Diversity, taxonomy, and biogeography of the reptiles inhabiting the highlands of the Cordillera Central (Serranía de Talamanca and Serranía de Tabasará) in western Panama

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To

my mother Ursula,

who showed me the power of perseverance

and encouraged my curiosity,

and to

my father Rainer,

who sowed my fascination for cold-blooded creatures

and taught me how to catch them.

Yet species are the cornerstone of our biology.

If we do not know our species, some or much of the ground is cut out from under our feet.

Ernest E. Williams 1977

Summary

With more than 10 000 known extant species, non-avian reptiles (henceforth called reptiles) are the second most speciose vertebrate group on earth. The more than 100 species newly described in each of the past years indicate that our knowledge on reptile species diversity is still far from being complete. This is especially true for the tropical regions of our planet, such as the Mesoamerican biodiversity hotspot. Forming the southeasternmost part thereof, Panama is a megadiverse country that together with Costa Rica constitutes Lower Central America (LCA). Many studies on Panamanian reptiles have concentrated on the country's central portion around the Canal. Fewer studies exist on the reptile fauna of western Panama's Cordillera Central, which accounts for the eastern part of the LCA highlands and was stated to house 155 of the 248 Panamanian reptile species in the most recent review (Jaramillo et al. 2010). The aim of the present study is to compile the most complete and updated picture possible of the taxonomy, diversity, and distribution of reptiles that occur from premontane elevations upwards along the Talamanca and Tabasará ranges. These two continuous mountain ridges account for the western two-thirds of the Cordillera Central between the Costa Rican border and 81°W near Santa Fé de Veraguas, extend through Bocas del Toro, Chiriquí, and Veraguas provinces as well as the indigenous autonomy territory Comarca Ngöbe-Buglé, and include the country's highest mountain, Volcán Barú with 3475 m asl.

For this purpose, I conducted four research travels with a total duration of more than 12 months in the period 2008–2010. Together with students and colleagues, 30 generalized research localities between 0 and 3475 m asl were visited to assemble a collection of 869 reptile specimens, almost all of which were documented photographically. Including specimens collected on other expeditions, photographic vouchers, and unequivocally identifiable own observations, I morphologically examined more than 1800 specimens and recorded detailed morphometric and pholidotic data from 826 of these. Furthermore, I generated 16S barcodes for 160 and received COI barcodes generated by the ColdCode project for 198 of these specimens. Additional 16S barcodes and morphological data for Panamanian and Costa Rican reptile specimens were provided by colleagues. To assess which species are present in my study area and how they are distributed, I performed a thorough search in literature and collection databases to obtain locality records for specimens and species occurrences, most of which I georeferenced myself. Summing up the records from all sources as well as those of my own examined specimens, my complete occurrence dataset comprises 14620 georeferenced occurrence records including 8795 from Bocas del Toro,

Chiriquí, Veraguas, and the Comarca Ngöbe-Buglé. To account for the variable quality of taxonomic evidence, I assigned each georeferenced record to one of the three quality categories "presence reported" (records without mention of a voucher specimen and non-type specimens listed in collection catalogues and databases), "specimen confirmed" (examined by others in a taxonomic context, i.e., a species description or generic revision), and "specimen examined" (examined by myself, including photos and personal observations of individuals with unmistakable identities). Similarly, I classify the occurrence of a given species in a given area either as "documented" whenever records exist from within the area in question, or evaluate its probability as "plausible" (records exist from less than 5 km from, or from both east and west of, the area, and the documented altitutinal distribution of the species suggests that it can occur at the elevations found within the area) or "possible" (none of the above, but the species' known geographic distribution strongly suggests its presence in the area). I provide all datasets which I generated for this study in Appendices.

Taxonomic analyses performed together with colleagues have resulted in the published descriptions of four new species which are included in the present work. The short-legged giant anole *Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013 differs from *D. microtus* in relative hind limb length and coloration pattern. All previous records of *D. microtus* from Panama were from Chiriquí and are actually attributable to *D. ginaelisae,* while the former species is newly documented to occur in western Bocas del Toro province. *Norops benedikti* (Lotzkat, Bienentreu, Hertz & Köhler 2011) differs from the other members of the *N. pachypus* complex in having a red dewlap with a yellow anterior margin (vs. solid red, solid yellow, or red with a yellow central blotch). The holotype and only known specimen of the cryptically colored snail-eater *Sibon perissostichon* Köhler, Lotzkat & Hertz 2010 differs from its congeners in having 17 oblique rows of dorsals at midbody (vs. 13 or usually 15 straight rows). The light-and-dark ringed coral snake-mimic *Sibon noalamina* Lotzkat, Hertz & Köhler 2012 is the only known species of *Sibon* having just five supralabials and only one of these posterior to the orbit, as well as a slight keeling on some dorsal scale rows in adults.

In the course of integrative taxonomic analyses including data from the respective Diploma theses of Joe-Felix Bienentreu for the *Norops pachypus* complex and Markus Gutpelet for the *N. kemptoni* complex, I compare morphological variation to genetic differentiation within selected groups and classify 15 genealogical lineages revealed by DNA barcoding within 7 anole species as Deep Conspecific Lineages (DCLs) because they lack consistent morphological differences to their nominal conspecifics. Apart from these, I provisionally classify 18 mitochondrial lineages found within six other anole species as Unconfirmed Genealogical Lineages (UGLs) since adequate analyses of morphological variation are beyond the scope of this study. I regard two additional UGLs from the Fortuna area to represent undescribed species although either the molecular or the morphological line of evidence is lacking: *Celestus* sp. exhibits differences in scalation to its geographically neighboring congeners *C. adercus* and *C. orobius,* but no reference barcodes of these species are available to compare them with my COI barcode of *Celestus* sp. In contrast, *Geophis* sp. is genetically differentiated from the other members of the *G. brachycephalus* complex found in my study area, but thorough morphological comparisons are still pending. Last, I found Panamanian dwarf geckos of the genus *Lepidoblepharis* with granular dorsals to comprise three different lineages distinguished by the configuration of their subdigital lamellae. 16S barcodes provided by Abel Batista attest that the Confirmed Genealogical Lineages (CGLs) *Lepidoblepharis* sp. 1 occurring in my study area and *Lepidoblepharis* sp. 2 from eastern Panama, both being short-toed and having fewer than 10 lamellae under their 4th toe, are genetically well-separated from the long-toed *L. xanthostigma* which has 12 or more 4th toe lamellae. Furthermore, my taxonomic analyses in combination with published data yield the hitherto most comprehensive and richly illustrated survey of the morphological variation exhibited by representatives of 30 dactyloid, two sphaerodactylid, and 11 dipsadid species along my study area. The 16S and/or COI barcodes I provide for 300 squamate individuals from Panama and Costa Rica representing 65 species recognized herein constitute the first DNA barcode reference library for Lower Central American reptiles. Ultimately, I summarize the taxonomic changes at the species-group level and faunistic additions that have occurred since the comprehensive treatment of Jaramillo et al. (2010), and argue that 20 nominal taxa traditionally and/or recently reported by different authors to be present in Panama should actually regarded as absent from the republic.

Taking into account these latter conclusions, my overall taxonomic results, and my georeferenced occurrence dataset, I regard the reptile fauna of Panama to comprise 265 species representing 109 genera in 33 families. This count includes the hitherto undescribed *Celestus* sp., *Geophis* sp., and *Lepidoblepharis* sp. 1 and 2, as well as *Dendrophidion crybelum* Cadle 2012 whose presence in the country I consider plausible since three of its paratypes have been collected less than 1 km from the Costa Rica-Panama border. My occurrence dataset reveals that 160 of these species have been documented to occur in my study area. Adding the 20 species whose occurrence therein I consider plausible, I report the total species richness of my study area as comprising 180 species representing 81 genera in 25 families. Of the 107 snake species occurring in the area, 52 pertain to the most speciose family Dipsadidae. Dactyloidae is the most species-rich lizard family holding 34 of the 68 lizard species, 27 of which pertain to the most speciose genus, *Norops.* Due to the relatively

small size of my study area (approximately 10 065 km^2), its relative species richness, or species density, of 178.8 species per 10 000 km^2 by far exceeds that of Panama (34.9) or any other Mesoamerican country (4.2–53.6). In view on their overall documented distribution, I regard the presence of 27 additional species in my study area as possible and provide an Appendix with distribution maps for these species. For the 180 species that are documentedly or plausibly (that is, most probably) present in my study area, I compiled standardized species accounts including authority and year of original description, common names, partial synonymies, reference to type material and locality, geographic distribution along with a point distribution map centered on my study area, diagnosis and standardized description, as well as notes on natural history and remarks on taxonomy, biogeography, and other aspects. I furthermore assess the conservation status of selected taxa by calculating Environmental Vulnerability Scores (EVS) and inferring appropriate IUCN categories. I illustrate 168 of the 180 species with color photographs, which are my own in the case of 121 species.

Concerning biogeography, my georeferenced dataset yields noteworthy extensions of their Panamanian and/or range-wide distribution for many species amounting to up to 180 km on the horizontal and about 1000 m on the vertical scale. Some of these, like the first record of *Potamites apodemus* from Panama, have already been published. For several species that were essentially known from a single site, the additional localities represented by my newly collected material span a three-dimensional geographic range for the first time. The relative comprehensiveness and up-to-dateness of my dataset is further testified by the increase in species numbers for any region, belt, or area analyzed over the results of previous authors. As an example, the species numbers I infer for Bocas del Toro (154), Chiriquí (171), and Veraguas (151) provinces range 40–96 higher than the correspondent figures of Young et al. (1999), while my list for the Comarca Ngöbe-Buglé (168 species) is the first to be compiled.

With over 150 reptile species, respectively, both the Serranía de Talamanca and the Serranía de Tabasará are each more species-rich than the adjacent Caribbean and Pacific lowlands together. Turtles and caimans enter the lower portion of my study area's premontane elevations, whereas only squamates are found well above 1000 m asl. From 800 m upwards, species richness gradually decreases until the highest Panamanian snake record lies at 2650 m for a *Rhadinaea calligaster*. Only the lizards *Mesaspis monticola* and *Sceloporus malachiticus* have been recorded above this elevation and up to 3420 m. Of the seven Holdridge life zones found in my study area, Premontane Wet Forest covers the largest portion and holds 97% of the species, more than half of which also occur in Lowland life zones, while the Montane Wet and Rain Forests together hold only 5%. The Am and Af Köppen climates roughly

corresponding to the combined Lowland and Premontane life zones each house more than twice as many species as the cooler Cw and Cf climates, respectively.

In view of their overall ranges, I classify 115 species of Central and/or South American distribution as widespread since they also occur outside LCA. With 65 remaining, more than a third of the species are endemic to LCA, including 21 species not known from outside Panama. Among these LCA endemics, 23 have considerable lowland ranges, including 8 Golfo Dulce endemics restricted to the Pacific versant of Costa Rica and western Panama. In contrast, the 42 Talamancan highland endemics are restricted to the LCA highlands, in the case of 16 small-scale highland endemics with a documented range spanning less than 100 km. For most of these small-scale endemics, I infer one of the IUCN Threatened categories and calculate EVS values indicating high vulnerability. Many other Talamancan and LCA endemics are Threatened or Data Deficient and medium or high vulnerability, whereas most widespread species are Least Concern and low vulnerability. Among the six protected areas established along the Talamanca and Tabasará ranges, Bosque Protector Palo Seco, Parque Internacional La Amistad, and Reserva Forestal La Fortuna hold the largest numbers of endemic and Threatened species. Nine LCA endemics, including two Talamancan small-scale endemics and four Threatened species, are neither documented nor inferred to occur in any of the protected areas, rendering the establishment of additional conservation areas necessary. This is especially urgent in the central Serranía de Tabasará where no protected area exists, while the conventional exploitation of its enormous mineral deposits, such as the repeatedly proposed open pit mining for copper in the so-called Cerro Colorado area around the Cerros Saguí and Santiago, would seriously threaten several species that are endemic to this mountain range with extinction.

About half of the species, including almost two-thirds of the LCA endemics, belong to genera of Middle American origin, while the South American lineages account for the lowest number of genera and species. Distributional range boundaries shared among different clades of highland anoles indicate that the crest of the Cordillera Central and Volcán Barú, as well as several depressions from the Fortuna area eastwards, constitute potential physiographic and climatic barriers that may have effected historic vicariance events triggering in situ speciation within the two most speciose lizard genera of my study area, *Norops* and *Dactyloa.*

The present work is the largest study on Panamanian reptile diversity assembled to date. Including four published species descriptions and the delineation of numerous genealogical lineages awaiting description or integrative corroboration, it considerably increases our knowledge on reptile alpha diversity both along the Cordillera Central and in Panama as a

whole. Moreover, my re-evaluation of diagnostic characters and variation summaries together with the standardized species accounts provide a solid basis for the identification of any of the 180 species comprising the reptile fauna of my study area. I further provide the hitherto most detailed, reproducible and comprehensive assessments of these species' geographical and ecological distribution, their occurrence in political subdivisions and protected areas, and conservation status. Directions for future studies building on the broad foundations laid out by this work include additional sampling throughout western Panama to fill taxonomic, genealogical, and geographic collection gaps, thorough integrative taxonomic studies of the UGL complexes revealed herein and other taxa to evaluate their taxonomic status, and comprehensive phylogeographic analyses to reconstruct the speciation events along and across the Cordillera Central that have produced such a diverse and unique reptile fauna.

Resumen

Diversidad, taxonomía y biogeografía de los reptiles en las tierras altas de la Cordillera Central (Serranía de Talamanca y Serranía de Tabasará) en el oeste de Panamá.

Con más de 10 000 especies actuales conocidas, los reptiles non-aviares (llamados reptiles en lo siguiente) son el segundo grupo de vertebrados con mayor riqueza en especies del planeta. Más de 100 especies han sido descritas durante cada uno de los últimos años, indicándonos que nuestro conocimiento acerca de la diversidad específica de reptiles todavía está lejos de ser completo. Esto aplica especialmente a las regiones tropicales de nuestro planeta, así como al hotspot de biodiversidad mesoamericano. Formando la parte más suroriental de este, Panamá es un país megadiverso y junto con Costa Rica constituye Centroamérica del Sur (abreviado LCA, por sus siglas en inglés Lower Central America). Muchos estudios acerca de los reptiles panameños Panamanian reptiles se han concentrado en la parte central del país, alrededor del canal. Menos trabajos existen sobre la fauna de reptiles de la Cordillera Central en el oeste de Panamá, la cual forma la parte oriental de las Tierras Altas de Talamanca o LCA y alberga 155 de las 248 especies de reptiles presentes en el país, según la sinopsis más reciente (Jaramillo et al. 2010). El objetivo de éste trabajo es compilar la síntesis más completa y actualizada posible acerca de la taxonomía, diversidad y distribución de los reptiles presentes en elevaciones premontanas y montanas a lo largo de las Serranías de Talamanca y Tabasará. Ubicadas entre la frontera con Costa Rica y 81°W cerca de Santa Fé de Veraguas, éstas dos cadenas montañosas constituyen los dos tercios más occidentales de la Cordillera Central, extendiéndose por las provincias de Bocas del Toro, Chiriquí y Veraguas

así como el territorio de autonomía indígena Comarca Ngöbe-Buglé, e incluyendo la cumbre más alta del país, el Volcán Barú con 3475 msnm.

Para esto, realicé cuatro viajes de investigación durante un total de más de 12 meses en el periodo comprendido entre los años 2008–2010. Junto con estudiantes y colegas, se visitaron 30 localidades generalizadas de estudio entre 0 y 3475 msnm, acumulando una colección de 869 especímenes de reptiles, la gran mayoría de los cuales se ha documentado fotográficamente. Incluyendo especímenes colectados por otras expediciones, registros fotográficos y observaciones propias inequívocamente identificables, examiné morfológicamente más de 1800 especímenes, recogiendo datos detallados de morfometría y folidosis de 826 de estos. Adicionalmente, generé códigos de barras 16S y recibí códigos de barras COI generado por el proyecto ColdCode para 160 y 198 de éstos especímenes, respectivamente. Algunos códigos de barras 16S y datos morfológicos adicionales fueron proporcionados por colegas. Con el fin de evaluar cuales especies están presentes dentro de mi área de estudio y como se distribuyen, realicé una investigación extensa en la literatura así como en bases de datos y catálogos de colecciones. Así obtive registros geográficos para especímenes y especies, la mayoría de los cuales georreferencié yo mismo. Sumando los registros de todas las fuentes con los de mis especímenes examinados, mi juego de datos geográfico completo comprende 14620 registros de ocurrencias georreferenciados, entre ellos 8795 provenientes de Bocas del Toro, Chiriquí, Veraguas y la Comarca Ngöbe-Buglé. Correspondiendo a la variable calidad de evidencia taxonómica, asigné a cada registro una de las siguientes tres categorías de calidad: "presence reported" (= presencia reportada: reportes que no hacen mención de especímenes voucher, y especímenes listados en catálogos de colecciones que no sean tipos), "specimen confirmed" (= espécimen confirmado: especímenes examinados por otros en un contexto taxonómico, por ejemplo para una descripción de especie o revisión de un género) y "specimen examined" (= especímen examinado: examinado por mí mismo, incluyendo fotos y observaciones propias de ejemplares con identidad inequívoca). De manera similar, clasifiqué la presencia de una especie dada en un área determinada como "documented" (= documentado) cuando existen registros provenientes del área concerniente, o evalué la probabilidad de su presencia como "plausible" (existen registros provenientes de distancias menores de 5 km del área, o de lugares tanto occidentales como orientales del área, y la distribución altitudinal documentada para la especie sugiere que puede ocurrir en las elevaciones presentes dentro del área) o "possible" (ninguno de los criterios arriba mencionados aplica, pero la distribución geográfica conocida de la especie sugiere su presencia en el área). Proporciono todos los juegos de datos que he generado para el presente estudio en anexos.

Análisis taxonómicos llevados a cabo junto con colegas han resultado en las descripciones ya publicadas de cuatro especies nuevas que son incluidas en el presente trabajo. El anolis gigante de patas cortas *Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013 se distingue de *D. microtus* en tener patas traseras relativamente más cortas y en el patrón de coloración. Todos los registros anteriores de *D. microtus* para Panamá provenían de Chiriquí y actualmente son referibles a *D. ginaelisae,* mientras la especie anterior es reportada por primera vez para Bocas del Toro. *Norops benedikti* (Lotzkat, Bienentreu, Hertz & Köhler 2011) difiere de los demás miembros del complejo de *N. pachypus* en tener el pliegue gular masculino rojo con el borde anterior amarillo (versus completamente rojo o amarillo, o rojo con una mancha central amarilla). El holotipo y único ejemplar conocido de la caracolera con coloración críptica *Sibon perissostichon* Köhler, Lotzkat & Hertz 2010 se distingue de otras especies del género *Sibon* en tener 17 hileras oblicuas de escamas dorsales en medio del cuerpo (versus 13 o usualmente 15 hileras rectas). La falsa coral de anillos claros y oscuros *Sibon noalamina* Lotzkat, Hertz & Köhler 2012 es la única especie conocida de *Sibon* con apenas cinco escamas supralabiales, sólo una de las cuales está ubicada posterior a la órbita, y algunas hileras de escamas dorsales ligeramente aquilladas en adultos.

En análisis taxonómicos integrales que incluyen datos provenientes de las respectivas tesis de diploma de Joe-Felix Bienentreu para el complejo *Norops pachypus* y de Markus Gutpelet para el complejo *N. kemptoni*, comparo la variación morfológica con la diferenciación genética en determinados grupos. Clasifico 15 líneas genealógicas reveladas a partir de códigos de barras de ADN dentro de 7 especies de anolis como Deep Conspecific Lineages (DCLs = profundas líneas coespecíficas), por carecer de diferencias morfológicas consistentes a sus coespecíficos nominales. Además, clasifico provisionalmente 18 líneas mitocondriales encontradas en otras seis especies de anolis como Unconfirmed Genealogical Lineages (UGLs = líneas genealógicas sin confirmar), porque análisis adecuados de su variación morfológica quedan fuera de los límites de esta tesis. Considero dos UGLs adicionales de la Reserva Forestal La Fortuna como especies no descritas, a pesar de que hace falta la linea de evidencia molecular o morfológica: *Celestus* sp. muestra diferencias de escamación a sus vecinos geográficos congenéricos *C. adercus* y *C. orobius,* pero ninguna secuencia de referencia existe de éstas dos especies para compararla con mi codigo de barras COI de *Celestus* sp. A la inversa, *Geophis* sp. es genéticamente diferenciada de los demás miembros del complejo *G. brachycephalus* presentes en mi área de estudio, pero carezco de comparaciones morfológicas profundas. Por último, descubrí que los guecos enanos del género *Lepidoblepharis* con escamas dorsales granulares en Panamá esconden tres líneas diferentes que se distinguen en la configuración de sus laminillas subdigitales. Códigos de barra 16S proporcionados por Abel

Batista comprueban que los Confirmed Genealogical Lineages (CGLs = líneas geneológicas confirmadas, es decir, especies propias) *Lepidoblepharis* sp. 1, presente en mi área de estudio, y *Lepidoblepharis* sp. 2 del este de Panamá, ambas de dedos cortos con menos de 10 laminillas debajo del cuarto dedo de pie, son genéticamente muy distantes de *L. xanthostigma* teniendo dedos largos con al menos 12 laminillas debajo del cuarto dedo de pie. En su totalidad, mis análisis taxonómicos en combinación con datos publicados dan como resultado la vista general más extensa y abundantemente ilustrada de la variación morfológica mostrada a lo largo de mi área de estudio por representantes de 30 especies de la familia Dactyloidae, dos de Sphaerodactylidae y 11 de Dipsadidae. Los códigos de barra 16S y/o COI que facilito para 300 individuos del orden Squamata provenientes de Panamá y Costa Rica representan 65 especies reconocidas en el presente trabajo y constituyen la primera biblioteca de referencia de códigos de barra de ADN para reptiles de LCA. Finalmente, resumo los cambios taxonómicos a nivel de especie que se han efectuados desde la más reciente sinopsis (Jaramillo et al. 2010), y concluyo que 20 taxa nominales que tradicionalmente y/o recientemente han sido reportados para Panamá por diferentes autores, en realidad no deben ser considerados como presentes en la república.

Tomando en cuenta éstas últimas conclusiones, mis resultados taxonómicos y mi juego de datos completo de ocurrencias georreferenciadas, deduzco que la fauna de reptiles de Panamá está compuesta por 265 especies en 109 géneros y 33 familias. Éste conteo incluye las especies no descritas *Celestus* sp., *Geophis* sp. y *Lepidoblepharis* sp. 1 y 2, así como *Dendrophidion crybelum* Cadle 2012, cuya presencia en el país clasifico como plausible, ya que tres paratipos se han hallado a menos de 1 km de la frontera entre Costa Rica y Panamá. Mi registro biogeográfico revela que 160 de estas especies han sido documentadas para mi área de estudio. Añadiendo las 20 especies cuya ocurrencia clasifico como plausible, considero que la riqueza total de especies de reptiles de mi área de estudio comprende 180 especies que representan 81 géneros y 25 familias. De las 107 especies de serpientes en el área, 52 pertenecen a la familia más rica en especies, Dipsadidae. Dactyloidae es la familia de saurios con el mayor número de especies, conteniendo 34 de las 68 especies de lagartijas, 27 de las cuales son miembros del género más especioso, *Norops*. Débido al tamaño relativamente pequeño de mi área de estudio (unos 10 065 km^2), su riqueza relativa o densidad de especies con 178.8 especies por 10 000 km^2 es mucho mayor que la de Panamá (34.9) o de cualquier otro país mesoamericano (4.2–53.6). Con base en su distribución total documentada, clasifico la presencia de 27 especies adicionales en mi área de estudio como posible, y facilito un apéndice con mapas de distribución para éstas. Para las 180 especies cuya presencia en mi área de estudio está documentada o plausible (es decir, más probable),

he elaborado informes sistemáticos estandarizados incluyendo la siguiente información: autor y año de la descripción original, nombres vernaculares, sinonimías parciales, referencias a material y localidad tipo, distribución geográfica con un mapa de distribución centrado en mi área de estudio, diagnosis y descripción estandarizada y notas acerca de su historia natural así como comentarios sobre taxonomía y biogeografía, entre otros aspectos. Para ciertas especies, además evalué el estatus de conservación calculando Environmental Vulnerability Scores (EVS = Puntajes de Vulnerabilidad Ambiental) y asignándolas a categorías de la UICN. Ilustro 168 de las 180 especies con fotografías a color, las cuales son de mí autoría en el caso de 121 especies.

Con respecto a la biogeografía, mi registro georreferenciado rinde extensiones notables de la distribución panameña y/o total para muchas especies, ascendiendo hasta 180 km en la escala horizontal y unos 1000 m en la escala vertical. Algunas de ellas, como el primer reporte de *Potamites apodemus* para Panamá, ya se han publicado. Para varias especies que básicamente fueron conocidas de un solo sitio, las localidades adicionales asociadas con el material examinado para ésta tesis abren un espacio tridimensional de distribución por primera vez. La relativa completitud y actualidad de mi juego de datos además se muestran en el incremento en el número de especies para cualquier región, piso altitudinal, o área administrativa analizada comparado con los resultados de autores anteriores. Como ejemplo, las riquezas de especies que derivo para las provincias de Bocas del Toro (154), Chiriquí (171) y Veraguas (151) son 40–96 mayores que los números correspondientes de Young et al. (1999), mientras mi lista para la Comarca Ngöbe-Buglé (168 especies) es la primera en ser compilada.

Con más de 150 especies de reptiles, respectivamente, tanto la Serranía de Talamanca como la Serranía de Tabasará son más ricas en especies que las tierras bajas adyacentes del Caribe y del Pacífico. Tortugas y caimanes entran en la parte inferior de las elevaciones premontanas de mi área de estudio, mientras que solo reptiles escamados habitan bien arriba de los 1000 msnm. De 800 msnm hacia arriba, la riqueza de especies disminuye gradualmente, hasta que la mayor altitud registrada en Panamá para una serpiente (*Rhadinaea calligaster*) se encuentra a 2650 msnm. Solo las lagartijas *Mesaspis monticola* y *Sceloporus malachiticus* se han reportado de elevaciones más altas y hasta 3420 msnm. De las siete zonas de vida del sistema de Holdridge que existen dentro de mi área de estudio, el Bosque Premontano Muy Húmedo cubre la mayor área y alberga 97% de las especies, de las cuales más de la mitad también ocurren en las zonas de vida de Tierras Bajas, mientras apenas el 5% de las especies habitan en los Bosques Montanos Muy Húmedos y Lluviosos. En su mayor parte correspondiendo a las zonas de vida Premontanas y de Tierras Bajas combinadas, los climas Am y Af del sistema de Köppen cada uno albergan más que el doble del número de especies que los climas más frescos Cw y Cf, respectivamente.

Con base en sus respectivas áreas de distribución total, clasifico 115 especies de distribución centro- y/o suramericana como ampliamente distribuidas porque ocurren en países fuera de LCA. Con las 65 especies restantes, más de la tercera parte de las especies de reptiles de mi área de estudio son endémicas para LCA, incluyendo 21 especies que solo se conocen de Panamá. Entre éstos endémicos de LCA, 23 tienen una gran parte de su distribución en las tierras bajas, incluyendo 8 endémicos de Golfo Dulce restringidas a la vertiente Pacífica de Panamá occidental y Costa Rica. Por otro lado, los 42 endémicos de las Tierras Altas de Talamanca solo ocurren en las Tierras Altas de LCA, en el caso de 16 microendémicos de tierras altas con un área de distribución documentada que se extiende por menos de 100 km. Para la mayoría de estos microendémicos de tierras altas, determino una de las categorías de amenaza de la UICN y calculo valores de EVS indicando alta vulnerabilidad. Muchos otros endémicos Talamanqueños y de LCA son considerados Amenazados o Datos Insuficientes y de vulnerabilidad media o alta, mientras la mayor parte de las especies de amplia distribución son de Preocupación Menor y de baja vulnerabilidad. Entre las seis áreas protegidas designadas a lo largo de las Serranías de Talamanca y Tabasará, el Bosque Protector Palo Seco, Parque Internacional La Amistad y la Reserva Forestal La Fortuna albergan los mayores números de especies endémicas y amenazadas. Para nueve endémicos de LCA, incluyendo dos microendémicos Talamancaneños y cuatro especies amenazadas, la presencia en una de las seis áreas protegidas no es documentada ni plausible. Por ello identifico la necesidad de establecer áreas protegidas adicionales. Esto es más urgente en la parte central de la Serranía de Tabasará, donde existe ninguna área protegida. Aquí, la explotación convencional de sus enormes yacimientos de mena, como por ejemplo la minería de cobre a cielo abierto propuesta varias veces en el llamado área de Cerro Colorado alrededor de los Cerros Saguí y Santiago, seriamente amenazaría varias especies endémicas de esta Serranía con la extinción.

Aproximadamente la mitad de las especies y casi dos tercios de los endémicos de LCA, son integrantes de géneros que se originaron en Mesoamérica, mientras que los grupos suramericanos contribuyen los menores números de géneros y especies. Límites de áreas de distribución compartidos entre diferentes clados de anolis de tierras altas indican que la cresta de la Cordillera Central y el Volcán Barú, así como diferentes depresiones desde La Fortuna al oriente, constituyen posibles barreras fisiográficas y climáticas que pueden haber causado eventos históricos de vicariancia, así ocasionando la especiación in situ dentro de los dos géneros de lagartijas más especiosos de mi área de estudio, *Norops* y *Dactyloa.*

La presente tesis es el mayor estudio de la diversidad de reptiles en Panamá realizado hasta la fecha. Incluyendo cuatro descripciones de nuevas especies ya publicadas y la delimitación de numerosas líneas genealógicas todavía esperando su descripción o confirmación integral, de manera considerable aumenta nuestros conocimientos acerca de la diversidad alfa de reptiles tanto a lo largo de la Cordillera Central, como en todo Panamá. Además, mi re-evaluación de características diagnósticas y resúmenes de variación, junto con los informes sistemáticos estandarizados, constituyen una base sólida para la identificación de cualquiera de las 180 especies contenidas en la fauna de reptiles de mi área de estudio. Adicionalmente, proporciono la hasta ahora más detallada, reproducible y extensa estimación de la distribución geográfica y ecológica, de presencia en áreas protegidas y administrativas, y del estatus de conservación de éstas especies. Indicaciones para estudios futuros que puedan basarse en el ámplio fundamento proporcionado por el presente trabajo incluyen muestreos adicionales para llenar vacíos geográficos y taxonómicos, estudios de taxonomía integral exhaustivos de los complejos de UGLs revelados en éste trabajo, así como de otros taxa, para evaluar su estatus taxonómico, y profundos estudios filogeográficos para reconstruir los eventos de especiación a lo largo y a través de la Cordillera Central que han producido una fauna de reptiles tan diversa y única.

Zusammenfassung

Diversität, Taxonomie und Biogeographie der Reptilien im Hochland der Cordillera Central (Serranía de Talamanca und Serranía de Tabasará) im westlichen Panama.

Mit über 10 000 bekannten rezenten Arten sind die Nicht-Vogel-Reptilien (fürderhin schlicht als Reptilien bezeichnet) die zweitartenreichste Wirbeltiergruppe der Erde. Die Neubeschreibungen von mehr als 100 Arten in jedem der letzten Jahre zeigen deutlich, dass unser Wissen über die Artenvielfalt der Kriechtiere noch sehr lückenhaft ist. Dies gilt besonders für die tropischen Regionen des Planeten wie beispielsweise den Mittelamerikanischen Biodiversitäts-Hotspot. Dessen südöstlichster Teil, Panama, ist ein Megadiversitätsland und bildet zusammen mit Costa Rica das Südliche Zentralamerika (kurz LCA für Lower Central America). Viele Studien an panamaischen Reptilien sind in der Umgebung des Panamakanals in der Landesmitte durchgeführt worden. Weit weniger bearbeitet ist die Reptilienfauna der Cordillera Central im Westen Panamas. Dieser Gebirgszug bildet den östlichen Teil des Talamanca- oder süd-zentralamerikanischen Hochlandes und beherbergt der aktuellsten Revision (Jaramillo et al. 2010) zufolge 155 der 248 aus Panama bekannten Reptilienarten. Das Ziel der vorliegenden Arbeit ist die

Zusammenstellung einer möglichst vollständigen und aktualisierten Übersicht über die Vielfalt, Taxonomie und Verbreitung der Reptilien, die ab der prämontanen Höhenstufe aufwärts entlang der Talamanca- und Tabasará-Höhenzüge vorkommen. Diese ineinander übergehenden Gebirgsketten bilden die westlichen zwei Drittel der panamaischen Cordillera Central und erstrecken sich von der Grenze zu Costa Rica bis 81°W bei Santa Fé de Veraguas durch die Provinzen Bocas del Toro, Chiriquí und Veraguas sowie das indigene Autonomiegebiet Comarca Ngöbe-Buglé und beinhalten Panamas höchsten Gipfel, den Volcán Barú mit 3475 m NN.

Zu diesem Zweck führte ich von 2008 bis 2010 vier Forschungsreisen mit einer Gesamtdauer von über 12 Monaten nach Panama durch. Gemeinsam mit Studenten und Kollegen wurden 30 generalisierte Untersuchungsorte zwischen 0 und 3475 m NN aufgesucht und 869 Belegexemplare von Reptilien gesammelt, von denen fast jedes fotografisch dokumentiert wurde. Einschließlich der von anderen Expeditionen stammenden Sammlungen, diverser Fotonachweise und sicher identifizierter eigener Beobachtungen habe ich über 1800 Individuen morphologisch untersucht und von 826 dieser Exemplare umfangreiche morphometrische und pholidotische Merkmale erfasst. Darüber hinaus generierte ich 16S Barcode-Sequenzen von 160 dieser Tiere und erhielt COI Barcodes für 198 weitere durch das ColdCode-Projekt. Zusätzliche 16S barcodes und morphologische Daten für Reptilien aus Panama und Costa Rica wurden mir von Kollegen zur Verfügung gestellt. Um die in meinem Untersuchungsgebiet vorkommenden Reptilienarten und ihre Verbreitung zu ermitteln führte ich eine umfangreiche Recherche in Literatur sowie in Sammlungskatalogen und -datenbanken durch und georeferenzierte die meisten der so erhaltenen geographischen Nachweise selbst. Mit sämtlichen Verbreitungspunkten aus allen Quellen und denen der von mir untersuchten Exemplare enthält mein Verbreitungs-Datensatz 14620 georeferenzierte Verbreitungspunkte, darunter 8795 aus Bocas del Toro, Chiriquí, Veraguas und der Comarca Ngöbe-Buglé. Um der sehr unterschiedlichen taxonomischen Glaubwürdigkeit verschiedener Nachweise gerecht zu werden, ordnete ich jeden einzelnen einer der drei Qualitätskategorien "presence reported" (= Vorkommen gemeldet: Berichte ohne Erwähnung von Belegexemplaren sowie in Katalogen und Datenbanken gelistete nicht-Typus-Exemplare), "specimen confirmed" (= Exemplar bestätigt: Belegexemplar wurde von anderen in einem taxonomischen Zusammenhang untersucht, z.B. einer Artbeschreibung oder Gattungsrevision) und "specimen examined" (= Exemplar untersucht: von mir selbst, inklusive Fotos und eigenen Beobachtungen von sicher bestimmbaren Exemplaren). In Anlehnung an diese Vorgehensweise klassifiziere ich das Vorkommen einer bestimmten Art in einem bestimmten Gebiet als "documented" (= dokumentiert), wann immer Nachweise aus dem fraglichen

Gebiet vorliegen oder evaluiere die Wahrscheinlichkeit eines Vorkommens entweder als "plausible" (= plausibel: Nachweise liegen weniger als 5 km entfernt oder aber sowohl östlich als auch westlich vom fraglichen Gebiet, und die dokumentierte vertikale Verbreitung der Art legt nahe, dass sie auf den im Gebiet vorgefundenen Meereshöhen existieren kann) oder als "possible" (= möglich: keines der oben genannten Kriterien trifft zu, aber die bekannte Verbreitung der Art lässt ihr Vorkommen im Gebiet als wahrscheinlich erscheinen). Ich stelle alle für diese Studie generierten Datensätze in Anhängen bereit.

Aus gemeinsam mit Kollegen durchgeführten taxonomischen Analysen sind die bereits publizierten Beschreibungen von vier für die Wissenschaft neuen Arten hervorgegangen, die in die vorliegende Arbeit aufgenommen wurden. Der kurzbeinige Riesenanolis *Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013 unterscheidet sich von *D. microtus* in relativer Beinlänge und Färbungsmuster. Alle bisherigen Berichte von *D. microtus* aus Panama kamen aus Chiriquí und bezogen sich in Wirklichkeit auf *D. ginaelisae,* wohingegen die erstgenannte Art erstmalig für die Provinz Bocas del Toro nachgewiesen wird. *Norops benedikti* (Lotzkat, Bienentreu, Hertz & Köhler 2011) unterscheidet sich von den anderen Mitgliedern des *N. pachypus*-Komplexes durch seine rote Kehlfahne mit gelbem Vorderrand (ganz rot, ganz gelb, oder rot mit zentralem gelben Fleck in den anderen Arten). Der Holotyp und einzige bekannte Vertreter der kryptisch gefärbten Schneckennatter *Sibon perissostichon* Köhler, Lotzkat & Hertz 2010 ist durch seine 17 schräg verlaufenden Reihen von Rückenschuppen um die Körpermitte von seinen 13 oder üblicherweise 15 gerade verlaufende Reihen aufweisenden Gattungsgenossen abgrenzbar. Die hell-dunkel geringelte falsche Korallenschlange *Sibon noalamina* Lotzkat, Hertz & Köhler 2012 ist die einzige bekannte Art der Gattung *Sibon* mit lediglich fünf Oberlippenschilden, von denen nur eines hinter der Augenhöhle liegt, und schwachen Kielen auf einigen Rückenschuppenreihen bei Adulti.

Im Zuge integrativer taxonomischer Analysen, die Daten aus den Diplomarbeiten von Joe-Felix Bienentreu über den *Norops pachypus*-Komplex und Markus Gutpelet über den *N. kemptoni*-Komplex mit einbeziehen, vergleiche ich die morphologische Variabilität mit der genetischen Differenzierung ausgewählter Gruppen. Ich klassifiziere 15 durch DNA Barcoding innerhalb von 7 nominellen Saumfingerechsenarten aufgezeigte genealogische Linien als Deep Conspecific Lineages (DCLs = stark ausgeprägte innerartliche Linien), da sie keine konsistenten morphologischen Differenzierungen zu ihren jeweiligen nominellen Artgenossen aufweisen. Achtzehn mitochondrielle Stammlinien innerhalb von sechs weiteren Saumfinger-Arten stufe ich provisorisch als Unconfirmed Genealogical Lineages (UGLs = unbestätigte genealogische Linien) ein, da morphologische Analysen angemessenen Umfangs weit jenseits des im Rahmen dieser Studie Machbaren liegen. Zwei weitere UGLs aus der La

Fortuna-Gegend erkenne ich als unbeschriebene Arten an, obwohl entweder die molekulare oder die morphologische Beweislinie fehlt: *Celestus* sp. weist Beschuppungsunterschiede zu seinen geographisch benachbarten Gattungsgenossen *C. adercus* und *C. orobius* auf, aber leider existieren keine Referenz-Sequenzen dieser Arten, die ich mit dem COI-Barcode von *Celestus* sp. vergleichen könnte. Im Gegensatz dazu ist *Geophis* sp. genetisch von den anderen im Untersuchungsgebiet vorkommenden Mitgliedern des *G. brachycephalus*-Komplexes differenziert, doch profunde morphologische Vergleiche stehen noch aus. Außerdem zeige ich, dass innerhalb panamaischer Laubstreu-Geckos der Gattung *Lepidoblepharis* mit granulären Rückenschuppen drei Linien existieren, die sich in der Konfiguration ihrer subdigitalen Lamellen unterscheiden. Von Abel Batista bereitgestellte 16S-Barcodes bestätigen, dass die Confirmed Genealogical Lineages (CGLs = bestätigte genealogische Linien) *Lepidoblepharis* sp. 1, der in meinem Untersuchunsgebiet vorkommt, und der ostpanamaische *Lepidoblepharis* sp. 2, beide kurzzehig mit weniger als 10 Lamellen unter dem vierten Zeh, sich auch genetisch deutlich von dem langzehigen *L. xanthostigma* mit 12 oder mehr Lamellen unter dem vierten Zeh unterscheiden. Darüber hinaus bieten meine taxonomischen Analysen in Verbindung mit bereits publizierten Daten die bisher umfassendste und am reichsten illustrierte Übersicht über die entlang meines Untersuchungsgebietes auftretende morphologische Variabilität bei Vertretern von 30 dactyloiden, zwei sphaerodactyliden und 11 dipsadiden Arten. Die für 300 squamate Individuen aus Panama und Costa Rica bereitgestellten 16S- und/oder COI-Barcodes repräsentieren 65 der hierin anerkannten Arten und stellen die erste DNA Barcode-Referenz-bibliothek für Reptilien des südlichen Zentralamerikas dar. Zuletzt fasse ich die taxonomischen Änderungen auf Artniveau und sonstige faunistische Zuwächse, die seit der letzten Reptilienliste Panamas (Jaramillo et al. 2010) erfolgt sind, zusammen und argumentiere dass 20 nominelle Taxa, die traditionell und/oder jüngst von verschiedenen Autoren für Panama angegeben wurden, nicht zur Fauna dieses Landes gehören.

Unter Berücksichtigung der letztgenannten Folgerungen, meiner taxonomischen Ergebnisse und meines Verbreitungs-Datensatzes komme ich zu dem Schluss, dass die Reptilienfauna Panamas 265 Arten umfasst, die sich auf 109 Gattungen in 33 Familien verteilen. Diese Zahlen enthalten vier bisher unbeschriebene Arten (*Celestus* sp., *Geophis* sp., *Lepidoblepharis* sp. 1 und 2) sowie *Dendrophidion crybelum* Cadle 2012, dessen Vorkommen in Panama ich als plausibel einstufe, da die Fundorte dreier Paratypen weniger als 1 km von der costaricanisch-panamaischen Grenze liegen. Mein geographischer Datensatz zeigt, dass 160 dieser Arten bisher für mein Untersuchungsgebiet nachgewiesen wurden. Unter Hinzunahme 20 weiterer Arten, deren Anwesenheit mir plausibel erscheint, gebe ich den

Gesamt-Artenreichtum der Reptilien meines Untersuchungsgebietes mit 180 Arten aus 81 Gattungen in 25 Familien an. Von den 107 im Gebiet vorkommenden Schlangenarten gehören 52 der artenreichsten Familie, Dipsadidae, an. Dactyloidae ist die artenreichste Echsenfamilie mit 34 der 68 Echsenarten, von denen 27 der artenreichsten Gattung, *Norops,* angehören. Aufgrund der vergleichsweise geringen Größe meines Untersuchungsgebietes (etwa 10 065 km^2) ist sein relativer Artenreichtum, also seine Artendichte, mit 178.8 Arten pro 10 000 km^2 weitaus höher als der von Panama (34.9) oder irgendeinem anderen mittelamerikanischen Land (4.2–53.6). Im Hinblick auf ihre bekannten Verbreitungsgebiete erachte ich das Vorkommen von 27 zusätzlichen Arten als möglich und stelle ihre Verbreitungskarten in einem Anhang bereit. Die 180 Spezies, deren Präsenz im Untersuchungsgebiet dokumentiert oder plausibel (will heißen: höchst wahrscheinlich) ist, charakterisiere ich in standardisierten Artenportraits. Diese enthalten Autor und Jahr der Erstbeschreibung, englische und spanische Trivialnamen, partielle Synonymielisten, Verweise auf Typusmaterial und -lokalität, Angaben zur geographischen Verbreitung mit einer auf mein Untersuchungsgebiet zugeschnittenen Punkt-Verbreitungskarte, Diagnosen und standardisierte Beschreibungen sowie Bemerkungen zur Naturgeschichte und Kommentare zur Taxonomie, Biogeographie und anderen Aspekten. Darüber hinaus beurteile ich den Gefährdungsstatus ausgewählter Arten durch die Berechnung von Environmental Vulnerability Scores (EVS) und die Herleitung der zutreffenden IUCN Kategorien. Ich illustriere 168 der 180 Arten mit Farbfotos, wobei 121 Arten von mir selbst aufgenommen wurden.

Im Hinblick auf die Biogeographie ergeben sich aus meinem Datensatz für die bekannten Verbreitungsgebiete vieler der betrachteten Arten bemerkenswerte Erweiterungen, die bis zu 180 km in der Horizontalen und bis zu 1000 m in der Vertikalen betragen. Manche davon, wie etwa der Erstnachweis von *Potamites apodemus* für Panama, sind bereits publiziert worden. Für diverse Arten, die bisher im Grunde nur von einem Ort bekannt waren, wird durch die Fundorte des von mir gesammelten Materials erstmalig ein dreidimensionaler Verbreitungsraum aufgespannt. Die weitgehende Vollständigkeit und Aktualität meines Datensatzes zeigen sich außerdem in den resultierenden Artenzahlen, die für jede analysierte Region, Höhenstufe oder Schutzzone höher sind als die von früheren Autoren angegebenen. So liegen beispielsweise die von mir abgeleiteten Zahlen der in den Provinzen Bocas del Toro (154), Chiriquí (171) und Veraguas (151) vorkommenden Reptilienarten um 40–96 über den entsprechenden Ergebnissen von Young et al. (1999), während meine Artenliste für die Comarca Ngöbe-Buglé (168 Arten) die erste ist, die jemals erstellt wurde.

Mit jeweils über 150 vorkommenden Arten sind sowohl die Serranía de Talamanca als auch die Serranía de Tabasará jeweils reicher an Arten als die angrenzenden karibischen und pazifischen Tieflandregionen zusammen. Während Schildkröten und Kaimane in den unteren Bereichen der prämontanen Höhenstufe meines Untersuchungsgebietes existieren, sind für gut über 1000 m NN liegenden Höhen ausschließlich squamate Reptilien nachgewiesen. Oberhalb von 800 m nimmt der Artenreichtum allmählich ab, bis auf 2650 m mit einer *Rhadinaea calligaster* der höchste Fundort für eine Schlange erreicht ist. Lediglich die Echsen *Mesaspis monticola* und *Sceloporus malachiticus* sind oberhalb dieser Meereshöhe und bis auf 3420 m nachgewiesen. Von den sieben in meinem Untersuchungsgebiet vorhandenen Klima- und Vegetationszonen nach Holdridge bedeckt der Prämontane Nasswald die größte Fläche und beherbergt 97% der Reptilienarten, von denen mehr als die Hälfte auch in den angrenzenden Tiefland-Zonen vorkommt, wohingegen lediglich 5% der Arten Montane Nass- und Regenwälder bewohnen. Die Am- und Af-Typen des Tropischen Regenklimas nach Köppen sind weitgehend deckungsgleich mit den Tiefland- und Prämontanen Zonen nach Holdridge und beherbergen jeweils mehr als doppelt so viele Arten wie die warmgemäßigten Cw- und Cf-Klimatypen zusammen.

Angesichts ihrer Verbreitungsgebiete klassifiziere ich 115 der im Untersuchungsgebiet vorkommenden Reptilienarten als weit verbreitet, da sie auch außerhalb des Südlichen Zentralamerikas (LCA) in Mittel- und/oder Südamerika vorkommen. Mit den 65 verbleibenden Arten ist mehr als ein Drittel der Fauna endemisch für LCA, einschließlich der 21 Arten, die nur aus Panama bekannt sind. Dreiundzwanzig dieser LCA-Endemiten haben einen beträchtlichen Teil ihrer jeweiligen Areale im Tiefland, darunter auch 8 Golfo Dulce-Endemiten, die nur auf der Pazifikseite Costa Ricas und des westlichen Panamas vorkommen. Demgegenüber sind die 42 Talamanca-Hochland-Endemiten ausschließlich entlang des LCA Hochlandes verbreitet, im Falle der 16 kleinräumigen Hochlandendemiten sogar mit dokumentierten Arealen von weniger als 100 km entlang des Gebirges. Für die meisten dieser kleinräumigen Endemiten leite ich eine der IUCN "Gefährdet"-Kategorien ("gefährdet", "stark gefährdet" oder "vom Aussterben bedroht") ab und errechne entsprechend hohe EVS-Werte, die eine starke Gefährdung anzeigen. Viele andere Talamanca- und LCA-Endemiten sind nach IUCN-Kriterien ebenfalls als gefährdet oder aufgrund ungenügender Datengrundlage derzeit gar nicht einzustufen und ihren EVS-Werten zufolge mittlerer oder starker Gefährdung ausgesetzt. Demgegenüber sind die meisten der weit verbreiteten Arten nach IUCN-Kriterien als nicht gefährdet oder mangels Daten nicht einstufbar, und anhand ihrer EVS-Werte als wenig gefährdet anzusehen. Von den sechs Schutzgebieten entlang der Talamanca- und Tabasará-Höhenzüge beherbergen Bosque Protector Palo Seco, Parque Internacional La Amistad, und Reserva Forestal La Fortuna die meisten endemischen und gefährdeten Arten. Das Vorkommen von neun LCA-Endemiten, darunter zwei kleinräumige

Hochlandendemiten und vier gefährdete Arten, in irgendeinem der sechs Schutzgebiete ist weder dokumentiert noch zu erwarten. Daraus folgt die Notwendigkeit der Einrichtung weiterer Schutzgebiete, besonders in der zentralen Serranía de Tabasará, die kein Schutzgebiet aufweist, während die konventionelle Ausbeutung ihrer enormen Erzvorkommen, wie etwa der wiederholt geplante Kupfertagebau in der so genannten Cerro Colorado-Gegend um die Cerros Saguí und Santiago, diverse für diesen Gebirgszug endemische Arten ernsthaft mit dem Aussterben bedrohen würde.

Etwa die Hälfte aller im Untersuchungsgebiet vorkommenden Arten und fast zwei Drittel der LCA-Endemiten gehören Gattungen mittelamerikanischen Ursprungs an, während die südamerikanischen Linien den kleinsten Anteil an den Gattungs- und Artenzahlen haben. Die weitgehende Deckungsgleichheit einiger in verschiedenen Artengruppen von Hochland-Saumfingerechsen vorgefundener Arealgrenzen deutet an, dass sowohl der Kamm der Cordillera Central und der Volcán Barú als auch verschiedene Pässe von der Fortuna-Depression ostwärts potentielle physiographische und klimatische Barrieren darstellen, die möglicherweise historische Vikarianzereignisse bewirkt haben und so im Zusammenhang mit der in situ-Speziation innerhalb der beiden artenreichsten Gattungen meines Untersuchungsgebietes, *Norops* and *Dactyloa,* stehen.

Die vorliegende Arbeit ist die bisher umfangreichste Untersuchung panamaischer Reptiliendiversität. Mit vier bereits publizierten Artbeschreibungen und der Abgrenzung zahlreicher genealogischer Linien, deren Beschreibung oder integrative Bestätigung noch aussteht, leistet sie einen beträchtlichen Beitrag zur Kenntnis der Alpha-Diversität von Reptilien, sowohl entlang der Cordillera Central als auch in Panama als Ganzem. Darüber hinaus bilden meine Neubewertungen diagnostischer Merkmale und Variabilitäts-Synopsen gemeinsam mit den standardisierten Artenportraits eine solide Basis für die Identifikation jeder der 180 in meinem Untersuchungsgebiet vorkommenden Arten. Des Weiteren präsentiere ich die bisher detailliertesten, nachvollziehbarsten und umfassendsten Analysen der geographischen und ökologischen Verbreitung, des Vorkommens in Verwaltungs- und Schutzgebieten, sowie der Gefährdung dieser Arten. Direktiven für weiterführende Studien, die auf dem breiten Fundament der vorliegenden Arbeit aufbauen können, beinhalten zusätzliche Inventarisierungsarbeit im Westen Panamas zur Schließung geographischer, genealogischer und taxonomischer Sammlungslücken, detaillierte integrativ taxonomische Studien der hierin identifizierten UGL-Komplexe und anderer Taxa zur Aufklärung ihres taxonomischen Status, sowie nicht zuletzt umfassende phylogeographische Analysen zur Rekonstruktion der Artbildungsprozesse im Bereich der Cordillera Central, welche eine derart diverse und einzigartige Reptilienfauna hervorgebracht haben.

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List of abbreviations

Abbreviation	meaning	category
+G	using a discrete Gamma distribution with 5 rate categories	phylogenetics
+I	assuming that a certain fraction of sites are evolutionary invariable	phylogenetics
2nd Canths	scales between second canthals	pholidosis
4finger	subdigital scales or lamellae under fourth finger	pholidosis
4fingerdist	subdigital scales or lamellae under distal phalanx of fourth finger	pholidosis
4fingerpad	subdigital scales or lamellae under phalanges ii-iv of fourth finger	pholidosis
4toe	subdigital scales or lamellae under fourth toe	pholidosis
4toedist	subdigital scales or lamellae under distal phalanx of fourth toe	pholidosis
4toepad	subdigital scales or lamellae under phalanges ii-iv of fourth toe	pholidosis
AB	Abel Batista	collector
AC	Arcadio Carrizo	collector, field tags
AGD	axilla-groin distance	morphometrics
AH	Andreas Hertz	collector, field tags
AIC	Akaike Information Criterion	phylogenetics
Am	tropical monsoon climate	Köppen climate type
ANAM	Autoridad Nacional del Ambiente	institution
asl	above sea level	geography
AU	Andreas Uselis	field assistant
Aw	tropical wet climate	Köppen climate type
Aw	tropical savanna climate	Köppen climate type
BI	Bayesian Inference	analysis
BIC	Bayesian Information Criterion	phylogenetics
BPPS	Bosque Protector Palo Seco	protected area
C.	Cerro (Spanish for "mountain", especially in mountain names)	geography
CA	Central America(n)	geography
ca.	circa (Latin for "approximately", "about")	Latin expression
Canths	total canthals	pholidosis
Canths enl.	enlarged canthals	pholidosis
Cf	temperate wet (or perhumid) climate	Köppen climate type
cf.	confer (Latin for "compare")	Latin expression
CGdR	Contraloria General de la República	institution
CO	circumorbitals	pholidosis
COL	Colombia	geography
CR	Critically Endangered	IUCN category
CRI	Costa Rica	geography
Cw	temperate wet & dry climate	Köppen climate type
D	dorsal, dorsals	pholidosis, morphology
DAG	dorsals between axilla and groin	pholidosis
DD	Data Deficient	IUCN status
D-HC	dorsals posteriorly (1 head length anterior to cloaca)	pholidosis
D-HH	dorsals anteriorly (2 head length posterior to head)	pholidosis
DHL	dorsals in one head length	pholidosis
D-MB	dorsals at midbody	pholidosis
Drows	enlarged dorsal rows	pholidosis
E	East	geography

Abbreviation	meaning	category
e.g.	exempli gratia (Latin for "for example")	Latin expression
EN	Endangered	IUCN category
et al.	et aliter (Latin for "and others", referring to people)	Latin expression
etc.	et cetera (Latin for " and others", referring to things, not people)	Latin expression
FH	Frank Hauenschild	collector, field tags
Fig(s).	Figure(s)	layout element
FL	femur length	morphometrics
FN	frontonasals	pholidosis
FO	Falk Ortlieb	field assistant
FP	frontoparietals	pholidosis
ft	foot, feet	unit (distance)
GK	Gunther Köhler	collector, field tags
GTR	General Time Reversible model	phylogenetics
gulars	gular rows	pholidosis
HIILV	Humedal de Importancia Internacional Lagunas del Volcán	protected area
HIISSPS	Humedal de Importancia Internacional San San Pond Sak	protected area
HKY	Hasegawa-Kishino-Yano model	phylogenetics
HL	head length	morphometrics
horDear	horizontal diameter of ear	morphometrics
horDT	horizontal diameter of tail	morphometrics
HW	head width	morphometrics
i.e.	id est (Latin for "that is")	Latin expression
IN	internasals	pholidosis
INL	infralabials	pholidosis
IO	interorbitals	pholidosis
IP	interparial plate	pholidosis
IP/SS	scales between IP and SS	pholidosis
IPL	interparietal length	morphometrics
IPW	interparietal width	morphometrics
IRI	interrictals	pholidosis
ISO	intersupraoculars	pholidosis
JC	Juan Castillo	field assistant
JFB	Joe-Felix Bienentreu	collector, field tags
JJK	Johannes Justus Köhler	collector, field tags
JS	Javier Sunyer	collector, field tags
JV	Joseph Vargas	collector, field tags
K2	Kimura 2-parameter model	phylogenetics
km	kilometer(s)	unit (distance)
L	lateral, laterals	pholidosis, morphology
LC	Least Concern	IUCN category
LCA	Lower Central America(n)	geography
LDF	Lowland (=Tropical) Dry Forest	Holdridge life zone
LMF	Lowland (=Tropical) Moist Forest	Holdridge life zone
LMMF	Lower Montane Moist Forest	Holdridge life zone
LMWF	Lower Montane Wet Forest	Holdridge life zone
loc., locs.	locality, localities	geography
loreal rows	horizontal loreal scale rows	pholidosis
loreals	total number of loreal scales	pholidosis
LS, LSt	Leonhard Stadler	collector, field tags

Abbreviation	meaning	category
LWF	Lowland (=Tropical) Wet Forest	Holdridge life zone
m	meter(s)	unit (SI, distance)
m asl	meter(s) above sea level	geography (elevation)
MB	midbody	pholidosis
MG	Markus Gutpelet	co-working student
MHCH	Museo Herpetológico de Chiriquí (Davíd, Chiriquí, Panamá)	collection
mi	mile(s)	unit (distance)
ML	Maximum Likelihood	analysis
mm	millimeter(s)	unit (distance)
MNPC	Monumento Natural Cerro Gaital	protected area
MNPC	Monumento Natural Los Pozos de Calobre	protected area
MP	Marcos Ponce	collector
Mya	Million years ago	unit (time)
N	North	geography
NA	North America(n)	geography
NE	Not Evaluated	IUCN status
NH	Nadim Hamad	collector, field tags
NT	Near Threatened	IUCN category
Occ	occipitals	pholidosis
p(p).	page(s)	bibliography
Par	parietals	pholidosis
PC	enlarged postcloacal scale(s), postcloacal(s)	pholidosis
PCL	postcloacal length	morphometrics
PCW	postcloacal width	morphometrics
PET	potential evapotranspiration	geography
PF	prefrontals	pholidosis
PILA	Parque Internacional La Amistad	protected area
PM	postmentals	pholidosis
PMMF	Premontane Moist Forest	Holdridge life zone
PMWF	Premontane Wet Forest	Holdridge life zone
PN	Parsimony Network analysis	analysis
PNAC	Parque Nacional Altos de Campana	protected area
PNCH	Parque Nacional Cerro Hoya	protected area
PNGDOTH	Parque Nacional General de División Omar Torrijos Herrera	protected area
PNSF	Parque Nacional Santa Fé	protected area
PNVB	Parque Nacional Volcán Barú	protected area
post Canths	scales between posterior canthals	pholidosis
Postoc	postoculars	pholidosis
PP	precloacal plate	pholidosis
PPant	precloacal plate anterior row	pholidosis
PPmar	precloacal plate marginals	pholidosis
PR	postrostrals	pholidosis
Preoc	preoculars	pholidosis
Qda.	Quebrada (spanish for "creek", "stream")	geography
RdL	Rosalba de Leon	field assistant
RFLF	Reserva Forestal La Fortuna	protected area
RFLT	Reserva Forestal La Tronosa	protected area
RFLY	Reserva Forestal La Yeguada	protected area
S	South	geography

Abbreviation	meaning	category
s	second(s)	unit (SI, time)
SA	South America(n)	geography
SAM	scales around midbody	pholidosis
SBL	sublabials	pholidosis
SBO	suboculars	pholidosis
SBO/SPL	scales between SO and SPL or interoculabials	pholidosis
SBO/SPL	interoculabials	pholidosis
SC	subcaudals	pholidosis
Serr.	Serranía (Spanish for "mountain range")	geography
SF	subfoveals	pholidosis
shank	shank length	morphometrics
SL	Sebastian Lotzkat	collector, field tags
SnL	snout length	morphometrics
sp. / spp.	species (singular/plural)	taxonomy
SPL	supralabials	pholidosis
SPL eye	supralabials contacting eye	pholidosis
SPO	supraorbitals, supraoculars	pholidosis
SS	supraorbital semicircles	pholidosis
ssp. / sspp.	subspecies (/plural)	taxonomy
STRI	Smithsonian Tropical Research Institute	institution
SVL	snout-vent length	morphometrics
T92	Tamura 3-parameter model	phylogenetics
Tab(s).	Table(s)	layout element
Tant	anterior temporals	pholidosis
TL	tail length	morphometrics
TN93	Tamura-Nei Model	phylogenetics
TOL	total length	morphometrics
Tpost	posterior temporals	pholidosis
UNACHI	Universidad Autónoma de Chiriquí	institution
V	ventral, ventrals	pholidosis, morphology
VAG	ventrals between axilla and groin	pholidosis
verDear	vertical diameter of ear	morphometrics
verDT	vertical diameter of tail	morphometrics
VHL	ventrals in one head length	pholidosis
vs.	versus (Latin for "as opposed to")	Latin expression
VU	Vulnerable	IUCN category
W	West	geography

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Preface

For billions of years, life on earth has pursued its survival through diversification in the course of a complex process that we call evolution, leaving us today with millions of unique life forms we refer to as species. One of these has undergone a tremendous cultural evolution and many of its individuals, to a certain extent liberated from the perpetual engagement in the harsh struggle for life, have enough leisure time to devote themselves to rather unnatural activities like fighting over unedible objects, sending greetings to other galaxies, or naming the other forms of life and in this event calling itself the knowledgeable man, *Homo sapiens.* Over all these distractions, most members of this species have forgotten that, intelligent as they may be, they are still only one facette of the utterly complex and heavily interdependent diversity of life.

The biological diversity on earth remains poorly understood, and we are still far from completely describing just its organismic components, not to speak of their interactions. Yet, diversity is rapidly declining, obviously due to the detrimental impact of mankind. More than ever, biodiversity research is a desperate race against time. While we discover new species or cryptic diversity among "well-known" species, we observe dramatic species declines and extinctions, irreplaceably loosing at a fast pace protagonists fulfilling their proper role in the biosphere – a role that may be crucial for the existence of many others, including ourselves.

This study is an attempt to compile the current picture on reptile diversity in the highlands of western Panama, by assembling all the scattered bits and pieces of knowledge provided by others and adding to it as many novel parts as possible myself. Regardless of the financial and temporal restrictions which limit the efficiency and comprehensiveness of my work, I recognize that such inventory cannot be complete at this time, even after more than a century of research in the area, and probably never will be. Nevertheless, I believe that I will leave this puzzle with quite some missing jigsaw pieces less than I received it.

1. Introduction

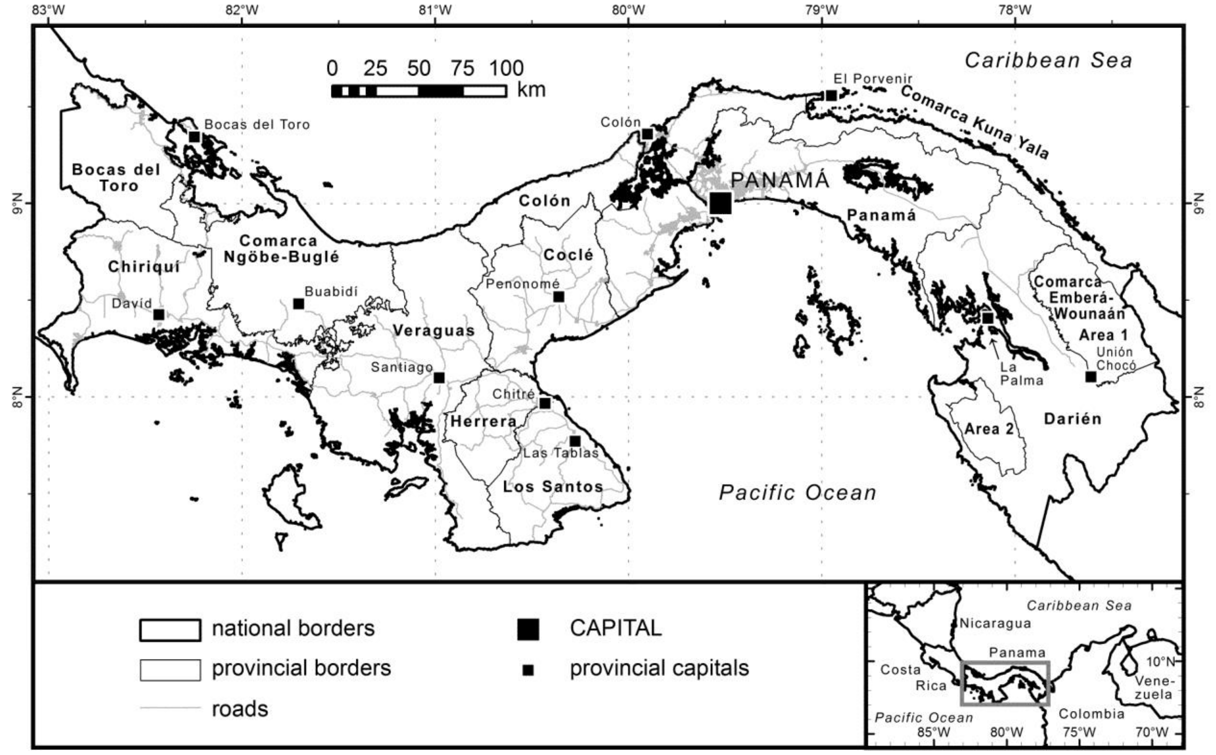
1.1 Panama: an overview

This first part of the introduction provides baseline information on Panama, its present environments, and its historical geology and biogeography. If not mentioned otherwise, geographic information and names are taken from the Mapa General de la República de Panamá (IGNTG 2000) and the Atlas Nacional Digital de la República de Panamá (IGNTG 2008), as well as from a few other key publications (Myers 1969b; Jaramillo et al. 2010).

1.1.1 Panama at a glance

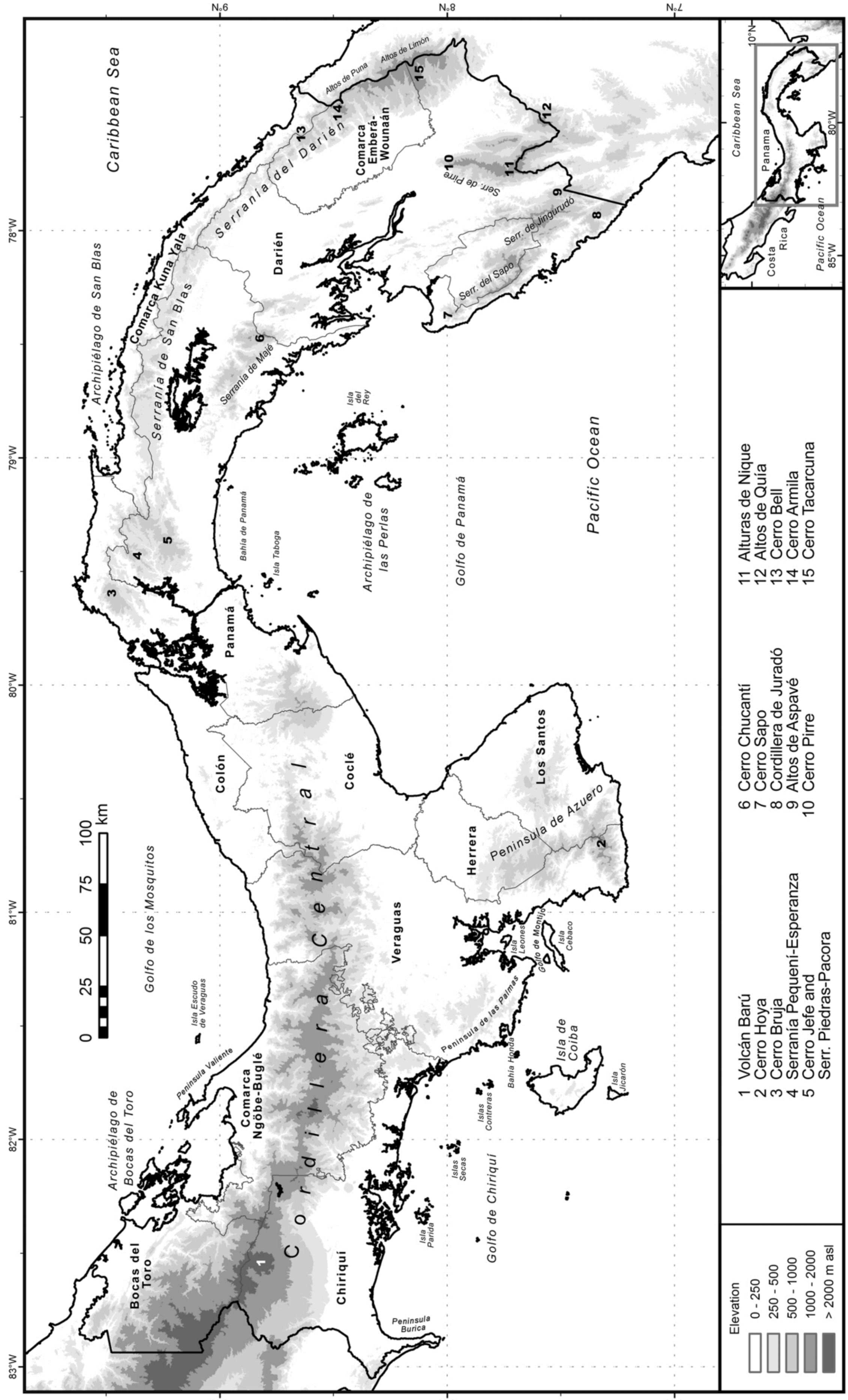
Panama is the southern- and easternmost country of Central America. It is bordered by Costa Rica to the west, Colombia to the east, the Caribbean Sea to the north, and the Pacific Ocean to the south. The elongate country has a longitudinal extension of 650 airline km from 83°03' to 77°09'W, and a latitudinal extension of 270 airline km from 7°12' to 9°39'N. Following the east-west-oriented sigmoidal shape of the country, its total length amounts to approximately 730 km. The width of the isthmus varies between 190 km at the Peninsula de Azuero and 50 km near the mouth of Río Chepo. Most of the republic's total area of approximately 75845 km^2 (including about 1232 km^2 inland water) is comprised by the mainland. Apart from the mainland, Panama has 1518 islands, islets, and keys, 1023 of these along the 1288 km of Caribbean and 495 along the 1701 km of Pacific coastline. Most of Panama's offshore land area is made up by the largest island Isla Coiba and a few other large islands in the Golfo de Montijo, the Archipiélago de las Perlas, and the Archipiélago de Bocas del Toro.

The Republic of Panama (República de Panamá) with its capital Panama City (Ciudad de Panamá) was established as such in 1903 after achieving its independence from Colombia. Presently, it contains 12 major political subdivisions (Map 1.1): The 9 provinces (Provincias) have essentially been unchanged since 1922, whereas the 3 indigenous autonomous regions known as Comarcas have been designated more recently (Comarca Kuna Yala as San Blas in 1938, Comarca Emberá-Wounaán in 1983, and Comarca Ngöbe-Buglé in 1997). Between 1903 and 1979, the so-called Canal Zone, extending to roughly 8 km on each side of the Panama Canal and comprising areas now belonging to Colón and Panamá provinces, was designated as territory of the USA, and completely returned to Panamanian control in 1999. The Provincias and Comarcas are again subdivided into 75 districts (Distritos), which in turn comprise between one and 24 Corregimientos, the smallest administrative subdivisions totaling 621 all over Panama.



Map 1.1: Panama: administrative subdivisions, provincial capitals, and major roads.

The approximately 3 400 000 inhabitants of Panama (www.contraloria.gob.pa/inec) are very unevenly distributed across the country, with the lowest population densities occurring along parts of the Caribbean drainage and in eastern Panama. About half of the population live in Panamá province, most of them in the greater urban area of Panama City. With the exception of Colón, which is the second largest city outside the capital's conurbanization and guards the Caribbean entrance to the Panama Canal, all other major cities are found in the Pacific drainage of central and western Panama, where most are lined up along the Panamerican Highway. More commonly referred to as Carretera Interamericana by Panamanians, this road constitutes the principal overland transport route of the country. It runs from the Costa Rican border at Paso Canoa to Panama City and into Darién Province, where it essentially ends around Yaviza, leaving the so-called Darien Gap around the border with Colombia impassable for road travel. The only roads that truly traverse the isthmus providing direct connections from coast to coast are the Transístmica between Panama City and Colón, and the road connecting Chiriquí and Bocas del Toro provinces via the Fortuna depression. Of utmost importance for the Panamanian economy is its other major transport route, the globally significant Panama Canal that was finally established in 1904.

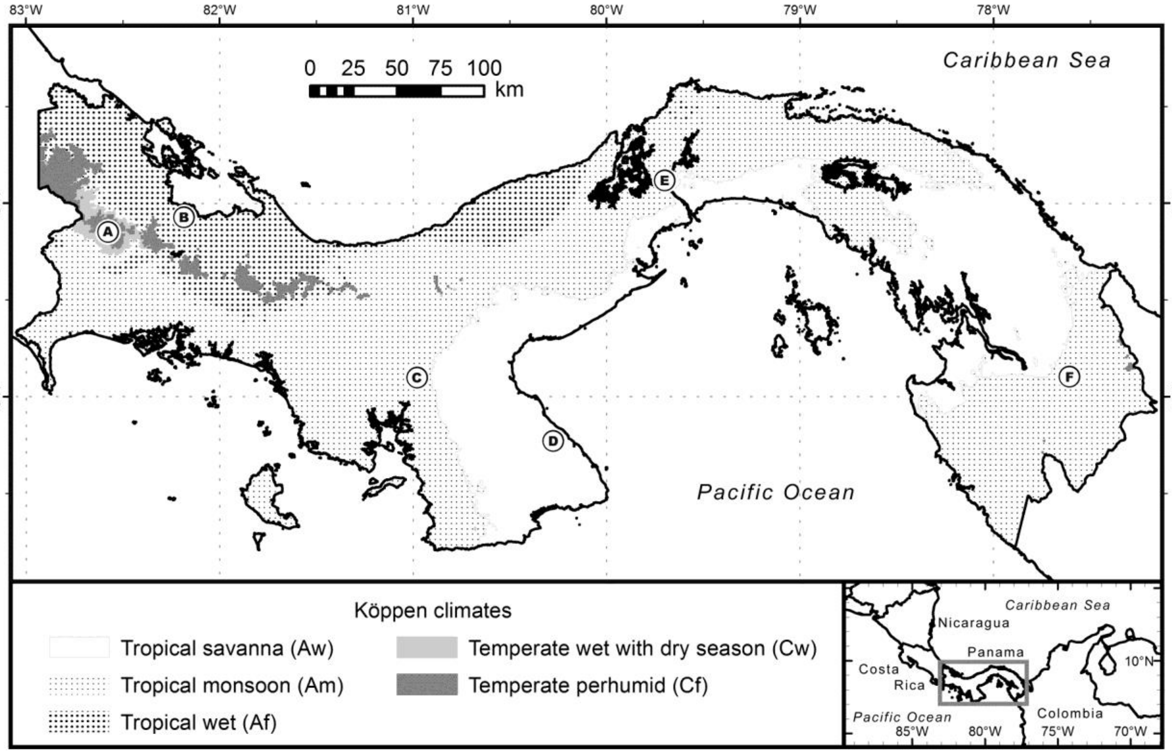


Map 1.2: Topography of Panama.

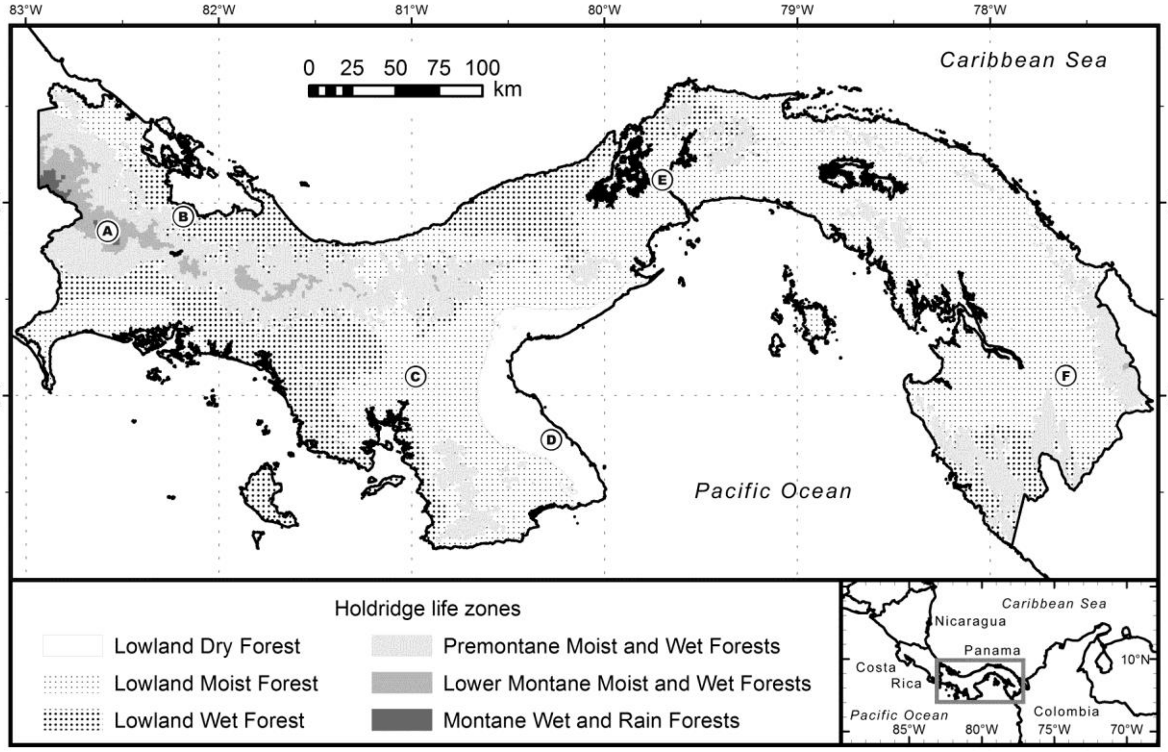
1.1.2 The Panamanian environment

Despite its small size, Panama has a very diverse environmental setting. Apart from its ubication in the tropical realm, the principal cause for the great variety of different habitats on this narrow isthmus is its manifold physiography. Map 1.2 shows the principal mountainous systems of Panama. The eastern highlands are composed of three separate systems: The elongate, mostly narrow, Caribbean range termed North Eastern Arch by Pérez-Santos (1999) forms a continuum paralleling the Caribbean coast from the Colombian border to the Canal, constituting the continental divide throughout its course. It originates near the easternmost corner of the country, forming the natural border to Colombia under the name Altos de Limón and, further north, Altos de Puna. North of Cerro Gandí it becomes much lower, and separates the Comarca Kuna Yala from the Comarca Emberá-Wounaán and Darién province as Serranía del Darién. From somewhere near 78°W it gradually changes direction from NW to W and is called Serranía de San Blas until N of Chepo, from where it again attains higher elevations and widens considerably to cover almost the entire width of the isthmus in Panamá and Colón provinces E of the canal, comprising the Serranías de Piedras-Pacora, Pequení-Esperanza, and the massif around Cerro Bruja. Prominent elevations throughout this range are, from south to north, Cerro Tacarcuna (1875 m asl), Cerro Tanela (1415 m), Cerro Armila (1421 m), Cerro Gandí (1160 m), Cerro Bell (1046 m), Cerro Sasardí (610 m), Cerro Brewster (899 m), Cerro Jefe (1007 m), and Cerro Bruja or Brujas (979 m). The other components of Panama's eastern highlands are smaller, isolated ranges located in the Pacific drainage and separated from the Caribbean arch by the extensive drainage systems of the Cañazas, Chepo, Chucunaque, and Tuira rivers. In eastern Panamá and northwestern Darién provinces, the Serranía de Majé, in the past often called Serranía de Cañazas (Myers 1969b, 2007), parallels the Pacific coast between the mouths of Río Chepo and Río Tuira, rising up to 1439 m at Cerro Chucantí. South of the mouth of Río Tuira, the Serranía del Sapo runs close to the Pacific coast through southwestern Darién province and Comarca Emberá-Wounaán, reaching elevations up to 1580 m at Cerro La Piña. To the southeast, it passes into the Serranía de Jingurudó. This range has its highest peaks above 1600 m and is connected to the smaller Cordillera de Juradó along the coast and Altos de Aspavé further inland. In their totality, the massifs from Cerro Sapo southward are sometimes referred to as Jaqué-Imamadó Divide (Myers 1969b). Between Río Balsas and Río Tuira in south-central Darién, the Serranía de Pirre quickly rises to above 1500 m along its southerly course, connecting to the even higher Alturas de Nique and Altos de Quia at the Colombian border.

West of the Canal, isolated highlands are found on the Peninsula de Azuero in the provinces of Herrera, Los Santos, and Veraguas, reaching up to 1559 m at Cerro Hoya. The westerly neighboring Peninsula de las Palmas contains a smaller and much lower hilly system. Panama's western backbone is the Cordillera Central, which runs from the Costa Rican border eastwards to western Panamá province. It holds the country's highest peaks, forms the continental divide, and is described in detail in chapter 1.2.



Map 1.3: Köppen climates in Panama. Localities marked with capital letters refer to Figure 1.1.



Map 1.4: Holdridge life zones in Panama. Localities marked with capital letters refer to Figure 1.1.

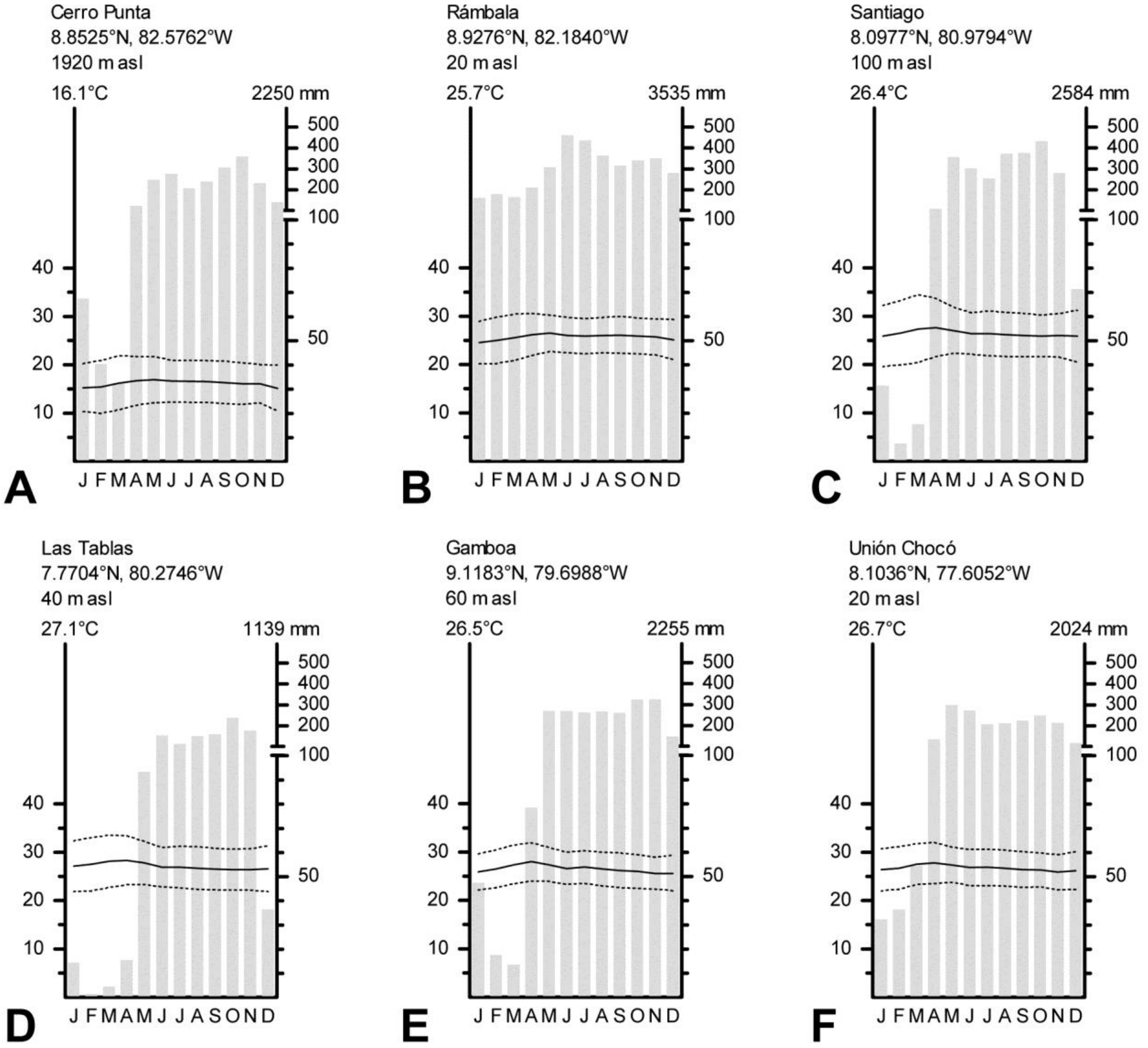


Figure 1.1: Climographs of selected localities plotted in Maps 1.3 and 1.4.

The principal factors determining the Panamanian climates are the country's ubication less than 10°N of the equator and between two seas, the seasonal regime of the trade winds, and the relief of the narrow isthmus. Panama's lowlands are tropical, whereas the highest peaks rise above the timberline and experience a temperate climate. Map 1.3 shows the Köppen climates (Köppen 1936) found within Panama. Most of the isthmus experiences tropical climates with mean annual temperatures above 18°C. These are either perhumid ("tropical wet" or Af climates, compare Fig. 1.1B) or have a dry season. Most tropical areas are subject to "tropical monsoon" climates (Am climates, compare Figs. 1.1A, C, E, and F) with a moderately pronounced dry season and total annual precipitation of usually 2000 mm or more. "Tropical savanna" or Aw climates (compare Fig. 1.1D; also called "tropical wet & dry", e.g., by Myers 1969b) receive a lower annual precipitation and a more pronounced dry season. The temperate climates of higher altitudes with mean annual temperatures below 18°C are largely restricted to western Panama’s Cordillera Central. These highland climates are mostly perhumid (Cf climates, also referred to as "temperate wet", e.g., by Myers 1969b) but in some places experience a usually short dry season (Cw climates, also termed "temperate wet & dry", e.g., by Myers 1969b; see Fig. 1.1A)

A different perspective on Panamanian climates is provided in Map 1.4 showing the life zones of the Holdridge (1967; 1971) system. The extent of the tropical Köppen climates is rather congruent with that of the Lowland and Premontane Holdridge life zones, while the Lower Montane and Montane life zones match the temperate Köppen climates. Incongruities among the subtypes of these principal climatic regimes are attributable to differences in the two classification schemes, probably mostly to the fact that the Holdridge system does not account for seasonal changes in precipitation. Only a small portion of Panama's lowlands is attributed to the Lowland (= Tropical) Dry Forest (LDF), while Lowland Moist Forest (LMF) and Lowland Wet Forest (LWF) each comprise a much larger area. The Premontane, Lower Montane, and Montane bioclimatic belts each encompass two different humidity provinces: humid and perhumid, that is, Moist Forest and Wet Forest, in the case of the former two, and perhumid and superhumid, that is, Wet Forest and Rain Forest, in the case of the latter. In view of the scale (as well as the fact that LMMF is restricted to a very small area at the border to Colombia in the Comarca Emberá-Wounaán), these two life zones are blended together in Map 1.4 for each of the highland belts, respectively (PMMF+PMWF; LMMF+LMWF; MWF+MRF). Map 1.8 provides a more detailed view of the Holdridge life zones for the Cordillera Central.

The standardized climographs in Figure 1.1 illustrate local climates for the six localities marked with capital letters in Maps 1.3 and 1.4. In view of its physiographic and climatic diversity, it is not surprising that Panama houses a multitude of different vegetation formations or habitats, as depicted in more detail for the Cordillera Central in chapter 1.2.3.

1.1.3 Tectonic history and historical biogeography of the Panamanian isthmus

The isthmus of Panama was the last portion of the Central American land bridge to be established during the Tertiary, leading to the closure of the sea connection between the Caribbean Sea and the Pacific Ocean called the Panama Portal. Located at the southwestern edge of the Caribbean Sea, Panama and Costa Rica constitute Lower Central America sensu Savage (2002). As presently understood (Roubik & Camargo 2012, Montes et al. 2012), the LCA landmasses together with Chocoan Colombia form a proper microplate surrounded by the SA, Caribbean, Nazca, and Cocos plates. This "Panamanian microplate" is comprised of the Chorotega block (Costa Rica and western Panama approximately to the Canal area), the Panama block (Panama east of the Canal area to around the Colombian border) and the Chocó block (adjacent Pacific Colombia). Their landmasses experienced initial uplifts at least since the Paleocene by the subduction of the Farallon plate under the Caribbean plate, way southwest of their contemporary ubication. After the fragmentation of the Farallon plate into the Cocos and Nazca plates, the Chorotega block as well as the northwesterly adjacent Chortis and southeasterly adjacent Chocó blocks slowly assumed their present positions, and with them probably a series of volcanic islands as the first indication of the future Central American land bridge. Major uplifts of what now is LCA are thought to have occurred since the Oligocene, owing to the continuing subduction of the northeasterly moving Cocos plate under the Chorotega block along the Middle American subduction zone, the subduction of the easterly moving Nazca plate under the Chocó block along the SA subduction zone, and complex tectonic interactions between the Cocos-Nazca axis and the Panamanian microplate.

The traditional view that the Panama Portal was not closed until the middle Pliocene some 3.5–3 Mya, or even later (see Savage 2002 and references therein), has recently been challenged by studies arguing for a much earlier formation of a CA land bridge during the Miocene or even the Oligocene, that was at least transitorily completed around 15 Mya and may have existed or at least been viable for terrestrial organisms as far back as 25 Mya (e.g., Montes et al. 2012, and references cited in the following paragraph). While both sides present strong arguments for their scenarios, at this point it must be stated that the exact paleogeography of the LCA land connection, i.e., the distribution, location, extent, and connectivity of emerged terrains over the last 35 million years remains unsatisfactorily understood.

Likewise, it is unclear since when exactly the first successful dispersals of biota over these islands occurred, though more and more studies support Miocene or Oligocene times. Molecular clocks applied to pitvipers suggest that the first ancestors of SA *Bothrops* arrived in SA during the Miocene about 10–23 Mya (Wüster et al. 2002; Castoe et al. 2009; Daza et al. 2010), and that SA and CA clades of *Lachesis* and *Porthidium* split around 6–14 (Wüster et al. 2002) or 1.6–8 Mya (Daza et al. 2010), while SA *Bothriechis* are thought to have diverged from the CA clade 5.5–12 Mya (Daza et al. 2010). Daza et al. (2009) inferred the genus *Leptodeira* to have colonized SA about 3.6–8 Mya. According to Daza et al. (2010), snake lineages dispersed between CA and SA between 0.8–22.8 Mya, with divergence maxima around 15 and 1–7 Mya. Head et al. (2012) found fossil vertebrae arguing for a dispersal of the genus *Boa* into CA before 19 Mya. Studies on other organisms suggest first crossings of the Panama Portal between 16–30 Mya by phletodontid salamanders (Elmer et al. 2013), 9–23

Mya by the eleutherodactylid genus *Pristimantis* (Pinto-Sanchez et al. 2012), 16–31 Mya by the palm genus *Copernicia* (Bacon et al. 2013), around 6 Mya by the annonacean genus *Guatteria* (Erkens et al. 2007), and between 19–27 Mya by the angiosperm family Caricaceae (Carvalho & Renner 2012). The results of the studies recounted above imply that at the traditionally assumed 3–3.5 Mya the Great American Biotic Interchange had already assumed its full magnitude, and strongly suggest that it had begun much earlier. During this major biogeographic event of overwhelming consequence for the biodiversity of the Neotropics, biota native to South America dispersed north into Central or even North America, while lineages with origins in Central and North America in turn colonized South America.

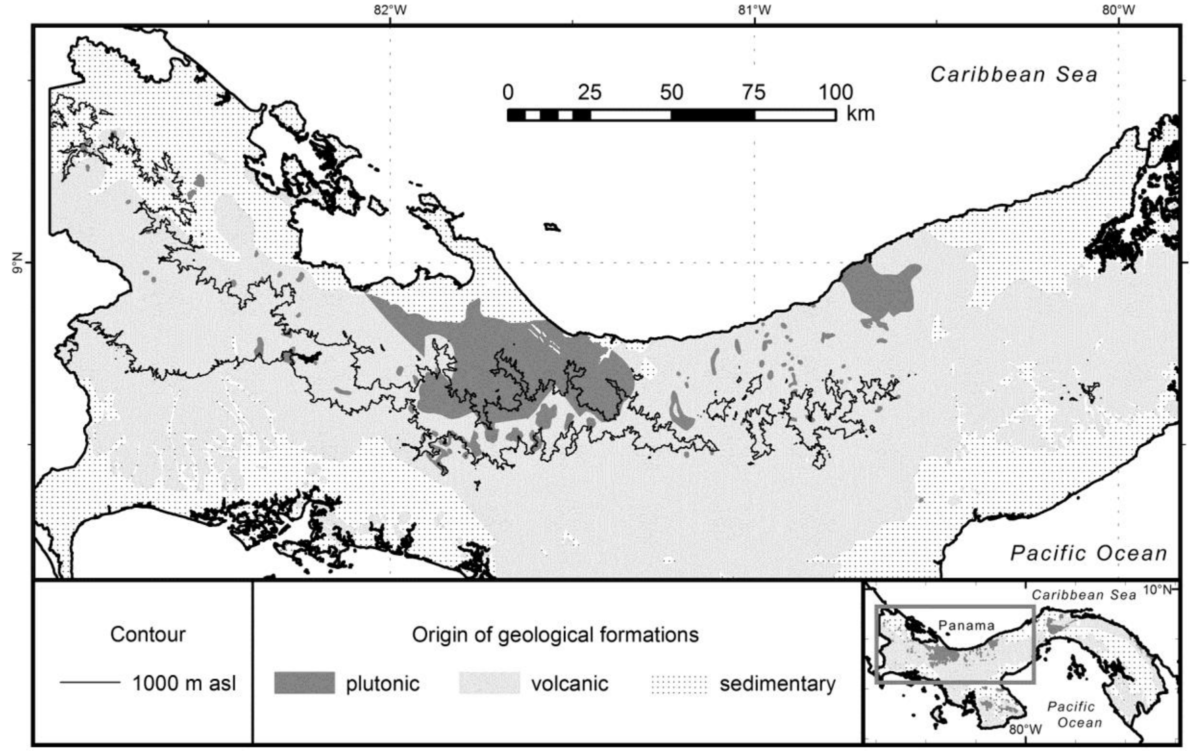
Presently, Lower Central America is one of the 25 biodiversity hotspots of the world as identified by Myers et al. (2000), is part of the Costa Rica-Chocó global plant megadiversity center with the highest number of vascular plant species and endemics (Barthlott et al. 2007), and holds some of the highest species densities and numbers of endemic species known also in terms of herpetofauna (Savage 2002; Wilson & Johnson 2010). On a Central American scale, the highlands of western Panama deserve special mention in the biogeographical context. Forming a continuum with Costa Rica's Cordillera de Talamanca, western Panama's Cordillera Central constitutes the eastern part of the Lower Central American Highlands, or Talamancan Highlands, sensu Savage (1966, 1982, 2002), which extend from northern Costa Rica through western Panama. Separated from the Nuclear Central American highlands of the Chortis block by the Nicaragua depression, and from the highlands of Darién and Colombia situated on the Panama and Chocó blocks by the lowlands of central Panama, these highlands are home to distinct evolutionary lineages believed to have evolved in situ (e.g., Savage 2002; Castoe et al. 2009). Moreover, the successively uplifting Talamancan Highlands seem to have increasingly isolated Caribbean populations of several lowland taxa from their relatives along the Pacific versant, acting as a barrier that induced vicariance events across the Lower Central American isthmus during the Plio- and Pleistocene (Daza et al. 2010; Cadle 2012a). Last but not least, these highlands' great altitudinal range and varied topography provide a multitude of different environments, allowing for extreme diversity among their inhabitants.

1.2 The Cordillera Central

The Cordillera Central is the single mountain range extending more or less centrally from the Costa Rican border eastwards, constituting the continental divide throughout western Panama and the southern and eastern part of the LCA highlands. The chiefly west-east-oriented range runs through Bocas del Toro and Chiriquí provinces, the Comarca Ngöbe-Buglé, as well as Veraguas, Colón, and Coclé provinces before ending in western Panamá province.

1.2.1 Geology

The LCA highlands are located on the Chorotega crustal block and form the southeastern part of the Middle American volcanic arc. Just as the majority of LCA's land mass, the Cordillera Central is thought to have been uplifted in the course of the complex tectonic interactions between the Caribbean, Cocos, Nazca, and SA plates (Savage 2002; Montes et al. 2012).



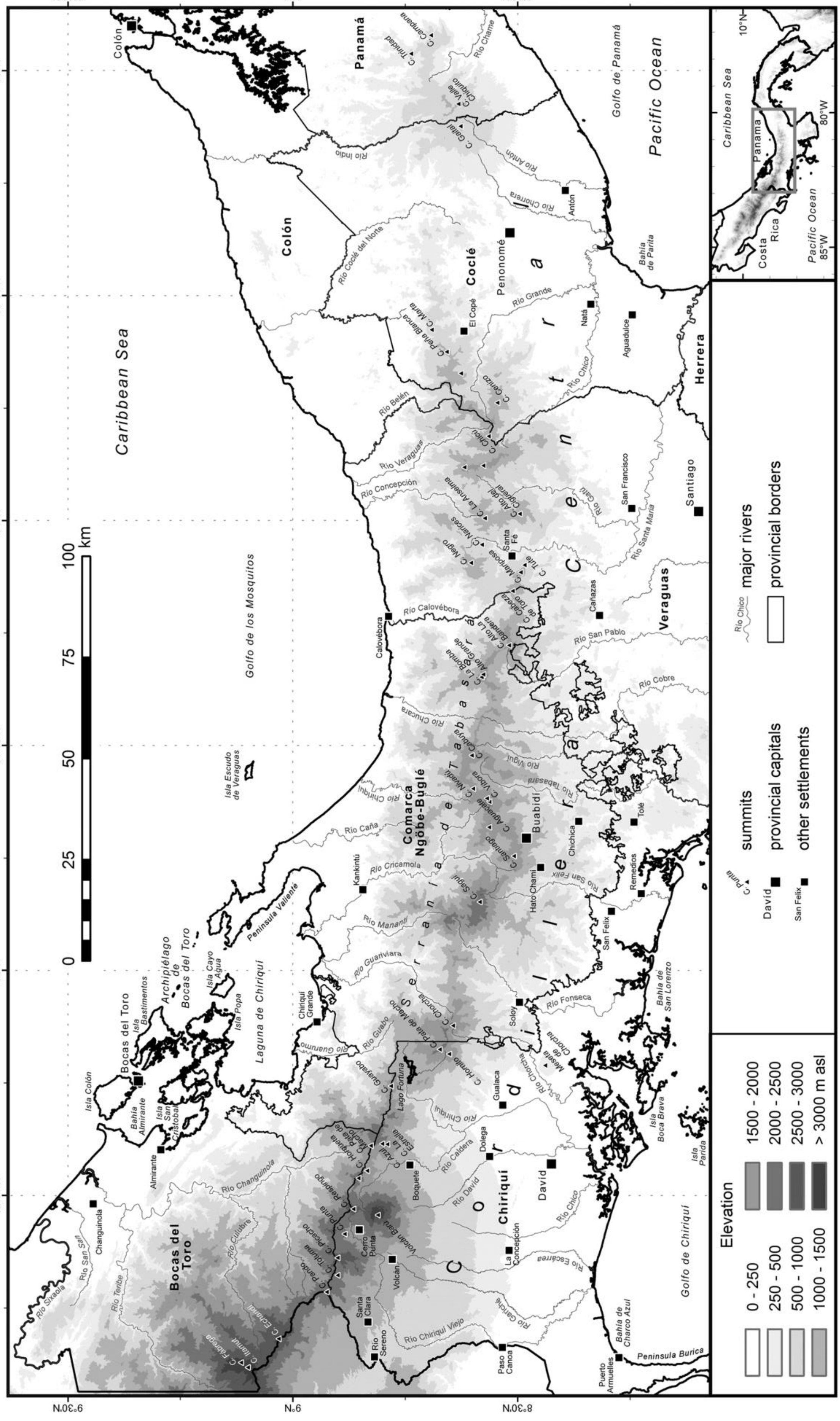
Map 1.5: Generalized geological formations along the Cordillera Central.

These interactions, including subductions, deformations, fractures, and faults, triggered strong volcanic activity along the present day isthmus of Panama. In consequence, the majority of the Cordillera Central is constituted by igneous rocks, chiefly in the form of volcanic outflows as shown in Map 1.5. Besides these, plutonic formations account for a considerable portion of the Caribbean versant along the Serranía de Tabasará and are also found in the western lowlands of Colón province. Most of these igneous components have emerged during the Tertiary, though some date back to the late Mesozoic and a certain fraction is of very recent Quaternary origin. It should be noted that the western portion of the Cordillera Central, with its northwest-southeasterly orientation (until somewhere between Cerro Santiago and the Río Tabasará), has experienced a slightly different geological evolution than the more easterly portions with their west-easterly course (IGNTG 2008). Marine sediments of Cretacic or Tertiary origin account for some premontane portions of the Cordillera's northern versant, especially in Bocas del Toro province, as well as for portions of the adjacent lowlands. Interspersed quaternary sediments accumulated by freshwater bodies complement the geological setting of the Cordillera Central (IGNTG 2008).

1.2.2 Physiography and toponymy

From west to east, the Cordillera Central can be divided physiographically into three consecutive sections, each of which accounts for roughly one-third of the Cordillera's total longitudinal extent in Panama: The Serranía (or Cordillera) de Talamanca, also called Cordillera Chiricana by some authors (e.g., Pérez-Santos 1999, though others define the Cordillera Chiriquana geologically and thus interpret it to end more to the east, as specified in chapter 1.2.1), extends from Costa Rica to the Fortuna depression. The easterly adjacent Serranía (seldom termed Cordillera) de Tabasará stretches between the Fortuna depression and the area around Santa Fé (also called Santa Fé de Veraguas) at about 81°W. For the easternmost third, between Santa Fé and the terminal Cerro Campana, no specific name other than "Cordillera Central" is widely used, though it is sometimes lumped together with the Serranía de Tabasará under that name (e.g., Pérez-Santos 1999) or as Cordillera Veragüense-Coclesiana (IGNTG 2008). Generally, the Panamanian Cordillera Central attains lower altitudes than the Talamancan Highlands of Costa Rica, and gradually lowers throughout its easterly course. Map 1.6 gives a topographic overview of this mountain range, its principal elevations mentioned below, and major rivers draining both versants.

Throughout the Serranía de Talamanca, i.e., from the Costa Rican Border to the Fortuna depression, the continental divide rarely drops below 2000 m, and never below 1500 m. All Panamanian peaks exceeding 3000 m are situated in this portion. Three of these, the Cerros Fábrega (3335 m), Itamut (3279 m), and Echandí (3163 m), tower near each other in the extreme west, where the crest of the Serranía de Talamanca constitutes the national border with Costa Rica.



Map 1.6: The Cordillera Central.

From Cerro Pando (2466 m) eastwards, the Talamancan ridge separates the provinces Bocas del Toro and Chiriquí. Prominent elevations along this section of the continental divide are Cerro Totuma (2625 m), Cerro Picacho (2986 m), Cerro Punta (2415 m), and Cerro Respingo (2850 m), which is connected by the Paso Respingo (2500 m) to Panama's highest mountain, Volcán Barú (3475 m). This impressive volcano is southernly offset from the main divide and also known as Volcán de Chiriquí. East of the Respingo pass, the continental divide lowers to almost 2000 m for the first time along its easterly course through Panama, creating a pass conveniently crossed by the trail known as Sendero Culebra W of the nameless peak (2352 m) above Cerro Horqueta (1943 m). The first pass below 2000 m asl, crossed by the trail known as Sendero Pianista, lies between these peaks and the massif called Cerro Pate Macho or Cerro Pata de Macho (higher than 2200 m) above Cerro Pianista. The latter massif also contains the southward projecting ridge of Cerro Azul (2310 m) and Cerro La Estrella (2250 m), and marks the border between Bocas del Toro and Comarca Ngöbe-Buglé on the Caribbean slopes. The easternmost summit of the Serranía de Talamanca is Cerro Guayabo (2088 m), east of which the elevation rapidly decreases to allow for the first passes below 1000 m. These passes, the westernmost of which is crossed by the Chiriquí-Bocas highway, are situated on the continental divide just north of the high valley of the Río Chiriquí known as the La Fortuna area. This valley of high beogeographic interest separates the Serranía de Talamanca from the Serranía de Tabasará.

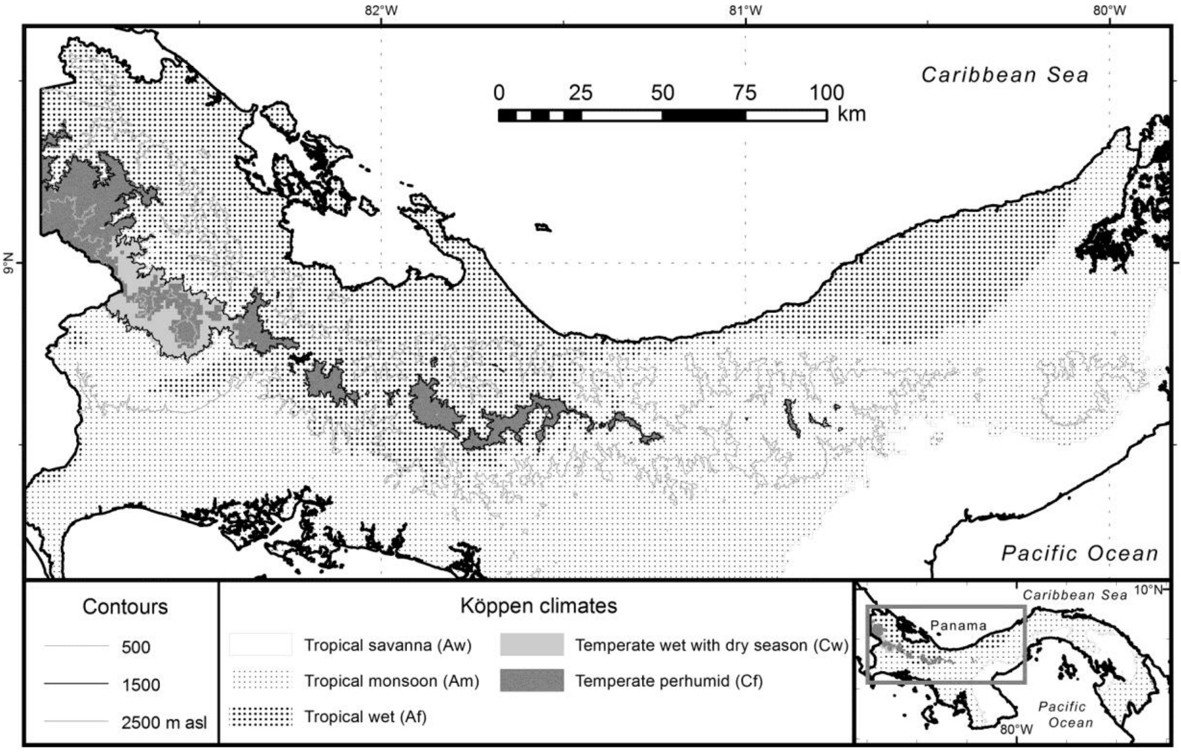
Throughout the Serranía de Tabasará, the 2000 m contour is exceeded only a few times, and the saddles between the higher massifs assume lower elevations than in the Talamancan ridge, in several cases well below 1500 m. To the south and southeast of the Fortuna depression, the Serranía de Tabasará has its western extreme containing three of its highest peaks: The elongate, L-shaped ridge of Cerro Pata de Macho (2192 m), part of the continental divide only at its easternmost tip, releases the headwaters of Río Chiriquí from its northern slopes. Cerro Hornito (2102 m) lies a little offset to the southwest, and Cerro Chorcha (2238 m; not to be confused with the much lower table mountain Meseta de Chorcha that stands out prominently from the adjacent lowlands) continues the continental divide to the east. From here, the Tabasará range runs as a narrow ridge eastward leaving several saddles below 1300 m, before it rises again towards its greatest massif comprising over ten square kilometers above 2000 m and culminating in the cone-shaped peak of Cerro Saguí or Cerro Ratón (2520 m). To the east, the continental divide drops towards the Cerro Colorado area to open a pass as low as 1400 m at Terminal de Hacha, and ascends again towards the last portion that contains peaks over 2000 m and is contiguous above the 1500 m contour. Those final really high mountains are Cerro Santiago (2127 m), an unnamed mountain (above

2100 m), and the nearby Cerros Aguacate (2292 m) and Víbora (2239 m). Prominent elevations further to the east along the Tabasará ridge include Cerro Nivadú (1845 m), Cerro Cabuya (1969 m), Cerro La Bomba (1850) and nearby Alto Grande (1933), Cerro Alto La Bandera (1760 m), and Cerro Cabeza de Toro (1412 m). The terminal elevations of the Tabasará range are Cerro Delgadito or Mariposa (1420 m; also called Cerro Tute or Cerro Los Gringos) and the narrow tower of Cerro Tute (1081 m) southwest of Santa Fé. Separated by a pass lower than 800 m, the next elevations are the twin peaks of Cerro Negro (1518 m) north of Santa Fé. Cerro Negro and the nearby narrow ridge of Cerro Narices are the last mountains west of the Río Santa María, which herein is considered the eastern limit of the Serranía de Tabasará.

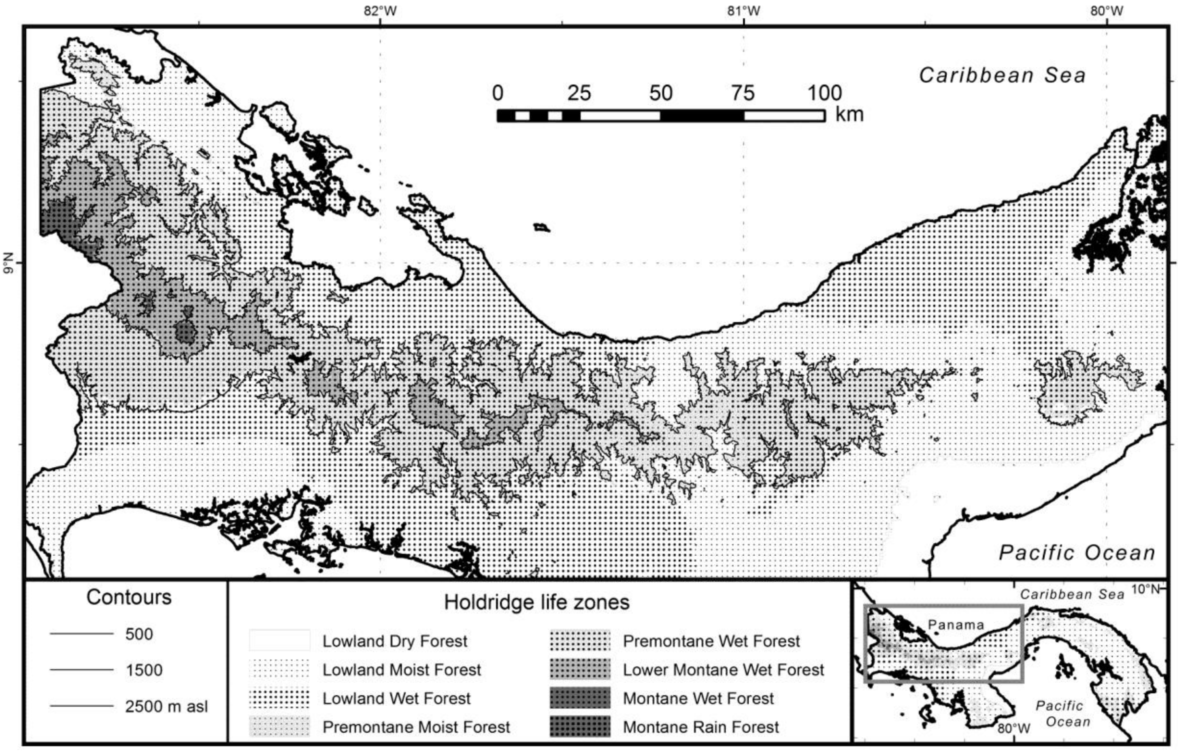
Throughout the easternmost third of the Cordillera Central, the remaining massifs above 1000 m are typically separated from each other by much lower saddles. The largest of these massifs are found in eastern Veraguas (Cerro La Anselma, 1504 m; Cerro Alto del Cigueral, 1510 m; unnamed mountain, 1964 m; unnamed mountain above 1870 m) and western Coclé province (Cerro Chicú, 1764 m; Cerro Cenizo, 1628 m; unnamed mountain above 1670 m; Cerro Peña Blanca, 1314 m; Cerro Marta, 1046). East of these, the continental divide drops below 500 m until eastern Coclé province, where it rises for the last time at the massif of Cerro Gaital (1185 m) surrounding El Valle de Antón. The main ridge continuing to the east into western Panamá province holds the peaks of Cerro Valle Chiquito (1120 m) and Cerro Trinidad (975 m). Cerro Campana (1047 m) marks the eastern end of the Cordillera Central, and thus of the Lower Central American Highlands.

1.2.3 Climate and vegetation

Along the Cordillera Central, local climates are chiefly determined by two factors. First, the elevation above sea level is directly correlated to the mean annual temperature. Thus, the range of mean annual temperatures throughout the Cordillera is wide, from above 27°C at certain places in the Pacific foothills to below 8°C around the summit of Volcán Barú. Secondly, the aspect, i.e., the ubication on the north or south face of the continental divide, exerts a certain influence on the total annual precipitation received, as well as on the rainfall seasonality experienced, by a given locality. While the northern slopes are predominantly perhumid owing to the humid air masses from the Caribbean Sea, the clouds seasonally get stuck along the continental divide, which effects a more or less pronounced dry season on the Pacific slopes depending on the exact site. Accordingly, the total annual precipitation varies between almost 4000 mm at some Caribbean localities and less than 1500 mm in some areas of the Pacific foothills. Located within the condensation zone of the humid air masses from the Caribbean, the crests and peaks above 1500 m asl are basically swathed in clouds during most, if not all, of the year.



Map 1.7: Köppen climates along the Cordillera Central.



Map 1.8: Holdridge life zones along the Cordillera Central.

A more detailed view of the five Köppen climates found along the Cordillera Central is provided in Map 1.7. The transition between tropical and temperate climates seems almost perfectly coincident with the 1500 m contour. While most of the temperate area is perhumid, the rain shadow of the Cordillera is quite evident especially in its higher western portion. In contrast to the Caribbean foothills and lowlands, which are perhumid ("tropical wet" climate, compare Fig. 1.1B) along large portions of the continental divide, the Pacific slopes obviously experience much more of a dry season resulting in monsoon or savanna climates.

Likewise, Map 1.8 shows the distribution of the 8 Holdridge life zones found along the Cordillera Central. In this more detailed view with the humidity provinces not lumped together for each of the highland bioclimatic belts as they were in Map 1.4, it becomes apparent that within the Premontane and Montane belts the wetter of the respective two humidity provinces prevails by far, and that all Lower Montane portions represent a single life zone, the Lower Montane Wet Forest. The four bioclimatic belts appear almost exactly separated by the 500, 1500, and 2500 m contours, thus nicely adhering to the elevational scheme provided by Savage (2002) for the Caribbean versant of Costa Rica. Only south of Volcán Barú, one might catch a glimpse of Savage's (2002) scheme for Costa Rica's Pacific versant with the elevational limits raised to 650, 1800, and 2700 m asl. This altitudinal shift in mean annual temperatures between the two versants is apparently supported by the WorldClim climate data, though to a somewhat minor extent. Nevertheless, whenever talking about elevations above sea level throughout this work, for the sake of simplicity I will refer to all elevations below 500 m asl as lowland, to those between 500–1500 m as premontane, to those between 1500–2500 m as lower Montane, and to those above 2500 m asl as montane (note lower case first letters in the elevational context as opposed to capitalized ones used for bioclimatic belts of the Holdridge life zone system).

The natural climax vegetation along most of the Cordillera's slopes are different types of forests ranging from evergreen broadleaf rain forests with high canopies at lowland to lower montane elevations over different types of cloud forest (sensu Myers 1969b) to the so-called elfin woodland or montane thicket with its gnarled trees and canopies that may be lower than 5 m along exposed ridges. Owing to the steepness of many slopes that usually increases with proximity to the Cordillera's crest on both versants, as well as to the sometimes torrential rains, these natural forest habitats are frequently subject to dynamic surface alterations in the form of landslides or singular tumbling trees. Thus, even in areas that can be considered rather pristine, it is common to find a mosaic of vegetation patches in different stages of succession. Only the highest elevations of the Talamanca range are located above the timberline, allowing for a treeless vegetation sometimes referred to as subparamo, paramo, or pluvial paramo (e.g., Savage 2002) that is dominated by low shrubs, herbs, and grasses. While the Pacific lowlands and premontane slopes of western Chiriquí are thought to have been completely covered by rainforests originally (McDiarmid & Savage 2005), it remains unclear whether the almost treeless savannas occupying a great portion of the Serranía de Tabasará's Pacific versant at premontane elevations are natural vegetation, maybe a fire climax, or the result of anthropogenic impact. Since a large portion of the Cordillera's surface is subject to anthropogenic activities, the natural vegetation has been altered in many areas and different types of secondary vegetation in various stages of succession, as well as agricultural areas, are widespread (see below).

Figures 2.1–2.8 show different aspects of natural and secondary vegetation as encountered around my research localities. An unparalleled account of the highland forests of Panama was published by Myers (1969b) and includes extensive descriptions of forest environments at different places in the Cordillera Central. Additional information on the region’s vegetation can be found in the accounts of Walters (1953), Myers (1971a, b), Adames (1977), Myers & Duellman (1982), and de Sousa (1999), among others.

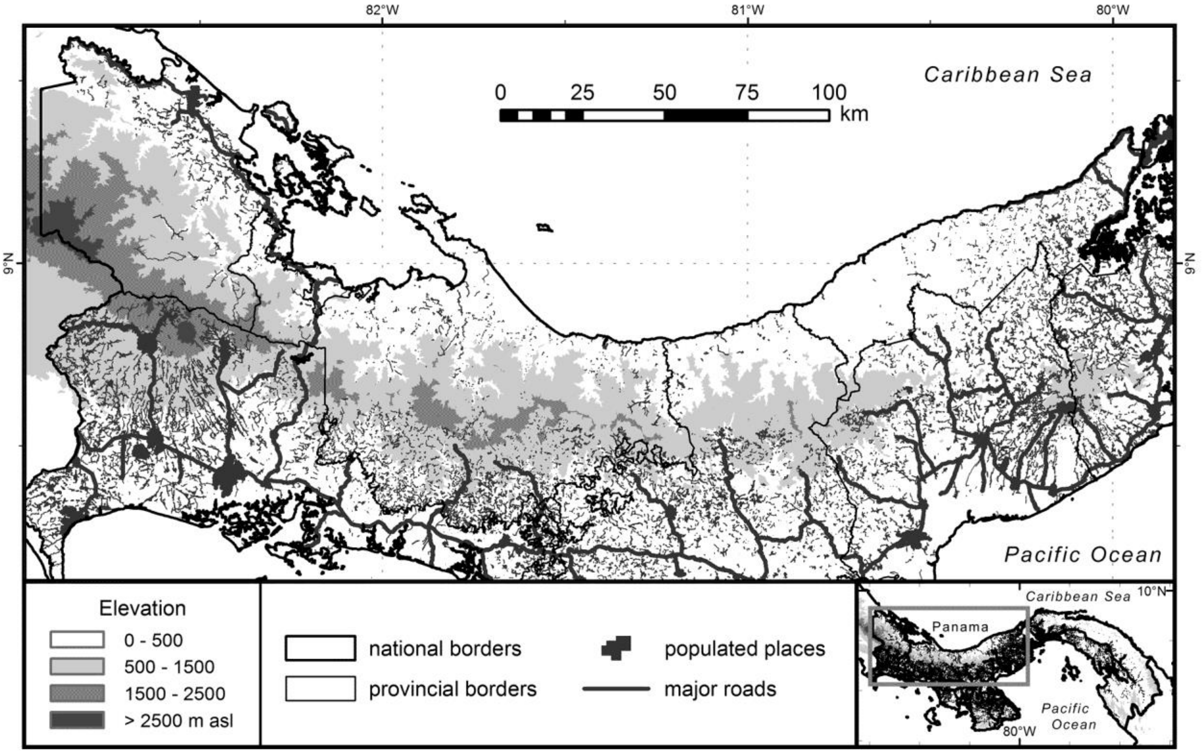
1.2.4 Human impact

The slopes of the Cordillera Central are rather steep in many areas, naturally discouraging human access. Especially the highest portions of the Talamanca and Tabasará ranges, typically rising steeply for the last few hundred meters towards the narrow crest of the continental divide, are barely suitable for human settlements or agricultural activities. Nevertheless, the lower portions on both faces of the Cordillera are home to humans. Map 1.9 shows settlements and roads along the Cordillera Central. The Pacific slopes are ascended by several roads leaving the Panamericana to the north, and appear densely packed with settlements especially at low and premontane elevations. With the exception of its western portion in Bocas del Toro and the eastern extreme in Colón province, the Caribbean versant is much less densely populated at low elevations, and very sparsely so at premontane elevations. Considerable human infrastructure above 2000 m asl is generally sparse except for some places in Chiriquí province, and practically absent above 2500 m except for some trails, trigonometric points, and the installations on Volcán Barú.

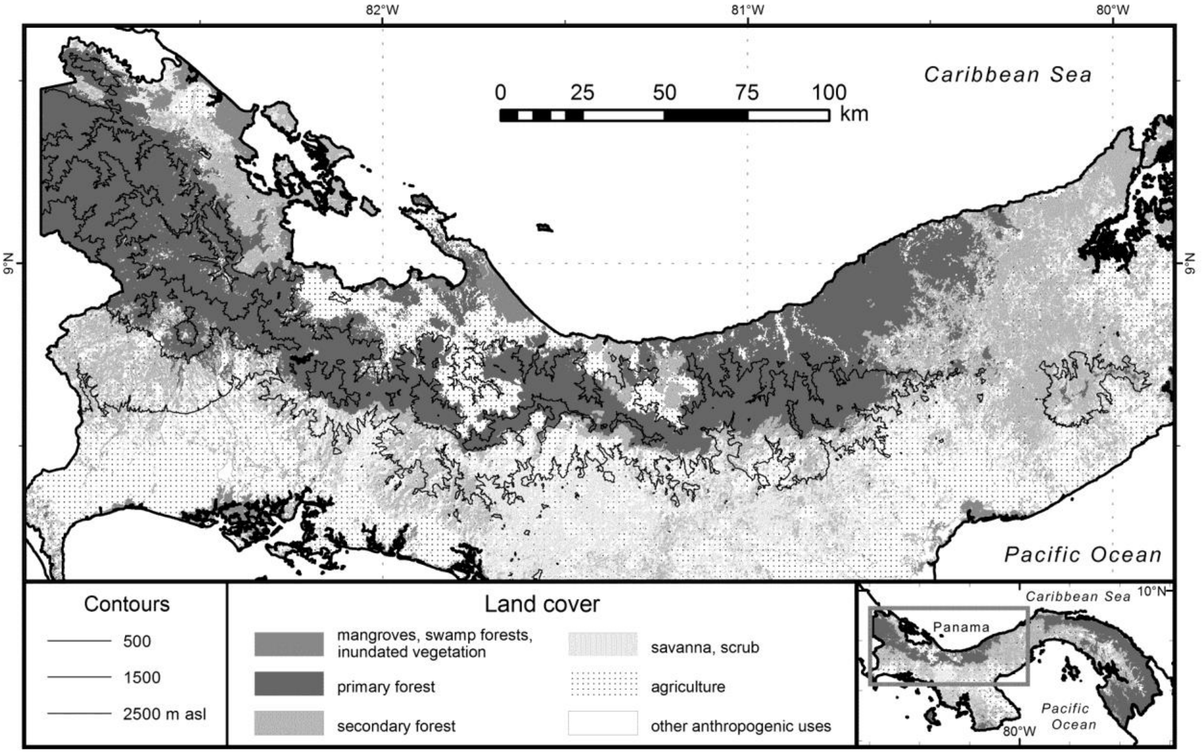
Very generalized land cover categories are drawn in Map 1.10 that provides a complementary picture: Mature forests are largely restricted to premontane and higher elevations of the Caribbean slopes, where they also subsist in different lowland areas. Along the Pacific versant, primary forest is almost completely absent from premontane and lowland areas owing to their population density and large-scale agriculture. Especially around the gently sloping Volcán Barú with its fertile soils, different crops and cattle are cultivated up to lower montane elevations. Generally speaking, the anthropogenically shaped mosaic of pastures, cropland, infrastructure, and scattered forest remnants chiefly remaining in the form of narrow strips of gallery forest along the numerous rivers extends as far up the Pacific slopes as feasible with respect to the terrain's inclination. Above these areas, and on the Caribbean slopes, small-scale subsistence farming has created numerous minor clearings, but in the recent past more and more subsistence farmers have ventured into cattle farming requiring larger clearings that increasingly intersect the forest also on the Caribbean slopes.

Given the growing population and increasing anthropogenic pressure, deforestation occurs at a fast pace in certain regions. According to the National Environment Authority (ANAM 2009a), the Comarca Ngöbe-Buglé had the highest deforestation rate within Panama during the last decade of the 20th century, losing more than one-fifth of its forest cover in just eight years. Thus, since the land cover area underlying Map 1.10 dates back to the year 2000, the area of primary forest as shown above has certainly shrunk in the meantime, notwithstanding that official numbers state deforestation along the Cordillera Central to have been minimal or even converted into reforestation in the period 2000–2008 (ANAM 2009a). While much of these contemporary losses of primary forest patches are attributable to an increasing demand for food to sustain the indigenous population that is rapidly growing, other causes have the potential to exert an equally negative, if not worse, impact on the Cordillera's environment.

First, the abundance of flowing water makes the region viable for the construction of hydroelectric dams. The most prominent existing example is the Lago Fortuna, a hydroelectric reservoir in the high valley of the Río Chiriquí with a water surface of approximately 10.5 km^2. Several other dams already exist, and many more are currently being constructed or planned, also on the hitherto somewhat less degraded Caribbean slopes. Second, the Cordillera Central houses enormous subsurface recources, i.e., mineral and metal deposits that appear somewhat concentrated around the plutonic rock formations (Map 1.5). While mining has historically taken place and is still ongoing in northern Veraguas and western Coclé provinces, the Serranía de Tabasará has hitherto largely escaped exploitation but might not always remain untouched. Especially the enormous copper deposit in the area known as Cerro Colorado, located between Cerro Saguí and Cerro Santiago in the central Tabasará range, has been in the focus of mining companies for a long time. Test drillings undertaken since the 1970s have caused severe pollution that alerted the indigenous inhabitants of the area and lead to the formation of a passionate protest movement which managed to halt exploitation until now. However, the region recently seems to have attracted increased attention again, encouraged by new laws that facilitate related activities (Naconeczny & Whysner 2010; Simms & Moolji 2011).

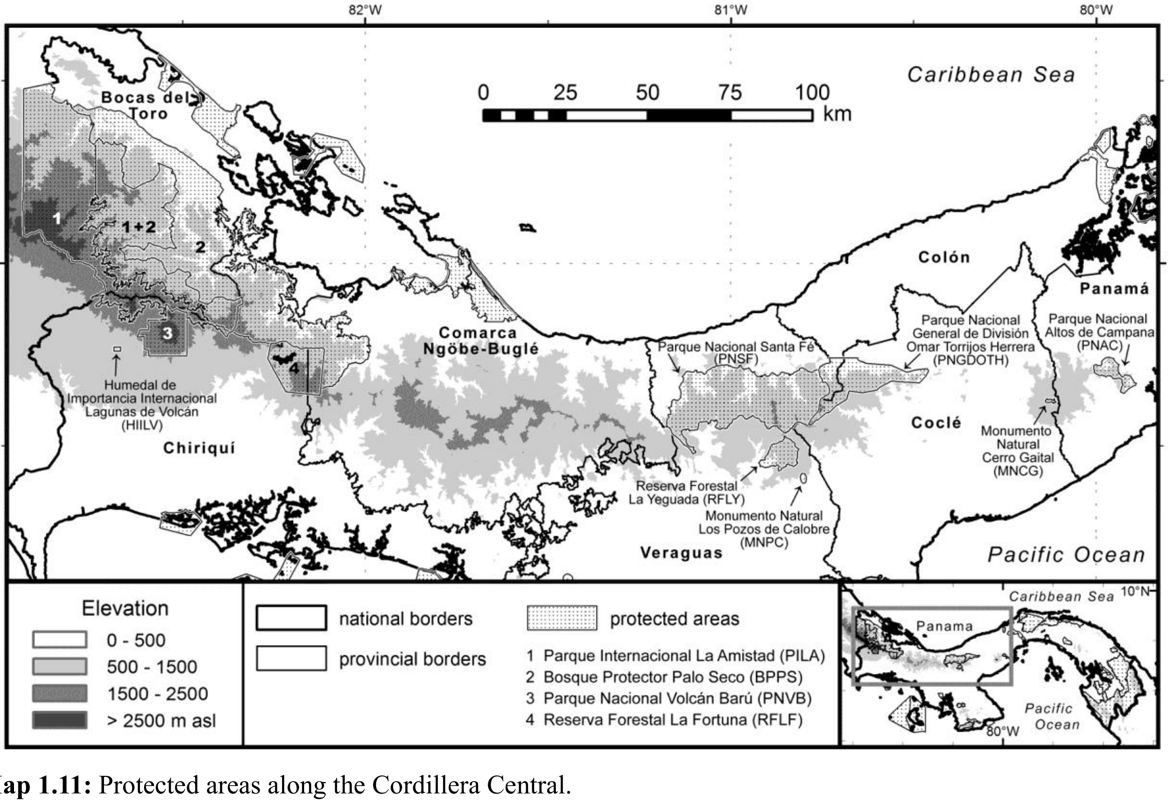


Map 1.9: Roads and settlements along the Cordillera Central.



Map 1.10: Forest cover and land use along the Cordillera Central (in the year 2000).

On the other hand, at least in theory, the natural environments and exuberant biodiversity of the Cordillera Central are not exposed to destruction shelterlessly. Since 1918, a total of 89 protected areas pertaining to 16 different management categories have been legally designated throughout Panama, covering almost 27000 km^2, or 36% of the country's terrestrial surface. (IGNTG 2008; ANAM 2009a). Beginning with the establishment of the La Yeguada Forest Reserve in Veraguas in 1960 and Parque Nacional Altos de Campana in 1966, eleven protected areas of 7 management categories have been designated along the Cordillera Central as shown in Map 1.11. While some are rather small, others cover vast areas, such as the Parque Internacional de Amistad that is shared with Costa Rica and covers 2070 km^2 of Panamanian territory. Most of the legally protected surface along the Cordillera Central comprises areas of rather difficult access on the Caribbean slopes which have retained much of their original forest cover. However, it should be noted that there are no protected areas in the Serranía de Tabasará except for its very extremes in the east and west. Moreover, a theoretical designatation of a given area as protected, even if a management plan exists, does not automatically prevent that area from becoming subject to deforestation, pollution, unsustainable exploitation, or other destructive anthropogenic actions. This also holds for Panama, where most protected areas lack adequate demarcation, facilities, staff, and enforcement of their legal status (Jaramillo et al. 2010).



Map 1.11: Protected areas along the Cordillera Central.

1.3 Reptile research in western Panama

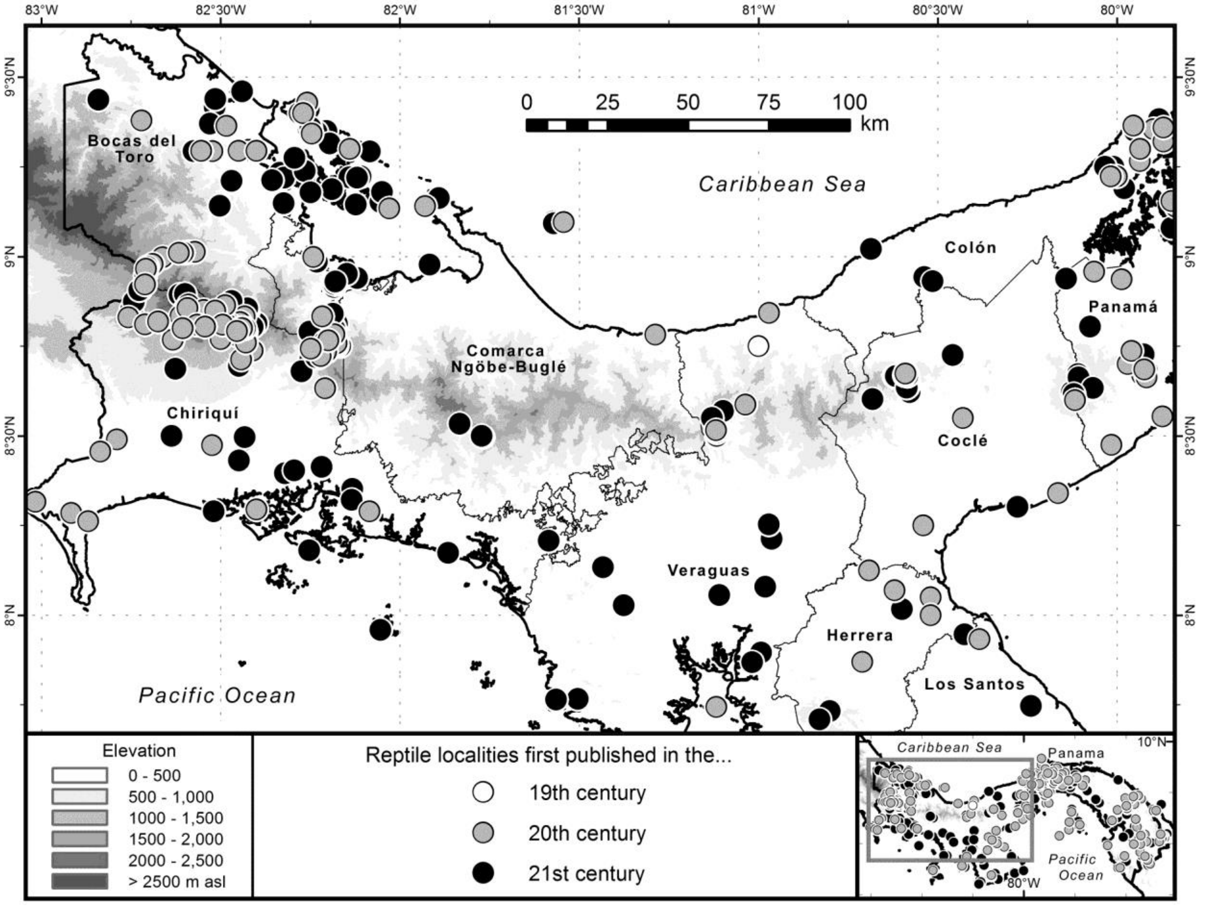
General accounts of the herpetology of Panama were provided by Myers (1972), Auth (1994), Young et al. (1999), Ibáñez et al. (2001), and Jaramillo et al. (2010). As pointed out by Ibáñez et al. (2001), most studies on ecological, life history, and behavioral aspects of Panama's reptiles have been carried out in the central portion of the country, around the watershed of the Panama Canal in Colón and Panamá provinces including the former Canal Zone. In the following, I present a historical summary of faunistic and taxonomic studies carried out west of the Canal watershed, emphasizing works west of Coclé and Colón provinces. Map 1.12 gives an overview of the localities referred to in these studies, whereas Map 1.13 pinpoints the type localities of reptiles which are clearly locatable in western Panama. Localities for which five or more reptile species have been published within a single publication are shown in Map 1.14. The maps in chapter 4 show published localities for specific taxa. The ubication of geographical features mentioned in this chapter can be seen in Maps 1.2 and 1.6.

Probably the first serious herpetological collection from western Panama was assembled by Josef Warszewicz (1812–1866), who, coming from Davíd over Boquete, climbed Volcán Barú and crossed the Cordillera Central down to the Caribbean coast in 1848 (Savage 1970), probably following a route close to a trail known nowadays as Sendero Culebra. At that time, the western Panamanian area presently comprising the provinces Bocas del Toro, Chiriquí, Veraguas, and the Comarca Ngöbe-Buglé was the province Veragua of Nueva Granada (present time Colombia; Savage 1970). Thus, many reptile species described during the 19th century from material collected in western Panama have the rather imprecise type locality "Veragua" for which different spellings and combinations with country names (e.g., Nueva Granada, New Grenada, Panama, or Costa Rica) have been used. Among these 19th century descriptions of species still valid today are those by Lichtenstein & Martens (1856: *Ameiva festiva* and *Sphaerodactylus lineolatus*), Peters (1863a: *Anolis humilis;* 1863c: *Bothriechis lateralis*), and Bocourt (1874: *Enyalioides heterolepis*). The most productive author of this era was Edward Drinker Cope (1860c: *Rhadinaea vermiculaticeps;* 1861c: *Anolis lemurinus;* 1862b: *A. limifrons;* 1868: *Dipsas articulata*), who also was the only one to designate a more specific type locality in some descriptions (1860c: *Tantilla reticulata;* 1861a: *Amastridium veliferum*; 1861b: *Leptophis depressirostris* and *Oxybelis brevirostris;* 1861c: *Anolis lionotus*): Cocuyos de Veraguas (sometimes spelled Cocuyas, Cucuyas, or Cucuyos; loc. 20 in Map 1.13), a mining site near the Río Concepción in northern Veraguas province (Myers 1974). However, since the name Chiriquí was already used for the Pacific, and Bocas del Toro for the Caribbean drainage of western "Veragua" (Savage 1970), some localities reported in those days can at least be assigned to one versant of the Cordillera Central. This applies to Peters' descriptions of *Anolis polylepis, A. palpebrosus, A. pulchripes,* and *A. obtusirostris* (Peters 1874; the latter three today considered synonyms of *A. lemurinus, A. limifrons,* and *A. biporcatus,* respectively) and *Coloptychon rhombifer* (Peters 1877) as well as to Boulenger's (1894) description of *Geophis championi,* all from "Chiriquí" (for the latter, Savage & Watling 2008 narrowed the type locality to "Boquete"). Likewise, the record of *Corallus annulatus* (as "*Xiphosoma annulata* Cope") from "Bocas del Toro, Columbia" (Brown 1893) can confidently be interpreted to refer to the Caribbean versant of western Panama.

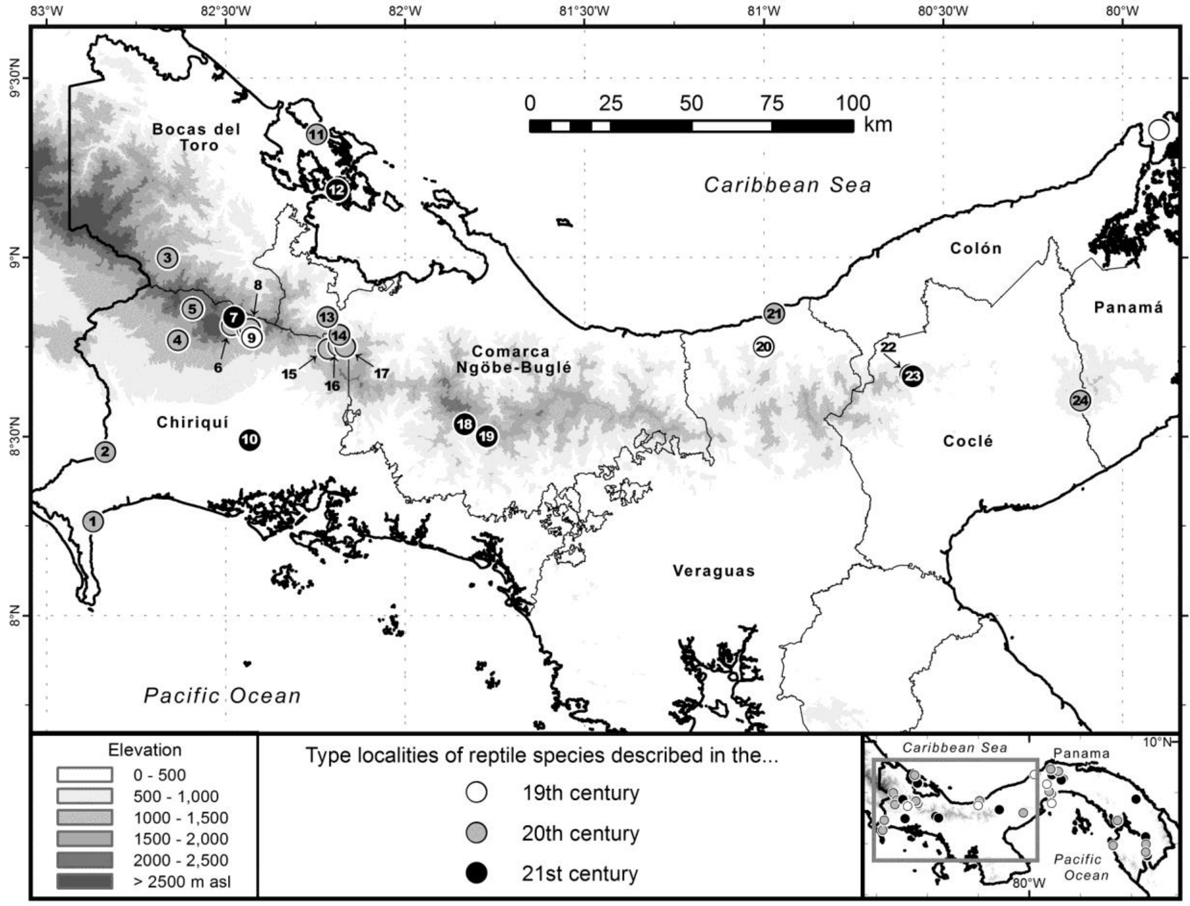
After Panama's independence in 1903 and the resumption of the canal construction works in 1904, the scientific exploration of the Panamanian isthmus mostly by US scientists experienced a considerable increase that is also reflected in a series of herpetological publications from western Panama. Among the earliest were the descriptions of *Sibon longifrenis* from near the town of Bocas del Toro (Stejneger 1909; Map 1.13: loc. 11), *Echinosaura panamensis* from La Loma (Barbour 1924; Map 1.13: loc. 13), and *Leposoma southi* from Progreso, Chiriquí (Ruthven & Gaige 1924; Map 1.13: loc. 2).

In the first half of the 20th century, the most influential explorer of the reptile fauna of western Panama was Emmett Reid Dunn (1894–1956), who, besides describing several new species and publishing local checklists, identified more than 10000 snake specimens in the course of the Panamanian Snake Census conducted by the Gorgas Memorial Laboratory under Dr. Herbert C. Clark (Myers 2003). From the mid-1920s to his death in 1956, Dunn published numerous taxonomic notes and revisions, as well as reports on particular collections, of Neotropical reptile taxa, which cannot all be recounted here although many involve Panamanian material. In 1923, he and Chester B. Duryea crossed the continental divide from Boquete, probably along a path close to the trail called Sendero Pianista today, a little east of Warszewicz's route (Dunn 1924a, b; Savage 1970). Their collection has served as a source for several species descriptions, especially their specimens from around La Loma, Bocas del Toro (also called Buenavista; today located in the Comarca Ngöbe-Buglé; loc. 13 in Map 1.13). Ten years later, Dunn published the first herpetofaunal list of El Valle de Antón in Coclé province (Map 1.13: loc. 24), therein listing 19 reptile species and describing *Dendrophidion clarkii* and *Morunasaurus groi* (Dunn 1933). In his paper on giant mainland anoles (Dunn 1937a), he provided the first records from Panama of *Anolis insignis* (Valle de Antón) and *A. microtus* (above Boquete, Chiriquí; but see chapter 4.1.3). Shortly thereafter, Dunn (1940) reported numerous new locality records for various reptile species and described *Bachia blairi* from Puerto Armuelles in the lowlands of western Chiriquí province (in Map 1.13: loc. 1), as well as *Anolis kemptoni* from Finca Lérida (Map 1.13: loc. 6) and *Trimetopon slevini* from near Boquete (Map 1.13: loc. 8). More noteworthy snake records from these two areas were published two years later (Dunn 1942).

Dunn's reports from around the town Boquete (Map 1.13: loc. 9) just east of Volcán Barú were complemented by a reptile collection of almost 700 specimens assembled in 1939 by Joseph R. Slevin, who listed 22 snake and 11 lizard species, including *Hydromorphus dunni* which he newly described (Slevin 1942). The next, and to this day the last, list of the snake fauna around Boquete (Dunn 1947) contained 28 species, also reporting 16 species for the nearby Finca Lérida and 7 for the surroundings of the town Volcán on the southwestern slopes of Volcán Barú. The account of Walters (1953), who reported four species from different sites around the volcano, concluded the series of reports from the vicinities of Boquete and Volcán Barú, the first area in the Cordillera Central to have its reptile fauna systematically sampled. Emmett Reid Dunn's last publications providing distributional data on the reptiles of western Panama were a comparison of the relative abundances of snake species from Coclé and Herrera with more easterly localities (Dunn 1949) and a revision of the genus *Nothopsis* (Dunn & Dowling 1957).



Map 1.12: Locality records published for reptiles in western Panama.



Map 1.13: Type localities of reptiles described from western Panama. (1) Puerto Armuelles: *Bachia blairi* (Dunn 1940); (2) Progreso: *Leposoma southi* Ruthven & Gaige 1924; (3) "Campo Mojica," a clearing on a trail at 1450 meters elevation, N slopes of Cerro Pando, upper watershed of Río Changena: *Anolis fungosus* Myers 1971; (4) El Volcán: *Anolis dunni* Dunn 1940; (5) on road about 4 km W of Cerro Punta, about 6000 feet [1829 m] elevation: *Anolis vociferans* Myers 1971 (synonymized with *A. salvini* by Köhler 2007); (6) Finca Lérida, 5300 feet [1615 m], above Boquete: *Anolis kemptoni* Dunn 1940; (7) eastern entrance to Sendero Quetzales, 8 km N of Boquete, approximately 08°49.0'N, 82°28.6'W: *Anolis magnaphallus* Poe & Ibáñez 2007; (8) near Boquete: *Trimetopon slevini* Dunn 1940; vicinities north of Boquete: *Hydromorphus dunni* Slevin 1942; (9) Boquete: *Geophis championi* Boulenger 1894 fide Savage & Watling (2008); (10) Los Algarrobos: *Anolis charlesmyersi* Köhler 2010; (11) Bocas del Toro: *Sibon longifrenis* (Stejneger 1909); (12) Cerro Brujo (9°11'16.4"N, 82°11'25.4"W), 10 m: *Anolis cryptolimifrons* Köhler & Sunyer 2008; (13) La Loma (= Buena Vista), Distrito de Chiriquí Grande, Provincia de Bocas del Toro (today Distrito de Kankintú, Comarca Ngöbe-Buglé): *Echinosaura panamensis* Barbour 1924 fide Uzzell (1965), *Geophis tectus* Savage & Watling 2008, *Rhadinaea persimilis* Dunn 1938 (synonymized with *Urotheca guentheri* by Myers 1974); (14) southwestern headwaters of Río Guabo, 780 m elev. (8°47'N, 82°11'W): *Sphenomorphus rarus* Myers & Donnelly 1991; (15) márgenes de Quebrada Frank (8°44'N, 82°13'W), 1100 m, en el lado oeste de la carretera: *Anolis casildae* Arosemena, Ibáñez & de Sousa 1992; (16) a orillas del Río Chiriquí, a unos 100 m de la desembocadura de la Quebrada Bijau (8°45'11"N, 82°11'07"W), entre 1050–1075 m: *Anolis exsul* Arosemena & Ibáñez 1994 (synonymized with *A. fortunensis* by Ponce & Köhler 2008); (17) márgenes del Río Chiriquí (8°45'N, 82°10'W), frente a la estacion hidrometeorologica del Instituto de Recursos Hidráulicos y Electrificación (IRHE) en Bijau, entre 1050–1075 m: *Anolis fortunensis* Arosemena & Ibáñez 1993; (18) near the headwaters of Río San Félix, ca. 2 km N Escopeta Camp, ca. 8°32'N, 81°50'W, 900 m: *Anolis gruuo* Köhler, Ponce, Sunyer & Batista 2007; (19) La Nevera, 8°29'45"N, 81°46'35"W (corrected to 8°30'N, 81°46'20"W by Lotzkat et al. 2010a), 1600 m: *Anolis datzorum, A. pseudokemptoni,* and *A. pseudopachypus* Köhler, Ponce, Sunyer & Batista 2007; (20) Cocuyos de Veraguas: *Amastridium veliferum* and *Anolis lionotus* Cope 1861, *Leptophis depressirostris* and *Oxybelis brevirostris* (Cope 1861), *Tantilla reticulata* Cope 1860; most probably also *Anolis lemurinus* Cope 1861, *Anolis limifrons* Cope 1862, *Dipsas articulata* (Cope 1868), and *Rhadinaea vermiculaticeps* (Cope 1860); (21) near the mouth of the Río Concepción, 1–10 meters elevation: *Anolis procellaris* Myers 1971 (synonymized with *A. carpenteri* by Fitch et al. 1976); (22) along the trails of Parque Nacional General de División Omar Torrijos Herrera, N of El Copé, Coclé Province, Panama, 8°40'18.9"N, 80°35'31.08"W: *Anolis ibanezi* Poe, Latella, Ryan & Schaad 2009, *Anolis kunayalae* Hulebak, Poe, Ibáñez & Williams 2007; (23) abandoned sawmill site on the continental divide, 9.7 km NNW of El Copé, PNGDOTH, La Pintada District, ca. 850 m (8°40'04"N, 80°35'6"W): *Celestus adercus* Savage, Lips & Ibáñez 2008; (24) El Valle de Antón: *Dendrophidion clarkii* and *Morunasaurus groi* Dunn 1933.

In the 1960s, Uzzell extended the distribution of *Echinosaura panamensis* to the eastern extreme of the Cordillera Central at El Valle and Cerro Campana (Uzzell 1965). Busack (1966) reported on a collection of 5 reptile species from Santa María in Herrera and 14 from Los Santos. In his revision of the genus *Geophis,* Downs (1967) examined 104 specimens collected in Panama, most from the collections of Dunn and Slevin. Besides the fact that little was published on reptiles of western Panama during the 1960s, it was in this decade that a major authority on the Panamanian reptile fauna initiated his studies: Charles W. Myers.

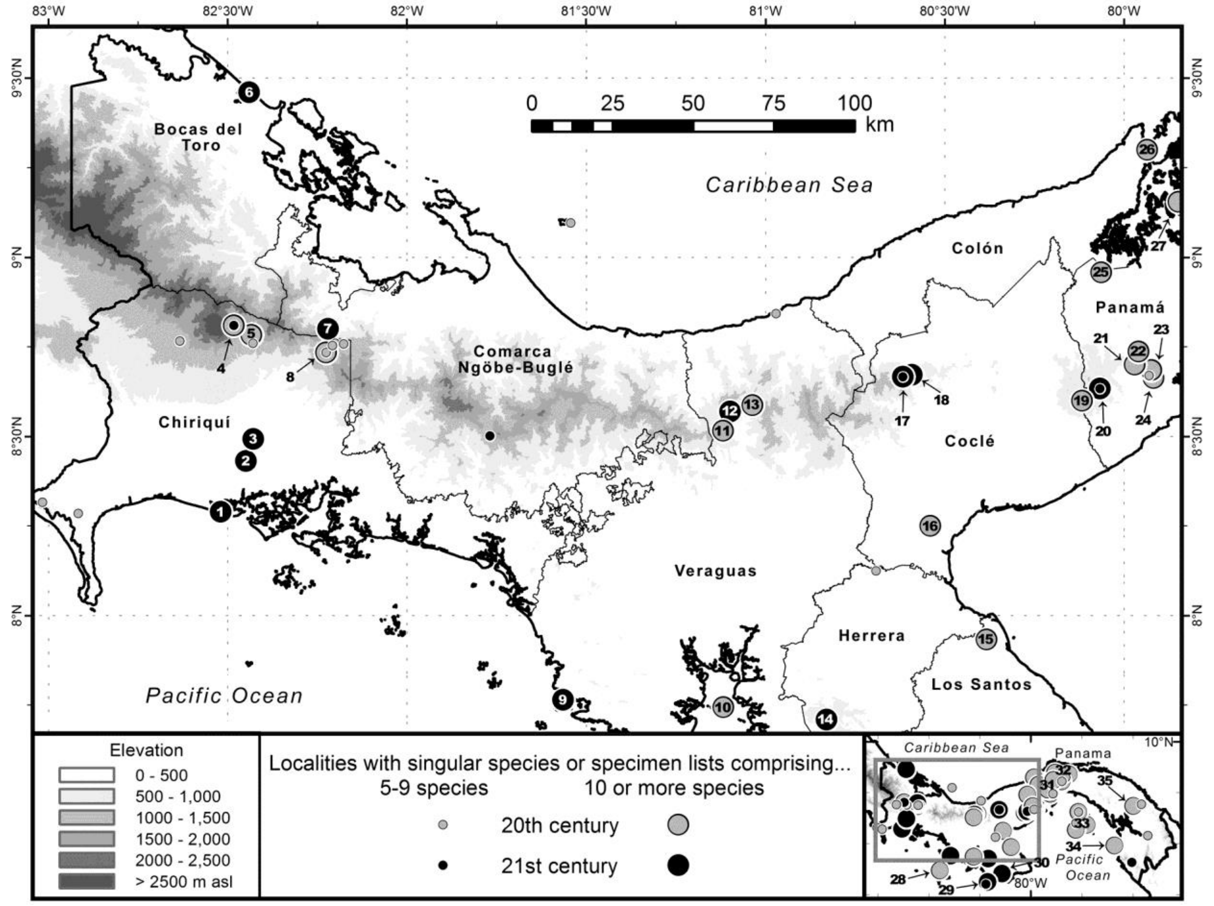
Myers entered Panama in 1964 to spend three years collecting throughout the country. He undoubtedly went further than former workers concerning the number of remote areas where he camped and collected for prolonged periods, including many cloud forest sites that are still hard to access nowadays. Possibly his most notable expedition was realized in 1966 together with Linda Trueb and William Duellman: Coming from Finca Hartmann at Santa Clara, Chiriquí, they crossed the continental divide at Cerro Pando next to the Costa Rican border and descended the Caribbean slopes down to 650 m, establishing four camps on the way and spending a whole month in the wild. As a first result of his field expeditions, Myers (1969b) presented an indispensable account of the cloud forest areas he had visited throughout Panama. The same year, he revised the Panamanian species of the snake genus *Coniophanes* (Myers 1969a). Since he seemingly did not take too much delight in "mere" species descriptions like the one of *Anolis procellaris* from northern Veraguas (Myers 1971a; Map 1.13: loc. 21), this was the first in his still enduring series of taxonomic revisions at genus or species group level that involved, or focused on, reptile populations from western Panama. It was followed, among others, by his studies of the *Anolis pentaprion* group including the description of the highland species *A. fungosus* and *A. vociferans* from the Cordillera Central (Myers 1971b; locs. 3 and 5 in Map 1.13), his review of Panamanian *Diploglossus* including the first country record for *D. bilobatus* from near Almirante (Myers 1973), his monumental revision of *Rhadinaea* (Myers 1974), as well as revisions of Panamanian populations of *Imantodes* (Myers 1982), *Atractus* and *Geophis* (Myers 2003), and most recently the resurrection of the genus *Rhadinella* for the *Rhadinaea godmani* species group (Myers 2011).

In between these solo works, Charles W. Myers co-authored other faunistic milestones like the first herpetofaunal species list for Barro Colorado Island in the Gatún lake (Myers & Rand 1969) and its update (Rand & Myers 1990), the first Panamanian record of *Sphenomorphus cherriei* coupled with the description of *S. rarus* from the Caribbean slopes of the Cordillera Central (Myers & Donnelly 1991; Map 1.13: loc. 14), the revalidation (Cadle & Myers 2003) and first locality record in western Panama (Myers et al. 2007) of *Dipsas nicholsi*, as well as several papers on amphibian diversity, one of which contains important geographic information on the Cerro Colorado area in the still underexplored Serranía de Tabasará (Myers & Duellman 1982). In the early 1980s, he was the first to co-author a species description (*Dendrobates arboreus* Myers, Daly & Martínez 1984) together with a Panamanian herpetologist, Victor C. Martínez Cortés.

A year earlier, Victor Martínez had published the first country record for *Atropoides picadoi* (Martínez 1983), which to my knowledge is the first publication of a Panamanian herpetologist on western Panamanian reptiles. The specimens reported therein were taken along Quebrada Arena near the La Fortuna hydroelectric reservoir. A first reptile inventory listing 24 species for this biogeographically interesting area comprising the high valley and headwaters of Río Chiriquí, characterized by Myers & Duellman (1982), had been published some years earlier by Myers (1977). As the La Fortuna dam was to be raised from 60 to 100 m in height, and the flooded area thus increased from 1.5 to more than 10 km^2, biological inventories of the area to be flooded were compiled in the 1980s by native researchers and students. Among these was the late Fernando A. Arosemena, a true field biologist who has collected reptiles at many places in western Panama. Their findings at Fortuna led to a series of publications by Panamanian reptile researchers, namely the first country records for *Anolis carpenteri* (Arosemena & de Sousa 1989, but see species account) and *Tantilla alticola* (Castillo et al. 1990, also mentioning other snake species found in the area), a morphological summary of the specimens of *Tantilla* and *Atropoides* collected at Fortuna (Solís 1991), and the descriptions of three species of anoles: *Anolis fortunensis* (Arosemena & Ibáñez 1993) and *A. casildae* (Arosemena et al. 1992) based on a single specimen each, and *A. exsul* (Arosemena & Ibáñez 1994) on the basis of three specimens (Map 1.13: locs. 15–17). The summary of their results (de Sousa 1999) lists a total of 39 reptile species from 15 more or less precise localities within the La Fortuna area, most of which had been declared a forest reserve (Reserva Forestal La Fortuna, RFLF) in 1976. A little later, Hofer & Bersier (2001) reported 28 reptile species from a transect in Bosque Protector Palo Seco (BPPS) on the Caribbean versant just next to Fortuna (loc. 7 in Map 1.14). Two of their specimens were also among the material of Nicholson et al. (2001), who presented additional data on the morphology and ecology of *A. casildae.* Almost a decade later, Chun (2010) revealed new facettes of the morphological variation of this very variable anole species. The latest reptile inventory from RFLF appeared in the Diploma thesis of Nadim Hamad (NH) (Hamad 2009), which is incorporated in the present work (see chapters 2.2.4, 2.3, and 3.1.4).

During the 1990s and the following decade, a number of faunistic inventories from different regions in western Panama were conducted mostly by Panamanian herpetologists. Unfortunately, not all of them were published, and the bulk of those that were published are rather difficult to obtain and as a consequence were usually neglected by subsequent comprehensive works (see below). The first of these was a list of 45 reptile species from the Serranía del Tute (comprising Cerro Tute and Cerro Mariposa, the latter of which is alternatively called Cerro Tute, Delgadito, or Los Gringos) west of Santa Fé de Veraguas at the eastern end of the Serranía de Tabasará (Martínez & Rodríguez 1994). Shortly thereafter, a team of authors including Victor Martínez and his former student Abdiel Rodríguez presented a herpetofaunal list for the nearby mountains Narices and La Anselma north of Santa Fé, which contained 35 reptile species and a modified version of their list for "Cerro Tute" containing merely 35 species (Martínez et al. 1995). Regrettably, the specimens they collected in both areas have been lost (Victor Martínez, personal communication), so some of their undetermined species and questionable identifications will never be resolved. Around the turn of the millenium, their work was continued by their student Arcadio Rodrigo Carrizo Díaz (AC), who reported 25 reptile species from the hitherto unexplored Cerro Negro northwest of Santa Fé in his Licenciatura thesis (Carrizo 2000). His Master thesis that summarized the reptile fauna of the general Santa Fé area (Carrizo 2010) and the Diploma thesis of Leonhard Stadler (LS), who resampled the reptiles of Cerro Mariposa near Alto de Piedra (Stadler 2010), are incorporated in the present work (see chapters 2.2.4, 2.3, and 3.1.4).

Together with various Panamanian and foreign colleagues, Victor Martínez and Abdiel Rodríguez have compiled herpetofaunistic inventories of several additional areas, mostly in Veraguas province and on the Peninsula de Azuero. Published inventories list 33 reptile species for Isla Coiba (de la Riva 1997; Pérez-Santos & Martínez 1997), 23 for Isla Leones (Martínez et al. 1999), 35 for the Reserva Forestal El Montuoso (Rodríguez et al. 2005), 27 for Bahía Honda and Isla Canales de Tierra (Martínez & Rodríguez 2005), and 32 for Reserva Forestal La Tronosa (Elizondo et al. 2007). As an ecological consultant, Victor Martínez has been involved in several area assessments and lists underlying management plans. While most of the underlying inventories are very hard or impossible to obtain, some of the resulting management plans or their appendices contain varying amounts of faunistic information. This applies to the Humedal de Importancia Internacional San San Pond Sak in the Caribbean lowlands close to Costa Rica (ANAM 2004, 2009b), the Refugio de Vida Silvestre Playa de la Barqueta Agrícola on the Pacific shore in Chiriquí (ANAM 2005b, based on Fuenmayor 2001), and Parque Nacional Cerro Hoya in southern Veraguas (ANAM 2005a, based on Martínez 1999). An overview of herpetofaunistic inventories from around the Gulf of Chiriquí, unfortunately lacking the respective lists in their full extent, was provided by Ibáñez (2006), including six species from the unobtainable inventory of Chorogo on the Peninsula de Burica (Fuenmayor 1997), for which three species were also mentioned by Araúz (1999).



Map 1.14: Localities for which single works mentioned in the text list 5 or more reptile species. Localities with lists of 10 or more species are numbered as follows: (1) Refugio de Vida Silvestre Playa La Barqueta Agrícola (Fuenmayor 2001; ANAM 2005b); (2) Botanical Garden of the UNACHI, Davíd (Batista & Ponce 2011); (3) Los Algarrobos (Lotzkat & Hertz 2011); (4) Finca Lérida (Dunn 1947); (5) Boquete and vicinities (Slevin 1942; Dunn 1947); (6) Humedal de Importancia Internacional San San Pond Sak (ANAM 2004, 2009b); (7) transect in BPPS (Hofer & Bersier 2001); (8) RFLF (Myers 1977; Castillo et al. 1990; de Sousa 1999; Hamad 2009; very generalized central point); (9) Bahía Honda and Isla Canales de Tierra (Martínez & Rodríguez 2005); (10) Isla Leones (Martínez et al. 1999); (11) Serranía del Tute and Cerro Mariposa (Martínez & Rodríguez 1994; Martínez et al. 1995; Stadler 2010); (12) Cerro Negro (Carrizo 2000, 2010); (13) Cerros Narices and La Anselma (Martínez et al. 1995); (14) Reserva Forestal El Montuoso (Rodríguez et al. 2005); (15) Los Santos (Busack 1966); (16) Aguadulce (Evans 1947); (17) PNGDOTH (Ray 2009); (18) PNGDOTH (Poe et al. 2009); (19) El Valle de Antón (Dunn 1933); (20) Altos del María (Ray 2009); (21) PNAC, locality 4 (Ibáñez et al. 1996); (22) PNAC, locality 5 (Ibáñez et al. 1996); (23) PNAC, locality 3 (Ibáñez et al. 1996); (24) PNAC, locality 1 (Ibáñez et al. 1996); (25) Cirí (Ibáñez et al. 1997); (26) Sherman (Ibáñez et al. 1997); (27) Isla Barro Colorado (Myers & Rand 1969; Rand & Myers 1990); (28) Isla Coiba (de la Riva 1997; Pérez-Santos & Martínez 1997); (29) Parque Nacional Cerro Hoya (Martínez 1999; ANAM 2005a); (30) Reserva Forestal La Tronosa (Elizondo et al. 2007); (31) different localities along the Panama Canal: Cocolí, Corte Culebra, Pequení, Tranquilla (Ibáñez et al. 1997); (32) different localities in the Serranía Piedras-Pacora, Parque Nacional Chagres: Río Las Cascadas, Cerro Azul, Cerro Brewster (= C. Guagaral), Cerro Jefe (Ibáñez et al. 1995); (33) different localities on the Archipiélago de las Perlas: Isla del Rey (= Isla San Miguel), Isla San José, Isla Saboga (Barbour 1906; Cochran 1946; Neal 2007); (34) around Cerro Sapo (Barbour 1923); (35) Lower Río Sucubtí (Breder 1946).

Along with their monumental inventories from central Panama listing 71 reptile species for Parque Nacional Chagres (Ibáñez et al. 1995) and 58 from six sites around the Panama Canal (Ibáñez et al. 1997), members of the Círculo Herpetológico de Panamá around Roberto Ibáñez published a comprehensive list of the herpetofauna of Parque Nacional Altos de Campana (PNAC), at the eastern end of the Cordillera Central, containing 86 reptile species (Ibáñez et al. 1996). Surprisingly, although many herpetological surveys have been conducted there since Myers first visited the mountains of present day Parque Nacional General de División Omar Torrijos Herrera (PNGDOTH) north of El Copé, Coclé province, in 1977 (Myers et al. 2007), it was not until very recently that a list of 56 snake species from that area was compiled by Julie M. Ray (2009). Still, no lizard inventory of this comparably well-studied site has been published. In her PhD thesis, Ray (2009) also reported the presence of 23 snake species from Altos del María near El Valle de Antón. Subsequently, Ray et al. (2012) presented a synopsis of the snail-eating snakes they found in these two areas. The latest reptile inventories of localities in western Panama again came from Chiriquí province, where Lotzkat & Hertz (2011; incorporated in the present work) reported 27 species from Los Algarrobos, and Batista & Ponce (2011) listed 25 species for the Botanical Garden of the Universidad Autónoma de Chiriquí in Davíd (UNACHI).

Apart from the inventories recounted above, distributional records from western Panama are found in a number of generic or species group revisions. For lizards, among the most fruitful revisions in this regard are those of the giant mainland anoles of the genus *Dactyloa* (Savage & Talbot 1978; Castañeda & de Queiroz 2011) and the genera *Lepidophyma* (Bezy & Camarillo 2002), *Ptychoglossus* (Harris 1994), and *Sphaerodactylus* (Harris & Kluge 1984). Many localities for voucher specimens are also found in the revisions of *Norops biporcatus* (Köhler & Vesely 2003), *N. capito* (Köhler et al. 2005) and the *N. humilis* group (Köhler et al. 2003, 2006). For snakes, the works on the genera *Dendrophidion* (Lieb 1988; Cadle 2012a, 2012b; Cadle & Savage 2012) and *Ninia* (Savage & Lahanas 1991), the *Geophis sieboldi* group (Savage & Watling 2008), and several species of *Sibon* (Savage & McDiarmid 1992) are worth mention. Two recent Diploma theses designed as integrative taxonomic revisions of cryptic anole species complexes in LCA, namely that of Joe-Felix Bienentreu (JFB) on the *Anolis pachypus* complex (Bienentreu 2011) and that of Markus Gutpelet (MG) on the *Anolis altae* complex (Gutpelet 2012), are in part based on material collected and/or examined by myself and incorporated in the present work (see chapters 2.2.4, 2.3, and 3.1.4).

During the last two decades, several distribution extensions for single species into or within western Panama, usually based on singular locality records, were published in the geographic distribution section of Herpetological Review for *Enyalioides heterolepis* (Nicholson 1998; Lips 1999), *Hemidactylus frenatus* (Jadin et al. 2010b), *Hydromorphus concolor* (Ponce et al. 2008a), *Leptophis nebulosus* (Ray 2011a), *Atropoides mexicanus* (Ray 2011b), and *Bothriechis lateralis* (Griffith et al. 2008). Published in the same journal, the first country records for *Clelia scytalina* (Solís et al. 1991), *Ninia sebae* (Ponce et al. 2008b), *Sibon lamari* (Jaramillo et al. 2008), *Bothriechis supraciliaris* (DeJesus 2007), *Lachesis melanocephala* (Dwyer & Perez 2009), and *Porthidium volcanicum* (Dwyer & den Burgh

2012) also originated from western Panama. In addition, the natural history section of the same journal yielded discrete distribution points for *Tantilla armillata* (Knight et al. 2012), *Tantilla reticulata* (Solórzano et al. 2012), and a generalized locality record for *Urotheca decipiens* (Montgomery et al. 2006). For almost a decade now, the open access online journal Check List has been publishing locality species lists and notes on geographic distribution which are easy to find and freely available to everyone. Distributional notes for Panamanian reptiles made their way into this journal only very recently, first through publications incorporated in the present work (Lotzkat et al. 2012a, b, c, 2014; Bienentreu et al. 2013). Subsequently, Myers et al. (2013) provided a record of *Tantilla alticola* from PNGDOTH and Ray et al. (2013) extended the distribution of *Trimetopon barbouri* to the same area.

A new era in terms of reptile species descriptions from western Panama dawned in 2007, when Hulebak et al. (2007) described *Anolis kunayalae* from PNGDOTH (Map 1.13: loc. 22), while Poe & Ibáñez (2007) separated *A. magnaphallus* from above Boquete (Map 1.13: loc. 7) from *A. pachypus.* In the subsequent years, *Celestus adercus* was described from PNGDOTH (Savage et al. 2008; loc. 23 in Map 1.13), and Poe et al. (2009) revealed the populations of *Anolis chocorum* from west of the Panama Canal to represent an undescribed species which they named *A. ibanezi* in honor of Roberto Ibáñez.

During the first decade of this century Abel Batista (AB) and Marcos Ponce (MP), two young herpetologists who had obtained their Licenciaturas at the UNACHI, undertook short expeditions to different sites in western Panama to collect amphibians and reptiles. In January 2006, they spent four weeks of collecting together with Gunther Köhler (GK), head of the Herpetology Section at the Senckenberg Research Institute Frankfurt, Germany, and his then PhD student Javier Sunyer (JS). This was the first of several field surveys realized in the course of this very productive cooperation between Panamanian and "Senckenbergian" herpetologists. In the region around Cerro Colorado, where only very little and sporadic collecting had taken place in the preceding decades, they gathered the type specimens of four new anole species within just 24 hours: *Anolis datzorum, A. gruuo, A. pseudokemptoni,* and *A. pseudopachypus* (Köhler et al. 2007; locs. 18 and 19 in Map 1.13). Having examined the types of both nominal taxa, Köhler (2007) placed *Anolis vociferans* Myers 1971 in the synonymy of *A. salvini* Boulenger 1885. Subsequently, Köhler & Sunyer (2008) revealed the existence of two additional species, formerly referred to as *A. limifrons,* in western Panama, which they named *A. apletophallus* and *A. cryptolimifrons.* Reviewing the morphological variation of highland anoles related to *A. kemptoni,* Ponce & Köhler (2008) placed *A. exsul* in the synonymy of *A. fortunensis.* Köhler et al. (2008) reported new localities for *A. auratus, A. fungosus, A. microtus,* and *A. polylepis* in Chiriquí and the Comarca Ngöbe-Buglé, adding comments on variation. Köhler (2010) demonstrated the populations of *A. pentaprion* from the Pacific versant of western Panama to represent a cryptic species which he described as *A. charlesmyersi*, based on types which Andreas Hertz (AH) and myself had collected in Los Algarrobos, Chiriquí (Map 1.13: loc. 10). The two of us had begun field work in western Panama for our respective PhD projects in the spring of 2008. The results of Bienentreu et al. (2013), Köhler et al. (2010a, 2012b), Lotzkat & Hertz (2011), and Lotzkat et al. (2010a, b, c; 2011; 2012a, b, c, d; 2013; 2014) are part of this PhD thesis and thus detailed in section 4.

Despite of the considerable number of publications recounted above, works presenting comprehensive data on the diversity and distribution of reptiles in western Panama are scarce. Owing not least to the great number of species involved and the resulting amount of relevant information, these comprehensive works are usually approximations of current knowledge at the time of their compilation. As a result, all are somewhat incomplete, that is, none of them incorporates all the single papers cited in the preceding paragraphs of this chapter. The very first checklist of Panamanian snakes (Smith 1958) already contained 128 species and subspecies, but lacked any information on their distribution. The first author who dared to compile a checklist and bibliography of the entire herpetofauna of Panama was Auth (1994), who listed 231 reptile species and provided short comments on the distribution within the country for some of them. Young et al. (1999) elaborated the only work considering the distribution of the entire herpetofauna among Panama's political subdivisions. Of the 228 reptile species included in their list, they reported 114 for Bocas del Toro, 130 for Chiriquí, 55 for Veraguas, 35 for Herrera, and 45 for Los Santos, totaling 169 species for Veraguas and the two provinces west of it, and 174 species for all provinces west of Coclé and Colón. Due to their approach at province level, it is unclear how many and which of the species they listed for the central provinces (66 for Coclé, 90 for Colón, and 142 for Panamá) would be found west of the Panama Canal watershed. Lamentably, Young et al. (1999) did not take into account the inventories from around Santa Fé, which would have considerably increased their species number for Veraguas, nor the Comarca Ngöbe-Buglé which already existed at that time. In the same year, Pérez-Santos (1999) published much more detailed information for 129 snake species occurring in the country, including altitudinal and ecological distribution. The point distribution maps in his book reveal the presence of 49 snake species in Chiriquí, 76 in Bocas del Toro, and 30 in Veraguas, totaling 94 species for Veraguas and the two provinces west of it. For twelve of these, his georeferences fall in the unmentioned Comarca Ngöbe-Buglé. The checklists of Ibáñez et al. (2001; 229 species) and Fundación PA.NA.M.A. (2007; 233 species) lack any geographic specification. In his first synopsis of Central American reptiles, Köhler (2003) mapped the distribution of 230 reptile species known to occur in Panama, 179 of these in western Panama. By the 2nd edition (Köhler 2008), these numbers had increased to 238 and 185, respectively. However, since most of these maps are on a Central American scale and present generalized areas of distribution, many of them should not be regarded as too precise. Recently, Ray & Knight (2013) provided general information, keys, and illustrations for 56 venomous snakes and some of their mimics known from Costa Rica and Panama. These authors state 153 snake species to occur in Panama, 48 of which are dealt with in their book. Their distribution maps include the country's current political subdivisions and show 44 of these species to occur in western Panama east to Veraguas (31 in Bocas del Toro, 37 in Chiriquí, 33 in the Comarca Ngöbe-Buglé, and 28 in Veraguas). The Reptile Database (www.reptile-database.org) provides information of variable extent for 270 reptile species currently listed for Panama (Uetz & Hošek 2014).

The most complete and up-to-date treatment of the entire Panamanian herpetofauna was compiled by Jaramillo et al. (2010), who analyzed the distribution of 248 reptile species (including 32 national endemics and 4 introduced geckos) occurring in the country among physiographic regions, vegetation zones, altitudinal belts, and protected areas. Of their four physiographic regions, one ("Eastern Panamanian Highlands") is clearly outside western Panama. Two others, the Caribbean Lowlands and the Pacific Lowlands, span the entire longitudinal extent of the isthmus along their respective versants. Thus, only the 155 species listed for their fourth region ("Isthmian Central American highlands", i.e., the Cordillera Central, which they obviously delineated just as I do in the present work) can clearly be attributed to western Panama. Since the treatment by Jaramillo et al. (2010) constitutes the starting point and basis for the present study, an excerpt of their list is given in Table 1.1.

Last but not least, much information on western Panamanian reptile species is contained in publications on the Costa Rican herpetofauna. For numerous species, detailed morphological data and black-and-white photographs can be found in the classic reviews of Taylor (1951, 1954, 1955, 1956). Brief notes on the presence, and in some cases on the distribution in western Panama, of 182 reptiles that also occur in Costa Rica can be found in the monumental opus of Savage (2002), which is above all the paramount source for condensed information on the morphology and biology of these species, and Central American herpetology in general. Solórzano (2004) provided information on the then 137 snake species known from Costa Rica, including 99 mentioned to occur in Panama, with distribution maps for all and illustrations of most species. A new field guide to the snakes of Costa Rica by McConnell (2014) provides basic information and distribution maps for 138 species, 105 of which also occur in Panama to my knowledge. Most notably, it contains 579 photos and drawings illustrating 136 of these species, including photos of Panamanian specimens for 58 species.

Table 1.1: Reptile species of Panama and the Cordillera Central (*) as listed by Jaramillo et al. (2010).

Family Alligatoridae
Caiman crocodilus
Family Crocodylidae
Crocodylus acutus
Family Cheloniidae
Caretta caretta
Chelonia mydas
Eretmochelys imbricata
Lepidochelys olivacea
Family Chelydridae
Chelydra acutirostris
Family Dermochelyidae
Dermochelys coriacea
Family Emydidae
Trachemys venusta
Family Geoemydidae
Rhinoclemmys annulata *
R. funerea
R. melanosterna
Family Kinosternidae
Kinosternon angustipons
K. leucostomum
K. scorpioides *
Family Testudinidae
Chelonoidis carbonaria
Family Amphisbaenidae
Amphisbaena alba
A. fuliginosa *
A. spurrelli
Family Anguidae
Celestus adercus *
Coloptychon rhombifer
Diploglossus bilobatus *
D. monotropis
D. montisilvestris
Mesaspis monticola *
Family Corytophanidae
Basiliscus basiliscus *
B. galeritus
B. plumifrons
B. vittatus
Corytophanes cristatus *
Family Eublepharidae
Coleonyx mitratus
Family Gekkonidae
Hemidactylus brooki
H. frenatus *
Lepidodactylus lugubris
Family Gymnophthalmidae
Anadia ocellata *
A. vittata *
Bachia blairi
B. pallidiceps
Cercosaura vertebralis
Echinosaura palmeri
E. panamensis *
Gymnophthalmus speciosus *
Leposoma rugiceps *
L. southi *
Ptychoglossus festae *
P. myersi
P. plicatus *
Family Hoplocercidae
Enyalioides heterolepis *
Morunasaurus groi *
Family Iguanidae
Ctenosaura similis
Iguana iguana *
Family Phyllodactylidae
Thecadactylus rapicauda *

Family Phrynosomatidae
Sceloporus malachiticus *
Family Polychrotidae
Anolis apletophallus *
A. aquaticus *
A. auratus *
A. biporcatus *
A. capito *
A. carpenteri
A. casildae *
A. chloris
A. chocorum *
A. cryptolimifrons
A. datzorum *
A. fortunensis *
A. frenatus *
A. fungosus *
A. gruuo *
A. humilis *
A. insignis *
A. intermedius *
A. kemptoni *
A. kunayalae *
A. latifrons
A. lemurinus *
A. limifrons *
A. lionotus *
A. magnaphallus *
A. microtus *
A. pachypus *
A. pentaprion *
A. poecilopus
A. polylepis *
A. pseudokemptoni *
A. pseudopachypus *
A. tropidogaster *
A. vittigerus *
A. vociferans *
A. woodi *
Polychrus gutturosus *
Family Sphaerodactylidae
Gonatodes albogularis *
Lepidoblepharis sanctaemartae
L. xanthostigma *
Sphaerodactylus argus
S. graptolaemus
S. homolepis
S. lineolatus *
Family Scincidae
Mabuya unimarginata *
Sphenomorphus cherriei
S. rarus *
Family Teiidae
Ameiva ameiva *
A. festiva *
A. leptophrys *
A. quadrilineata *
Cnemidophorus lemniscatus
Family Xantusiidae
Lepidophyma flavimaculatum *
Family Anomalepididae
Anomalepis mexicanus
Helminthophis frontalis *
Liotyphlops albirostris *
Family Boidae
Boa constrictor *
Corallus annulatus
C. ruschenbergerii
Epicrates maurus *

Family Colubridae
Amastridium veliferum *
Atractus clarki
A. darienensis
A. depressiocellus
A. hostilitractus
A. imperfectus
Chironius exoletus *
C. flavopictus *
C. grandisquamis *
Clelia clelia *
C. equatoriana
C. scytalina *
Coniophanes bipunctatus
C. fissidens *
C. joanae
Dendrophidion nuchale *
D. paucicarinatum *
D. percarinatum *
D. vinitor *
Diaphorolepis wagneri
Dipsas articulata *
D. nicholsi
D. temporalis
D. tenuissima
D. viguieri
Drymarchon melanurus *
Drymobius margaritiferus *
D. rhombifer *
Enuliophis sclateri *
E. flavitorques *
Erythrolamprus bizona *
E. mimus *
Geophis bellus
G. brachycephalus *
G. championi *
G. godmani *
G. hoffmanni *
G. talamancae *
G. tectus *
Hydromorphus concolor *
H. dunni *
Imantodes cenchoa *
I. gemmistratus
I. inornatus *
I. phantasma
Lampropeltis triangulum *
Leptodeira annulata *
L. rubricata
L. septentrionalis *
Leptophis ahaetulla *
L. depressirostris *
L. nebulosus
L. riveti *
Liophis epinephelus *
L. lineatus
Masticophis mentovarius
Mastigodryas melanolomus *
M. pleei
Ninia atrata
N. celata *
N. maculata *
N. psephota *
N. sebae
Nothopsis rugosus *
Oxybelis aeneus *
O. brevirostris *
O. fulgidus *
Oxyrhopus petolarius
Phimophis guianensis

Pliocercus euryzonus *
Pseudoboa neuwiedii
Pseustes poecilonotus *
Rhadinaea calligaster *
R. decorata *
R. godmani *
R. pulveriventris *
R. sargenti
R. vermiculaticeps *
Rhinobothryum bovallii *
Scaphiodontophis venustissimus
Sibon annulatus *
Sibon argus *
S. lamari
S. longifrenis
S. nebulatus *
Siphlophis cervinus
S. compressus *
Spilotes pullatus *
Stenorrhina degenhardtii *
Tantilla albiceps
T. alticola *
T. melanocephala *
T. reticulata
T. ruficeps *
T. schistosa *
T. supracincta *
Tretanorhinus mocquardi
T. nigroluteus
Trimetopon barbouri *
T. pliolepis *
T. slevini *
Urotheca decipiens *
U. fulviceps
U. guentheri *
U. pachyura *
Xenodon rabdocephalus *
Family Elapidae
Pelamis platura
Micrurus alleni *
M. ancoralis
M. clarki
M. dissoleucus
M. dumerilii
M. mipartitus *
M. mosquitensis
M. multifasciatus *
M. nigrocinctus *
M. stewarti *
Family Leptotyphlopidae
Leptotyphlops goudotii
L. macrolepis
Family Tropidophiidae
Trachyboa boulengeri
Ungaliophis panamensis *
Family Viperidae
Atropoides mexicanus *
A. picadoi *
Bothriechis lateralis *
B. nigroviridis *
B. schlegelii *
B. supraciliaris *
Bothrops asper *
B. punctatus
Cerrophidion godmani *
Lachesis acrochorda
L. melanocephala *
L. stenophrys *
Porthidium lansbergii
P. nasutum *

1.4 Objectives of this study

As depicted in the preceding chapter, a considerable amount of herpetological studies has been carried out in western Panama, and many of these have dealt with reptiles inhabiting the Cordillera Central. Nevertheless, these studies without exception have their taxonomic or geographic restrictions, i.e., most result from discrete inventory projects conducted over limited periods of time in comparably small areas, or focus on one or a few species. Thus, the total information generated on the diversity of reptiles along Panama's Cordillera Central is scattered in small fractions across numerous publications, several of which are somewhere between difficult and impossible to obtain. Moreover, for large tracts of this mountain range, very little or nothing has been published at all.

The present study attempts to summarize what is known about the reptile taxa populating the Cordillera Central of western Panama, and to complement this summary with newly generated data especially for areas poorly sampled in the past. The aim is to compile the most complete and up-to-date picture possible of the taxonomy, diversity, and distribution of reptiles that occur in this mountainous system from premontane elevations upwards. For the sake of manageability, the focus area of this study is restricted to the Serranías de Talamanca and Tabasará, i.e., the western two-thirds of the Cordillera Central between the Costa Rican border and Santa Fé de Veraguas at 81°W.

Specific objectives are:

– Which reptile species have been reported from within the study area by previous workers?

– Which reptiles can be detected in the study area during own field excursions?

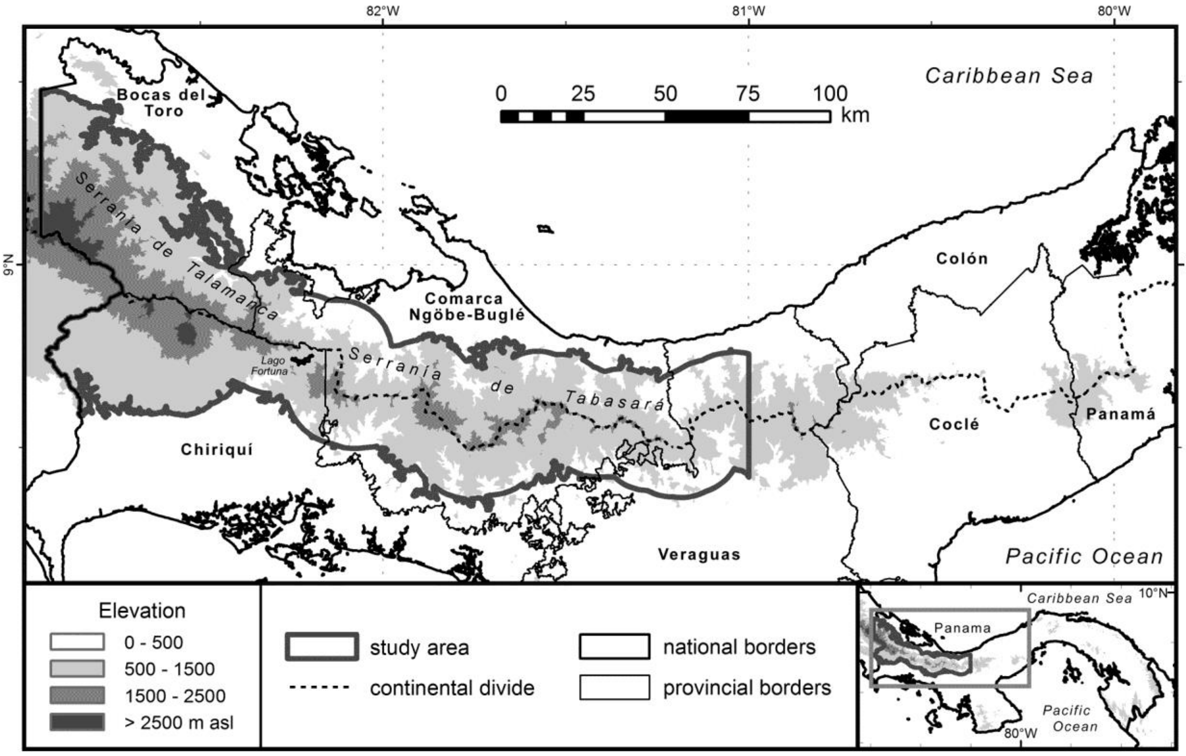
– What is the current taxonomic arrangement of the area's reptile fauna, i.e., which names are properly assigned to the reptile populations living in the area?

– How are the members of the area's reptile fauna distributed?

– Which spatial patterns of diversity among the reptile fauna of the study area can be recognized?

2. The study area

General aspects concerning physiography, climate, and vegetation of the entire Cordillera Central including the study area have been dealt with in chapter 1.2. In this section, I first specify the extent of my study area (chapter 2.1) within the highlands of western Panama as shown in Map 2.1. Throughout this large area of interest, selected localities, as representative as possible of the different altitudinal belts on the two versants, were visited to sample their reptile fauna. Map 2.2 shows the ubication of these research localities. In chapter 2.2, their geography, climate, and vegetation are briefly characterized. Finally, chapter 2.3 specifies the periods during which field work was undertaken at the different localities by co-workers and myself.

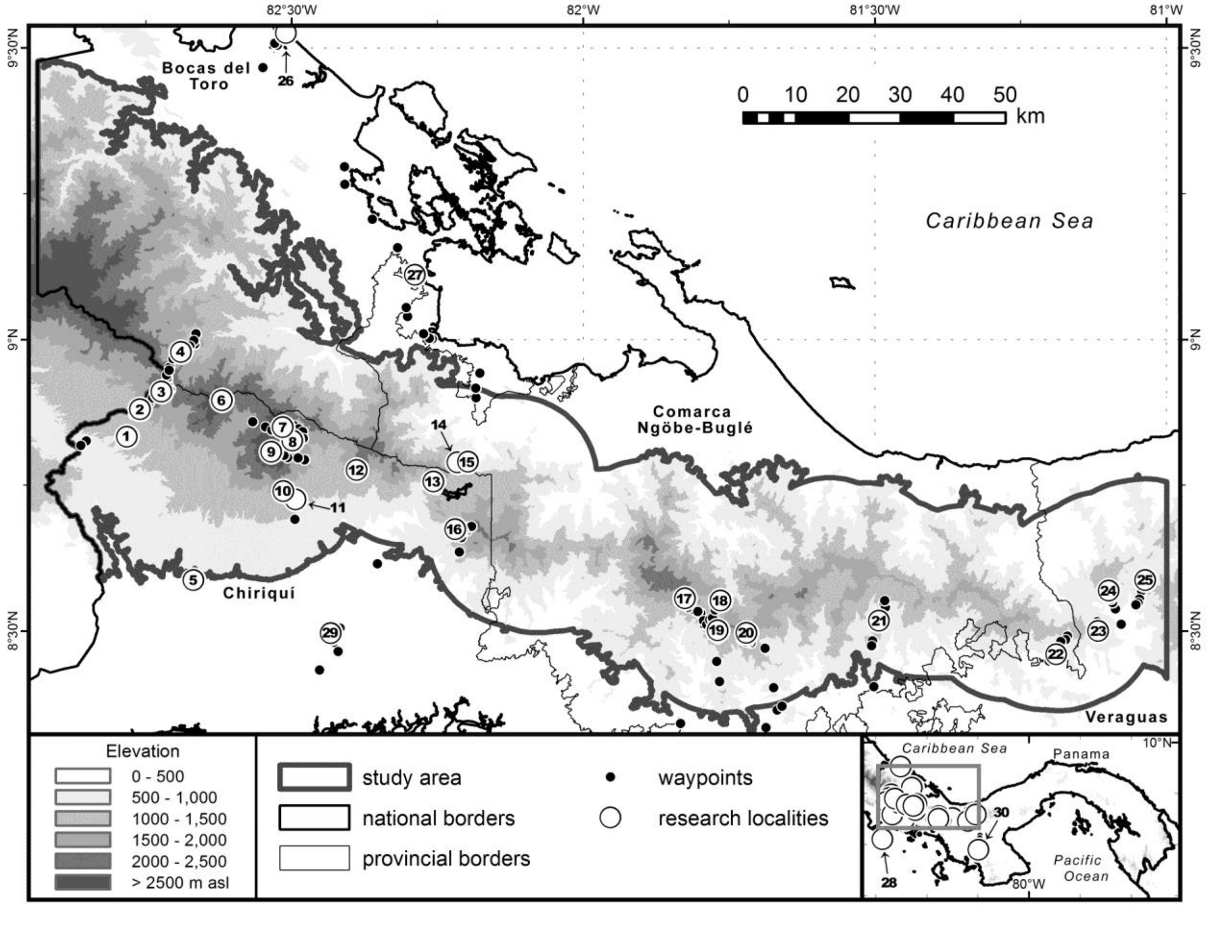


Map 2.1: Extent of the study area.

2.1 Extent

The study area comprises about two-thirds of the Cordillera Central of western Panama, namely the Serranía de Talamanca and the Serranía de Tabasará. The former stretches from the Costa Rican border (approximately 82°56'–82°43'W, depending on latitude) east-southeastwards to the Fortuna depression (around 82°12'W), while the latter continues the continental divide eastwards to the valley of Río Santa María at Santa Fé, slightly west of

81°W. The combined longitudinal extension of both ranges is roughly 210 km, their combined length along the winding continental divide about 260–270 km. Generally, the study area comprises all areas of premontane and higher elevations (i.e., above 500 m asl), but extends to a distance of 15 km from the continental divide at narrower portions. With its horizontal dimensions of approximately 10065 km^2, the study area covers a little more than 13.3% of the total area of the republic of Panama. In their totality, elevations above 500 m asl along the two ranges are found between ca. 9°30'N at the Caribbean foothills in extreme western Panama to approximately 8°20'N along the Pacific slopes in the Comarca Ngöbe-Buglé. The airline latitudinal extension of areas above 500 m asl is very variable along the study area, ranging from just 7 km at certain places in the Serranía de Tabasará to around 90 km west of Volcán Barú.



Map 2.2: Research localities in the study area and adjacent lowlands. White circles representing the 30 generalized research localities are approximately centered over the waypoints pertaining to their respective locality. (1) Santa Clara; (2) Hacienda Café de Eleta; (3) Jurutungo; (4) Changena trail; (5) Volante; (6) Las Nubes; (7) Sendero Los Quetzales; (8) Sendero La Cascada; (9) Volcán Barú; (10) Potrerillos Arriba; (11) Cabecera de Cochea; (12) Cerro Altrillería; (13) Cerro Guayabo; (14) Headwaters of Río Chiriquí Malí; (15) Willie Mazú; (16) Lost & Found Ecohostel, Río Hornito, and Cerro Pata de Macho; (17) Cerro Saguí; (18) Hacha trail; (19) La Nevera and western slopes of Cerro Santiago; (20) Buabidí and eastern slopes of Cerro Santiago; (21) Alto Tólica and Guayabito; (22) Los Valles and El Paredón; (23) Cerro Mariposa; (24) Cerro Negro; (25) Río Chilagres; (26) San San Pond Sak; (27) Road to Almirante (comprising all the waypoints that are roughly aligned along the coast); (28) Peninsula Burica; (29) Los Algarrobos; (30) Finca La Providencia.

2.2 Research localities

In the following, I introduce and characterize the highland localities at which field work was performed, roughly from west to east, in chapters 2.2.1–2.2.4, and mention some lowland localities where complementary sampling took place in chapter 2.2.5. Given the nature of certain places and field expeditions, I summarize several nearby or otherwise logistically connected singular collection points to describe them as one generalized research locality. The 30 generalized research localities and interspersed waypoints are shown in Map 2.2. All waypoints are listed in Appendix 1. Figures 2.1–2.8 show selected environments found at my research localities. Table 2.1 provides an overview of the waypoints, altitudinal range, recorded temperature range, mean annual temperature and total annual precipitation, as well as Holdridge life zones and Köppen climates for each generalized research locality. For selected localities, climate data is illustrated in Figure 2.9.

2.2.1 Serranía de Talamanca

This portion of the Cordillera Central comprises the country's highest mountains and with BPPS and PILA the two largest protected areas within my study area. Being rather densely populated, the Pacific slopes are well accessible on paved and dirt roads up to just a few hundred meters below the continental divide in many areas. Consequently, most of my research localities lie on the S versant, just as one of the herpetologically best-sampled regions of Panama, the Boquete area.

Santa Clara

Map 2.2: Locality 1; Figs. 2.1A–C.

On invitation by the owner, Enrique Caballero, three short visits were paid to the Finca Ecológica "Don Chavo" which is adjacent to the road from Volcán to Río Sereno. The building housing the small shop "Abarrotería La Sorpresa" (WP 174), vis-a-vis an abandoned gas station at a road crossing, served as a base. From this point, we worked downhill throughout the Finca which is bordered to the S and W by two small creeks. The mostly narrow strips of gallery forest along these creeks retain some old trees, whereas most of the secondary forest growing in the lower portions of the finca appears to be in a rather early successional stage. In its upper portions, the finca holds open grassland partly planted with plantain, and shade coffee plantations with old trees. Most searching was performed along the border creeks as well as a path leading down to the W creek near its junction with the S one, as well as around the shade coffee plantations next to WP 174.

Hacienda Café de Eleta

Map 2.2: Locality 2; Fig. 2.1D.

Through a contact to the management of Hacienda Café de Eleta mediated by Porfírio Yangüez, we spent two nights camping next to the utility shed of that estate (WP 29) near the community Piedra Candela just E of the road leading to Jurutungo. Our searches concentrated on nearby coffee and citrus plantations as well as the gallery forest along the Río Candela.

Jurutungo

Map 2.2: Locality 3; Fig. 2.1E–H.

On invitation by the owner, Porfírio Yangüez, AH and myself visited his finca at Jurutungo, in the high valley of the Río Candela, four times, i.e., once during each research trip to Panama. The finca's main building (WP 59) at almost exactly 2000 m asl was reached by car from Río Sereno, and served as a convenient base to explore its surroundings up- as well as downhill along the Pacific slopes. The vegetation around the finca and along the road to Jurutungo consists of gallery forest along the Río Candela and its tributaries, montane and cloud forest along the slopes, and large patches of interspersed cattle pastures often retaining singular trees. A few more estates are scattered along the road leading to the finca. Several small paths lead up towards the continental divide, some of which we followed to the Costa Rican border near the summit of Cerro Pando (WP 67) and an unnamed peak (WP 61) E of it to sample the elfin forest that covers the exposed ridges. Most significantly, a much used cattle trail (the "camino a Bocas") leads onto the crest of the Talamancan range N of Jurutungo, which it then follows N along the Costa Rican border. All collection sites from the large border monument on this trail (WP 77; Fig. 2.2A) northwards are attributed to the general locality Changena trail.

Changena trail

Map 2.2: Locality 4; Figs. 2.2A–D.

This generalized locality comprises all collection sites between the large border monument (WP 77) on the continental divide N of Jurutungo and the lowest point we reached at Río Clarito while roughly following the route of the 1966 Duellman, Trueb & Myers expedition.

The uppermost portions of this trail, along or close to the continental divide, were visited several times during our stays at Jurutungo in 2008 and 2009, and a provisional camp was established at WP 179 about 1 airline km N of the border monument just below the continental divide, to spend a few nights there during each of our two visits to Jurutungo in 2009. In 2010, AH and myself followed the cattle trail further N to about 1.9 airline km N of the border monument (WP 270), where a branch descends to the right onto the Caribbean slopes, continuing the "camino a Bocas" cattle trail. Always following this trail, we established our camp 1 or "upper camp" on the 1st cattle pasture along a small tributary of Río Changena (WP 271). After following this creek for about 2 km, the trail ascents the ridge left of it, which it follows before descending to Río Changena itself, where we established our camp 2 or "middle camp" at WP 275. From here, the trail leads N up the next ridge over a large cattle pasture, bends more E where it enters forest, and more N again where it descends onto the next very large pasture which holds a constantly inhabited house around its upper limit at WP 279. From here, the trail becomes somewhat unvisible on the pasture, and we followed the directions of the Ngöbe inhabiting the mentioned house N to the banks of Río Clarito, where we established our camp 3 or "lower camp" at WP 280. Vegetation along the Changena trail comprises elfin forest along the ridges, gallery forest along the streams, other montane forests on the slopes, and medium-sized to very large open pastures. The hooves of hundreds of cows being driven along this trail each year have created deep, almost impassable mud along large portions of the trail, and their excrements are washed into the streams which are situated downhill of the trail and/or pastures, rendering their water not too safe to drink.

Volante

Map 2.2: Locality 5; Fig. 2.2E.

Following an invitation of the owner Tapio Linderhaus, AH and myself (in the company of a film crew consisting of Caroline d'Orville and Dustin auf der Springe) spent two nights near the settlement Volante at the private reserve "Finca Volante", which is integrated in a conservation project aiming at protecting and interconnecting Squirrel Monkey populations (www.saimiri.org). Being surrounded chiefly by pastures, this reserve itself holds a rather mature gallery forest along the Río Escárrea which forms its W limit, and various stages of forest succession throughout most of its remaining area.

Las Nubes

Map 2.2: Locality 6.

The park ranger and biological station "Las Nubes" lies on the slopes of Cerro Picacho N of Cerro Punta and is accessible by car via this town. This place is one of the main gateways for hikes and research in the PILA, and definitely the one most frequented by tourists and students, in a way that for students of Biology at the UNACHI and many other people it is synonymous with PILA. JFB and Frank Hauenschild (FH) spent a couple of nights in this area in 2009.

Sendero Los Quetzales

Map 2.2: Locality 7; Figs. 2.2F–H.

The Sendero Los Quetzales is a prominent hiking trail that can be walked in a single day, connecting Cerro Punta and Boquete via Bajo Grande, Paso Respingo, and the high valley of the Río Caldera N of Volcán Barú as well as the Alto Chiquero and Bajo Mono areas. The core section of the trail is guarded by the park ranger stations Alto Respingo right on the Respingo pass to the W and Alto Chiquero to the E. Apart from recent landslides, the rocky areas near Refugio Las Rocas, and the gravel streambed of the upper Río Caldera, vegetation along the core section consists of different forms of rather mature montane forest including oak cloud forest ("bosque de roble"). Outside the core section, pastures and plantations dominate. In the spring of 2009, AH and myself walked the trail from Bajo Grande to Bajo Mono and spent one night each at the Refugio Las Rocas (WP 158) and at Quebrada El Silencio (WP 160), where wooden shelters provide small dry areas. In the autumn of the same year, FH and JFB walked the trail in the same direction, camping at Alto Respingo instead of Las Rocas and in this event working their way up a little on the ridge leading S to Volcán Barú.

Sendero La Cascada

Map 2.2: Locality 8; Figs. 2.3A–B.

Informally known as Sendero La Cascada (a name probably applied to many trails leading to waterfalls throughout Panama), this footpath leads from the road branch Alto Quiel–Alto Chiquero–Boquete (WP 169) W, up the valley of a tributary to the Río Caldera, until reaching a scenic waterfall ("la cascada") the bottom of which is at about 1870 m asl. We visited this place two times in 2009, camping next to the trail about 400 airline m downstream from the waterfall. Vegetation in this canyon mostly consists of rather mature montane forest, while the area below the waterfall is dominated by rocks and open vegetation and the lower half of the valley bears interspersed pastures.

Volcán Barú

Map 2.2: Locality 9; Figs. 2.3C–E.

Panama's highest mountain, Volcán Barú, is in theory accessible by road until shortly below its highest summit. However, only few cars can cope with the state of the dirt road leading to the military and broadcasting facilities ("las antenas"), from where a footpath leads up the short remaining distance to the volcano's peak at 3475 m asl. In November 2009, together with AH, Andreas Uselis (AU), FH, Falk Ortlieb (FO), and JFB, I mounted a strong-looking car in Boquete that was supposed to take us all the way to the "antenas" but broke around 2600 m asl. Fortunately, a much stronger car picked us up while we were trying to reach the summit by foot. We then supplied ourselves with water at the constantly guarded installations and descended to the camping site "Los Fogones" (WP 201) where we spent two nights before descending to the camping site "Los Mamecillos" (WP 198) for a 3rd night. On the descent to that camp site, we paid a visit to an old crater of the volcano that was described and pictured by Slevin (1942: p. 466–467, Fig. 1). This crater's flat floor is almost entirely covered by grass and herbs. Otherwise, the vegetation along the road to the "antenas" consists of mostly mature montane forests until, beginning at Los Fogones around 3300 m asl, the trees become smaller and more scattered to disappear towards the very summit, which holds a kind of subparamo vegetation of herbs, grasses, and dwarf shrubs.

Potrerillos Arriba

Map 2.2: Locality 10; Figs. 2.3F–G.

Invited by the UNACHI Biology student Juan Castillo, we spent two nights on his family's Finca "Los Mameyes" which is situated some 5–6 airline km NNW of Potrerillos Arriba and next to the Río Pedro, a tributary to the Río Cochea. A "rancho" (wooden hut) on the border between pasture and forest at WP 186 served as our base. From here, we sampled downhill towards Río Pedro and along that river, in gallery and secondary forest as well as along cattle pastures.

Cabecera de Cochea

Map 2.2: Locality 11; Fig. 2.3H.

Through the contact of Meike Piepenbring to the owner who is simply known as Don Rodrigo, AH and I could spend two nights in a rancho (WP 109) on his finca at Cabecera de Cochea, a community that is accessible via Potrerillos Arriba and comprises several scattered properties along the headwaters of the Río Cochea. We mostly concentrated our searches in the gallery forest along the Río Cochea just below the rancho, with sparse collecting along the fence tree rows on the pastures around the rancho.

Cerro Altrillería

Map 2.2: Locality 12.

Situated E of Boquete, N of Alto Jaramillo, and S of Cerro La Estrella, this summit is part of the southwestern extension of the easternmost large massif within the Serranía de Talamanca. Having accessed the area via Boquete and Alto Jaramillo, JFB and FH spent some time here in 2009, sampling in elfin forest and pastures.

2.2.2 La Fortuna and Palo Seco

The surroundings of the Fortuna hydroelectric reservoir have received much biological attention since the 1970s, nowadays being the herpetologically second most studied region within my study area. Most sampling undertaken in the general Fortuna area in the course of my study concentrated S of the Fortuna lake, around the Lost & Found Ecohostel and the nearby W slopes of Cerro Pata de Macho.

Cerro Guayabo

Map 2.2: Locality 13.

This is the easternmost peak of the Serranía de Talamanca exceeding 2000 m asl, E of which elevation rapidly decreases towards the high valley of the Río Chiriquí holding the Fortuna reservoir. JFB and FH ascended this mountain on a dirt road branching off next to the Fortuna dam and spent some time collecting here in 2009.

Headwaters of Río Chiriquí Malí

Map 2.2: Locality 14; Figs. 2.4A–B.

Almost exactly at the Fortuna pass, i.e., at the place where the road from Chiriquí to Almirante finally crosses the continental divide (WP 193; background of Fig. 2.4C), more than 8 km by road after the Fortuna dam when coming from Chiriquí, a small paved road leading to the "casa de control" of the oil pipeline that crosses the Cordillera Central diverges to the left. Following this road, one soon comes to a small cutout on its left side where the road bends to the right after a comparably long straight portion. From this cutout, a footpath steeply descends to the valley on the left. About 50 m above the point where this path reaches a creek flowing towards Río Chiriquí Malí, AH and I established a camp next to that stream in October 2009 and returned to this site on several occasions in 2010. Apart from recent landslides, the valley is forested with obviously secondary forest on the slope ascending towards the access road, and a more mature forest on the opposite slope.

Willie Mazú

Map 2.2: Locality 15; Figs. 2.4D–E.

This small private reserve is situated next to km 68 of the road from Fortuna to Almirante. Its name laid out with white stones, entrance, and edifications are visible uphill from the road and situated around 510 m asl (WP 250) where the road crosses a tributary of Río Guabo, vis-a-vis the small "Minicafé Isabel" serving delicious smoked meat and other homemade specialties. By permission of the owner, Wilberto Martínez, AH and I could visit this area several times in 2010. From the reserve's buildings, we walked up the main path along the river to set up a camp right on the path at about 640 m asl (WP 251), where the path comes very close to the river for the first time after leaving the buildings. From here, we sampled mostly uphill along the existing paths leading through at least partly mature forest.

Lost & Found Ecohostel, Río Hornito, and Cerro Pata de Macho

Map 2.2: Locality 16; Figs. 2.4F–H.

After our first rather accidental visit in 2008, the Lost & Found Ecohostel became one of our primordial study sites and bases throughout all research trips beginning with NH's Diploma thesis on its herpetofauna, chiefly owing to the friendliness and cooperation of the owners, Andrew Bennett and Patrick McGreer, as well as their staff members. The hostel itself (WP 22; Fig. 2.4F) is situated around 1250 m asl within RFLF, on a steep west-facing slope some 100 elevational meters above the road leading from lowland Chiriquí to La Fortuna, shortly after the abandoned toll station at Valle de la Mina. It can only be reached by foot from the road but rewards the visitor with a unique atmosphere and what probably is the most beautiful view of the Serranía de Talamanca that one can get. From here, the hostel's principal hiking trail leads up a narrow ridge and down on the other side towards Río Hornito (called Río de Oro on the hostel's hiking maps), which flows into the Fortuna lake. Following a trail upstream, AH and I crossed the river around 1300 m asl (WP 52) and opened a path up the W slope of Cerro Pata de Macho in 2008, establishing a provisional campsite next to a small creek at WP 50. From here, we established a trail further uphill and founded a more suitable campsite somewhat off the main path at WP 54, overlooking a tributary to Río Hornito which we baptized "Río Perdido" for its relative remoteness. Along the large ridge separating Río Perdido from the stream paralleling it to the N, we continued the main path up to 1800 m asl in 2008, and a little further to roughly 1870 m asl (WP 183) in 2009. Vegetation around the Lost & Found Ecohostel includes shade coffee plantations and open secondary vegetation as well as mostly secondary forest on the adjacent slope. Descending towards Río Hornito, the forest becomes less disturbed, until mature forest dominates on the slopes of Cerro Pata de Macho, including elfin forests on the small peaks and narrow ridges above 1700 m asl. This mature forest is frequently interspersed with secondary patches obviously owing to landslides, and contains more or less extensive areas of hardly penetrable bamboo thickets. Hamad (2009) provided a description of the natural environment of this area.

2.2.3 Central Serranía de Tabasará

Located within the Comarca Ngöbe-Buglé, the central portion of the Serranía de Tabasará is unquestionably the least explored and worst accessible part of my study area, even on the Pacific slopes. At the time of our field work, only a few dirt roads lead up these rugged mountains. Most sampling took place in the area around the Cerros Saguí and Santiago, known as the Cerro Colorado area and accessible from San Félix over Hato Chamí on a road constructed for mining purposes. This road is served by public transport in the form of strong cars ("chivas", literally translating to [mountain] goats) which usually serve the "Terminal de Hacha" from the bus terminal in San Félix. Owing to the desastrous ecological consequences of past test drills, the indigenous Ngöbe and/or Buglé population in many places is highly suspicious of any stranger entering their territory, and often could hardly be convinced that some Europeans would take on the effort of climbing the steep slopes regardless of weather or light conditions without any commercial benefit. Fortunately, in most cases these obstacles could be overcome with friendly openness, patient explanations, and a special permit issued to us by the chief general of the Ngöbe.

Cerro Saguí

Map 2.2: Locality 17; Figs. 2.5A–B.

This large massif lies at the end of the so-called "Cerro Colorado road" and is best accessible via the village Ratón about 5 airline km NW of the Terminal de Hacha. From this village, where even a small store selling basic supplies is found, AH and I walked up onto the ridge

NE of it that constitutes the continental divide, spending the first night in a provisional camp on a cattle pasture just above the settlement. The next day we continued atop this ridge to the NW until reaching the end of the pasture at roughly 1860 m asl, where Gabriel Morales Palacio was constructing a rancho with a thatched roof of palm fronds. Being asked for a suitable camping site, he pointed us towards the adjacent valley on the Caribbean (i.e., NE) slope of the divide, where a stream called Quebrada Juglí on most maps (but called Río Cricamola by him and other locals) marks the N limit of his family's finca "Alto Cedro". With his permission, we camped two nights next to that river at 1700 m asl (WP 263) and worked our way up the ridge on its opposite side up to 2033 m (WP 269) instead of further pursuing the path that continues uphill along the divide from where we met our host. Apart from cattle pasture and corn plantations, vegetation in this area consists of gallery forest along Quebrada Juglí, montane forest on the slopes, and elfin forests on the exposed ridges. Descending on foot, it took us about 3 hours to reach the Terminal de Hacha, where we learned after one hour of waiting that no car would be going down to San Félix that day anymore. Being under time pressure, we decided to walk downhill at 15:45, passed our roadside campsite at La Nevera about one hour later, and at 19:25 arrived at Hato Chamí where we could persuade drivers of the local transport cooperative to take us to San Félix.

Hacha trail

Map 2.2: Locality 18; Fig. 2.5C.

This trail, known among some adventurous tourists as the "Cricamola trail", is a major travelling and transport route for the Ngöbe communities inhabiting the Caribbean slopes along the Río Cricamola, in its totality leading from the continental divide down to the large Ngöbe settlement of Kankintú in the Caribbean lowlands. It begins at the so-called "Terminal de Hacha", the endpoint of most cars leaving to "Cerro Colorado" or "Hacha" from San Félix, which is situated on a pass slightly lower than 1400 m asl (WP 256) and was reached in 2–4 hours by these cars in times when the road was still unpaved above Hato Chamí. From here, the dirt road descending the Caribbean slopes quickly turns into a footpath along the narrow canyon of the Río Marabí. Once the canyon opens into a wider valley, that river joins the Río Flor (or Flores) which comes from the right and has its headwaters at La Nevera. AH and I established a first camp next to a small bridge crossing the Río Flor at 1216 m asl (WP 286) to collect in its close vicinities as well as upriver to the houses of Augustín and Manuel Ábrego, whom we had already met in 2008 at La Nevera. After 2 nights, we descended further on the unmistakable trail along the Río Flor, reaching the village of Hacha (also known as Río Hacha or Quebrada de Hacha) just below the junction of the Ríos Flor and Hacha (the latter and larger of which comes in from the E, and is called Río Moi on the Mapa General de la Republica) after about one hour. About 1 airline km downstream of this village, we accidentally crossed the Río Hacha on one of the utterly frightening "bridges" which are so typical for this area, only to find that we now were on the path leading W to the village of Suiche along the Quebrada Juglí and actually should have stayed on its right (i.e., E) side. After returning to the correct bank, approximately another airline km further downstream we reached a small shop (Abarrotería Lopez), shortly below which the Río Hacha enters an impressive canyon flanked by towering rocks. Just before this canyon we turned right into the valley of a small creek where we established a very uncomfortable camp quite inside the streambed around 990 m asl (WP 291) to sample in the surroundings, including alongside the stairs over which the trail winds along the mentioned canyon. In the second night spent here, we packed and walked all the way up to the Terminal de Hacha within approximately 4 hours while collecting along the way. The vegetation along this trail is dominated by pastures, scrub, and cropland in the valley and adjacent slopes, with interspersed forest patches mostly constrained to the steepest slopes and minor areas of gallery forest. Above the junction of Río Flor and Río Marabí, more forest is left.

La Nevera and western slopes of Cerro Santiago

Map 2.2: Locality 19; Figs. 2.5D–H; 2.6A.

This is another major research locality where AH and I spent prolonged periods. Right next to the road to Cerro Colorado, shortly after it has reached its highest point before gradually descending again towards the Terminal de Hacha, a provisional camp was established at 1700 m asl (WP 6) during the first explorative trip we made by car together with GK, LS, and NH in 2008. This point is just before a very narrow and rather open portion of the divide called "La Nevera" (the freezer) by the locals. It had been visited already in 2006 by GK, AB, JS, and MP and is the type locality of *Anolis datzorum, A. pseudokemptoni,* and *A. pseudopachypus* as corrected by Lotzkat et al. (2010a). From here, several small streams forming the headwaters of Río Flor flow down the Caribbean slopes. Descending one of these, we established a more suitable camp above a small stream at 1580 m asl (WP 100) in the company of Caroline d'Orville and Dustin auf der Springe in 2008. From this base, we collected down the adjacent creek as well as up the next stream behind the easterly ascending small ridge. Ascending the canyon of the latter stream, we worked our way up again onto the continental divide to an elfin forest covered cone (WP 105, 1814 m) along the ridge ascending towards Cerro Santiago from the W. Apart from various stages of succession where some of the here apparently frequent landslides have come down (including streambeds washed naked and broadened as if by glaciers), the slopes in this area hold rather mature montane forest, and the ridges are covered with seemingly pristine elfin forest. In 2010, AH and I camped one night along the road above Hato Chamí around 1480 m asl (WP 229; Fig. 2.6A) after our car had made it very clear that it would not manage to surmount the first steep ascent between Hato Chamí and La Nevera. Here, we collected in secondary and gallery forest with interspersed plantations.

Buabidí and eastern slopes of Cerro Santiago

Map 2.2: Locality 20; Figs. 2.6B–E.

According to most maps, Buabidí (also known as Alto Tugrí, Hato Tugrí, Llano Tugrí, Buäbtí, or Buapití) is the capital of the Comarca Ngöbe-Buglé. However, this does not mean that this community of scattered properties on the SE slopes of Cerro Santiago is easily accessible. Travelling in a strong car with the advantage of the dry season, it took AB, AH, and myself more than 3 hours to reach Buabidí from Tolé next to the Carretera Interamericana via Chichica and Peña Blanca. Here, we camped at 1241 m asl (WP 140) next to the house of Don Amado, who guided us to a lake ("la laguna") about 1.5 km WNW in the first night. When MP arrived the next day, we were lead by our host about 1.7 airline km NNW to a campsite next to Quebrada Ardilla, a tributary to Río Rey, at 1532 m asl (WP 143). Here, we collected along this creek and reached the continental divide E of Cerro Santiago (WP 148 at 1718 m) via the valley of Río Rey itself. Vegetation around Buabidí mainly consists of savanna interspersed with pasture, plantations, and forest patches. From Quebrada Ardilla upwards, more and more area is covered by montane forest, but open areas in various stages of succession persist.

Alto Tólica and Guayabito

Map 2.2: Locality 21; Figs. 2.6F–H.

The settlements of Alto Tólica and Guayabito are situated on the same ridge ascending towards the continental divide. A dirt road diverging from the paved road to Buenos Aires (which branches off the Carretera Interamericana about halfway between the large Ríos Viguí and Cobre) at Chumí (or El Chumico) leads up this ridge and becomes hardly passable for cars already at the beginning of the ascent onto Cerro Tólica, a bit below Alto Tólica. In this village, the uppermost point which we managed to drive to, we were rather reluctantly housed in the community school at 1052 m asl (WP 232) and sampled nearby pasture, savanna, and gallery forest. Although the steep and rocky ascent to the pass over Cerro Tólica at ca. 1317 m asl is the only major obstacle on the way, the road to Guayabito is only coped with by very suitable cars with utterly determined drivers. We were bound to walk the road leading through almost completely treeless savanna, pastures, and plantations over Alto Galera to Guayabito and needed around 3 hours for the ca. 7.5 airline km. In Guayabito, which has a small café serving simple food and coffee as well as small stores selling basic supplies, we were again housed in the school facilities (WP 294 at 1130 m). From here, a path continues along the ridge over a steep slope covered mostly by open vegetation but holding also a small patch of shade coffee with some old trees. Continuous closed forest is only reached around 1500 m asl.

Most lamentably, the local people in the mentioned settlements are extremely suspicious, not to say hostile, toward strangers entering their lands without special permission. On our first trip on which we slept in Alto Tólica and only walked up to the forest above Guayabito for one night, AH and I were confronted with a Bugudai (Ngöbe guardian) the next morning, prevented from leaving, and forced to pay a fine of US$ 20,-. On the next trip together with MP, we carried our permit issued by the chief general of the Ngöbe, which helped us being received not too reluctantly in Alto Tólica, but was not recognized at all in Guayabito, where we had to explain ourselves to the entire community whose members demanded rediculously huge sums from us and told us to "better not return without carrying sufficient amounts of bucks". Both times, we were happy and relieved when having returned to the lowlands safe and sound in the end.

2.2.4 Eastern Serranía de Tabasará

Towards its E end, the Serranía de Tabasará only attains elevations above 1500 m asl at a few points. Around Santa Fé de Veraguas, were its passes drop well below the 1000 m contour repeatedly, my easternmost premontane research localities are found.

Los Valles and El Paredón

Map 2.2: Locality 22; Fig. 2.7A.

The village of Los Valles lies right at the border between Veraguas province and the Comarca Ngöbe-Buglé and is accessible on a paved road from Cañazas. Neither Los Valles nor Cañazas have a gas station, so travellers are well advised to stock up on combustible at where the road to Cañazas branches off the Carretera Interamericana. In Los Valles, we were kindly permitted to stay overnight at the ANAM station (WP 240, 402 m asl) by the ANAM officer José Carpintero, who even accompanied us on our night search along the Río Corita that runs through agricultural land. The next day, we crossed the river into the Comarca Ngöbe-Buglé and took the dirt road to El Paredón, where the local leader Antonino Santos allowed us to camp next to his son Inocencio's house at the "Piedra Pintada" (WP 243 at 454 m) that bears ancient and modern petroglyphs. From here, we walked and sampled uphill through savanna with forest patches into the almost completely forested valley of the Río Rasca up to a little more than 4 airline km NNE of the "painted stone", about 2 km S of the continental divide.

Cerro Mariposa

Map 2.2: Locality 23; Figs. 2.7B–D.

This mountain, also known as Cerro Los Gringos, Delgadito, or Tute, is the principal elevation of the so-called Serranía del Tute (also containing the real Cerro Tute) which markes the E end of the continuous Tabasará range. Arcadio Carrizo introduced us to this place as well as to the family Peña Solís who run a restaurant with rooms to let at the W extreme of the village Alto de Piedra, which lies just W of Santa Fé along the road to Calovébora. Together with Jurutungo and the Lost & Found Ecohostel, this restaurante (WP 17 at 867 m asl) became one of our main bases for field work, beginning with the Diploma thesis field work of LS in 2008. Above this estate and the adjacent roadside with their open vegetation, forest covers almost the entire mountain except for its treeless northern peak. A detailed description of its natural environment was provided by Stadler (2010).

Cerro Negro

Map 2.2: Locality 24; Figs. 2.7E–G.

This mountain NNW of Santa Fé was first inventorized herpetologically by AC in the course of his Licenciatura thesis (Carrizo 2000) and constituted a major study site for his Master thesis (Carrizo 2010). Together with him, AH and I chartered a car in Santa Fé which took us over dirt roads to the community of Bermejo, or more exactly to the "entrada al Salto Bermejo" (WP 90), the branching of a trail which leads to a waterfall of the Río Bermejo (also known as Río Bermedero or Bermejito). From here, a trail on the E slope of this river's valley leads essentially N through forest and clearings until the last large clearing offering a view S onto Cerro Mariposa is reached after 4–5 hours, or about 3.5 airline km. Crossing another creek behind this clearing, we established a camp next to a small clearing with plantain at 700 m asl (WP 90). From here, we opened a trail for collecting up the adjacent, completely forested ridge of Cerro Negro.

Río Chilagres

Map 2.2: Locality 25; Fig. 2.7H.

The Río Chilagres or Chilargre is a small tributary to the Río Santa María. We accessed it together with AC under the guidance of Señor Roberto, following the apparently much frequented trail that runs along the Río Santa María for about two hours after having crossed to the river's E bank NNE of the community Piragual. About halfway to Río Chilagres, this trail passes a rancho with thatched roof. Just below the mouth of the Río Chlagres, the trail crosses the Río Santa María again to the W bank. Just before this crossing, a branch to the right leads to another thatched roof rancho about 100 m upstream along the Chilagres (WP 40 at 476 m asl). From this base, we collected in the gallery forest along both rivers and premontane forests on the adjacent slopes.

2.2.5 Complementary lowland localities

In between the main field work in the highlands of the Cordillera Central, several lowland localities were visited, which are briefly described in the following.

San San Pond Sak

Map 2.2: Locality 26; Figs. 2.8A–B.

The Humedal de Importancia Internacional (Wetland of International Importance) San San Pond Sak (Ramsar site No. 611) covers the entire Caribbean coastal strip between Almirante and the border to Costa Rica. Invited by REWE, Chiquita, and the GIZ, we visited the Centro Boca San San at the mouth of the Río San San (WP 209), which is operated by the Asociación de Amigos y Vecinos de la Costa y de la Naturaleza (AAMVECONA) to collect in coastal vegetation, mangrove, pasture, and flooded forests. Selected environments were described by Lotzkat et al. (2012b), the entire area by ANAM (2004, 2009b).

Road to Almirante

Map 2.2: Locality 27; Figs. 2.8C–D.

Together with Rosalba de León (RdL) and Johannes Justus Köhler (JJK), AH and I conducted targeted sampling of beta anoles of the *limifrons* complex (see chapter 4.1.7.4) along the road leading from the gas station and restaurante "Marismar #2" in Chiriquí Grande (km 0) to Almirante around km 68 and on to Changuinola and Costa Rica. This road runs through pasture, intensively as well as extensively cultivated areas, secondary growth, and gallery forest along the rivers it crosses. Other reptile taxa were also collected whenever encountered. The WPs 126 (a house in Punta de Peña) and 106 (road Fortuna–Chiriquí Grande about 5.6 km on road before reaching Restaurante Marismar) are also included in this locality.

Peninsula Burica

Map 2.2: Locality 28; Fig. 2.8E.

In 2010, AH and I spent two nights on the Peninsula de Burica along the Costa Rican border together with my sister, Anna Lotzkat. A few hours of nighttime collecting were performed along small creeks, and specimens found dead on the road were also secured.

Los Algarrobos

Map 2.2: Locality 29; Figs. 2.8F–G.

Together with different long-term companions such as Diploma students and interns, AH and I used different houses rented in the village of Los Algarrobos as our headquarters on all four research trips to Panama. Through the contacts of Meike Piepenbring, who owns a residence (WP 1) on the W outskirts of that village that we could occupy during the initial days of our 2008 stay as well as througout our 2010 stay, we were perfectly integrated into the local community and soon felt at home in Los Algarrobos. Whenever work and recreation schedules allowed it, AH and I, often accompanied by others, performed some collecting, chiefly along different ways leading S to the Río Majagua, nearby pastures and secondary vegetation, but also inside the village itself. Several snake specimens were brought to me by local people who had killed or badly injured them. Lotzkat & Hertz (2011) published a herpetological inventory of Los Algarrobos and surroundings, which contains a general description of the area.

Finca La Providencia

Map 2.2: Locality 30; Fig. 2.8H.

During the above all recreational round trip together with my sister in 2010, we spent two nights in the main building (WP 217) of the Finca La Providencia which is owned and operated by the family of Arcadio Carrizo and located on the NW Azuero Peninsula. Sporadic collecting was undertaken during the daytime horse tour, and dedicated searches performed each night in gallery forest, around ponds, and in open pasture.

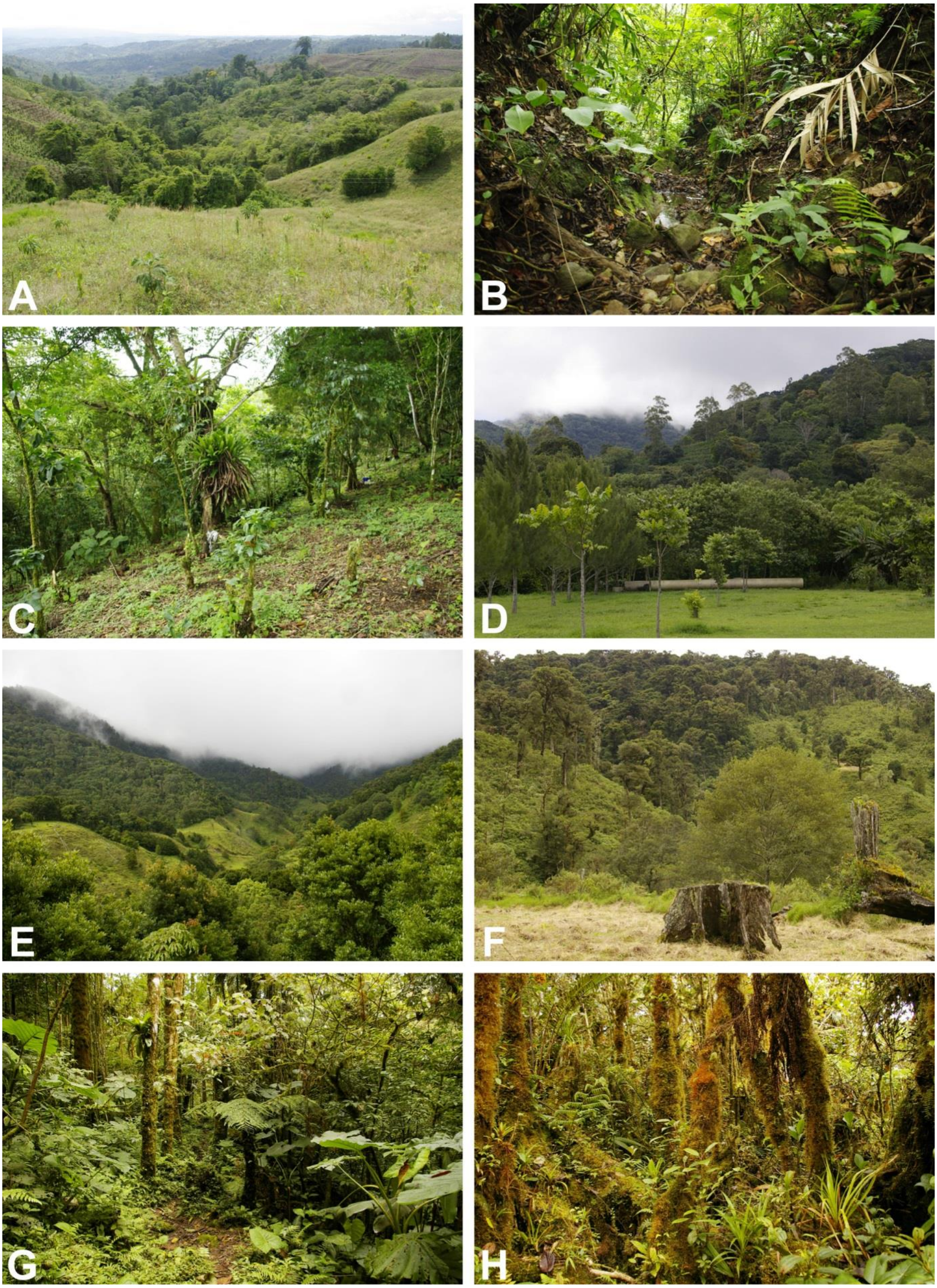


Figure 2.1: Representative environments in the Serranía de Talamanca. (A–C) Santa Clara: (A) view downhill onto clearing, gallery forest, and surrounding intensive coffee plantations from ca. 1200 m asl near WP 174; (B) southern border creek near WP 175, 1130 m asl; (C) shade coffee plantation near WP 174; (D) Hacienda Café de Eleta, clearing and forest fragments at WP 29, 1437 m asl; (E–H) Jurutungo: (E) view of valley towards continental divide hidden in clouds, from WP 86 at 1954 m asl; (F) pasture, secondary growth and border of forest near WP 64, ca. 2020 m asl; (G) forest trail near WP 63, 2070 m asl, (H) elfin forest on summit of Cerro without name at WP 61, 2460 m asl. (A, B) modified from Lotzkat et al. (2012a), (E, G, H) from Lotzkat et al. (2011).

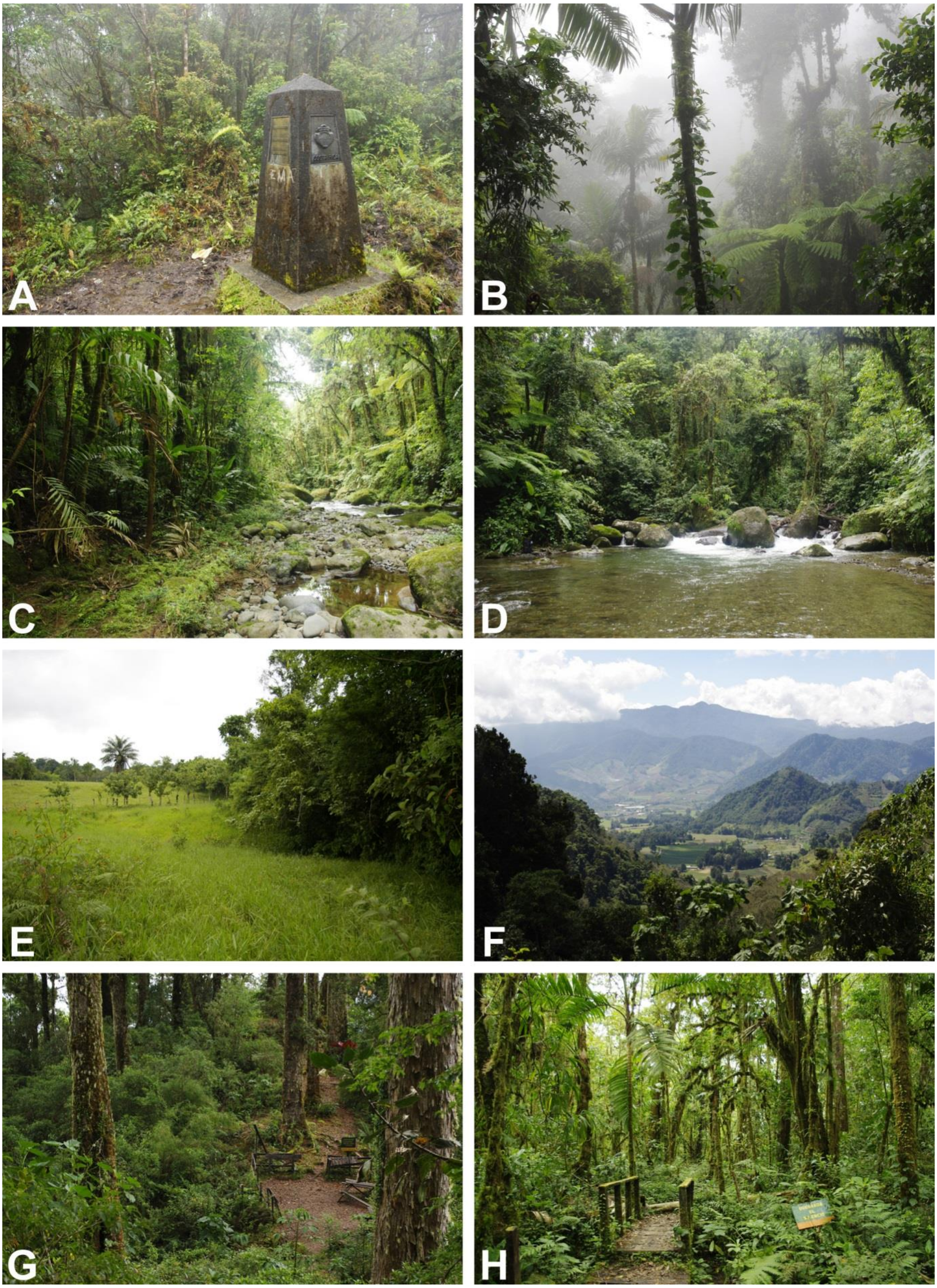


Figure 2.2: Representative environments in the Serranía de Talamanca. (A–D) Changena trail: (A) international border monument on continental divide at WP 77, 2447 m asl; (B) cloud forest just below continental divide near WP 181, 2310 m asl; (C) Río Changena near "middle camp" at WP 275, 1640 m asl; (D) Río Clarito near "lower camp" at WP 280, 1240 m asl; (E) Volante: pasture outside, and secondary forest inside private reserve near WP 88, ca. 470 m asl; (F–H) Sendero Los Quetzales: (F) view from ascent to Paso Respingo over valley of Cerro Punta and Bajo Grande towards Cerro Picacho; (G) oak cloud forest between Refugios Las Rocas (WP 159) and Quebrada El Silencio (WP 160), ca. 2250 m asl; (H) Quebrada Silencio near WP 160, 2130 m asl. (A–C) modified from Lotzkat et al. (2011).

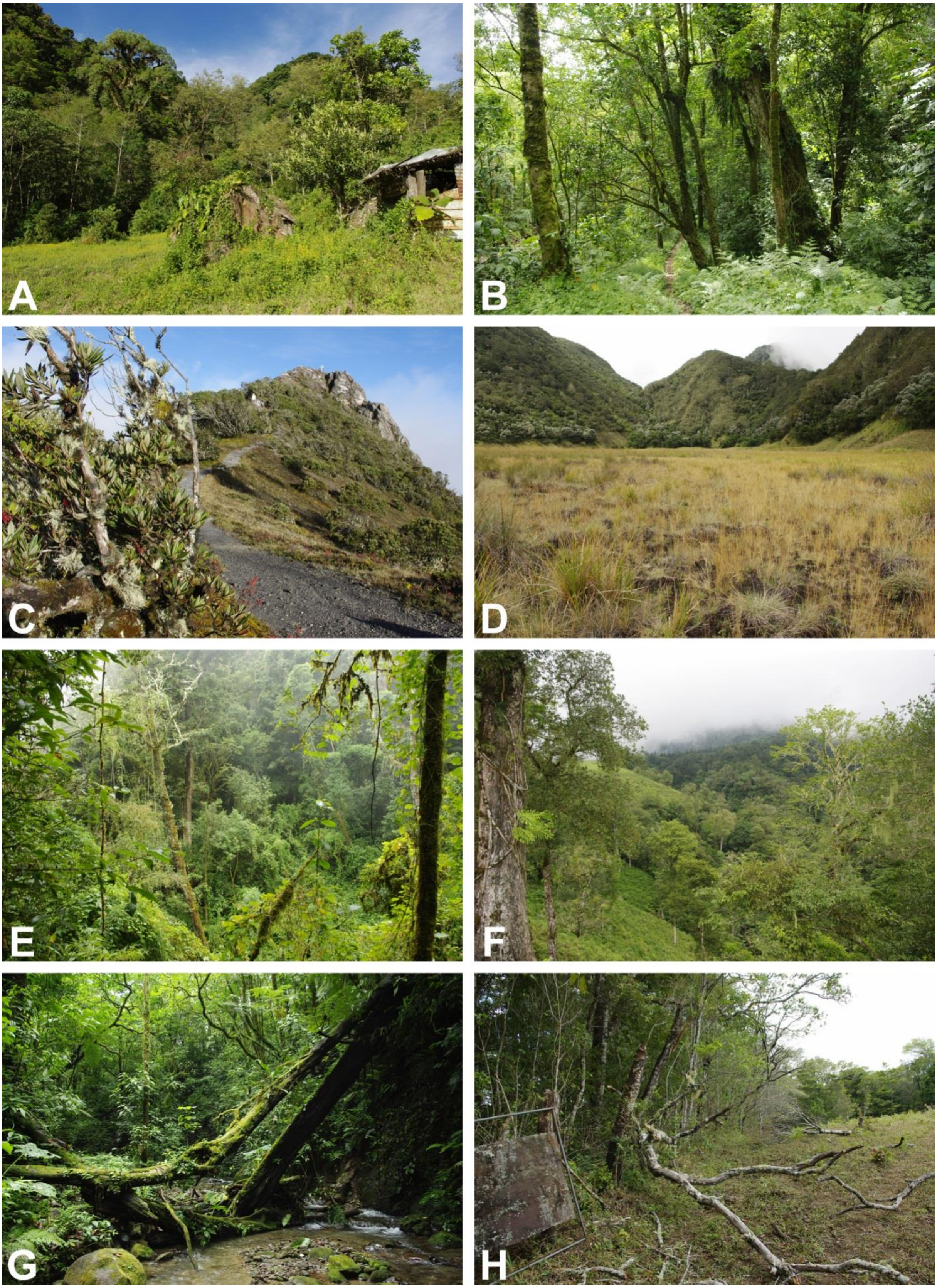


Figure 2.3: Representative environments in the Serranía de Talamanca. (A, B) Sendero La Cascada: uppermost clearing along trail at WP 173, 1680 m asl; (B) forest near camp at WP 171, 1830 m asl; (C–E) Volcán Barú: (C) last portion of ascent to summit at WP 200, 3475 m asl; (D) floor of crater at WP 204, 2970 m asl; (E) forest near Area de Acampar Los Mamecillos at WP 198, ca. 2580 m asl; (F, G) Potrerillos Arriba: (F) view from rancho at WP 186 onto pasture, secondary forest, and gallery forest along the valley of Río Pedro; (G) Río Pedro near WP 188, ca. 1320 m asl; (H) Cabecera de Cochea: border of pasture and secondary forest below rancho at WP 109, ca. 1150 m asl.

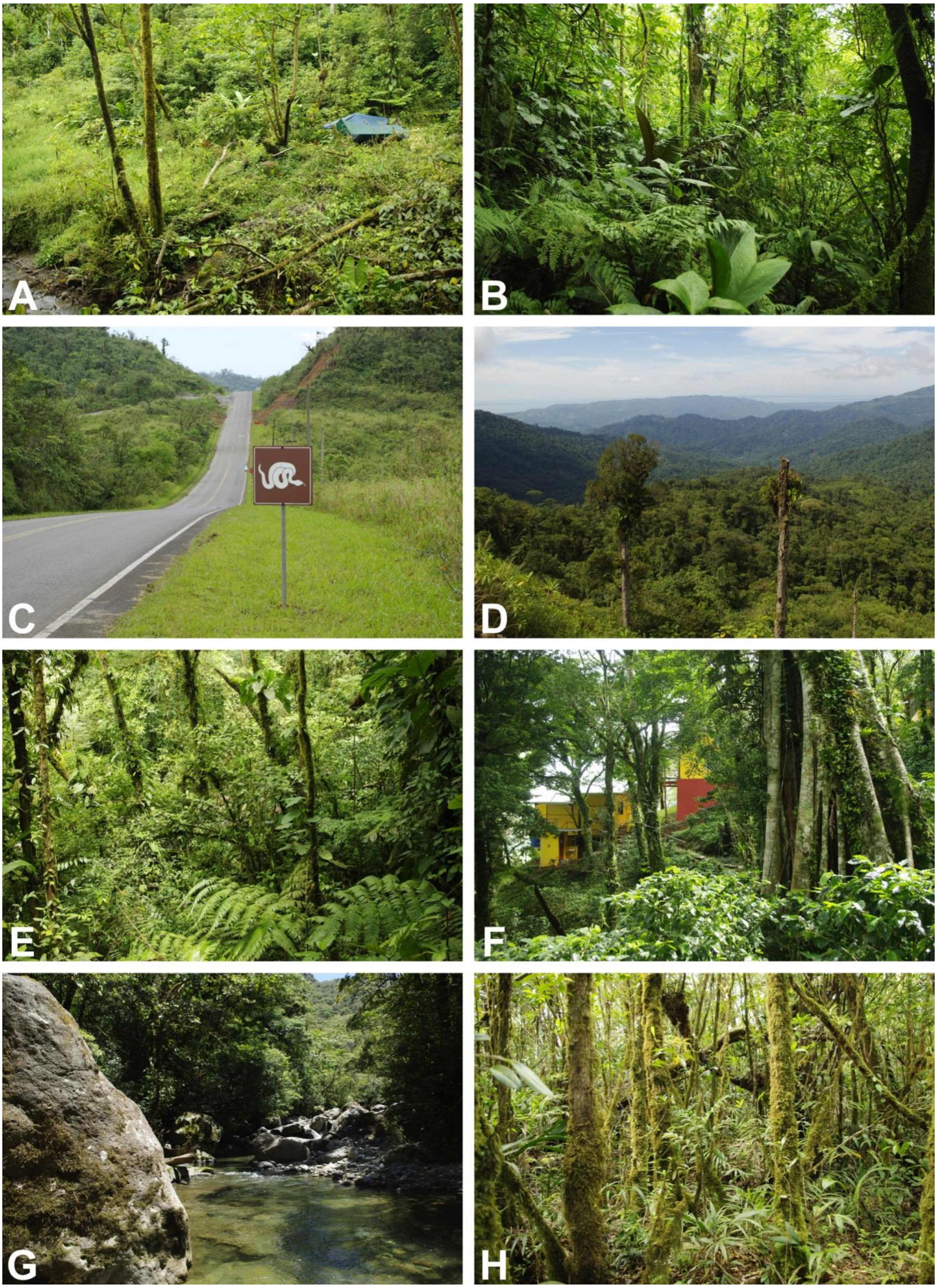


Figure 2.4: Representative environments around the Fortuna depression. (A, B) Headwaters of Río Chiriquí Malí: (A) secondary growth along N bank of stream, campsite at WP 194, 1054 m asl, and (B) forest on slope S of stream, ca. 1070 m asl; (C) road from Fortuna to Chiriquí Grande, crossing valley of Quebrada Arena before reaching continental divide in background at WP 193, 1090 m asl; (D) view onto Caribbean slopes from road to Chiriquí Grande, one turn N of continental divide; (E) Willie Mazú: forest near camp at WP 251, ca. 640 m asl; (F–H) Lost & Found, Río Hornito, and Cerro Pata de Macho: (F) Lost & Found Ecohostel: buildings in shade coffee plantation, WP 22, 1250 m asl; (G) Río Hornito at crossing to ascent, WP 52, 1304 m asl; (H) low canopy cloud forest on plateau between WPs 55 and 56, ca. 1750 m asl. (B, E) modified from Lotzkat et al. (2013).

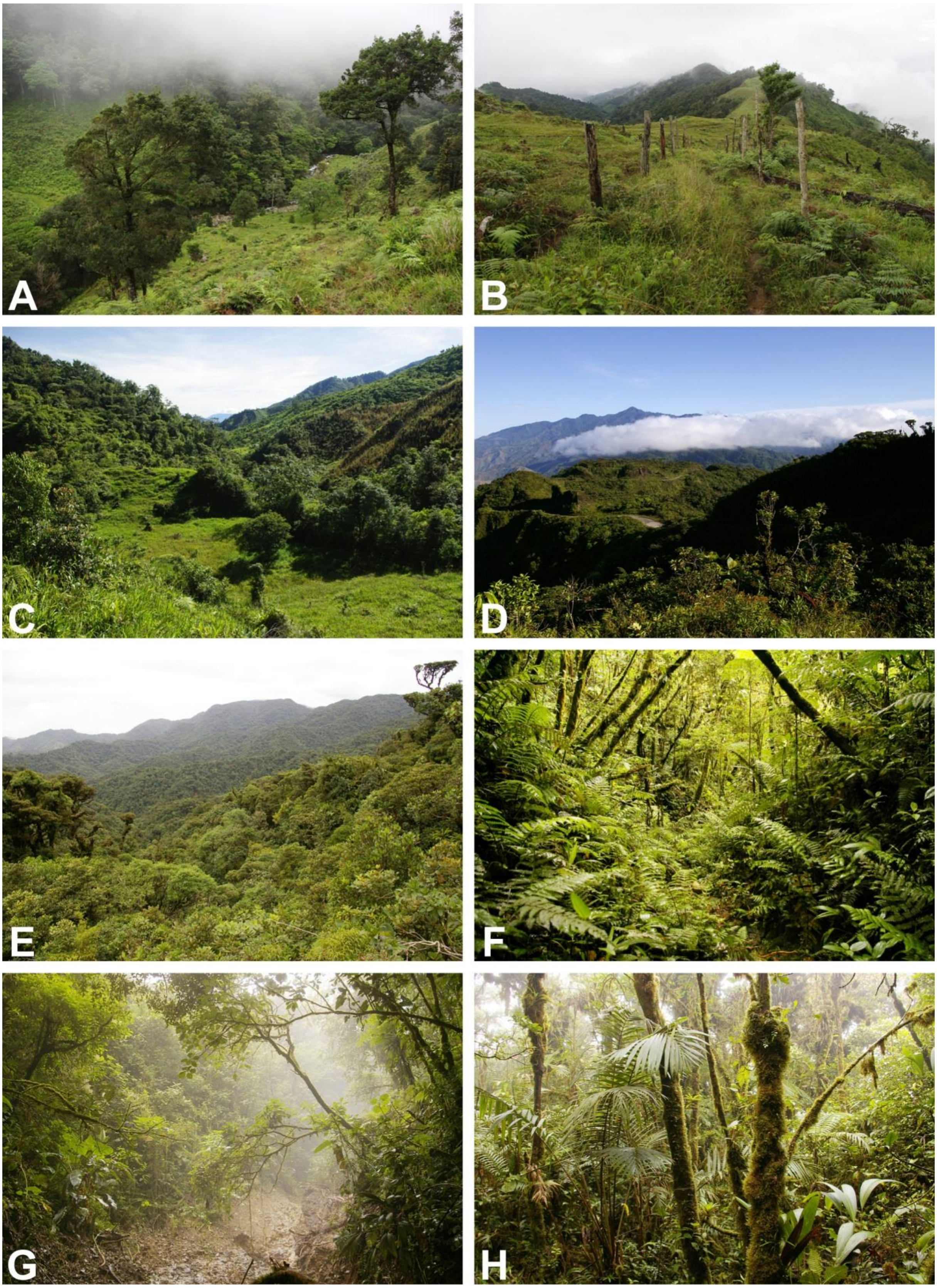


Figure 2.5: Representative environments in the Serranía de Tabasará. (A, B) Cerro Saguí: (A) looking down into the valley of Quebrada Juglí from ca. 1800 m asl above WP 263; (B) looking E along the continental divide between Ratón and Quebrada Juglí, near WP 262, ca. 1840 m asl; (C) Hacha trail: looking S, down the valley of Río Flor near WP 286, ca. 1220 m asl; (D–H) La Nevera and W slopes of Cerro Santiago: (D) looking W along continental divide onto Cerro Saguí and (E) NE onto Cerro Santiago from La Nevera at WP 6, 1699 m asl; (F) cloud forest stream just below WP 6, ca. 1600 m asl; (G) bed of "ascent creek" washed out by landslide, near WP 104, ca. 1700 m asl; (H) elfin forest at WP 105, ca. 1810 m asl. (A) modified from Bienentreu et al. (2013), (C and E–G) from Lotzkat et al. (2014).

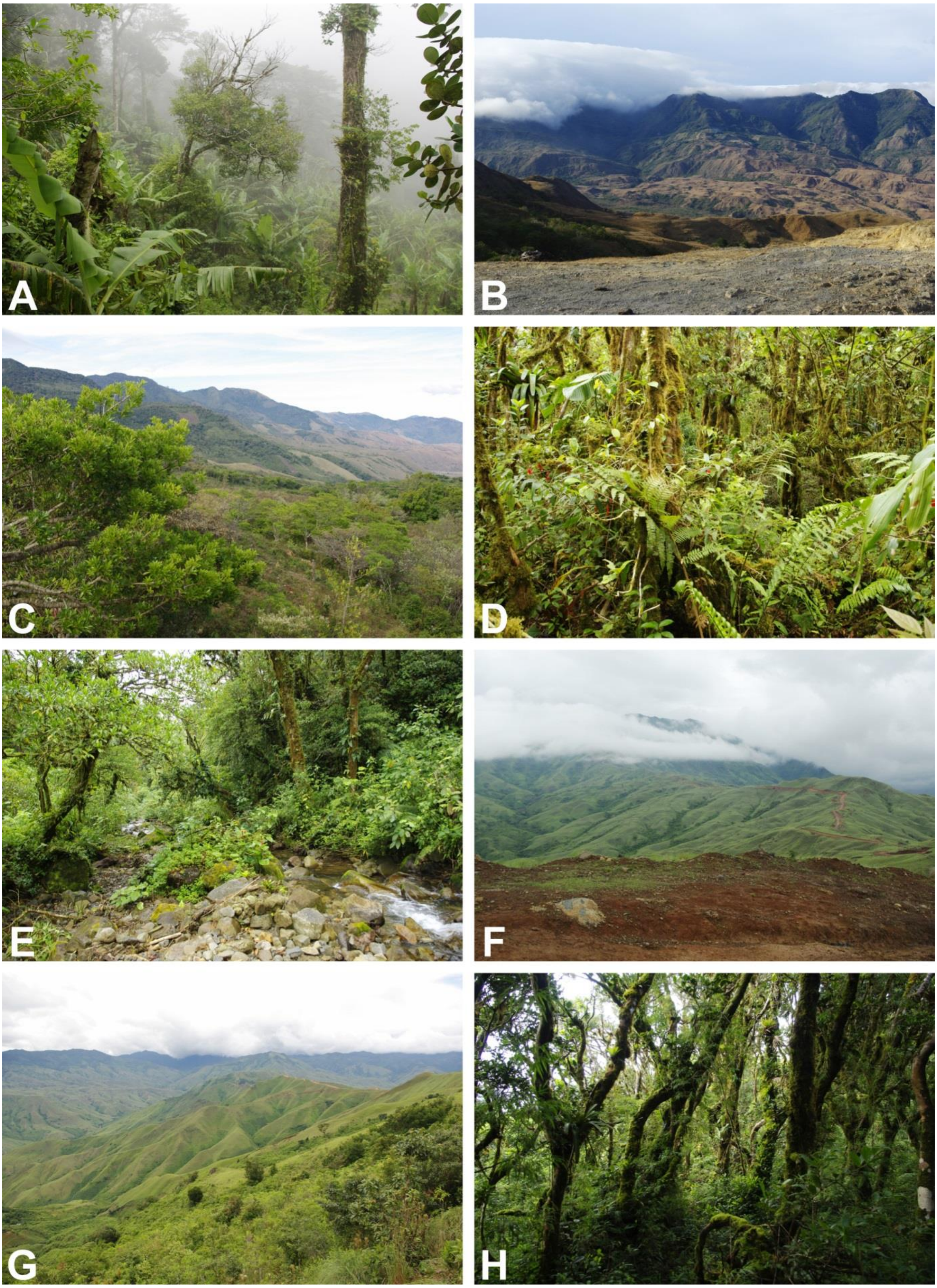


Figure 2.6: Representative environments in the Serranía de Tabasará. (A) mixed plantation along road to Cerro Colorado above Hato Chamí, WP 229, ca. 1480 m asl; (B–E) Buabidí and E slopes of Cerro Santiago: (B) view N towards Buabidí from E of Cerro Peña Blanca, around 1000 m asl; (C) view E from Buabidí at WP 140, 1241 m asl; (D) forest along trail to Río Rey near Quebrada Ardilla, between WPs 143 and 147, around 1530 m asl; (E) Río Rey close to continental divide at WP 147, 1546 m asl; (F–H) Alto Tólica and Guayabito: (F) view N along ridge and road leading to Alto and Cerro Tólica (hidden in clouds) from around 700 m asl; (G) view N towards Guayabito and continental divide from Paso Tólica at WP 234, 1317 m asl; (H) forest above Guayabito near WP 295, 1522 m asl. (A, C, D) modified from Lotzkat et al. (2012c), (E) from Lotzkat et al. (2014).

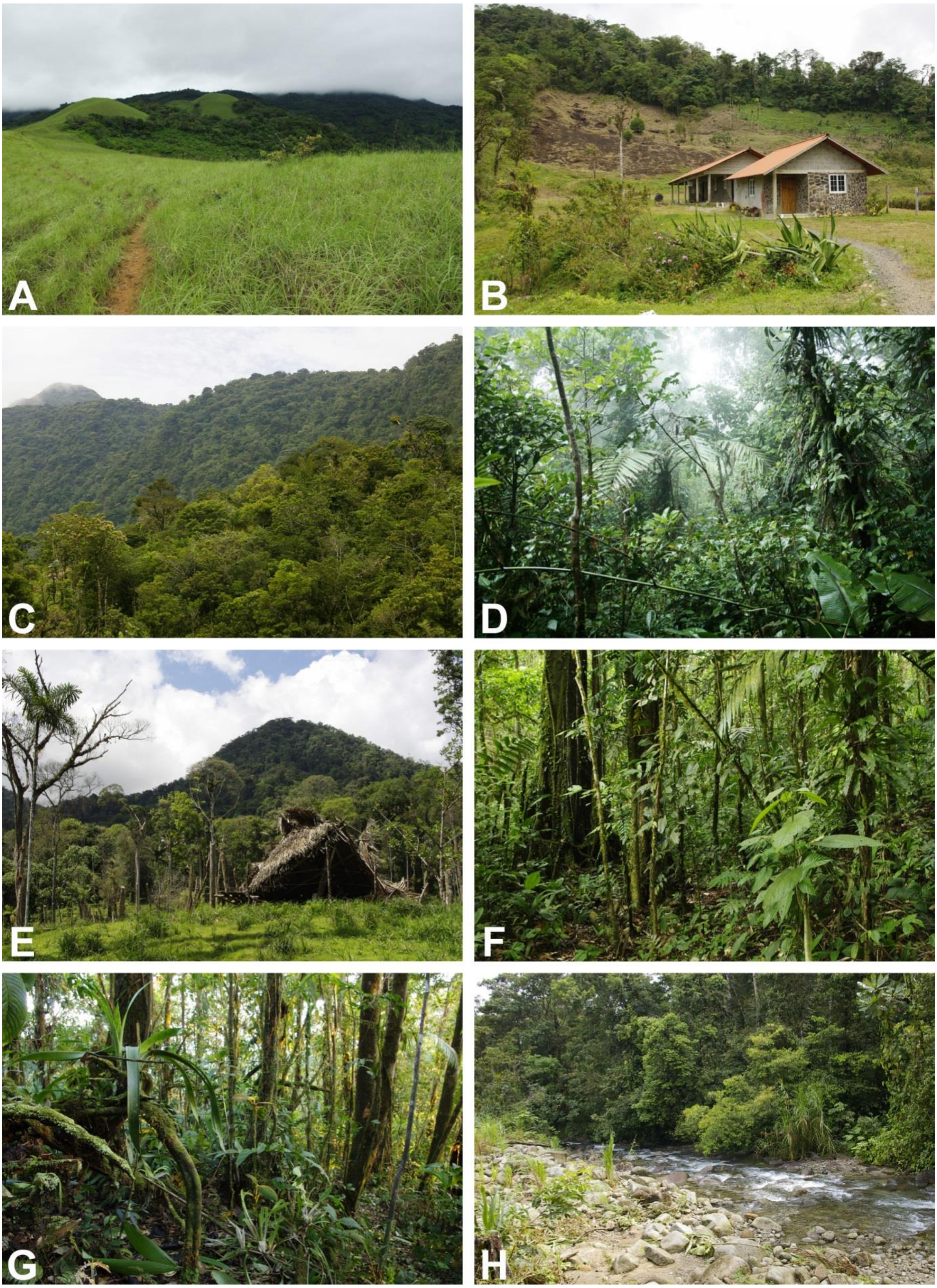


Figure 2.7: Representative environments in the Serranía de Tabasará. (A) Above El Paredón: view N towards valley of Río Rasca from around 600 m asl; (B–D) Cerro Mariposa: (B) forest edge behind restaurant at Alto de Piedra, WP 17, 867 m asl; (C) view S from WP 17 along ridge leading up Cerro Mariposa; (D) forest on Cerro Mariposa near WP 39, 1280 m asl; (E–G) Cerro Negro: (E) broken rancho on last clearing before camp at WP 94, 722 m asl; (F) forest next to camp at WP 95, 700 m asl; (G) forest on ridge above camp, near WP 153, around 1140 m asl; (H) Río Chilagres at WP 40, 476 m asl. (D) modified from Lotzkat et al. (2012c).

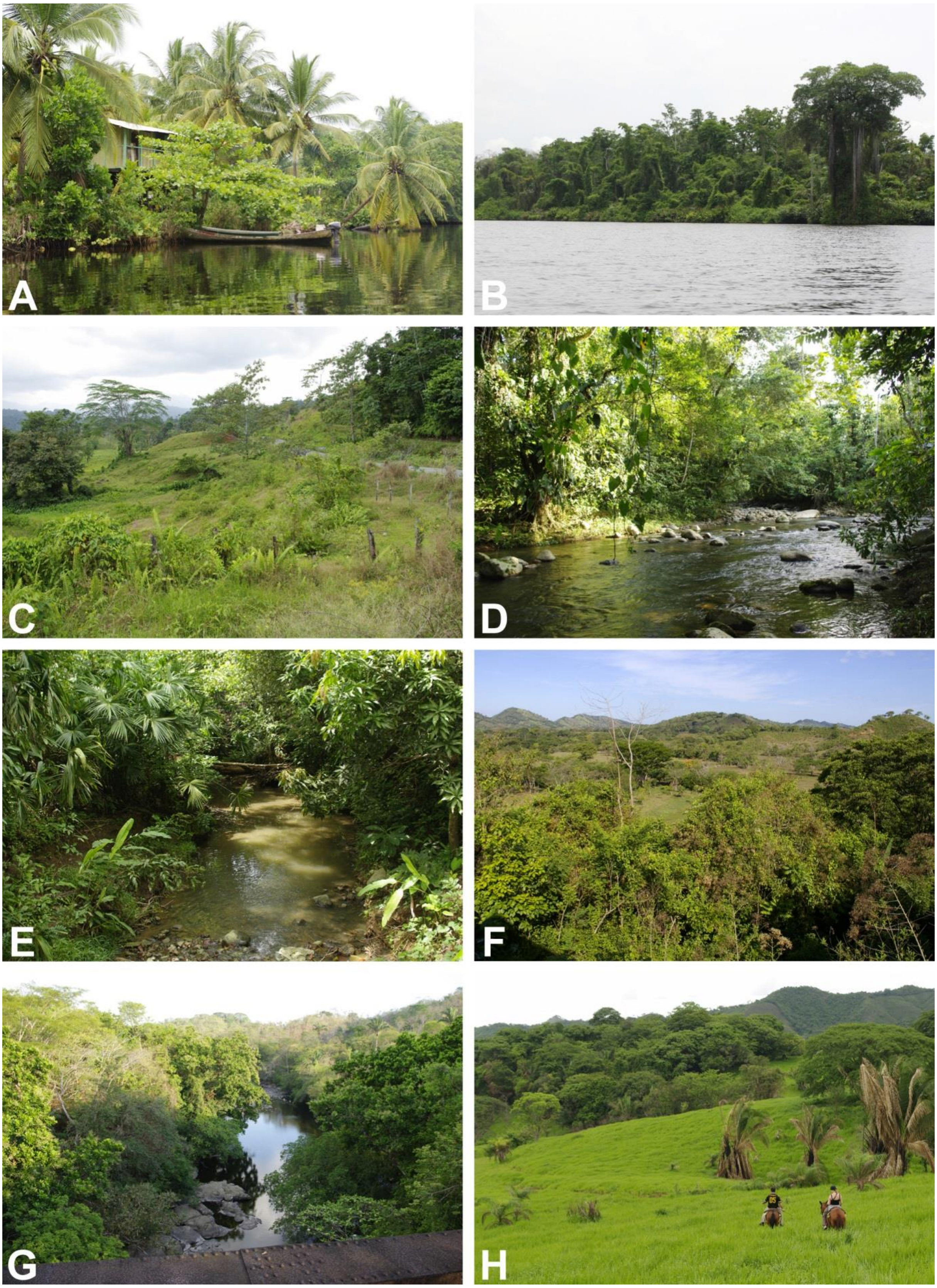


Figure 2.8: Representative environments in the lowlands. (A, B) San San Pond Sak: (A) coastal vegetation at Boca San San, WP 209, 1 m asl; (B) flooded Sangruillo forest at Río Negro near WP 213, 8 m asl; (C, D) road to Almirante: (C) shortly after km 23, branch to Palma Real and Punta Róbalo, WP 116, 46 m asl; (D) gallery forest of Río Miramar at km 13, WP 115, 23 m asl; (E) Peninsula Burica: creek near Tallón, between WPs 223 and 224, around 60 m asl; (F, G) Los Algarrobos: (F) view W over pasture and scrubland from Casa de la Alemana at WP 1, 141 m asl; (G) Río Majagua viewn from old railway bridge at WP 167, 88 m asl; (H) Finca La Providencia: pasture and forest patches near WP 218, around 60 m asl.

Table 2.1: Synopsis of the generalized research localities.

	generalized locality	WPs	elevation [m asl]	recorded temperature range [°C]	mean annual temperature [°C]	annual precipitation [mm]	recorded daily precipitation [mm]	Holdridge life zones	Köppen climates
1	Santa Clara	27; 174–178; 228	1088–1220	15.6–25.1	20.3–20.8	3273–3331	0–55.3	PMWF	Am
2	Hacienda Café de Eleta	29–31	1380–1437	no record	18.8–19.3	2810–2969	no record	PMWF	Am, Cw
3	Jurutungo	57–76; 79–86	1596–2464	9.6–18.2	13.5–18.1	2420–2618	0–63	PMWF, LMWF	Cf, Cw
4	Changena trail	77; 78; 179–181; 207; 270–282	1240–2447	11.1–20.2	13.6–19.2	2407–2730	0–0.4	PMWF, LMWF	Am, Cf, Cw
5	Volante	87–89	430–480	19.1–27.1	24.6	3304	no record	LWF	Am
6	Las Nubes	JFB 68–85	1963–2526	11.1–19.7	13.6–15.8	2295–2532	no record	LMWF	Cf
7	Sendero Los Quetzales	155–165; JFB 11–22	1688–2555	6.6–20.6	12.1–16.5	2208–2573	no record	LMWF	Cf, Cw
8	Sendero La Cascada	169–173	1585–1866	13.6–19.6	14.8–17.8	2225–2376	0.4–105.1	LMWF	Cf, Cw
9	Volcán Barú	195–204	1618–3475	4.6–13.6	7.9–17.9	2274–2799	no record	LMWF, MRF	Cf, Cw
10	Potrerillos Arriba	186–191	960–1422	14.1–28.1	18.7–22.0	2491–3302	no record	PMWF	Af, Am, Cw
11	Cabecera de Cochea	107–111	1090–1174	16.6–29.2	20.1–21.0	2747–3025	0	PMWF	Am
12	Cerro Altrillería	JFB 88–94	1930–2050	13.7–18.7	15.9	2266	no record	LMWF	Cf
13	Cerro Guayabo	JFB 27–56	1200–1785	17.2–24.7	18.0–20.4	2387–2927	no record	PMWF, LMWF	Af, Am, Cf
14	headwaters of Río Chiriquí Malí	193–194	1054–1090	17.6–22.6	20.6–21.2	3056–3333	2.2–44.5	PMWF	Af
15	Willie Mazú	250–255; 283–284	510–778	19.6–26.1	22.2–23.4	3449–3494	0–8.5	PMWF	Af
16	Lost & Found Ecohostel, Río Hornito, and Cerro Pata de Macho	22–26; 32; 47–56; 183; 215–16; 226; 227	1125–1876	13.7–24.6	16.8–20.3	2332–2906	0–75.5	PMWF, LMWF	Af, Am, Cf
17	Cerro Saguí	9–14; 257–269	1472–2033	13.2–23.1	16.2–20.0	2413–2744	0.4–2.7	PMWF, LMWF	Af, Cf
18	Hacha trail	256; 285–292	953–1393	15.1–21.1	19.2–21.2	2636–2899	7.6	PMWF	Af
19	La Nevera and W slopes of Cerro Santiago	6–8; 15; 16; 99–105; 205; 206; 229; 230	1431–1814	12.6–20.7	17.4–19.2	2477–2633	0–130.5	PMWF, LMWF	Af, Cf

Table 2.1: continued.

	generalized locality	WPs	elevation [m asl]	recorded temperature range [°C]	mean annual temperature [°C]	annual precipitation [mm]	recorded daily precipitation [mm]	Holdridge life zones	Köppen climates
20	Buabidí and E slopes of Cerro Santiago	139–149	1191–1718	14.1–20.2	17.7–20.3	2491–2737	0	PMWF, LMWF	Af, Cf
21	Alto Tólica and Guayabito	231–239; 293–295	396–1527	17.6–26.1	19.4–24.4	2560–2976	no record	LWF, PMWF	Af, Am
22	Los Valles and El Paredón	240–249	402–805	20.6–28.6	22.3–24.4	2554–2639	no record	LMF, PMMF	Am
23	Cerro Mariposa	17–19; 35–39; 192	855–1437	14.7–32.7	19.6–21.7	2434–2494	0–82.3	PMMF, PMWF	Am
24	Cerro Negro	90–97; 151–154	448–1163	16.1–24.6	20.6–24.5	2467–2620	0–30.6	LMF, PMMF, PMWF	Am
25	Río Chilagres	40–43	387–476	17.2–27.6	23.6–24.6	2623–2684	16.6–35.5	LMF, PMMF	Am
26	San San Pond Sak	208–214	1–24	21.2–32.1	26.2–26.4	2539–2574	no record	LMF	Af
27	road to Almirante	106; 114–126	17–85	no record	24.7–25.8	2785–3579	no record	LMF, LWF	Af
28	Peninsula Burica	220–225	2–74	no record	25.9–26.2	2470–2533	no record	LMF	Am
29	Los Algarrobos	1; 2; 45; 112; 167; 168; 182; 184; 185	67–162	21.2–31.7	26.1–26.4	2826–3010	0–56.7	LMF	Am
30	Finca La Providencia	217–218	41–56	no record	26.7–26.8	2993–3000	no record	LMF	Am

The following Figure 2.9 illustrates the climatic setting of selected research localities. While the annual climographs are based on the interpolated climate data of the WorldClim database (Hijmans et al. 2005; www.worldclim.org), the temperature curves represent values measured directly with iButtons. Likewise, the latter are attributed with the elevation recorded directly at the site of measuring, whereas the climographs bear the elevation of the corresponding grid cell in the WorldClim data, that is, the mean value of a square of approximately 0.81 km^2.

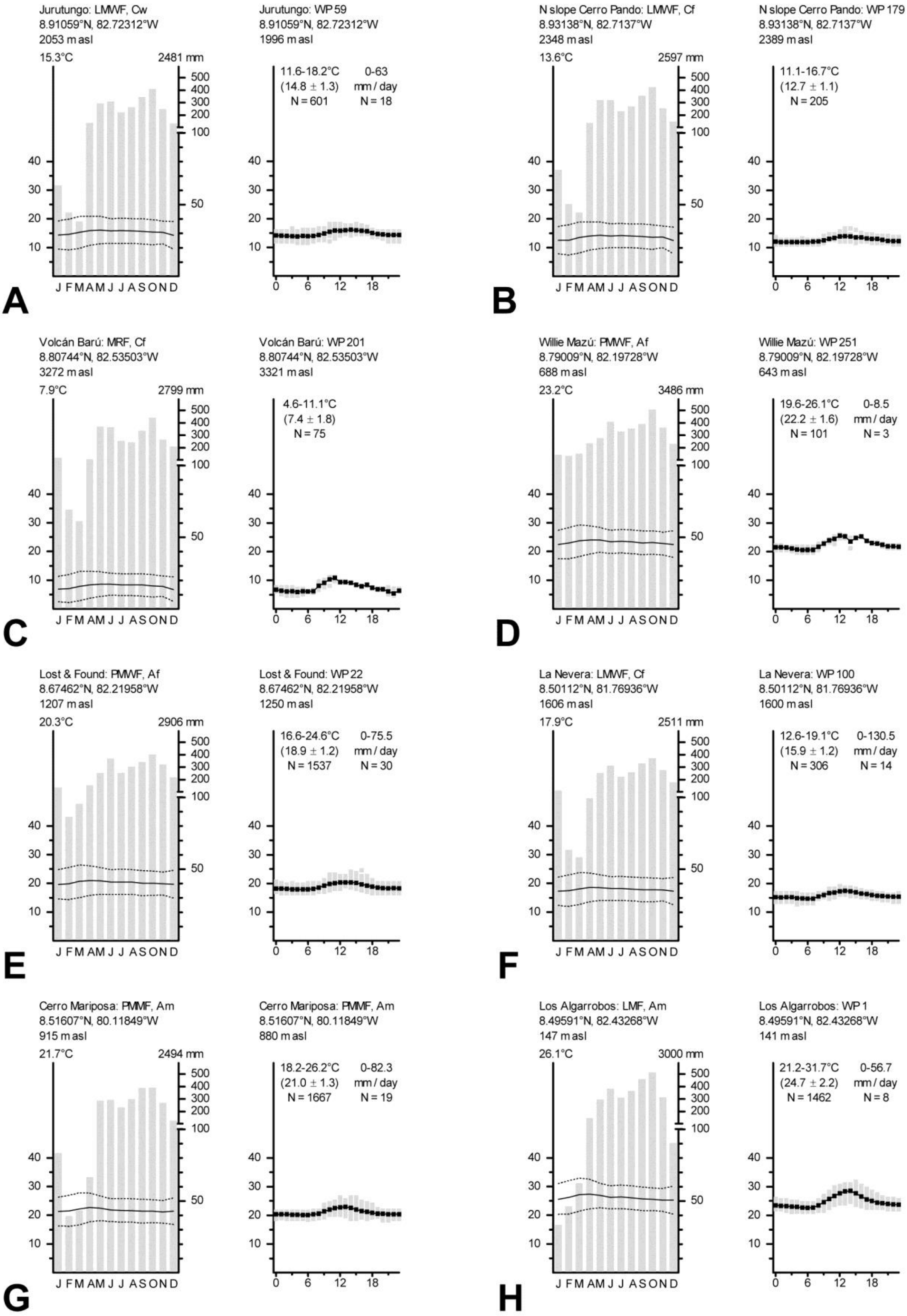


Figure 2.9: Climate of selected research localities. For each locality, a climograph derived from the WorldClim database (left) is accompanied by a graph of air temperature (right; mean values in black) recorded with iButtons at the specified waypoint for which the WorldClim data was extracted. Precipitation values per day recorded by AH are additionally given were applicable. (A) Jurutungo, finca at WP 59; (B) N slope Cerro Pando, camp at WP 179; (C) Volcán Barú, camping site Los Fogones, WP 201; (D) Willie Mazú, camp at WP 251; (E) Lost & Found Ecohostel, WP 22; (F) La Nevera, camp at WP 100; (G) Cerro Mariposa, WP 18; (H) Los Algarrobos, WP 1.

2.3 Research periods

Together with Andreas Hertz (AH), I realized four research trips to Panama between 2008 and 2010. During the first stay of almost four months from 06.05–30.08.2008, we were accompanied by the Diploma students NH and LS, each of whom elaborated a herpetofaunal inventory of a restricted area for their respective Diploma theses: NH explored the herpetofauna of the forests of La Fortuna surrounding the Lost & Found Ecohostel, while LS inventorized that of Cerro Mariposa near Alto de Piedra. At the beginning of this stay, we took a first explorative trip to different localities within the Cordillera Central by car in the company of GK. Throughout much of 2008 and 2009, the Master student AC sampled the herpetofauna of the area around Santa Fé de Veraguas as detailed in his thesis (Carrizo 2010), partially in the company of AH and myself. The second trip took place from 14.02.–29.04.2009 and included a joint expedition to the Serranía de Tabasará with AB and MP. Shortly before, targeted sampling of beta anoles of the *limifrons* complex was carried out along the road to Almirante in the company of JJK and RdL, who also spend one night on Cerro Pata de Macho with us. Later, RdL accompanied us at Santa Clara. During our third trip (17.09.–07.12.2009) we were in the company of the diploma students JFB and FH, who mostly realized independent collecting trips on their own. During this period, AH and myself were supported by the field assistants FO and AU. At San San Pond Sak, we were accompanied by RdL. The last period of field work occurred from 10.05.–18.08.2010, including some days spent with AC at Finca La Providencia, and a short trip together with MP to Guayabito. Table 2.2 provides a synopsis of the periods spent at the different generalized highland localities by myself and the accompanying colleagues and assistants. Other expeditions that have contributed material and data incorporated into this work are specified in chapter 3.1.4.

Table 2.2: Collecting time spent by myself and coworkers at the highland research localities per research trip.

	generalized locality	2008 1st trip 06.05–30.08.	2009 2nd trip 14.02.–29.04.	2009 3rd trip 17.09.–07.12.	2010 4th trip 10.05.–18.08.	total man-nights
1	Santa Clara		14.–16.04.: AH, RdL, SL	20.–22.10.: AH, AU, FH, FO, JFB, SL	17.–20.06.: AH, SL	24
2	Hacienda Café de Eleta	15.–17.05.: AH, GK, LS, NH, SL				10
3	Jurutungo	05.–18.07.: AH, SL	18.–19.04., 21.–23.04.: AH, SL	17.–18.11., 20.–22.11.: AH, AU, FO, SL	12.–13.07.: AH, SL	46
4	Changena trail		19.–21.04.: AH, SL	18.–19.11.: AH, AU, FO, SL 19.–20.11.: AH, SL	13.–18.07.: AH, SL	20
5	Volante	22.–24.07.: AH, SL				4

Table 2.2: continued.

	generalized locality	2008 1st trip 06.05–30.08.	2009 2nd trip 14.02.–29.04.	2009 3rd trip 17.09.–07.12.	2010 4th trip 10.05.–18.08.	total man-nights
6	Las Nubes			09.–13.11.: FH, JFB		8
7	Sendero Los Quetzales		06.–08.04.: AH, SL	19.–21.10.: FH, JFB		8
8	Sendero La Cascada		12.–13.04.: AH, SL	12.–14.10.: AH, AU, FH, FO, JFB, SL		14
9	Volcán Barú			04.–07.11.: AH, AU, FH, FO, JFB, SL		18
10	Potrerillos Arriba			14.–16.10.: AH, AU, FH, FO, JC, JFB, SL		14
11	Cabecera de Cochea		13.–15.03.: AH, SL			4
12	Cerro Altrillería			16.–18.11.: FH, JFB		4
13	Cerro Guayabo			25.–28.10.: FH, JFB		6
14	headwaters of Río Chiriquí Malí			28.–31.10.: AH, SL	09.–10.06., 11.–12.06., 10.–11.08.: AH, SL	12
15	Willie Mazú				01.–02.07., 22.–24.07.: AH, SL	6
16	Lost & Found Ecohostel, Río Hornito, and Cerro Pata de Macho	14.–15.05., 17–18.05.: AH, GK, LS, NH, SL 16.–28.06.: AH, LS, NH, SL 18.–27.07., 12.–21.08.: LS, NH	27.–29.02., 07.–11.03.: AH, SL 19.–20.03.: AH, JJK, RdL, SL	29.09.–06.10.: AU, FH, FO, JFB, SL	16.–20.05., 08.–09.06., 10.–11.06., 04.–05.07.: AH, SL	159
17	Cerro Saguí	10.–11.05.: AH, GK, LS, NH, SL			06.–09.07.: AH, SL	11
18	Hacha trail				25.–29.07.: AH, SL	8
19	La Nevera and W slopes of Cerro Santiago	09.–10.05., 11.–12.05.: AH, GK, LS, NH, SL 07.–19.08.: AH, SL		09.–14.11.: AH, AU, FO, SL	22.–23.06.: AH, SL	56
20	Buabidí and E slopes of Cerro Santiago		23.–26.03.: AB, AH, SL 24.–26.03.: MP			11
21	Alto Tólica and Guayabito				23.–25.06.: AH, SL 31.07.–03.08.: AH, MP, SL	10
22	Los Valles and El Paredón				25.–27.06.: AH, SL	4
23	Cerro Mariposa	12.–14.05.: AC, AH, GK, LS, NH, SL 27.–30.05.: AH, SL 27.05.–10.06., 04.–13.07., 01.–09.08.: LS, NH	04.–05.04.: AH, SL	24.–26.10.: AU, FO, SL	06.–08.08.: AH, SL	92
24	Cerro Negro	28.–31.07.: AC, AH, SL	31.03.–03.04.: AC, AH, SL			18
25	Río Chilagres	30.05.–01.06.: AC, AH, SL 01.–04.06.: AH, SL				12

3. Materials and methods

This section details the procedures untertaken to acquire (3.1–3.3) and process (3.4–3.6) the data underlying the results and discussion. I describe the sampling of reptile specimens in chapter 3.1, the extraction of taxonomically useful data from these specimens in chapter 3.2, and the acquisition of distribution records from different sources in chapter 3.3. I depict how taxonomic conclusions were reached under 3.4, how taxonomic and distribution data were integrated to assess reptile diversity under 3.5, and the methodology for cartography and biogeographical analyses under 3.6.

3.1 Field work

In this chapter, I describe all technical aspects of my field work: how specimens were encountered and secured (3.1.1), and the way they were documented and preserved (3.1.2), as well as the collection of environmental data around collection sites (3.1.3) and the contributions of other collectors (3.1.4). All field work realized by myself together with AH, and in many cases together with other accompanying workers, during the research periods specified in the preceding chapter 2.3 was legitimized by the Dirección de Áreas Protegidas y Vida Silvestre of the Autoridad Nacional del Ambiente (ANAM), Panama City, Panama, through the following collecting permits: SE/A-30-08, SC/A-8-09, SC/A-28-09, and SC/A-21-10. For the Comarca Ngöbe-Buglé, additional access and work permits were issued by Cacique General Rogelio Moreno (chief general of the Ngöbe), San Félix, and by Cacique Regional Angel Pitá for the districts Müna and Ñürün.

3.1.1 Sampling

At each of the research localities introduced in chapter 2.2, I tried to survey as much of available vegetation types and elevations for reptiles as the duration of the stay permitted. In some cases, paths spanning the desired elevational range had to be newly opened by AH and me. By far most of the sampling was conducted in the form of opportunistic searches without temporal or spatial constraints both at day- and nighttime. Since many diurnal species, like anole lizards or colubrid snakes, are easier to spot and catch at night, more than half of the searching was performed in the dark. Slowly walking along footpaths or streams, and often standing still for a minute or two, the surrounding habitat was visually scanned for present reptiles. I tried to distribute my attention equally among all strata of the surrounding environment, i.e., the ground and various height levels of the vegetation. Naturally, animals located above a certain distance from ground are less likely to be spotted, and usually I paid little attention to vegetation higher than 10 m. I made an effort to specifically search microhabitats known to be favorable for reptiles. Above ground, I focused on climbable vegetation features like branches, lianas, and leaves on which many species sleep at night, as well as rough or loose bark and epiphytic vegetation like mosses, liverworts, ferns, and bromeliads that could serve as perching or hiding places. Near the ground level, I turned over logs, rocks, leaves, and other debris to uncover hidden animals. For these microhabitat searches, as well as for many other purposes, an extendable potato rake (Wolf Multistar ZMTS pole, with an iL-M3 head bearing three prongs on one side and a blade on the other) was extremely useful.

In 2008, arrays of pitfall traps were operated by AH and myself at Jurutungo, La Fortuna, and La Nevera, as well as by NH and LS at La Fortuna and Cerro Mariposa. These traps consisted of one central 10 l plastic bucket and three peripheral 10 or 7.5 l buckets connected to the central one by drift fences made of plastic sheets, 0.4–0.5 m in height, and in some cases flanked by funnel traps of wire mesh. The array was described in detail by Hamad (2009) and Stadler (2010). Since the few animals caught in these traps did not justify the time and effort required to install and operate them, they were only used once again, in 2010 at the Lost & Found Ecohostel.

Encountered reptiles were usually caught by hand. For venomous snakes, a telescopic snake hook (M&S Reptilien, Weigheim, Germany) was employed. In some cases, venomous or not yet identified snakes were immobilized on the ground by gently pressing them down with the extendable potato rake. The capture of many individuals spotted two or more meters above ground in the vegetation would not have been possible without bending or pulling the branch or liana on which the animal was located down with the potato rake until the animal could be reached by hand. In cases were the perch of the animal was too high to be bent into reach, a short but decisive pull with the rake would usually cause it to fall down into my hands. In very few cases, prolonged agitation of the perch was necessary. According to size, the captured individuals were placed in mesh bags of different sizes, or transparent plastic bags containing fresh leaves, that were tied to the backpack for transport. For large and venomous snakes I used closed fabric bags. Usually, the specimens were processed the next day.

3.1.2 Documentation and preservation

For every collected specimen and most observed reptiles, I noted the date and time as well as the place (geographic coordinates, elevation above sea level, see 3.1.2.1) of encounter. I further noted the habitat type were the encounter occurred as well as substrate, position, altitude above ground, and activity of the animal. Any peculiarity observed in an animal, such as broken or regenerated tails, wounds or scars, prominent ectoparasites or coloration features, were also noted. Detailed color descriptions (see 3.1.2.3) were recorded for selected individuals. Almost every collected and most observed reptiles were documented photographically (see 3.1.2.2).

3.1.2.1 Georeferencing

While in the field, I recorded geographic coordinates and altitude above sea level of 296 waypoints (see Appendix 1) using a Garmin etrex Summit GPS receiver with a barometric altimeter, or, in some cases, copying readings from the GPS units of AH, NH, and LS. At every study site, the first waypoint was set upon arrival at the working base, be it a house or a campsite. Whenever possible, the barometric altimeter was calibrated using known elevations (e.g., before departing to the field, or leaving camp) or the unit's autocalibration function when enough satellites were received. Within a research locality, waypoints were set along all trails and streams where sampling took place, usually at prominent spots that are somehow recognizable. The quality of signal and amount of satellites receivable at a given place in the steep relief and often dense forest also effected the exact ubication of some waypoints.

Not every reptile found or captured received a proper waypoint. Instead, animal encounters were attributed to the nearest waypoint. In many cases, the assigned waypoint was visible from the actual place of the encounter. In by far most cases, the airline distance between assigned waypoint and actual spot of encounter is less than 100 m, only in singular cases greater than 200 m, and in no case greater than 500 m. To account for the steepness of the terrain in many places, elevation was recorded separately for many encounters.

3.1.2.2 Photography

In 2008, I used a Pentax *ist DL, and since 2009 a Pentax K200D. Lenses used with both cameras were a smc Pentax DA 18–55 mm F3.5–5.6, a Pentax-F Zoom 70–200 mm, and a Tamron SP AF 90 mm F2.8 Di Macro lens. During sampling, the camera's built-in flash was used if necessary. During the photo sessions at the camp, I used two small Novoflex makroblitz as twin flashs, mounted on a Manfrotto 330B Macro Bracket Support. For habitat photos in forests, the camera was often mounted on a tripod.

Whenever possible, mainly depending on the animal's activity and weather conditions, I photographed a reptile specimen before catching it to document the position of the animal at the time of encounter, and in anole lizards also their coloration. I also frequently used the camera to document other aspects of animal encounters like elevation, temperature and air humidity, or into which bag a certain animal was placed. Before preserving or freeing the captured animals, they were photographed more extensively. Special attention was payed to photograph diagnostic features of the animal in question, like the cloacal region or undersides of hands and feet in many lizards. Most important in this regard was the dewlap of anoles, which was photographed in every individual captured. To extend dewlaps, I utilized the standard forceps of genuine Swiss Army Knives since their broad, flat apex prevents even thin-skinned dewlaps from damage and functions as an approximate scale (width = 3 mm in the models of both suppliers).

3.1.2.3 Color descriptions

Standardized descriptions of the coloration in life were recorded for at least one specimen of most collected species using the Naturalist's Color Guide (Smithe 1975–1981), usually between photographing and preserving a specimen. Securing the animal in one hand and the color guide in the other or on my lap, I held the pattern element in question next to the similarly colored color swatches of the guide until a swatch matched the color in question. Intermediate colors were expressed as "color x with a suggestion of color y." The color descriptions are given in the respective species accounts in telegraphic style, with the singular statements separated by semicolons, and all capitalized color names and corresponding color codes (the latter in parentheses) being those of Smithe (1975–1981).

In species capable of pronounced metachrosis, like anoles, a color description can only be a snapshot of a momentary state. In order not to describe different elements of their coloration at different stages of metachrosis, I first recorded the pattern elements, leaving blank spaces for the colors. When this was done, the anole in my hand had usually become accustomed to being held in my hand and reached a rather stable coloration state. Since this procedure appeared to cause less stress in the handled specimens, I followed it in all color descriptions after the first weeks of field work. Specimens of which I recorded color descriptions were photographed from all sides to complement the written description.

3.1.2.4 Euthanasia and preservation

Specimens were euthanized by the pericardian injection of T61 (Intervet International, Unterschleißheim, Germany). In 2009 and 2010, most collected specimens were weighed using Pesola scales. Immediately after euthanasia, relative hind limb length was determined in anoles by recording the point reached by the tip of the fourth toe when the extended hind limb was adpressed along the straightened specimen. Tissue samples of selected individuals were cut before they came in contact with formalin, from the left hand or preferably regenerated tails in lizards, or from the edges of ventrals and first dorsal rows on the posterior half of body in snakes, and stored in 98% non-denatured ethanol. Whenever possible, the hemipenes of male specimens were everted by injecting 70% ethanol into the hemipenial pockets after manually pre-everting the hemipenes. Specimens were then preserved by injecting a solution of 5–10 mL absolute (i.e., 36%) formalin in 1 L of 96% ethanol into the body cavity and thighs, preferably also sprinkling everted hemipenes and extended dewlaps with this solution. In lizards, all injections were applied through the cloacal opening, with the exception of large-bodied individuals that also received injections into their forelimbs. In snakes, beginning at the cloacal opening, subsequent injections were applied roughly every 10 cm anterior to the preceding one. Thus preserved specimens received a field number that was tied to the anterior third of the body in snakes, to the left hind limb just above the knee in lizards, or around the body just above the waist in very small or smooth-scaled lizards. Last, specimens were stored in 70% ethanol.

3.1.3 Additional data collection

Apart from the data directly associated with the collected specimens (compare 3.1.2), I recorded environmental variables at certain places whenever AH and myself stayed at least one night at a given place. Equivalent data were also obtained by JFB, NH, FH, and LSt (see 3.1.4).

To obtain air temperature values, we employed the iButton dataloggers Thermochron (DS1922L-F5) and Hygrochron (DS1923-F5; all produced by Dallas Semiconductor, Corp., a wholly owned subsidiary of Maxim Integrated Products, Inc.), connected to the computer via the DS9094B USB adapter and programmed with the 1-Wire Drivers software (with 1-Wire Viewer; available at http://www.maxim-ic.com/products/ibutton/software/resources.cfm) to record values at intervals of one hour. These dataloggers, firmly clipped onto so-called iButton fobs (DS9093A-G) to which I had attached robust strings, were tightly knotted to trees or lianas approximately two meters above ground in shaded places. Many datalogger positions at several localities were reemployed during repeated visits in different years. Five Hygrochron iButtons also allowed for the recording of relative air humidity (RH). However, the high rainfall and air humidity often lead to a saturation of the air with water, that is, condensation of water vapor and fog formation. As a result, the membrane through which RH is measured by the Hygrochron was covered by a drop of water most of the time at most places, leading to constant recordings of values above 100% RH over prolonged periods of time, and thus rendering the RH datasets worthless. The datasets obtained from the iButtons, processed in Microsoft Excel and visually displayed with GraphPad Prism, are incorporated in the descriptions of the generalized research localities in chapter 2.2, as well as in the natural history sections of some species accounts (chapter 4.2.2). Additionally, AH measured precipitation in mm/day at several localities where we stayed for more than one night using a Conrad Electronics KW-9015 rain gauge. These data are included in the descriptions of some generalized research localities in chapter 2.2. On a few occasions, air temperature and RH were directly recorded at the time and place of encountering certain specimens using a Voltcraft HT-200 Thermo-/Hygrometer.

3.1.4 Contributing works

As stated in chapters 2 and 3.1.3, I did not personally collect all specimens that I have examined, nor all environmental data presented herein. Instead, I add to the 664 specimens tagged with my own field numbers (SL 113–776) the collections made by several colleagues in western Panama, partly under my supervision and tutelage, as depicted in the following.

Many specimens examined for the present study have been collected by expeditions lead between 2006 and 2011 by Gunther Köhler (GK) and involving different colleagues, especially AB, AC, MP, JS, and JV. These specimens usually have GK field numbers and are housed in the collections of SMF and MHCH. Since their graduations around the turn of the millenium, AB and MP have accumulated the bulk of the collection at MHCH. Some of these specimens have been donated to SMF, in which case their MHCH collection numbers assume the role of field numbers. Specimens labelled with JS field numbers were collected in the course of Javier Sunyer's PhD field work in Nicaragua and will be deposited at SMF.

Four German diploma students have been collecting reptiles in Panama with me and also recorded environmental data that is used herein during their respective field work. In 2008, Nadim Hamad and Leonhard Stadler repeatedly visited their respective study areas together. NH realized a herpetofaunal inventory in the vicinities of the Lost & Found Ecohostel, where he preserved 26 reptile specimens (with field numbers ranging between NH 001–048), while

LSt inventorized the herpetofauna of Cerro Mariposa, assembling a sample of 50 individuals (with field numbers ranging from LSt 001–125). In 2009, Joe-Felix Bienentreu and Frank Hauenschild conducted targeted collecting of members of the *Norops pachypus* (JFB) and *Diasporus diastema* (FH) complexes, respectively, to obtain material for their respective Diploma theses concerned with the phylogeography of these groups (Bienentreu 2011; Hauenschild 2011). During the trips realized autonomously by these two students and involving some sites never visited by AH and myself (see chapters 2.2. and 2.3), JFB also collected members of other reptile taxa which he encountered. His collection comprises 80 specimens (field numbers JFB 001–080).

During 2008 and 2009, Arcadio Carrizo visited different localities around Santa Fé in the course of his Master thesis (Carrizo 2010). During his stay at Río Chilagres and two periods at Cerro Negro, he was accompanied by AH and myself (see Tab. 2.2). The bulk of the material collected by AC has been integrated into the collection of SMF, including 49 squamate specimens with field numbers ranging between AC 014–221.

3.2 Laboratory work

The specimens collected by my contributing workers and myself were examined at the laboratories of the Senckenberg Research Institute Frankfurt, Germany. In order to determine their taxonomic identity, I analyzed two complementing aspects: external morphology (chapter 3.2.1) and molecular genetics (chapter 3.2.2).

3.2.1 External morphology

As characters of external morphology, I employed general aspects of coloration such as color and pattern recorded in the field and, if feasible, reassessed in the preserved specimen, as well as morphometrics (measurements and proportions) and pholidosis (scale counts and qualities). Whenever rendered necessary by the small size of the studied specimen or trait, characters were recorded with the aid of a dissecting microscope (Leica MZ 12). Sketches to aid counting and line drawings were made using a camera lucida attachment for this dissecting microscope.

Table 3.1 summarizes the mensural characters recorded in lizards and snakes, and the way they were obtained. Snout-vent length and tail length measurements were taken to the nearest mm along a meter stick, other measurements to the nearest 0.1 mm with precision calipers.

Dimensions of scales, eyes, and ears were measured at the longest or widest points along the longitudinal (length) or perpendicular (width or height) axis of the body, respectively.

Table 3.1: Morphometric characters recorded in lizards and snakes.

Abbreviation	Character	definition
characters obtained from lizards and snakes:		
SVL	snout-vent length	from tip of snout to cloacal opening
TL	tail length	from cloacal opening to tip of tail incomplete: remaining TL+x regenerated: original part+regenerated part
HL	head length	Sauria: from tip of snout to anterior margin of ear opening Serpentes: from tip of snout to posterior edge of mandibular bone
HW	head width	at broadest point; usually equal to the distance between oral ricti
SnL	snout length	from tip of snout to anterior border of orbit
characters obtained from lizards only:		
horDT	horizontal diameter of tail	measured at the point reached by the heel of the extended hind leg
verDT	vertical diameter of tail	measured at the point reached by the heel of the extended hind leg
shank	shank length	from tip of bent knee to base of bent heel
FL	femur length	from midline of body to tip of knee when femur held perpendicular to body
AGD	axilla-groin distance	from posterior insertion of forelimb to anterior insertion of hind limb
PCL	postcloacal length	length of largest enlarged postcloacal scale
PCW	postcloacal width	width of largest enlarged postcloacal scale
horDear	horizontal diameter of ear	measured on external ear opening
verDear	vertical diameter of ear	measured on external ear opening
IPL	interparietal length	length of interparietal plate
IPW	interparietal width	width of interparietal plate

Characters derived from these direct measurements are total length (TOL = SVL + TL) and various proportions, especially "relative" lengths obtained through division of any measurement by SVL (except relative tail length in snakes, for which I use the traditionally employed TL/TOL).

Concerning scalation, I recorded a number of scale counts as meristic, and scale shape and surface structure as qualitative characters. Scale nomenclature largely follows Köhler (2008) and Savage (2002), as well as Avila-Pires (1995) for Gekkota, Harris (1994) for Teiformata, Köhler & Sunyer (2008) and Köhler et al. (2007; 2012b) for anoles, and Savage et al. (2008) for Anguimorpha. General abbreviations for scales and scale groups not separately defined in the following tables are D (dorsals), L (laterals) V (ventrals), PC (enlarged postcloacal scales), PP (precloacal plate), IP (interparietal plate), SS (supraorbital semicircles), SBO (suboculars), SPO (supraorbitals), SPL (supralabials), INL (infralabials), SBL (sublabials, the scales ventrally bordering the INL), PM (postmentals), PR (postrostrals), and IN (internasals). Table 3.2 specifies the pholidotic characters I recorded from the different lizard groups.

Table 3.2: Pholidotic characters recorded in lizards.

Abbreviation	**Character**	**definition**
meristic characters of head scalation:		
loreal rows	horizontal loreal scale rows	Iguania: maximum number of horizontal rows, each comprising at least two loreal scales
loreals	total number of loreal scales	Iguania: all scales between canthals, SPL, and anterior extension of SO row; including adjacent scales posteriorly to below level of center of eye if SO and SPL not in contact
		Teiformata, Scinciformata, Gekkota: minimum number of scales between postnasal and orbit or preocular
SBO/SPL	scales between SBO and SPL	minimum number of scale rows separating suboculars from supralabials
SPL	supralabials	number of supralabial scales to level below center of eye
INL	infralabials	number of infralabial scales to level below center of eye
IO	interorbitals	Dactyloidae: minimum number of scales separating SS
		others: minimum number of scales separating SPO
IP/SS	scales between IP and SS	Dactyloidae: minimum number of scales separating IP from SS
		others: minimum number of scales separating IP from SPO
SBO	suboculars	continuous scale row bordering the orbit below
SPO	supraorbitals	Dactyloidae: number of enlarged (largest diameter at least twice the height of rostral scale) scales in supraorbital disc
		others: number of enlarged supraorbitals ("median supraoculars" of Savage et al. 2008, "supraoculars" of Harris 1994)
Canths enl.	enlarged canthals	Dactyloidae: number of enlarged posterior canthal scales
Canths	total canthals	total number of canthal scales
post Canths	scales between posterior canthals	Dactyloidae: minimum number of scales separating right and left posterior canthals
2nd Canths	scales between second canthals	Dactyloidae: minimum number of scales separating right and left second (i.e., directly anterior to posterior) canthals
PM	postmentals	number of scales bordering the mental plate posteriorly (excluding INL)
PR	postrostrals	number of scales bordering the rostral plate posteriorly (excluding SPL)
IN	internasals	minimum number of scales separating right and left nasals (excluding upper or circumnasals in Dactyloids)
FN	frontonasals	Anguimorpha, Teiformata, Scinciformata: scales between rostral and prefrontal (synonymous with IN)
PF	prefrontals	Anguimorpha, Teiformata, Scinciformata: number of scale(s) directly anterior to frontal plate
FP	frontoparietals	Anguimorpha, Teiformata, Scinciformata: number of scale(s) posterior to frontal and anterior to parietals and IP
Par	parietals	Anguimorpha, Teiformata, Scinciformata: number of scales laterally bordering the IP
Occ	occipitals	Anguimorpha, Teiformata, Scinciformata: number of enlarged scales bordering the parietals and IP posteriorly (first postparietals of Harris 1994)

Table 3.2: continued.

Abbreviation	Character	definition
meristic characters of body scalation:		
DHL	dorsals in one head length	number of middorsal scales at midbody counted longitudinally along one-half HL and doubled
VHL	ventrals in one head length	number of midventral scales at midbody counted longitudinally along one-half HL and doubled
Drows	enlarged dorsal rows	number of enlarged longitudinal rows of middorsal scales at midbody
DAG	dorsals between axilla and groin	number of middorsal scales between axilla and groin; counted longitudinally between two threads looped around axillae just posterior to forelimbs and around groin just anterior to hind limbs, respectively
VAG	ventrals between axilla and groin	number of midventral scales between axilla and groin; counted like DAG
SAM	scales around midbody	number of longitudinal scale rows around midbody; if feasible, counted on right side from midventer to middorsum and doubled
4toe	subdigital scales or lamellae under fourth toe	counted from base of digit to claw
4toepad	subdigital lamellae under phalanges ii-iv of fourth toe	Dactyloidae: counted from base of digit to distal end of dilated pad
4toedist	subdigital scales or lamellae under distal phalanx of fourth toe	Dactyloidae: counted from the scale or lamella distally adjacent to the end of the dilated pad to claw
4finger	subdigital scales or lamellae under fourth finger	counted from base of digit to claw
4fingerpad	subdigital lamellae under phalanges ii-iv of fourth finger	Dactyloidae: counted from base of digit to distal end of dilated pad
4fingerdist	subdigital scales or lamellae under distal phalanx of fourth finger	Dactyloidae: counted from the scale or lamella distally adjacent to the end of the dilated pad to claw
gulars	gular rows	Teiformata: number of transverse rows of gular scales between ear-to-ear gular crease and collar, including the latter
PPmar	precloacal plate marginals	Teiformata: number of scales of the precloacal plate bordering vent = posterior transverse row of scales within the precloacal plate
PPant	precloacal plate anterior row	Teiformata: number of scales of the precloacal plate anterior to marginals = anterior transverse row of scales within the precloacal plate
qualitative characters of body scalation:		
C, G, R, H	scale shape	C = cycloid G = granular R = rectangular H = hexagonal
s, k, (k), r, str, wr	scale surface state	s = smooth k = keeled; (k) = slightly keeled r = rugose str = striate wr = wrinkled

In lizards, bilaterally symmetrical characters such as lateral head scalation or toe lamellae were usually only counted on the right side. In snakes, the lateral head scalation was recorded for both sides. When variation in the bilateral symmetry of scale characters is present, they are given separated by a slash (right side/left side). Table 3.3 summarizes the pholidotic characters recorded in the different groups of snakes and how they were taken.

Table 3.3: Pholidotic characters recorded in snakes.

Abbreviation	Character	definition
meristic characters of head scalation:		
Preoc	preoculars	Caenophidia except Viperidae: scale(s) bordering the orbit anteriorly and in contact with either the supraocular or the supralabials or both, but never with the nasal
loreals	loreals	Caenophidia except Viperidae: scale(s) bordering the nasal posteriorly and in contact with prefrontal and SPL, as well as with preocular(s) or orbit
Postoc	postoculars	Caenophidia except Viperidae: scale(s) bordering the orbit posteriorly and in contact with either the supraocular or the supralabials or both
Tant	anterior temporals	Caenophidia except Viperidae: scale(s) bordering the postoculars posteriorly and in contact with either the parietal or the supralabials or both
Tpost	posterior temporals	Caenophidia except Viperidae: scale(s) bordering the anterior temporals posteriorly (or separated from orbit or postoculars by parietal-supralabial-contact) and in contact with either the parietal or the supralabials or both
SPL	supralabials	total number of supralabial scales
SPL eye	supralabials contacting eye	number of supralabial scales bordering orbit which of the consecutively numbered (starting anteriorly) SPL(s) are in contact was also noted
INL	infralabials	total number of infralabial scales
Canths	total canthals	Viperidae: number of enlarged canthal scales, not counting postrostrals or preoculars that may co-form the canthus
SF	subfoveals	Viperidae: minimum number of scales separating lacunal(s) from SPL
ISO	intersupraoculars	Boidae and Viperidae: minimum number of scales separating right and left supraoculars
IRI	interrictals	Boidae and Viperidae: minimum number of scales separating right and left oral ricti
CO	circumorbitals	Boidae and Viperidae: number of scales bordering orbit, including supraocular(s)
SBO/SPL	interoculabials	Boidae and Viperidae: minimum number of scale rows separating suboculars (first circumorbital ring) from supralabials
meristic characters of body scalation:		
V	ventrals	from the anteriormost scale bordered on both sides by the first dorsal row to the scale anterior to cloacal scute; not counting partial ventrals
SC	subcaudals	from the first subcaudal scale contacting its counterpart from the other side to the scale anterior to the tail spine
D-HH	dorsals anteriorly	number of longitudinal rows of dorsals one head length posterior to head
D-HH	dorsals at midbody	number of longitudinal rows of dorsals at midbody (halfway between head and cloaca)
D-HC	dorsals posteriorly	number of longitudinal rows of dorsals one head length anterior to cloaca

Table 3.3: continued.

Abbreviation	Character	definition
qualitative characters of body scalation:		
e, d	cloacal scute	e = entire d = divided
s, k, (k), str	dorsal scale surface state	s = smooth k = keeled; (k) = slightly keeled str = striate

Additional observations, such as the presence and number of femoral and precloacal pores in lizards or apical pits (AP) in snakes, were noted separately if present. The terminology for hemipenial morphology follows Myers et al. (1993) and Savage (1997). Terminology for anole dewlap morphology follows that of Fitch & Hillis (1984) especially for scutellation, and Savage (2002) for dewlap size (very small = posterior extent well anterior to axilla; small = extending to front limb insertion; moderate = extending to slightly beyond front limb insertion; large = extending to one-fourth to one-half distance between axilla and groin).

I myself recorded the characters detailed above from 826 specimens (573 lizards + 253 snakes). Additional datasets were provided by JFB for 194 members of the *Norops pachypus* complex, by MG for some individuals related to *Norops kemptoni,* as well as by GK for several type and other examined specimens listed in recent species group revisions and species descriptions from Panama (Köhler 2007, 2010; Köhler et al. 2007, 2010b, 2012b). All these specimens were also examined by myself, but without recording the full set of characters. Including these, this holds for about 260 specimens in the collections of FMNH, MCZ, MHCH, MVUP, and SMF, chiefly from central and eastern or the lowlands of western Panama. Furthermore, I include in my examined specimens 450 individuals which I personally observed and most of which I photographed, but which I did not collect, as well as 105 specimens photographed in life by others. I list all specimens that I have examined in Appendix 2.

Data were entered and processed in Microsoft Excel. Throughout this work, summarized values are given as minimum–maximum, followed by mean ± standard deviation in parentheses for samples comprising three or more individuals. Selected datasets were analyzed and visualized with GraphPad Prism (univariate analyses and diagrams), Statistica (multivariate analyses and diagrams), and ArcGIS (mapping). All figures and maps were graphically enhanced using Adobe Photoshop, and if necessary layouted in Adobe InDesign.

3.2.2 DNA barcoding

To complement the morphological data in the study of selected groups, I employed two fragments of mitochondrial DNA that have become established in DNA barcoding efforts of herpetofauna worldwide: a part of the 16S rRNA gene (henceforth called 16S) and a portion of the gene coding for the cytochrome c oxidase subunit I (henceforth called COI).

For most 16S sequences, JFB and I performed DNA extraction and amplification in the Grunelius-Möllgaard Laboratory for Molecular Evolution of the Senckenberg Research Institute Frankfurt, partly with the help of AH and MG. We extracted DNA from small (1–3 mm^3) tissue pieces following the protocol of Ivanova et al. (2006). To eliminate potential PCR-inhibiting contaminants, the tissue samples were incubated for at least 10 hours in 200 µL low PBS buffer (20 µL PBS in 180µL of water) before overnight digestion with the vertebrate lysis buffer at 56°C. After extraction, DNA was eluted in 50 µL TE buffer. A fragment of the mitochondrial 16S rRNA gene was amplified in an Eppendorf Mastercycler® pro using the following program we had agreed upon after several test runs described in detail by Bienentreu (2011): initial denaturation for 2 min at 94°C; followed by 40 cycles with denaturation for 35 s at 94°C, hybridization for 35 s at 48.5°C, and elongation for 60 s at 72°C; final elongation for 10 min at 72°C. Reaction mix for each sample contained 1 µL DNA template, 14 µL water, 2.5 µL PCR-buffer x10, 1 µL 25 mM $MgCl_2$, 4 µL 2.5 mM dNTPs (Invitrogen), 0.5 µL (containing 2.5 units) Taq Polymerase (PeqLab), and 1 µL (containing 10 pmol) of each primer (forward: L2510, 5'-CGCCTGTTTATCAAAAACAT-3'; reverse: H3056, 5'-CCGGTCTGAACTCAGATCACGT-3'; eurofins MWG Operon). The PCR products were then sent to the laboratory center of the Biodiversität und Klima-Forschungszentrum (BiK-F) in Frankfurt for automated sequencing. The raw trace files of returned by the staff of BiK-F were manually checked and both strands assembled in Geneious (Drummond et al. 2010). This way, JFB and I generated a total of 160 16S barcodes.

Additional 16S barcodes obtained in a similar way were provided by AB for two specimens of *Lepidoblepharis*, by MG for 28 anoles related to *Norops kemptoni* (including 16 from Panama), and by JJK for 16 members of the *Norops limifrons* complex (including 13 from Panama). Two additional 16S as well as all COI sequences of specimens from the collections of MHCH and SMF were generated by colleagues working for the ColdCode project for barcoding amphibians and reptiles in the Kunming Institute of Zoology, China, to whom I had sent small tissue pieces of 349 specimens in 98% non-denatured ethanol. I later received a FASTA file with an alignment of the readily assembled sequences. Last, Luis Canseco provided me with sequence fragments of the mitochondrial cytochrome b gene (hereafter called cyt-b) for 15 members of the genus *Geophis*. Thus, all in all, at my disposition were sequence fragments for 300 squamate individuals from Panama and Costa Rica, including 16S barcodes for 207 and COI barcodes for 198 individuals (the total as well as the COI counts including one that could not unambiguously assigned to a certain specimen, see chapter 4.1.7.1). For 105 specimens, I had both 16S and COI barcodes. The availability of DNA barcodes is indicated in the list of examined specimens (Appendix 2). The few comparative sequences of either fragment downloaded from GenBank are mentioned in the results of the respective analyses. The individual 16S and COI sequence files not downloaded from GenBank were named with a four-lettered abbreviation of the species name (the first letter of the generic name and usually the first three letters of the epithet) and five digits for the individual's field number (JFB abbreviated to JF, LSt to LS, and GK to G) or collection number when no separate field number was known (MHCH abbreviated to M; SMF: five digits without preceding letter) and appear with these names in the trees in chapter 4.

Sequences were aligned with MUSCLE (Edgar 2004) using the default settings in Geneious. Alignments were manually checked and exported as NEXUS, PHYLIP, or MEGA files. Using MEGA5 (Tamura et al. 2011), I computed uncorrected pairwise genetic distances between individuals as well as within and between groups, identified the best-fitting substitution model using Akaike Information Criterion (corrected, AIC) and Bayesian Information Criterion (BIC), and conducted Maximum Likelihood (ML) analyses (with 1000 or, usually and if not otherwise mentioned, with 10000 bootstrap replicates). Abbreviations for substitution models are those used in MEGA5: GTR for General Time Reversible; HKY for Hasegawa-Kishino-Yano; TN93 for Tamura-Nei; T92 for Tamura 3-parameter; K2 for Kimura 2-parameter; +G for using a discrete Gamma distribution with 5 rate categories; +I for assuming that a certain fraction of sites are evolutionarily invariable. Using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003), I performed Bayesian inferences of phylogeny (BI) under the likelihood models determined in MEGA, in two parallel runs with four chains each, sampling trees every 1000 generations. If not indicated otherwise in the respective results section, BI analyses were run over $2x10^7$ generations, and the initial 25% (i.e., 5000 of the 20000 sampled trees) discarded as burn-in after assessing verifying the previous convergence of the parallel runs by visually checking the log file. If not specified otherwise, scale bars for trees refer to the number of substitutions per site. Using TCSv1.21 (Clement et al. 2000), I conducted statistical parsimony network (PN) analyses, with gaps considered as a fifth character state and a parsimony probability of 95% (Hart & Sunday 2007) that in most cases resulted in a connection limit of 9 or 10 steps. In some cases, I manually in- or decreased this connection limit in subsequent analyses to check for further connections or fragmentations. In these networks, each node represents a unique haplotype separated from the next by one substitutional step. Small circles represent unsampled haplotypes. Sequences differing only in missing or ambiguous characters were grouped in one haplotype.

3.3 Research in literature, databases, and catalogues

For a comprehensive summary of the status quo of knowledge on reptile diversity and distribution in the Cordillera Central, I performed a thorough revision of scientific books and journal articles, traceable theses and reports, as well as catalogues and databases of scientific collections to compile a comprehensive point dataset of georeferenced species occurrences.

Regarding primary literature, I examined all references mentioned in chapter 1.3, with the exception of gray literature that I was unable to obtain. In addition to this near complete set of published information from western Panama, updated to December 2013, I consulted some key publications for localities in central and eastern Panama, such as faunal lists and recent distribution extensions (Barbour 1906, 1923; Breder 1946; Cochran 1946; Evans 1947; Telford 1971; Jaramillo & Ibáñez 2003; Neal 2007; Sosa et al. 2012).

Concerning catalogues and databases, in November 2010 I obtained records from different institutions through a search for the keywords "reptil" and "Panama" in the HerpNET data portal (http://www.herpnet.org). Later, I obtained additional records through species-specific searches in the HerpNET portal (Lotzkat et al. 2012b; Bienentreu et al. 2013). I further consulted the handwritten reptile catalogue of the Museo de Vertebrados de la Universidad de Panama (MVUP), Panama City, Panama, after photographing all available pages on 16 August 2010. I directly searched the field catalogues of all expeditions to Panama by members of Senckenberg's herpetology department. I also downloaded the catalogue of the Círculo Herpetológico de Panamá (CHP; accessed on 11 October 2011 through the GBIF data portal, http://ara.inbio.ac.cr/SSTN-IABIN/datasets/resource/37). Last, GK provided me with partly georeferenced lists of the Panamanian reptile specimens that he had examined and identified during his respective visits at FMNH and MCZ in 2012.

I entered all records into separate Excel sheets – one each for every catalogue or database query, one for the remaining literature. The records from Breder (1946), Ibáñez et al. (1995; 1996; 1997), and Pérez-Santos (1999) were digitized by interns. Georeferencing was mainly done in DIVA-GIS (www.diva-gis.org) using the geographical datasets and procedures specified in chapter 3.6.1, whenever necessary with additional information obtained via

Google Earth (https://earth.google.de), from the internet, or the literature mentioned above. Table 3.4 sums up the georeferenced occurrences obtained from the different sources.

Table 3.4: Number of georeferenced records obtained from different sources. Preceding the slash are the total number of records from throughout Panama (or LCA where applicable), following the slash the number of records from Veraguas province and west of it. Datasets which I received as digital tables are marked with an asterisk (*).

Source	total records	records with given coordinates	records georeferenced myself	final total of georeferenced records
Pérez-Santos (1999)*	532/437	0/0	481/396	481/396
other literature	4613/2744	929/422	4069/2527	4499/2668
HerpNET search*	13276/2329	1522/75	2232/2232	2290/2290
MVUP catalogue	529/529	13/13	446/446	453/453
CHP catalogue*	1630/255	0/0	403/211	403/211
FMNH examined by GK*	1713/386	1242/386	564/277	1271/386
MCZ examined by GK*	3260/284	0/0	2851/249	2851/249
GK field notes 2006-2010*	408/389	406/387	57/56	408/389
GK field notes 2011*	152/128	148/124	4/4	152/128
Total	**26113/7481**	**4260/1407**	**11107/6398**	**12808/7170**

All georeferences, self-assigned or not, were checked visually in DIVA-GIS. Among the very numerous specimen records obtained from MVUP, SMF, and via HerpNET, I only georeferenced the records coming from within or west of Veraguas province. For the specimen records provided by Pérez-Santos (1999) and in the CHP catalogue, I further included the records from Coclé province. For many records, after georeferencing them I further corrected or complemented other associated information such as the pertinence to a certain province or blatant misspellings in place names. For records without specified elevation, approximate values were extracted as described in chapter 3.6.1. I updated the specific taxonomy to be consistent with the current status of knowledge, incorporating the results of published studies and my taxonomical conclusions presented in chapter 4.1. I checked all records species-wise for plausibility, making further adjustments to coordinates (e.g., records of an unmisidentifiable sea turtle 10 km inland from the coastline) or species names (e.g., records of exclusively montane species from elevations near sea level) where necessary. Whenever I judged the occurrence of a certain species at the stated and georeferenced locality highly improbable, I considered the possibility of a misidentification and replaced the specific epithet with "sp." (for example, I changed several *Norops polylepis* from the Caribbean foothills to *Norops* sp.). In the case of any correction, the original information was kept verbatim within a separate column. Extra columns were created for own comments on species or specimens, locality, and elevation.

According to the quality of taxonomic evidence, I classified each record as one of the following: The category "reported" accomodates all records not substantiated by any voucher specimen (as it is the case in most faunal lists), or merely cited specimens that are not explicitly stated to have been examined by the author(s) in a taxonomic context (such as all records of Pérez-Santos 1999), as well as all specimens from collection catalogues except primary types of valid species. Records in the category "specimen confirmed" are based on voucher specimens that have been examined and their identification confirmed by a scientific authority (such as material examined for taxonomic revisions or species descriptions, or the FMNH specimens examined by GK). The last category "specimen examined" was only assigned when the specimen underlying the record has been examined by myself (such as most SMF specimens from Panama), including photos of reliable provenance showing clearly identifiable species. Having in this way homogenized the occurrence datasets from different sources, I combined them into a single dataset for further analyses (provided in Appendix 6).

3.4 Taxonomy

This chapter elucidates the methodology employed for different aspects of taxonomy in this work: First, I outline the taxonomic arrangements applied in this study to the Panamanian reptile fauna at genus level and above (3.4.1), and from which sources I adopted them. Then, I explain how I used morphological and molecular data to address taxonomic problems and uncertainties at species level and draw my own taxonomic conclusions (3.4.2).

3.4.1 Higher level taxonomy

I am fully aware that the monophylum Reptilia includes the monophylum Aves, and that the exclusion of birds renders reptiles paraphyletic. Nevertheless, throughout this work I use the terms "reptile" and "Reptilia" in the traditional way, i.e., synonymous with non-avian reptiles. Since higher level phylogeny and taxonomy is far beyond the scope of this study, I adopted contemporary taxonomic arrangements at the genus level and above from a variety of sources. I am aware that the phylogeny of reptiles is not fully resolved yet, and thus subject to frequent changes just as the corresponding taxonomy, and explicitly refrain from attempting to reflect the most recent classification concepts, especially for squamates. Instead, I decided to take a road halfway between the conservative and progressive approaches, and to adopt recent alterations, especially at the family level, of the more "traditional" arrangement as it has been employed, among others, at least partly by Savage (2002), Köhler (2008), and Jaramillo et al.

(2010), whenever they reflect important evolutionary divergences so that the additional taxonomic complexity is compensated by the benefit of a clearer view on major aspects of the presumed phylogenetic reality. The taxonomic arrangement used herein is largely congruent with that of The Reptile Database (Uetz & Hošek 2014).

Within the subclass Anapsida and its only order Testudines, I follow the taxonomy of Rhodin et al. (2010). For the subclass Archosauria, order Crocodylia, I follow Man et al. (2011). In the subclass Lepidosauria, order Squamata, diversity is highest and systematics more complicated (see Pyron et al. 2013 for the most updated and broadly based concepts). Since adopting current views inevitably leads to an increase in family numbers, I adopted some higher level groups as proposed but not ranked by Vidal & Hedges (2009) to keep closely related families together in lists and the like. On The Reptile Database (Uetz & Hošek 2014), some of these taxa are ranked as suborders, some as infraorders, and others are unranked. For traditional reasons, I retain at suborder level the taxa Amphisbaenia, Serpentes, and "Sauria", although the latter is paraphyletic (expressed by the quotation marks) with respect to the other two, as repeatedly shown (see Pyron et al. 2013 and references therein).

Within the suborder "Sauria", I recognize at the infraorder level the monophyletic taxa Anguimorpha (family in Panama: Anguidae), Gekkota (families in Panama: Eublepharidae, Gekkonidae, Phyllodactylidae, and Sphaerodactylidae following Gamble et al. 2008a, b), Iguania (families in Panama: Corytophanidae, Dactyloidae, Hoplocercidae, Iguanidae, Phrynosomatidae, and Polychrotidae following Townsend et al. 2011), Scinciformata (families in Panama: Mabuyidae, Sphenomorphidae, and Xantusiidae following Hedges & Conn 2012), and Teiformata (families Teiidae and Gymnophthalmidae). For generic taxonomy within Scinciformata I follow Hedges & Conn (2012) for Mabuyidae and Linkem et al. (2011) for Sphenomorphidae. For generic taxonomy of Dactyloidae (anoles), I follow Nicholson et al. (2012). Within the suborder Serpentes, I recognize as infraorders "Scolecophidia" (families in Panama: Anomalepididae and Leptotyphlopidae), "Macrostomata" (families in Panama: Boidae and Tropidophiidae following Wiens et al. 2012), and Caenophidia, although each of the former two is paraphyletic with regard to the following (e.g., Wiens et al. 2012; Pyron et al. 2013). For caenophidian families I follow Zaher et al. (2009) in recognizing Colubridae, Dipsadidae, Elapidae, and Viperidae.

3.4.2 Species concept and delineation

In evaluating species boundaries within the populations of reptiles found in western Panama, I follow the unified species concept (de Queiroz 2005a, b, 2007). As lines of evidence for species delimitation, I apply phenotypic criteria (external morphology: coloration, morphometrics, and pholidosis) that include species recognition traits at least in the case of one of my target groups (Dactyloidae: dewlap size and coloration), and a criterion for reproductive isolation (genetic distinctness of the 16S and COI genes) where possible. For the taxa for which I lack DNA barcodes, I rely entirely on external morphology. In this case, I recognize populations as separate evolutionary lineages at species level if they exhibit consistent, preferably non-overlapping morphological differences to other populations, based on the assumption that these differences reflect divergent evolutionary histories (Frost & Kluge 1994).

In integrating molecular and morphological results, I roughly follow the approaches of Vieites et al. (2009) and Jansen et al. (2011). However, since data on genetic divergence of the 16S or COI barcodes is unavailable for most reptile species of Panama, I refrain from pre-defining thresholds of genetic distance to qualify lineages for classification. Instead, I identify the smallest diagnosable terminal clusters recovered with strong bootstrap supports of at least 70% in the ML analyses, or posterior probabilities >0.9 in the BI analyses, and use these terminal clades as a starting point. Next, I integrate molecular (BI, ML, PN) and morphological (morphometrics, pholidosis, and coloration) evidence to classify these lineages adopting the terminology of Jansen et al. (2011). A lineage is classified as a confirmed genealogical lineage (CGL) when it is supported by molecular (i.e., not only recovered in BI, ML, and MP analyses, but also forming an independent haplotype network in PN analysis at a connection limit that leaves well-defined species in the same alignment isolated from each other in independent networks) as well as morphological (i.e., showing consistent, preferably non-overlapping differences to the other lineages) evidence. The classification as a deep conspecific lineage (DCL) is applied to a lineage that lacks either molecular (i.e., not recovered in BI or ML analyses, or its haplotype network connected to that of other lineages at a connection limit that leaves well-defined species in the same alignment isolated from each other in independent networks in PN analysis) or morphological (i.e., lacking consistent differences to the other lineages) distinctness, or both. Third, I classify as an unconfirmed genealogical lineage (UGL) any lineage for which the analyses of available DNA barcodes indicate a profound genealogical divergence from other lineages that would qualify for recognition as a CGL, but morphological data was unavailable to me or, as it is mostly the case, was not analyzed in the framework of this study for whatever reason. Since no 16S and only very few COI sequences of Panamanian reptiles were available for comparison at the when I conducted these analyses, the identified lineages were assigned to nominal species according to morphology.

3.5 Diversity

In this section, I detail how I ascertained the total species richness of my study area (3.5.1) and outline the structure of the species accounts that also include other aspects of diversity (3.5.2).

3.5.1 The reptile fauna of the Cordillera Central

Species richness is one fundamental measure of biodiversity, and the one that I most focus on herein. To assess how many and which species occur within the study area, I combined the georeferenced datasets of my examined specimens (1717 georeferenced records from Panama, including 1610 from Veraguas province and west of it, plus 58 from Nicaragua and Costa Rica) with the combined dataset resulting from my research in literature, databases, and catalogues (12801 georeferenced records from Panama, including 7170 from Veraguas province and west of it, plus 7 from Nicaragua and Costa Rica) as well as three much smaller datasets that had been generated as a basis for four publications which are incorporated in this work (Bienentreu et al. 2013; Lotzkat et al. 2012a, b, 2013). With 14620 georeferenced records (including 8795 Panamanian records from Veraguas province and west of it), the resulting "all-inclusive" dataset encompasses all distributional information available to me for reptiles in western Panama and is updated to December 2013. As a knowledge base for the general distribution of reptiles I relied on Savage (2002) and Köhler (2008) for Lower Central America, on Sasa et al. (2010) for Costa Rica, and on Jaramillo et al. (2010) for Panama.

For each species in the dataset, I first checked for records from within the study area that would immediately classify a species as "documented" (appearing as "X" in tables). If a species had not been recorded from within the study area, I evaluated the probability of its presence. I regard the occurrence of a species within my study area as "plausible" ("(x)" in tables) if it has been recorded at a location less than 5 km from, and its documented altitudinal distribution suggests that it can occur at the predominantly premontane elevations of, my study area. The same holds for species that have been recorded at appropriate elevations both west and east of my study area along the course of the Lower Central American Highlands. I regard the occurrence of a species within my study area as "possible" ("x?" in tables) if the above mentioned criteria do not apply, but its known distribution strongly suggests that it could well range into my study area (e.g., species that have been found at PNGDOTH, or wide-ranging lowland species known to occur at premontane elevations elsewhere). In contrast, I regard a species as "absent" from my study area if my combined data suggest at least one of the following: (a) the quality of evidence for an existing record is very meager (e.g., a mere mention in an unpublished thesis or report, without any information on why a given observation or specimen was attributed to the listed species); (b) the taxonomic identity of an existing record is to be regarded erroneous according to current knowledge; (c) current knowledge on the species' horizontal and vertical distribution does not suggest an occurrence in my study area.

3.5.2 Species accounts

For all species which I regard as present in my study area (i.e., those of documented or plausible occurrence), I compiled species accounts that are largely standardized. However, their individual content and length somewhat reflect the amount of own experience that I have with the respective species. Thus, the accounts of certain species for which I have generated extensive data or provide important novelties are more voluminous than those of species which I have never collected. For species whose occurrence in my study area I regard as possible, a distribution map is given in Appendix 7.

The head of every species account starts with the currently valid scientific name, taxonomic authority, and year of original description. Common names in English and Spanish are given if they have been published (Frank & Ramus 1995; Savage 2002; Solórzano 2004; Guyer & Donnelly 2005; Fundación PA.NA.M.A. 2007; Ray & Knight 2013; Uetz & Hošek 2014; but not all common names appearing in these publications are necessarily listed herein) or are actually used by people, and in some cases newly proposed. Next, the corresponding figures or maps in this work are specified. The following synonymy is partial in two ways: First, it is in most cases restricted to literature focusing on Lower Central American reptiles, chiefly those references mentioned in chapters 1.3, 3.3, and 3.5, as well as other publications referred to in the text. Second, the synonymies only list references dealing with the respective species under a different name than that used for it in the present work. In compiling these synonymies, I payed special attention to the exact spelling of the synonymous scientific names. That is to say, I included as synonyms also those apparent misspellings differing in a single letter from another listed synonym, or from the name used for the respective species in the present work (e.g., *Diploglossus bilabatus* instead of *D. bilobatus*), without adding a "sic!" each time to corroborate such misspellings. The reference to type material and the type locality is taken from Köhler 2008, McCranie 2011, Uetz & Hošek 2014, or from the respective original descriptions if these are cited. Just as throughout this work, quotation marks indicate verbatim transcripts from cited references, with own amendments set in square brackets.

Based on the same references (among these, mainly from a few comprehensive works: Perez-Santos 1999; Young et al. 1999; Savage 2002; Campbell & Lamar 2004; Solórzano 2004; Köhler 2008; Sunyer 2009; Jaramillo et al. 2010; Rhodin et al. 2010; Sasa et al. 2010; Wilson & Johnson 2010; McCranie 2011; Ray & Knight 2013; Uetz & Hošek 2014) and my own dataset of examined specimens, the species' distribution is first summarized in its totality, then detailed within Panama and the Cordillera Central including my study area, respectively. All georeferenced point records from my combined datasets are plotted on a standardized distribution map according to the quality of evidence (see category definitions in chapter 3.3).

A usually brief diagnosis allows to distinguish the species from similar ones occurring in or close to the study area. The subsequent description summarizes important characteristics of external morphology such as maximum size and standard scale counts. The morphological variation among my examined material is not separately specified, since the original data tables are provided in Appendix 4. As an exception, selected counts and proportions derived exclusively from my sample and therefore possibly not reflecting the total known variation in the species concerned are included for the sake of comparability and marked with an asterisk (*; e.g., 4finger counts for geckos, which are not mentioned in the comprehensive works used as the main sources for the morphological summaries, or maximum SVL values of snakes which are omitted in most comprehensive works). A generalized summary of the coloration in life is followed by standardized color descriptions of selected individuals only for species of which I have examined specimens. In these individual color descriptions, the capitalized colors and color codes (the latter in parentheses) are those of Smithe (1975–1981). Brief notes on the coloration in preservative conclude the description. If no additional references are given, the coloration and other morphological summaries blend information from the comprehensive works mentioned in the preceding paragraph with my own data and photos available to me.

The natural history notes combine prominent life history traits from other sources (if not otherwise specified, these are again the comprehensive works recounted above) with own observations. For selected species, i.e., Panamanian national and small-scale Talamancan highland endemics, an assessment of the conservation status is provided in a separate paragraph. Where applicable, a species account is concluded with remarks on taxonomy, relationships, morphology, or distribution, especially if my findings in any of these regards are incongruent to published opinions, e.g., extend the known distribution or variability.

3.6 Biogeography

In this section, I depict how I obtained, processed, and analyzed geographical data (3.6.1) and conducted the biogeographical analyses (3.6.2).

3.6.1 Spatial data: sources, processing, management, and analysis

If not specifically stated otherwise, all coordinates and maps presented in this work are in geographic coordinate system and WGS 1984 datum. Spatial datasets in the form of shapefiles (.shp) or raster datasets (often received as ASCII files that were converted to .grd gridfiles for use in DIVA-GIS and ESRI raster files for use in ArcGIS) were obtained from different sources. Polygon shapefiles of administrative areas as well as point shapefiles of gazetteers for CA and SA countries were obtained from the DIVA-GIS website (www.diva-gis.org/gdata; see sources linked therein for original sources of data). The NASA SRTM digital elevation model version 3 (Jarvis et al. 2006) was downloaded from http://srtm.csi.cgiar.org at a resolution of 3 arc seconds (equalling about 90 m at Panamanian latitudes). Monthly climate data at a resolution of 30 arc seconds (equalling about 900 m at Panamanian latitudes; Hijmans et al. 2005) was downloaded from the WorldClim database (www.worldclim.org) for the area surrounding and including Panama (tile 23).

Different geographical datasets used for display and/or analysis in this work were obtained directly from the Dirección de Cartografía of the Contraloria General de la República (CGdR) through the intermediation of the Vicerrectoría de Investigación y Posgrado of the UNACHI. In particular, these were polyline shapefiles of rivers and roads as well as polygon shapefiles of urban areas, populated places, urban neighborhoods, and administrative areas (Provincias, Distritos, Corregimientos). Several other datasets used throughout this work were downloaded from the GIS Data Portal of the Smithsonian Tropical Research Institute (STRI); (http://mapserver.stri.si.edu/geonetwork/srv/en/main.home). In particular, these were a point shapefile for populated places, polyline shapefiles for rivers and roads, and polygon shapefiles for administrative areas (Provincias, Distritos, Corregimientos, protected areas), drainage systems, geology, and forest cover (the latter both for the years 1990 and 2000).

Most of the shapefiles downloaded from the STRI's mapserver as well as all shapefiles received from the Contraloría General were projected in NAD 1927 datum and UTM coordinate system (UTM zone 17, North hemisphere). I used the "Project" tool of ArcMap to transform these to WGS 1984 datum and geographic coordinate system, the spatial reference used throughout this work. Datasets created in DIVA-GIS (see below) are automatically created in this geographic reference but lack a corresponding projection (.prj) file. This file was created in ArcCatalog via specifying the geographic reference in the "Properties..." window of such datasets. The other way round, whenever I needed to measure areas, I projected and transformed data from the geographic coordinate system and WGS 1984 datum to UTM (zone 17 N) and NAD 1927 datum.

Since the content and data quality exhibited by the respective equivalent shapefiles obtained from CGdR and STRI differed, I combined the best-fitting features from each of the respective two equivalent shapefiles to obtain the best possible shapefiles in the case of political subdivisions, i.e., Corregimientos, Distritos, and Provinces, using the SRTM elevation data as a basic reference for the extent of land areas. In several occasions, shapefiles of neighboring and/or overlapping geographic extent were combined in ArcMap using the "Append" and "Merge", or "Union" Tools, or clipped using the "Clip" or "Intersect" tools.

Chiefly in the case of SRTM elevation data, neighboring raster datasets were combined to a single raster in DIVA-GIS using the "Merge" function. Several raster datasets were masked to exclude grid cells outside Panama using the "Clip (Data Management)" tool in ArcMap with a self-constructed polygon shapefile of Panama's land borders and a marine area including all the republic's islands as the clipping feature. I derived contour polygon shapefiles from elevational and climatic data with Arc Map's "Contour (Spatial Analyst)" tool.

Point locality data for specimens or species occurrences was obtained in two ways: In the case of own collections and observations, the corresponding coordinates recorded in the field were downloaded directly from the GPS unit using Garmin MapSource (download.garmin.com/software) or the freeware MyGPS (http://www.faureragani.it/mygps). Other distributional points were georeferenced manually, mainly in DIVA-GIS. If a locality record bore geographic coordinates, these were verified and, if plausible and necessary, converted to decimal degrees for further use. However, most locality records in the data sources recounted above lack coordinates, and some come with clearly erroneous ones. I georeferenced these records whenever their associated information (such as verbal locality descriptors, elevation, collector, and so on) allowed for deducing an unequivocal locality. Localities for my georeferences were traced employing the datasets mentioned in the preceding paragraphs as well as the literature recounted in chapters 1.3 and 3.3, the Mapa General de la República de Panamá (IGNTG 2000), the Atlas Nacional Digital de la República de Panamá (IGNTG 2008), different topographic maps at a 1:50 000 scale issued over the past decades by IGNTG (some available at http://mapserver.stri.si.edu/geonetwork/srv/en/main.home), as well as Google Earth (https://earth.google.de) and in some cases consultations with friends and colleagues. If the given locality was unspecified within or along a larger geographical feature (e.g., an island, district, city, stream, or a polygon defined by corner points), I referenced it in the middle of that feature. Unless very precise locality information allowed for more, I usually restricted the precision of my georeferences to three decimals, which is roughly equivalent to 110 m at Panamanian latitudes. Point datasets obtained in these ways were copied from the Excel sheet in which they were assembled, pasted into a tab-delimited text file, imported into DIVA-GIS using the "Import Points to Shapefile ... from text file (.TXT)" function and assigned a spatial reference in ArcCatalog. All georeferences, self-assigned or not, were checked visually (most additionally using the "Check Coordinates" function) for correctness and plausibility in DIVA-GIS and corrected if necessary. For records lacking altitudinal information, I derived an approximate elevation using the "Extract Values by Points ... from Grid or Stack" function of DIVA-GIS on my combined dataset to assign the corresponding SRTM elevation to each point record devoid of an elevational value.

I created GIS layers of approximate Köppen climates and Holdridge life zones from the WorldClim 30s monthly climate data. For this purpose, I first specified the tile 23 dataset as the active climate database in DIVA-GIS. Next, I used DIVA-GIS to create gridfiles of the WorldClim raw data (altitude, alt; monthly mean temperature, tmean1–12; monthly minimum temperature, tmin1–12; monthly maximum temperature, tmax1–12; monthly precipitation, prec1–12) as well as of the 19 BIOCLIM variables which DIVA-GIS calculates from these raw data (BIO1–19) with the "Climate Data to Map" function. From these gridfiles, the bioclimatic layers were derived as detailed in the following two paragraphs, if not otherwise specified using the commands in the "Grid" menu of DIVA-GIS.

For the Köppen (1936) climates, I first reclassed the BIO6 grid (mean temperature of coldest month), reclassifying values above 18 (A climates) to 1, and values below 18 (C climates; tile 23 contains no value below -3°C that would indicate D or E climates) to 3, creating the output file koeppen_zones_lca.grd. Second, I determined the climate type for the C climates. For this purpose, I used "Overlay: Divide" to divide BIO13 (precipitation wettest month) by Bio 14 (precipitation driest month) and reclassified the resulting gridfile so that all values above 10 (w type with dry season) would assume 0.02 and all values lower than or equal to 10 (f type, perhumid) would assume 0.06, creating the output file koeppen_types_C_lca.grd. Third, I determined the climate type for the A climates in a multi-step procedure. Having reclassed all cells of BIO14 with values above 60 to "nodata" in the output file precminlessthan60_lca.grd, I used "Overlay: Substract" to substract it from the newly created allcells_100_lca.grd (in which all cells had been set to the value 100), thus creating the output file 100-precminlessthan60_lca.grd. Using "Scalar", I multiplied the latter file by 25, and substracted the output file 25mal_100-precminlessthan60_lca.grd from BIO12 (annual precipitation) using "Overlay: Substract" to create the output file BIO12-25mal_100-precminlessthan60_lca.grd. I reclassed this file so that all values below 0 (w type) would assume 0.2, and all values above 0 (m type) would assume 0.4, creating the output koeppen_types_A_lca.grd. To account for f type climates, I reclassed BIO14 again, with all values of 60 or higher changed to 0.6 and all below 60 changed to 0, creating koeppen_types_A_0isworm0,6isf_lca.grd. Fourth, I used the "Make Stack" function (Stack menu) to create a stack of the four resulting gridfiles (koeppen_zones_lca, koeppen_types_C_lca, koeppen_types_A_lca, koeppen_types_A_0isworm0,6isf_lca.grd) and used "Calculate: Sum" (Stack menu) with "NULL as zero" checked to create a gridfile summing up the values from all grids. This gridfile was again reclassed (values of 0–0.7 set to NODATA; A climate values around 1.2 to 1.2, around 1.4 to 1.4, and around 1.6 to 1.6 to eliminate the second decimal accounting for C types; C climate values of 3.x2 to 3.2 and of 3.x6 to 3.6 to eliminate the first decimal accounting for A types) and the output stored as koeppen_climates_lca.grd. This resulting file was reclassed a last time (1.2=Aw to 1, 1.4=Am to 2, 1.6=Af to 3, 3.2=Cw to 4, 3.6=Cf to 5) and stored as koeppen_climates_lca_integer.grd, which I imported into ArcGIS and then clipped it to koeppen_pan using the "Clip (Data Management)" tool in ArcMap as described above. Last, I derived the polygon shapefile koeppen_pan.shp through the "Contour (Spatial Analyst)" tool.

The Holdridge (1967, 1971) life zones could be obtained a little more straightforward. First, I used "Scalar" to obtain the potential evapotranspiration by multiplying BIO1 (annual mean temperature; here synonymous with mean biotemperature since no cell in tile 23 has a value below 0) by 58.93, creating pet_lca.grd. Second, I used "Overlay: Divide" to obtain the PET ratio dividing PET_lca.grd by BIO12 (annual precipitation), creating pet_ratio_lca.grd. Third, I obtained the altitudinal belts by reclassing BIO1 (3–6°C to 5, Subalpine; 6–12°C to 4, Montane; 12–18°C to 3, Lower Montane; 18–24°C to 2, Premontane; 24–30°C to 1, Lowland), creating alt_zones_lca.grd. Fourth, I obtained decimals denoting the humidity provinces by reclassing PET_ratio_lca.grd (1–2 to 0.2, subhumid or Dry; 0.5–1 to 0.4, humid or Moist; 0.25–0.5 to 0.6, perhumid or Wet; 0–0.25 to 0.8, superhumid or Rain), creating pet_ratio_reclassed_lca.grd. In the fifth step, I used "Overlay: Add" to sum up alt_zones_lca.grd and pet_ratio_reclassed_lca.grd, creating holdridge1_lca.grd, which was reclassed to integer values (1.2 to 12, 1.4 to 14, ..., 3.2 to 32, and so on) in holdridge_lca_integer.grd. This resulting file was exported to ArcGIS where I clipped it to holdridge_pan using the "Clip (Data Management)" tool in ArcMap as described above, and derived the polygon shapefile holdridge_pan.shp through the "Contour (Spatial Analyst)" tool.

All maps shown in the present work were created in ArcMap and enhanced in Adobe Photoshop. Bar and line graphs displaying distributional information were created in GraphPad Prism (www.graphpad.com).

3.6.2 Biogeographical classifications and analyses

In the following sections, I depict how I analyzed the distributional data obtained from different sources. All biogeographical analyses described in the sections 3.6.2.1–5 were restricted to the reptile species documented herein to occur in my study area, and if not otherwise specified carried out on the "all-inclusive" dataset introduced in chapter 3.5.1 that combines all point records of any of the three quality categories from all sources. Species occurrences in geographical features (such as physiographic regions, altitudinal belts, protected areas, or provinces) were evaluated analogously to the occurrence in my study area employing the categories ("documented", "plausible", and "possible") and corresponding criteria depicted in chapter 3.5.1. As with the reptile fauna of my study area, total species numbers given for geographical features are the sum of documented and plausible occurrences, which are plotted separately in the corresponding diagrams, and do not include the possible occurrences which are only specified in the corresponding tables. Throughout chapter 4.3, percentages without decimals usually represent values that have been rounded to the next percent.

3.6.2.1 Ecological and physiographic distribution

For the distribution among physiographic regions, I only considered the distribution of my study area's reptile species in and along my study area, i.e., from 81°W westwards. Thus, I modified the ecoregions of Jaramillo et al. (2010) as follows: Instead of their "Central American highlands" comprising the entire Cordillera Central, I employed the Serranía de Talamanca and Serranía de Tabasará as defined in chapters 1.2.2 and 2.1 and refrained from considering the eastern third of the Cordillera Central. Likewise, I assessed the distribution within the Caribbean and Pacific lowlands, respectively, only from 81°W westwards. Species that within my study area are exclusively documented from the Fortuna depression were scored as "documented" for either the Talamanca or Tabasará range based on the exact provenance of the record(s), and scored as "plausible" for the respective other segment of the Cordillera Central.

For the distribution among Holdridge life zones and Köppen climates, I first used the "Extract Values by Points ... from Polygons" function of DIVA-GIS to extract documented occurrences among life zones and Köppen climates throughout Panama for each species from the Holdridge and Köppen polygon shapefiles, respectively. In a second step, I evaluated additional plausible and possible occurrences among the different climatic regimes along my study area for each species. In this evaluation, as well as in the results, I only considered the 7 Holdridge life zones (LMF, LWF, PMMF, PMWF, LMWF, MWF, MRF) and the 4 Köppen climates (Am, Af, Cw, Cf) found in and along my study area. That is, two life zones (LDF, LMMF) and one Köppen climate (Aw) only found east of 81° W are not considered herein.

The altitudinal distribution of each species was assessed on two levels: First, I derived each species' total elevational range (i.e., the maximum and minimum elevations inhabited throughout a species' geographical range) from my combined dataset and the elevational limits given in the references mentioned in chapters 1.3, 3.3, and 3.5. Second, I derived the elevational range covered by each species along the Cordillera Central and in the adjacent lowlands of western Panama based on the values given by Jaramillo et al. (2010) for Panama and my combined dataset. I critically evaluated the maximum and minimum values obtained from any source and only adopted them if they seemed plausible, as discussed for several species in their respective species accounts (chapter 4.2.2). In evaluating a species' presence in altitudinal 100 m segments, I simply interpolated the elevational limits for the Cordillera Central, assuming that a species would in principle occur at any elevation within these limits. In evaluating a species' presence in altitudinal belts (lowland, premontane, lower montane, and montane as defined in chapter 1.2.3), I distinguished between documented and plausible presences based on the altitudinal values associated with the georeferenced records in my combined dataset.

3.6.2.2 Distribution patterns and endemism

Based on its overall distribution as derived from literature and my dataset (see 3.5.2) and reported in its respective species account, I determined the general distribution pattern of each species documented herein to occur in my study area as follows: I consider a species to be a Lower Central American (LCA) endemic if its documented distribution does not exceed LCA as defined in chapter 1.1.3, i.e., Panama and Costa Rica. If a species ranges outside these two countries, I classify it as widespread. Within these two general categories, I further distinguish several distribution patterns. Widespread species are denoted as widespread in Central America (CA) if their range includes at least LCA and Nicaragua, as CA + Colombia or LCA + Colombia if they additionally occur in Colombia, and as widespread in South America (SA) if their range includes at least one SA country beyond Colombia. LCA endemics are generally categorized as lowland + premontane endemics if their distributional records are restricted to these altitudinal belts and include several lowland records. Those LCA lowland + premontane endemics that are restricted either to the Caribbean (e.g., *Norops cryptolimifrons*) or Pacific (e.g., *Norops polylepis*) versant of Costa Rica and/or Panama are denoted as such. If a species is exclusively known from the Talamancan highlands of LCA, (entailing that its distribution within Panama is restricted to the Cordillera Central; e.g., *Rhadinaea calligaster*), I categorize it as a Talamancan highland endemic regardless of singular lowland records that may exist. Talamancan highland endemics whose documented range does not significantly exceed 100 airline km (e.g., *Norops pseudokemptoni*) are further classified as Talamancan small-scale endemics.

In evaluating its distribution pattern, I further denoted whether a species reaches the southern/eastern or northern/western limit of its geographical range within or along my study area.

3.6.2.3 Distribution among protected areas and conservation

Abbreviations used for protected areas along my study area are BPPS (Bosque Protector Palo Seco), HIILV (Humedal de Importancia Internacional Lagunas del Volcán), PILA (Parque Internacional La Amistad), PNSF (Parque Nacional Santa Fé), PNVB (Parque Nacional Volcán Barú), and RFLF (Reserva Forestal La Fortuna). Abbreviations for other protected areas in Panama that are mentioned in the text are HIISSPS (Humedal de Importancia Internacional San San Pond Sak), MNPC (Monumento Natural Los Pozos de Calobre), MNCG (Monumento Natural Cerro Gaital), PNAC (Parque Nacional Altos de Campana), PNCH (Parque Nacional Cerro Hoya), PNGDOTH (Parque Nacional General de División Omar Torrijos Herrera, often referred to as "El Copé"), RFLT (Reserva Forestal La Tronosa), RFLY (Reserva Forestal La Yeguada). To obtain the documented occurrences of the study area's reptile species within the six protected areas established within my study area (BPPS, PILA, HIILV, PNVB, RFLF, and PNSF; see Map 1.11), I used the "Extract Values by Points ... from Polygons" function of DIVA-GIS to extract the records per protected area from the STRI shapefile of protected areas. Since BPPS and PILA exhibit a large overlap and only the presence in BPPS was extracted during this procedure, I had to create a separate shapefile only containing the PILA (selecting its polygon and using the "Selection to New Shapefile" function in DIVA-GIS) in order to obtain all records from this park. In a second step, I manually evaluated additional plausible and possible occurrences for each species.

Analogously to Jaramillo et al. (2010; and Wilson & Johnson 2010 in general), I applied two measures assessing the conservation status of my study area's reptile species. The first of these is the classical assignment to one of the IUCN Red List categories (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; or the listing as DD = Data Deficient when the available data does not allow for an assessment) according to IUCN (2001) guidelines. In this framework, I checked the IUCN Red List (IUCN 2014) for an existing official assessment of each species. For the many species that have not been officially assessed for the IUCN Red List (then listet as NE = Not Evaluated), I adopted the IUCN assessments that Jaramillo et al. (2010) provided for 244 native species. Since much of the distributional information on my study area's reptile fauna as presented herein has apparently not been available to or used by these authors and several species have been added to the Panamanian reptile fauna since their treatment, I further conducted own IUCN assessments for selected species. For the sake of manageability, I restricted my own assessments to species which I consider to have the highest conservation priority, that is, which are either Talamancan highland small-scale endemics or Panamanian endemics or both, and further included assessments already compiled by myself in the course of several studies incorporated in this work (Lotzkat et al. 2012a, c, 2013, 2014).

Recognizing that for most of the resulting 29 species assessed by myself virtually nothing is known concerning their population size, status, dynamics, and trends as well as their life history, my own IUCN assessments are without exception based on the IUCN (2001) criterion B, that is, geographic range. As the more objectively measurable variable, I decided to employ criterion B1 (extent of occurrence) rather than B2 (area of occupancy). I obtained each assessed species' extent of occurrence by using the "Points to convex Polygon" function of DIVA-GIS (in the case of the assessments presented by (Lotzkat et al. 2012a, c, 2013, 2014) or the "Minimum Bounding Geometry: Convex Hull" Tool of ArcMap (for the remaining assessments). The resulting polygons were projected to UTM coordinate system (zone 17N) and NAD 1927 datum and cleared of any portion overlapping the sea with the "Clip" tool of ArcMap, using a shapefile with the combined outlines of Costa Rica and Panama as the clip feature. Last, I calculated each polygon's area by applying the "Calculate Geometry: Area" (output set to square km) command of ArcMap to the field "area" which I had newly created in the shapefile's attribute table. The value thus obtained as the extent of occurrence for a given species formed the basis of my corresponding IUCN assessment in combination with different subcriteria, as separately detailed in the respective species accounts (chapter 4.2.2). While up to three IUCN assessments (IUCN 2014; Jaramillo et al. 2010; own) are synoptically listed in the corresponding table (Tab. 4.31) in chapter 4.3.3 for comparison, I usually used the respective highest (i.e., most threatened) category inferred for each species as the resulting IUCN category. This resulting categories appear in the summations found at the foot of the table as well as in the corresponding figures, and serve as a basis for further discussion. As an exception from this rule, I gave the results of my own assessments priority in a few cases where the data available to me clearly showed that the earlier assignments (IUCN 2014; Jaramillo et al. 2010) to higher threat categories are inappropriate.

The second measure assessing the conservation status of my study area's reptile species is the Environmental Vulnerability Score (EVS). As with the IUCN assessment, I adopt the EVS values calculated by Jaramillo et al. (2010) for most species, but calculated own EVS for the same species whose IUCN category I assessed. In these cases, I obtained the EVS as described by Jaramillo et al. (2010): According to best knowledge and available data, each species received three separate subscores: one for the extent of its total geographic range (1 = widespread in- and outside of Panama; 2 = widespread in Panama, peripheral outside Panama; 3= widespread outside Panama, peripheral in Panama; 4 = LCA endemic; 5 = Panamanian national endemic; 6 = only known from the vicinity of the type locality in Panama), one for the extent of ecological distribution as determined by the occurrence in "forest formations", that is, in generalized Holdridge life zones (1 = occurs in five life zones; 2 = in 4 life zones; 3 = in 3 life zones; 4 = in 2 life zones; 5 = in 1 life zone; for this purpose, I combined LMF with LWF, and MWF with MRF as done by Jaramillo et al. 2010), and the last for the degree of persecution by humans (1 = fossorial, typically escaping human notice; 2 = semifossorial, or nocturnal arboreal or aquatic, non-venomous and usually non-mimicking, sometimes escaping human notice; 3 = terrestrial and/or arboreal or aquatic, generally ignored by humans; 4 = terrestrial and/or arboreal or aquatic, thought to be harmful (often mistakenly) and may be killed on sight; 5 = venomous species or mimics thereof, killed when encountered; 6 = species exploited by humans for meat, eggs, or skin). The summation of these subscores as detailed in the respective species accounts (see 4.2.2) resulted in the final EVS of an evaluated species.

Following Jaramillo et al. (2010), I consider species with EVS values from 3–8 as low, those with 9–11 as medium, and those with values above 11 as high vulnerability species. As with the IUCN assessments, both the EVS of Jaramillo et al. (2010) and my own EVS are tabulated, but a resulting EVS value is used in the summations found at the foot of Tab. 4.31, the corresponding figures, and as a basis for further discussion. As in the case of the IUCN assessments (see above), I usually used the highest score inferred for a given species as its resulting EVS except for a few cases where the data available to me clearly showed that the EVS calculated by Jaramillo et al. (2010) are outdated (especially as a result of novel distributional data presented herein) or otherwise inappropriate.

Last, I combined the occurrences in protected areas and conservation assessments to determine the occurrence among my study area's protected areas for those species which are assignable to the IUCN Threatened categories (CR, EN, VU) or assessed as DD, as well as those considered highly vulnerable according to their EVS.

3.6.2.4 Historical source units

In order to shed some light on my study area's historical biogeography and its reptile fauna's source units, I assigned the native reptile genera (that is, all genera except the introduced *Hemidactylus*) of my study area to three historical source units, namely the North American Element, Middle American, and South American Element as characterized by Savage (2002). Using the composition of these units as presented by Savage (2002: p. 802–806) as a starting point and finding it consistently applicable to most genera, I incorporated recent findings in phylogeny and phylogeography (especially Macey et al. 1999; Gamble et al. 2008a, b; Savage et al. 2008; Linkem et al. 2011; Harvey et al. 2012; Hedges & Conn 2012) to reconfirm or reconsider the assignments of Savage (2002) wherever necessary and applicable.

3.6.2.5 Phylogeographic boundaries as suggested by highland anoles

While thorough phylogeographic studies are far beyond the scope of this study, I try to provide a starting point for such studies by identifying shared geographic patterns of speciation. For this purpose, I exemplarily compared the geographic distribution of highland anoles inhabiting my study area. I restricted my comparison to anole species that are endemic to premontane and/or higher elevations of the Talamancan highlands and from which I have obtained DNA barcodes. In a subset of my examined specimens restricted to the barcoded individuals, I labeled each specimen according to its genealogical lineage as inferred separately for each clade of highland anoles in chapters 4.1.3–6. Using the "Minimum Bounding Geometry: Convex Hull" Tool of ArcMap, I created a bounding polygon around all records of barcoded specimens pertaining to a given lineage. Using the "Buffer" tool of ArcMap (side type: full; end type: round; distance: 4 km), I extended each polygon by 4 km for better display and visibility. On the thus generated distribution maps of genealogical lineages, I manually placed black bars as symbols for gene flow barriers between all pairs of geographically neighboring, closely related lineages. To facilitate comparison and interpretation, I layouted a graphical synopsis of these maps together with the corresponding details of the trees shown in Fig. 4.1.

3.6.2.6 Distribution of Panamanian reptiles among the western provinces

Last, I evaluated the distribution of Panama's reptile species among the four political subdivisions which overlay my study area, i.e., the provinces of Bocas del Toro, Chiriquí, and Veraguas, and the Comarca Ngöbe Buglé. Other than the biogeographical analyses described in the preceding sections 3.6.2.1–5, this analysis is neither restricted to the species reported herein to occur in my study area, nor to the area west of 81°W. Rather, it encompasses all reptile species reported to occur in Panama in the present work, and considers the entire geographical area occupied by the four administrative divisions. Again, I evaluated the documented, plausible, and possible species occurrences as for my study area (see 3.5.1). Novelties concerning the distribution of certain species among the four political subdivisions as well as plausible and possible occurrences in the Comarca or any of the provinces are mentioned and, if necessary, substantiated in the respective species accounts in chapter 4.2.2.

4. Results

From single species and species groups to an entire fauna and its distribution in space: In this section, I first present the results of my taxonomical analyses of selected reptile groups from the Cordillera Central and briefly summarize other authors' recent species descriptions from the area (4.1). Next, I combine these new findings with other available point distribution information to assess the study area's total species richness, and characterize each species in a short account including a distribution map (4.2). Then, I analyze biogeographical aspects of the area's reptile fauna such as the distribution among political subdivisions, protected areas, altitudinal belts, and climatic regimes, as well as endemism and shared patterns of distribution (4.3).

4.1 Taxonomy

In the following chapters 4.1.1–4.1.11, I address selected issues of morphological and/or genetic variability observable among certain reptile populations and assess inhowfar they can be interpreted as intraspecific variation, or rather represent interspecific distinctions warranting taxonomic conclusions. Before proceeding to the faunistic level, I summarize the genetic distances inferred and the unnamed genealogical lineages identified in this study in chapter 4.1.10, as well as all taxonomic changes that have occurred since the list of Jaramillo et al. (2010) in chapter 4.1.11.

Among the 869 specimens from western Panama collected in the period 2008–2010 by AC, AH, FH, JFB, LS, NH, and myself, I could more or less readily identify 114 (including 54 lizards and 56 snakes) of the nominal species listed by Jaramillo et al. (2010), among these 107 based on specimens from the study area. However, several specimens could not be doubtlessly assigned to any species listed by these authors or by Köhler (2008) using the literature available until 2010. Moreover, closer examinations of external morphology and/or the analysis of DNA barcodes revealed the existence of two or more lineages within some nominal taxa. Figure 4.1 roughly aligns and compares a ML tree of 182 16S barcodes with that of 183 COI barcodes generated from Panamanian reptiles (each being the tree with the highest log likelihood of 1000 bootstrap replicates, with *Sphenodon punctatus* NC_004815.1 as the outgroup; the corresponding alignments and distance matrices are provided in Appendix 5.1) and indicates the chapters containing the correspondent taxonomic analyses.

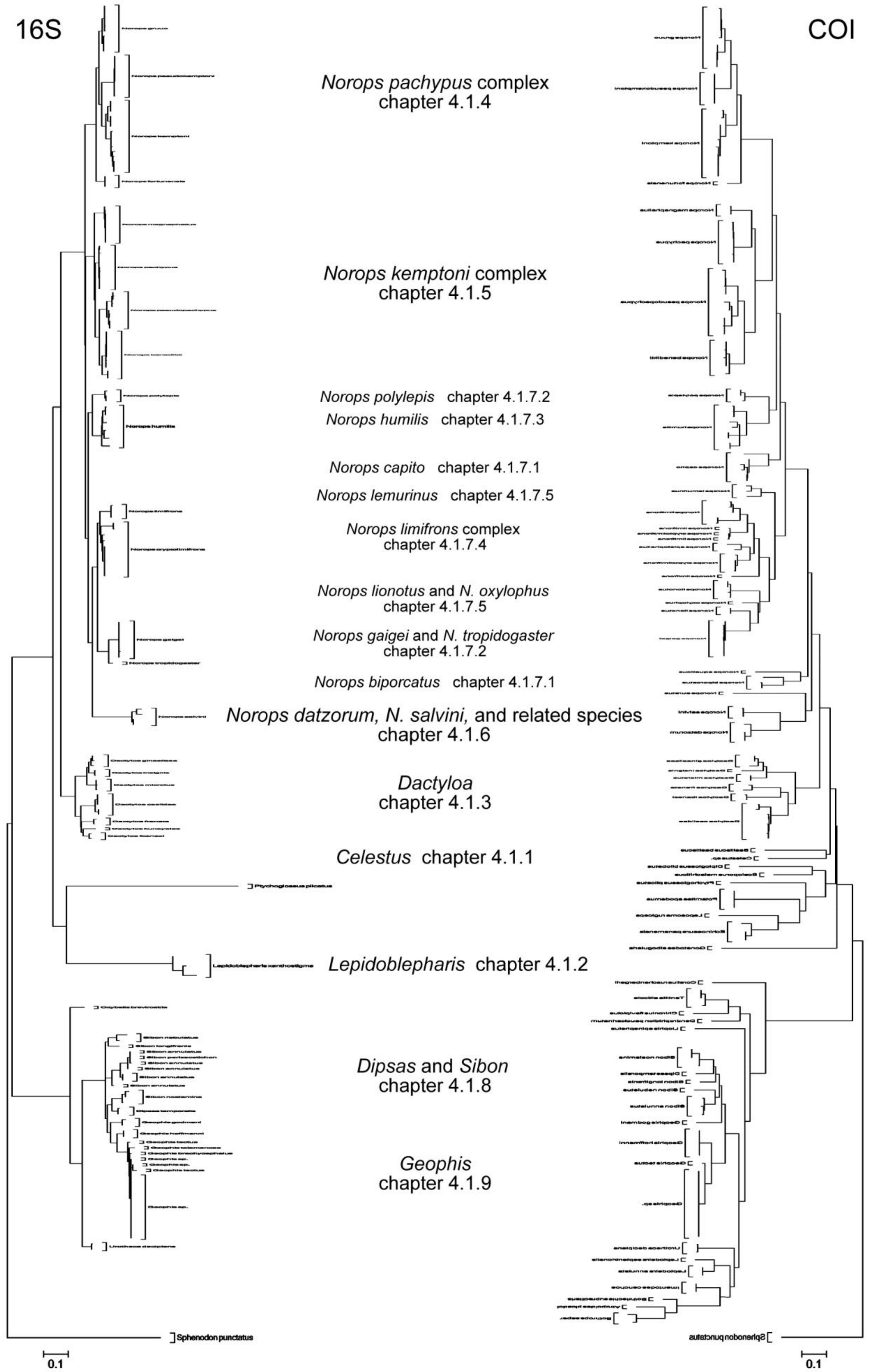


Figure 4.1: Overview of DNA barcodes from Panamanian reptiles and taxonomic issues addressed in this work.

Anoles make up a large portion of the specimens collected by myself and coworkers, and thus dominate the trees shown in Figure 4.1 as well as the taxonomic analyses below. This is partly due to the nature of our collecting and the fact that anoles are highly spottable as well as easy to catch at night, but on the other hand also reflects an undisputable aspect of Central American reptile diversity. Anoles are the most speciose lizard group of the Panama, accounting for about 41% of the country's lizard species and almost 15% of its entire reptile fauna as listed by Jaramillo et al. (2010). Until 2010, 39 species of *Anolis* had been reported for Panama (Jaramillo et al. 2010; Köhler 2008, 2010). As many as ten of these had been described during just four years in the first decade of this century (Köhler et al. 2007, Poe and Ibáñez 2007, Hulebak et al. 2007, Köhler and Sunyer 2008, Poe et al. 2009, Köhler 2010), suggesting that quite some taxonomic work remains to be done, especially among species groups inhabiting the comparatively less studied highlands of Panama.

4.1.1 Anguimorpha, Anguidae: The genus *Celestus*

As currently understood, the genus *Celestus* comprises 29 species of small to medium-sized lizards distributed in the Caribbean region, with 12 species on the Central American mainland (Savage et al. 2008; Uetz & Hošek 2014). Its presence in Panama was first revealed by Savage et al. (2008), who described the species *C. adercus* based on a single specimen (MVUP 1894, formerly CHP 4870) from "the abandoned sawmill site on the continental divide, 9.7 km NNW of El Copé, Parque Nacional General de División Omar Torrijos Herrera, La Pintada District, Coclé Province, Panama, ca. 850 m (8°40'04"N, 80°35'06"W)", shown as locality 23 in Map 1.13. On 30.09.2009, Gabriel Palacios secured an anguid lizard (SMF 90177, field no. SL 449; Fig. 4.2) on the grounds of the Lost & Found Ecohostel (WP 22) in the Fortuna area. The juvenile (SVL = 35 mm) with incomplete tail (15 mm left) is readily identified as a representative of *Celestus* by the absence of a claw sheath (Figs. 4.2I–L), and constitutes the second specimen of this genus collected in Panama.

In Table 4.1, key morphological characteristics of the specimen are compared to those of the four known Lower Central American species as provided by Köhler (2008), Savage (2002), Savage & Lips (1993), and especially Savage et al. (2008). Employing the keys and descriptions provided by these authors, I am unable to assign this specimen confidently to any species of *Celestus* that is known from Costa Rica or Panama, or the remaining Central American mainland. The fact that its suboculars and postoculars are juxtaposed posterioventral to the orbit keys out the Mexican species *C. eneagrammus, C. ingridae,* and *C. legnotus* as well as the Costa Rican *C. cyanochloris.* Its single large frontonasal and markedly keeled caudal scales rule out *C. atitlanensis, C. montanus, C. rozellae, C. scansorius,* and the Costa Rican *C. hylaius,* leaving this little specimen somewhere between *Celestus adercus* and *C. orobius.*

Table 4.1: Pholidotic characters of *Celestus* from Costa Rica and Panama.

	C. adercus	***C. cyanochloris***	***C. hylaius***	***C. orobius***	***Celestus* sp.**
Loreals	3	2	2–3	1–2	2
Canthals present	ii+iii	ii+iii	ii+iii	ii+iii	ii+iii
Postoculars and suboculars	juxtaposed	continuous	juxtaposed	juxtaposed	juxtaposed
SAM	31	32–34	31–33	33	33
Transverse rows of dorsals	79	65–73	76–81	66	72
Transverse rows of ventrals	86	73–77	84–92	75	77
4th toe lamellae	24	20–25	22–27	21–22	24–25
4th finger lamellae	?	16–18	15–20	15–17	19
Precloacal scales	8	10–12	10–12	8	10
Caudal scales	k, str	k, str	str	k, str	k, str
Subcaudal scales	k	k	some (k)	k	k, str

The only characters truly matching any of these two species' descriptions are the number of toe lamellae that would advocate the affiliation with *Celestus adercus,* and the presence of two loreals that would argue for *C. orobius*. Unfortunately, the available COI barcode does not aid identification because no sequences of *Celestus* are available for comparison at this time. Since the morphological variation of both *C. adercus* and *C. orobius* is not too well known, the juvenile from Fortuna might still be a representative of either of these species. However, published photos of *C. orobius* (Savage et al. 2008) show much stouter animals with broader heads and a different color pattern. On the other hand, the lack of a third loreal can be regarded as a profound distinction from *C. adercus* (J.M. Savage, pers. comm. May 2012). Considering these and manifold more subtle incongruities to both species in question, I recognize the specimen as representative of a hitherto undescribed form, and refer to it as *Celestus* sp. In the following, I provide a description of its morphology, adopting the format and terminology of Savage et al. (2008).

Celestus sp.

Figures 4.2; 4.94F; Map 4.24.

Scalation: Rostral much broader than high, distinctly visible from above, in contact with nasals, first SPL and anterior IN on both sides; anterior IN (supranasals) narrower than posterior ones; FN and PF fused into a single large plate with slightly concave posterior margin, much wider than long, bordered by posterior IN, frontal, the two anterior median supraoculars, and on left side also by anterior (ii) canthal (on right side excluded from canthal ii by contact between posterior internasal and anterior median supraocular); frontal narrow, much longer than wide; FP small, widely separated by frontal; IP about the size of parietals and separating them, posteriorly touching smaller interoccipital; parietal separated from supraocular by uppermost temporal (and FP); nasal single, large nostril above suture between SPL 1 and 2; 2 roughly quadrangular postnasals; two loreals; first loreal about as high as long at its highest portion, in contact with posterior IN (separating canthal ii from upper postnasal) on left side; second loreal larger, slightly longer than high; canthal ii quadrangular, longer than wide (right) / wider than long (left), not fused with second loreal, smaller than second loreal, touching loreals one and two, posterior IN, and canthal iii, as well as upper postnasal on right side and prefrontal and anterior median supraocular on left side; canthal iii about the size of canthal ii, longer than wide, contacting anterior most lateral and median supraoculars, canthal ii, second loreal, and small upper preocular, as well as posterior IN on right side; five median supraoculars; first two median supraoculars contact PF; 3 small lateral supraoculars; a moderately large anterior superciliary about the size of canthal iii; 6/7 smaller superciliaries, posterior one enlarged; 5/4 primary temporals, lowermost four contacting postoculars; 6 scales between postocular and ear opening; four large postoculars juxtaposed to suboculars; three suboculars, posterior subocular large, on left side rectangular; median subocular elongate, narrow; anterior subocular small; 9/10 SPL, 6/7 to level below center of eye; 9 INL, 6 to level below center of eye; mental about as wide as rostral; an azygous PM; four pairs of enlarged chin shields, followed posteriorly by two pairs of less enlarged ones, first pair in contact with one another and second and third INL, second to fourth pair separated by one to four, 5th pair by 6, 6th pair by 8 scales; cycloid D, L, and V body scales striate without a median keel; 72 D from interoccipital to base of tail; 77 transverse rows of V scales from postmental to vent; 33 SAM; digits laterally compressed (compressedness increasing distally) with slightly rounded lamellae; finger lengths 4>3>2>5>1, with 3 almost equal to 4 in length, 19 lamellae under 4th finger; toes relatively long and slender, lengths 4>3>5>2>1; 24/25 lamellae under 4th toe; 10 precloacal scales; D and L caudal scales as well as SC cycloid, striate with a strong median keel except on very base of tail.

Measurements: in mm and %SVL: SVL 35; horDT 2.6 (7.4%), verDT 2.7 (7.7%); horDear 0.4 (1.1%), verDear 0.3 (0.9%); AGD 19.1 (54.6%); shank 3.8 (10.9%); SnL 3.0 (8.6%); HL 7.5 (21.4%); HW 4.9 (14%).

Coloration in life: See Figures 4.2A–E and species account in chapter 4.2.2.

Coloration in preservative: See Figures 4.2F–L and species account in chapter 4.2.2.

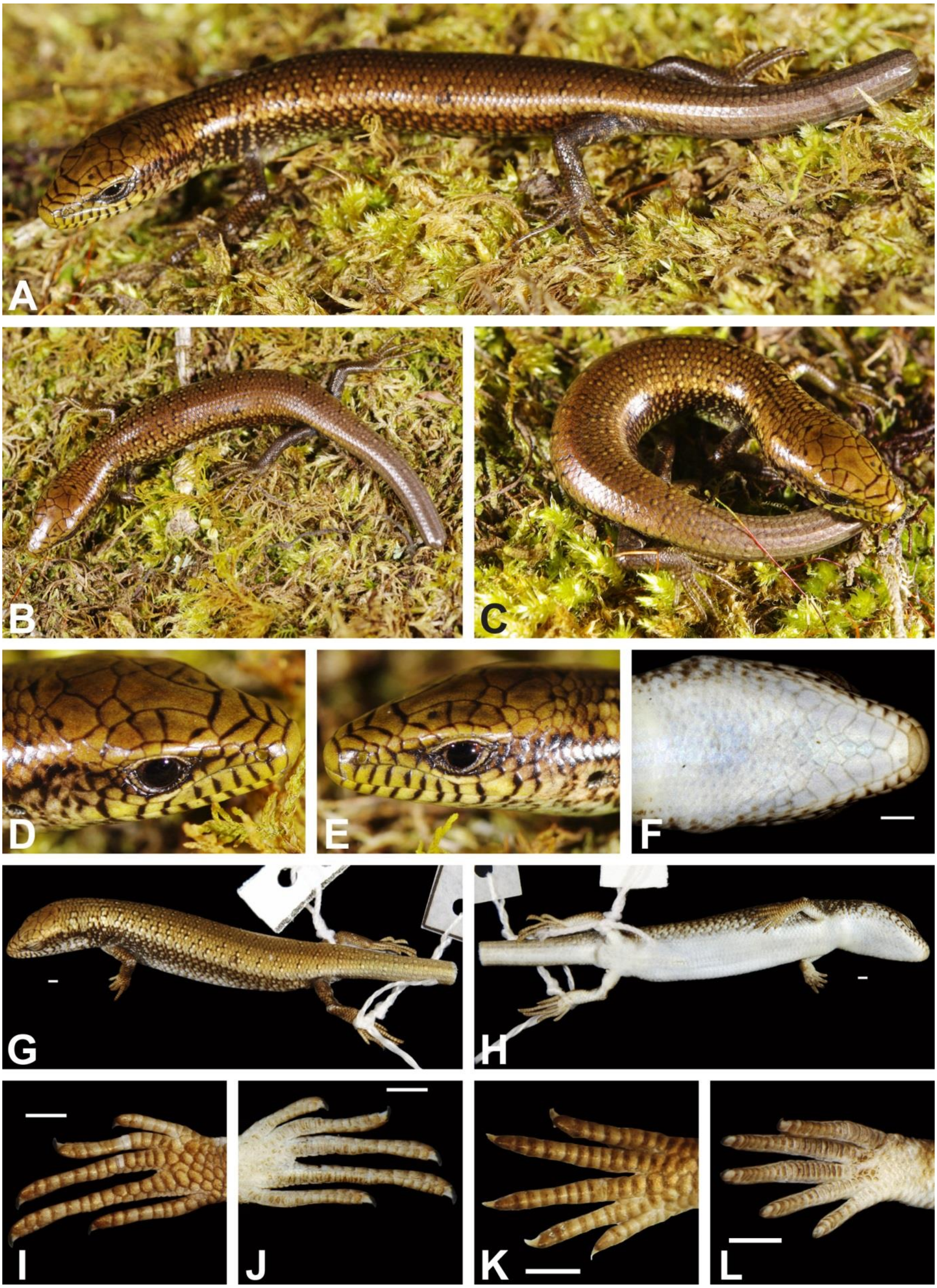


Figure 4.2: *Celestus* sp. from La Fortuna. (A–C) entire specimen in life; (D, E) dorsolateral views of (D) right and (E) left side of head in life; (F–L) preserved specimen: (F) ventral view of head, contours of mental plate and chin shields accentuated for better visibility; (G) dorsolateral and (H) ventrolateral view of entire specimen; (I) dorsal and (J) ventral view of left foot; (K) dorsal view of right hand; (L) ventral view of left hand. All scale bars equal 1 mm and are next to the first finger or toe in hands and feet.

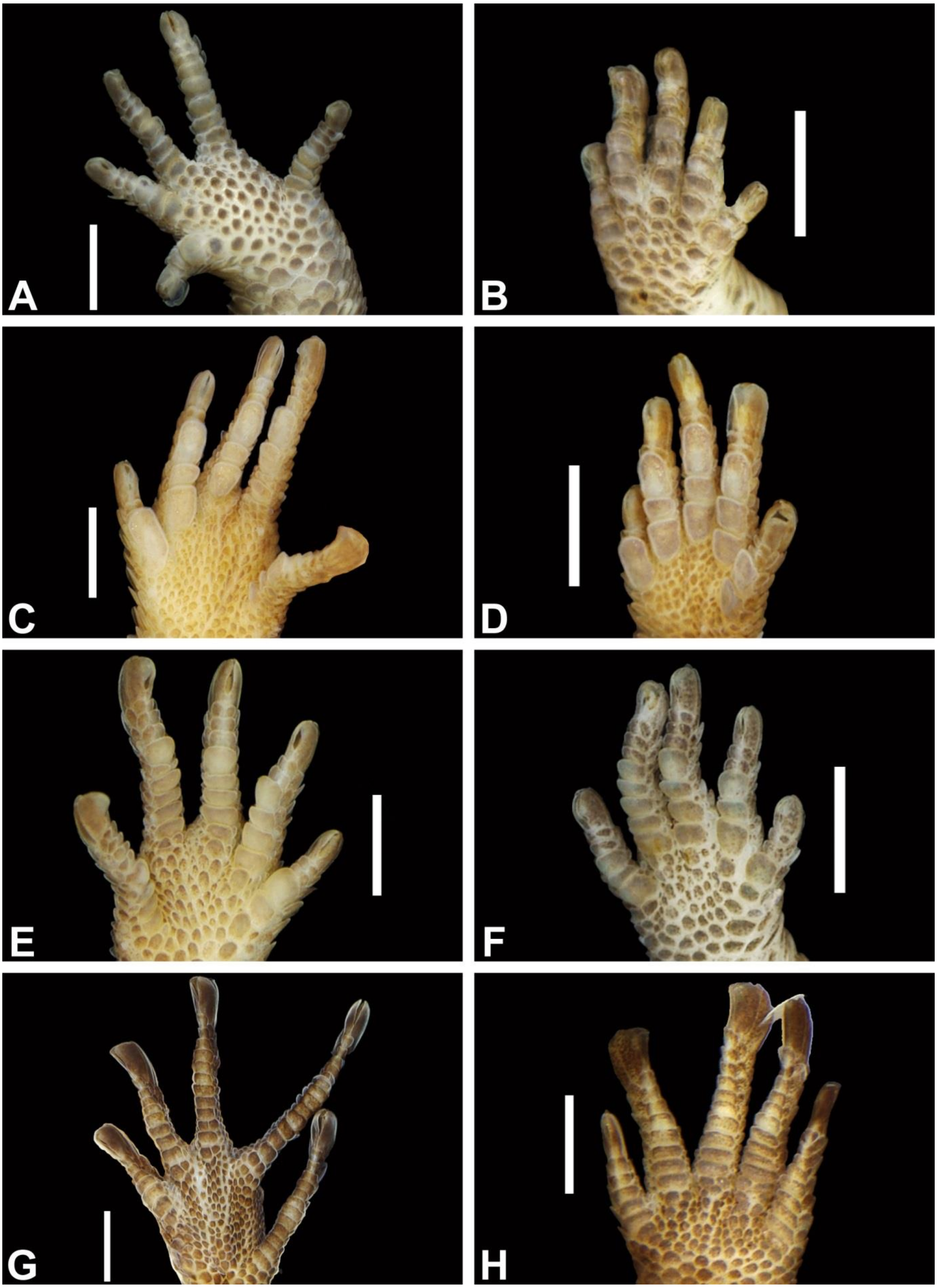


Figure 4.3: Hands (right column) and feet (left column) of Panamanian *Lepidoblepharis.* (A, B) *L. sanctaemartae:* (A) left foot of AB 385 and (B) right hand of AB 250; (C, D) *Lepidoblepharis* sp. 1: (C) left foot and (D) left hand of SMF 89963; (E, F) *Lepidoblepharis* sp. 2: (E) right foot of SMF 81954 and (F) right hand of AB 415; (G, H) *L. xanthostigma:* (A) left foot of SMF 90190 and (B) left hand of SMF 89576. All scale bars equal 1 mm and are located next to the first finger or toe.

4.1.2 Gekkota, Sphaerodactylidae: The genus *Lepidoblepharis*

Geckos of the genus *Lepidoblepharis* are small, terrestrial lizards typically inhabiting the leaf litter of forests (Savage 2002). Most of the 16–18 recognized species (Avila-Pires 2001; Uetz & Hošek 2014) are distributed in northern SA south to Brazil and Ecuador, while only two species have been documented to occur in Central America (Avila-Pires 2001; Köhler 2008): *Lepidoblepharis sanctaemartae* that ranges from Venezuela to west-central Panama, and *L. xanthostigma* occurring from Colombia to Nicaragua. These two species are readily distinguished from each other: *Lepidoblepharis sanctaemartae* has large, flat, imbricate dorsal body scales and 6–8 lamellae under its fourth toe that in consequence would be classified as short for a member of this genus. In contrast, *L. xanthostigma* has small, granular, non-imbricate dorsals and 11–14 lamellae under its fourth toe, thus being classified as a long-toed member of the genus (Ayala & Castro 1983; Lamar 1985; Köhler 2008). The only identification key available for Central American *Lepidoblepharis* (Köhler 2008) omits the lamellar counts and relies entirely on the obvious difference in dorsal scutellation. As a consequence, all members of the genus that bear granular dorsals were identified as *L. xanthostigma* in the field. However, closer examination of the specimen SMF 89963 (field number AC 079), collected in July 2008 by AC, AH, and myself at Cerro Negro, Veraguas, revealed it to have much fewer subdigital lamellae than other sphaerodactylids identified as *L. xanthostigma* from my study area. Moreover, the lamellae under its fingers and toes show a peculiar dimorphism, with 1–3 proximal ones greatly enlarged longitudinally, each about 3–4 times as long as any of the "normal" lamellae. Additionally, this specimen's median subcaudal scales are only slightly enlarged laterally, in contrast to the very prominently enlarged median subcaudal scales of typical long-toed *L. xanthostigma* which are more than two times wider than the neighboring subcaudal scales. Struck by these obvious differences, I examined all specimens referable to the genus *Lepidoblepharis* collected in CA that are housed in the collection of SMF: two specimens from Costa Rica; 12 specimens from Nicaragua including five uncatalogued ones collected by JS; and 36 individuals from Panama including 20 uncatalogued ones collected by AB and MP. Furthermore, I examined photos taken by GK at FMNH and MCZ, including 16 Panamanian and 2 Costa Rican specimens housed at FMNH, the Costa Rican holotype of *L. xanthostigma* (MCZ 11658), and individuals of most SA species. The comparative material is listed in Appendix 2.

In the course of this examination it became obvious that Panamanian *Lepidoblepharis* with granular dorsals comprise three morphologically distinct lineages: the long-toed *L. xanthostigma* and two short-toed lineages. Including the short-toed *L. sanctaemartae* with its imbricate dorsals, there are four different members of this genus in Panama. Figure 4.3 shows the feet (left column) and hands (right column) of these four lineages. In the short-toed *L. sanctaemartae,* the proximal lamellae are slightly larger than (at most twice as long as) the distal one(s). The short-toed *Lepidoblepharis* sp. 1 has 1–3 proximal lamellae greatly enlarged, up to four times longer than the distal one(s). The short-toed *Lepidoblepharis* sp. 2 exhibits a lamellar configuration similar to that of *L. sanctaemartae.* The only long-toed representative of the genus in Panama is *L. xanthostigma,* whose lamellae become shorter rather gradually towards the claw.

Apart from the number and quality of their subdigital lamellae, the four lineages can be distinguished by other characters found on the ventral surfaces of these tiny lizards. Figure 4.4 shows ventral views of the anterior portion of the tail of representative specimens from each lineage. All Panamanian *Lepidoblepharis* have a single median series of enlarged SC that originates less than ten scales posterior to the cloacal opening. Throughout this series, slightly larger and wider scales alternate with slightly smaller and narrower ones, as already noted for *L. xanthostigma* by Taylor (1956). The larger scales are bordered laterodistally by two scales, the smaller ones by one, forming a regular tail sequence of 1'1" (codification after Rivero-Blanco 1979 fide Avila-Pires 1995: 1 = single midventral scale; ' = bordered laterodistally by one scale; " = bordered laterodistally by two scales). In *L. xanthostigma,* the enlarged SC typically are at least twice as wide as the laterally adjacent SC and much wider than long (twice as wide as long in most examined specimens). Moreover, their posterior margins are straight, or almost so, oriented at right angle to the longitudinal axis of the tail (Fig. 4.4D). In *Lepidoblepharis* sp. 2, the median SC are also conspicuously wider than long, but neither twice as wide as the neighboring scales nor twice as wide as they are long. Their posterior margins may be straight as in *L. xanthostigma* (this is the case in most specimens that I have examined) or rounded (an example of the latter variant is shown in Fig. 4.4C). The median SC of *L. sanctaemartae* exhibit similar relative dimensions as those of the aforementioned lineage, but their posterior margins are rounded in all specimens I examined (Fig. 4.4A). Finally, *Lepidoblepharis* sp. 1 has its median SC only slightly larger than the neighboring scales, about as long as wide, with rounded posterior margins in all examined specimens (Fig. 4.4B). It must be noted that the state of the enlarged median SC can only be assessed reliably on original tails, or the original portion of a regenerated tail. Regenerated tails or tail portions generally exhibit a modified scale structure, and this also applies to the median subcaudal series in all specimens that I have examined. For example, in *L. xanthostigma* the median SC under regenerated tail portions are shaped very irregularly, may become much shorter and at the same time much wider, fuse with regular SC to extend almost to or even onto the lateral surfaces, and/or be arranged in pairs or groups of three.

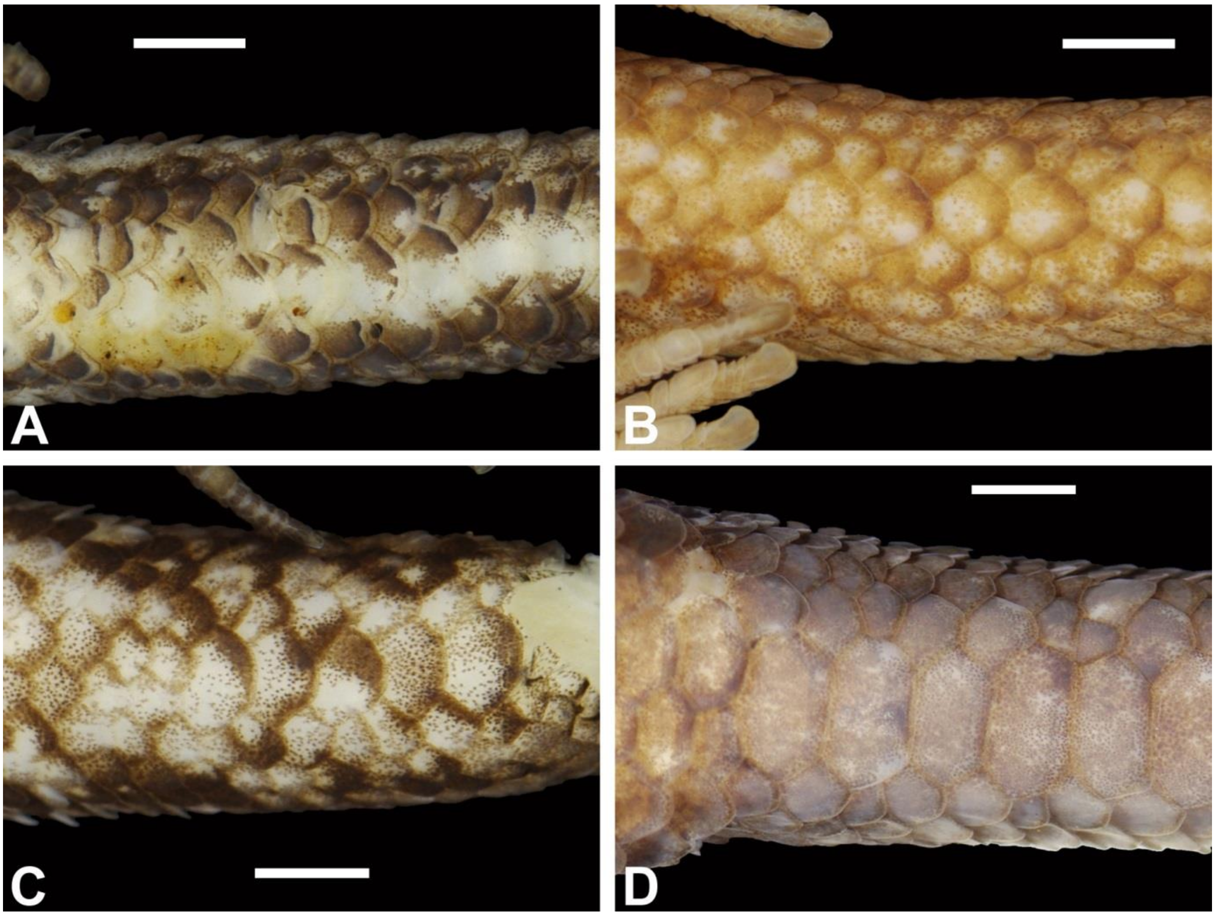


Figure 4.4: Enlarged median subcaudal scales in Panamanian *Lepidoblepharis.* (A) *L. sanctaemartae:* AB 250; (B) *Lepidoblepharis* sp. 1: SMF 89963; (C) *Lepidoblepharis* sp. 2: AB 415; (D) *L. xanthostigma:* SMF 90189. All scale bars equal 1 mm.

The posterior border of the mental plate as well as the number and size of the postmentals (PM) contacting it are a character widely used in *Lepidoblepharis* systematics, and can also help to distinguish among the four Panamanian lineages as illustrated by representative examples in Figure 4.5. In *L. sanctaemartae,* the mental plate has a concave posterior border that may be rounded or obtusely angular with a single median cleft and usually three, sometimes up to five PM (Fig. 4.5A). In *Lepidoblepharis* sp. 1, two paramedian clefts demarcate a convex median portion of the posterior mental border, that results vaguely M-shaped in its totality, and the number of PM is higher with 5–7 in the examined specimens (Fig. 4.5B). *Lepidoblepharis* sp. 2, exhibits a similar configuration with two paramedian clefts and a vaguely M-shaped posterior mental border, but with 3–7 has a wider range of PM (Fig. 4.5C). In *L. xanthostigma,* the posterior mental border may be slightly concave (Fig. 4.5D), somewhat M-shaped (Fig. 4.11M), or straight (Fig. 4.11L) and is bordered by 3–6 PM. Most specimens (21 of the 26 examined) lack clefts in the posterior border of the mental plate, but some specimens exhibit one (three of the 12 specimens from Nicaragua) or two (two of the 12 specimens from Panama) short and usually weakly developed paramedian or lateral clefts. The number of PM varies from three to six.

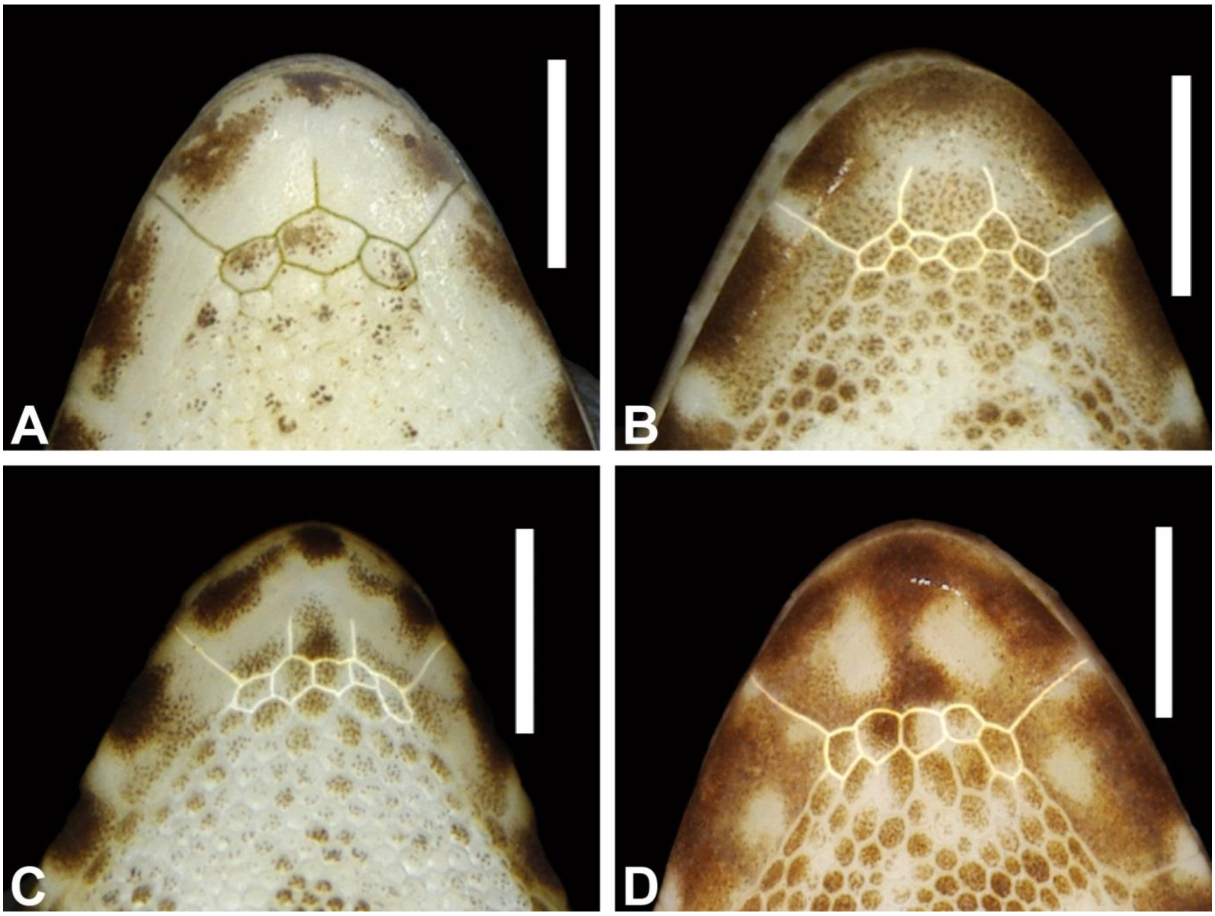


Figure 4.5: Mental plate and postmental scales in Panamanian *Lepidoblepharis.* (A) *L. sanctaemartae:* AB 250; (B) *Lepidoblepharis* sp. 1: AB 018; (C) *Lepidoblepharis* sp. 2: AB 415; (D) *L. xanthostigma:* SMF 90189. Posterior border of mental and outlines of postmentals accentuated, all scale bars equal 1 mm.

Another character that I found to be quite diagnostic among the four lineages involved has to date largely been neglected in taxonomic studies of the genus *Lepidoblepharis,* although discussed in detail by Taylor (1956) and Taylor & Leonard (1956): the escutcheon scales on the venter, and partly also on the subfemoral surfaces, of male individuals. Largely or completely lacking pigmentation, these glandular scales more or less conspicuously contrast with the surrounding V or subfemoral scales. Apart from allowing for confidently determining the sex of all but very young individuals, the number and arrangement of the escutcheon scales is quite different between the four lineages as shown by representative examples in Figure 4.6: The examined males of *L. sanctaemartae* have a V escutcheon consisting of 64–92 scales that spans 9–11 scales in length and 11–12 in width, which I consider as long and, since it spans most of the V body surface, also as relatively wide. Along the V surface of the thigh, no subfemoral escutcheon scales are distinguishable (Fig. 4.6A). Examined males of *Lepidoblepharis* sp. 1 (Fig. 4.6B) have a V escutcheon consisting of 57–68 scales that is short (6–8 scales along a central longitudinal row of ventrals) but involves most if not all longitudinal rows of V at its central level (12–15 scales), and can thus be considered as relatively wide. As in the former species, they lack a discernible subfemoral escutcheon. In the male specimens of *Lepidoblepharis* sp. 2 which I examined, the V escutcheon consisting of 38–61 scales is short (6–7 scales) and relatively narrow (10–13 scales in width, leaving out some longitudinal rows of V on each side). Additionally, all examined males of this lineage have a clearly visible subfemoral escutcheon consisting of 4–5 scales arranged in a single row under each thigh (Fig. 4.6C). In my examined males of *L. xanthostigma,* the V escutcheon contains 36–90 scales and may be short or long: As noted by Taylor (1956), it is usually shorter in smaller males (6–8 scales in the two Panamanian males with SVL < 30 mm) and long in larger males (10–12 scales in the four Panamanian males with SVL > 30 mm). The V escutcheon may appear rather narrow to wide (8–13 scales), though it never covers all longitudinal rows of V at its widest level. Most examined males (11 of 13) have a distinct subfemoral escutcheon at least under one thigh, comprising 1–7 scales in 1–2 rows per side (Fig. 4.6D).

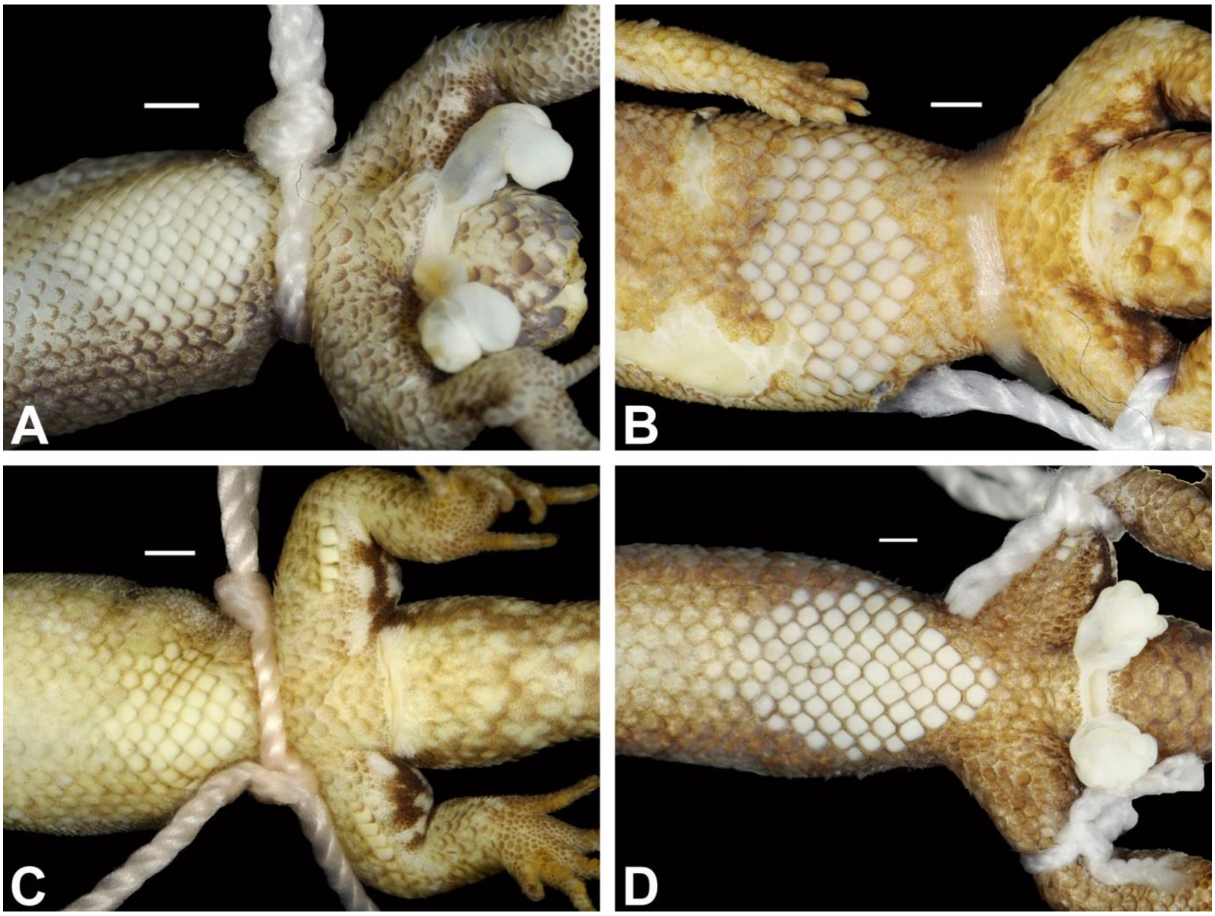


Figure 4.6: Escutcheon scales in males of Panamanian *Lepidoblepharis.* (A) *L. sanctaemartae:* ventral escutcheon of AB 385 (SVL = 22 mm) comprising 92 scales, 10 scales long x 12 wide; (B) *Lepidoblepharis* sp. 1: ventral escutcheon of SMF 89963 (SVL = 27 mm) comprising 57 intact scales (an original total of 61 is assumed considering the symmetrical scale arrangement of the non-damaged portions), 7 long x 14 wide; (C) *Lepidoblepharis* sp. 2: ventral escutcheon with 46 scales, 7 long x 11 wide, and subfemoral escutcheon with 4 scales per side, of SMF 81951 (SVL = 25 mm); (D) *L. xanthostigma:* ventral escutcheon with 75 scales, 12 long x 11 wide, and subfemoral escutcheon with 2 scales per side (no additional scales hidden under strings), of SMF 90189 (SVL = 35 mm). All scale bars equal 1 mm.

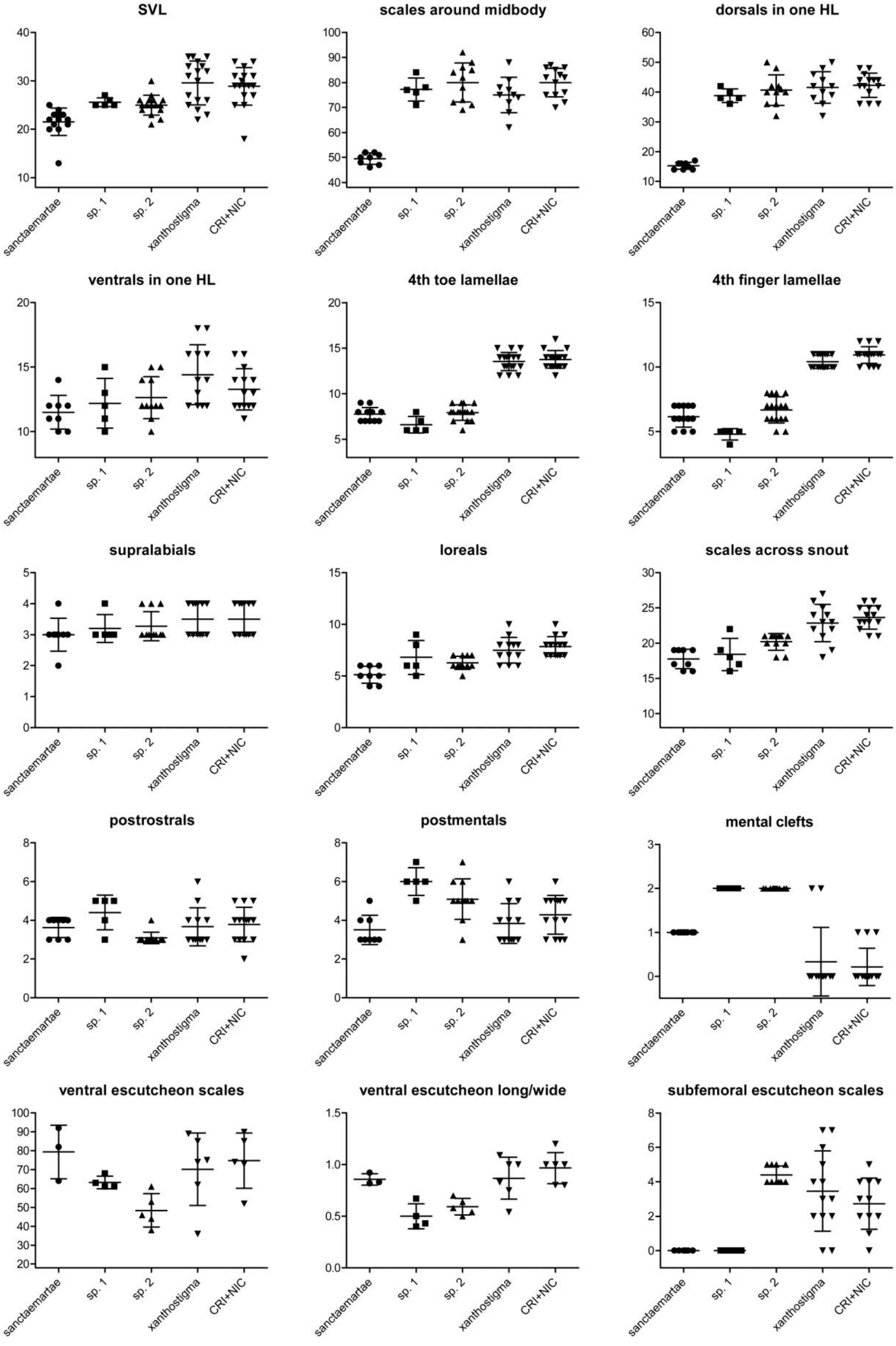


Figure 4.7: Selected morphological characteristics of Central American *Lepidoblepharis.* Horizontal bars represent mean ± standard deviation. CRI+NIC comprises the specimens of *L. xanthostigma* from Costa Rica and Nicaragua, whereas all other specimens are from Panama.

Other characters usually employed in *Lepidoblepharis* systematics, as rostral shape and numbers of postrostrals, loreals, or scales across snout, appear less helpful in distinguishing the three Panamanian lineages with granular dorsals. In Figure 4.7, selected morphological characters are compared for the four Panamanian lineages and the combined specimens from Costa Rica and Nicaragua.

Table 4.2: Uncorrected p-distances in the 16S rRNA gene of the five *Lepidoblepharis* and nine anoles used in the molecular analyses. Individual p-distances in lower-left, mean distances between lineages in upper-right matrix. Mean distances within a lineage are in **bold** face.

		Dactyloa ibanezi	***Norops pachypus***		***N. pseudopachypus***		***N. kemptoni***		***N. gruuo***		***Lepidoblepharis xanthostigma***			***Lepidoblepharis* sp. 1**	***Lepidoblepharis* sp. 2**
		LSt 049	JFB 027	SL 201	JFB 010	SL 520	SL 402	SL 590	SL 355	SL 761	SL 558	SL 750	SL 760	AB 018	AB 415
D. ibanezi	LSt 049		0.128		0.133		0.132		0.124			0.203		0.219	0.216
N. pachypus	JFB 027	0.129	**0.002**		0.065		0.098		0.092			0.200		0.206	0.191
	SL 201	0.126													
N. pseudo-pachypus	JFB 010	0.141	0.070	0.068	**0.035**		0.089		0.094			0.211		0.206	0.196
	SL 520	0.125	0.063	0.060											
N. kemptoni	SL 402	0.132	0.101	0.100	0.100	0.082	**0.010**		0.072			0.200		0.211	0.212
	SL 590	0.132	0.095	0.095	0.094	0.079									
N. gruuo	SL 355	0.121	0.091	0.089	0.094	0.091	0.076	0.069	**0.023**			0.194		0.209	0.210
	SL 761	0.128	0.095	0.093	0.096	0.093	0.074	0.067							
L. xantho-stigma	SL 558	0.198	0.200	0.202	0.212	0.208	0.193	0.196	0.188	0.194					
	SL 750	0.206	0.200	0.202	0.213	0.207	0.201	0.205	0.191	0.199	0.031	**0.029**		0.114	0.126
	SL 760	0.206	0.198	0.200	0.217	0.209	0.199	0.203	0.193	0.199	0.033	0.023			
***L.* sp. 1**	AB 018	0.219	0.205	0.207	0.214	0.198	0.208	0.214	0.206	0.212	0.117	0.116	0.110		
***L.* sp. 2**	AB 415	0.216	0.190	0.192	0.206	0.185	0.211	0.212	0.208	0.212	0.122	0.125	0.131	0.106	

In order to assess genetic differentiation among the lineages with granular dorsals, I compared the 16S barcodes of three specimens of *Lepidoblepharis xanthostigma* collected by myself with the 16S barcodes provided to me by AB of one *Lepidoblepharis* sp. 1 and one *Lepidoblepharis* sp. 2 which he had collected in central and eastern Panama, respectively. To aid recognition of species boundaries, I analyzed them together with 9 anole barcodes including two individuals each of four *Norops* species more or less closely related to each other (see chapters 4.1.4 and 4.1.5) and one specimen of *Dactyloa.* A specimen of the dipsadid snake *Sibon nebulatus* served as the outgroup. The manually refined alignment (provided in Appendix 5.2) contained 554 positions, of which (excluding the outgroup) 192 were variable and 147 parsimony-informative. The uncorrected p-distances calculated for the 14 lizard sequences are summarized in Table 4.2. Among the three individuals of long-toed *L. xanthostigma,* p-distances range from 2.3–3.3%, which is within the range of intraspecific p-distances calculated for *N. gruuo* and *N. pseudopachypus.* The p-distances between the two short-toed specimens (10.6%) and between any short-toed specimen and representatives of *L. xanthostigma* (11.0–13.1%) are larger than any of the interspecific distances within the genus *Norops*, some even as high as the distances observed between *Norops* and *Dactyloa*, indicating a genetic differentiation at species level.

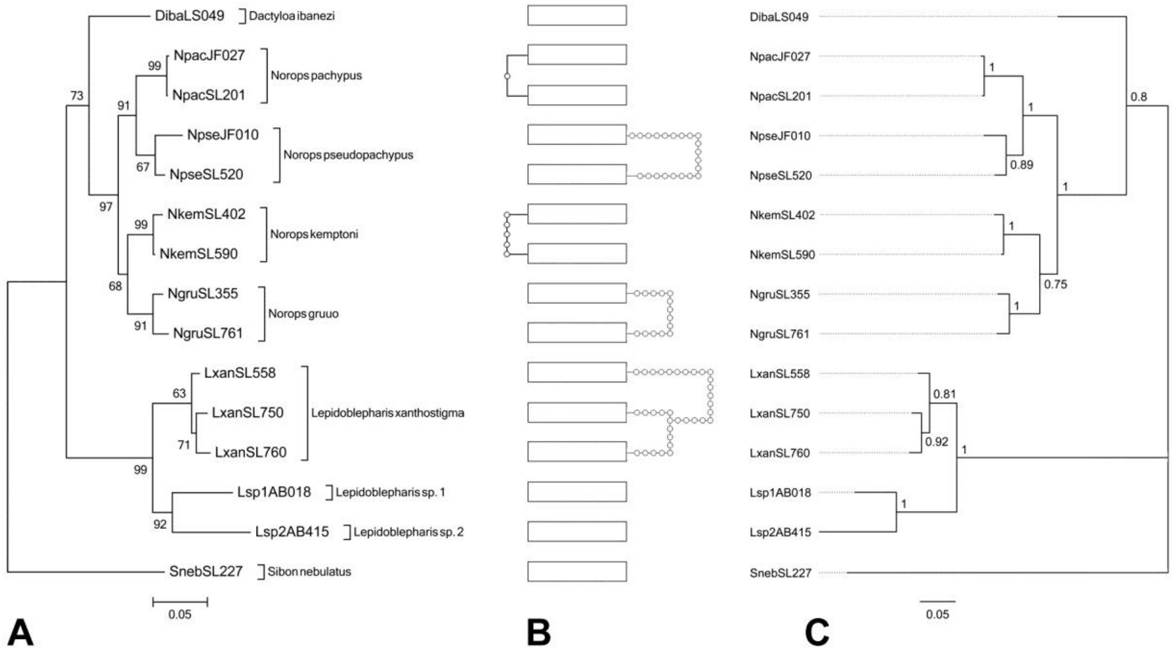


Figure 4.8: Results of molecular analyses. (A) Consensus tree from Maximum Likelihood analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps (black, left) and additional connections resulting from increasing the connection limit to 30 steps (gray, right). (C) Consensus tree from Bayesian analysis.

The GTR+G model was determined as the best-fitting substitution model. The results of the ML, PN (95% parsimony probability resulting in a connection limit of 10 steps, manually increased to 30 steps in subsequent analyses), and BI analyses are shown in Figure 4.8. With the exception of *Lepidoblepharis xanthostigma* and *Norops pseudopachypus,* all putatively specific lineages are supported by bootstrap values > 90% in the ML, and posterior probabilities of 1 in the BI analysis. The relatively high genetic distances between the sampled individuals of all lineages except *N. pachypus* and *N. kemptoni* prevent their haplotypes to be connected in the PN analysis with a 95% parsimony probability. Only after manually increasing the connection limit to 30 steps in subsequent analyses, each morphological lineage's sampled haplotypes are connected within a common haplotype network. The largest number of substitutional steps are found between the sampled individuals of *N. pseudopachypus* (22) and *L. xanthostigma* (27 and 30), respectively. This profound genetic differentiation reveals the existence of distinct genealogical lineages within each of these two morphospecies, as also reflected by the relatively long branches within, and the low bootstrap values and posterior probabilities for, their respective clades in the ML and BI analyses.

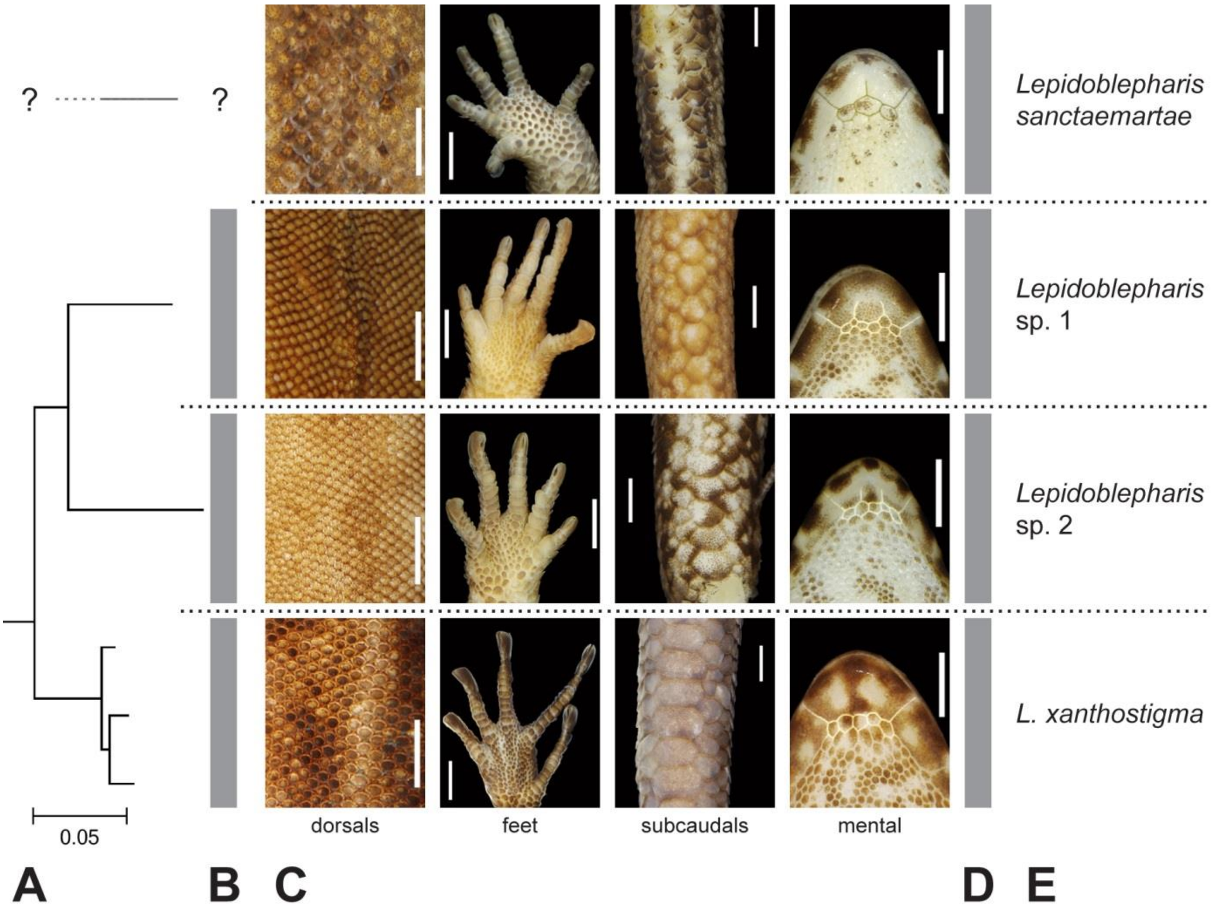


Figure 4.9: Integration of morphological and molecular evidence. (A) ML tree of sampled voucher specimens; (B) lineages as confirmed by molecular evidence; (C) synopsis of selected morphological characteristics found to distinguish the inferred CGLs from each other; (D) lineages as confirmed by morphological evidence; (E) taxonomic identities of inferred CGLs.

Morphological and molecular results are summarized and compared in Figure 4.9. Although no molecular data for *L. sanctaemartae* was available, its large, imbricate dorsals combined with the other morphological distinctions revealed above constitute sufficient evidence to accept it as a CGL among Panamanian *Lepidoblepharis.* For this CGL, the applicable taxonomic identity is obviously and unequivocally that which I have employed throughout this chapter. Ruthven (1928) described Panamanian populations of *L. sanctaemartae* as a new subspecies, *L. s. fugax,* which he diagnosed from the nominal subspecies found around the type locality in the Santa Marta mountains of northern Colombia by the higher number of postmentals. He stated that in the Panamanian subspecies "the mental scute is usually bordered posteriorly by five, or less frequently four, scales" (p. 2) as opposed to the "usually three large scales" (p. 3) found in the nominal subspecies. Since four of the eight specimens which I examined have only three postmentals, I cannot reconfirm this subspecific distinctiveness.

The results of the molecular analyses unanimously confirm the existence of three deeply differentiated genealogical lineages among Panamanian *Lepidoblepharis* with granular dorsals, corresponding to those already revealed by the morphological comparisons. Integrating morphological and molecular evidence, I recognize the three lineages with granular dorsals as separate CGLs. That is, Panama is home to four well-differentiated species instead of just two as hitherto assumed. Table 4.3 summarizes the variation in selected morphological characters among the four species of *Lepidoblepharis* found in Panama as exhibited by the examined material. For the three CGLs with granular dorsals, my taxonomic conclusions are as follows.

The nominal species *L. xanthostigma* has been described from "Zent, near Puerto Limon, Costa Rica", a locality in the Caribbean lowlands of Limón province in eastern Costa Rica (Noble 1916). This type locality is situated roughly 100 km NW of my westernmost collection site of *L. xanthostigma* (San San Pond Sak, specimens SL 558 and SL 563). The Panamanian specimens treated throughout this chapter as *L. xanthostigma* exhibit an overwhelming congruence in their morphological variation to the specimens from Costa Rica and Nicaragua, as shown in Figure 4.7 and Table 4.3. Moreover, the Panamanian specimens comply with the descriptions of *L. xanthostigma* provided by different authors (Taylor 1956; Ayala & Castro 1983; Lamar 1985; Savage 2002; Köhler 2008), as well as with the photos of the holotype (MCZ 11658) available from the MCZ collection database (mczbase.mcz.harvard.edu). Thus, the assignment of the long-toed Panamanian specimens to this nominal taxon can confidently be reconfirmed. Since the high genetic differentiation among populations of *L. xanthostigma* revealed by the analyses of 16S barcodes is not correlated with any consistent morphological distinctions in my sample, I preliminarily classify the corresponding genealogical lineages as DCLs pending further study.

Table 4.3: Selected morphological characters of Lower Central American *Lepidoblepharis*. For *L. xanthostigma,* variation for specimens from Panama only and Lower Central America as a whole (LCA: Costa Rica, Panama, and Nicaragua) is shown separately

	Lepidoblepharis sanctaemartae	***Lepidoblepharis* sp. 1**	***Lepidoblepharis* sp. 2**	***L. xanthostigma***	
	N = 14	N = 5	N = 16	Panama N = 17	LCA N = 34
SVL	13–25 (21.6 ± 2.58)	25–27 (25.6 ± 0.89)	21–30 (25.0 ± 2.07)	22–35 (29.6 ± 4.54)	18–35 (29.2 ± 4.17)
TL	12–21 (16.5 ± 6.36) n = 2	31 n = 1	18–31 (24.4 ± 4.83) n = 5	23–49 (35.3 ± 9.71) n = 7	23–49 (35.3 ± 7.70) n = 11
TL / SVL	0.92–0.95 (0.94 ± 0.02) n = 2	1.15 n = 1	0.82–1.24 (1.01 ± 0.15) n = 5	0.89–1.4 (1.17 ± 0.18) n = 7	0.89–1.4 (1.18 ± 0.15) n = 11
HL / SVL	0.2–0.22 (0.21 ± 0.01) n = 8	0.2–0.23 (0.21 ± 0.01)	0.2–0.25 (0.22 ± 0.01) n = 11	0.19–0.24 (0.22 ± 0.01) n = 12	0.19–0.24 (0.22 ± 0.01) n = 26
Dorsals	flat, imbricate	granular	granular	granular	granular
VHL	10–14 (11.5 ± 1.31) n = 8	10–15 (12.2 ± 1.92)	10–15 (12.6 ± 1.63) n = 11	12–18 (14.4 ± 2.31) n = 12	11–18 (13.8 ± 2.0) n = 26
DHL	14–17 (15.3 ± 1.16) n = 8	36–42 (38.8 ± 2.28)	32–50 (40.6 ± 5.14) n = 11	32–50 (41.5 ± 5.32) n = 11	32–50 (42.0 ± 4.57) n = 25
4 toe lamellae	7–9 (7.8 ± 0.73)	6–8 (6.6 ± 0.89)	6–9 (7.9 ± 0.85)	12–15 (13.5 ± 1.01)	12–16 (13.6 ± 0.98)
4 finger lamellae	5–7 (6.2 ± 0.80)	4–5 (4.8 ± 0.45)	5–8 (6.7 ± 1.01)	10–11 (10.4 ± 0.51)	10–12 (10.7 ± 0.64)
SPL	2–4 (3.0 ± 0.53) n = 8	3–4 (3.2 ± 0.45)	3–4 (3.3 ± 0.47) n = 11	3–4 (3.5 ± 0.52) n = 12	3–5 (3.6 ± 0.58) n = 26
PM	3–5 (3.5 ± 0.76) n = 8	5–7 (6.0 ± 0.71)	3–7 (5.1 ± 1.04) n = 11	3–6 (3.8 ± 1.03) n = 12	3–6 (4.1 ± 1.02) n = 26
PR	3–4 (3.6 ± 0.52) n = 8	3–5 (4.4 ± 0.89)	3–4 (3.1 ± 0.3) n = 11	3–6 (3.7 ± 0.98) n = 12	2–6 (3.7 ± 0.92) n = 26
Clefts in posterior border of mental	1 (1 ± 0) median n = 8	2 (2 ± 0) paramedian	2 (2 ± 0) paramedian n = 11	0–2 (0.33 ± 0.78) short, lateral n = 12	0–2 (0.27 ± 0.60) short, lateral n = 26
loreals	4–6 (5.1 ± 0.83) n = 8	5–9 (6.8 ± 1.64)	5–7 (6.3 ± 0.65) n = 11	6–10 (7.5 ± 1.24) n = 12	6–10 (7.7 ± 1.09) n = 26
scales across snout	16–19 (17.8 ± 1.39) n = 8	16–22 (18.4 ± 2.30)	18–21 (20.2 ± 1.17) n = 11	18–27 (22.8 ± 2.66) n = 12	18–27 (23.3 ± 2.16) n = 26
SAM	46–52 (49.5 ± 2.27) n = 8	71–84 (77.2 ± 4.66)	69–92 (80.0 ± 7.8) n = 11	62–88 (75.0 ± 7.04) n = 10	62–88 (77.8 ± 6.66) n = 23
Ventrals at MB		15–19 (17.4 ± 1.52)	16–20 (18.2 ± 1.17) n = 11	16–20 (18.3 ± 1.3) n = 12	16–21 (18.9 ± 1.23) n = 26
Dorsals at MB		53–67 (59.8 ± 5.36)	52–74 (61.8 ± 7.61) n = 11	44–69 (57.3 ± 6.67) n = 10	44–69 (59.1 ± 6.03) n = 23
Ventral escutcheon scales	64–92 (79.3 ± 14.19) n = 3	61–68 (63.3 ± 3.30) n = 4	38–61 (48.4 ± 8.85) n = 5	36–89 (70.2 ± 19.22) n = 6	36–90 (72.3 ± 16.63) n = 11
Ventral escutcheon long	9–11 (10.0 ± 1.0) n = 3	6–8 (6.8 ± 0.96) n = 4	6–7 (6.8 ± 0.45) n = 5	6–12 (9.3 ± 2.34) n = 6	6–12 (9.7 ± 1.97) n = 12
Ventral escutcheon wide	11–12 (11.7 ± 0.58) n = 3	12–15 (13.8 ± 1.26) n = 4	10–13 (11.6 ± 1.14) n = 5	8–13 (10.8 ± 1.72) n = 6	8–13 (10.6 ± 1.24) n = 12
Subfemoral escutcheon scales per thigh	0 n = 6	0 n = 8	4–5 (4.4 ± 0.52) n = 10	0–7 (3.5 ± 2.33) n = 13	0–7 (3.1 ± 1.98) n = 24

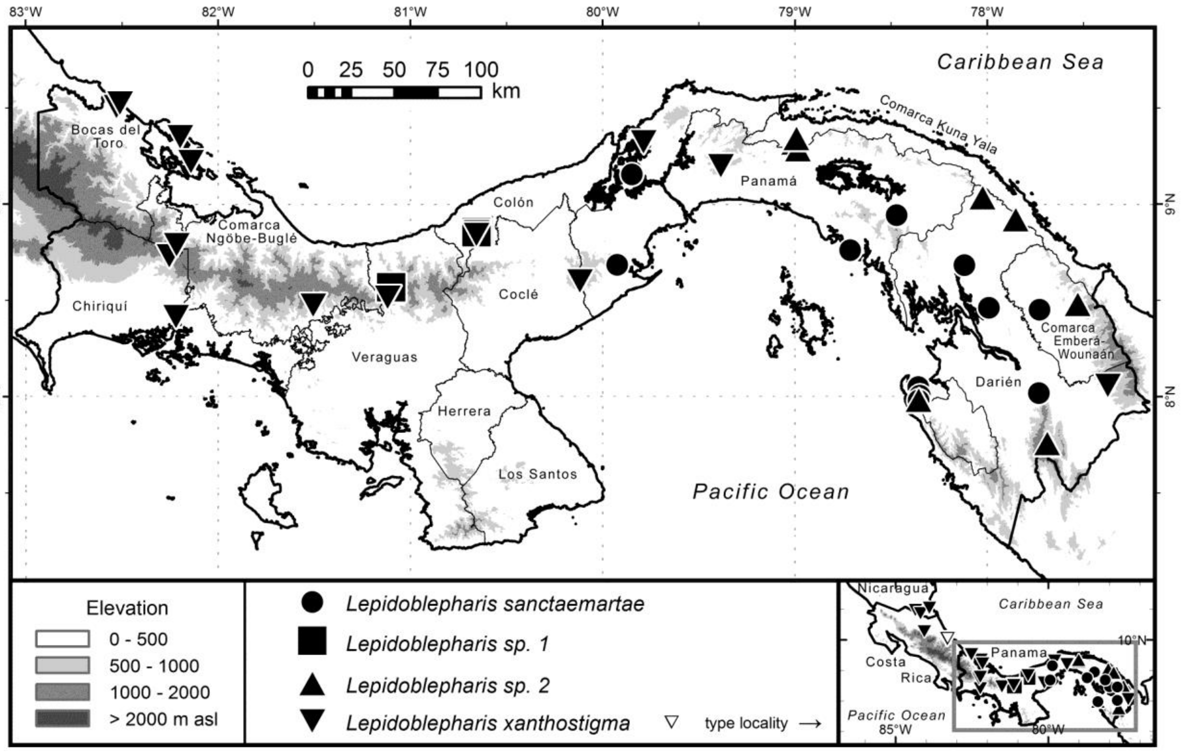
This leaves to be clarified the taxonomic identities of the two short-toed CGLs with granular dorsals. To date, seven species of the genus *Lepidoblepharis* have been reported to possess ten or less lamellae under the 4th toe, i.e., to be short-toed. Two of these, *L. miyatai* Lamar 1985 and *L. sanctaemartae,* possess imbricate dorsal scales and thus are out of question as possible names for the two CGLs. The five remaining species with short toes and granular dorsals are *L. buchwaldi* Werner 1910, *L. microlepis* (Noble 1923), *L. montecanoensis* Markezich & Taphorn 1994, *L. peraccae* Boulenger 1908, and *L. williamsi* Ayala & Serna 1986. For the two relatively recently and rather meticulously described species *L. montecanoensis* and *L. williamsi,* photographs of type specimens are available from the MCZ collection database, and the authors of the latter species have even made the effort to adorn its description with line drawings of diagnostic features. In contrast, no illustrations have been published for the remaining three species. Especially *L. microlepis* and *L. peraccae* are apparently known only from one or a few specimens, and no sound descriptions of their morphology exist. At the time of their respective descriptions, the subdigital lamellae had not yet been recognized as a primordial character for distinguishing members of the genus. In the case of *L. microlepis,* it is not even sure if we are dealing with a short-toed species, since Lamar (1985) stated it to have ten or fewer lamellae under the 4th toe, but Markezich & Taphorn (1994) reported it to have more than ten. However, the latter authors based their statement on the key of Parker (1926), who stated all species with granular dorsals that he examined (including *L. peraccae* and *L. microlepis*) to have 10 or more lamellae under the 4th toe. Anyway, *L. microlepis* has been considered a "problematic" species (Lamar 1985; Markezich & Taphorn 1994; Avila-Pires 2001) and a possible synonym of *L. peraccae* (Ayala & Serna 1986) or *L. xanthostigma* (Ruthven 1928; Peters & Donoso-Barros 1970).

Fortunately, these uncertainties could be overcome with photos of preserved specimens taken by colleagues. For *Lepidoblepharis buchwaldi,* GK provided me with photos he had taken of the specimen MCZ 151710. Photographs of the respective holotypes of *L. microlepis* and *L. peraccae* kindly provided by David Dickey (AMNH) and Patrick Campbell (BMNH). The holotype of *L. microlepis* (AMNH R-18229) has 9 lamellae under the 4th toe, which are more narrow basally and distally than around the central portion of the toe, and 6 under the 4th finger. Most notably, it has only slightly enlarged SC with rounded posterior margins and a regular tail sequence of 1'1'. The holotype of *Lepidoblepharis peraccae* (BMNH 1908.5.29.46) has 10 lamellae under the 4th toe and 8 under the 4th finger, which in both cases appear to gradually decrease in size towards the claw. A first conclusion to be drawn from the examination of these images is that *L. microlepis* is neither conspecific with *L. peraccae* nor *L. xanthostigma.*

The possibility that the CGL *Lepidoblepharis* sp. 1 represents either of the five hitherto described short-toed species with granular dorsals can confidently be ruled out, since the illustrations and photographs available to me show none to have the subdigital lamellae as conspicuously enlarged as it is the case in *Lepidoblepharis* sp. 1. Moreover, although AB, GK, and MP have accumulated many specimens of *Lepidoblepharis* from eastern Panama representing all remaining CGLs, *Lepidoblepharis* sp. 1 has until now only been collected west of the Panama Canal in the provinces of Colón and Veraguas (Map 4.1). Based on current knowledge, I thus consider this CGL to be absent from eastern Panama. This would render its occurrence in Colombia and the possibility that the taxon has been formally described from that country in the past very unlikely. Thus, I recognize *Lepidoblepharis* sp. 1 as an undescribed species that I include in the reptile fauna of my study area.

In contrast, the CGL *Lepidoblepharis* sp. 2 has only been collected east of the Panama Canal, both in the Caribbean and the Pacific drainage (Map 4.1). Its collection sites suggest that it should also be present in Colombia, and thus might well represent a species with short toes described from that country. The pertinence to *L. montecanoensis* or *L. williamsi* can again be ruled out, since the illustrations available to me clearly show that none of these species has the proximal lamellae as enlarged as *Lepidoblepharis* sp. 2, nor distinctly enlarged median SC. *Lepidoblepharis microlepis* and *L. peraccae* also lack a set of distinctly and homogeneously enlarged proximal lamellae. While the photos of the latter species available to me do not include ventral views of the tail, *L. microlepis* is further distinguished from all Panamanian lineages examined herein by its tail sequence of 1'1'. *Lepidoblepharis buchwaldi* does exhibit enlarged median SC in the characteristic 1'1" sequence similar to those of *Lepidoblepharis* sp. 2 as well as slightly enlarged proximal lamellae, but has a single median cleft in the posterior mental border. Thus, I recognize this CGL as a second undescribed species of the genus in Panama. Yet, considering that the CGL is apparently absent from western Panama and almost certainly does not occur in my study area, it clearly falls outside the scope of the present study. The taxonomic actions revealed to be necessary will be taken in the course of an integrative revision of Central American *Lepidoblepharis* which is the subject of ongoing work by AB, myself, and various colleagues (Batista et al. in prep. a).

The provenances of all examined specimens from CA are shown in Map 4.1. Two species of *Lepidoblepharis* are herein documented occur in my study area: *Lepidoblepharis* sp. 1 and *L. xanthostigma.* Standardized descriptions of these species are provided in their respective species accounts in chapter 4.2.2. Figures 4.10 and 4.11 illustrate their morphological variation. Last, the following key sums up the diagnostic features and should allow for a doubtless identification of any Panamanian *Lepidoblepharis.*



Map 4.1: Collection localities of Central American *Lepidoblepharis* specimens examined in this study.

Key to the species of *Lepidoblepharis* in Panama

1. Dorsals cycloid, flat, and imbricate; 7–9 lamellae under 4th toe, 5–7 under 4th finger; a single median cleft in posterior border of mental .... ***Lepidoblepharis sanctaemartae***

   Dorsals granular, not imbricate, usually raised with a pointed or keeled appearance **2**

2. Twelve or more lamellae under 4th toe, 10 or more under 4th finger; posterior border of mental usually without, sometimes with 1–2 short lateral clefts; median subcaudal scales greatly enlarged, more than twice as wide as the adjacent subcaudals and wider than long .... ***L. xanthostigma***

   Less than 10 lamellae under 4th toe and 4th finger; posterior border of mental with two pronounced paramedian clefts; median subcaudal scales not or only slightly enlarged, rarely wider than long **3**

3. Median subcaudal scales only slightly enlarged; 6–8 lamellae under 4th toe, 4–5 under 4th finger; 1–3 proximal subdigital lamellae per digit greatly enlarged, up to 4 times as long as the distal one(s); males with a ventral escutcheon consisting of 61–68 scales (6–8 scales long and 12–15 wide), but without distinct femoral escutcheon scales .... ***Lepidoblepharis* sp. 1**

   Median subcaudal scales distinctly enlarged; 6–9 lamellae under 4th toe, 5–8 under 4th finger; 1–6 proximal subdigital lamellae per digit slightly enlarged, at most twice as long as the distal one(s); males with a ventral escutcheon consisting of 38–61 scales (6–7 scales long and 10–13 wide), and 4–5 conspicuous subfemoral escutcheon scales per thigh .... ***Lepidoblepharis* sp. 2**

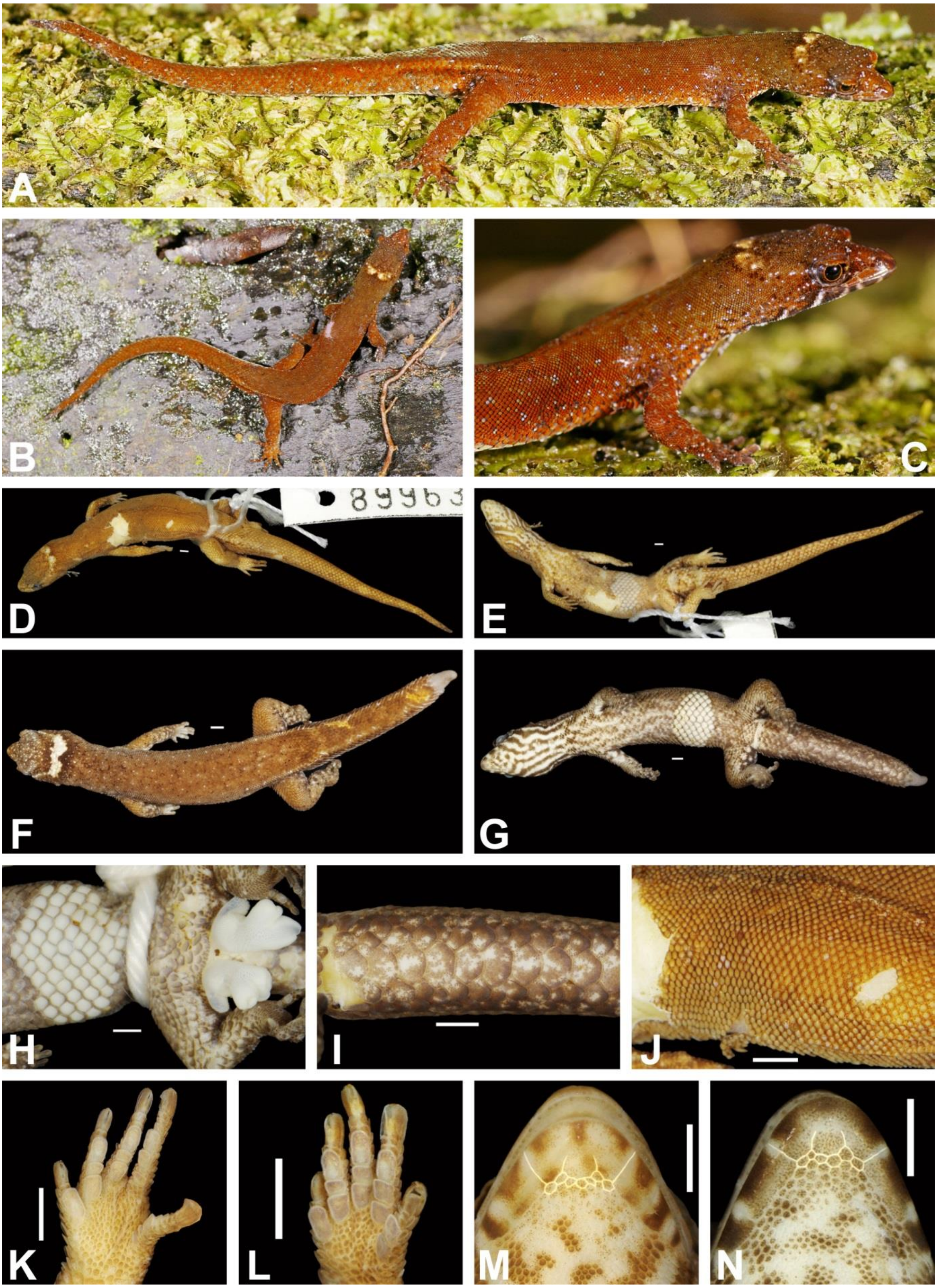


Figure 4.10: *Lepidoblepharis* sp. 1. (A–C) Adult male SMF 89963 from Cerro Negro in life and (D, E) after approximately 5 years in preservative; (F) dorsal and (G) ventral view of preserved male AB 1251 from Petaquilla, Colón province; (H–I) preserved male AB 018 from Petaquilla: (H) detail of ventral surface showing ventral escutcheon and everted hemipenes, (I) ventral view of base of tail showing slightly enlarged subcaudal scales comparatively wide for this species; (J–M) details of SMF 89963: (J) dorsolateral view of left side of midbody showing granular dorsals; (K) ventral view of left foot, (L) ventral view of left hand, (M) ventral view of chin area; (N) ventral view of chin area of AB 018.

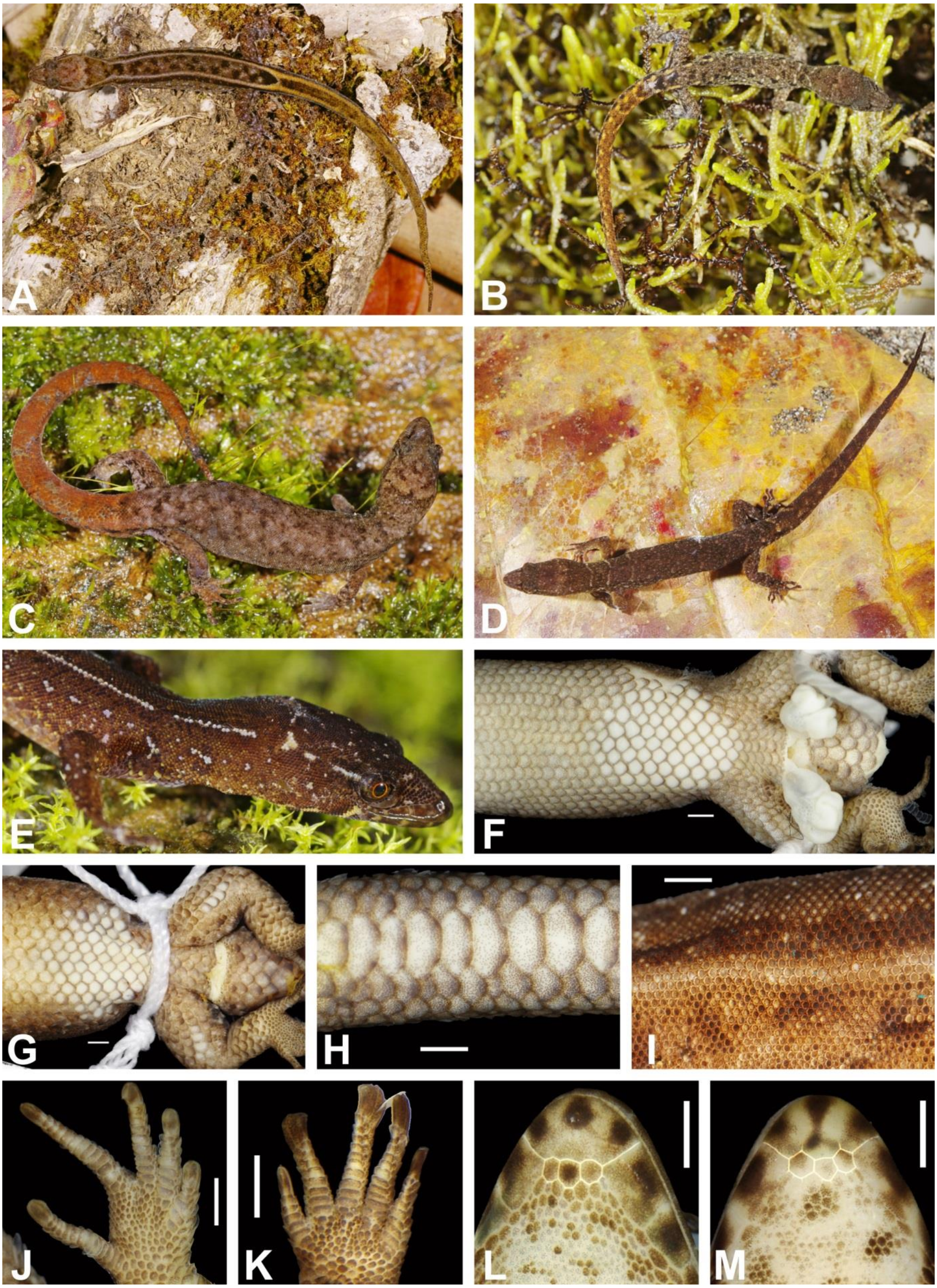


Figure 4.11: *Lepidoblepharis xanthostigma.* (A) Adult male SMF 89576 and (B) juvenile SMF 91559 from Cerro Mariposa; (C) adult male SMF 91558 from Alto Tólica; (D) female MHCH 2338 from San San Pond Sak; (E) adult male SMF 90189 from headwaters of Río Chiriquí Malí; (F) ventral view of SMF 91558 showing ventral and rather undistinct subfemoral escutcheon as well as everted hemipenes; (G) ventral and very distinct subfemoral escutcheon of SMF 89576; (H) subcaudal scales of SMF 91558; (I) dorsolateral view of right side of midbody showing granular dorsals of SMF 89576; (J) ventral view of right foot of SMF 85005 from Meseta de Chorcha and (K) ventral view of left hand of SMF 91558; (L) ventral view of chin area of SMF 91558; (M) ventral view of chin area of SMF 85005.

4.1.3 Iguania, Dactyloidae: The giant alpha anoles of the genus *Dactyloa* in the highlands of western Panama, with the description of a new species formerly referred to as *D. microtus*

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Abstract: Six species of giant alpha anoles of the genus *Dactyloa* are known to occur in western Panama: *Dactyloa casildae, D. frenata, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus.* Based on own material collected along the highlands in Bocas del Toro, Chiriquí, and Veraguas provinces and the Comarca Ngöbe-Buglé of western Panama, we review their variation in morphological characters and the 16S rRNA mitochondrial gene. Our results support all six nominal taxa, but reveal considerable genetic differentiation between populations of the two highland species, *D. casildae* and *D. microtus,* respectively, from different localities. Correlated morphological differences confirm the existence of a cryptic species among populations currently assigned to *D. microtus,* which we describe as *Dactyloa ginaelisae* sp. nov. We provide point distribution maps, morphology and color descriptions, photographs in life, conservation status assessments, and an identification key for all seven species.

Key words: *Anolis, Dactyloa*, Lower Central America, Cordillera Central, Talamancan highlands, Tabasará range, morphology, 16S barcoding, conservation.

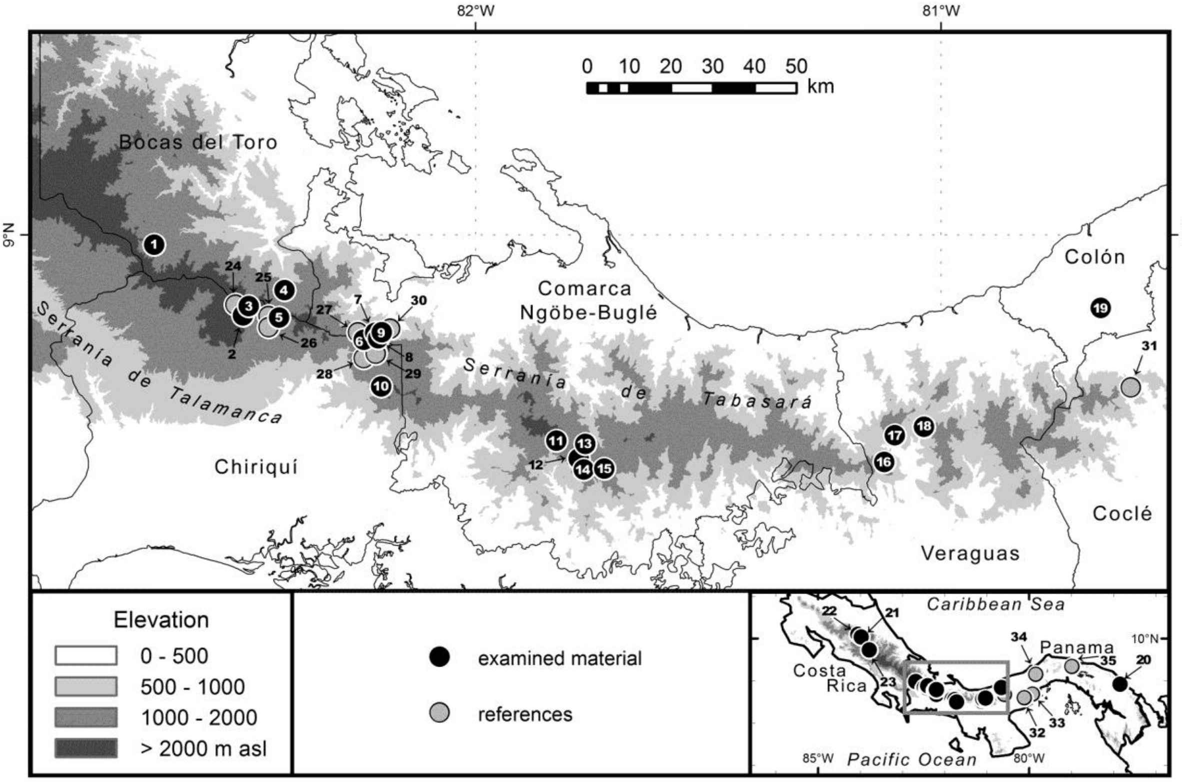
The anoline fauna of Lower Central America (Costa Rica and Panama) is composed of two principal lineages (Savage 2002; Köhler 2008). Most species are referable to the beta section of Etheridge (1959), and have been included in the genus *Norops* Wagler by Guyer & Savage (1986). These anoles are typically of small to moderate size and rather inconspicuously colored with a predominance of brownish or grayish tones. Besides these, some representatives of Etheridge's (1959) alpha section are also found in the region (Köhler 2008; Jaramillo et al. 2010). These moderately-sized to large anoles exhibit a usually more colorful appearance typically including green tonalities and most of them were referred to the genus *Dactyloa* Wagler by Guyer & Savage (1986) — a taxonomic conclusion discussed controversially ever since (see Poe 2004, Köhler 2008, Nicholson et al. 2012, and references therein). Recently, Castañeda & de Queiroz (2011) provided molecular evidence for the monophyly of the *Dactyloa* clade of anoles. Moreover, they confirmed the close relationship among most Central American members of the *Dactyloa* clade that were included in their analysis within a monophylum roughly corresponding to the *latifrons* species group of Williams (1976) and the *latifrons* series of Savage & Guyer (1989). A year later, Nicholson et al. (2012) elevated eight major anole lineages to generic status, thereby also re-erecting the genera *Norops* and *Dactyloa.* We are well aware that the discussion about anole classification is ongoing, but see no problem in recognizing the monophyletic *Norops* and *Dactyloa* clades formally as genera.

To our knowledge, nine species of *Dactyloa* occur in Lower Central America (Savage 2002; Köhler 2008; Jaramillo et al. 2010): *Dactyloa casildae* (Arosemena, Ibáñez & de Sousa 1992), *D. chloris* (Boulenger 1898), *D. chocorum* (Williams & Duellman 1967), *D. frenata* (Cope 1899), *D. ibanezi* (Poe, Latella, Ryan & Schaad 2009), *D. insignis* (Cope 1871), *D. kunayalae* (Hulebak, Poe, Ibáñez & Williams 2007), *D. latifrons* (Berthold 1845), and *D. microtus* (Cope 1871). Additionally, the presence of *D. purpurescens* (Cope 1899) in eastern Panama has been suggested by Chun (2010), but to our knowledge no voucher specimens from Panama exist. Of the nine confirmed species, *D. chloris, D. chocorum,* and *D. latifrons* range from northwestern South America to eastern or central Panama and have not been reported from west of the Panama Canal (Köhler 2008; Poe et al. 2009; Jaramillo et al. 2010).

The other six species, without exception members of the *Dactyloa latifrons* species group *sensu* Nicholson et al. (2012), are known to occur in western Panama: *Dactyloa frenata* and *D. insignis* are widely distributed at lower elevations in Panama and Costa Rica (Köhler 2008). *Dactyloa ibanezi* comprises populations from central Panama to eastern Costa Rica formerly referred to as *D. chocorum* (Poe et al. 2009), whereas *D. microtus* is an endemic of the Lower Central American (or Talamancan) highlands of Costa Rica and western Panama (Savage 2002; Köhler 2008). The remaining two species are endemic to Panama: *Dactyloa kunayalae* has been reported from east-central to western Panama (Hulebak et al. 2007), and *D. casildae* is only known from three nearby localities in the western Cordillera Central (Nicholson et al. 2001; Chun 2010).

In general, little is known about these giant anoles suspected to be canopy dwellers of primary forests. Among the six species concerned here, the two wide-ranging lowland species *Dactyloa frenata* and *D. insignis* may be regarded as comparably well-studied, considering that both species had been collected in considerable numbers already at the time of Savage &

Talbot (1978), and color photographs from different parts of their range have been published (Savage 2002; Köhler 2003, 2008; Fläschendräger & Wijffels 2009; Uetz & Hošek 2014). Still, *D. frenata* is the only species having several aspects of its behavior and ecology studied (Scott et al. 1976; Losos et al. 1991). For the remaining four species, comparatively few specimens are traceable in public collections, and only scanty data on variation in pholidosis and coloration is available.



Map 4.2: Collection localities of *Dactyloa* specimens in western Panama (main map) and Lower Central America (inset). Black circles represent examined specimens and reliable photo records listed in Appendix 2, gray circles stand for other localities that are mentioned in the text and listed in Appendix 6. One symbol may summarize several localities close to each other. See text for abbreviations and details. (1) Río Changena; (2) Bajo Mono, Sendero La Cascada; (3) Alto Chiquero; (4) Sendero El Pianista, Casa de Calixto; (5) Sendero Pianista, 1500 m; (6) Cerro Guayabo; (7) headwaters of Río Chiriquí Malí; (8) Quebrada Arena; (9) Willie Mazú; (10) Cerro Pata de Macho; (11) Cerro Saguí; (12) Río Flor; (13) Río Hacha; (14) W slope Cerro Santiago, La Nevera; (15) E slope Cerro Santiago, Quebrada Ardilla; (16) Cerro Mariposa; (17) Cerro Negro; (18) Río Chilagres; (19) Distrito de Donoso: between Botija, Brazo, Petaquilla, and Río del Medio; (20) Camp Summit; (21) La Palma; (22) Cerro Dantas; (23) Parque Nacional Tapantí; (24) Sendero Quetzales on N slope Volcán Barú, 7000 ft = 2130 m; (25) Cerro Horqueta; (26) Boquete; (27) BPPS, transect of Hofer & Bersier (2001); (28) Smithsonian station at RFLF; (29) Quebrada Frank; (30) Road to Almirante, 400 m; (31) PNGDOTH north of El Copé; (32) Valle de Antón; (33) Altos de Campana; (34) Isla Barro Colorado; (35) Nusagandí.

Mostly between 2008 and 2010, our surveys around 18 different sites at premontane and lower montane elevations throughout the study area (Map 4.2) produced 68 voucher specimens representing all six species mentioned above to occur in western Panama, some of which represent noteworthy distributional range extensions or show undocumented morphological variation. In particular, we obtained the largest known samples of the hitherto sparsely collected highland endemics *Dactyloa casildae* and *D. microtus*. We take this opportunity to review the intra- and interspecific variation exhibited by the populations of *Dactyloa* along the Cordillera Central west of Santa Fé, as well as to summarize and update their geographic distribution.

Additional locality records for Panama and Costa Rica were taken from the original species descriptions mentioned in the preceding paragraphs of this chapter and other references (Barbour 1923; Dunn 1937a; Slevin 1942; Breder 1946; Myers 1971, 1977; Savage & Talbot 1978; Rand & Myers 1990; Martínez & Rodríguez 1994; Martínez et al. 1995; Ibáñez et al. 1995, 1996, 1997; de Sousa 1999; Hofer & Bersier 2001; Nicholson et al. 2001; Savage 2002; ANAM 2004, Köhler 2008; Köhler et al. 2008; Chun 2010; Castañeda & de Queiroz 2011), as well as from the catalogues of CHP and MVUP. For the 16S barcodes, the manually refined final alignment (18 *Dactyloa* and one *Norops humilis* as outgroup; provided in Appendix 5.3) contained 543 positions, of which, excluding the outgroup, 95 were variable and 83 parsimony-informative. For the COI barcodes, the final alignment (18 *Dactyloa* and one *Norops humilis* as outgroup; provided in Appendix 5.3) contained 565 positions, of which, excluding the outgroup, 182 were variable and 162 parsimony-informative. For both genes, HKY+G was determined as the best-fitting substitution model, ML and MP analyses were run with 10000 bootstrap replicates, BI was run over $2x10^6$ generations (discarding the initial 10%, i.e., 200 of the 2000 trees that were sampled every 1000 generations, as burn-in), and PN analyses were performed with a parsimony probability of 95% resulting in a connection limit of 10 steps. For the COI alignment, the connection limit was manually increased to 30 substitutional steps in subsequent analyses.

Most collected representatives of the genus *Dactyloa* could readily be identified to species level using the key to Central American anoles of Köhler (2008). The discrepancies we observed between the featured key characters and the animal at hand, especially in coloration (*Dactyloa casildae* and *D. microtus*), relative hind limb length (*D. kunayalae* and *D. microtus*), head scalation (*D. insignis* and *D. microtus*) and current taxonomy (*D. chocorum* vs. *D. ibanezi*), could be overcome by consulting the more recent species descriptions (Hulebak et al. 2007; Poe et al. 2009) as well as other color descriptions and color photographs of the species in question (Nicholson et al. 2001; Savage 2002; Köhler 2003, 2008; Köhler et al. 2008; Chun 2010), some of which only became available during our investigation. From the beginning of our field work, we were impressed by the ample variation in coloration pattern among individuals identified as representatives of *D. casildae* and *D. microtus,* whereas all representatives of the remaining four species presented a rather reliable specific color and pattern.

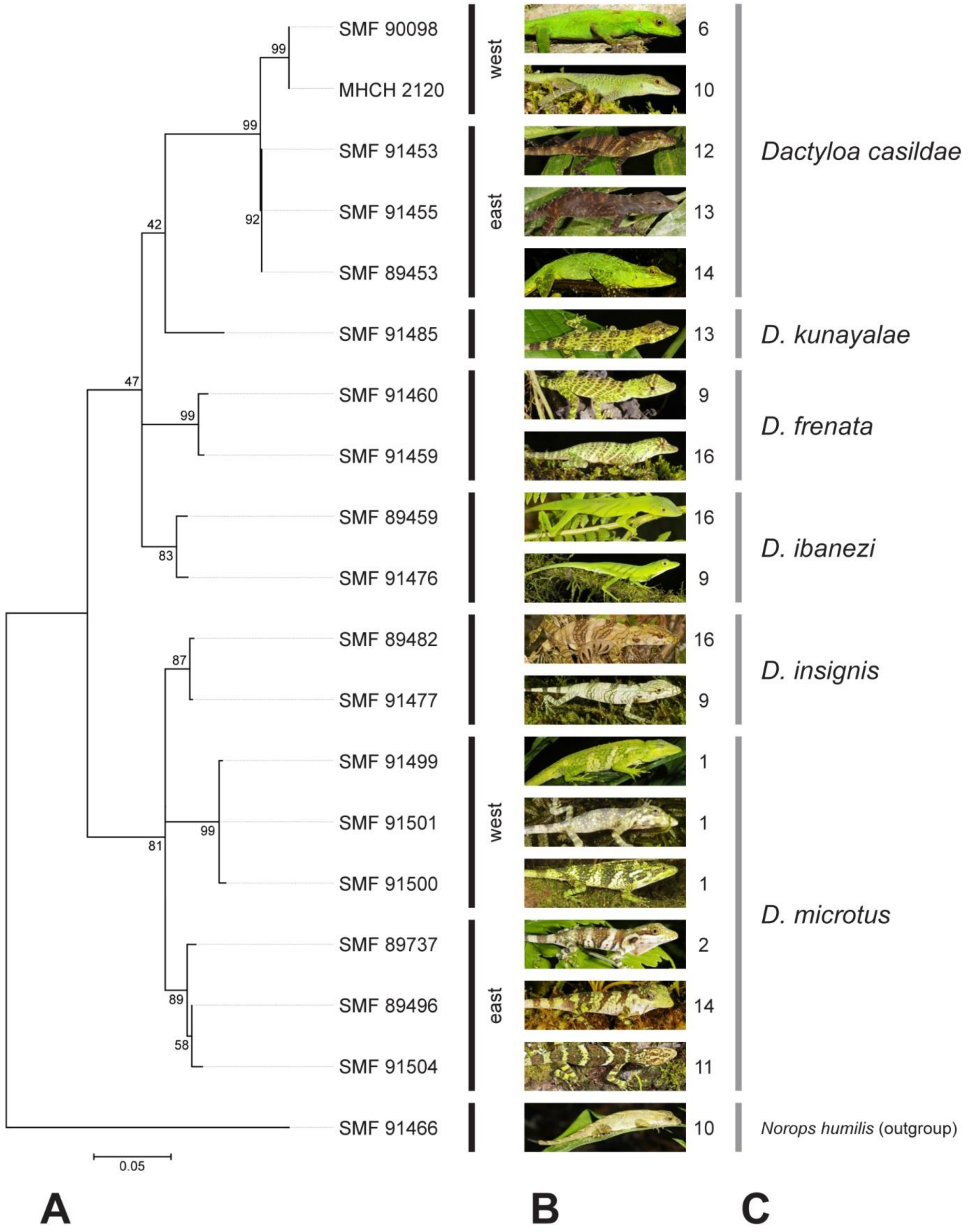


Figure 4.12: Comparison of 16S barcoding and morphology for *Dactyloa* from my study area. (A) Maximum likelihood consensus tree for the 16S barcodes of 19 Panamanian anoles. Black bars demarcate smallest well-supported clusters. (B) Sampled individuals in life, with locality numbers referring to Map 4.2. (C) Taxonomic identity derived from morphology on the basis of available literature.

A comparison of the morphological identification using available literature to the smallest diagnosable terminal clusters recovered in our ML analysis of 16S barcodes obtained from representative individuals (Fig. 4.12) shows congruence for all species except *Dactyloa casildae* and *D. microtus,* respectively, that appear composed of two lineages each. Within both nominal taxa, the respective subclades do not reflect color variants, but appear correlated with geographical longitude of the collection sites: The western clade of *D. casildae* comprises animals from near the type locality (Map 4.2: locality 29) at RFLF, while individuals collected east of RFLF between Cerro Saguí and Cerro Santiago cluster together as "*D. casildae* east". The mean *p*-distance within each of these two subclades is 0.0%, and 1.7% between the two subclades. In the case of *D. microtus,* the western lineage contains our three westernmost individuals (from Río Changena in Bocas del Toro Province; loc. 1 in Map 4.2), while the specimens from east of Volcán Barú form "*D. microtus* east". The respective mean *p*-distances within these subclades are 0.37% (west) and 0.88% (east), while the mean *p*-distance between the two lineages is 3.9%. The complete *p*-distance matrix for the 16S barcodes is shown in Table 4.4.

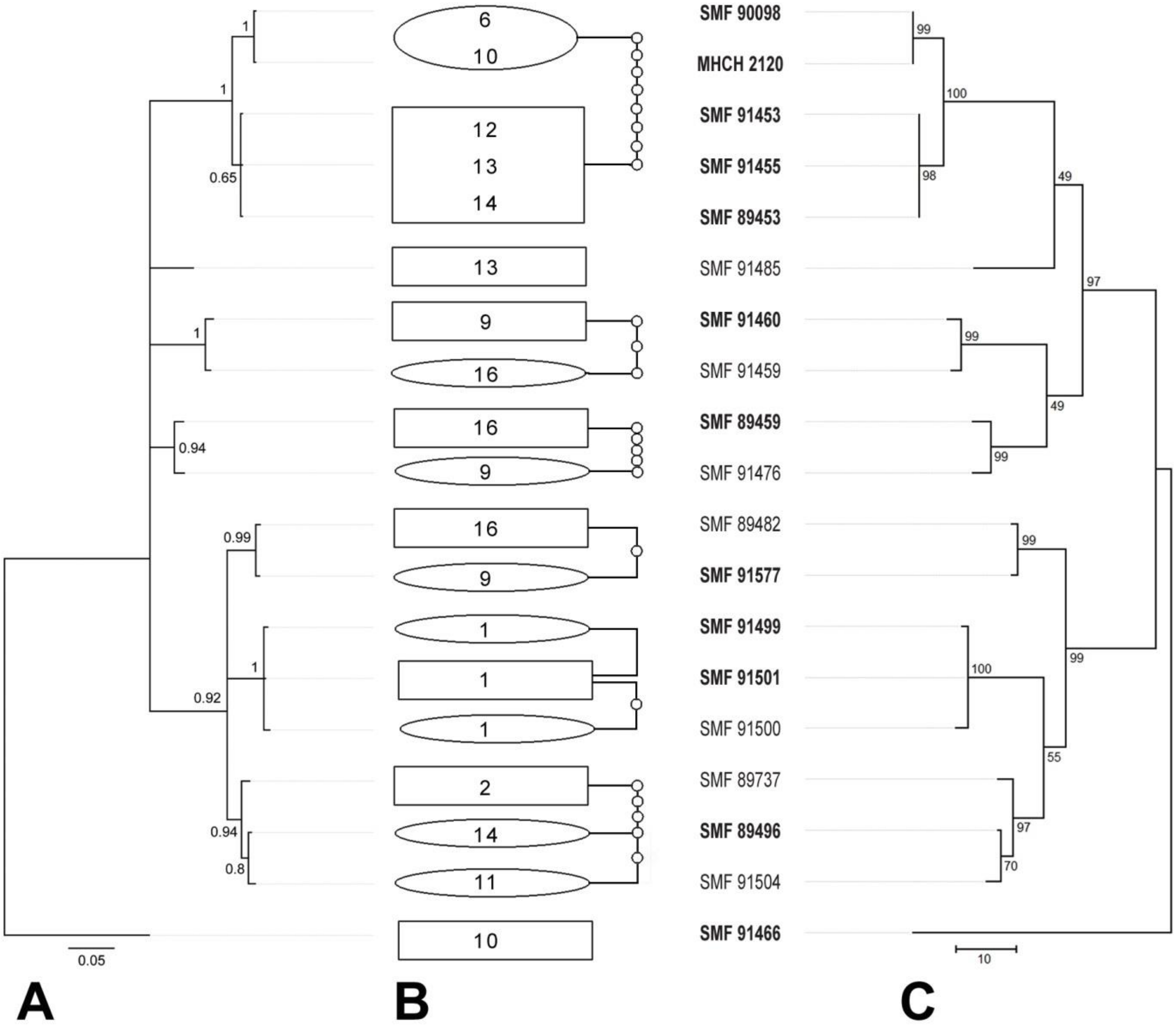


Figure 4.13: Results of 16S analyses. (A) Consensus tree from Bayesian analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps. Small circles represent unsampled haplotypes, rectangles the probably ancestral haplotypes. Locality numbers refer to Map 4.2. Collection numbers in **bold face** indicate individuals for which also COI barcodes are available. (C) Consensus tree from Maximum Parsimony analysis. Scale bar refers to number of changes over whole sequence.

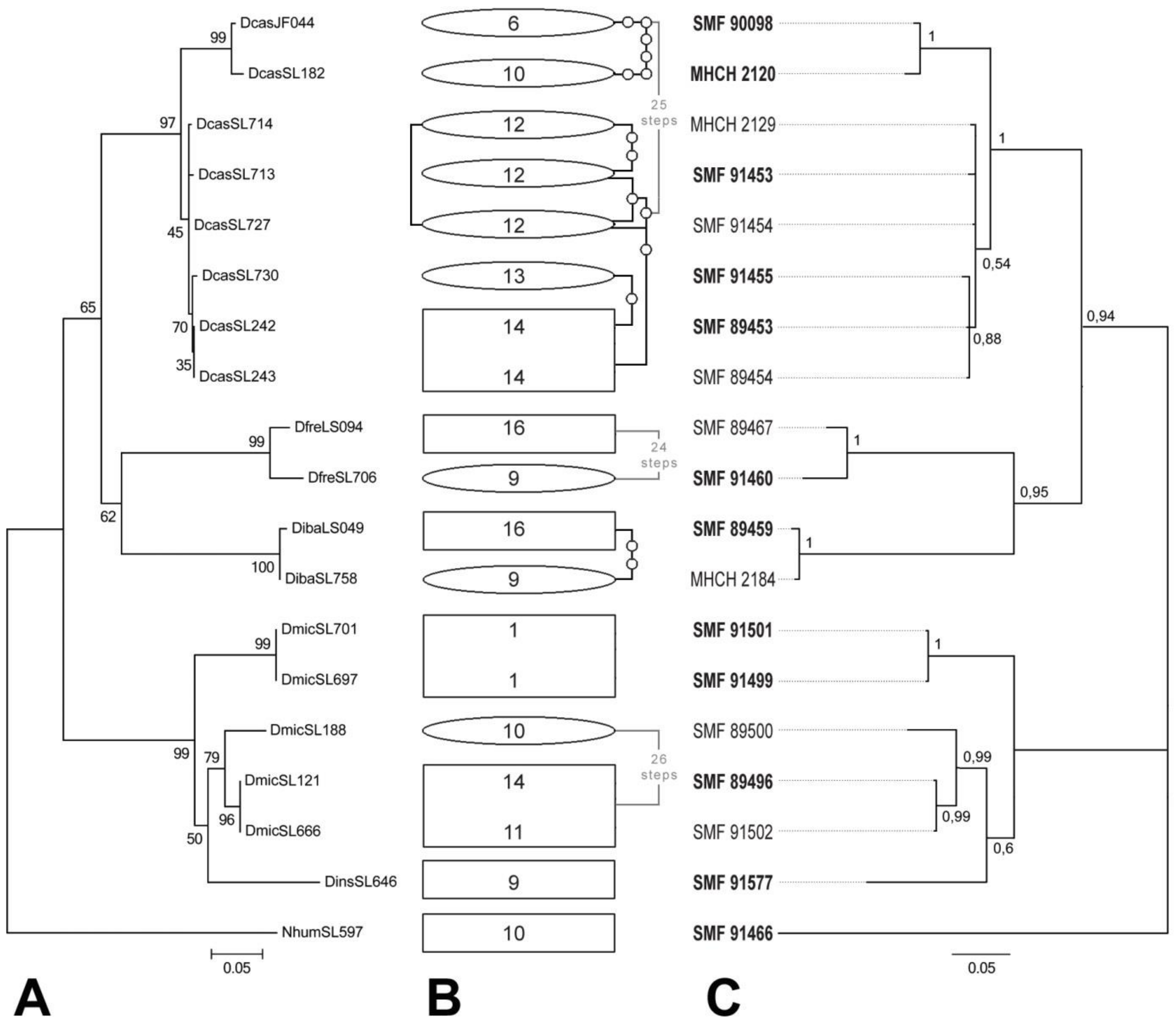


Figure 4.14: Results of COI analyses. (A) Consensus tree from ML analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps (black) and additional connections resulting from increasing the connection limit to 30 steps (gray); small circles represent unsampled haplotypes, rectangles the probably ancestral haplotypes. Locality numbers refer to Map 4.2. Collection numbers in **bold face** indicate individuals for which also 16S barcodes are available. (C) Consensus tree from BI analysis.

The trees inferred from my BI (Fig. 4.13A) and MP (Fig. 4.13C) analyses of the 16S alignment show similar topologies. Besides minor differences, the same terminal clades are recovered in all analyses. The PN analysis (Fig. 4.13B) yields independent haplotype networks for each *Dactyloa frenata, D. ibanezi, D. insignis,* and *D. kunayalae.* The western and eastern subclades of *D. casildae* appear united in a fourth independent subnetwork, whereas the western and eastern lineages of *D. microtus* are represented by two unconnected subnetworks. The analyses of the COI barcodes (Fig. 4.14) yield similar results. However, the uncorrected p-distances (Table 4.5) are generally higher, leaving the haplotypes within several lineages unconnected to each other at the 95% parsimony probability connection limit of 10 steps. Only after increasing the connection limit to 30 steps, haplotype networks analogous to those of the 16S barcodes are recovered, with as many as 24 (within *D. frenata*), 26 (within *D. microtus* east), or 29 (between *D. casildae* east and west) substitutional steps between sampled haplotypes. A preliminary alignment including COI sequences available on GenBank revealed the barcodes of *D. casildae* and *D. frenata* from RFLF (accession numbers JN112726.1 and JN112745.1) to cluster within my samples of these nominal species, while an alledged *D. insignis* from RFLF (JN112756.1; MVUP 2021) is most closely related to my *D. microtus* west (results not pictured; see Appendix 5.3 and species accounts).

According to the smallest diagnosable clusters inferred by the molecular analyses, we separated our material assigned to *Dactyloa casildae* and *D. microtus,* respectively, into "west" and "east" for the morphological comparisons. Individuals without 16S or COI barcodes were assigned according to their morphology and, in the case of *D. casildae* and *D. microtus,* collection site. A comparison of morphometric and pholidotic characters (selected characters plotted in Fig. 4.15) shows that the six nominal species are readily distinguishable from each other morphologically. Furthermore, *D. casildae* west and east show great overlap in all characters, *i.e.,* no relevant morphological differentiation from each other. Concerning most characters, this also holds for the two subclades of *D. microtus*. However, the western specimens show lower values for relative shank length and accordingly in relative hind limb length. Apart from these proportions, we found some qualitative characters to differ consistently between the lineages of *D. microtus* in our sample (see below).

To gain another perspective on differentiation in mensural and meristic characters, I conducted a discriminant function analysis (DFA) based on two morphometric and four pholidotic characters (shank length/SVL, TL/SVL, loreals, 2nd Canths, SAM, 4toe) that correctly classified 85.1% of all specimens (71.4% of *Dactyloa casildae* west, 63.6% of *D. casildae* east, 100% of each *D. kunayalae, D. ibanezi, D. frenata, D. insignis,* and *D. microtus* west, and 92% of *D. microtus* east). In the scatterplot of canonical scores (Figure 4.16), the polygons of *D. kunayalae, D. ibanezi, D. frenata,* and *D. insignis* do not overlap any other polygon. In contrast, the respective polygons of *D. casildae* west and *D. casildae* east largely (>50%) overlap one another, and the respective polygons of *D. microtus* west and *D. microtus* east show a minimal overlap. The first function is DS = -0.76492 (shank length/SVL) +0.16048 (tail length/SVL) -0.18694 (total number of loreals) -0.27281 (2nd Canths) -0.63966 (scales around midbody) -0.04644 (4toe), with an eigenvalue of 37.30403 and a proportion of explained variance of 79.95%. The second function is DS = -0.230353 (shank length/SVL) -0.374134 (tail length/SVL) -0.396223 (total number of loreals) +0.082657 (2nd canths) +0.473025 (scales around midbody) +0.880354 (4toe), with an eigenvalue of 5.112135 and a cumulative proportion of explained variance of 90.91%.

Table 4.4: Uncorrected *p*-distances in the 16S rRNA gene of the 19 anoles used in the molecular analyses. Mean distances within a lineage are in **bold** face.

		Norops humilis	*Dactyloa microtus* west			*D. insignis*		*D. microtus* east			*D. casildae* west		*D. casildae* east			*D. kunayalae*	*D. frenata*		*D. ibanezi*	
		SMF 91466 (JX083219)	SMF 91500 (JX083220)	SMF 91499 (JX083221)	SMF 91501 (JX083222)	SMF 89482 (JX083223)	SMF 91477 (JX083224)	SMF 89737 (JX083225)	SMF 89496 (JX083226)	SMF 91504 (JX083227)	SMF 90098 (JX083228)	MHCH 2120 (JX083229)	SMF 89453 (JX083230)	SMF 91453 (JX083231)	SMF 91455 (JX083232)	SMF 91485 (JX083233)	SMF 91460 (JX083234)	SMF 91459 (JX083235)	SMF 89459 (JX083236)	SMF 91476 (JX083237)
Norops humilis	SMF 91466		0.137			0.123		0.125			0.140		0.144			0.121	0.132		0.123	
Dactyloa microtus west	SMF 91500	0.136																		
	SMF 91499	0.138	0.006	**0.004**		0.044		0.039			0.105		0.101			0.090	0.090		0.086	
	SMF 91501	0.136	0.004	0.002																
D. insignis	SMF 89482	0.123	0.047	0.045	0.043	**0.004**		0.033			0.098		0.089			0.082	0.084		0.085	
	SMF 91477	0.123	0.045	0.043	0.041															
D. microtus east	SMF 89737	0.129	0.041	0.039	0.038	0.032	0.034													
	SMF 89496	0.123	0.036	0.038	0.036	0.030	0.032	0.009	**0.009**		0.107		0.098			0.085	0.081		0.078	
	SMF 91504	0.123	0.041	0.043	0.041	0.034	0.036	0.011	0.006											
D. casildae west	SMF 90098	0.140	0.107	0.105	0.103	0.098	0.099	0.105	0.105	0.111	**0.000**		0.017			0.068	0.079		0.071	
	MHCH 2120	0.140	0.107	0.105	0.103	0.098	0.099	0.105	0.105	0.111										
D. casildae east	SMF 89453	0.144	0.103	0.101	0.099	0.088	0.090	0.096	0.096	0.101	0.017	0.017								
	SMF 91453	0.144	0.103	0.101	0.099	0.088	0.090	0.096	0.096	0.101	0.017	0.017	0.000	**0.000**		0.064	0.071		0.070	
	SMF 91455	0.144	0.103	0.101	0.099	0.088	0.090	0.096	0.096	0.101	0.017	0.017	0.000	0.000						
D. kunayalae	SMF 91485	0.121	0.092	0.090	0.088	0.083	0.081	0.083	0.085	0.089	0.068	0.068	0.064	0.064	0.064		0.068		0.051	
D. frenata	SMF 91460	0.134	0.092	0.090	0.088	0.085	0.086	0.081	0.079	0.085	0.081	0.081	0.073	0.073	0.073	0.068	**0.007**		0.050	
	SMF 91459	0.130	0.092	0.090	0.088	0.081	0.083	0.081	0.079	0.085	0.077	0.077	0.069	0.069	0.069	0.068				
D. ibanezi	SMF 89459	0.121	0.086	0.085	0.083	0.083	0.083	0.075	0.073	0.079	0.070	0.070	0.068	0.068	0.068	0.051	0.051	0.051	**0.011**	
	SMF 91476	0.125	0.086	0.088	0.086	0.086	0.086	0.079	0.077	0.083	0.073	0.073	0.071	0.071	0.071	0.051	0.049	0.049		

Table 4.5: Uncorrected *p*-distances in the COI gene of the 19 anoles used in the molecular analyses. Mean distances within a lineage are in **bold** face.

		Norops humilis	*Dactyloa microtus* west		*D. insignis*	*D. microtus* east			*D. casildae* west		*D. casildae* east						*D. frenata*		*D. ibanezi*	
		SMF 91466	SMF 91499	SMF 91501	SMF 91477	SMF 89500	SMF 89496	SMF 91502	SMF 90098	MHCH 2120	SMF 89453	SMF 91453	SMF 91455	MHCH 2129	SMF 91454	SMF 89454	SMF 89467	SMF 91460	SMF 89459	MHCH 2184
Norops humilis	SMF 91466		0.184		0.205	0.188			0.182		0.171						0.188		0.213	
Dactyloa microtus west	SMF 91499	0.184	**0.000**		0.120	0.092			0.171		0.158						0.175		0.188	
	SMF 91501	0.184																		
D. insignis	SMF 91477	0.205	0.120	0.120		0.099			0.181		0.163						0.187		0.188	
D. microtus east	SMF 89500	0.196	0.103	0.103	0.099															
	SMF 89496	0.184	0.087	0.087	0.099	0.046	**0.031**		0.163		0.146						0.167		0.171	
	SMF 91502	0.184	0.087	0.087	0.099	0.046	0.000													
D. casildae west	SMF 90098	0.182	0.170	0.170	0.179	0.166	0.158	0.158	**0.012**		0.055						0.166		0.143	
	MHCH 2120	0.182	0.172	0.172	0.184	0.172	0.163	0.163												
D. casildae east	SMF 89453	0.172	0.159	0.159	0.165	0.150	0.145	0.145	0.051	0.057							0.147		0.130	
	SMF 91453	0.170	0.159	0.159	0.161	0.147	0.145	0.145	0.055	0.060	0.007									
	SMF 91455	0.172	0.159	0.159	0.165	0.150	0.145	0.145	0.055	0.060	0.004	0.011	**0.005**							
	MHCH 2129	0.170	0.158	0.158	0.163	0.149	0.143	0.143	0.051	0.057	0.005	0.005	0.009							
	SMF 91454	0.168	0.156	0.156	0.161	0.147	0.142	0.142	0.051	0.057	0.004	0.004	0.007	0.002						
	SMF 89454	0.172	0.159	0.159	0.165	0.150	0.145	0.145	0.051	0.057	0.000	0.007	0.004	0.005	0.004					
D. frenata	SMF 89467	0.182	0.172	0.172	0.181	0.168	0.159	0.159	0.172	0.172	0.149	0.149	0.149	0.145	0.145	0.149	**0.042**		0.159	
	SMF 91460	0.193	0.179	0.179	0.193	0.168	0.173	0.173	0.159	0.163	0.149	0.149	0.149	0.145	0.145	0.149				
D. ibanezi	SMF 89459	0.216	0.189	0.189	0.191	0.179	0.172	0.172	0.143	0.145	0.131	0.133	0.129	0.131	0.131	0.131	0.159	0.163	**0.005**	
	MHCH 2184	0.211	0.188	0.188	0.186	0.173	0.166	0.166	0.142	0.143	0.129	0.131	0.127	0.129	0.129	0.129	0.154	0.159		

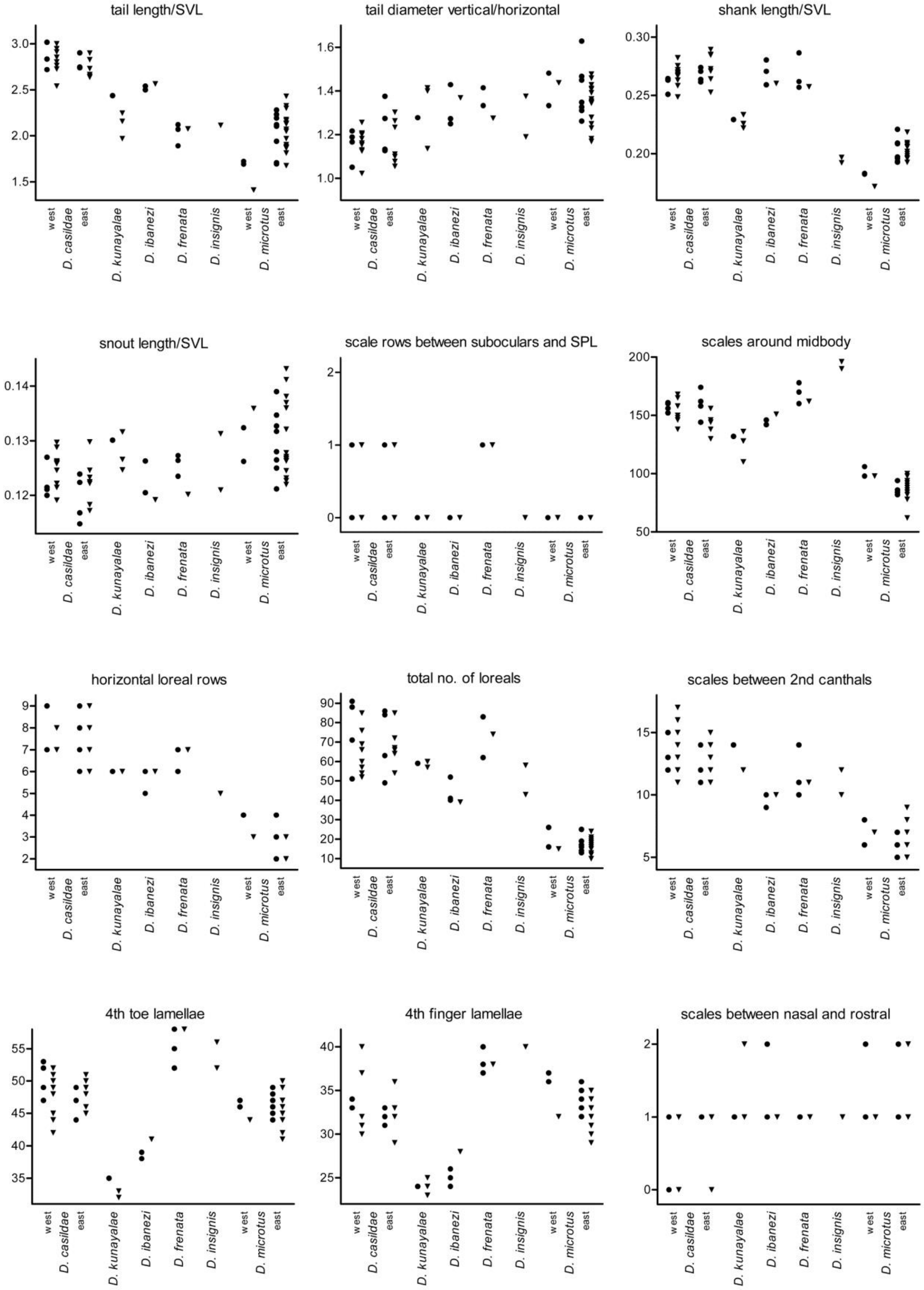


Figure 4.15: Variation in selected morphological characters among our sample of *Dactyloa* from western Panama, separated by males (circles, left) and females (triangles, right) for each lineage. See text for details.

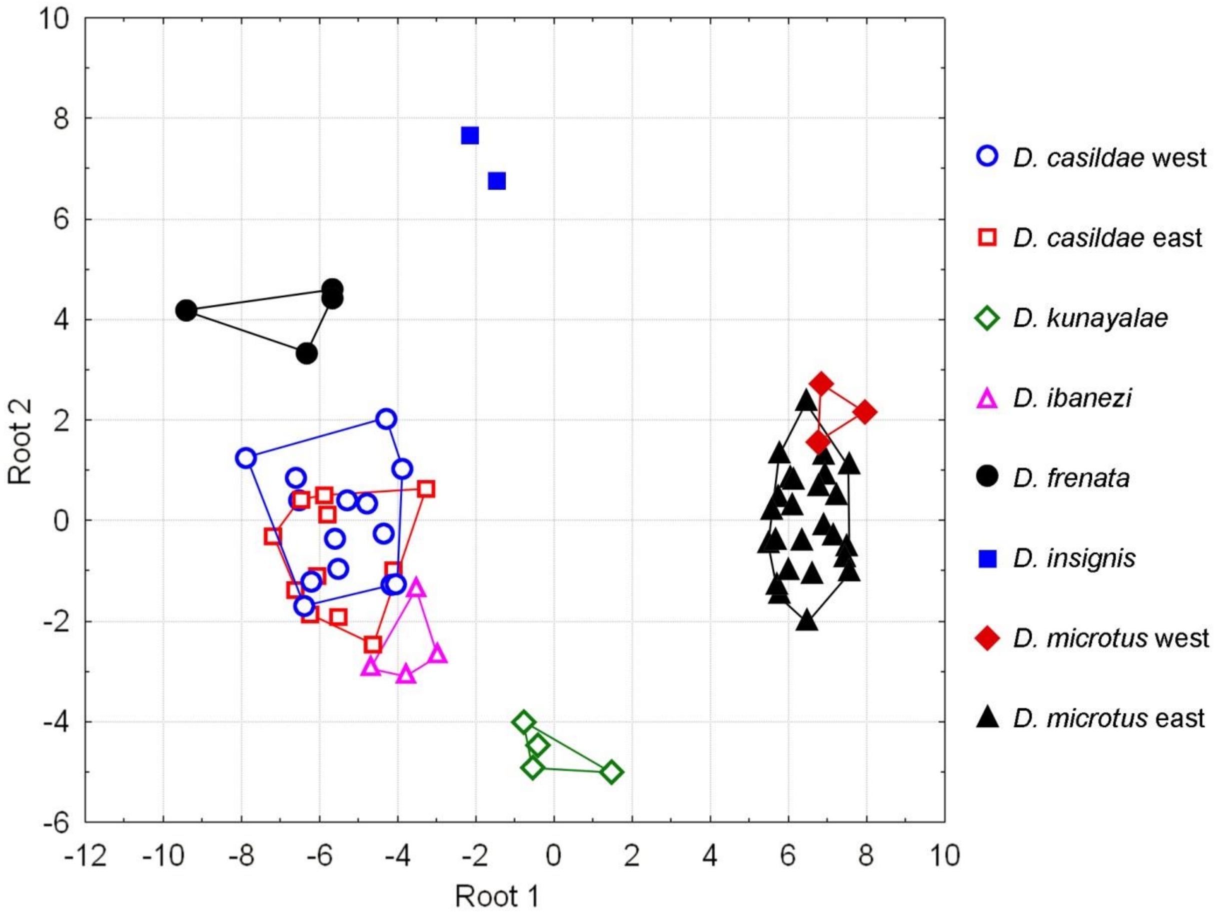


Figure 4.16: Discriminant function analysis of the eight *Dactyloa* lineages using two morphometric and four pholidotic characters. See text for details.

In Figure 4.17, molecular and morphological evidence are summarized and compared, and species boundaries inferred accordingly. Without question, we recognize the perfectly diagnosable nominal species *Dactyloa frenata, D. ibanezi, D. insignis,* and *D. kunayalae.* Based on the combined evidence, we regard the two subclades of *D. casildae* as DCLs, since they exhibit a great overlap in morphological characters as well as a comparably low differentiation in their 16S barcodes, which are connected in a single haplotype network. The distinctness of their COI barcodes is much more pronounced but proportionally so, i.e., still in the range of that found within *D. frenata* and *D. microtus* east. The two subclades referred to *D. microtus* present a different scenario. Concerning 16S barcodes, each lineage forms an unconnected haplotype network, and the mean *p*-distance between the two subclades (3.9%) is comparably high, that is, in the range of the respective mean *p*-distances between the well-diagnosable species *D. insignis* and each of the two subclades (west: 4.4%; east: 3.3%). Similar *p*-distance values have been found between pairs of closely related species of beta-anoles, as for example between *Norops gaigei* and *N. tropidogaster* (4.1% according to Köhler et al. 2012b), or between *N. limifrons* and *N. cryptolimifrons* (4.3%; Köhler, J.J., and Lotzkat, unpublished data). That is to say, the genetic distance in the 16S barcodes between *D.*

microtus west and *D. microtus* east may well be interpreted to reflect a differentiation at species level. The p-distances of the COI barcodes are more than twice as high but follow the same pattern, with the mean value between the two subclades (9.2%) similar to those between *D. insignis* and either of the subclades (west: 10.2%; east: 9.9%). Among our sample, several morphological differences between the two subclades are also consistent. Integrating all evidence, we recognize the two subclades as CGLs. Before taking the next step and assigning the name *Dactyloa microtus* to one of these two CGLs, it seems necessary to summarize and clarify the morphological differences exhibited by their representatives among our material.

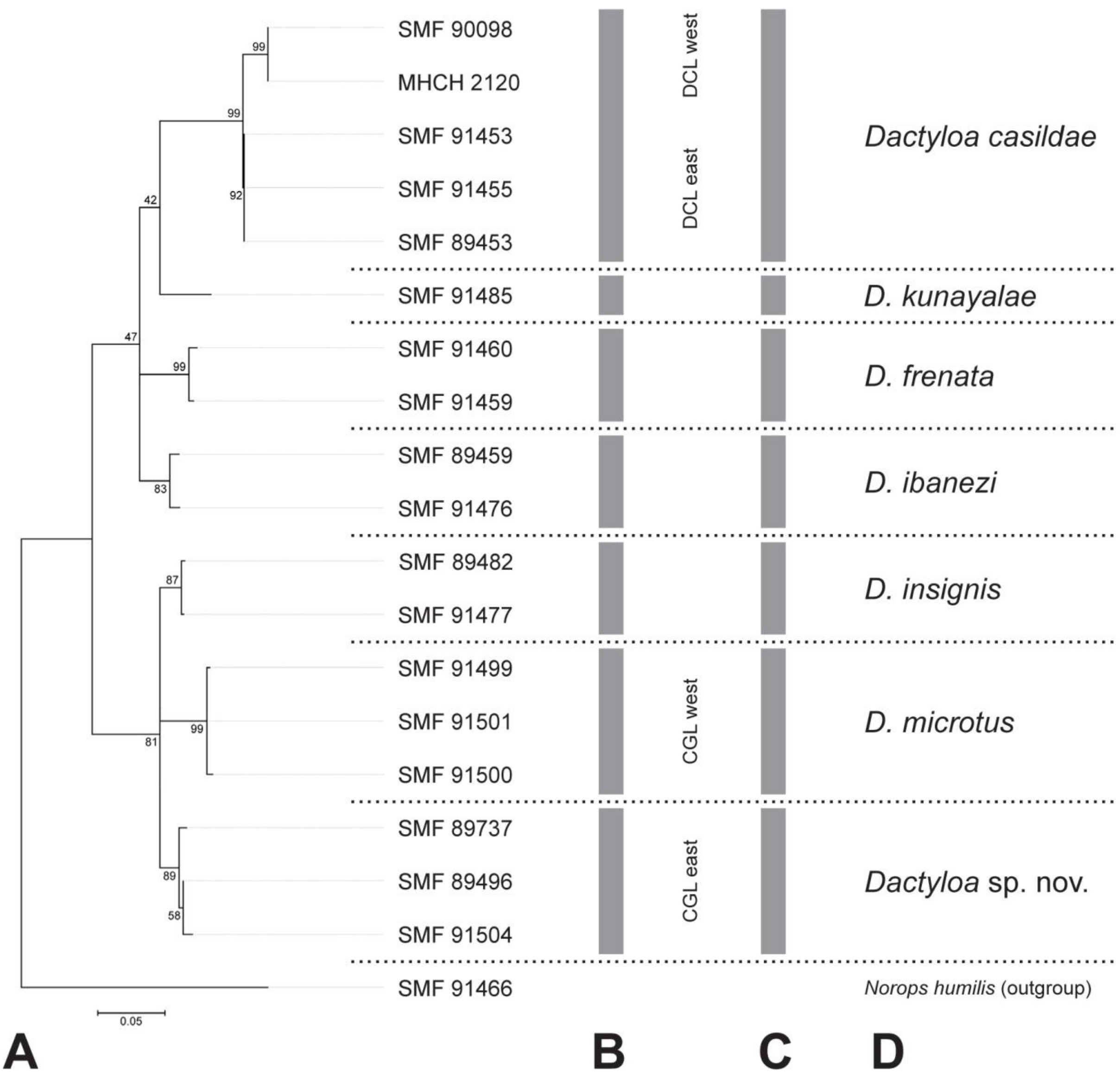


Figure 4.17: Integration of morphological and molecular evidence. (A) ML tree of sampled voucher specimens; (B) Lineages as confirmed by molecular evidence; (C) Lineages as confirmed by morphological evidence; (D) Taxonomic identities of inferred CGLs.

Regarding body proportions, the two CGLs show a slight but determined divergence in relative length of the hind limb. Numerically, this is expressed in lower values for relative shank length and relative femur length in the western CGL. Consequently, the tip of the fourth toe of the hind limb (when adpressed along straightened specimen) reaches to a point between shoulder and tympanum in two specimens of the western CGL, and to the tympanum in the third. In individuals of the eastern CGL, the tip of the fourth toe reaches at least to the anterior border of the ear opening, in most specimens to a point between tympanum and eye, and in a few even to the posterior border of the eye.

Regarding coloration, the CGLs differ markedly in the pattern of stripes between eye and shoulder. The eastern pattern basically is the same as pictured by Savage & Talbot (1978: Fig. 3M): The light coloration of the supralabials, usually originating somewhere anterior to level of orbit, continues posteriorly as a rather horizontal, well-demarcated, light "postsupralabial" stripe that passes above or across the ear opening and above the dark preaxillary blotch. In most specimens, this light stripe then bends ventrally and descends to somewhere above the shoulder, thus forming the upper and posterior boundaries of the prominent dark preaxillary blotch, which is situated between ear opening and shoulder. More or less distinctly, it also bifurcates at or just posterior to the ear opening, in a way that the ventrally bound ramification constitutes the anterior and lower limits of the dark preaxillary blotch. The light horizontal postsupralabial stripe is paralleled above by a very prominent dark postorbital stripe that is well-delineated by darker borders and extends from the posterior border of the orbit to a level above the dark preaxillary blotch. Posterior to the level of the ear opening, this dark postorbital stripe tends to bend up rather than down, and may merge diffusely into the first transverse dorsal band in some individuals, or vaguely connect dorsally to its counterpart from the other side of the neck, thus forming a usually diffuse dark nuchal band in other specimens (Figs. 4.12; 4.19; 4.20). In contrast, the western individuals exhibit a modified pattern with the dark postorbital stripe being more ventrally orientated and terminating around the ear opening or just anterior to it, thus preventing the light postsupralabial stripe from passing horizontally above or across the ear. Instead, the light stripe follows the direction of the dark postorbital stripe and bends ventrally behind the corner of the mouth to run directly towards the shoulder. Both the light and the dark stripe have lost their clear-cut distinctness at the level of the ear opening. Moreover, our members of the western GCL have another, yet less defined, light postorbital stripe bordering the dark postorbital stripe dorsally. A light transverse pattern element that seems like an interconnection between the lower and the upper light stripe extends over the ear and borders the dark postorbital stripe posteriorly. Accordingly, the three individuals have two dark preaxillary blotches: a small lower one situated ventrally to the lower light stripe at the level of the tympanum, and a larger upper one that, lying between the more or less diffuse posterior extensions of the two light stripes, seems like an extension of the dark postorbital stripe (Figs. 4.12; 4.27). While in individuals of the eastern CGL the described pattern of stripes is usually very contrasting, sharply demarcated, and well retained in preservative, it appears somewhat less contrasting and demarcated, and more blurred in preservative, in our three animals of the western CGL (compare Figs. 4.29R and T). Other differences we found in coloration and scalation between the representatives of the two CGLs in our material appear to be more variable in the light of material from Costa Rica, and are mentioned in the species accounts in chapter 4.2.2.

Morphologically, both CGLs are largely consonant with published character descriptions of *Dactyloa microtus* (Cope 1871, 1876; Boulenger 1885; Dunn 1937a; Taylor 1956; Savage & Talbot 1978; Savage 2002; Köhler 2008), but show differential conformance in certain characters. For example, the shorter hind limbs found in the western subclade comply better with the alleged degree of short-leggedness of *D. microtus,* while the salmon to pink dewlap as well as the pattern of stripes between eye and shoulder exhibited by our eastern CGL match the correspondent color descriptions. However, at least since Dunn (1937a) reported specimens from Boquete (Map 4.2: loc. 26; close to the collection site of our eastern CGL's westernmost individual), descriptions of *D. microtus* combined information from Costa Rica and Panama, and must have been based on representatives of both clades. The descriptions preceding this date are less informative, lacking common nomenclatural standards, partially contradicting, and contain no information on coloration in life.

Cope (1871) originally described *Dactyloa microtus* from "San José, Costa Rica." Savage (1974) regarded the type locality to be "near San José; probably from near La Palma" (loc. 21 in Map 4.2). Since the original description of *D. microtus* does not clearly specify all characters that separate the two CGLs among our sample, I examined the holotype (USNM 31282; Figs. 4.18A–H) as well as photos I could obtain showing individuals of *D. microtus* from Cerro Dantas (Map 4.2: loc. 22) and Parque Nacional Tapantí (Map 4.2: loc. 23; Figs. 4.18I–L), as well as from an undefined locality in Costa Rica (Savage 2002: plate 258). Concerning the pattern of stripes between eye and shoulder, all four Costa Rican animals clearly correspond to our CGL "west." Our measurements of the holotype (shank length = 18.6 mm; SVL = 106 mm; shank length/SVL = 0.175) confirm the degree of short-leggedness reported by Savage & Talbot (1978), and fall within the range exhibited by our material of CGL "west" (shank length/SVL = 0.172–0.183; mean 0.179 ± 0.006), whereas the values found in our material of CGL "east" are higher (0.193–0.221; mean 0.203 ± 0.008). In conclusion, our western CGL is morphologically concordant with the holotype of *D. microtus,* and with animals of this species found north and south of its type locality. Thus, we assign

CGL "west" to this nominal taxon. In consequence, no scientific name is available for our eastern CGL, and therefore we describe it as a new species below.

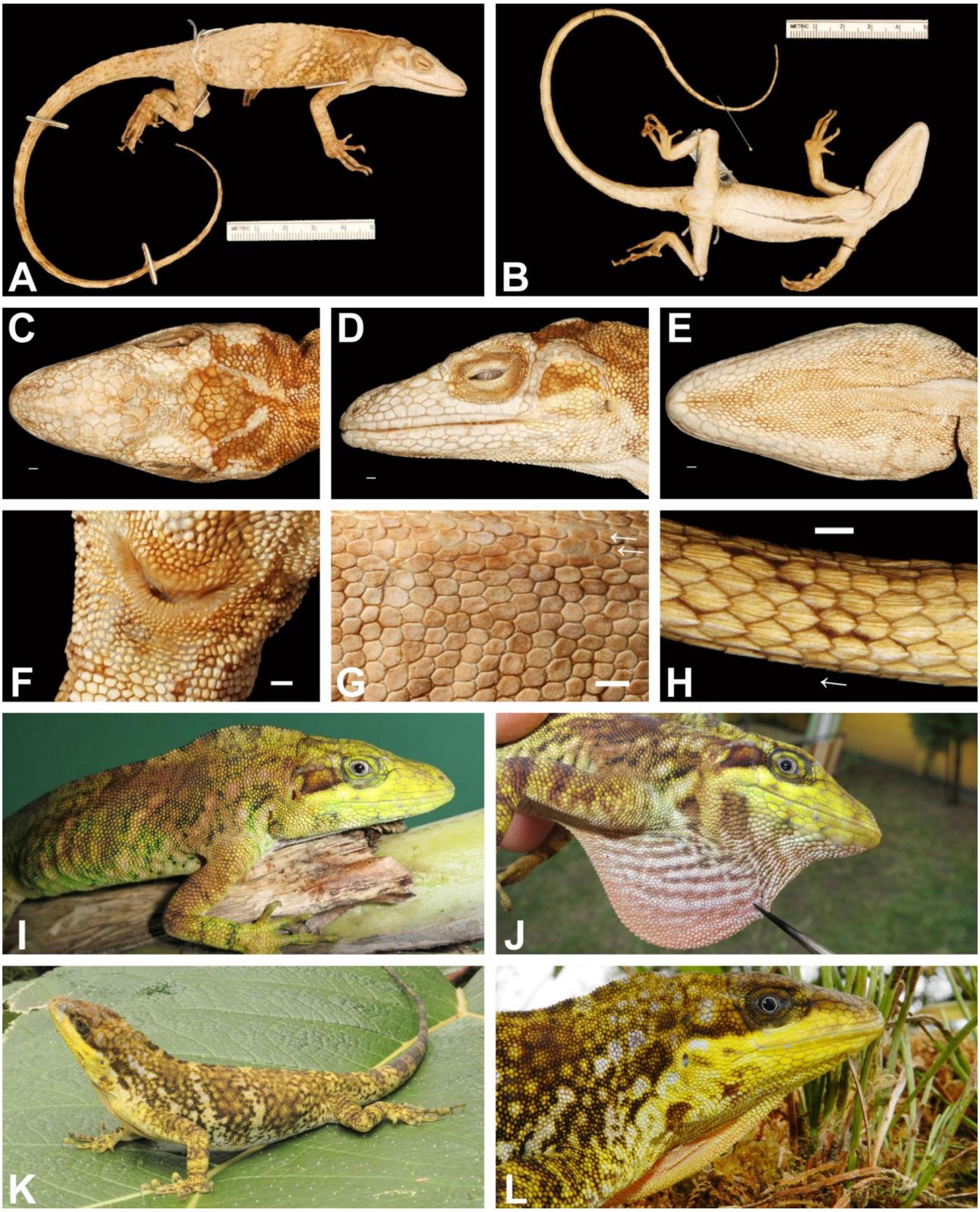


Figure 4.18: Specimens of *Dactyloa microtus* from Costa Rica: (A–H) holotype USNM 31282, adult female, SVL = 106 mm: entire specimen photographed by James Poindexter in (A) lateral and (B) ventral view; (C) dorsal, (D) lateral, and (E) ventral view of head; (F) ventral view of cloacal region showing lack of enlarged postcloacal scales; (G) detail of dorsal scales at midbody, arrows indicate middorsal rows (photos C–G by GK); (H) detail of subcaudal scales, each bearing more than one prominent keel; (I, J) individual photographed by Mason Ryan at Parque Nacional Tapantí, Cartago province; (K, L) individual photographed by Daniel Cascante at Cerro Dantas, Heredia province. Scale bars = 1 mm, all arrows point posteriorly.

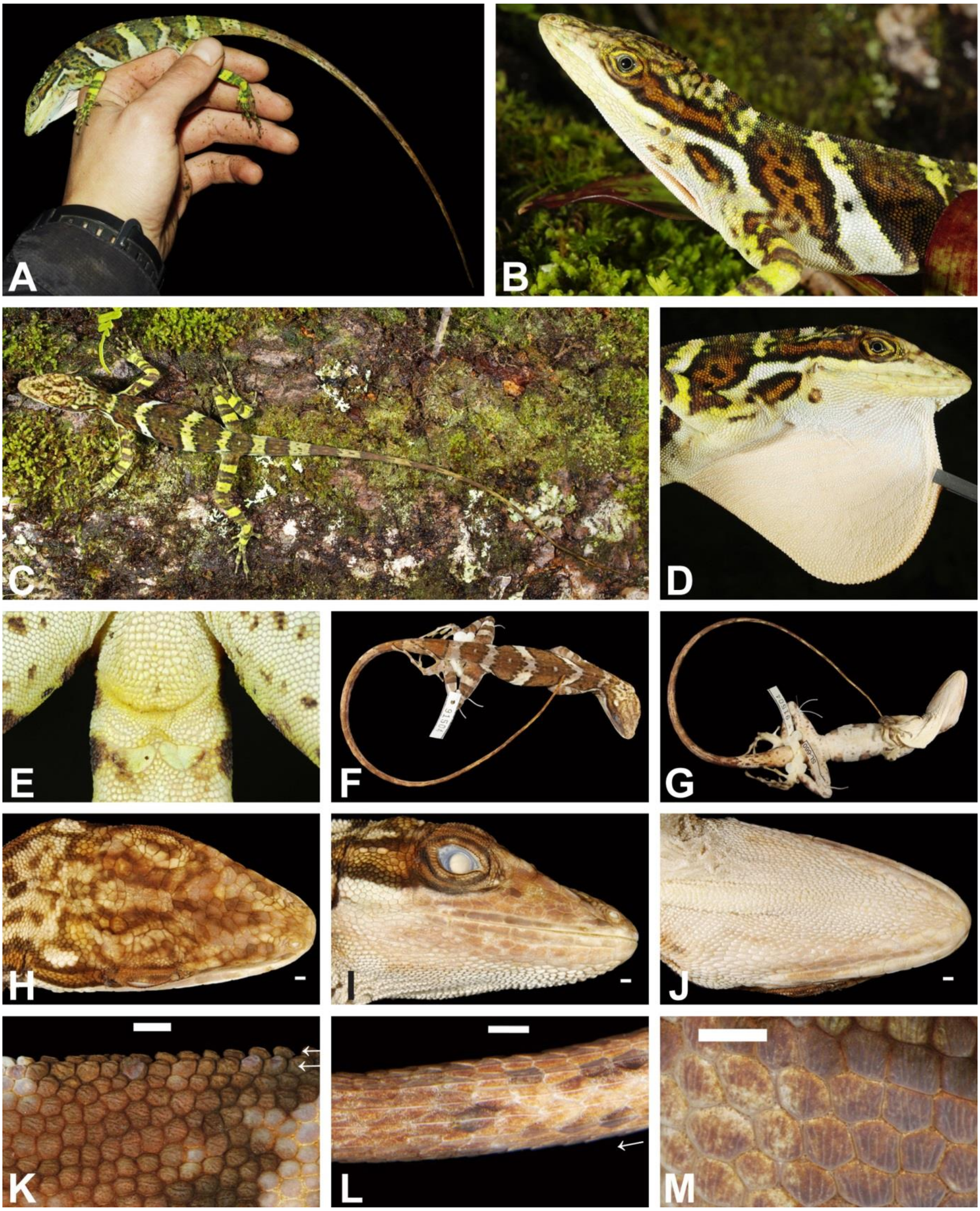


Figure 4.19: Holotype of *Dactyloa ginaelisae* sp. nov. (SMF 91504, adult male, SVL = 107 mm), (A–E) in life: (A) lateral view at time of capture; (B) portrait the next day; (C) dorsal view of entire specimen; (D) dewlap (width of forceps = 3 mm); (E) ventral view of cloacal region showing enlarged postcloacal scales; (F–M) specimen after approximately two years in preservative: (F) dorsal and (G) ventral view of entire specimen; (H) dorsal, (I) lateral, and (J) ventral view of head; (K) detail of dorsal scales at midbody, arrows indicate middorsal rows; (L) detail of subcaudal scales with one prominent keel; (M) detail of multicarinate scales on upper surface of right forearm. Scale bars = 1 mm, all arrows point posteriorly.

Dactyloa ginaelisae **sp. nov.**

Figures 4.12; 4.19; 4.20; 4.28G–I; 4.29R–S; 4.96H.

Anolis microtus: Dunn (1937a: in part.); Slevin (1942); Taylor (1956: in part.); Peters & Donoso-Barros (1970: in part.); Savage & Talbot (1978: in part.); Arosemena et al. (1992: in part.); Auth (1994: in part.); Young et al. (1999); Ibáñez et al. (2001); Köhler et al. (2008); Fläschendräger & Wijffels (2009: in part.); Hamad (2009: in part.); Lotzkat et al. (2010a); Jaramillo et al. (2010); Stadler (2010); Castañeda & de Queiroz (2011: in part.); Uetz & Hošek (2014: photo).

Dactyloa microtus: Savage & Guyer (1989: in part.); Savage (2002: in part.); Köhler (2003, 2008: in part.)

Anolis ginaelisae: Uetz & Hošek (2014).

Holotype. SMF 91504 (Figs. 4.12; 4.19; 4.20S–T), adult male, from the banks of Quebrada Juglí (Fig. 2.5A) on the southeastern slope of Cerro Saguí (also known as Cerro Ratón; locality 11 in Map 4.2) at Finca Alto Cedro, about 2 km north-northeast of the village Ratón, 8.5576°N, 81.8262°W, 1710 m asl, Corregimiento de Piedra Roja, Distrito de Kankintú, Comarca Ngöbe-Buglé, Panama; collected by Andreas Hertz and Sebastian Lotzkat on 08 July 2010; original field number SL 660.

Paratypes. Collected by Sebastian Lotzkat and Andreas Hertz, if not indicated otherwise. All from the Comarca Ngöbe-Buglé, Panama. Southeastern slope of Cerro Saguí (Map 4.2: loc. 11): MHCH 2240, juvenile female, same collecting data as holotype; MHCH 2239 and SMF 91503, females, near type locality, 8.5561°N, 81.8252°W, 1700 m asl, 07 July 2010; SMF 91502, juvenile female, about 850 m NNE of type locality, 8.5636°N, 81.8217°W, 1960 m asl, 08 July 2010. Western slope of Cerro Santiago, La Nevera (Map 4.2: loc. 14): SMF 89496 and 89497, juvenile female and adult female, 8.4997°N, 81.7724°W, 1700 m asl, 11 May and 17 August 2008; SMF 85069, juvenile female, 8.5000°N, 81.7722°W, 1600 m asl, collected by Abel Batista, Gunther Köhler, Marcos Ponce, and Javier Sunyer on 22 January 2006; SMF 89498, male, 8.5011°N, 81.7694°W, 1580 m asl, 14 August 2008; MHCH 2235, juvenile female, 8.5018°N, 81.7689°W, 1560 m asl, 10 August 2008; MHCH 2238, female, 8.4989°N, 81.7682°W, 1620 m asl, 11 November 2009; MHCH 2234, female, 8.5032°N, 81.7675°W, 1530 m asl, 10 August 2008; SMF 90133, female, 8.4954°N, 81.7673°W, 1810 m asl, 11 November 2009. Eastern slope of Cerro Santiago, Quebrada Ardilla (Map 4.2: loc. 15): MHCH 1338, female, 8.4974°N, 81.7228°W, 1600 m asl, 24 March 2009.

Referred specimens. Apart from the material collected by ourselves and listed in Appendix 2, all specimens reported as *Dactyloa microtus* that have been collected in Panama to our knowledge are referrable to *D. ginaelisae* in view of their collection localities (localities 24–26 in Map 4.2) in the vicinities of Boquete, where we also collected three specimens of this species: ANSP 22418 and 22419 from above Boquete (Dunn 1937a; Savage & Talbot 1978); CAS 79598 from the north slope of Volcán Barú (Slevin 1942); MVUP 966 from Cerro Horqueta and MVUP 969 from Bajo Mono near Boquete (MVUP catalogue); CHP 1038 from Cerro Horqueta (CHP catalogue).

Diagnosis. A large species (maximum SVL 112 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this genus found in western Panama (*D. casildae, D. frenata, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus*). These species share a moderate to large adult size (SVL > 70 mm), a large dewlap and enlarged postcloacal scales in males, and smooth or faintly keeled ventrals. *Dactyloa ginaelisae* can readily be distinguished from these six species by its color pattern described below and shown in Figs. 4.12, 4.19, 4.20, 4.29R–S, and 4.96H. It further differs from all mentioned species except *D. microtus* by its low numbers of horizontal loreal rows (4 or fewer in *D. ginaelisae* vs. 5 or more) and total loreal scales (25 or fewer in *D. ginaelisae* vs. 39 or more), and by its low number of scales around midbody (100 or usually much fewer in *D. ginaelisae* vs. 110 or more). Moreover, *D. ginaelisae* differs from *D. casildae, D. frenata,* and *D. ibanezi* in having short legs (tip of fourth toe of adpressed hind limb reaching to a point between tympanum and eye, very rarely to posterior border of eye, in *D. ginaelisae* vs. beyond eye; shank length/SVL = 0.22 or less in *D. ginaelisae* vs. 0.25 or more). Among the short-legged species of *Dactyloa* in western Panama, *D. ginaelisae* further differs from *D. insignis* in having fewer subdigital lamellae under the fourth toe (50 or fewer in *D. ginaelisae* vs. 52 or more) as well as under the fourth finger (36 or fewer in *D. ginaelisae* vs. 40), and from *D. kunayalae* in having more subdigital lamellae under the fourth toe (41 or more in *D. ginaelisae* vs. 35 or fewer) as well as under the fourth finger (29 or more in *D. ginaelisae* vs. 25 or fewer). *Dactyloa ginaelisae* is very similar to *D. microtus,* from which it differs in having longer legs (tip of fourth toe of adpressed hind limb reaching to a point between tympanum and eye in *D. ginaelisae* vs. to a point between shoulder and tympanum in *D. microtus;* shank length/SVL = 0.19 or more in *D. ginaelisae* vs. 0.183 or less) and by its conspicuous and clear-cut coloration pattern between eye and shoulder (a prominent light stripe extending from supralabials posteriorly above or a across the ear before bending down towards shoulder, delineating a dark preaxillary blotch above and posteriorly, and paralleled above by a dark postorbital stripe with darker borders that extends at least to a level above the preaxillary blotch in *D. ginaelisae* vs. light postsupralabial and dark postorbital stripe oriented more ventrally and losing their conspicuousness around ear).

Description of the holotype. Adult male as indicated by everted hemipenes (Fig. 4.19G), a pair of enlarged postcloacal scales (Fig. 4.19E), and presence of large dewlap (Fig. 4.19D); SVL 107 mm; tail complete; TL 244 mm, tail length/SVL ratio 2.28; tail compressed in cross section, tail height 7.0 mm, tail width 4.3 mm; axilla to groin distance 45.0 mm; HL 29.1 mm, HL/SVL ratio 0.27; snout length 14.2 mm; HW 16.7 mm; longest toe of adpressed hind limb reaching to a point between tympanum and eye; shank length 22.3 mm, shank length/SVL ratio 0.21, shank length/HL ratio 0.77; longest finger of extended forelimb reaching well beyond tip of snout; longest finger of adpressed forelimb reaching to anterior insertion of hind limbs; prefrontal ridges distinct, parietal ridges conspicuously protruding; scales on snout mostly rugose to wrinkled; 5 postrostrals; 6 scales between nasals; scales in distinct prefrontal depression wrinkled; supraorbital semicircles differentiated, composed of very rugose and partly wrinkled scales, separated by a minimum of 2 scales; supraorbital disc composed of 15 enlarged rugose scales; one slightly elongated, keeled anterior superciliary, followed posteriorly by a much smaller, keeled, elongate scale; about 2 rows of small keeled scales extending between enlarged supraorbitals and superciliary; interparietal plate not distinct, no parietal eye visible; canthal ridge distinct, composed of 5 large (posterior) and 1 small (anterior) canthal scales; 7 scales present between second canthals; 8 scales present between posterior canthals; 19/20 (right side/left side) wrinkled loreal scales in a maximum of 3 horizontal rows; subocular scales flat, wrinkled, subocular row well-defined; 7 supralabials to level below center of eye; ear opening 1.1 x 2.2 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 6 postmentals; 7 infralabials to level below center of eye; sublabials enlarged, about as high as INL anterior to level of orbit, first two sublabials posterior to mental greatly enlarged, higher than INL; keeled granular to elongate scales present on chin and throat; dewlap large, extending well onto body, anterior insertion at a level halfway between orbit and tip of snout, posterior insertion at a level between one-fourth and one-third the distance between axilla and groin, with about 5 gorgetal-sternal rows 2–4 scales wide, becoming more diffuse posteriorly; low nuchal and dorsal crests present, dorsum of body with elevated, wrinkled scales, 2 middorsal rows of prominently protruding, keeled, but not otherwise enlarged scales, largest dorsal scales about 0.8 x 0.8 mm (length x width); about 42 medial dorsal scales in one HL; about 72 medial dorsal scales between axilla and groin; lateral scales raised, rugose to wrinkled, average size 0.7 mm in diameter, with minute granules occupying varying portions of the interspaces between them; ventrals at midbody smooth, subimbricate, about 0.5 x 0.5 mm (length x width); about 57 ventral scales in one HL; about 88 ventral scales between axilla and groin; about 94 scales around midbody; caudal scales strongly keeled, without whorls of enlarged scales, subcaudal scales with a single prominent keel; a pair of greatly enlarged postcloacal scales, larger one about 1.8 x 3.1 mm (length x width); tube-like axillary pocket not developed; scales on anterodorsal surface of thigh and on dorsal surface of forearm multicarinate, imbricate; digital pads dilated, dilated pad about 3 times width of non-dilated scales under distal phalanx; distal phalanx narrower than and raised from dilated pad; 33/35 lamellae under phalanges ii to iv of 4th toe; 12/13 scales under distal phalanx of 4th toe; 24 lamellae under phalanges ii to iv of 4th finger; 12/11 scales under distal phalanx of 4th finger.

The completely everted hemipenis is a medium-sized, bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; large asulcate processus and ridge present; a knob-like processus present on each lateral side of truncus below base of apex; lobes finely calyculate, truncus with transverse folds.

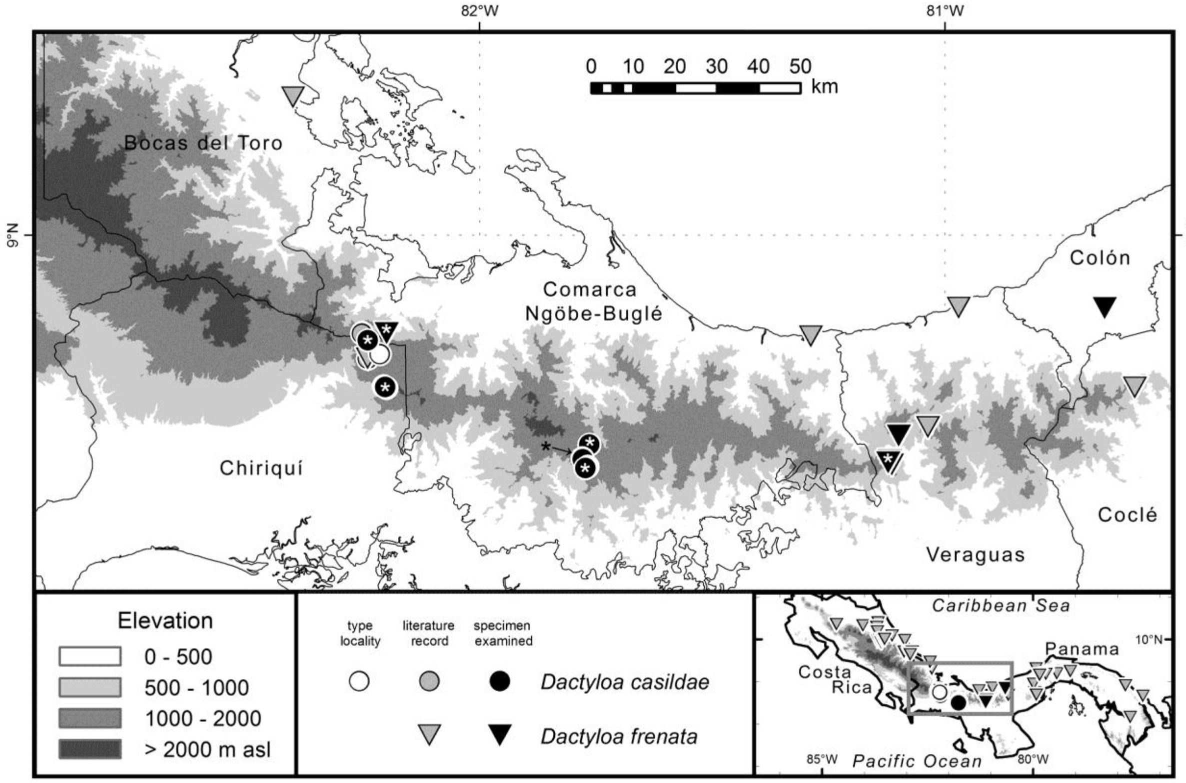
Coloration in life. The coloration in life, including two stages of metachrosis, is shown in Figs. 4.19A–E. The holotype represents the most contrastingly colored morph known for the species, with the dark crossbands on the dorsal and lateral surfaces of body, limbs, and anterior portion of tail well-delineated against the very light ground color by darker bands. Equally well-demarcated are the dark postorbital stripe extending posteriorly to above shoulder, and the large, elongate preaxillary blotch. The dirty to bright white supralabial stripe extends below the dark postorbital one, over and across the ear, to above the posterior portion of the preaxillary blotch, where it curves down towards the shoulder. Otherwise, no detailed notes of the holotype were taken. Coloration after approximately two years of preservation in 70% ethanol (Figs. 4.19F–M) is similar to that in life, apart from that all reddish, greenish, and bluish tonalities have faded.

Variation. The paratypes and referred specimens agree well with the holotype in terms of general morphometrics and pholidosis (see Tables 4.6 and 4.7), but are very variable in coloration (Fig. 4.20). For details, see species account in chapter 4.2.2.

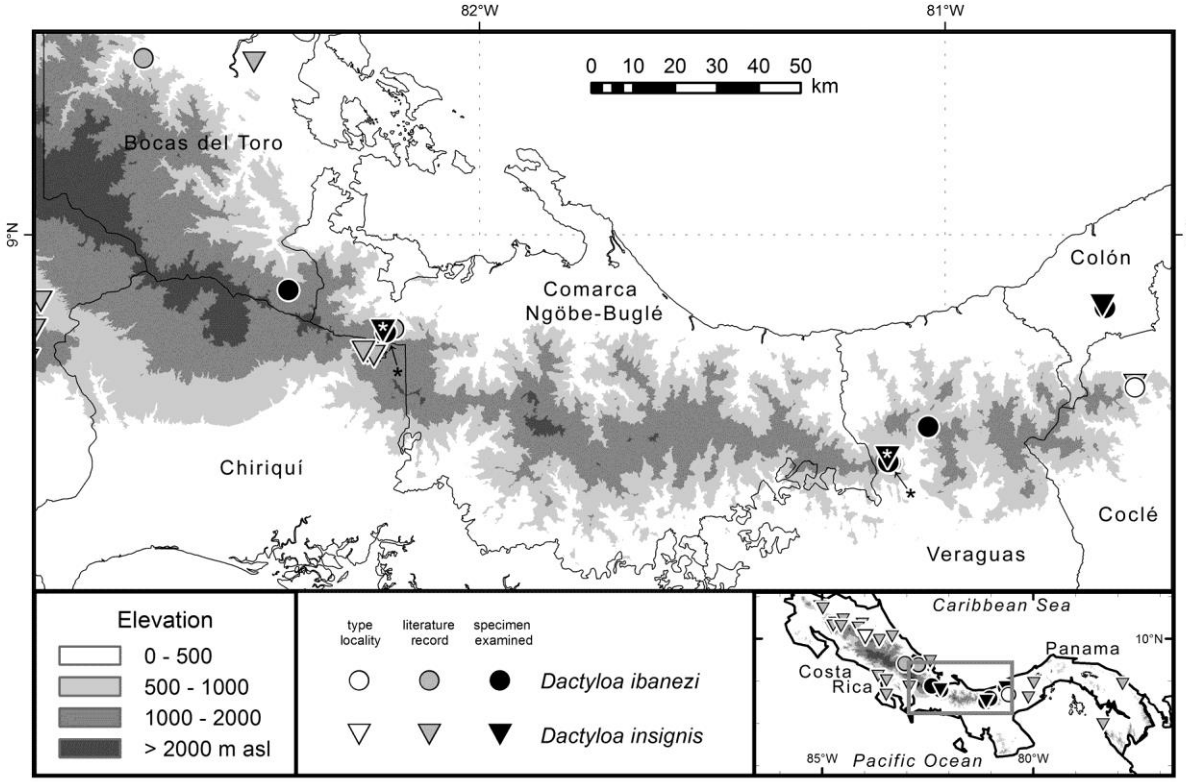
Geographic distribution. See Maps 4.5 and 4.39, and species account in chapter 4.2.2.

Natural history notes, Conservation, Remarks. See species account in chapter 4.2.2.

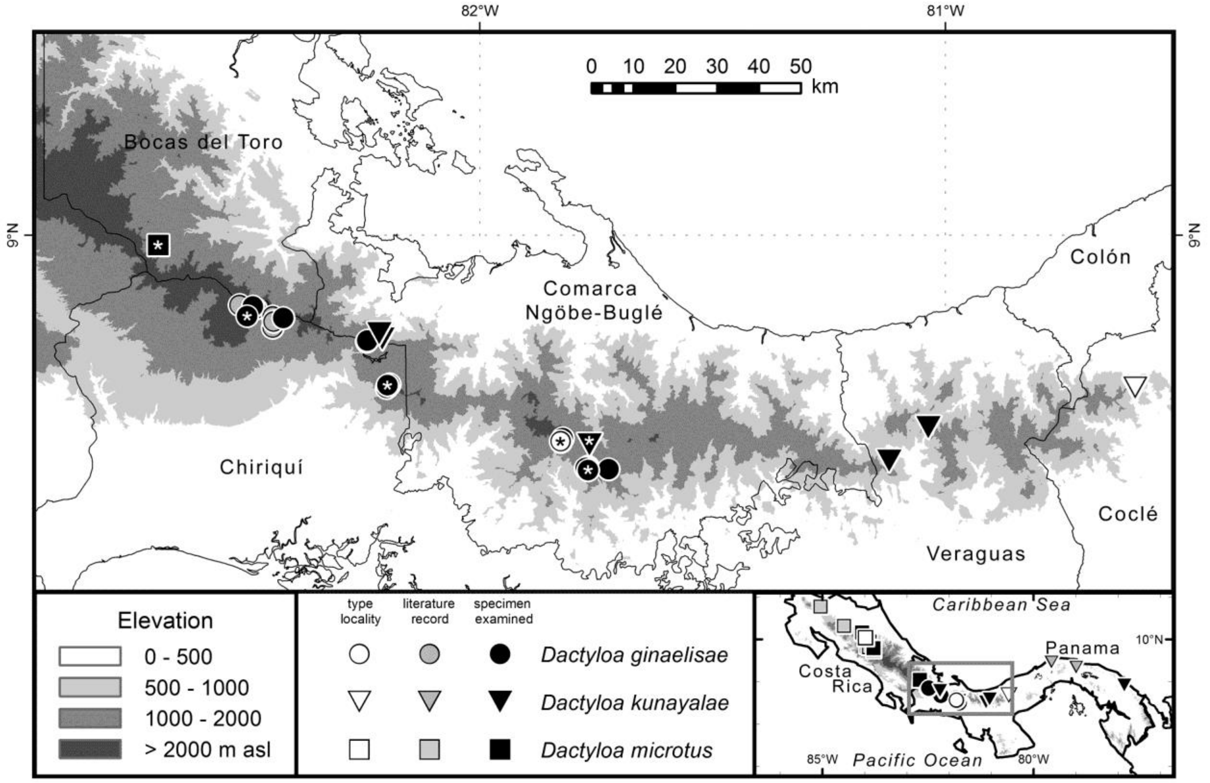
Etymology. Sebastian Lotzkat dedicates this exceptionally beautiful new species to his even more enchanting fiancée Gina Elisa Moog, who has made more than a third of his life worthwhile by now, in deepest gratitude for that wonderful time and pleasant anticipation of a mutual future.



Map 4.3: Distribution of *Dactyloa casildae* and *D. frenata* in western Panama (main map) and Lower Central America (inset). Localities of specimens with DNA barcodes included in the molecular analyses are marked with an asterisk (*). Records of *D. frenata* from Colombia, such as the type locality, are not shown.



Map 4.4: Distribution of *Dactyloa ibanezi* and *D. insignis* in western Panama (main map) and Lower Central America (inset). Localities of specimens with DNA barcodes included in the molecular analyses are marked with an asterisk (*).



Map 4.5: Distribution of *Dactyloa ginaelisae, D. kunayalae,* and *D. microtus* in western Panama (main map) and Lower Central America (inset). Localities of specimens with DNA barcodes included in the molecular analyses are marked with an asterisk (*).

The species accounts in chapter 4.2.2 summarize the morphological variation and geographical distribution of the now seven species of *Dactyloa* in western Panama, largely matching the format of the species description above. With the exception of maximum sizes, both their diagnosis and the description sections exclusively present data obtained from our material. Whenever relevant for identification, values for scale counts or proportions from other sources that exceed the ranges exhibited by our sample, as well as other incongruities or completions to our results, are mentioned in their concluding remarks sections. Table 4.6 presents a synopsis of the measurements and proportions, Table 4.7 of the scale counts among our material. The morphological variation among our material is illustrated by selected individuals in Figures 4.19–4.29. Concerning geographical distribution, our specimens of *Dactyloa ibanezi* and *D. insignis* fill gaps in the respective species' documented distribution. For the remaining taxa, our collection yields horizontal and/or vertical range extensions. The upper vertical limit for *D. frenata* is raised to 900 m asl (Stadler 2010). For *D. casildae,* our records expand the known range about 56 km southeastwards and 320 m uphill (Nicholson et al. 2001). The range of *D. ginaelisae* is extended 6 km further east from the records of Köhler et al. (2008), and onto the Caribbean slopes of western Panama. Our findings of *D. kunayalae* raise the altitudinal maximum by 250 m, and originate from up to 180 km west of the documented range (Hulebak et al. 2007). Regarding political subdivisions, we report for the first time *D. microtus* from Bocas del Toro province, *D. kunayalae* from Chiriquí and Veraguas provinces, *D. ibanezi* from Colón province, and *D. ibanezi, D insignis,* and *D. kunayalae* from the Comarca Ngöbe-Buglé. Maps 4.3–4.5 condense the current picture of their distribution, while Maps 4.37–43 illustrate the distribution of each species separately.

Although our records yield distributional range extensions for several species, we believe that dedicated sampling at additional localities will further expand certain ranges. In particular, we expect both *Dactyloa casildae* and *D. ginaelisae* to occur still more to the east along the Serranía de Tabasará than now documented. Likewise, the upper elevational limit for *D. casildae* and other species is probably not reached yet, and those of *D. ginaelisae* and *D. microtus* should be reconfirmed using modern GPS technology. Taking into account the continuous presence of suitable habitat along the Caribbean slopes of the Serranía de Talamanca in BPPS and PILA, it seems very likely that both *D. casildae* and *D. kunayalae* will be documented west of the currently westernmost localities, and most probably range into Bocas del Toro province. We also suspect that *D. ibanezi* occurs in the Pacific drainage around the Fortuna dam in Chiriquí province. Another interesting target for future surveys is the ubication of the geographic boundary between *D. ginaelisae* and *D. microtus,* including the possibility of hybridization between the two closely related species along a putative contact zone, as revealed for cryptic species pairs of *Norops* (Köhler et al. 2010b; Köhler et al. 2012a; also see chapters 4.1.4, 4.1.5, and 4.1.7.4)

All seven species of *Dactyloa* in western Panama reach an adult size that is large for anoles (SVL > 70 mm), have smooth or only slightly keeled ventrals at midbody, a large to very large dewlap as well as enlarged postcloacal scales in males, and lack caudal autotomy. Depending on individual size and color phase, especially young representatives of the genus *Dactyloa* occurring in western Panama might at first glance be confused with sympatric beta anoles of the genus *Norops* that reach moderate or large sizes, *i.e., N. aquaticus* Taylor, *N. biporcatus* Wiegmann, *N. capito* Peters, *N. lionotus* Cope, and *N. woodi* Dunn. Nevertheless, a closer examination will readily distinguish members of *Dactyloa* found in western Panama from the mentioned beta anoles (character states for the latter in parentheses) by their smooth to only slightly keeled ventrals that in any case seem smooth to the naked eye (ventrals obviously very strongly keeled), their large male dewlap (male dewlap at most moderate in *N. biporcatus* and *N. capito,* large in the other species), and their enlarged postcloacal scales in males (only present in *N. lionotus* and *N. woodi,* absent in the other species). Especially in combination with Figures 4.19–29, the following key will allow for the reliable identification of any living or preserved individual of *Dactyloa* encountered in the Cordillera Central.

Key to the species of *Dactyloa* in Panama

1. Legs short: tip of fourth toe of hind limb (adpressed along straightened specimen) reaching at most to posterior border of eye, shank length/SVL ratio < 0.24; suboculars and supralabials in contact **2**

   Legs long: tip of fourth toe of hind limb (adpressed along straightened specimen) reaching at least to center of eye, usually to a point anterior to eye, shank length/SVL ratio 0.25 or greater; suboculars and supralabials in contact or separated by one scale row **5**

2. At least one, often two or more, sublabials posterior to mental plate greatly enlarged; four or fewer horizontal rows of loreal scales; interparietal plate usually not distinct, usually no visible parietal eye; dorsal scales about the size of ventral scales; all scales on anterodorsal surface of thigh multicarinate; ear opening very small, less high than supralabials and infralabials together; 41–50 lamellae under fourth toe (base of digit to claw), 29–37 under fourth finger; male and female dewlap salmon, pink, or yellow **3**

   Sublabials not greatly enlarged, less high than adjacent infralabials; five or more horizontal rows of loreal scales; interparietal plate usually distinct, with visible parietal eye; dorsal scales smaller than ventral scales; most scales on anterodorsal surface of thigh smooth or unicarinate; ear opening moderate to large, higher than supralabials and infralabials together; numbers of lamellae under fourth toe and fourth finger higher or lower; dewlap coloration different **4**

3. Legs short: tip of fourth toe of hind limb (adpressed along straightened specimen) reaching to a point between anterior border of ear opening and posterior border of eye, shank length/SVL ratio 0.19–0.22; conspicuous and clear-cut coloration pattern between eye and shoulder, with a prominent light stripe extending from supralabials posteriorly above or a across the ear before bending down towards shoulder, delineating a dark preaxillary blotch above and posteriorly, and paralleled above by a dark postorbital stripe with darker borders that extends at least to a level above the preaxillary blotch .... ***Dactyloa ginaelisae*** (Figs. 4.12; 4.19; 4.20; 4.28G–I; 4.29R–S; 4.96H)

   Legs very short: tip of fourth toe of hind limb (adpressed along straightened specimen) reaching to a point between shoulder and ear, shank length/SVL ratio < 0.183; pattern of stripes between eye and shoulder more diffuse, with the light postsupralabial stripe not passing above or across the ear, and just as the dark postorbital stripe being oriented more ventrally, both losing their conspicuousness around level of ear opening .... ***Dactyloa microtus*** (Figs. 4.12; 4.18; 4.27; 4.29T–U; 4.97D)

4. Subdigital lamellar pads strongly dilated, more than three times width of distal phalanx; more than 50 lamellae under fourth toe (base of digit to claw); 190 or more scales around midbody; scales on anterodorsal surface of thigh smooth, only on anterior edge unicarinate with a few bi- or tricarinate; male dewlap orange or red, female dewlap brownish, mottled .... ***Dactyloa insignis*** (Figs. 4.12; 4.25; 4.29K–M; 4.97B)

   Subdigital lamellar pads barely dilated, less than two times width of distal phalanx; 35 or fewer lamellae under fourth toe (base of digit to claw); fewer than 150 scales around midbody; scales on anterodorsal surface of thigh unicarinate; male dewlap white with an orange-yellow margin; female dewlap white with a light yellow margin .... ***Dactyloa kunayalae*** (Figs. 4.12; 4.26; 4.28M–O; 4.29N–Q; 4.97C)

5. Body homogeneously green (turning bluish in preservative) with a series of parallel, oblique narrow dark lines on flanks; bright yellow completely encircling the eye; ear opening moderate, about as high as supralabials and infralabials together; suboculars and supralabials in contact; male dewlap orange with or without a white

margin, female dewlap dark orange, purple, or violet .... ***Dactyloa ibanezi*** (Figs. 4.12; 4.24; 4.28J–L; 4.29H–J; 4.97A)

Body pattern different: with broad bars, blotches, spots, or ocelli; if homogeneously green, then without narrow dark oblique lines on flanks; if bright yellow coloration present around the eye, then not completely encircling it but interrupted by darker stripes radiating from the eye; ear opening large, higher supralabials and infralabials together; suboculars and supralabials in contact or separated by one scale row; male dewlap mostly white **6**

6. Series of dark blotches or ocelli form oblique transverse bands on dorsum, flanks, limbs, and anterior portion of tail; a pronounced light-colored interorbital bar with dark anterior and posterior borders; light and dark stripes radiating from eye in all directions; tail length 1.9–2.1 times SVL; nasal separated from rostral by one or two scales; suboculars and supralabials separated by one scale row; male dewlap cream white, female dewlap brown .... ***Dactyloa frenata*** (Figs. 4.12; 4.23; 4.28D–F; 4.29E–G; 4.96G)

Coloration variable: unicolor, mottled, or with broad dark transverse bands; no pronounced interorbital bar; a dark pre- and/or postorbital stripe often present, but no light and dark stripes radiating from eye in all directions; tail length more than 2.5 times SVL; nasal in contact with rostral or separated from rostral by one scale; suboculars and supralabials in contact or separated by one scale row; male dewlap white with yellow and blue or green scales, female dewlap with contrasting yellow and green or blue striped or reticulate pattern ....***Dactyloa casildae*** (Figs. 4.12; 4.21; 4.22; 4.28A–C; 4.29A–D; 4.96F)

The hemipenes of the five species for which we have everted ones available are described for the first time in this study. The male reproductive organs among these species are rather similar in general build (Fig. 4.28), varying mostly in their degree of bilobatedness, from only slightly bilobated in *Dactyloa ibanezi* to distinctly bilobated in *D. ginaelisae.* However, this variation does not at all compare to the profound differences in hemipenial morphology exhibited by Central American mainland beta anoles of the genus *Norops,* where several extreme cases of hemipenial divergence concerning size and shape among very closely related and otherwise cryptic species have been documented (e.g., Köhler 2009, Köhler et al. 2010, 2012; Köhler, J.J. et al. 2012). Moreover, compared to the male reproductive organs of most species of *Norops,* the hemipenes among species of *Dactyloa* described herein are very small relative to the animals' body size. This is also the case in other alpha anoles for which we have everted hemipenes available. However, we refrain from inferring much of a phylogenetic signal from the hemipenial morphology among our sample. Yet, it seems that among anoles of the genus *Dactyloa,* or alpha anoles in general, the morphology of the male reproductive organ is less of a driving force in speciation than in their relatives of the beta section. In this context, we eagerly anticipate the examination of the everted hemipenes of adult males of *D. insignis,* and even more of *D. microtus.*

In our molecular analyses, *Dactyloa ibanezi* nests between the other five species. Hence, our results advocate the allocation of *D. ibanezi* in the *latifrons* clade of Castañeda and de Queiroz (2011), who did not include the species in their analysis but, just as Poe et al. (2009), assumed a close relationship with *D. chocorum* that they found to nest within the *latifrons* clade. Thus, our results reconfirm the formal inclusion in the latifrons species group as undertaken by Nicholson et al. (2012). Concerning *D. kunayalae,* our results reconfirm the species' allocation in the same species group as already suggested by the position that one of the paratypes (CHP 5505 fide Hulebak et al. 2007) assumed in the phylogeny of Nicholson et al. (2005, labeled "*Anolis* new species 1"). Thus, all seven *Dactyloa* species that occur in western Panama can confidently be regarded as members of the *latifrons* clade sensu Castañeda and de Queiroz (2011), and accordingly of the *latifrons* species group sensu Nicholson et al.(2012). Regarding the relative position of *D. casildae* in this clade, we are confident that our topology (*D. casildae* more closely related to *D. frenata* than to *D. microtus* as also recovered by Castañeda and de Queiroz 2011, and to *D. kunayalae* not sampled by these authors), better reflects evolutionary reality than the topology recovered by Nicholson et al. (2005, partly also 2012; *D. casildae* more closely related to *D. microtus* than to *D. frenata* and *D. kunayalae*), since this view is strongly supported by morphological characters.

In the case of *Dactyloa microtus* as recognized traditionally, high genetic differentiation (similar to that observed between *D. insignis* and *D. microtus*) along with corresponding morphological discrepancies clearly show that the nominal taxon *D. microtus* as understood in the past contains two well-separated genealogical lineages, which merit recognition as two separate species. It may seem surprising that the often very contrastingly colored individuals of *D. ginaelisae* that have been collected around Boquete have not attracted the attention of taxonomists earlier on. The small number of specimens of "*D. microtus*" in collections worldwide (Savage 2002), along with the unavailability of color photographs of the species until recently, have certainly contributed to the fact that these two species, which are not even too cryptic in their external morphology, have been treated under one name for the now 76 years that have passed since the first specimens from Panama became available (Dunn 1937). In the light of this taxonomic history, it seems a little ironic that *D. ginaelisae* is now more comprehensively documented and known from more voucher specimens than is *D. microtus* some 140 years after its original description. Considering the morphological differences among *D. insignis* from different regions in LCA pointed out by Savage & Talbot (1978) and the COI barcode of MVUP 2021 (see species account), this nominal species might represent a similar case as *D. ginaelisae* and *D. microtus.* Unfortunately, our small and exclusively female sample precludes that we contribute to the solution of this question at this point.

Table 4.6: Selected measurements and proportions among our sample of *Dactyloa* from western Panama.

		Dactyloa casildae **♂ 8, ♀ 17**	***D. frenata*** **♂ 3, ♀ 1**	***D. ginaelisae*** **♂ 8, ♀ 17**	***D. ibanezi*** **♂ 3, ♀ 1**	***D. insignis*** **♀ 2**	***D. kunayalae*** **♂ 1, ♀ 3**	***D. microtus*** **♂ 2, ♀ 1**
SVL	♂	46–114 (92.13 ± 25.23)	55–132 (86.33 ± 40.45)	41–112 (80.75 ± 30.49)	76–78 (77.33 ± 1.15)		103	65–68
	♀	37–99 (75.35 ± 15.57)	94	37–108 (80 ± 23.4)	78	64–124	57–85 (68.67 ± 14.57)	39
Tail length	♂	126–335 (246.33 ± 79.36)	104–280 (177.67 ± 91.43)	70–250 (169.88 ± 77.23)	193–195 (194 ± 1.41)		251.0	112–115
	♀	94–283 (212.29 ± 49.55)	195	62–231 (164.13 ± 57.84)	200	262	123–191 (146.67 ± 38.42)	55
Total length	♂	172–446 (333.33 ± 106.5)	159–412 (264 ± 131.87)	111–362 (250.63 ± 107.65)	269–273 (271 ± 2.83)		354.0	177–183
	♀	131–379 (288.36 ± 66.24)	289	99–339 (242.81 ± 81.03)	278	386	180–276 (215.33 ± 52.78)	94
Tail length/SVL	♂	2.72–3.02 (2.83 ± 0.12)	1.89–2.12 (2.03 ± 0.12)	1.69–2.28 (2.03 ± 0.23)	2.5–2.54 (2.52 ± 0.03)		2.44	1.69–1.72
	♀	2.54–3 (2.78 ± 0.13)	2.08	1.68–2.43 (2.05 ± 0.21)	2.56	2.11	1.97–2.25 (2.12 ± 0.14)	1.41
verDT/horDT	♂	1.05–1.38 (1.19 ± 0.1)	1.33–1.41 (1.36 ± 0.05)	1.26–1.63 (1.39 ± 0.12)	1.25–1.43 (1.32 ± 0.1)		1.28	1.33–1.48
	♀	1.02–1.3 (1.16 ± 0.08)	1.28	1.17–1.48 (1.34 ± 0.1)	1.37	1.19–1.38	1.14–1.41 (1.32 ± 0.16)	1.44
AGD/SVL	♂	0.39–0.45 (0.42 ± 0.02)	0.40–0.44 (0.42 ± 0.02)	0.39–0.43 (0.41 ± 0.01)	0.33–0.45 (0.4 ± 0.07)		0.42	0.41–0.43
	♀	0.39–0.46 (0.42 ± 0.02)	0.42	0.41–0.46 (0.43 ± 0.01)	0.44	0.41–0.44	0.4–0.43 (0.41 ± 0.01)	0.39
Shank length/SVL	♂	0.25–0.27 (0.26 ± 0.01)	0.26–0.29 (0.27 ± 0.02)	0.19–0.22 (0.2 ± 0.01)	0.26–0.28 (0.27 ± 0.01)		0.23	0.18
	♀	0.25–0.29 (0.27 ± 0.01)	0.26	0.19–0.22 (0.2 ± 0.01)	0.26	0.19–0.2	0.22–0.23 (0.23 ± 0.01)	0.17
Femur length/SVL	♂	0.29–0.33 (0.31 ± 0.01)	0.29–0.3 (0.29 ± 0.01)	0.23–0.27 (0.26 ± 0.01)	0.31–0.33 (0.32 ± 0.01)		0.27	0.23
	♀	0.27–0.33 (0.31 ± 0.02)	0.30	0.23–0.3 (0.26 ± 0.01)	0.31	0.24	0.26	0.23
HL/SVL	♂	0.26–0.28 (0.27 ± 0.01)	0.25–0.27 (0.26 ± 0.01)	0.25–0.3 (0.28 ± 0.01)	0.25–0.26 (0.25 ± 0.01)		0.27	0.27–0.28
	♀	0.26–0.29 (0.27 ± 0.01)	0.25	0.25–0.3 (0.27 ± 0.01)	0.25	0.25–0.26	0.27–0.28 (0.28 ± 0.01)	0.29
HW/SVL	♂	0.16–0.19 (0.17 ± 0.01)	0.15–0.18 (0.17 ± 0.02)	0.16–0.18 (0.17 ± 0.01)	0.14–0.16 (0.14 ± 0.01)		0.16	0.18
	♀	0.16–0.19 (0.18 ± 0.01)	0.15	0.16–0.2 (0.17 ± 0.01)	0.15	0.14–0.16	0.16–0.18 (0.17 ± 0.01)	0.18
HL/HW	♂	1.44–1.66 (1.56 ± 0.06)	1.49–1.62 (1.55 ± 0.07)	1.51–1.74 (1.61 ± 0.08)	1.64–1.84 (1.75 ± 0.1)		1.68	1.56–1.61
	♀	1.42–1.62 (1.53 ± 0.05)	1.59	1.46–1.65 (1.56 ± 0.06)	1.69	1.62–1.76	1.55–1.66 (1.59 ± 0.06)	1.60
Snout length/SVL	♂	0.11–0.13 (0.12 ± 0.01)	0.12–0.13 (0.13 ± 0.01)	0.12–0.14 (0.13 ± 0.01)	0.12–0.13 (0.12 ± 0)		0.13	0.13
	♀	0.12–0.13 (0.12 ± 0)	0.12	0.12–0.14 (0.13 ± 0.01)	0.12	0.12–0.13	0.12–0.13 (0.13 ± 0)	0.14
Snout length/HL	♂	0.43–0.46 (0.45 ± 0.01)	0.47–0.50 (0.48 ± 0.02)	0.44–0.49 (0.47 ± 0.02)	0.48–0.49 (0.48 ± 0)		0.48	0.46–0.47
	♀	0.43–0.48 (0.46 ± 0.01)	0.49	0.46–0.51 (0.48 ± 0.01)	0.47	0.49–0.50	0.46–0.47 (0.46 ± 0)	0.47
IP length/SVL	♂	0.01–0.02 (0.02 ± 0)	0.02		0.02		0.02	0.03
	♀	0.01–0.03 (0.02 ± 0)	0.01	0.02	0.02	0.01	0.01–0.02 (0.02 ± 0)	0.03
PA/SVL	♂	0.01–0.02 (0.02 ± 0)	0.01–0.02 (0.01 ± 0)	0.02–0.03 (0.03 ± 0)	0.02		0.01	0.05

Table 4.7: Selected pholidotic characters among our sample of *Dactyloa* from western Panama.

	Dactyloa casildae **♂ 8, ♀ 17**	***D. frenata*** **♂ 3, ♀ 1**	***D. ginaelisae*** **♂ 8, ♀ 17**	***D. ibanezi*** **♂ 3, ♀ 1**	***D. insignis*** **♀ 2**	***D. kunayalae*** **♂ 1, ♀ 3**	***D. microtus*** **♂ 2, ♀ 1**
4toepad	31–42 (37.1 ± 2.6)	38–43 (40.8 ± 2.1)	29–36 (32.9 ± 1.8)	28–30 (29 ± 0.8)	37–41	20–24 (21.8 ± 1.7)	32–34
4toedist	8–14 (11.2 ± 1.3)	14–17 (15 ± 1.4)	11–14 (12.4 ± 1.2)	10–11 (10.3 ± 0.5)	15	11–12 (11.3 ± 0.5)	12–13
4toe	42–53 (48.3 ± 2.9)	52–58 (55.8 ± 2.9)	41–50 (45.3 ± 2.5)	38–41 (39.3 ± 1.3)	52–56	32–35 (33 ± 1.4)	44–47
4fingerpad	18–25 (21.4 ± 1.5)	24–27 (25.3 ± 1.3)	19–24 (21.8 ± 1.4)	15–17 (16.5 ± 1)	25–27	12–13 (12.5 ± 0.6)	22–25
4fingerdist	9–19 (11.2 ± 2.1)	13	9–13 (10.9 ± 1)	8–11 (9.3 ± 1.3)	13–15	11–12 (11.5 ± 0.6)	10–12
4finger	29–40 (32.5 ± 2.4)	37–40 (38.3 ± 1.3)	29–36 (32.6 ± 1.7)	24–28 (25.8 ± 1.7)	40	23–25 (24 ± 0.8)	32–37
Number of scales between SS	2–5 (3.6 ± 0.8)	3–4 (3.8 ± 0.5)	1–3 (1.7 ± 0.6)	2	4	4–5 (4.3 ± 0.5)	2
Number of scales between IP and SS	2–5 (3.9 ± 0.8)	5	3	2–3 (2.8 ± 0.5)	3–5	4–6 (4.8 ± 1)	1
Number of scales between suboculars and SPL	0–1	1	0	0	0	0	0
Number of SPL to level below center of eye	6–8 (7 ± 0.4)	9–11 (9.8 ± 1)	6–8 (7.4 ± 0.7)	7–8 (7.8 ± 0.5)	8	8–9 (8.5 ± 0.6)	6–8
Number of INL to level below center of eye	6–9 (6.9 ± 0.7)	9–11 (9.8 ± 1)	5–9 (6.5 ± 0.9)	6–9 (7.5 ± 1.3)	8	8–9 (8.5 ± 0.6)	6–7
Total number of loreals	49–91 (68.5 ± 12.6)	62–83 (70.3 ± 10.2)	10–25 (17 ± 3.4)	39–52 (43 ± 6.1)	43–58	57–60 (58.3 ± 1.5)	15–26
Number of horizontal loreal scale rows	6–9 (7.6 ± 0.9)	6–7 (6.8 ± 0.5)	2–4 (3 ± 0.5)	5–6 (5.8 ± 0.5)	5	6	3–4
Number of postrostrals	6–11 (8.3 ± 1.2)	7–8 (7.3 ± 0.5)	4–8 (5.8 ± 1)	6–7 (6.5 ± 0.6)	6–7	7–8 (7.5 ± 0.6)	5–7
Number of postmentals	6–9 (7.6 ± 0.9)	8–11 (9.3 ± 1.5)	4–7 (5.7 ± 0.9)	6–8 (6.5 ± 1)	6–8	7–8 (7.8 ± 0.5)	6–8
Number of scales between nasals	5–8 (6.8 ± 0.9)	8–11 (9.8 ± 1.5)	3–7 (4.6 ± 0.9)	5–7 (6.5 ± 1)	6–8	7–9 (8 ± 0.8)	5
Number of enlarged Canthals	4–6 (4.8 ± 0.5)	5–7 (5.8 ± 1)	4–5 (4.7 ± 0.5)	5–6 (5.8 ± 0.5)	6	6–7 (6.3 ± 0.5)	3–6
Total number of Canthals	7–10 (8.6 ± 1)	9–10 (9.8 ± 0.5)	6–9 (7 ± 0.8)	8	8–9	9–10 (9.5 ± 0.6)	7–9
Number of scales between 2nd canthals	11–17 (13.2 ± 1.6)	10–14 (11.5 ± 1.7)	5–9 (7 ± 1)	9–10 (9.5 ± 0.6)	10–12	12–14 (12.5 ± 1)	6–8
Number of scales between posterior canthals	13–17 (14.8 ± 1.1)	11–14 (12.5 ± 1.3)	6–12 (7.9 ± 1.2)	11–13 (12 ± 0.8)	11–15	14–16 (14.8 ± 1)	8–9
Number of scales separating circumnasal or anterior nasal from rostral	0–1	1	1–2	1–2	1	1–2	1–2
Number of enlarged dorsal scale rows	0–2	0–2	0	0–2	0–2	0–2	0
Number of medial dorsal scales in one HL	43–68 (51.7 ± 5.4)	50–60 (53.8 ± 4.3)	31–48 (37.8 ± 4.2)	47–50 (48.5 ± 1.3)	49–72	46–53 (49.5 ± 3.5)	32–46
Number of medial ventral scales in one HL	46–83 (58.3 ± 8)	20–62 (46.3 ± 18.2)	40–61 (48.7 ± 6.3)	46–60 (53.3 ± 5.9)	44–60	48–63 (54.5 ± 6.2)	42–48
Number of scales around midbody	130–174 (150.7 ± 10.8)	160–178 (167.5 ± 8.2)	62–100 (87.2 ± 7.7)	142–151 (145.3 ± 4.3)	190–196	110–136 (126.5 ± 11.5)	98–106
Number of dorsal scales between axilla and groin	72–99 (87.2 ± 6.9)	90–98 (92.8 ± 3.6)	52–78 (63.4 ± 6.4)	84–97 (90.8 ± 5.4)	111–145	82–87 (83.8 ± 2.4)	50–55
Number of ventral scales between axilla and groin	65–86 (76.7 ± 6.2)	87–102 (92.3 ± 6.7)	61–88 (73.9 ± 6.6)	80–96 (86.8 ± 8.1)	85–104	67–92 (78.8 ± 10.4)	49–73

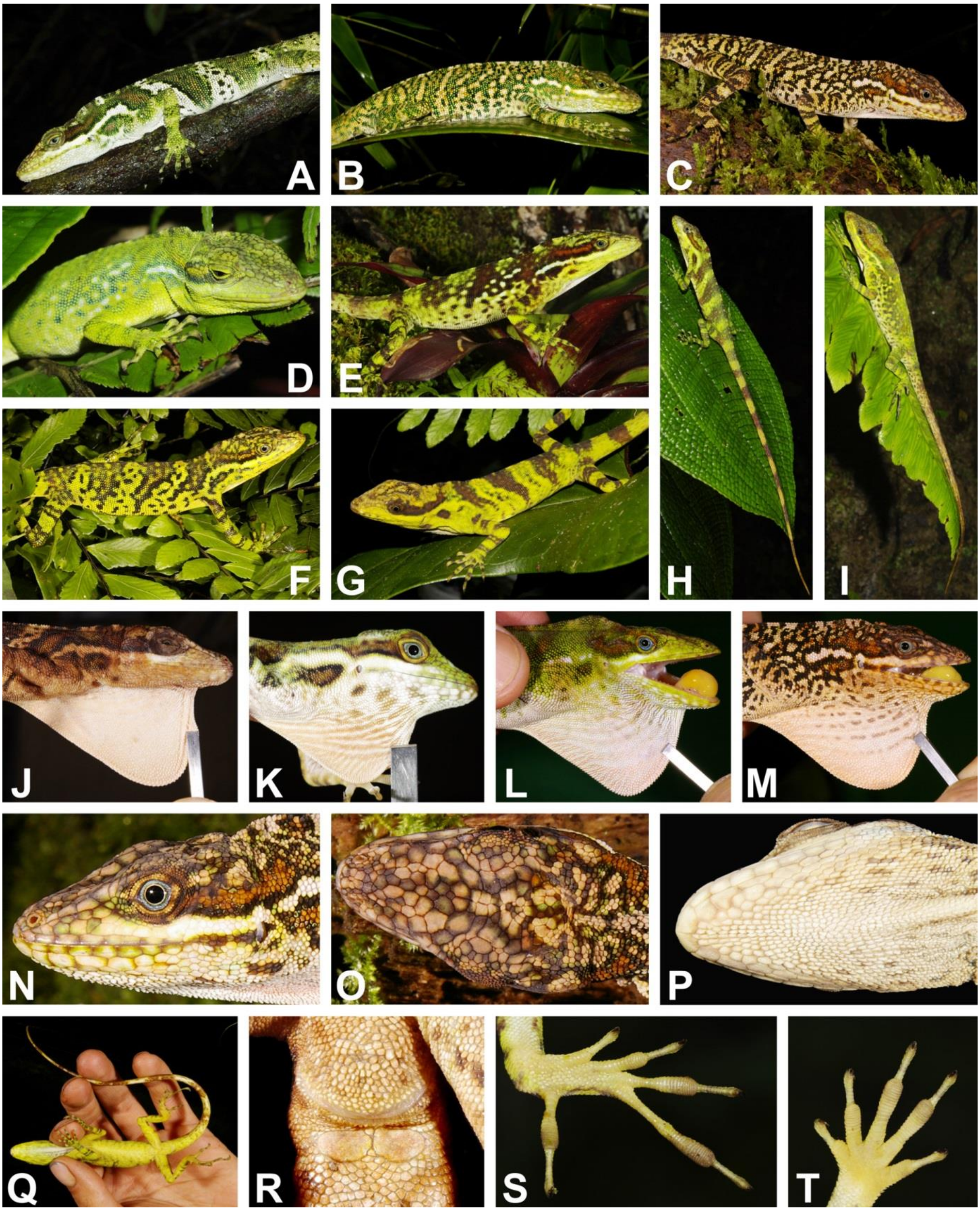


Figure 4.20: Specimens of *Dactyloa ginaelisae* from Chiriquí and the Comarca Ngöbe-Buglé: (A) adult male MHCH 2237 from RFLF; (B) female SMF 89501 from RFLF in sleeping position and (C) the next day; (D) female SMF 91503 from Cerro Saguí in sleeping position and (E) the next day; (F) female SMF 89497 and (G) female MHCH 2234 from La Nevera; (H) uncollected female juvenile and (I) uncollected female from La Nevera; (J–M) dewlaps of (J) adult male SMF 89738 from RFLF, (K) male juvenile SMF 89737 from PNVB, (L) female SMF 89499 from RFLF, and (M) female SMF 89501; (N) lateral, (O) dorsal, and (P) ventral views of head of SMF 89501; (Q) ventral view of MHCH 2234; (R) enlarged postcloacal scales of SMF 89738; ventral views of (S) left foot and (T) left hand of male holotype SMF 91504 from Cerro Saguí.

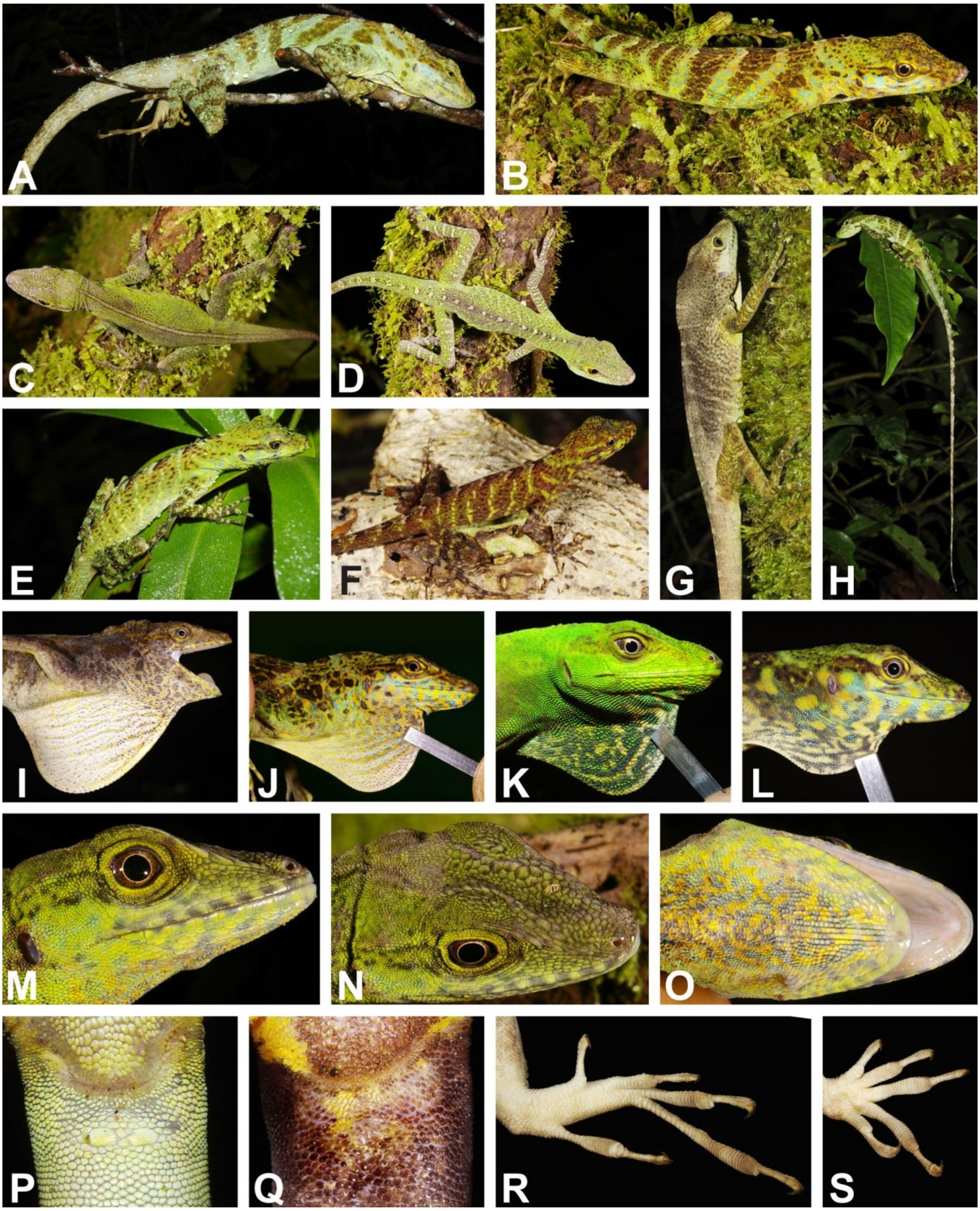


Figure 4.21: Specimens of *Dactyloa casildae* from RFLF, Chiriquí (if not otherwise mentioned from western slope of Cerro Pata de Macho): (A) adult male SMF 89673 in sleeping position; (B) subadult male MHCH 2121; (C) female SMF 89458; (D) female MHCH 2120; (E) female juvenile MHCH 2123 in sleeping position and (F) the next day; (G) uncollected adult male exhibiting brown phase at night; (H) female juvenile MHCH 2127 in sleeping position; (I–L) dewlaps of (I) adult male SMF 89673, (J) subadult male MHCH 2121, (K) female SMF 90098 from Cerro Guayabo, and (L) female juvenile MHCH 2127; (M) lateral, (N) dorsolateral, and (O) ventral views of head of SMF 89458; cloacal regions of (P) uncollected male shown in G showing enlarged postcloacal scales, and of (Q) male SMF 89673 lacking enlarged postcloacal scales; (R) left foot and (S) left hand of SMF 89673.

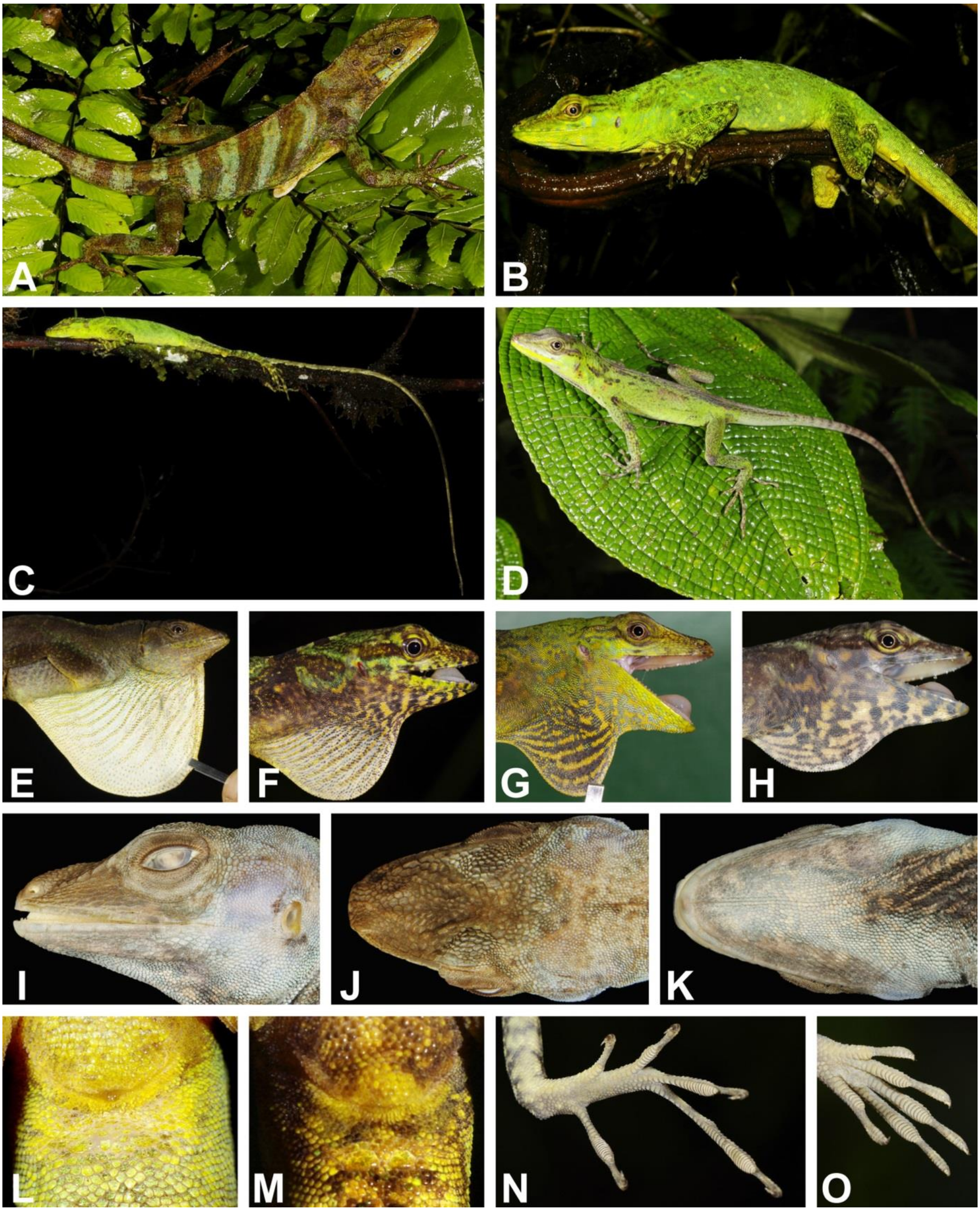


Figure 4.22: Specimens of *Dactyloa casildae* from the Comarca Ngöbe-Buglé: (A) adult male SMF 89454, and (B) adult female SMF 89453 in sleeping position, from La Nevera; (C) uncollected female from Río Flor; (D) female juvenile MHCH 2126 from La Nevera; (E–H) dewlaps of (E) adult male SMF 91454 and (F) male juvenile SMF 91453 from Río Flor; (G) female MHCH 2122 from La Nevera, and (H) female juvenile MHCH 2129 from Río Flor; (I) lateral, (J) dorsal, and (K) ventral views of head of preserved female SMF 89452 from La Nevera; enlarged postcloacal scales of (L) SMF 91454 and (M) SMF 91453; ventral views of (N) left foot and (O) left hand of MHCH 2129.

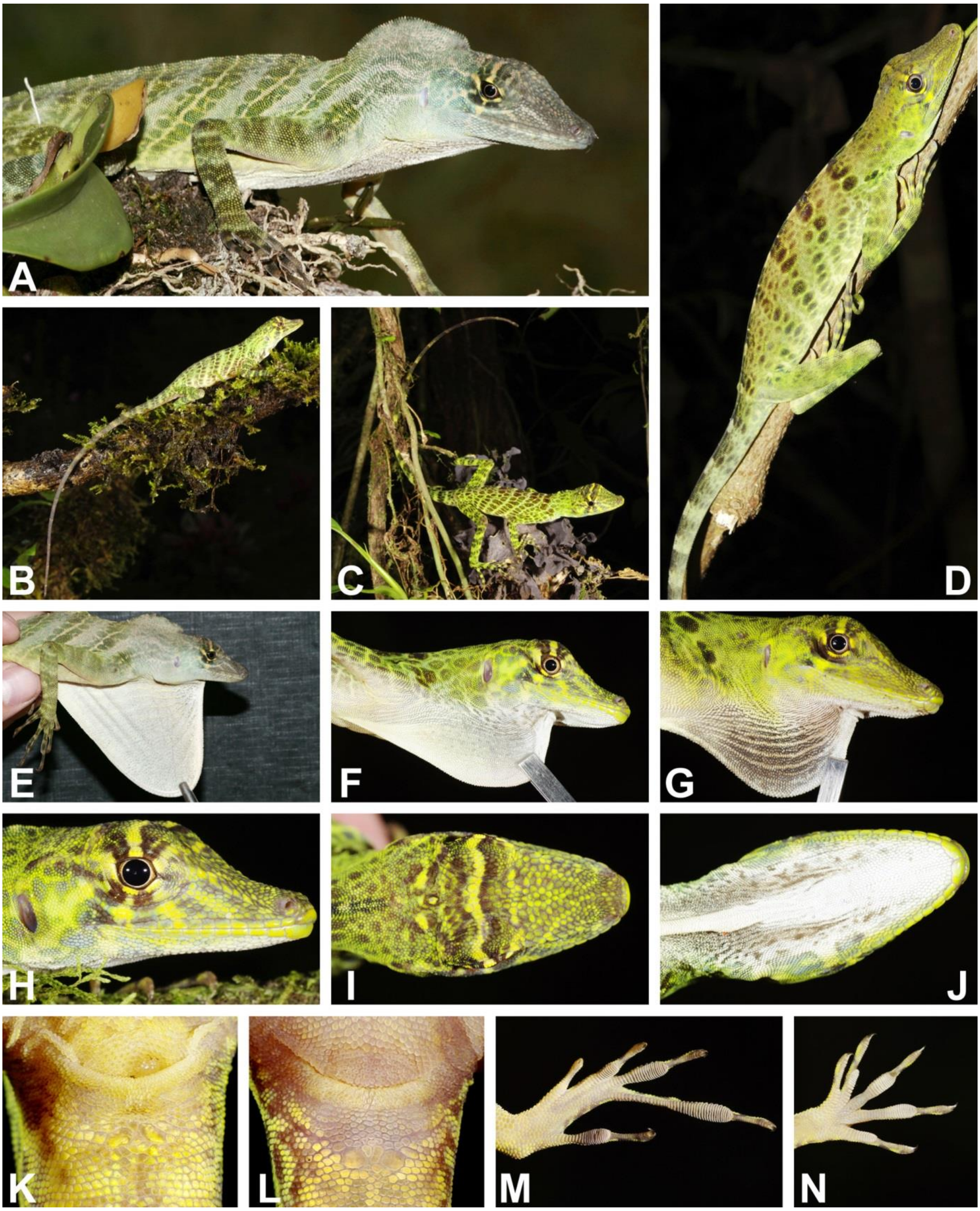


Figure 4.23: Specimens of *Dactyloa frenata* from western Panama: (A) adult male SMF 89467 from Cerro Mariposa, photo by Nadim Hamad and Leonhard Stadler; (B) juvenile male SMF 91459 and (C) young male SMF 91460 from Willie Mazú; (D) female SMF 89897 from Cerro Negro; (E–G) dewlaps of (E) adult male SMF 89467, photo by Nadim Hamad and Leonhard Stadler, (F) young male SMF 91460, and (G) female SMF 89897; (H) lateral, (I) dorsal, and (J) ventral views of head of SMF 91460; enlarged postcloacal scales of (K) SMF 91460 and (L) SMF 91459; ventral views of (M) left foot and (N) left hand of SMF 91460.

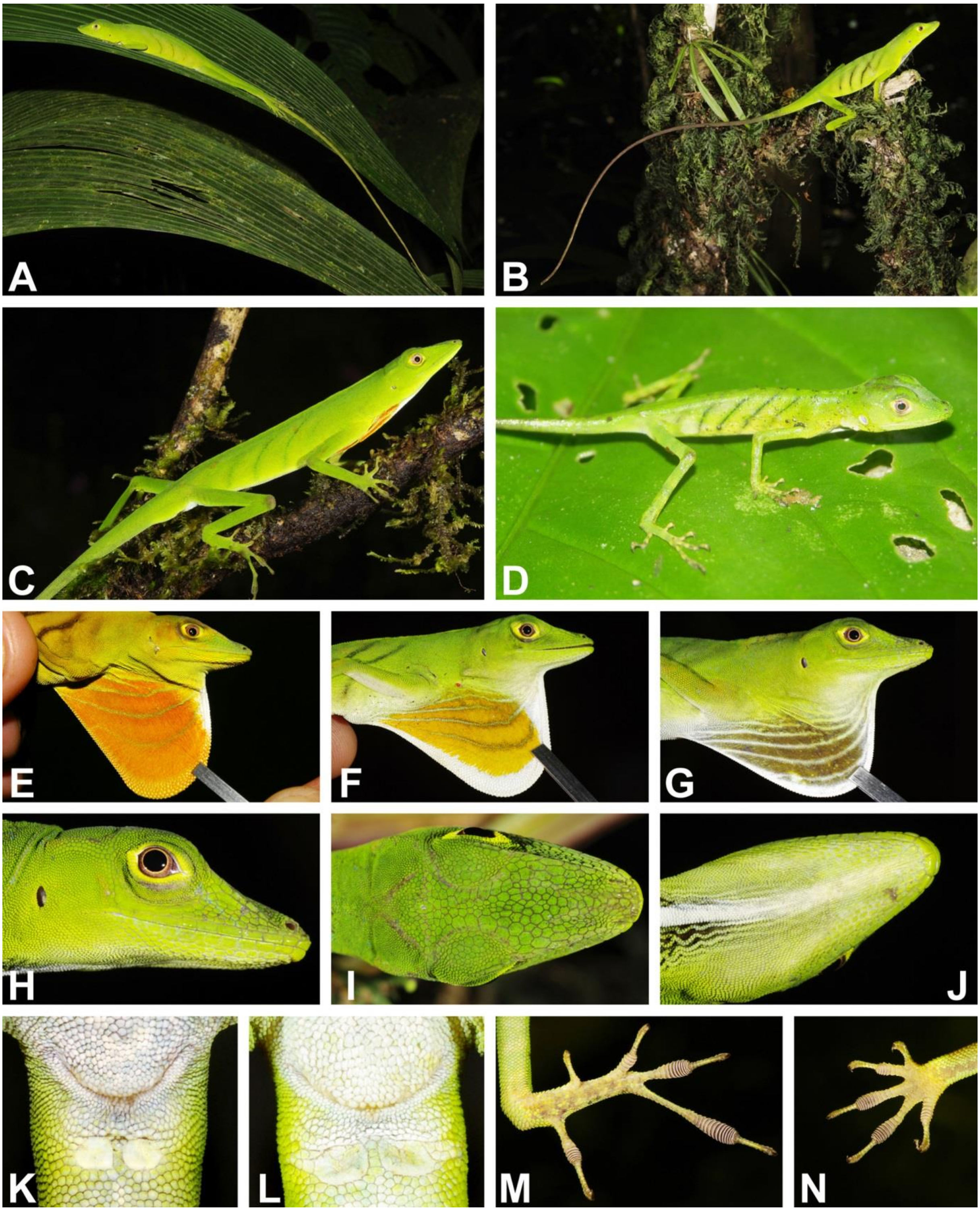


Figure 4.24: Specimens of *Dactyloa ibanezi* from western Panama: (A) female SMF 91475 from Willie Mazú in sleeping position and (B) the next day; (C) male MHCH 2184 from Cerro Mariposa; (D) juvenile from Sendero Pianista, photo by Johannes J. Köhler; (E–G) dewlaps of (E) male paratype SMF 89459 from Cerro Mariposa, (F) male SMF 91476 from Willie Mazú, and (G) female SMF 91475; (H) lateral, (I) dorsal, and (J) ventral views of head of SMF 91475; enlarged postcloacal scales of (K) SMF 89459 and (L) MHCH 2184; ventral views of (M) left foot and (N) right hand of SMF 89459.

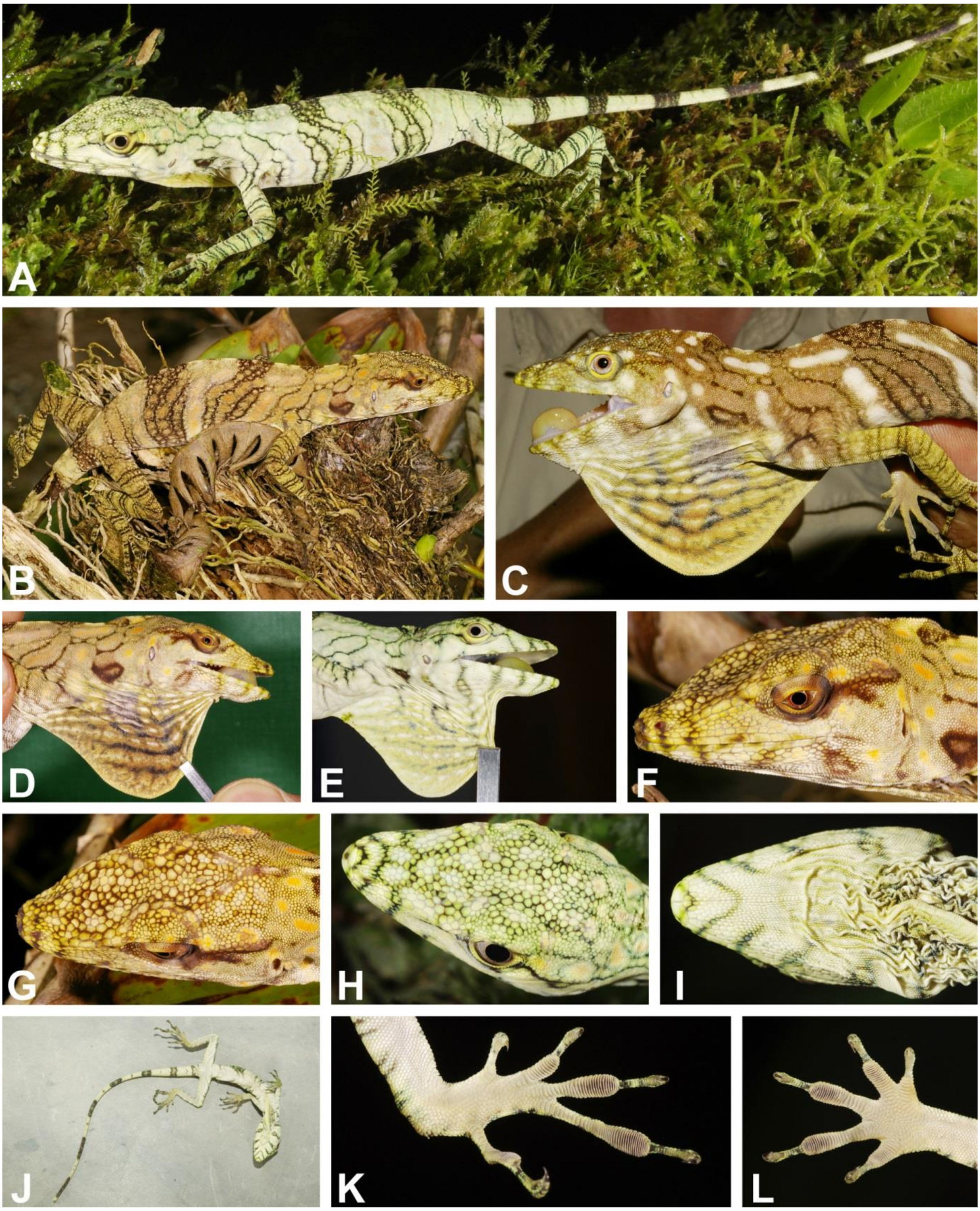


Figure 4.25: Female specimens of *Dactyloa insignis* from western Panama: (A) juvenile female SMF 91477 from Willie Mazú; (B) adult female SMF 89482 from Cerro Mariposa at daytime, and (C) at night immediately after capture; (D–E) dewlaps of (D) SMF 89482 and (E) SMF 91477; (F) lateral and (G) dorsal views of head of SMF 89482; (H) dorsal and (I) ventral views of head of SMF 91477; ventral views of (J) entire specimen, (K) left foot, and (L) right hand of SMF 91477.

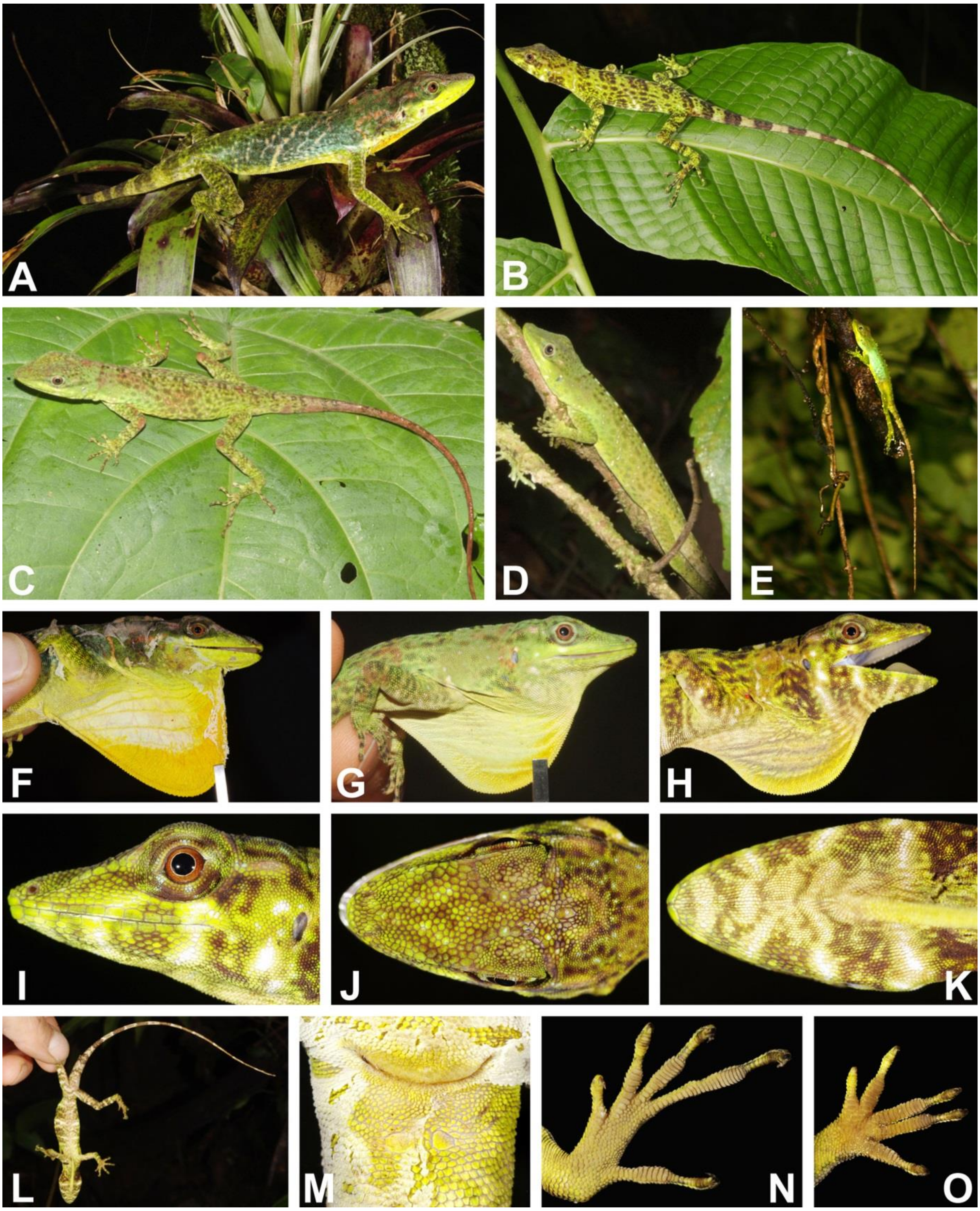


Figure 4.26: Specimens of *Dactyloa kunayalae* from western Panama: (A) adult male SMF 91484 from BPPS; (B) young female SMF 91485 from Río Hacha; (C) female SMF 96009 from Cerro Mariposa; (D) SMF 96009 in sleeping position; (E) uncollected, probably male specimen from Río Chilagres; (F–H) dewlaps of (F) male SMF 91484, (G) female SMF 96009, and (H) young female SMF 91485; (I) lateral, (J) dorsal, and (K) ventral views of head of SMF 91485; (L) ventral view of SMF 91485; (M) enlarged postcloacal scales of SMF 91484; ventral views of (N) left foot and (O) left hand of SMF 91485.

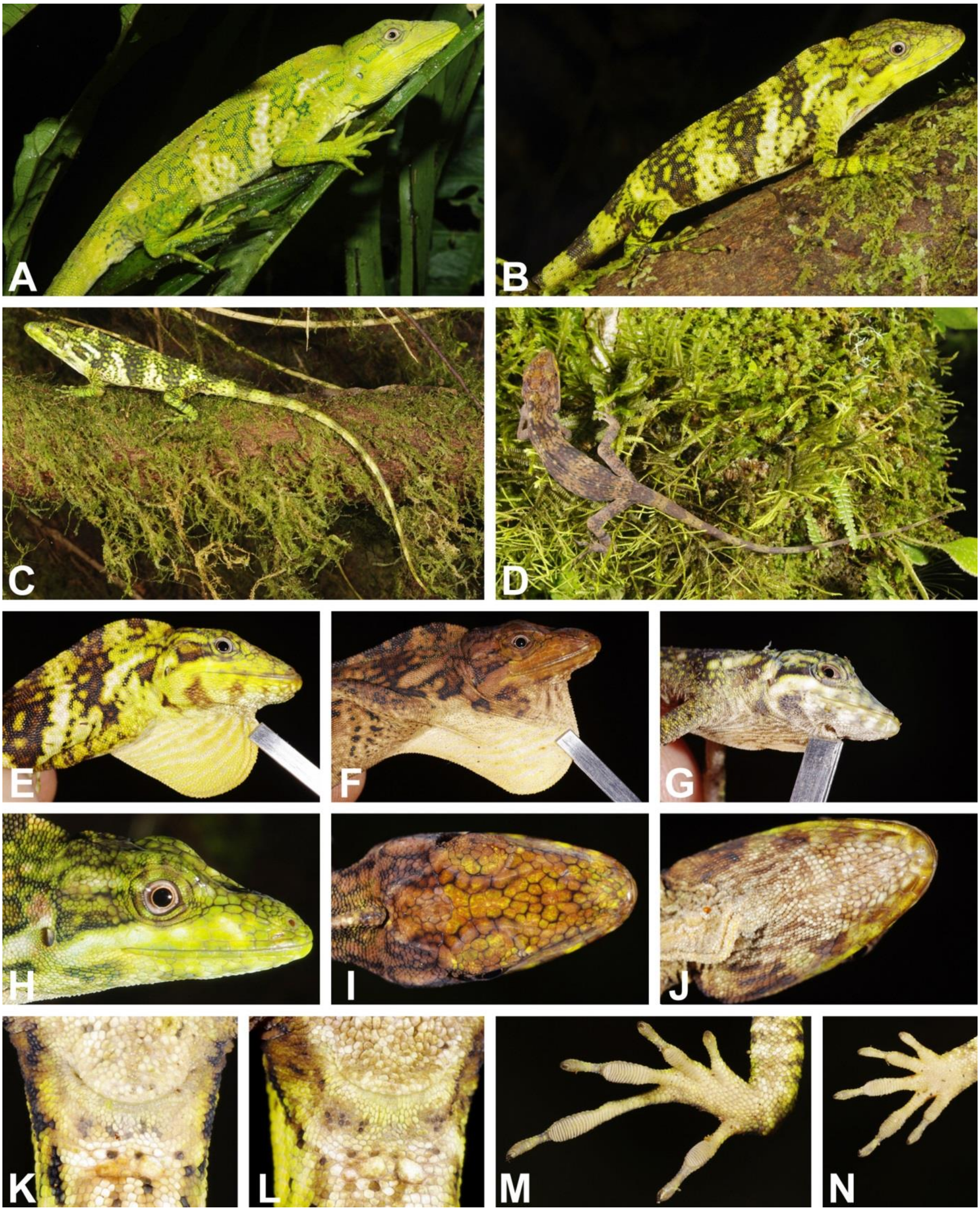


Figure 4.27: Specimens of *Dactyloa microtus* from Río Changena, Bocas del Toro: young male SMF 91499 in (A) sleeping position and (B) the next day; (C) and (D) young male SMF 91500; (E–G) dewlaps of (E) young male SMF 91499, (F) young male SMF 91500, and (G) female hatchling SMF 91501; (H) lateral, (I) dorsal, and (J) ventral views of head of SMF 91500; enlarged postcloacal scales of (K) SMF 91500 and (L) SMF 91499; ventral views of (M) right foot and (N) right hand of SMF 91500.

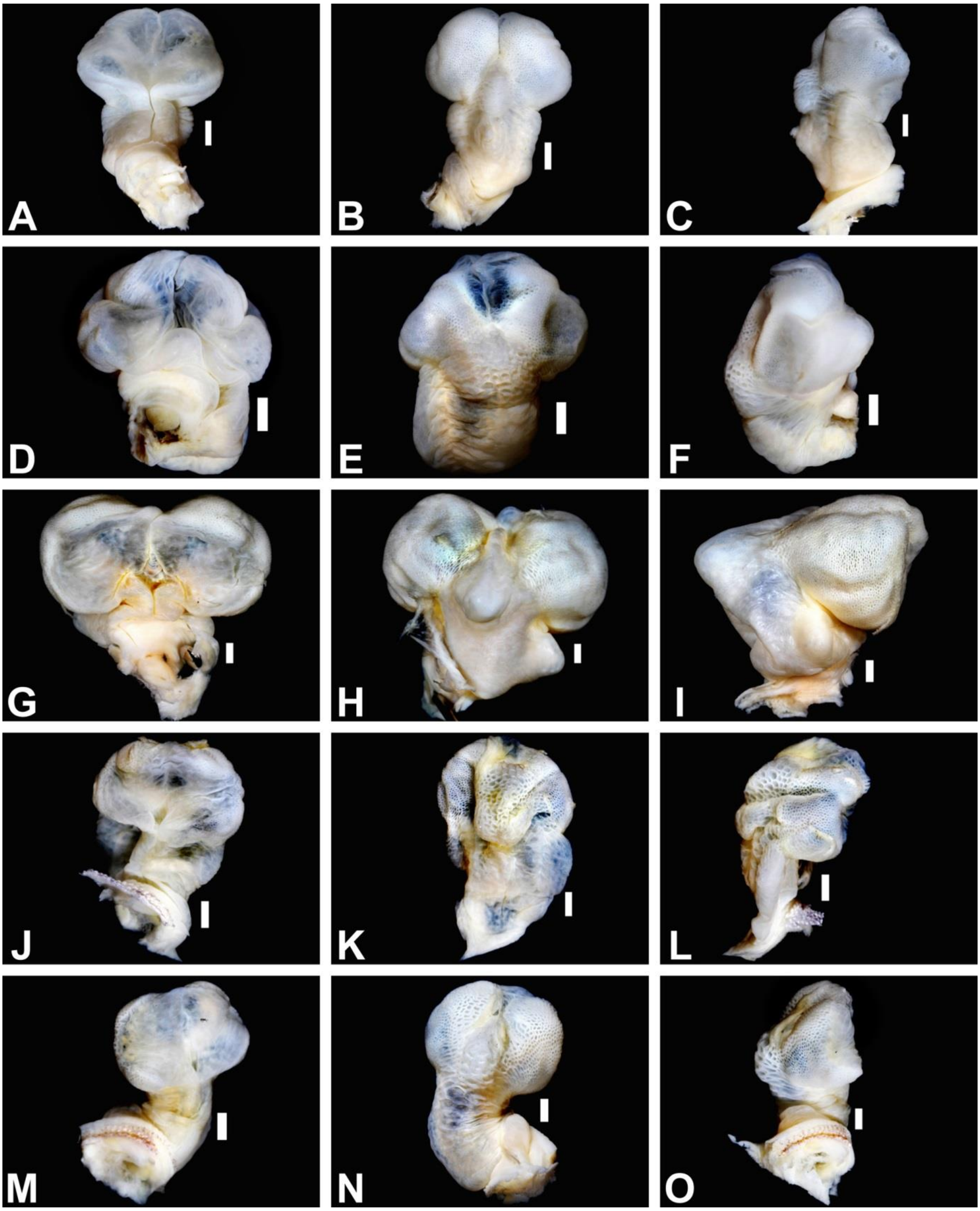


Figure 4.28: Hemipenes of *Dactyloa* from western Panama: (A–C) *Dactyloa casildae,* SMF 91454: (A) sulcate, (B) asulcate, and (C) lateral view; (D–F) *Dactyloa frenata,* SMF 89467: (D) sulcate, (E) asulcate, and (F) lateral view; (G–I) *Dactyloa ginaelisae,* SMF 89498: (G) sulcate, (H) asulcate, and (I) lateral view; (J–L) *Dactyloa ibanezi,* MHCH 2184: (J) sulcate, (K) asulcate, and (L) lateral view; (M–O) *Dactyloa kunayalae,* SMF 91484: (M) sulcate, (N) asulcate, and (O) lateral view; all scale bars equal 1 mm.

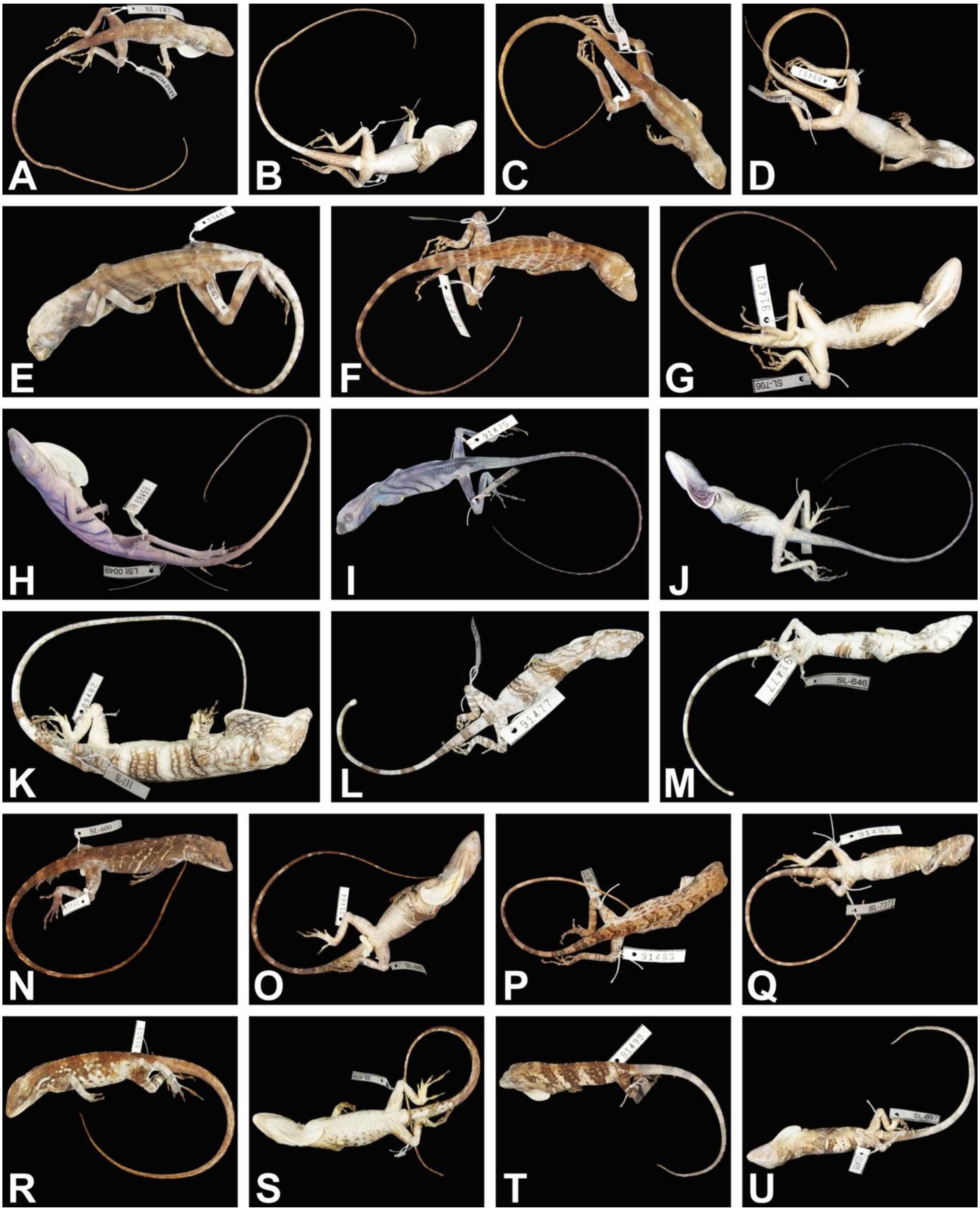


Figure 4.29: Preserved specimens of *Dactyloa* from western Panama: (A–D) *Dactyloa casildae,* (A) and (B) young male MHCH 2121, SVL = 69 mm; (C) and (D) female SMF 89453, SVL = 81 mm; (E–G) *D. frenata,* (E) male SMF 89467, SVL = 132 mm, (F) and (G) young male SMF 91460, SVL = 72 mm; (H–J) *D. ibanezi,* (H) male paratype SMF 89459, SVL = 78 mm, (I) and (J) female SMF 91475, SVL = 78 mm; (K–M) *D. insignis,* (K) adult female SMF 89482, SVL = 124 mm, (L) and (M) juvenile female SMF 91477, SVL = 64 mm; (N–Q) *D. kunayalae,* (N) and (O) male SMF 91484, SVL = 103 mm; (P) and (Q) young female SMF 91485, SVL = 64 mm; (R) and (S) *D. ginaelisae,* female SMF 91503, SVL = 100 mm; (T) and (U) *D. microtus,* young male SMF 91499, SVL = 65 mm.

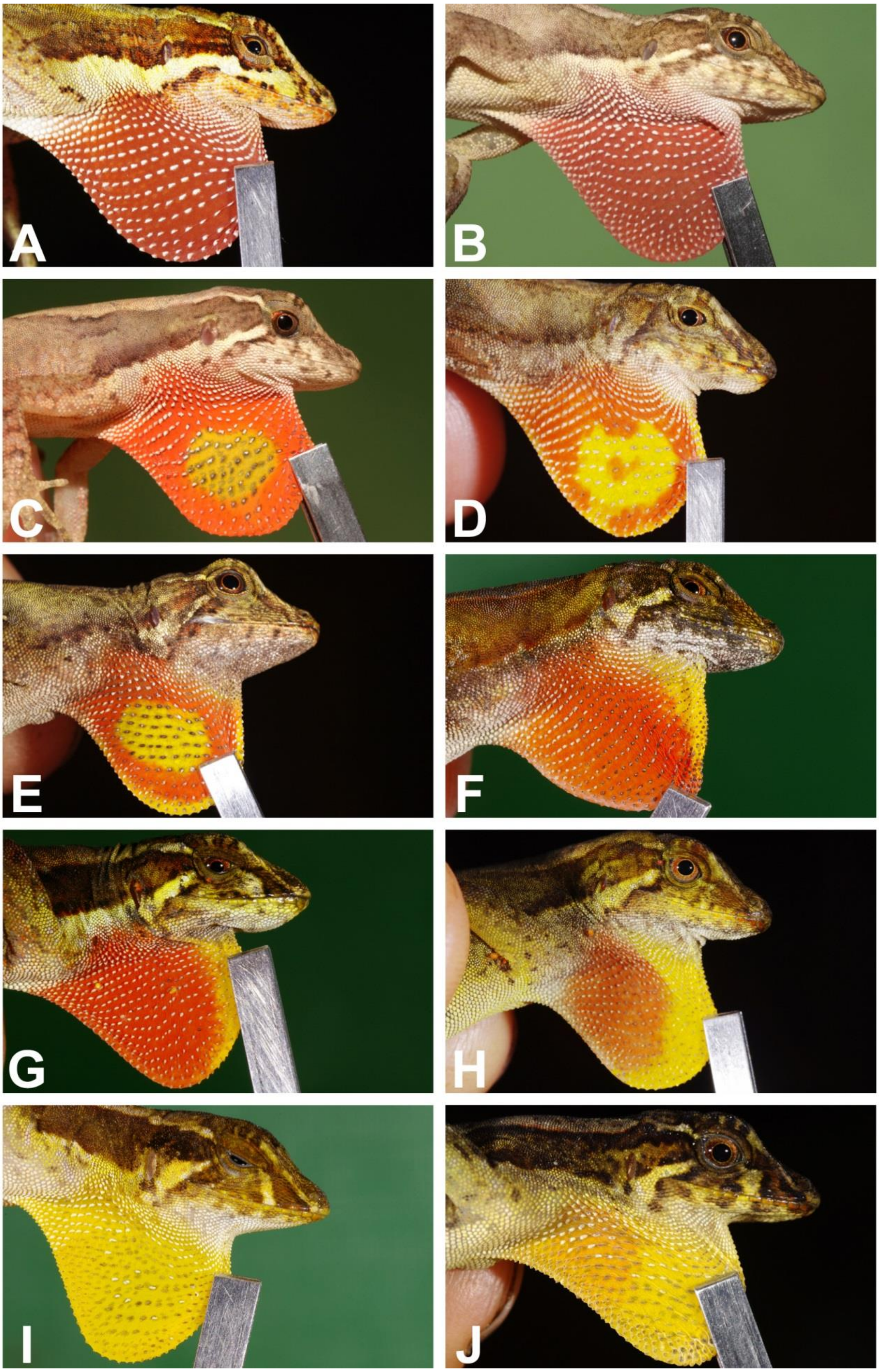


Figure 4.30: Dewlaps of anoles related to *Norops pachypus* representative of the five OTUs: (A) OTU A (SMF 89729, Sendero La Cascada, Bajo Mono, Chiriquí, Panama); (B) OTU B (GK 2297, road from San José de la Montaña to Birrí, Heredia, Costa Rica; photo by GK); (C) OTU C (GK 2355, road from San Isidro de El General to Cerro de la Muerte, San José, Costa Rica; photo by GK); (D) OTU C (SL 439, Jurutungo, Chiriquí, Panama); (E) OTU C (SL 524, Jurutungo); (F) OTU D (SMF 89507, Jurutungo); (G) OTU D (SMF 89506, Jurutungo); (H) OTU D (SMF 90149, N slope Cerro Pando, Bocas del Toro, Panama); (I) OTU E (SMF 89519, La Nevera, Comarca Ngöbe-Buglé, Panama); (J) OTU E (SL 510, La Nevera).

4.1.4 Iguania, Dactyloidae: The *Norops pachypus* complex

The Lower Central American highlands are home to several groups of very similar to truly cryptic species of anoles. One of these species complexes comprises *Norops pachypus* (Cope 1876) and its recently described close relatives *N. magnaphallus* (Poe & Ibáñez 2007) and *N. pseudopachypus* (Köhler, Ponce, Sunyer & Batista 2007). Together with *N. tropidolepis* (Boulenger 1885), which inhabits montane elevations in the Costa Rican highlands (Guanacaste, Puntarenas, Alajuela, Heredia, Cartago, and San José provinces), the aforementioned species are extremely similar to each other in terms of habitus, general appearance, coloration, habitat, and probably also in behavior and ecology. They are separable mostly by the distinct coloration of the male dewlap, which seems to be stable within each of the four species, as presently understood. Discrepancies in dewlap coloration among male representatives of the *N. pachypus* complex at certain localities aroused our suspicion and lead to the description of a fifth species that is presented in chapter 4.1.4.1. The species composition as suggested by dewlap coloration is compared to the phylogenetic signal inferred from DNA barcodes in chapter 4.1.4.2. For more information on each species see their respective species accounts in chapter 4.2.2.

4.1.4.1 A new species of *Norops* (Squamata: Iguania: Dactyloidae) formerly referred to as *N. pachypus* from the Cordillera de Talamanca of western Panama and adjacent Costa Rica

[Modified from Lotzkat et al. (2011) who used the generic name *Anolis;* see Appendix 8 for original publication]

Abstract: We describe *Norops benedikti* from lower montane elevations of the Cordillera de Talamanca in Bocas del Toro and Chiriquí provinces of western Panama, and adjacent Puntarenas province of eastern Costa Rica. The new species is very similar to *N. magnaphallus, N. pachypus, N. pseudopachypus,* and *N. tropidolepis,* which inhabit the same mountain range. It differs from these species in the coloration of the male dewlap, which is red with a yellow anterior margin (versus male dewlap solid purplish red in *N. magnaphallus* and *N. tropidolepis,* red with a central yellow blotch in *N. pachypus,* and solid yellow in *N. pseudopachypus*), and in pholidotic characters.

Key words: *Norops pachypus* complex, cryptic species, Lower Central America, Cordillera Central, Talamancan highlands, Cerro Pando, conservation, morphology.

Our surveys along western Panama's Cordillera Central produced numerous specimens of the three species of the *Norops pachypus* complex previously documented to occur in Panama (*N. magnaphallus, N. pseudopachypus,* and *N. pseudopachypus*). Yet, within the supposed distributional ranges of *N. pachypus* and *N. magnaphallus,* and most notably close to sites where we had collected individuals exhibiting the respective typical phenotype of either species, we came across individuals that are not distinguishable at first sight, but indeed differ substantially from these two taxa in terms of male dewlap coloration, dorsal head scalation, and tongue coloration. We herein compare them to the four nominal species of the *N. pachypus* complex (*N. magnaphallus, N. pachypus, N. pseudopachypus,* and *N. tropidolepis*), and describe them as representative of a new species.

Juvenile and subadult specimens (SVL<30 mm, except for the larger-bodied *Norops magnaphallus* and *N. tropidolepis:* SVL<35 mm) were excluded from the statistical analyses. Our designations of nasal scalation types are shown in Figure 4.33. We conducted automatized temperature measurements at the type locality of the new taxon every hour, over a total of 205 hours distributed among three periods (40 hours from 20:00 hr. on 19 April 2009 to 11:00 hr. on 21 April 2009; 40 hours from 20:00 hr. on 18 November 2009 to 11:00 hr. on 20 November 2009; 125 hours from 12:00 hr. on 13 July 2010 to 16:00 hr. on 18 July 2009). An exclusive list of all specimens examined for this chapter by JFB, including those from Costa Rica, is provided in the Appendix of the original publication.

To assess the distinctness of the populations in question, we compared them to the four currently recognized species inhabiting the highlands of Costa Rica and/or Panama with which they are most likely to be confused: *Norops magnaphallus, N. pachypus, N. pseudopachypus,* and *N. tropidolepis.* Since the male dewlap is the main distinguishing feature in this species cluster, we only considered male specimens with associated data on dewlap coloration for the statistics. According to their dewlap coloration, and in the case of identical dewlap coloration among geographically widely separated samples also according to geography, we separated the material into Operational Taxonomic Units (OTUs) as follows:

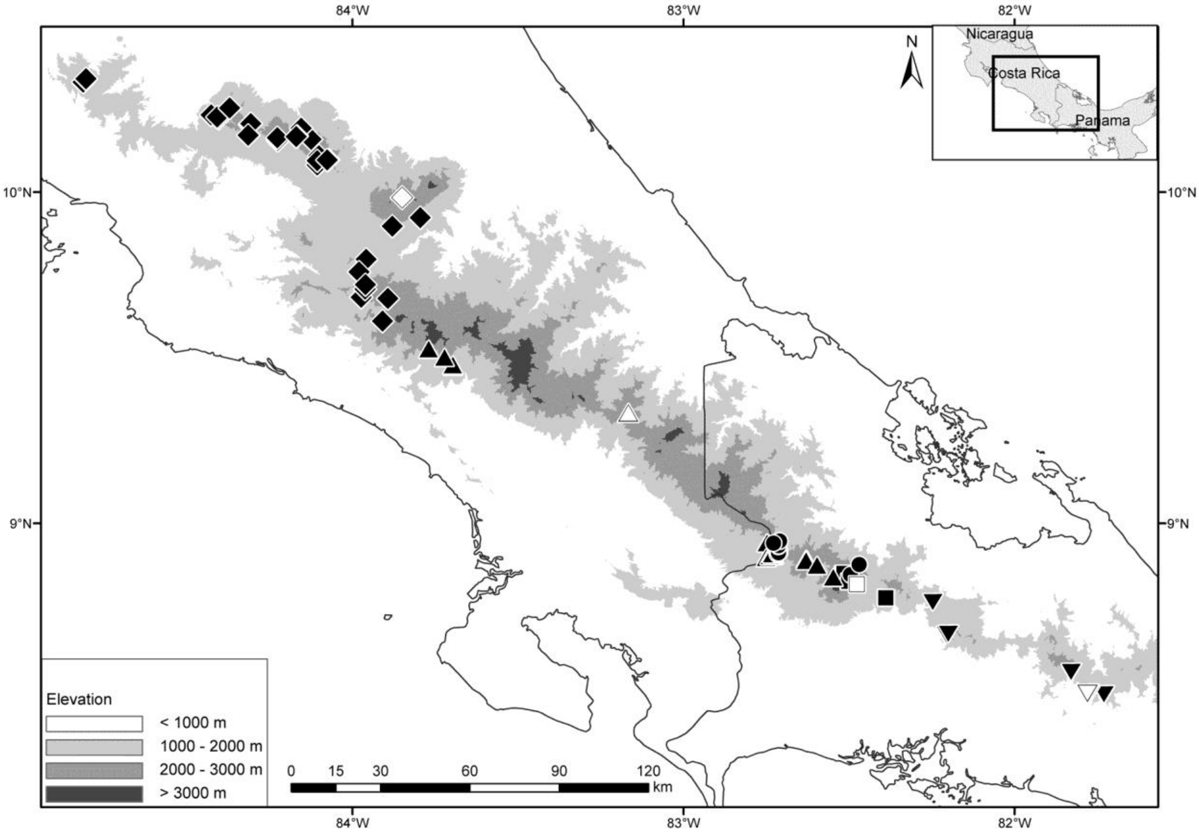
A: uniform purplish red — from the Boquete area in western Panama (Fig. 4.30A)

B: uniform purplish red — from Costa Rica (Fig. 4.30B)

C: red with central yellow blotch and (potentially) a narrow yellow margin (Figs. 4.30C–E)

D: red with anterior yellow margin, but without central yellow blotch (Figs. 4.30F–H)

E: uniform yellow, in some cases grading into orange-yellow posteriorly (Figs. 4.30I–J)



Map 4.6: Geographical distribution of OTUs. Squares represent OTU A, diamonds OTU B, upright triangles OTU C, circles OTU D, inverted triangles represent OTU E. Hollow symbols represent the type localities (from west to east) of *Norops tropidolepis*, *N. pachypus, N. magnaphallus,* and *N. pseudopachypus.* Map by AH.

In total, we could assign 143 male specimens to the respective OTUs. Map 4.6 shows the geographic distribution of these individuals: OTUs B in the west and E in the east are separated geographically from the remaining OTUs. OTUs A, C, and D occur very close to each other in western Panama and extreme eastern Costa Rica. We then employed statistics to a subset of 61 adult males (marked in the Appendix of the original publication with an asterisk; N = 8 for OTU A, N = 10 for OTU B, N = 10 for OTU C, N = 17 for OTU D, N = 16 for OTU E) to further assess morphological differentiation among OTUs. An analysis of standard morphometric and pholidotic characters among these 61 specimens showed little morphological differentiation among OTUs for most characters (Figure 4.31). However, dorsal head scales of OTUs D and E are generally smaller and more numerous, and their supraorbital semicircles less conspicuous, than those of OTUs A–C. This is most obviously reflected in OTUs D and E exhibiting more scale rows between the supraorbital semicircles, and more scales between supraorbital semicircles and the interparietal plate. Individuals of OTUs D and E also have slightly more scales between posterior and second canthals, respectively, than those belonging to OTUs A, B, and C. Furthermore, in the field we observed differences in tongue coloration among members of OTUs: Individuals with a type D dewlap invariably had a very dark gray (almost blackish) tongue (as well as the members of

OTU E examined for this trait), whereas those with type A and C dewlaps (as well as the members of OTU B examined for this trait) had a very light gray tongue.

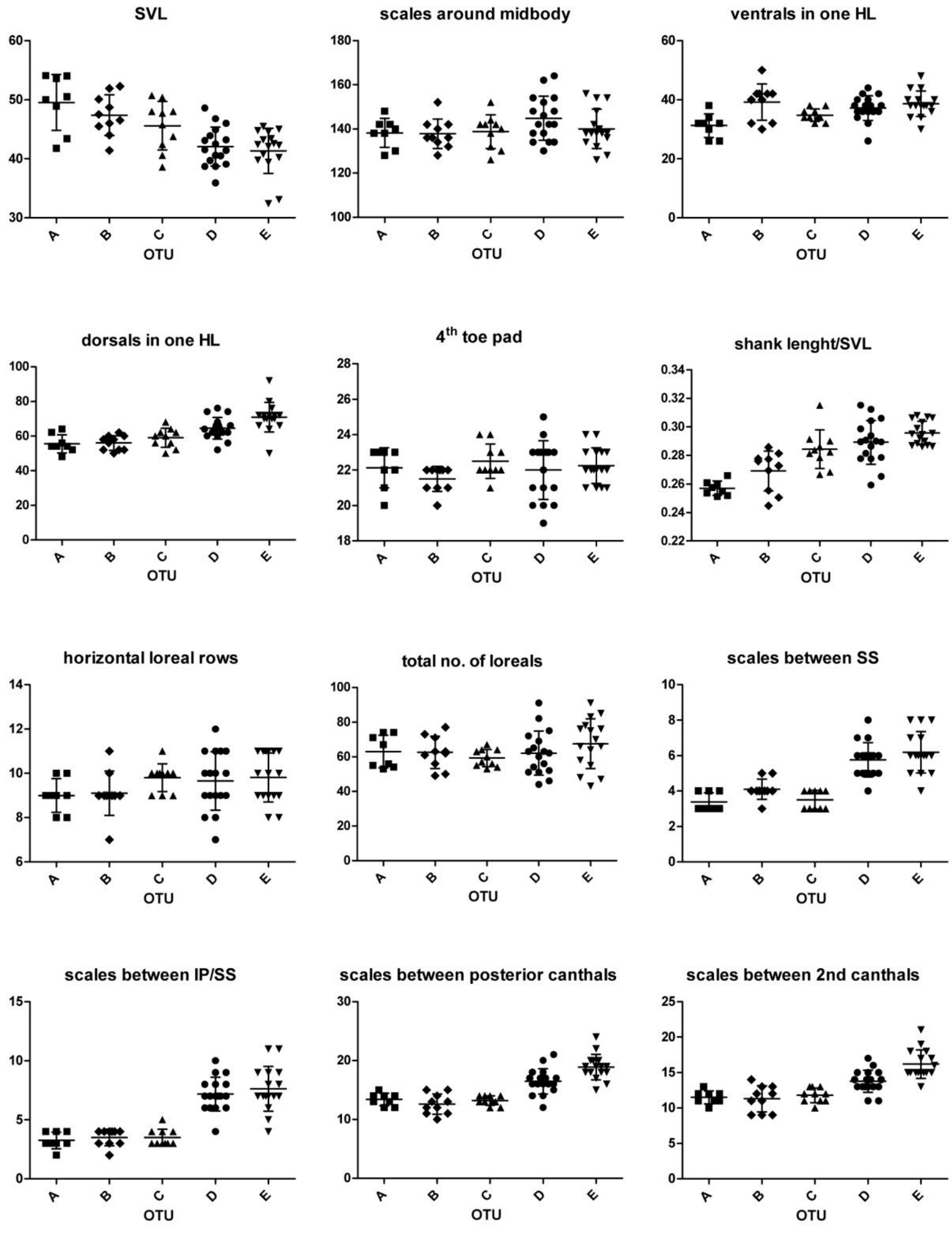


Figure 4.31: Scatterplots (bars indicate mean ± one standard deviation) showing the variation in selected morphological characters among OTUs. Symbols match those of Map 4.6.

We conducted a discriminant function analysis (DFA) based on two morphometric and four pholidotic characters (SVL, shank length/SVL, ventrals in one HL, dorsals in one HL, IO, scales between 2^{nd} canthals) that correctly classified 80.3% of all specimens (100% of OTU A, 70% of OTUs B and C, 88.2% of OTU D, and 75% of OTU E). In the scatterplot of canonical scores (Figure 4.32), each OTU's polygon overlaps another one (A, B), two (D, E), or four (C) polygons of other OTUs. The first function is DS = +0.082180 (SVL) +0.636003 (shank length/SVL) -0.236048 (ventrals in one HL) +0.404230 (dorsals in one HL) +0.477532 (IO) +0.461402 (scales between 2^{nd} canthals). The second function is DS = -0.433741 (SVL) -0.166431 (shank length/SVL) +0.683449 (ventrals in one HL) -0.590546 (dorsals in one HL) +0.719675 (IO) -0.663412 (scales between 2^{nd} canthals).

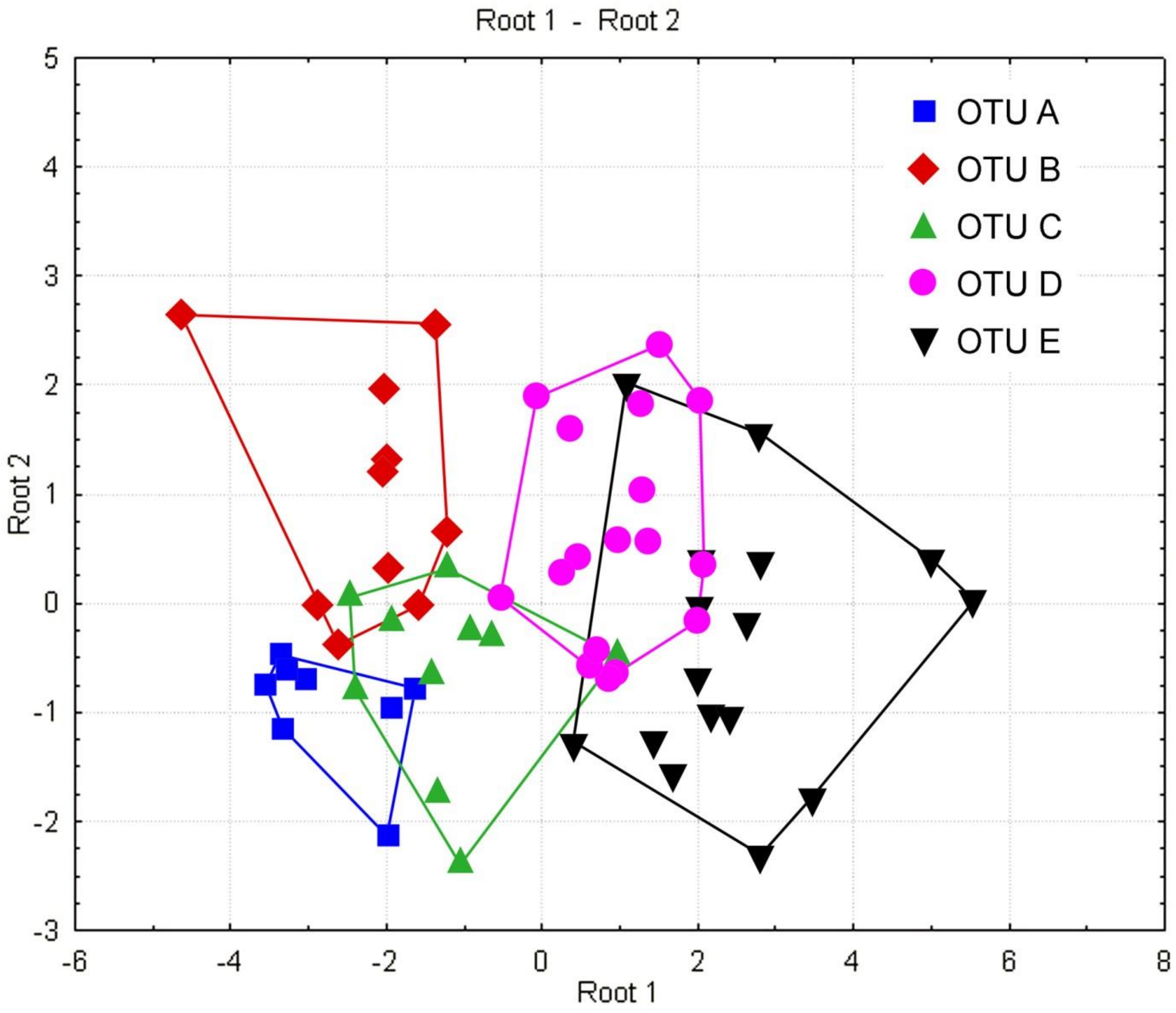


Figure 4.32: Discriminant function analysis of OTUs. Symbols match those of Map 4.6.

We consider the male dewlap to be of superior importance in the separation of anole species, given its significance in inter- and intraspecific recognition and intraspecific courtship behavior, and thus in the establishment and maintenance of species boundaries *in situ*. This view has been supported by various authors (Fitch & Hillis 1984, Savage 2002, Poe & Ibáñez 2007, Köhler et al. 2007) and is reflected in the current taxonomic arrangement of the *Norops pachypus* complex.

Although there is a certain overlap among OTUs in body proportions and scale counts, the differences in these morphological characters as well as in tongue coloration constitute strong evidence for the specific distinctness of all five OTUs. Concerning OTUs A, C, and D, another line of evidence is that all three OTUs occur in close proximity to each other (Maps 4.6 and 4.7). For example, we observed individuals of OTUs C and D at less than 100 m distance from each other near the border of Costa Rica and Panama. Despite much fieldwork in the areas where the ranges of these three OTUs meet, we found no indication of hybridization. This allows for the conclusion that these three OTUs represent distinct species that occur in close parapatry, if not partially in sympatry, with each other, while maintaining their phylogenetic integrities along with their dewlap patterns. In view of this combined evidence, we feel obliged to recognize each OTU as a distinct species.

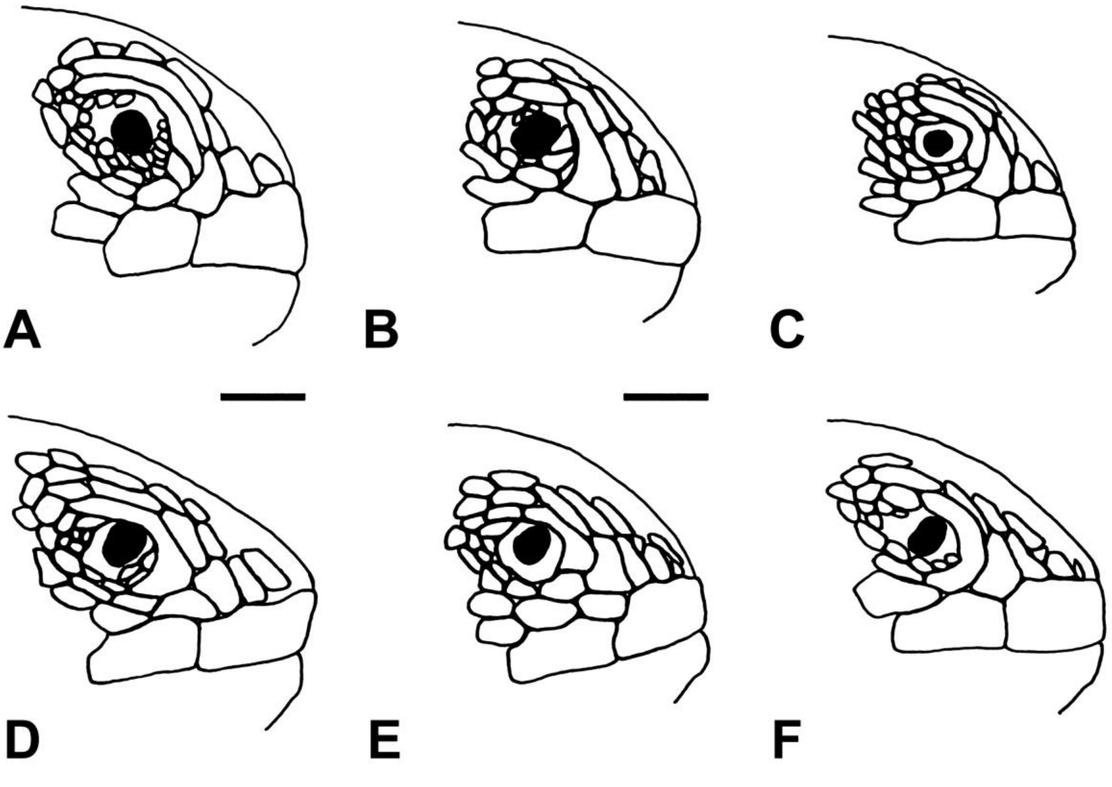


Figure 4.33: Designation of nasal scalation types. (A) Type A (SMF 90149); (B) Type B (SMF 92134); (C) Type C (SL 678); (D) Type D (SMF 85264); (E) Type E (SMF 89506); (F) Type F (85272). Scale bars equal 1 mm. See text for details. Drawings by JFB.

All our OTUs, except OTU D, are clearly assignable to currently recognized species: Occurring in the Cordillera de Tilarán, Cordillera Central, and the northwesternmost portion of the Cordillera de Talamanca in Costa Rica, our OTU B clearly represents the nominal taxon *Norops tropidolepis,* which has its type locality at Volcán Irazú (eastern part of Costa Rica's Cordillera Central; see Map 4.6). The name *N. curtus* (Boulenger) remains in the synonymy of *N. tropidolepis,* as the type locality (La Estrella, Cartago province, westernmost portion of the Costa Rican Cordillera de Talamanca) is situated within the range of *N. tropidolepis* (see also comments in Savage 2002). For OTU E, the name *N. pseudopachypus* is applicable in concordance with the original description and the type locality La Nevera in the Serranía de Tabasará. We assign the name *N. magnaphallus* to OTU A, given its restricted distribution in the area around Boquete, the diagnostic solid purplish red dewlap, and the fact that we collected numerous individuals near this taxon's type locality. The name *N. pachypus* (type locality "Cerro Utyum" in the border region of Limón and Puntarenas provinces in Costa Rica) has been tied to the populations exhibiting a red dewlap with a central yellow blotch (fide Savage 2002), allowing the assignment of OTU C to this nominal taxon. Moreover, in the original description Cope (1876, p.122) stated this taxon to have "four rows between supraorbital series and occipital scale", which in our terminology would signify "four scales between supraorbital semicircles and the interparietal plate", which is a typical trait for members of our OTU C. For OTU D, formerly also referred to *N. pachypus,* no scientific name was available when we conducted this study, and therefore we described it as a new species (Lotzkat et al. 2011). The core of the species description is provided below, additional information in the species account in chapter 4.2.2.

Norops benedikti **(Lotzkat, Bienentreu, Hertz & Köhler 2011)**

Figures 4.30F–H, 4.33–4.36; 4.97G.

Anolis benedikti: Lotzkat et al. (2011); Uetz & Hošek (2014).
Anolis pachypus: Taylor (1956); Peters & Donoso-Barros (1970); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Fundación PA.NA.M.A. (2007); Poe & Ibáñez (2007); Köhler et al. (2007); Jaramillo et al. (2010); Sasa et al. (2010); all in part.
Anolis sp.: Bienentreu (2011).
Norops pachypus: Savage (2002); Köhler (2008); Savage & Bolaños (2009); all in part.

Holotype. SMF 90149 (Figs. 4.30H; 4.34; 4.35A and F), adult male, from the north slope of Cerro Pando, leaving the cattle trail to the right after following it to about 1000 m airline north of the large border monument (Fig. 2.2A), 8.9333°N, 82.7131°W, 2310 m asl, Parque Internacional La Amistad (PILA), Bocas del Toro Province, Panama, close to the border with Costa Rica; collected by AH and SL on 19 November 2009; original field number SL 529.

Paratypes. Collected by SL and AH, if not indicated otherwise. All from the PILA in Panama. Bocas del Toro: north slope Cerro Pando: SMF 89744, male, near type locality, 8.9314°N, 82.7137°W, 2390 m asl, 19 April 2009; SMF 89745–6, male and female, same locality as holotype, 2330 and 2310 m asl, 20 April 2009; SMF 90148, juvenile male, near type locality, 8.9354°N, 82.7128°W, 2280 m asl, 19 November 2009; SMF 91508, male, SL 677–8, subadult male and female, along tributary to Río Changena, 8.9474°N, 82.7098°N, 1980–2000 m asl, 13 July 2010; SMF 91507, female, along tributary to Río Changena, 8.9524°N, 82.7093°N, 1960 m asl, 14 July 2010; SMF 91505–6, SL 686, 695, females, Río Changena, 8.9785°N, 82.6901°N, 1640–1660 m asl, 14–17 July 2010; SMF 91509, juvenile, between Río Clarito and Río Changena, 8.9887°N, 82.6749°N, 1820 m asl, 17 July 2010; Chiriquí: south slope Cerro Pando, Jurutungo: SMF 85276–7, males, 8.9083°N, 82.7168°W, 2010–2100 m asl, collected by Gunther Köhler on 11 January 2006; SMF 85272–3, subadult males, 8.9109°N, 82.7144°W, 2060 m asl, collected by Gunther Köhler on 10 January 2006; SL 202, female, 8.9119°N, 82.7095°W, 2250 m asl, 6 July 2008; SMF 89505, female, 8.9111°N, 82.7159°W, 2020 m asl, 8 July 2008; SMF 89506, male, 8.9121°N, 82.7096°W, 2200 m asl, 8 July 2008; SMF 89507, male, 8.9114°N, 82.7129°W, 2070 m asl, 15 July 2008.

Referred specimens. See Appendix of original publication (provided in Appendix 8).

Diagnosis. A medium-sized species (maximum SVL 48.6 mm in males, 48.1 mm in females) of the genus *Norops* sensu Nicholson et al. (2012), that is most similar in external morphology to *N. magnaphallus, N. pachypus, N. pseudopachypus,* and *N. tropidolepis*. These four species and *N. benedikti* share narrow toe pads, long legs (tip of fourth toe of adpressed hind limb reaches to a point anterior to eye), a dark interorbital bar, and usually at least the indication of a lyriform marking on the occipital region, keeled dorsal scales on head and body, weakly keeled ventral scales at midbody, and the lack of enlarged postcloacal scales in males. *Norops benedikti* can be distinguished readily from all four aforementioned species by the coloration of the male dewlap which is red with a yellow anterior portion comprising just the anterior margin or, at most, the anterior third of the dewlap (versus solid purplish red in *N. magnaphallus* and *N. tropidolepis,* red with a central yellow blotch in *N. pachypus,* and solid yellow, sometimes grading into orange-yellow on the posterior portion, in *N. pseudopachypus*). In addition, *N. benedikti* differs from *N. magnaphallus, N. pachypus,* and *N. tropidolepis* in having more scale rows between the supraorbital semicircles (usually five or more in *N. benedikti,* versus four or fewer in *N. magnaphallus, N. pachypus,* and usually four or fewer, rarely five, in *N. tropidolepis*), and more scales between supraorbital semicircles and interparietal plate (usually five or more, rarely four, in *N. benedikti,* versus four or fewer in *N. magnaphallus, N. tropidolepis,* and usually four or fewer, rarely five, in *N. pachypus*). Furthermore, *N. benedikti* differs from *N. magnaphallus*, *N. pachypus,* and *N. tropidolepis* in having a very dark (almost blackish) gray tongue (versus a very light gray tongue in *N. magnaphallus*, *N. pachypus,* and *N. tropidolepis*). At first sight, individuals of *N. benedikti* might be confused with similarly-colored *N. humilis.* Yet, regardless of sex or age, individuals of the latter species have at least eight longitudinal rows of greatly enlarged, visibly keeled median dorsal scales that are larger than the ventrals, whereas *N. benedikti* has a maximum of two slightly enlarged middorsal rows, the scales of which are smaller than the ventrals. Males of *N. humilis* have a red dewlap with a complete (i.e., bordering the whole dewlap) yellow margin, whereas males of *N. benedikti* exhibit yellow coloration only on the anterior portion of their otherwise solid red dewlap.

Description of the holotype. Adult male as indicated by everted hemipenes and presence of moderate-sized dewlap (Fig. 4.30H); snout-vent length 48.6 mm; tail length 81.7 mm, tail complete; tail slightly compressed in cross section, tail height 2.2 mm, tail width 1.8 mm; axilla to groin distance 18.7 mm; head length 11.9 mm, head length/snout-vent length ratio 0.24; snout length 5.3 mm; head width 8.1 mm; longest toe of adpressed hind limb reaching to snout; shank length 12.6 mm, shank length/head length ratio 1.1; longest finger of extended forelimb reaching about 4.2 mm beyond tip of snout; longest finger of adpressed forelimb reaching to anterior insertion of hind limbs; scales on snout keeled; 5 postrostrals; 5 scales between nasals; scales in distinct prefrontal depression distinctly keeled; supraorbital semicircles differentiated, separated by a minimum of 7 scales; supraorbital disc composed of 14 slightly enlarged keeled scales; 3 elongated superciliaries; about 5 rows of small keeled scales extending between enlarged supraorbitals and superciliaries; interparietal plate slightly enlarged, 0.6 x 0.3 mm (length x width), surrounded by small scales; 10 scales present between interparietal plate and supraorbital semicircles; canthal ridge distinct, composed of 5 large (posterior) and 3 small (anterior) canthal scales; 15 scales present between second canthals; 17 scales present between posterior canthals; 93/95 keeled loreal scales in a maximum of 12 horizontal rows; subocular scales granular, subocular row ill-defined; 8 supralabials to level below center of eye; ear opening 0.8 x 1.5 mm (length x height); mental distinctly wider than long, almost completely divided medially, bordered posteriorly by 7 postmentals; 8 infralabials to level below center of eye; sublabials undifferentiated; slightly keeled granular scales present on chin and throat; dewlap moderate-sized, extending well onto chest, anterior insertion at level of anterior border of orbit, posterior insertion at level of axilla, with about 10 somewhat irregular, partially interrupted gorgetal-sternal rows of 20–26 scales per row; dorsum of body with keeled scales, 2 medial rows of slightly enlarged scales, largest dorsal scales subimbricate, about 0.40 x 0.35 mm (length x width); about 66 medial dorsal scales in one head length; about 112 medial dorsal scales between axilla and groin; lateral scales pointed, granular and homogeneous, average size 0.18 mm in diameter; ventrals at midbody weakly keeled, slightly mucronate, and subimbricate, about 0.30 x 0.40 mm (length x width); about 42 ventral scales in one head length; about 58 ventral scales between axilla and groin; about 162 scales around midbody; caudal scales strongly keeled, without whorls of enlarged scales; no enlarged postcloacal scales; tube-like axillary pocket not developed; scales on dorsal surface of forelimb strongly keeled, mucronate and imbricate, about 0.30 x 0.45 mm (length x width); digital pads dilated, dilated pad about 2 times width of non-dilated scales on distal phalanx; distal phalanx narrower than and raised from dilated pad; 23/22 lamellae under phalanges II–IV of 4th toe; 9/10 scales under distal phalanx of 4th toe; 15 lamellae under phalanges II–IV of 4th finger; 9 scales under distal phalanx of 4th finger.

The completely everted hemipenis is a stout bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips and opening at base of apex into two broad concave areas, one on each lobe; a large asulcate ridge-like processus present; lobes strongly calyculate, truncus with transverse folds.

Coloration in life. The dewlap (Fig. 4.30H) was recorded as follows: Flame Scarlet (15) with a suggestion of Chrome Orange (16) on posterior three fourths, Orange Yellow (18) on anterior fourth and anterior margin; dewlap scales Sepia (119) and dirty white. Otherwise, no detailed notes of the holotype were taken; Figures 4.35A and F show the entire holotype in life.

Coloration after 18 months of preservation in 70% ethanol is similar to that in life, apart from that all reddish shades have faded, especially on the dewlap that now is dirty white.

Variation. The paratypes and referred specimens agree well with the holotype in terms of general morphology and pholidosis (see Table 4.9). Four of the 32 examined specimens (SMF 89507, 91505; SL 686, 695) have only four scales between the supraorbital semicircles. Two specimens (SMF 89507, 91505) have only four scales between the supraorbital semicircles and the interparietal plate. Among the 17 adult males included in statistical analyses, the variability in the nasal region (Fig. 4.33) was recorded as follows: Type A 1 specimen (5.9%); Type B 2 specimens (11.8%); Type C 4 specimens (23.5%); Type D 5 specimens (29.4%); Type E 3 specimens (17.6%); Type F 2 specimens (11.8%). For information on variability in color and pattern, see Figs. 4.35, 4.36, and 4.97G, as well as species account in chapter 4.2.2.

Natural history notes. See species account in chapter 4.2.2.

Geographic distribution. See Maps 4.7, 4.8, and 4.46, as well as species account in chapter 4.2.2.

Etymology. The specific name is a patronym for Benedikt Stökl, Germany, in recognition of the financial support of taxonomic research provided by Karsten Lutz through the BIOPAT initiative.

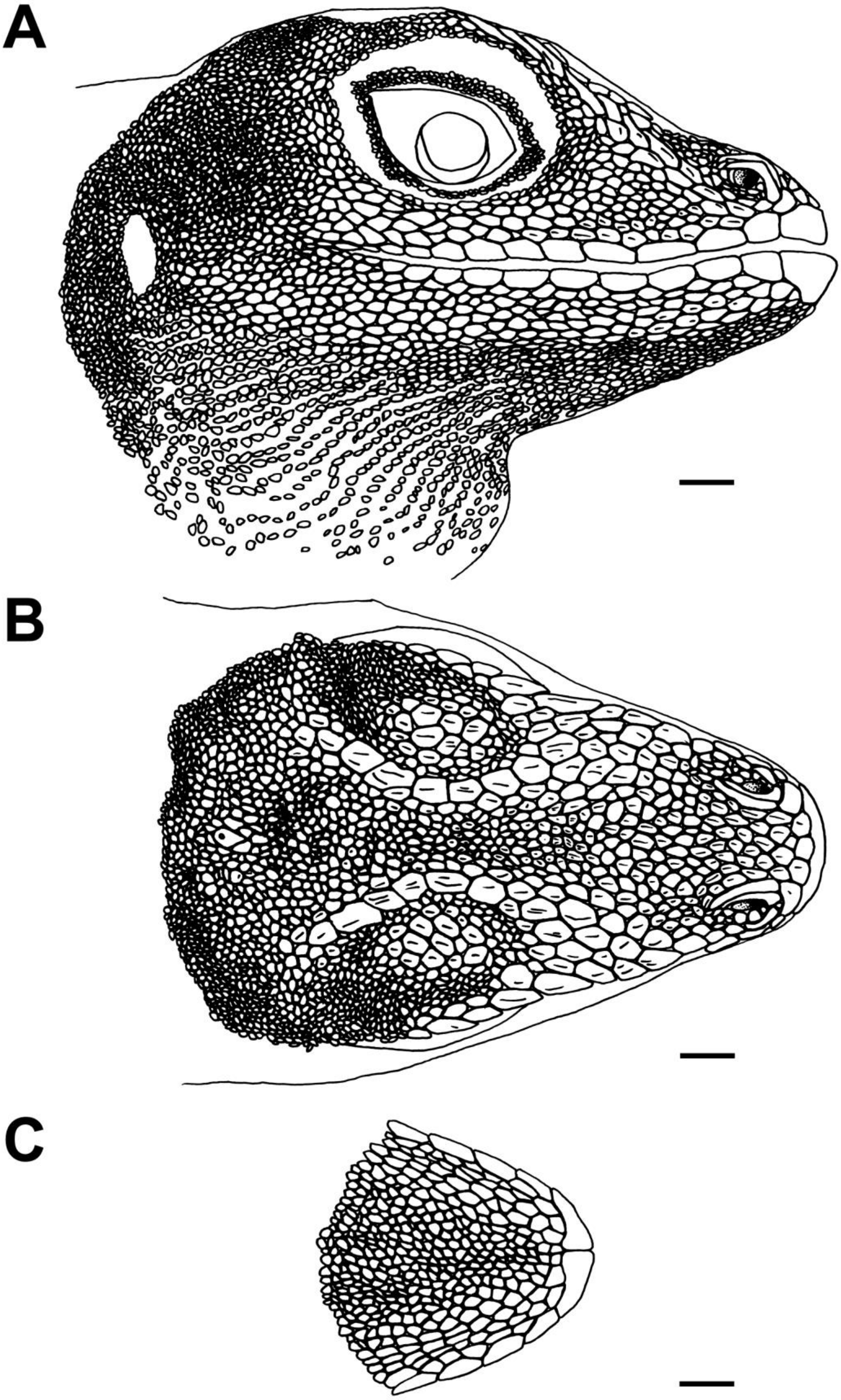
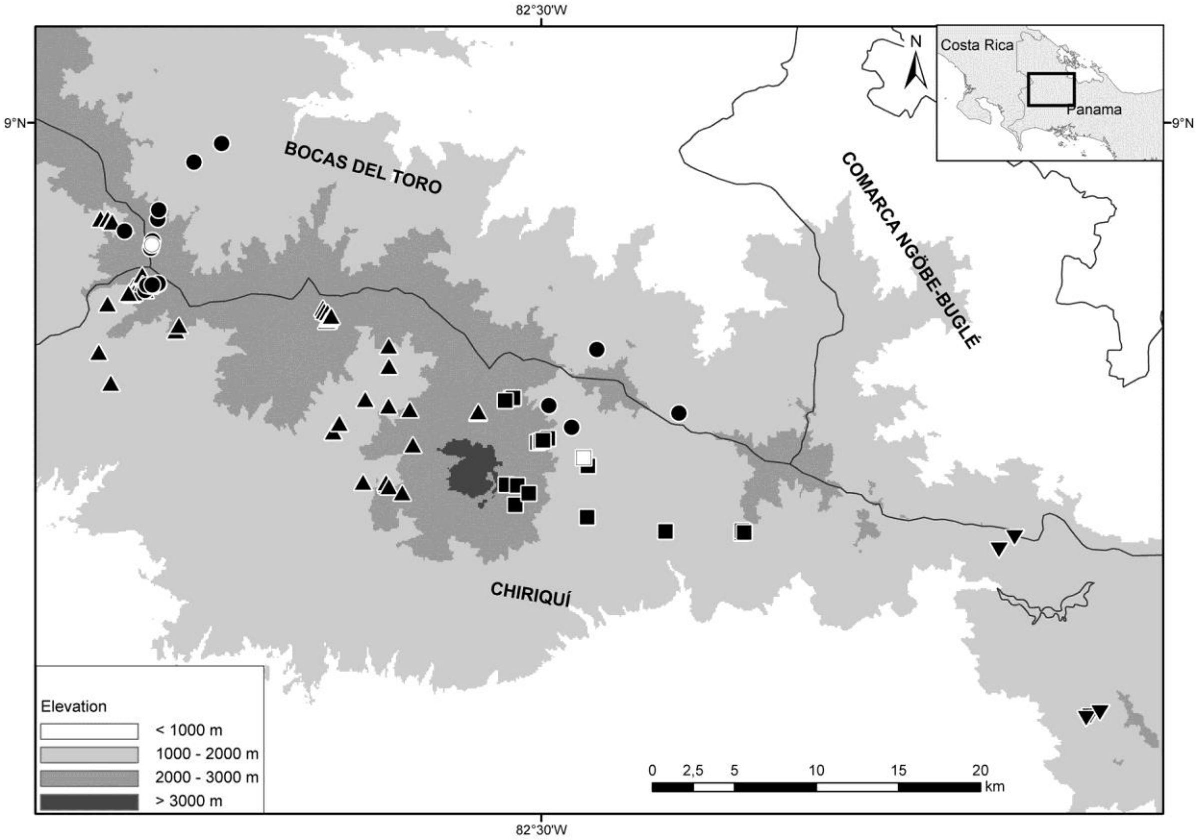


Figure 4.34: Head of holotype (SMF 90149) of *Norops benedikti:* (A) lateral (right side), (B) dorsal, and (C) ventral views. Scale bars equal 1 mm. Drawings by JFB.



Map 4.7: Collection localities of *Norops benedikti* (circles) and other members of the *N. pachypus* complex (*N. magnaphallus:* squares; *N. pachypus:* upright triangles; *N. pseudopachypus:* inverted triangles) in western Panama and adjacent Costa Rica. Hollow symbols represent type localities. Map by AH.

4.1.4.2 Barcoding the *Norops pachypus* complex

In order to verify the taxonomic arrangement of the *Norops pachypus* complex based on external morphology as presented by Lotzkat et al. (2011; preceding section), in the following I analyze the molecular data available for these lizards. To this end, I reanalyze all Panamanian and three Costa Rican 16S barcodes that were generated and first analyzed in the course of JFB's Diploma thesis (Bienentreu 2011), and complement these analyses with those of the correspondent COI barcodes sequenced by the ColdCode project.

For the 16S barcodes, the manually refined final alignment of 56 sequences (51 individuals of the *Norops pachypus* complex as well as the two *N. gruuo,* two *N. kemptoni,* and one *Dactyloa ibanezi* that already served as outgroups in chapter 4.1.2) contained 538 positions, of which, excluding the outgroups, 71 were variable and 62 parsimony-informative. For the COI barcodes, the final alignment of 30 taxa (identical outgroups and 25 individuals of the *N. pachypus* complex) contained 561 positions, of which, excluding the outgroups, 163 were variable and 147 parsimony-informative.

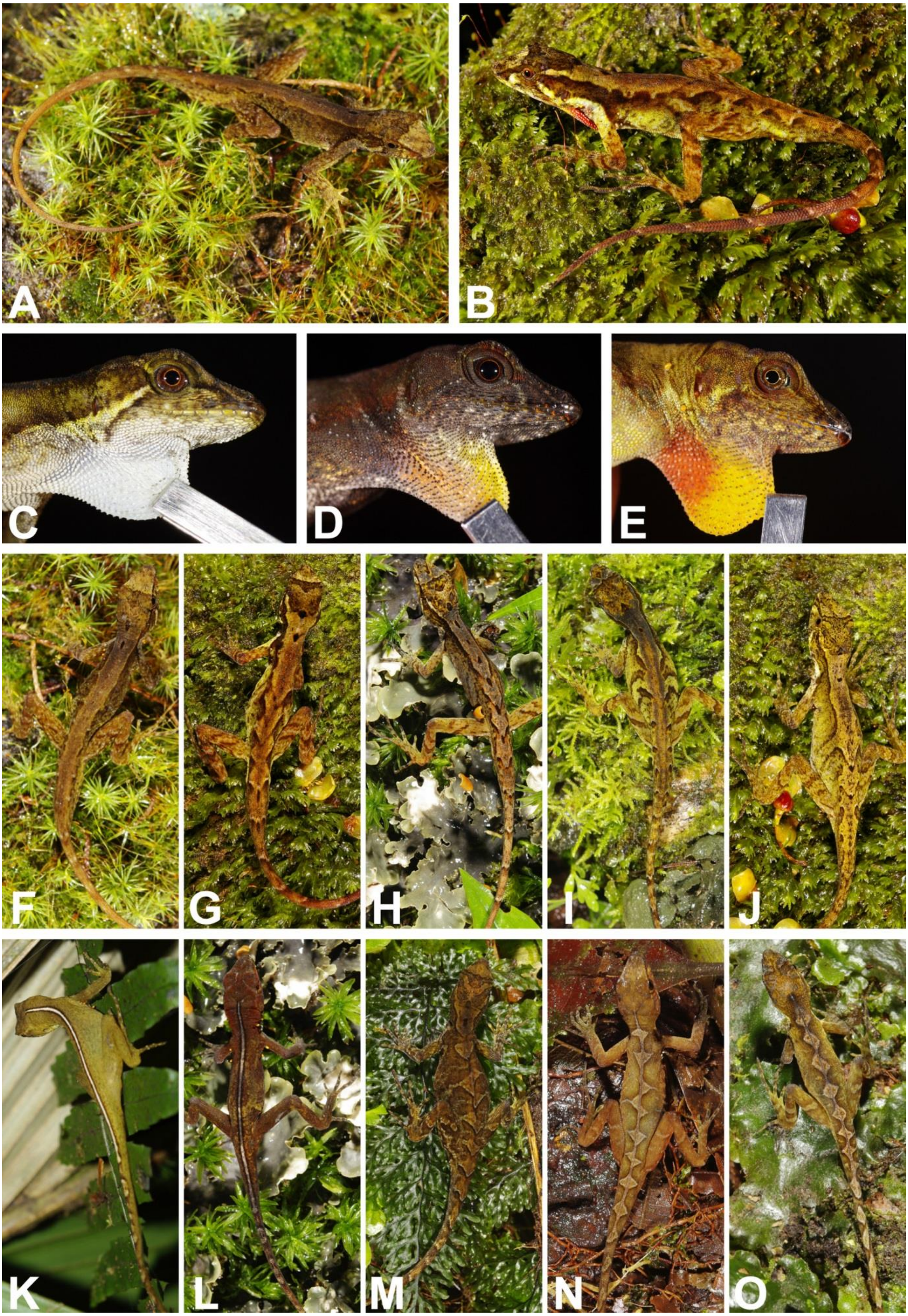


Figure 4.35: Type specimens of *Norops benedikti* in life: (A) male holotype (SMF 90149); (B) male from Jurutungo, SMF 89506; (C–E) female dewlaps: (C) SMF 91506; (D) SL 695; (E) SMF 89746; (F–O) variation in dorsal patterns: (F) SMF 90149, male holotype; (G) SMF 89506, male; (H) SMF 89745, male; (I) SMF 91508, male; (J) SL 202, female; (K) SMF 89746, female, at night; (L) SMF 89746 the next day; (M) SMF 91507, female; (N) SL 686, female; (O) SMF 91505, female.

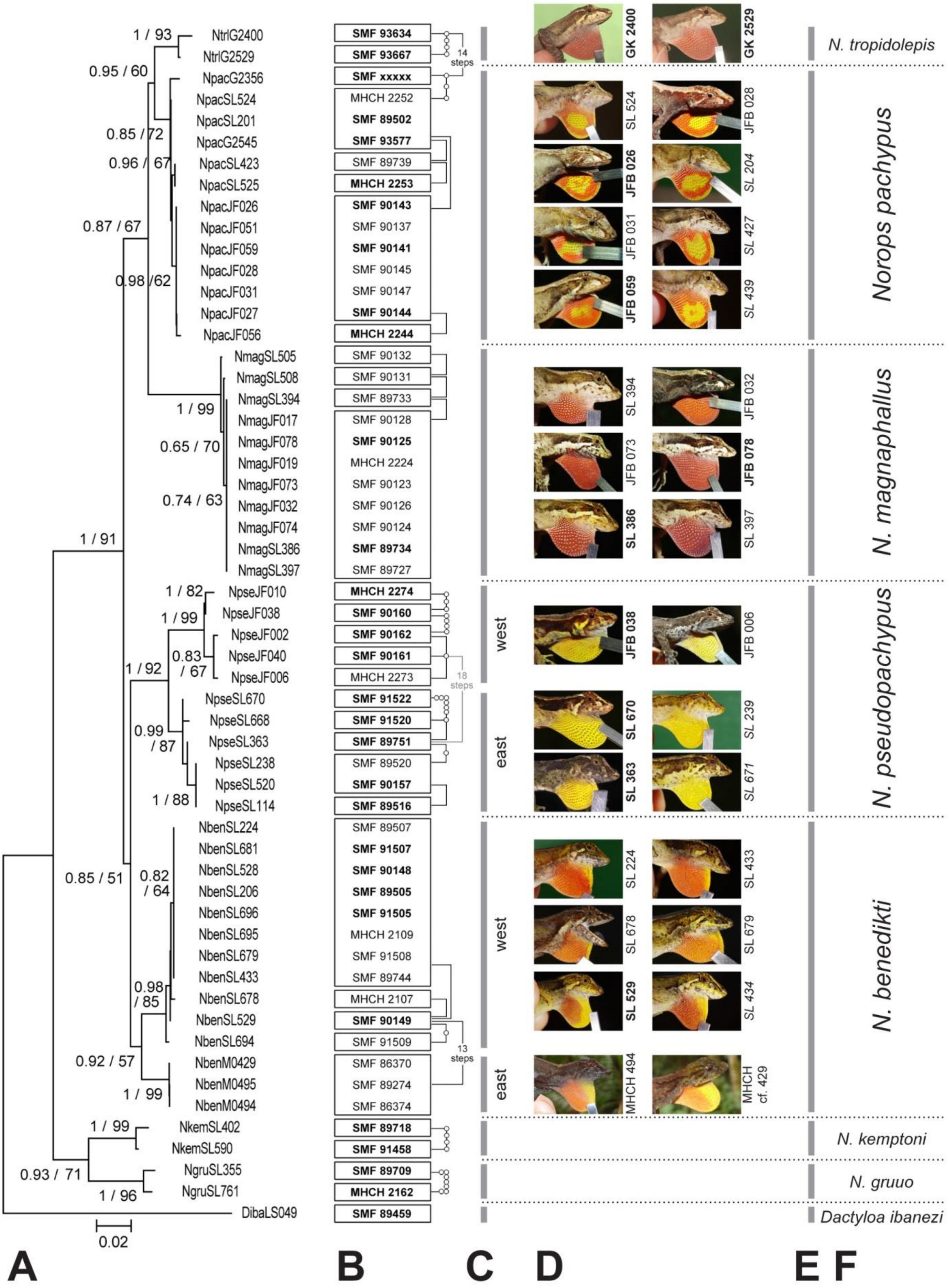


Figure 4.36: Integration of 16S barcodes and morphology for the *Norops pachypus* complex. (A) ML consensus tree, bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 9 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the 16S barcodes. (D) Dewlaps of sampled or syntopical males in life; field numbers of males without barcode in *italics,* photos of GK and JFB specimens taken by the respective collector. (E) Lineages diagnosable through morphology. (F) Taxonomic identity of inferred CGLs. In (B) and (D), collection and field numbers in **bold face** indicate individuals for which also COI barcodes are available. See text for details.

For both genes, T92+G was determined as the best-fitting substitution model. The alignments and distance matrices underlying the following results are provided in Appendix 5.4. Table 4.8 gives an overview of the mean values of uncorrected p-distances found for both barcodes within and between the different lineages.

Table 4.8: Mean values of uncorrected p-distances in 16S (lower left) and COI (upper right, in *italics*) barcodes among members of the *Norops pachypus* complex and outgroups. Mean distances within a lineage are in **bold** face.

	Dactyloa ibanezi	***Norops kemptoni***	***N. gruuo***	***N. benedikti***	***N. b.* west**	***N. b.* east**	***N. pseudopachypus***	***N. p.* west**	***N. p.* east**	***N. magnaphallus***	***N. pachypus***	***N. tropidolepis***
Dactyloa ibanezi	**–**	*0.190*	*0.177*	*0.210*	*0.210*	–	*0.216*	*0.216*	*0.216*	*0.206*	*0.196*	*0.205*
Norops kemptoni	0.123	***0.011*** **0.008**	*0.102*	*0.157*	*0.157*	–	*0.190*	*0.182*	*0.196*	*0.195*	*0.187*	*0.193*
N. gruuo	0.113	0.057	***0.043*** **0.010**	*0.160*	*0.160*	–	*0.188*	*0.179*	*0.195*	*0.170*	*0.193*	*0.182*
N. benedikti	0.119	0.076	0.079	***0.015*** **0.011**	–	–	*0.111*	–	–	*0.136*	*0.134*	*0.135*
***N. b.* west**	0.117	0.074	0.079	–	***0.015*** **0.002**	–	–	*0.106*	*0.115*	*0.136*	*0.134*	*0.135*
***N. b.* east**	0.125	0.082	0.081	–	0.028	**–** **0.0**	–	–	–	–	–	–
N. pseudo-pachypus	0.120	0.086	0.088	0.050	–	–	***0.056*** **0.020**	–	–	*0.148*	*0.131*	*0.134*
***N. p.* west**	0.128	0.092	0.090	–	0.053	0.055	–	***0.007*** **0.007**	*0.082*	*0.151*	*0.135*	*0.140*
***N. p.* east**	0.115	0.082	0.087	–	0.049	0.047	–	0.028	***0.032*** **0.012**	*0.146*	*0.127*	*0.128*
N. magna-phallus	0.125	0.085	0.089	0.059	0.061	0.050	0.066	0.068	0.065	***0.018*** **0.001**	*0.116*	*0.130*
N. pachypus	0.110	0.083	0.084	0.046	0.046	0.046	0.056	0.062	0.053	0.046	***0.008*** **0.003**	*0.089*
N. tropidolepis	0.118	0.079	0.081	0.048	0.051	0.039	0.058	0.062	0.056	0.055	0.027	***0.048*** **0.010**

Figure 4.36 integrates the results of the 16S barcode analyses with the morphological distinctions revealed in the previous section. In principle, each nominal species forms its own clade in both ML and BI analyses (Fig. 4.36A). Yet, the molecular perspective offers some additional insights into certain relationships. *Norops tropidolepis* and *N. pachypus* appear very closely related to each other with individual p-distances of just 2.3–2.9%. On the contrary, both *N. benedikti* and *N. pseudopachypus* are revealed to comprise a western and an eastern genealogical lineage, respectively, that are separated by similar to slightly higher p-distances (2.5–3.1% between the two clades of *N. benedikti*, and 2.7–3.5% between those of *N.*

pseudopachypus). Within each of these two nominal species, the subclades reflect geography: *Norops benedikti* "west" come from the type locality and adjacent slopes, while *N. benedikti* "east" have been collected E of Volcán Barú, at a minimum airline distance of 25 km. In the case of *N. pseudopachypus*, lineage "west" comprises animals from RFLF, separated by more than 40 airline km from the eastern lineage's representatives that were collected at the type locality and the nearby Cerros Saguí and Santiago. With the sole exception of *N. pseudopachypus* east, within each of the 7 distinct genealogical lineages of the *N. pachypus* complex, as well as within the two outgroup taxa *N. gruuo* and *N. kemptoni,* mean as well as individual p-distances are lower than 1%. Interestingly, this even holds for *N. pachypus,* within which the individual GK 2356 from central Costa Rica is separated by just 0.58–0.96% from its conspecifics collected more than 120 km to the east.

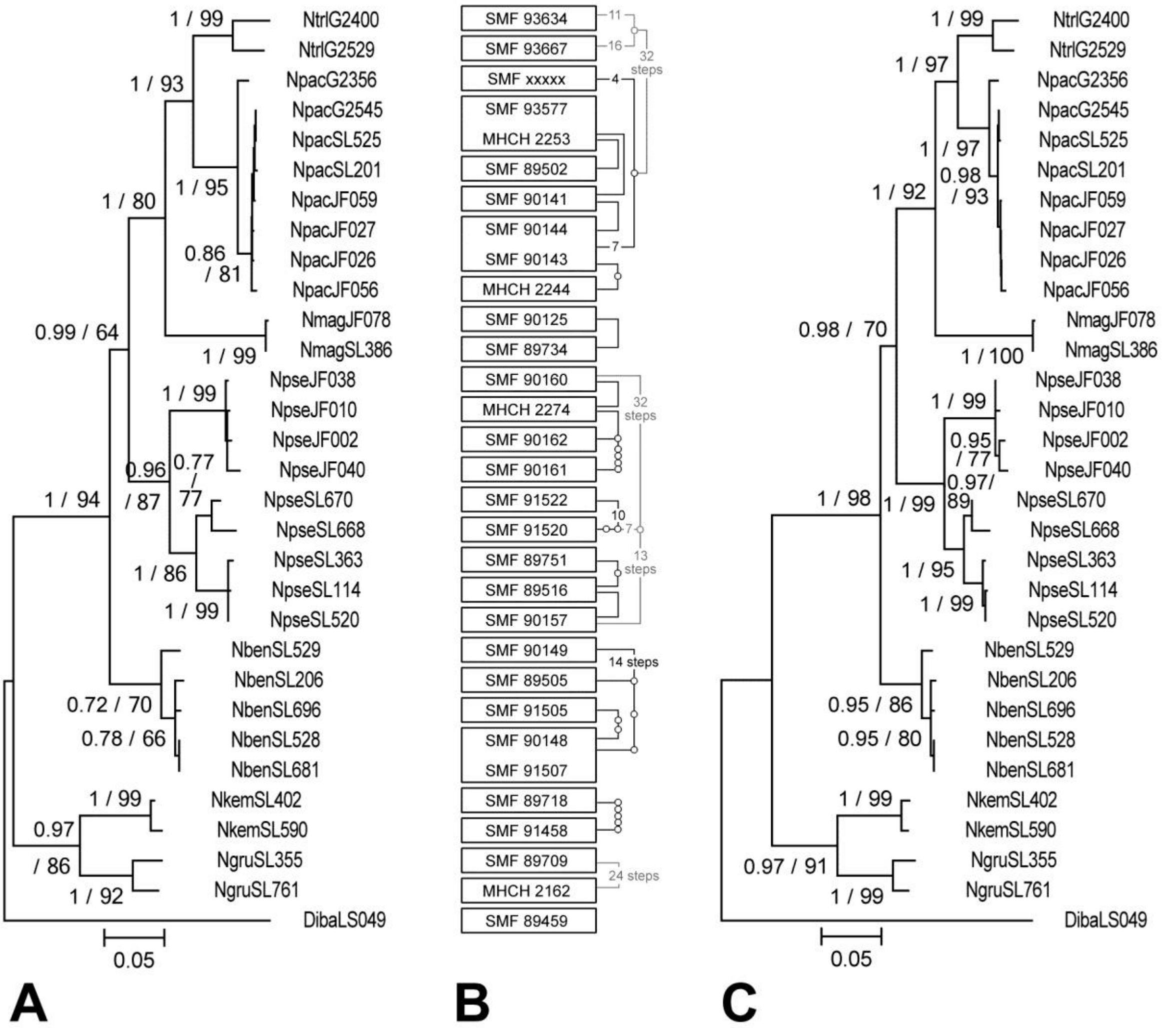


Figure 4.37: Results of COI and combined analyses. (A) Consensus tree from ML analysis of COI barcodes. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Consensus tree from ML analysis of concatenated 16S and COI alignments. In (A) and (C), bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. See text for details.

The PN analysis (Fig. 4.36B) complements the inferred trees with a very similar picture. Applying the connection limit of 9 steps calculated for a 95% parsimony probability (black connections with haplotype symbols instead of numbers), the seven lineages inferred in the ML and BI analyses, as well as each of the three outgroup lineages, are recovered as discrete haplotype networks. Increasing the connection limit to 14 steps calculated for a 90% parsimony probability (black connections with substitution step numbers), the two lineages of *N. benedikti* join to form a single network, just as *N. pachypus* and *N. tropidolepis* do. The eastern and western lineage of *N. pseudopachypus* only become connected if the 95% connection limit is doubled to 18 substitutional steps (gray connection with step number). That is, eastern and western *N. pseudopachypus* are more divergent in their 16S rRNA gene than representatives of *N. tropidolepis* from those of *N. pachypus.*

As seen in the genus *Dactyloa* (chapter 4.1.3) and shown for the *N. pachypus* complex in Table 4.8, the individual differentiation in the COI fragment analyzed is far more pronounced than that found in the 16S barcode. While individual 16S p-distances (see Appendix 5.4) do not exceed 7.1% within the *N. pachypus* complex, 9.6% among the analyzed *Norops,* and 13.1% when including *Dactyloa,* these values rise to 15.3, 20.3, and 22.1%, respectively, when analyzing the COI alignment. Still, the COI barcodes yield congruent results in outline, with the lamentable exception that no eastern individuals of *N. benedikti* yielded sequences of this gene. The remaining lineages are recovered accordingly in the consensus trees from the ML and BI analyses (Fig. 4.37A). Within each of the 6 sampled lineages of the *N. pachypus* complex, as well as within the two outgroup taxa *N. gruuo* and *N. kemptoni,* mean as well as individual p-distances range from 0.2–5.5%. Owing to the higher divergence in the COI fragment, the connection limit of 10 steps calculated for a 95% parsimony probability in the PN analysis (Fig. 4.37B: black connections with haplotype symbols) leaves singular to several individuals of each *N. pachypus, N. benedikti, N. pseudopachypus* east, and the outgroup *N. gruuo* unconnected to the respective network(s) or other individuals of their respective lineages. At a connection limit of 14 steps calculated for a 90% parsimony probability (Fig. 4.37B: black connections with substitution step numbers), the former two lineages blend into a joint haplotype network each. Doubling the 95% connection limit to 20 steps, also *N. pseudopachypus* east is merged into a proper network (Fig. 4.37B: gray connections with step numbers). Still more substitutional steps lie between the sampled individuals of the remaining three lineages, where 24 steps are needed to connect the two *N. gruuo,* 27 to join the two *N. tropidolepis,* and 41 (not shown in Fig. 4.37B) to join the respective networks of *N. pseudopachypus* east and west. In contrast to the results from their 16S barcodes, the sampled COI barcodes of *N. pachypus* differ from those of *N. tropidolepis* by a minimum of 47 substitutional steps, i.e., appear more divergent than those of *N. pseudopachypus* east and west. In conclusion, while the 95% parsimony probability networks rather well reflect the smallest well-supported clusters found in ML and BI analyses of the 16S barcode, to achieve a congruent network layout for the COI barcodes the connection limit has to be two- or threefold higher than that calculated for a 95% parsimony probability. Yet, besides exhibiting such unequal genetic differentiation as well as certain differences in the topology of the inferred trees, the two barcode fragments fundamentally complement each other, as it was to be expected by their location in the same organelle, and is evidenced by the increased robustness of all principal nodes when analyzing their concatenated alignments (Fig. 4.37C).

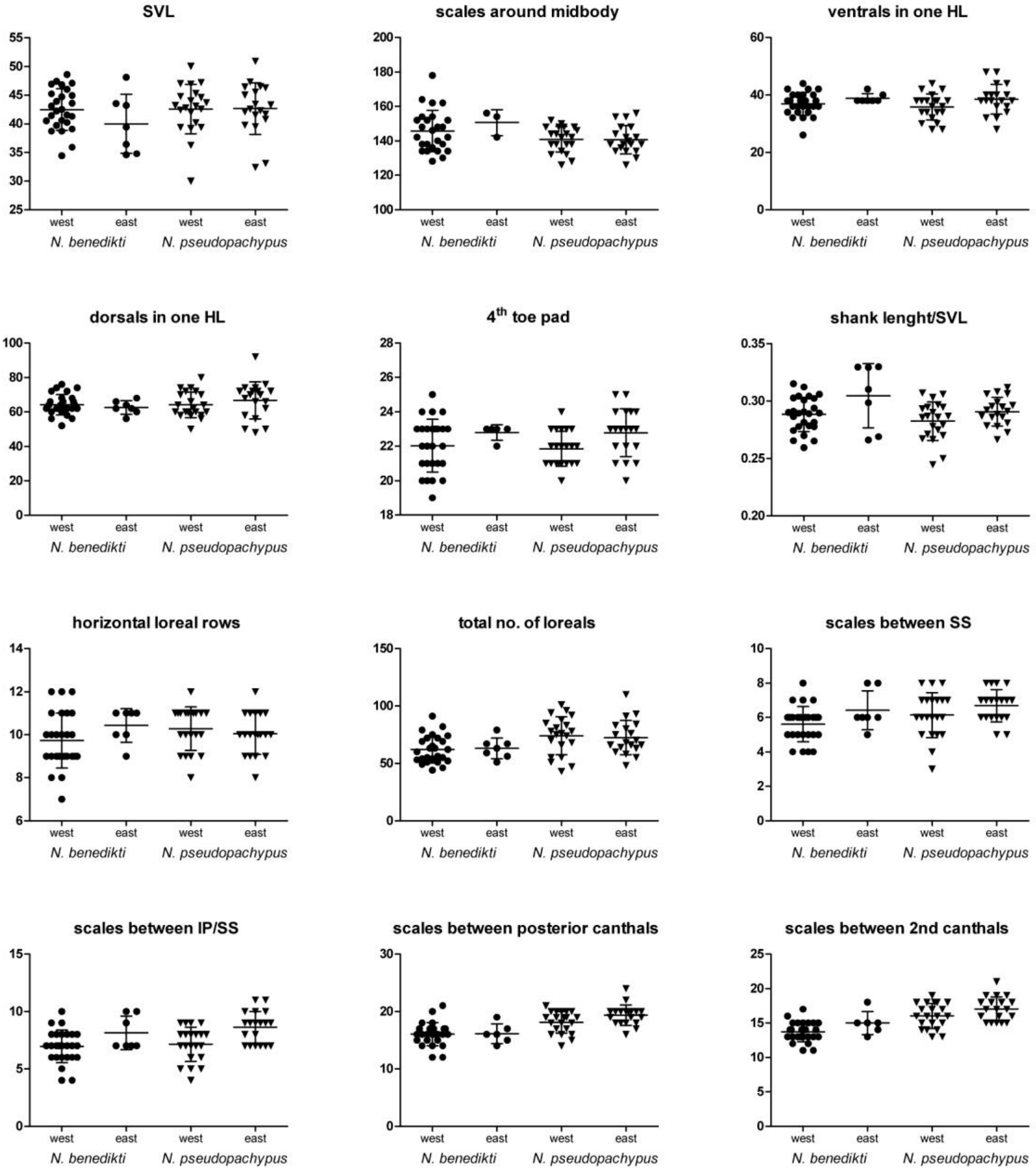
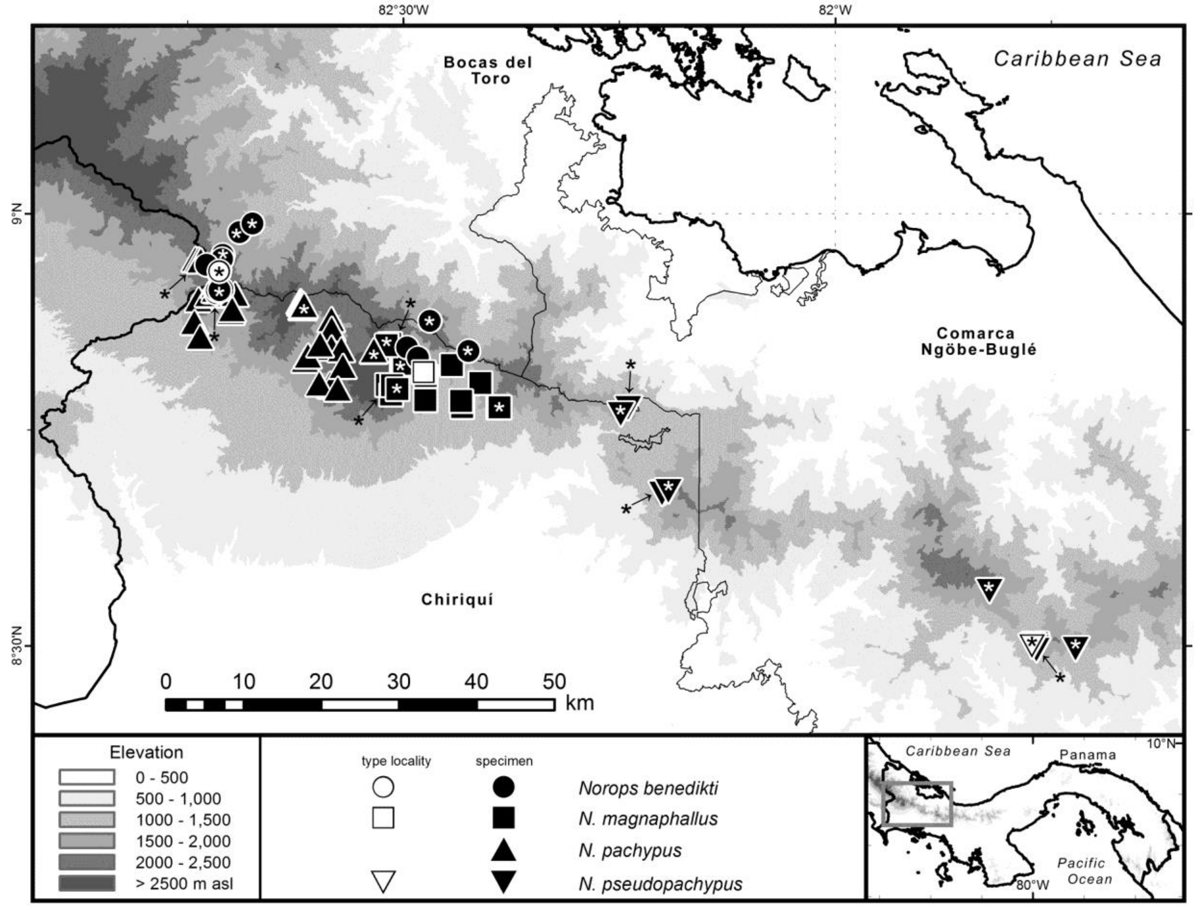


Figure 4.38: Scatterplots (bars indicate mean ± one standard deviation) showing the variation in selected morphological characters (the same ones as plotted in Fig. 4.31) among the eastern and western lineages of *Norops benedikti* and *N. pachypus,* respectively. Modified from data prepared by JFB.

Since each species boundary inferred in the previous section from male dewlap coloration is strongly supported by the analyses of both 16S and COI barcodes, the integration of morphological and molecular results as elaborated in Figure 4.36 results in the recognition of the five nominal taxa as CGLs. Further, *Norops benedikti* and *N. pseudopachypus* appear composed of an eastern and a western lineage each. Notwithstanding the undisputable genetic distinctness of the respective two lineages within each of the two species, they are not separable on the basis of morphology as exemplarily illustrated by the large overlaps in pholidotic and morphometric characters plotted in Figure 4.38. Moreover, the variation in male dewlap coloration found in both nominal species (extent of the yellow anterior border in *N. benedikti,* extent and intensity of orange shadings on posterior portion in *N. pseudopachypus*) is apparently not correlated with geography. Since I was unable to find any consistent morphological differentiations between the respective two lineages of either species, I must regard these lineages as DCLs at this point. Thus, my integrative approach reconfirms the five species as delineated in the previous chapter. Table 4.9 summarizes selected morphological characters of these five species.

While the coloration of the male dewlap generally is one of the most important cues in the identification of anole species, it is the only reliable character of external morphology for species differentiation within the *Norops pachypus* complex. Among these five species, a doubtless identification of a given individual in the field is only possible on the basis of male dewlap coloration in life. Other characters allow at most the differentiation between certain groups of species, as it is the case with head scalation. In three species (*Norops magnaphallus, N. pachypus,* and *N. tropidolepis*), the dorsal head scales are rather large, including very conspicuous and well-differentiated SS separated from each other, as well as from the IP, by usually four or fewer scales. In the remaining two species (*N. benedikti* and *N. pseudopachypus*), the dorsal head scales are generally much smaller and more numerous compared to those of the three other species, resulting in ill-defined supraorbital semicircles separated from each other, as well as from the interparietal plate, by usually five or more scales.Contrary to the view presented by Savage (2002), the ventral scale surface has no diagnostic value at all as demonstrated Bienentreu (2011). The assignment of females, juveniles, or preserved males to either species may appear possible on the basis of head scalation and collection locality, but should be treated with caution considering the occasional "outliers" (Fig. 4.31), and especially with regard to interspecific contact zones, some of which have a complex geography and most of which remain unknown. Another character that apparently separates *N. benedikti* and *N. pseudopachypus* from the other three species is their very dark, almost blackish gray tongue. The coloration of the tongue, along with the overall pigmentation of the inside of mouth, has to our knowledge largely been neglected by herpetologists, although Myers (1971b) proposed its taxonomic significance. Unfortunately, dark pigmentation of the tongue seems to fade much more rapidly in alcoholic preservatives than the pigmentation of external surfaces.

For the four species that occur in Panama, Map 4.8 gives an overview of the known distribution in western Panama. An overview of the variability in coloration among the type series of *Norops benedikti* has been provided in Fig. 4.35. Similarly, the variation among the examined material is pictured for the other Panamanian species in Figures 4.39–4.41. More illustrations of the exuberant variability in color and especially pattern of these lizards were provided by Bienentreu (2011: Figs. 33–38). Standardized characterizations of the four Panamanian members of the *N. pachypus* complex are found in their respective species accounts in chapter 4.2.2.



Map 4.8: Distribution of *Norops benedikti, N. magnaphallus, N. pachypus,* and *N. pseudopachypus* in western Panama and and immediately adjacent eastern Costa Rica. Based on specimens examined by Köhler et al. (2007), Bienentreu (2011), and Lotzkat et al. (2011) as well as the type series of *N. magnaphallus* as reported by Poe & Ibáñez (2007). Localities of barcoded specimens analyses are marked with an asterisk (*).

Table 4.9: Selected measurements, proportions, and scale characters of *Norops benedikti, N. magnaphallus, N. pseudopachypus, N. pachypus,* and *N. tropidolepis.* Modified from Bienentreu (2011) and Lotzkat et al. (2011).

		Norops benedikti	***N. pachypus***	***N. pseudopachypus***	***N. magnaphallus***	***N. tropidolepis***
		♂ 20 **♀ 14**	**♂ 36** **♀ 33**	**♂ 27** **♀ 13**	**♂ 16** **♀ 14**	**♂ 10** **♀ 10**
SVL	♂	34.6–48.6 (41.6 ± 3.5)	38.2–52.6 (47.3 ± 3.8)	30.0–46.9 (41.0 ± 4.0)	40.5–54.1 (48.6 ± 4.5)	41.4–52.3 (47.4 ± 3.5)
	♀	34.4–49.9 (43.0 ± 5.0)	37.0–56.9 (48.2 ± 4.2)	39.4–50.9 (45.9 ± 3.0)	42.8–58.9 (51.2 ± 4.8)	44.7–54.1 (49.9 ± 3.0
TL / SVL	♂	1.22–2.16 (1.76 ± 0.21)	1.61–2.03 (1.84 ± 0.11)	1.61–2.06 (1.90 ± 0.13)	1.04–1.75 (1.60 ± 0.19)	1.72–2.18 (1.99 ± 0.18)
	♀	1.42–1.90 (1.67 ± 0.11)	1.42–1.72 (1.62 ± 0.07)	1.63–1.81 (1.74 ± 0.07)	1.38–1.57 (1.48 ± 0.7	1.62–1.91 (1.76 ± 0.11)
verDT / horDT	♂	1.00–1.43 (1.19± 0.10)	1.11–1.43 (1.25 ± 0.09)	1.06–1.29 (1.19 ± 0.09)	1.11–1.45 (1.25 ± 0.10)	1.05–1.31 (1.21 ± 0.08)
	♀	1.10–1.27 (1.18 ± 0.06)	1.06–1.36 (1.21 ± 0.08)	1.07–1.36 (1.17 ± 0.09)	1.05–1.28 (1.18 ± 0.07)	1.05–1.38 (1.21 ± 0.11)
HL / SVL	♂	0.24–0.31 (0.27 ± 0.02)	0.23–0.28 (0.25 ± 0.01)	0.24–0.29 (0.26 ± 0.01)	0.24–0.28 (0.26 ± 0.01)	0.25–0.26 (0.26 ± 0.01)
	♀	0.24– 0.29 (0.26 ± 0.02)	0.23–0.27 (0.25 ± 0.01)	0.23–0.27 (0.25 ± 0.01)	0.24–0.27 (0.25 ± 0.01)	0.23–0.26 (0.24 ± 0.01)
HL / HW	♂	1.43–1.68 (1.52 ± 0.07)	1.39–1.61 (1.53 ± 0.05)	1.43–1.69 (1.55 ± 0.07)	1.47–1.66 (1.56 ± 0.05)	1.47–1.61 (1.54 ± 0.04)
	♀	1.44–1.60 (1.51 ± 0.05)	1.41–1.58 (1.51 ± 0.04)	1.51–1.67 (1.56 ± 0.05)	1.47–1.68 (1.56 ± 0.05)	1.49–1.62 (1.56 ± 0.04)
Shank length / SVL	♂	0.26–0.33 (0.29 ± 0.02)	0.25–0.32 (0.27 ± 0.01)	0.25–0.31 (0.29 ± 0.01)	0.23–0.27 (0.25 ± 0.01)	0.24–0.29 (0.27 ± 0.01)
	♀	0.25–0.33 (0.29 ± 0.02)	0.24–0.28 (0.26 ± 0.01)	0.24–0.30 (0.28 ± 0.01)	0.22–0.27 (0.24 ± 0.02)	0.24–0.26 (0.25 ± 0.01)
AGD / SVL	♂	0.31–0.45 (0.39 ± 0.03)	0.35–0.46 (0.40 ± 0.03)	0.34–0.43 (0.39 ± 0.02)	0.33–0.44 (0.39 ± 0.03)	0.37–0.40 (0.38 ± 0.01)
	♀	0.34–0.45 (0.41 ± 0.04)	0.37–0.47 (0.41 ± 0.02)	0.38–0.43 (0.41 ± 0.01)	0.37–0.45 (0.40 ± 0.02)	0.39–0.44 (0.41 ± 0.01)
Subdigital lamellae under phalanges II–IV of 4th toe		19–25 (22.1 ± 1.5)	19–24 (21.7 ± 1.1)	20–25 (22.3 ± 1.3)	20–24 (22.5 ± 1.0)	20–25 (21.9 ± 1.1)
Number of scales between SS		4–8 (5.8 ± 1.1)	2–5 (3.5 ± 0.7)	3–8 (6.4 ± 1.2)	2–4 (3.3 ± 0.6)	2–5 (3.7 ± 0.9)
Number of scales between IP and SS		4–10 (7.2 ± 1.5)	2–5 (3.4 ± 0.7)	4–11 (7.9 ± 1.6)	2–4 (3.1 ± 0.6)	2–5 (3.5 ± 0.7)
Number of scales between SBO and SPL		2 (2.0 ± 0.0)	2–3 (2.0 ± 0.2)	1–2 (1.9 ± 0.4)	2 (2.0 ± 0.0)	1–32 (2.0 ± 0.3)
Number of SPL to level below center of eye		5–8 (6.3 ± 0.7)	5–7 (5.9 ± 0.5)	5–8 (6.5 ± 0.6)	6–9 (7.2 ± 0.7)	5–8 (6.5 ± 0.8)
Number of INL to level below center of eye		5–8 (6.7 ± 0.8)	5–8 (6.5 ± 0.7)	4–8 (6.9 ± 0.9)	6–9 (7.8 ± 0.7)	5–7 (6.5 ± 0.6)
Total number of loreals		44–91 (62.3 ± 11.1)	41–75 (56.8 ± 7.2)	43–110 (73.3 ± 15.7)	47–97 (61.9 ± 13.0)	47–77 (61.9 ± 8.7)
Number of horizontal loreal scale rows		7–12 (9.9 ± 1.2)	7–11 (8.9 ± 0.9)	8–12 (10.2 ± 1.0)	7–12 (8.6 ± 1.4)	6–11 (8.7 ± 1.1)
Number of postrostrals		5–9 (6.6 ± 0.9)	4–7 (6.0 ± 0.8)	5–8 (6.5 ± 0.8)	5–9 (7.0 ± 0.9)	5–8 (6.8 ± 0.9)
Number of postmentals		5–8 (6.3 ± 0.8)	4–8 (5.7 ± 0.7)	6–8 (6.3 ± 0.6)	5–9 (6.7 ± 0.9)	5–8 (6.2 ± 0.8)
Number of scales between nasals		5–10 (6.6 ± 1.1)	5–9 (6.4 ± 0.8)	6–8 (6.8 ± 0.6)	6–9 (6.9 ± 0.7)	5–8 (6.7 ± 0.7)
Number of scales between 2nd canthals		11–18 (14.0 ± 1.6)	9–14 (11.6 ± 1.1)	13–21 (16.5 ± 1.8)	10–14 (11.6 ± 1.0)	9–14 (11.7 ± 1.6)
Number of scales between posterior canthals		12–21 (16.2 ± 1.9)	10–16 (13.0 ± 1.1)	14–24 (18.7 ± 1.9)	11–15 (13.1 ± 1.1)	10–16 (12.8 ± 1.9)
Number of medial dorsal scales in one HL		52–76 (63.8 ± 5.5)	42–68 (53.1 ± 5.7)	48–92 (65.4 ± 9.2)	42–64 (51.3 ± 5.9)	42–62 (51.3 ± 6.2)
Number of medial ventral scales in one HL		26–44 (37.2 ± 3.7)	28–42 (33.5 ± 3.2)	28–48 (37.1 ± 5.0)	26–40 (31.4 ± 3.7)	28–50 (35.0 ± 6.2)
Number of scales around midbody		128–178 (146.6 ±11.7)	126–158 (141.4 ± 6.2)	126–156 (140.9 ±7.7)	122–148 (137.3 ±6.2)	128–152 (138.3 ±5.4)
Number of dorsal scales between axilla and groin		83–113 (99.5 ± 8.0)	72–104 (86.8 ± 6.5)	84–119 (100.0 ± 9.1)	69–102 (82.4 ± 10.0)	66–92 (82.4 ± 7.4)
Number of ventral scales between axilla and groin		41–63 (52.1 ± 5.1)	42–58 (50.9 ± 3.2)	47–65 (54.8 ± 4.5)	41–56 (47.0 ± 3.5)	46–66 (52.8 ± 4.5)

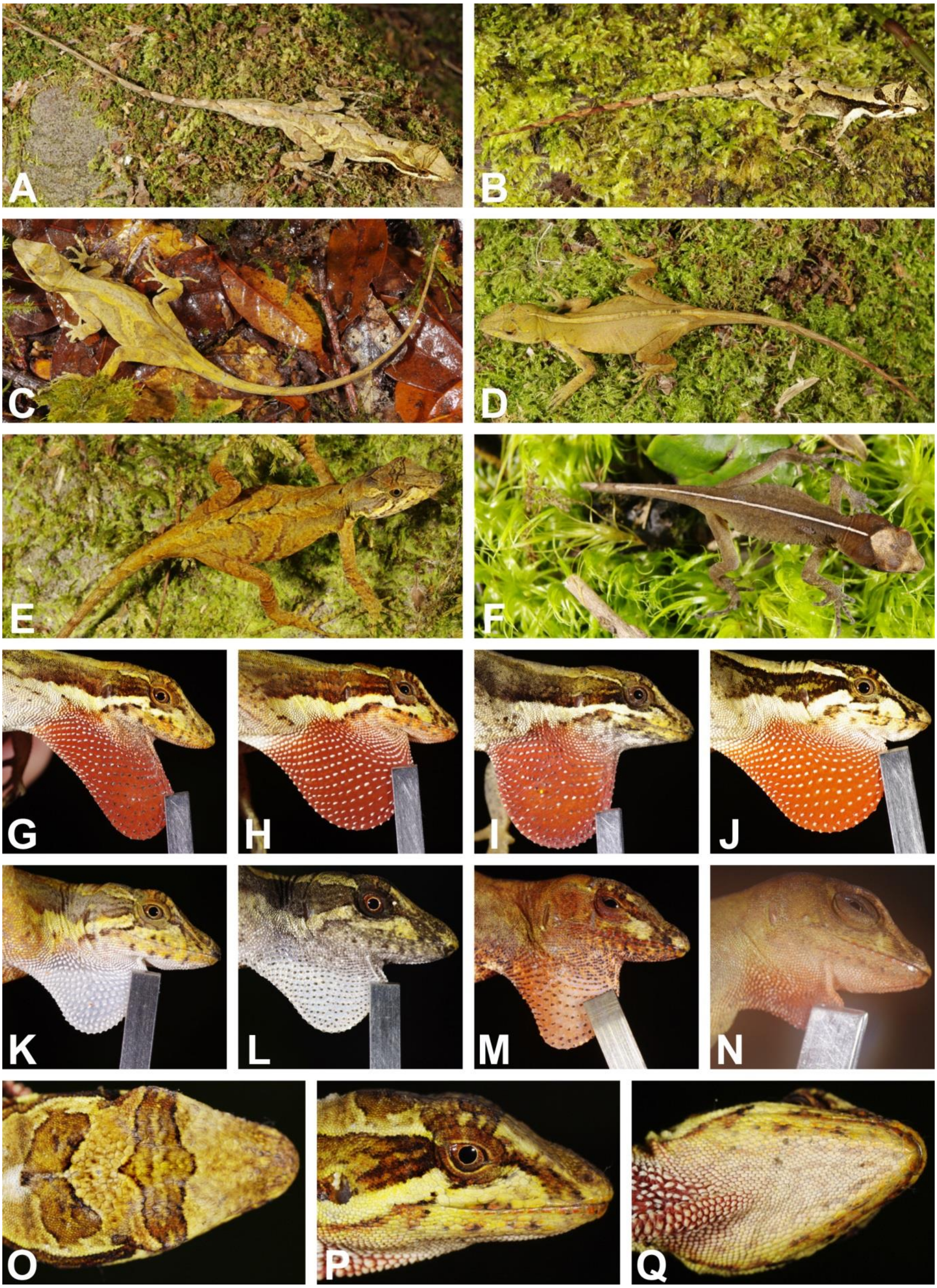


Figure 4.39: Individuals of *Norops magnaphallus* from the slopes of Volcán Barú. (A) Adult male MHCH 2232 and (B) subadult male MHCH 2229 from Sendero Los Quetzales; (C–E) adult females: (C) SMF 90131 from Area de Acampar Mamecillos, (D) MHCH 2233 and (E) SMF 89730 from Sendero La Cascada; (F) small juvenile SMF 90132 from Las Zarzamora; (G–J) male dewlaps: (G) SMF 89728 and (H) SMF 89729 from Sendero La Cascada, (I) SMF 89731 and (J) MHCH 2229 from Sendero Los Quetzales; (K–M) female dewlaps: (K) SMF 89730, (L) SMF 89736 from Sendero Los Quetzales, (M) uncollected female from Sendero La Cascada; (N) dewlap of SMF 90132; (O) dorsal, (P) lateral, and (Q) ventral view of head of 89734 from Sendero Los Quetzales.

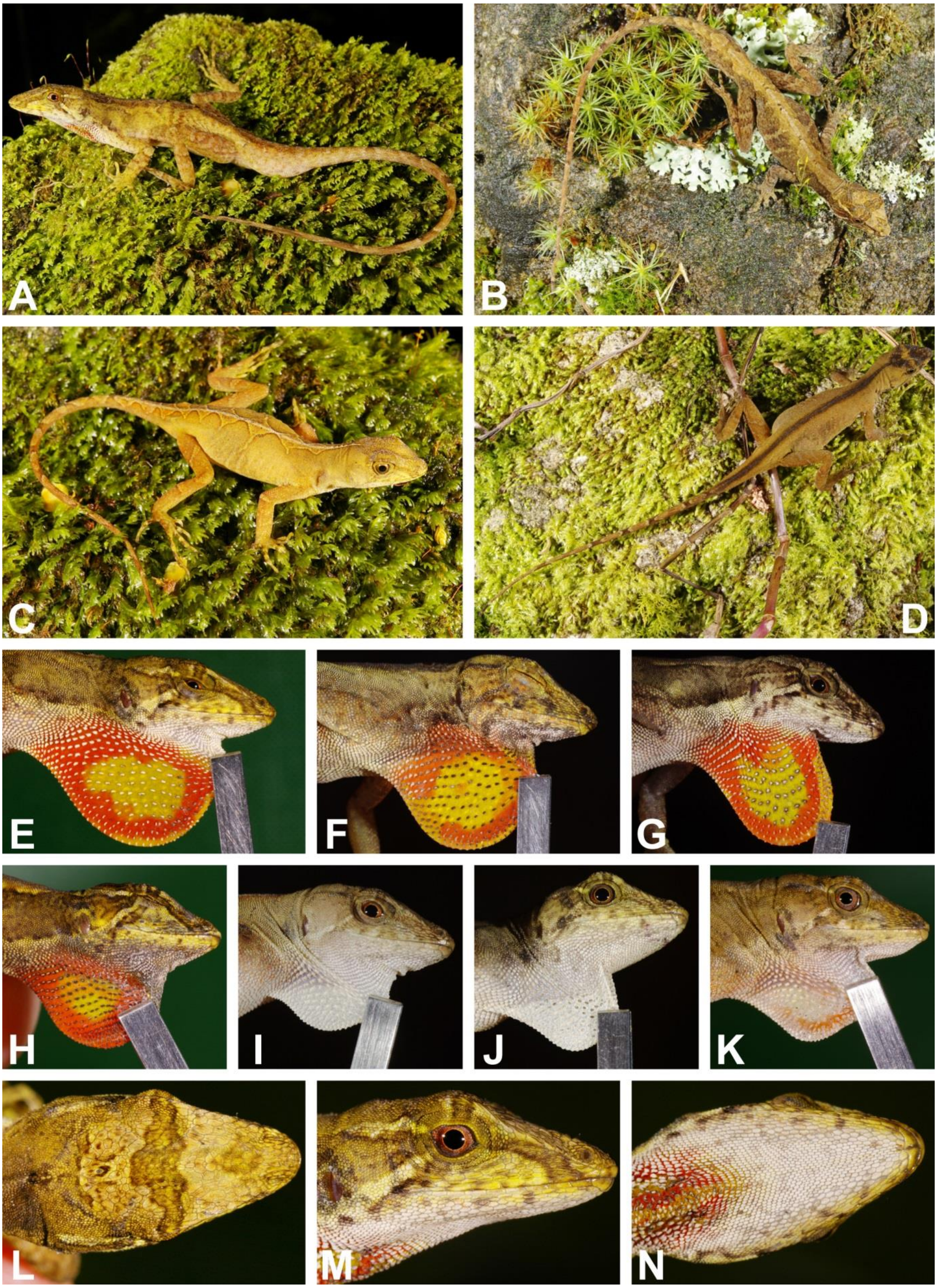


Figure 4.40: Individuals of *Norops pachypus* from Jurutungo. (A) Adult male SMF 89504; (B) adult male MHCH 2252; (C) adult female SMF 89502; (D) adult female SMF 89742; (E–H) male dewlaps: (E) SMF 89504; (F) SMF 89743, (G) SMF 89740, (H) uncollected male; (I–K) female dewlaps: (I) MHCH 2249, (J) MHCH 2253, (K) MHCH 2247; (L) dorsal, (M) lateral, and (N) ventral view of head of SMF 89504.

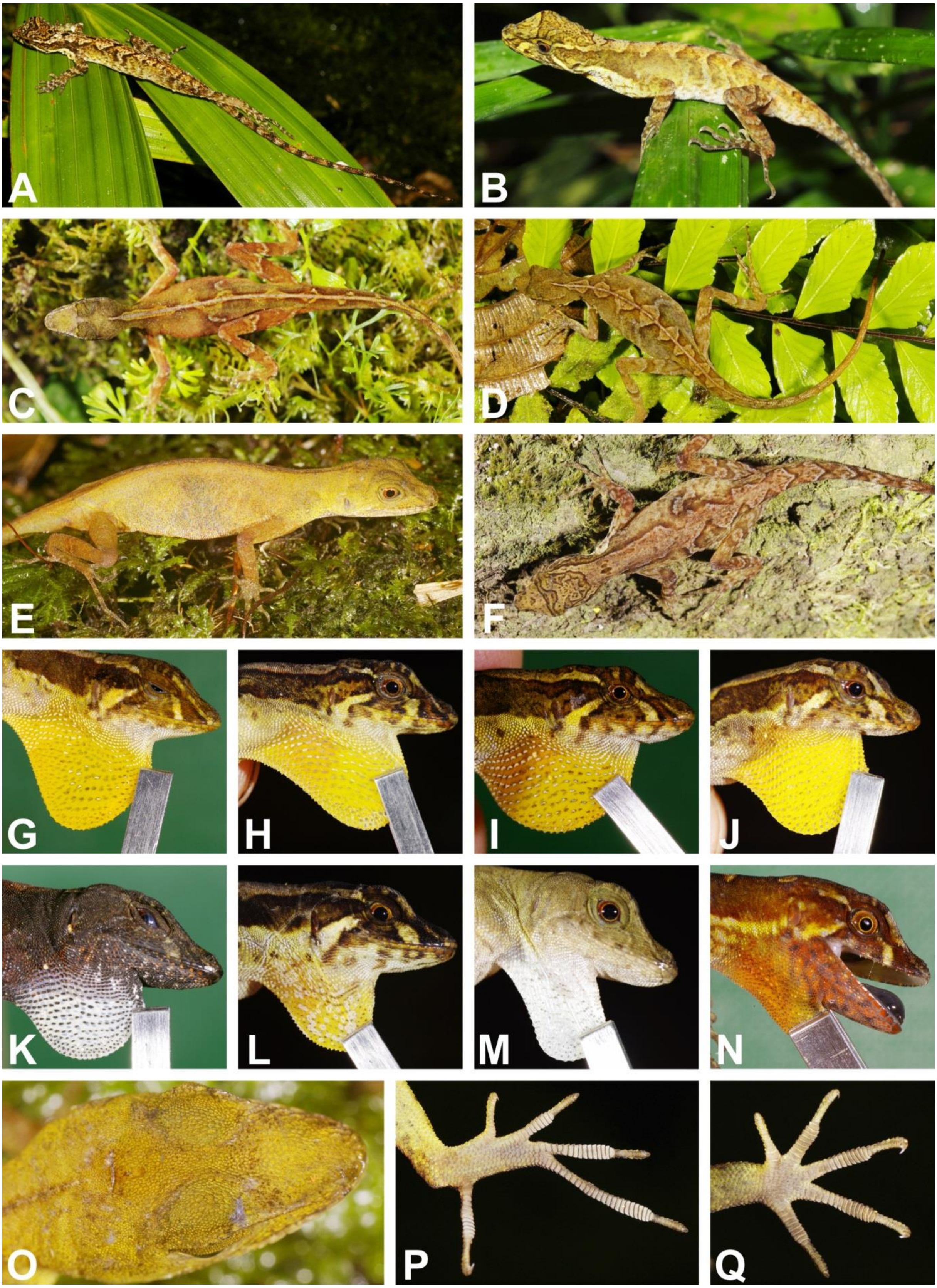


Figure 4.41: Individuals of *Norops pseudopachypus.* (A) Adult male SMF 89518 from La Nevera in sleeping position; (B) uncollected male from La Fortuna; (C–F) adult females: (C) uncollected and (D) SMF 89520 from La Nevera, (E) SMF 89526 and (F) SMF 89754 from La Fortuna; (G–J) male dewlaps: (G) SMF 89519 and (H) MHCH 2282 from La Nevera, (I) SMF 89524 and (J) MHCH 2284 from La Fortuna; (K–N) female dewlaps: (K) SMF 89520 and (L) MHCH 2283 from La Nevera, (M) MHCH 2285 from La Fortuna, (N) juvenile MHCH 2276 from La Nevera; (O) dorsal view of head of SMF 89526 showing numerous tiny scales in frontal and parietal areas; ventral views of (P) left foot and (Q) left hand of male SMF 91522 from Cerro Saguí, exemplary for all members of the *N. pachypus* complex.

4.1.5 Iguania, Dactyloidae: The *Norops kemptoni* complex

Another case of cryptic species diversity in the Cordillera Central that has long remained unrecognized is presented by *Norops kemptoni* and its close relatives. Since the first member of this group of highland anoles to be described was *N. altae* (Dunn 1930b) from Costa Rica, these short-legged species of slender appearance are often collectively referred to as the *Norops* (or *Anolis*) *altae* complex (Ponce & Köhler 2008; Köhler 2009, 2011; Gutpelet 2012). However, since this chapter is exclusively dedicated to their diversity in the Panamanian portion of the LCA highlands, I will refer to them as the *Norops kemptoni* complex throughout the following. In Panama, the first species to be formally recognized was *Anolis kemptoni* Dunn 1940, described from Finca Lérida near Boquete (loc. 6 in Map 1.13). More than half a century later, *A. fortunensis* Arosemena & Ibáñez 1993 and *A. exsul* Arosemena & Ibáñez 1994 were described from the La Fortuna area, with a distance of about 2 km between their respective type localities (locs. 16 and 17 in Map 1.13). The next name added to this clade was *N. pandoensis* Savage & Guyer 1998, described from La Changuinolita in the Las Tablas area of extreme southeastern Costa Rica, on the southwestern slopes of Cerro Pando close to the border with Panama. Not even a decade later, Hulebak & Poe (2006) synonymized this species with *N. kemptoni.* The following year, Köhler et al. (2007) described *A. gruuo* and *A. pseudokemptoni* from the central Serranía de Tabasará (locs. 18 and 19 in Map 1.13). Shortly thereafter, Ponce & Köhler (2008) examined 46 specimens of the *N. kemptoni* complex from western Panama, including all specimens of *N. exsul, N. fortunensis, N. gruuo,* and *N. pseudokemptoni* known at that time. Their analyses of morphological variation lead to the placement of *N. exsul* in the synonymy of *N. fortunensis.* Thereafter, news about the *N. kemptoni* complex from Panama were restricted to distribution extensions for *N. fortunensis* (Hamad 2009 and Lotzkat et al. 2010c; both based on erroneous identifications, see below) and *N. gruuo* (Stadler 2010; Lotzkat et al. 2012c). The latest taxonomic additions to this group again came from Costa Rica, namely *N. monteverde* (Köhler 2009) and *N. tenorioensis* (Köhler 2011). In his recent Diploma thesis (Gutpelet 2012), for which I had provided material as well as morphological and molecular data and also assumed a partial tutorship, MG analyzed morphological and/or molecular data for a grand total of 368 specimens of the aforementioned species, whose validity he essentially reconfirmed. Similar to Köhler (2011), he concluded that dewlap coloration and hemipenial morphology should be regarded as the primordial characters to distinguish between the species of this clade.

In the following, I examine the robustness of the taxonomic arrangement of the *Norops kemptoni* complex in western Panama. Other than previous workers (Ponce & Köhler 2008; Köhler 2009, 2011; Gutpelet 2012), I use DNA barcodes as a starting point. For this purpose, I reanalyze all Panamanian and 3 Costa Rican 16S sequences that were included in the analyses of Gutpelet (2012), and complement these with the correspondent COI barcodes provided by the ColdCode project. For the 16S barcodes, the manually refined final alignment of 45 sequences (37 Panamanian and 3 Costa Rican, i.e., 40 individuals of the *N. kemptoni* complex as well as the two *N. pachypus,* two *N. pseudopachypus,* and one *Dactyloa ibanezi* that already served as outgroups in chapter 4.1.2) contained 537 positions, of which, excluding the outgroups, 63 were variable and 58 parsimony-informative. For the COI barcodes, the final alignment of 30 taxa (identical outgroups and 25 Panamanian individuals of the *N. kemptoni* complex) contained 561 positions, of which, excluding the outgroups, 163 were variable and 147 parsimony-informative. For both genes, T92+G was determined as the best-fitting substitution model. The alignments and distance matrices underlying the following results are provided in Appendix 5.5. Table 4.10 gives an overview of the mean values of uncorrected p-distances found for both barcodes within and between the different lineages.

Table 4.10: Mean values of uncorrected p-distances in 16S (lower left) and COI (upper right, in *italics*) barcodes among members of the *Norops kemptoni* complex and outgroups. Mean distances within a lineage are in **bold** face.

	Dactyloa ibanezi	***Norops pachypus***	***N. pseudopachypus***	***N. gruuo***	***N. g.* west**	***N. g.* east**	***N. pseudokemptoni***	***N. kemptoni***	***N. k.* west**	***N. k.* east**	***N. fortunensis***
Dactyloa ibanezi	–	*0.199*	*0.219*	*0.179*	*0.178*	*0.180*	*0.194*	*0.189*	*0.190*	*0.189*	*0.182*
Norops pachypus	0.113	***0.005*** **0.002**	*0.129*	*0.194*	*0.197*	*0.189*	*0.195*	*0.186*	*0.183*	*0.187*	*0.184*
N. pseudopachypus	0.129	0.055	***0.082*** **0.031**	*0.189*	*0.192*	*0.185*	*0.188*	*0.189*	*0.182*	*0.190*	*0.190*
N. gruuo	0.124	0.084	0.083	***0.025*** **0.009**	–	–	*0.088*	*0.098*	–	–	*0.099*
***N. g.* west**	0.122	0.083	0.080	–	***0.004*** **0.001**	*0.043*	*0.084*	–	*0.090*	*0.097*	*0.101*
***N. g.* east**	0.128	0.085	0.088	–	0.016	**0.001** **0.001**	*0.093*	–	*0.091*	*0.103*	*0.098*
N. pseudokemptoni	0.134	0.094	0.093	0.046	0.045	0.049	***0.002*** **0.001**	*0.119*	*0.107*	*0.122*	*0.113*
N. kemptoni	0.128	0.085	0.084	0.047	–	–	0.055	***0.020*** **0.016**	–	–	*0.089*
***N. k.* west**	0.133	0.085	0.086	–	0.043	0.046	0.055	–	***0.009*** **0.008**	*0.039*	*0.096*
***N. k.* east**	0.122	0.084	0.082	–	0.048	0.051	0.055	–	0.025	***0.009*** **0.006**	*0.098*
N. fortunensis	0.120	0.078	0.087	0.044	0.043	0.046	0.069	0.053	0.050	0.056	**–** **0.0**

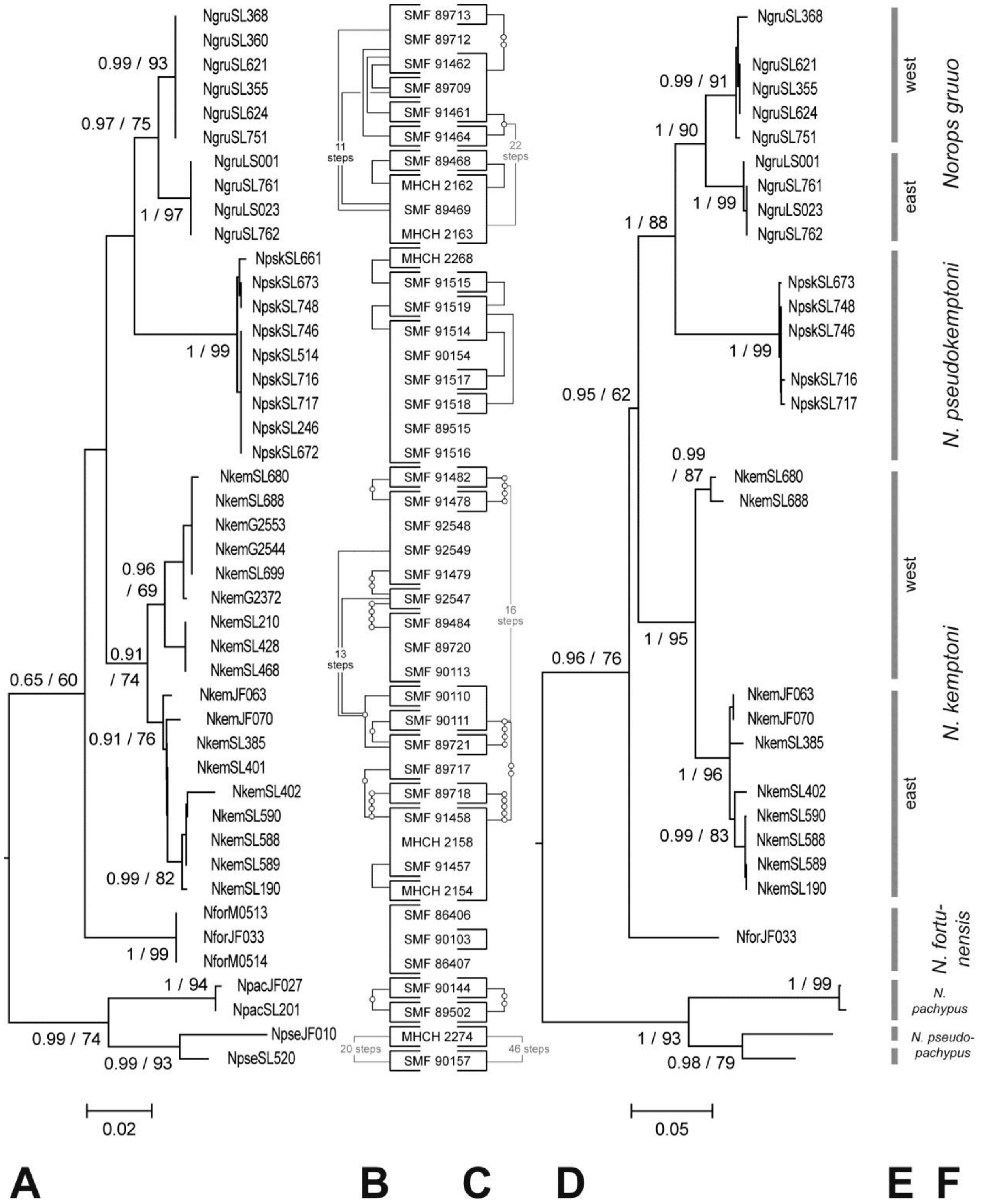


Figure 4.42: Results of DNA barcode analyses of the *Norops kemptoni* complex. (A) Consensus tree from ML analysis of 16S barcodes. (B) Parsimony network of 16S barcodes with a 95% parsimony probability resulting in a connection limit of 9 steps drawn with haplotype symbols on the left side of the correspondent collection numbers. (C) Parsimony network of COI barcodes with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols on the right side of the correspondent collection numbers. (D) Consensus tree from ML analysis of COI barcodes. (E) Lineages diagnosable through barcoding. (F) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding analyses. In (A) and (D), bootstrap values shown at selected nodes are preceded by posterior probabilities from correspondent BI analyses, and the outgroup *Dactyloa ibanezi* is not shown. In (B) and (C), additional connections acheived by manually increasing the connection limit are indicated by the number of necessary steps, in gray or black as specified in the text.

The results of the analyses of the 16S and COI alignments are visualized in Figure 4.42, omitting the *Dactyloa* outgroup for layout reasons. As in the case of the *Norops pachypus* complex, the nominal species form discrete clades in both 16S and COI analyses. Due to the higher p-distances in the COI fragment, these clades are inferred with higher support values in the corresponding tree. However, it should be noted that within the *N. kemptoni* complex the discrepancies in corresponding p-distances between 16S and COI barcodes are not as pronounced as they were found to be in the *N. pachypus* complex, with the mean COI distances less frequently being much more than twice as high as the respective 16S distances. Again, the DNA barcodes reveal the presence of two distinct genealogical lineages, respectively, in two of the analyzed species, which are correlated with the western longitude of the specimens' collection sites. Within *N. gruuo,* the western lineage contains animals from near the type locality and the single individual from Guayabito, while the eastern lineage is made up by the population from Veraguas. Between individuals of these two lineages lies a minimum airline distance of 40 km, and uncorrected p-distances of 1.5–1.9% in the 16S or 4.1–4.5% in the COI barcode. Within *N. kemptoni,* the western lineage comprises the three Costa Rican individuals as well as Panamanian specimens originating from Jurutungo, the Changena trail, and the SE slopes of Volcán Barú at Potrerillos Arriba. This lineage essentially includes the OTUs 1–3 of Ponce & Köhler (2008), or the western "half" of the OTUs 8 and 9 of Gutpelet (2012). Moreover, it must comprise the populations described by Savage & Guyer (1998) as *N. pandoensis,* since the individuals GK 2544 and GK 2553 have been collected about one kilometer from the type locality of that nominal taxon according to Gutpelet (2012). The eastern lineage's areal begins in close neighborhood to the western lineage's population from Potrerillos Arriba, with its westernmost representatives collected at an airline distance of only 9.4 km at Sendero La Cascada and Sendero Los Quetzales on the N and NE slopes of the volcano. Given the close proximity of Sendero La Cascada to that taxon's type locality at Finca Lérida (about 2–3 km depending on where exactly on this large estate Dunn collected the holotype), this lineage is most likely to comprise the population originally described as *N. kemptoni* (though the single paratype from Volcán surely pertains to the western lineage identified herein). The eastern lineage also includes animals found further east at Cerro Altrillería and, surprisingly, the population from Cerro Pata de Macho at RFLF that had been identified as *N. fortunensis* based on the key of Ponce & Köhler (2008), and in consequence erroneously published as such (Hamad 2009; Köhler et al. 2010a; Lotzkat et al. 2010a, c). The genetic distances between the two lineages of *N. kemptoni* range from 2.1–3.4% in the 16S or 3.4–4.3% in the COI barcode. From the perspective of parsimony, the haplotype networks provide a similar view. For the 16S barcode (Fig. 4.42B), the 95% parsimony probability (black connections with haplotype symbols) requires a connection limit of 9 substitutional steps, leaving all respective haplotypes within each of the six lineages inferred for the *Norops kemptoni* complex interconnected, as well as the two outgroup individuals of *N. pachypus*. Lowering the parsimony probability to 90% (black connections with step numbers) raises the connection limit to 14 steps and adds connections between the two respective lineages within *N. gruuo* and *Norops kemptoni,* whereas still more substitutional steps (gray connections with substitution step numbers) are required to interconnect the two haplotypes of the outgroup *N. pseudopachypus,* representative of two genetically distinct clades classified as DCLs in the previous section. For the COI fragment (Fig. 4.42C), the 95% parsimony probability requires a connection limit of 10 substitutional steps and results in a congruent picture. Lowering the parsimony probability to 90% raises the connection limit to 14 steps that do not entail further connections yet. The interconnection of eastern and western haplotypes of *N. kemptoni* requires a minimum of 19 steps, while for *N. gruuo* 23 steps are needed. That is, roughly doubling the 95% parsimony probability connection limit will result in COI haplotype networks congruent with the nominal species of the *N. kemptoni* complex, whereas a still two-fold higher number of steps separate the two outgroup haplotypes of *N. pseudopachypus*.

According to the lineages evident in all molecular results, I separated the examined specimens into these six groups for the morphological comparisons. Figure 4.43 shows the variation in standard meristic and mensural characters for the six lineages. Although among the characters plotted are the ones found to be the most variable, no lineage shows consistent, non-overlapping differences to any other lineage, in none of the examined characters. On the one hand, this holds for the four nominal species as currently recognized. Moreover, it also applies to the two genealogical lineages found in *N. gruuo* and *N. kemptoni,* respectively. The eastern and western lineages of *N. kemptoni* appear almost completely congruent in all examined characters. While the eastern and western lineages of *N. gruuo* do show certain differences in some characters, which is expressed in divergent respective mean values, there is always a considerable overlap of the observed character states between the two lineages. These results essentially reconfirm those of Hulebak & Poe (2006), Ponce & Köhler (2008), and Gutpelet (2012), yet they go a little further: Even the high number of loreals in *N. pseudokemptoni,* used in the key of Ponce & Köhler (2008) and consequently also that of Köhler (2008) to distinguish that species from the other members of this complex, is now revealed to overlap with that of all other lineages in the light of an increased sample size. In other words, standard anole measurements and scale counts are useless for lineage separation or species identification in the *N. kemptoni* complex. As with the relatives of *N. pachypus,* morphological species delimitation is bound to rely on qualitative characters.

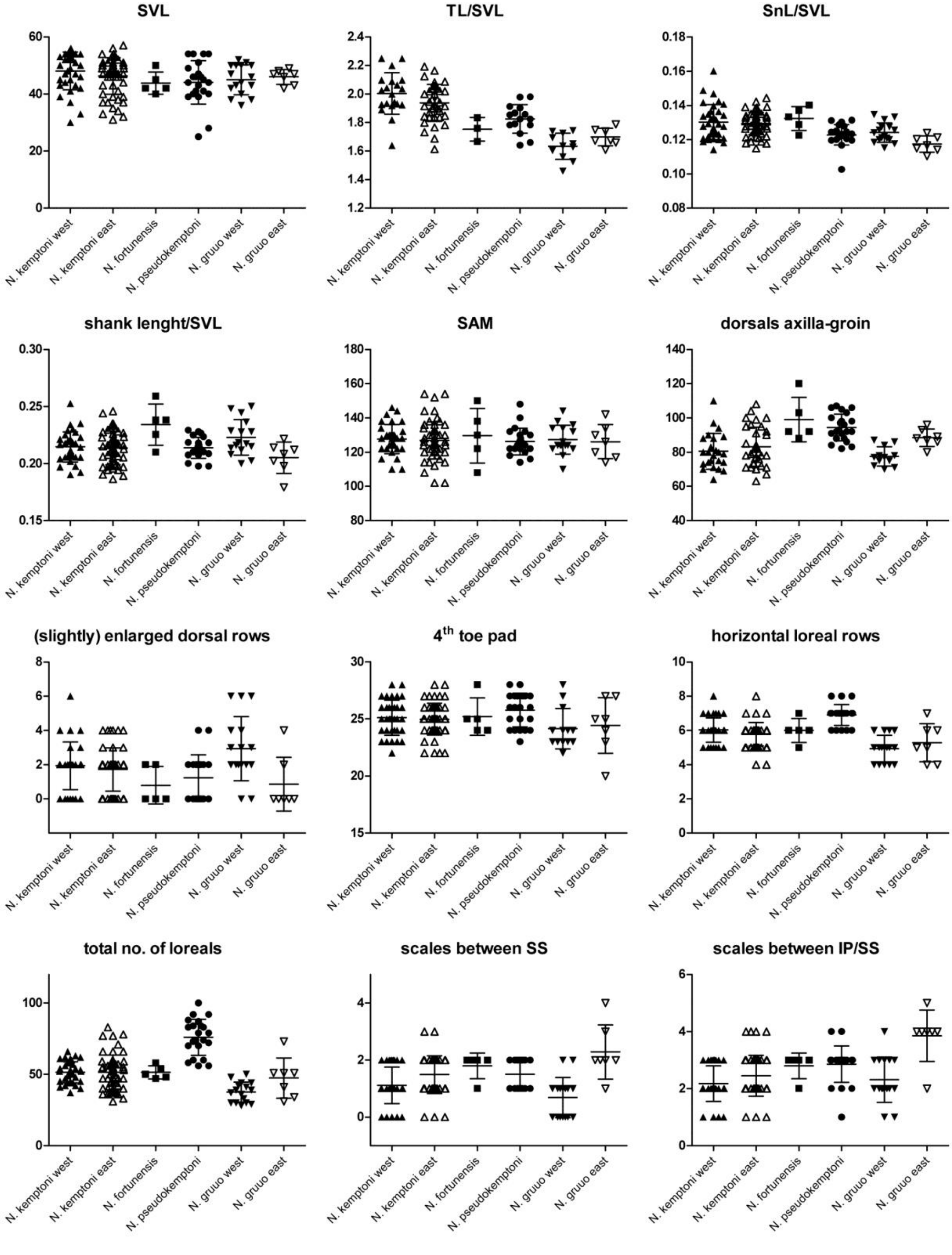


Figure 4.43: Variation (bars indicate mean ± one standard deviation) in selected morphometric and pholidotic characters among the lineages of the *Norops kemptoni* complex as inferred from DNA barcodes.

The first of these that comes to mind is of course the coloration of the male dewlap in life, shown in Figures 4.45–49. Indeed, its rather unicolor orange dewlap immediately separates males of *Norops gruuo* (Figs. 4.45 and 4.47) from those of the other lineages. Within this nominal species, representatives of the eastern lineage seem to have a slightly larger dewlap than that of most members of the western lineage, but there are also males with a comparably large dewlap (larger than reported by Ponce & Köhler 2008) in the Central Serranía de Tabasará. Apart from a usually present small light-colored portion located at the anterior base next to the chin area, the dewlap of male *N. pseudokemptoni* (Figs. 4.45 and 4.49) may appear almost solid red or, in most cases, exhibit lighter reddish tonalities in its posterior third or two-thirds. Regardless of their pertinence to the western or eastern lineage, the dewlap of male *N. kemptoni* (Figs. 4.45 and 4.48) may vary similar to that of *N. pseudokemptoni,* i.e., appear unicolor red or have the posterior portion grading into lighter colors from the red palette, with the difference that some individuals have a light-colored portion located more centrally along the dewlap's base than those of *N. pseudokemptoni.* The statement of Arosemena & Ibañez (1993, 1994) that *N. kemptoni* differs from *N. fortunensis* (and its now synonym *N. exsul*) by its small dewlap is simply untenable in view of the large appendages found in all males of this complex. Yet, all three males of *N. fortunensis* which I know (Figs. 4.45 and 4.46) had a red dewlap whose posterior portion is not grading into something that could be called pink, orange, or lavender as in the two aforementioned taxa, but instead is dominated by greenish shadings. In all taxa, the female dewlap is much smaller than the large male one, and chiefly white. Exceptions are young females of *N. gruuo* that have a reddish orange dewlap (Fig. 4.47L), and females of *N. pseudokemptoni,* whose yellow to orange dewlap has been used as a diagnostic character (Köhler et al. 2007; Ponce & Köhler 2008; Köhler 2008). However, some females in my sample have a white dewlap (Fig. 4.49).

Another qualitative character that has been stated to separate these taxa is the state of the ventral scale surface, that has been said to be smooth in all nominal species except *N. kemptoni* (Arosemena & Ibañez 1993, 1994; Köhler et al. 2007; Ponce & Köhler 2008; Köhler 2008). Yet, this character loses much of its significance in the light of my material, since several males of *N. kemptoni*, mostly from the eastern lineage*,* have perfectly smooth ventrals. On the other hand, one male of *N. gruuo* from Veraguas has very faintly keeled ventrals. The "conspicuous dark and pale banding" on the tail of *N. gruuo* (Köhler et al. 2007; Ponce & Köhler 2008; Köhler 2008), that in my experience may be present or not in representatives of all six genealogical lineages (compare Figs. 4.46–4.49), should definitely not be considered a diagnostic character. This leaves us with the second paramount feature to distinguish between cryptic anole species: their hemipenes, shown in Figure 4.44. In *N. pseudokemptoni* and both lineages of *N. gruuo,* the male reproductive organ is large and bilobated, whereas it is much smaller and unilobate in *N. fortunensis* and both lineages of *N. kemptoni.* The bilobated hemipenes of *N. gruuo* and *N. pseudokemptoni* differ markedly in the relative length and width of the lobes, which are much longer compared to the truncus in the former species (compare Figs. 4.44C and D). Contrarily to Ponce & Köhler (2008), I cannot find a pronounced difference between the hemipenes of *N. fortunensis* and both lineages of *N. kemptoni*. As described by these authors, in both the eastern and the western lineage of *N. kemptoni* the apex is strongly calyculate and bears a processus on the asulcate surface. While these features have been stated to be absent in *N. fortunensis* by Ponce & Köhler (2008), I find them maybe less pronounced but clearly present in the completely everted hemipenis of the young male SMF 90103 (Fig. 4.44A), and even discernable in low quality photos of the organs of the holotypes of *N. exsul* and *N. fortunensis* provided to me by MP. Thus, the hemipenis loses its diagnostic value in this case.

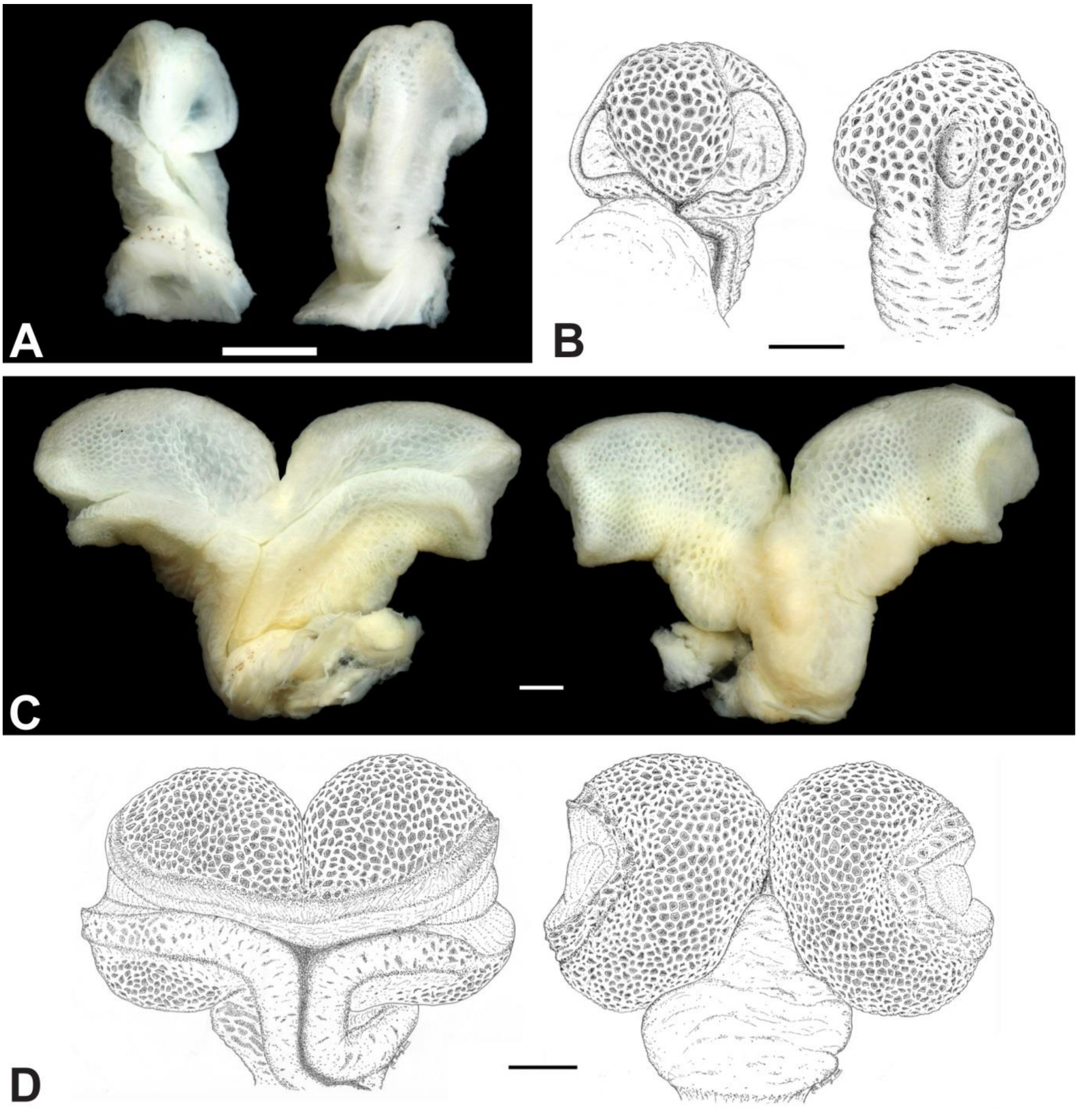
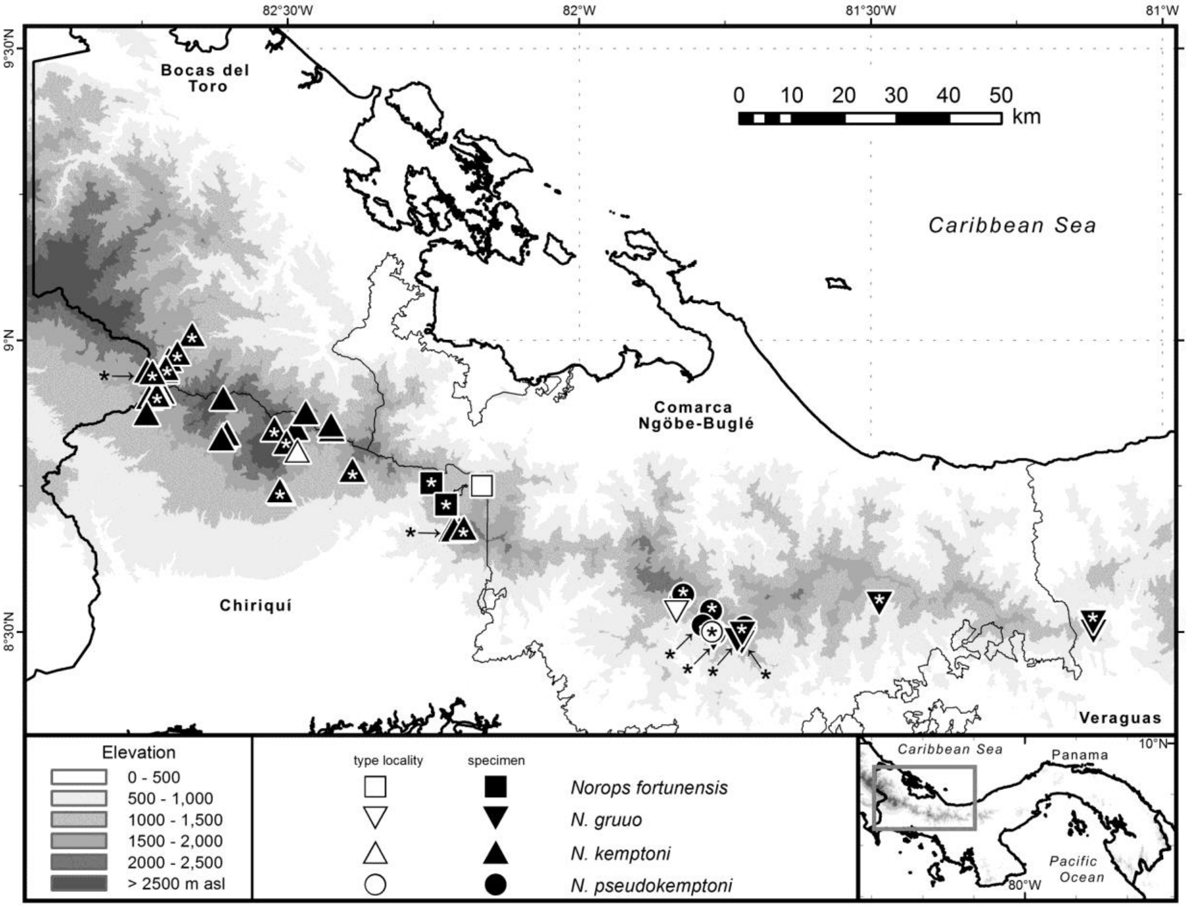


Figure 4.44: Hemipenes in the *Norops kemptoni* complex. (A) *N. fortunensis,* young male SMF 90103; (B) *N. kemptoni,* SMF 85406; (C) *N. gruuo,* SMF 89711; (D) *N. pseudokemptoni,* holotype SMF 85420. Sulcate views left, asulcate views right; all scale bars equal 1 mm. Drawings in (B) and (D) by Milan Vesely, modified from Köhler et al. (2007); photos in (A) and (C) by GK.

Molecular and morphological results are integrated in Figure 4.45. Since neither of the eastern or western genealogical lineages found within *N. kemptoni* nor *N. gruuo* exhibits any consistent, non-overlapping morphological distinctions from the respective other lineage within the respective nominal species, I must regard the two lineages within *N. kemptoni,* as well as those of *N. gruuo,* as DCLs. This leaves the taxonomic arrangement of this group of closely related lizards as it is. Table 4.11 summarizes the qualitative characters which have been demonstrated to be somewhat helpful for identifying any member of this complex. Updating the quantitative morphological data provided by previous authors (Ponce & Köhler 2008, Gutpelet 2012), Table 4.12 summarizes selected morphometric and pholidotic characteristics among the four species of the *N. kemptoni* complex treated herein, based exclusively on Panamanian material. Map 4.9 provides an overview on the distribution of all four species in western Panama, while the morphological variation among them pictured in Figures 4.46–4.49. For more information on each species see their respective species accounts in chapter 4.2.2.



Map 4.9: Distribution of *Norops fortunensis, N. gruuo, N. kemptoni,* and *N. pseudokemptoni* in western Panama and and immediately adjacent eastern Costa Rica. Based on specimens examined by Köhler et al. (2007), Ponce & Köhler (2008), Gutpelet (2012), and Lotzkat et al. (2012c). Localities of specimens with DNA barcodes included in the molecular analyses are marked with an asterisk (*).

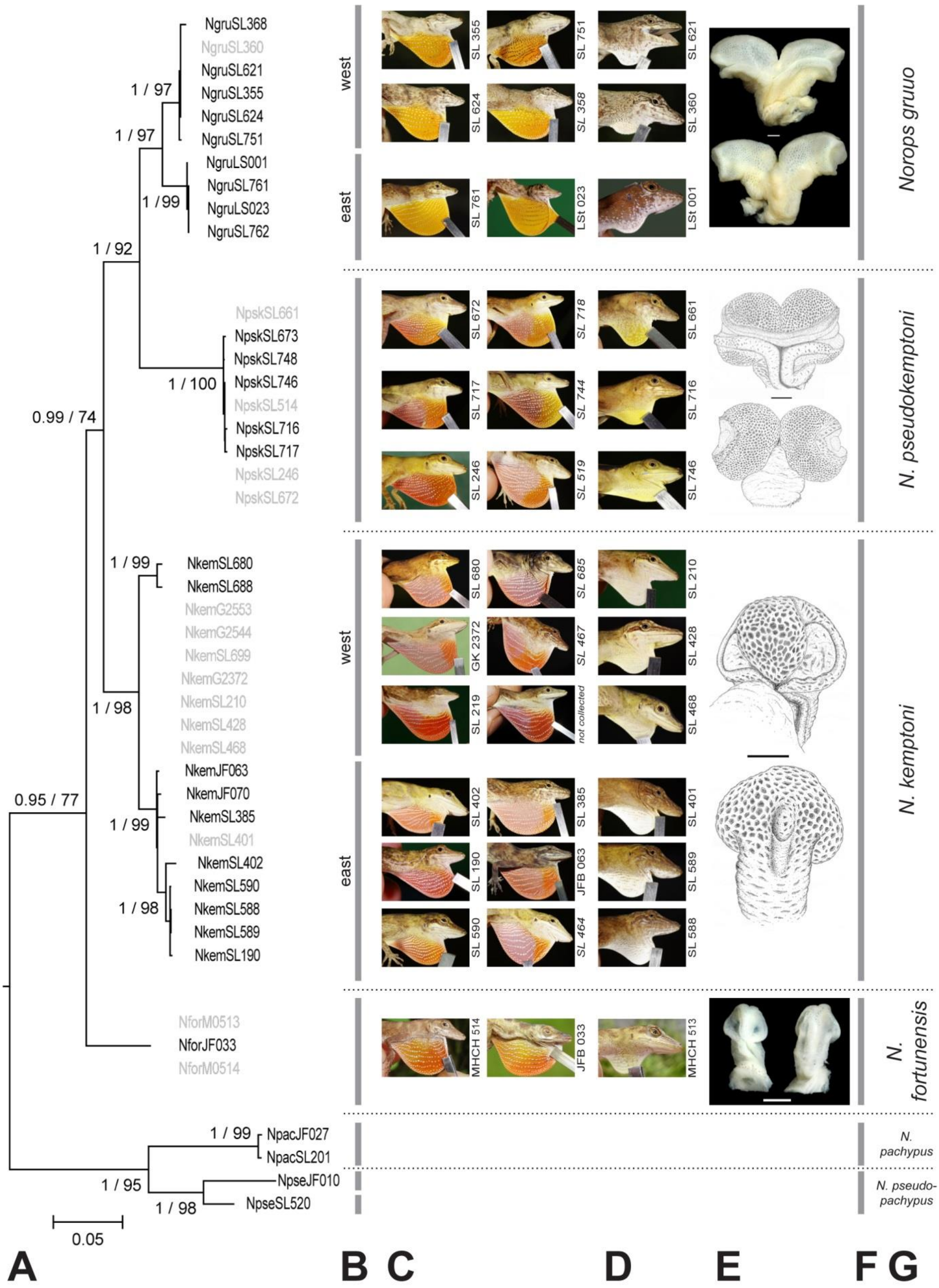


Figure 4.45: Integration of molecular and morphological lines of evidence for the *Norops kemptoni* complex. (A) Consensus tree from ML analysis of concatenated 16S and COI alignments, with additional specimens only represented by 16S barcodes inserted in light gray; for more details see legend of Fig. 4.42. (B) Lineages as inferred from the DNA barcodes in Fig. 4.42. (C) Dewlaps of sampled or syntopical males, the latter labelled in *italics*. (D) Dewlaps of sampled females in life. (E) Representative hemipenes from Fig. 4.44; sulcate view above or left of asulcate view, scale bars = 1 mm. (F) Lineages diagnosable from morphology. (F) Taxonomic identity of inferred CGLs. Photos of GK and JFB specimens taken by the respective collector, those of MHCH specimens by MP. See text for details.

Table 4.11: Synopsis of qualitative diagnostic characters in the *Norops kemptoni* complex.

	Norops fortunensis	***N. gruuo***	***N. kemptoni***	***N. pseudokemptoni***
male dewlap	red posterior portion always with greenish or greenish-yellow hue small light-colored area may be present on anterior half of base	orange mostly unicolor	red unicolor or posteriorly with magenta or similar hue, but never greenish small light-colored area may be present on anterior half of base	red unicolor or posteriorly with magenta or similar hue, but never greenish small light area usually present at anteriormost base next to chin
female dewlap	white	white in adults orange in juveniles	white rarely yellowish	yellow or orange rarely white
hemi-penis	unilobate base of tail not swollen in adult males	bilobate, long lobes base of tail usually swollen in adult males	unilobate base of tail not swollen in adult males	bilobate, short lobes base of tail always swollen in adult males
ventrals	smooth	smooth or faintly keeled	keeled or smooth	smooth

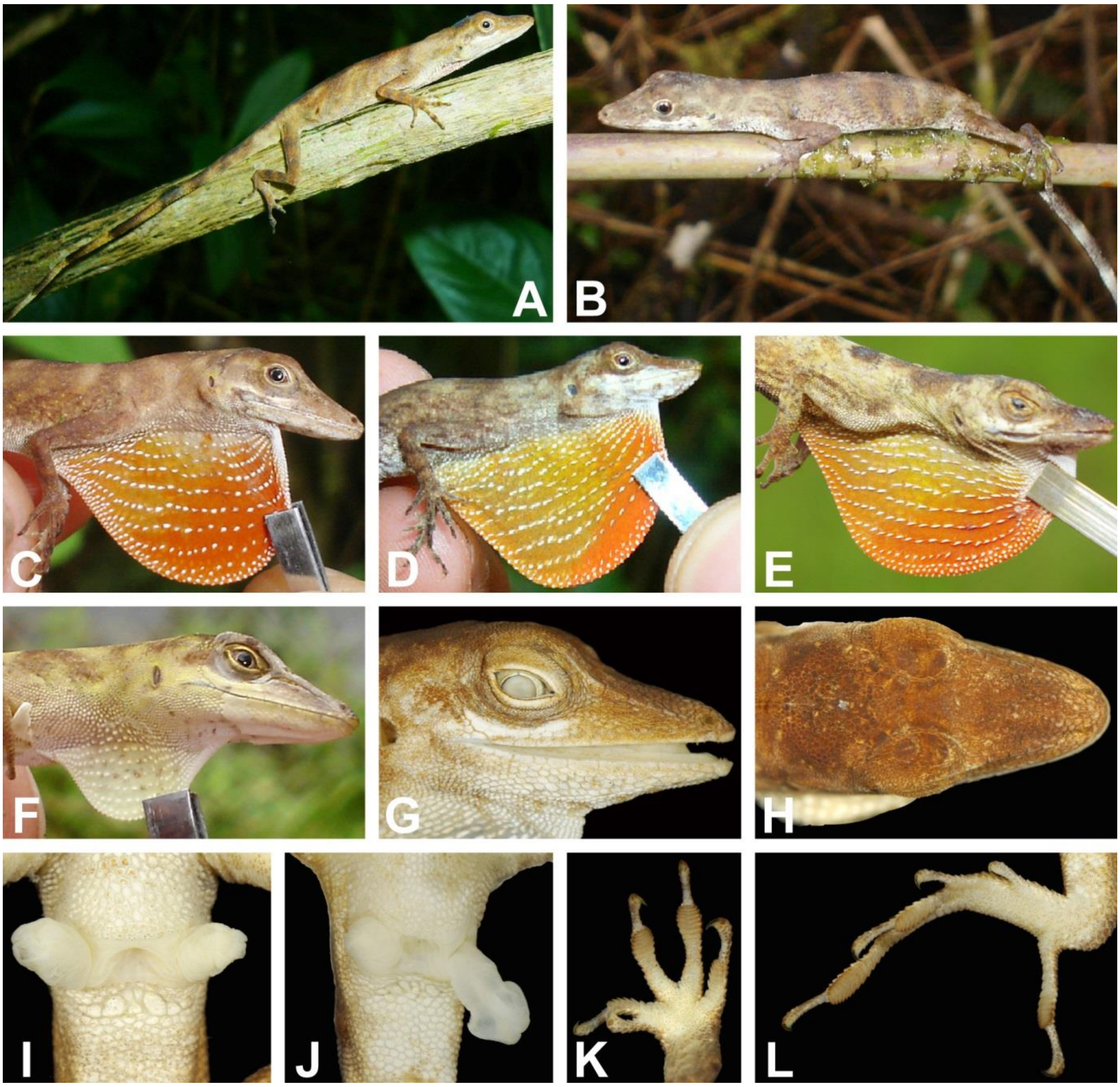


Figure 4.46: Individuals of *Norops fortunensis.* (A) Male SMF 86408; (B) individual of the series SMF 86405–7; (C–E) male dewlaps: (C) SMF 86407, (C) SMF 86408, (E) SMF 90103; (D) dewlap of female SMF 86406; (G) lateral and (H) dorsal view of head of SMF 86407; enlarged postcloacal scales of (I) SMF 86407 and (J) SMF 90103; (K) left hand and (L) right foot of SMF 86407. Photos (A, C, F) by MP, (B,D) by AB, (E) by JFB.

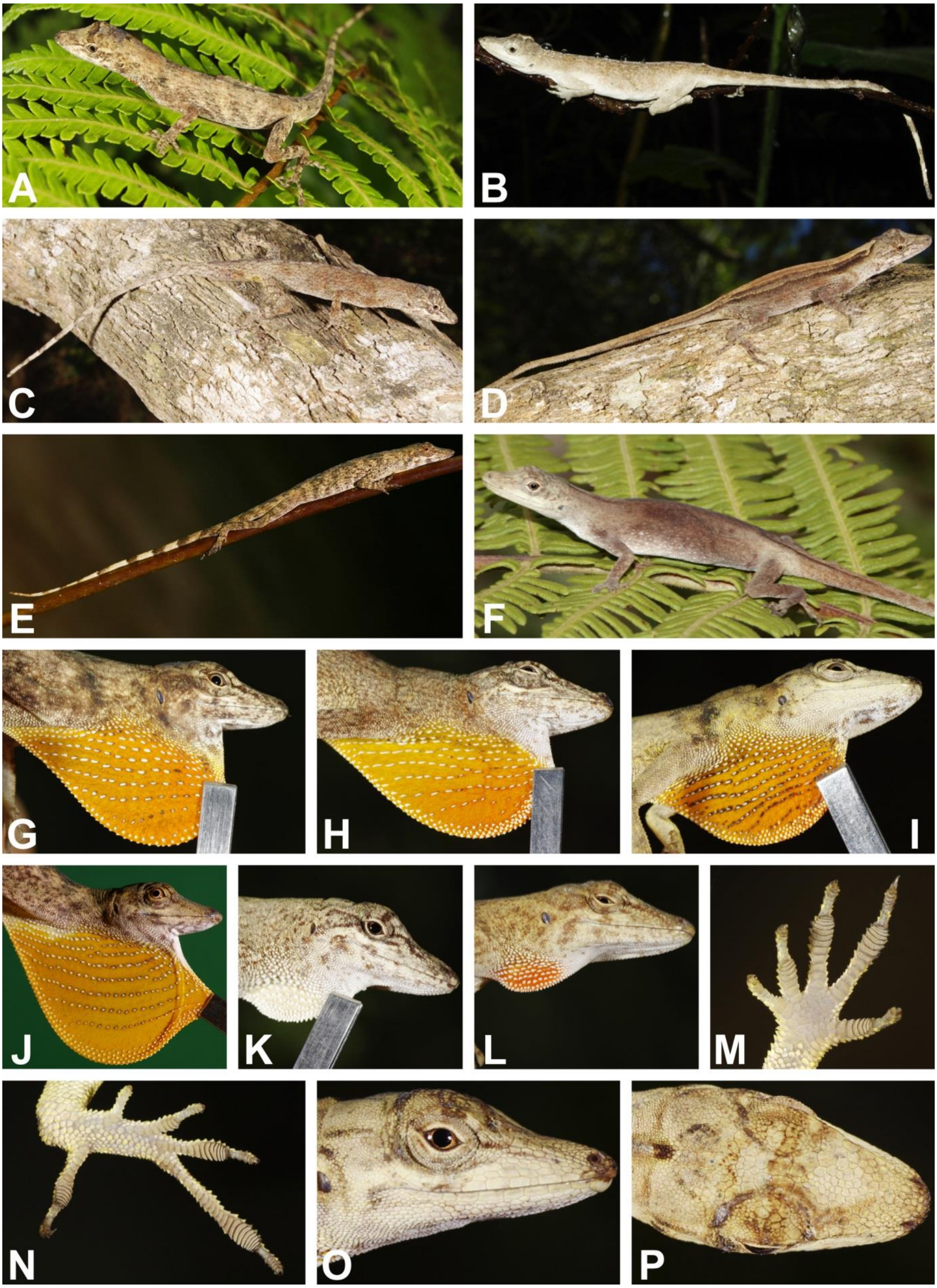


Figure 4.47: Individuals of *Norops gruuo* from the Serranía de Tabasará. (A) male (SMF 91461) from north of Hato Chamí; (B) female (SMF 91462) from north of Hato Chamí in sleeping position; (C) male (SMF 89711) from near Buabidí; (D) female (SMF 89710) from near Buabidí; (E) male (SMF 89469) from Cerro Mariposa; (F) female (SMF 89471) from Alto de Piedra; (G)–(J) male dewlaps, width of forceps 3 mm: (G) SMF 91461; (H) SMF 89711; (I) SMF 91464 from north of Guayabito; (J) SMF 89469; (K)–(L) female dewlaps: (K) SMF 89712 from near Buabidí, adult; (L) MHCH 2160 from near Buabidí, subadult; (M) left hand and (N) left foot of SMF 91464 in ventral view; (O) lateral and (P) dorsal view of head of male SMF 89709 from near Buabidí. Modified from Lotzkat et al. (2012c).

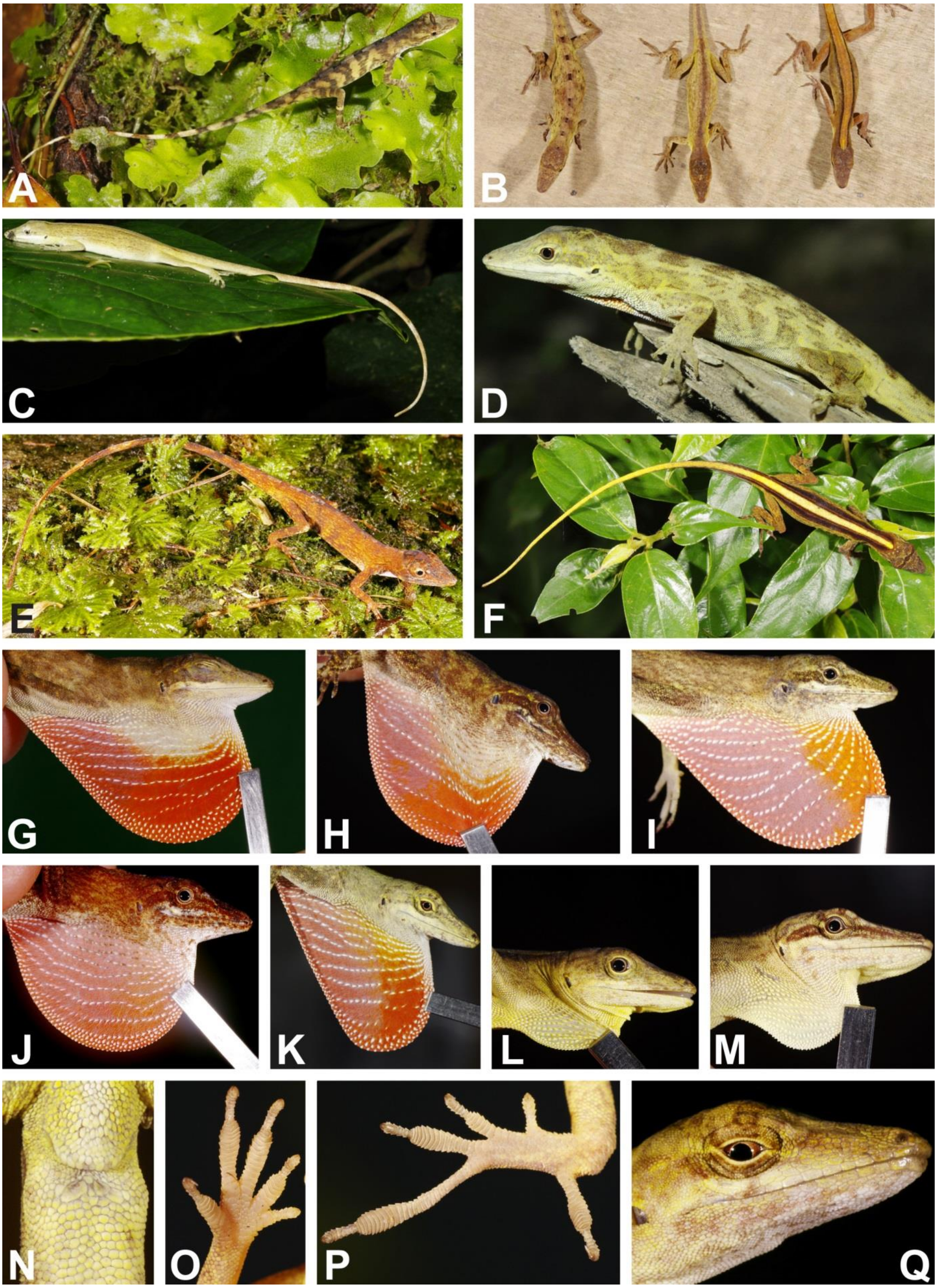


Figure 4.48: Individuals of *Norops kemptoni* from Bocas del Toro and Chiriquí. (A) Male SMF 91480 from Río Changena; (B) three female (SMF 89483, uncollected, SMF 89484) examples for body pattern variation from Jurutungo; (C) female MHCH 2188 in sleeping position and (D) male MHCH 2192 from Sendero La Cascada; (E) male SMF 89466 and (F) female SMF 91457 from RFLF; (G–K) male dewlaps: (G) SMF 89485 from Jurutungo, (H) SMF 90112 from Potrerillos Arriba, (I) SMF 89716 from Sendero La Cascada, (J) SMF 89466, (K) SMF 89705 from RFLF; (L–M) female dewlaps: (L) SMF 91479 from Río Changena, (M) SMF 89720 from Jurutungo; (N) enlarged postcloacal scales of SMF 89705; ventral views of (O) right hand and (P) right foot of SMF 91481 from Changena trail; (Q) lateral view of head of female SMF 89462 from La Fortuna.

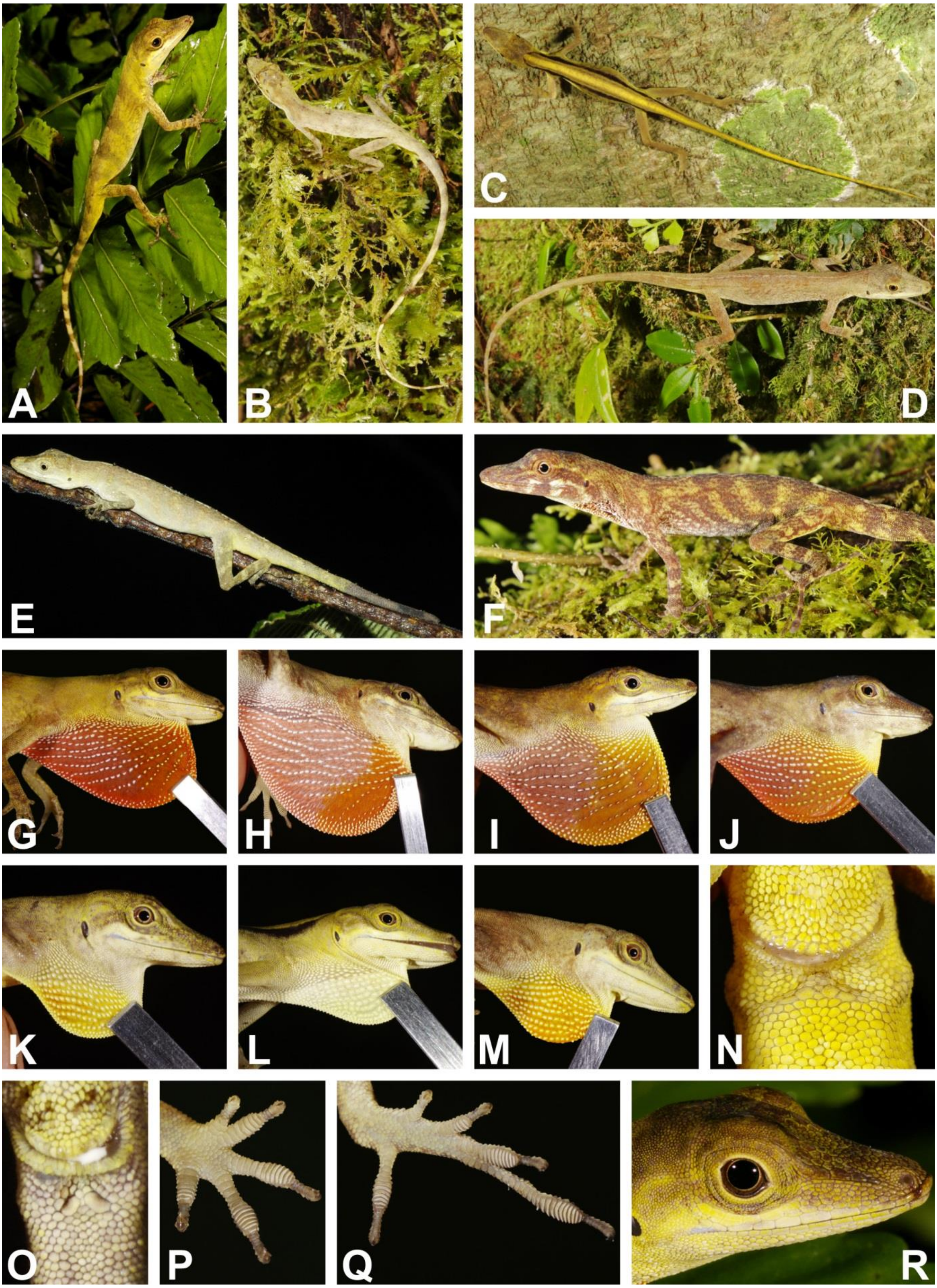


Figure 4.49: Individuals of *Norops pseudokemptoni* from the Comarca Ngöbe-Buglé. (A) Young male SMF 89515 and (B) female SMF 90154 from La Nevera; (C) female SMF 91519 from Terminal de Hacha; (D) female SMF 89750 from above Río Rey; (E) male SMF 90156 from La Nevera in sleeping position and (F) the next day; (G)–(J) male dewlaps: (G) SMF 89515; (H) SMF 90156; (I) MHCH 2271 from Río Flor; (J) SMF 91516 from Cerro Saguí; (K)–(M) female dewlaps: (K) SMF 90154; (L) SMF 91519; (M) SMF 89750; (N)–(O) cloacal region showing enlarged postcloacal scales of (N) adult male SMF 90156 with swollen base of tail, and (O) juvenile male MHCH 2267; (P) left hand and (Q) left foot of MHCH 2268 in ventral view; (R) lateral view of head of SMF 89515. Modified from Lotzkat et al. (2014).

Table 4.12: Selected measurements, proportions, and scale characters of *Norops fortunensis, N. gruuo, N. kemptoni,* and *N. pseudokemptoni.* Modified from Gutpelet (2012) and Lotzkat et al. (2012c, 2014).

		Norops fortunensis	***N. gruuo***	***N. kemptoni***	***N. pseudokemptoni***
		♂ 3 **♀ 2**	**♂ 10** **♀ 13**	**♂ 39** **♀ 50**	**♂ 11** **♀ 11**
SVL	♂	40–45 (42.3 ± 2.52)	38–52 (44.9 ± 3.7)	32–54 (45.8 ± 6.4)	25–54.5 (43.6 ± 9.6)
	♀	42–50 (46.0 ± 5.7)	36–51 (45.6 ± 5.3)	30–57 (47.9 ± 6.5)	39–55 (45.5 ± 6.2)
TL / SVL	♂	1.67–1.83 (1.75 ± 0.12)	1.60–1.79 (1.67 ± 0.07)	1.69–2.25 (1.96 ± 0.13)	1.80–1.98 (1.89 ± 0.07)
	♀	no intact tails	1.46–1.75 (1.65 ± 0.10)	1.61–2.25 (1.95 ± 0.15)	1.64–1.91 (1.77 ± 0.09)
verDT / horDT	♂	1.27–1.37 (1.33 ± 0.05)	1.15–1.41 (1.25 ± 0.09)	1.12–1.47 (1.26 ± 0.09)	1.08–1.33 (1.21 ± 0.09)
	♀	1.28–1.32 (1.30 ± 0.02)	1.07–1.29 (1.19 ± 0.07)	1.0–1.41 (1.24 ± 0.09)	1.08–1.29 (1.16 ± 0.07)
HL / SVL	♂	0.26–0.27 (0.26 ± 0)	0.25–0.27 (0.26 ± 0.01)	0.25–0.30 (0.27 ± 0.01)	0.26–0.28 (0.26 ± 0.01)
	♀	0.25–0.28 (0.26 ± 0.02)	0.24–0.28 (0.26 ± 0.01)	0.24–0.28 (0.26 ± 0.01)	0.23–0.27 (0.25 ± 0.01)
HL / HW	♂	1.78–1.88 (1.83 ± 0.05)	1.61–1.89 (1.71 ± 0.08)	1.61–1.99 (1.77 ± 0.08)	1.52–1.86 (1.75 ± 0.11)
	♀	1.6–1.89 (1.75 ± 0.20)	1.59–1.77 (1.65 ± 0.06)	1.55–1.87 (1.75 ± 0.07)	1.69–1.86 (1.75 ± 0.04)
SnL / SVL	♂	0.12–0.14 (0.13 ± 0.01)	0.11–0.13 (0.12 ± 0.01)	0.11–0.16 (0.13 ± 0.01)	0.12–0.13 (0.12 ± 0.00)
	♀	0.13–0.14 (0.13 ± 0.01)	0.11–0.13 (0.12 ± 0.01)	0.11–0.14 (0.13 ± 0.01)	0.10–0.13 (0.12 ± 0.01)
Shank length / SVL	♂	0.21–0.24 (0.23 ± 0.02)	0.21–0.25 (0.23 ± 0.01)	0.20–0.25 (0.22 ± 0.01)	0.21–0.23 (0.22 ± 0.01)
	♀	0.23–0.26 (0.24 ± 0.02)	0.18–0.25 (0.21 ± 0.02)	0.19–0.24 (0.21 ± 0.01)	0.20–0.23 (0.21 ± 0.01)
AGD / SVL	♂	0.42–0.47 (0.44 ± 0.03)	0.40–0.45 (0.43 ± 0.02)	0.38–0.49 (0.43 ± 0.02)	0.41–0.46 (0.43 ± 0.02)
	♀	0.45–0.45 (0.45 ± 0.01)	0.42–0.47 (0.44 ± 0.02)	0.39–0.49 (0.45 ± 0.02)	0.42–0.48 (0.45 ± 0.02)
Subdigital lamellae under phalanges II–IV of 4th toe		24–28 (25.2 ± 1.6)	20–28 (24.3 ± 2.0)	22–28 (25 ± 1.4)	23–28 (25.8 ± 1.5)
Number of scales between SS		1–2 (1.8 ± 0.4)	0–4 (1.2 ± 1.1)	0–3 (1.3 ± 0.7)	1–2 (1.5 ± 0.5)
Number of scales between IP and SS		2–3 (2.8 ± 0.4)	1–5 (2.8 ± 1.1)	1–4 (2.3 ± 0.7)	1–4 (2.8 ± 0.7)
Number of scales between SBO and SPL		0	0	0	0
Number of SPL to level below center of eye		6–9 (7.8 ± 1.3)	7–9 (7.9 ± 0.6)	6–9 (7.7 ± 0.9)	6–9 (7.3 ± 0.8)
Number of INL to level below center of eye		6–9 (8.0 ± 1.4)	6–9 (7.7 ± 0.9)	6–10 (7.7 ± 1.0)	7–9 (8.2 ± 0.9)
Total number of loreals		47–58 (51.4 ± 4.6)	28–73 (40.5 ± 10.5)	31–83 (51.4 ± 10.5)	56–100 (76.2 ± 12.5)
Number of horizontal loreal scale rows		5–7 (6.0 ± 0.7)	4–7 (5.0 ± 0.98)	4–8 (5.9 ± 0.7)	6–8 (7.1 ± 0.7)
Number of postrostrals		5–8 (6.6 ± 1.1)	6–10 (7.9 ± 1.3)	5–9 (6.4 ± 0.8)	7–10 (7.9 ± 1.0)
Number of postmentals		5–6 (5.8 ± 0.4)	5–8 (6.1 ± 0.5)	4–8 (6.0 ± 0.8)	4–8 (6.0 ± 1.1)
Number of scales between nasals		6–9 (7.6 ± 1.1)	6–9 (7.3 ± 0.7)	5–9 (7.0 ± 0.8)	6–9 (8.0 ± 0.8)
Number of scales between 2nd canthals		8–12 (10.6 ± 1.5)	7–13 (9.5 ± 1.7)	6–13 (8.3 ± 1.3)	8–12 (10.3 ± 1.1)
Number of scales between posterior canthals		10–15 (12.0 ± 1.9)	9–15 (11.1 ± 1.8)	7–14 (9.7 ± 1.6)	8–15 (11.7 ± 1.9)
Number of medial dorsal scales in one HL		48–56 (51.2 ± 3)	42–57 (48.9 ± 4.3)	34–70 (53.0 ± 6.8)	50–80 (60.37 ± 7.7)
Number of medial ventral scales in one HL		43–51 (48.4 ± 3.2)	37–48 (42.8 ± 3.4)	33–58 (44.8 ± 6.8)	35–61 (47.9 ± 6.5)
Number of scales around midbody		108–150 (129.6 ± 15.9)	110–144 (126.9 ± 8.7)	102–154 (127.2 ± 10.0)	114–148 (126.5 ± 8.5)
Number of dorsal scales between axilla and groin		88–120 (99.0 ± 13.0)	70–96 (81.5 ± 7.6)	63–110 (82.1 ± 11.0)	82–107 (94.2 ± 7.9)
Number of ventral scales between axilla and groin		69–83 (76.2 ± 6.3)	61–83 (70.3 ± 5.3)	51–86 (65.4 ± 7.8)	65–87 (72.9 ± 6.0)

4.1.6 Iguania, Dactyloidae: *Norops datzorum*, *N. salvini,* and related species

[In part modified from Bienentreu et al. (2013) who used the generic name *Anolis;* see Appendix 8 for original publication]

A third distinct cluster of *Norops* found along the Cordillera Central are the species closely related to *N. pentaprion.* These lizards differ markedly from the above analyzed *N. pachypus* and *N. kemptoni* complexes in having very short legs (adpressed hind limb at most reaching to the ear opening) and very short tails (TL/SVL < 1.5), combined with a black throat lining and blueish-grayish tissue at the corners of the mouth (Myers 1971b; Köhler 2010; Bienentreu et al. 2013). *Anolis pentaprion* was described by Cope (1862b) from "New Grenada, near the river Truando" (present day Colombia). Two decades later, Boulenger (1890) described *A. panamensis* from "Panama", that was later synonymized with *A. pentaprion* (Dunn 1930b). This action was confirmed by Myers (1971b) in his review of what he termed the *pentaprion* species group, which included a redefinition of *A. pentaprion* as well as the descriptions of *A. fungosus* from "Campo Mojica" on the northern slopes of Cerro Pando (loc. 3 in Map 1.13) and *A. vociferans* from near Cerro Punta on the western slopes of Volcán Barú (loc. 5 in Map 1.13). Köhler (2007) judged the holotype and several Panamanian specimens of the latter species to be conspecific with the holotype and only known specimen of *A. salvini,* a species that Boulenger (1885) had described from "Guatemala", pointed out probable mixups in locality data underlying Boulenger's original description, and accordingly declared *A. vociferans* a junior synonym of *A. salvini.* However, neither Sasa et al. (2010) nor Jaramillo et al. (2010) followed this decision and listed the species as *Anolis vociferans*. In the most recent taxonomic review of the *pentaprion* species group, Köhler (2010) provided an extensive review of relevant synonymies for the seven species he recognized throughout Central America, designated the specimen SMF 83608 as the neotype for *A. pentaprion,* and described the populations from the Pacific versants of Costa Rica and extreme western Panama as a new species, *A. charlesmyersi,* for which AH and myself had the honor of collecting the three type specimens. Most recently, Bienentreu et al. (2013) published new localities as well as morphological and acoustical data on *N. salvini.* In the following, I present a brief review of the *pentaprion*-like anoles inhabiting the Cordillera Central and adjacent lowlands, inspired by the new specimens and DNA barcodes that have become available after the review of Köhler (2010). Since *Norops datzorum* (Köhler, Ponce, Sunyer & Batista 2007) is revealed to be rather closely related to *N. salvini* in analyses of COI barcodes (Figs. 4.1 and 4.50), and is somewhat likely to be confused with *N. salvini* given their overall morphological similarities, I include it in the following analyses.

For the COI barcodes, the manually refined final alignment of 14 sequences (three *Norops datzorum* and two *N. salvini,* as well as the nine anoles already employed as outgroups in chapters 4.1.2, 4.1.4, and 4.1.5) contained 562 positions, of which, excluding the outgroups, 104 were variable and 84 parsimony-informative. For the 16S barcodes, the final alignment of 13 taxa (identical outgroups and five *N. salvini*) contained 546 positions, of which, excluding the outgroups, 23 were variable and 9 parsimony-informative. For both genes, T92+G was determined as the best-fitting substitution model. The alignments and distance matrices underlying the following results are provided in Appendix 5.6.

Figure 4.50 shows the results of the COI analyses. Apart from the by now well-known relationships among the outgroup representatives of the *kemptoni* and *pachypus* complexes, the respective clades *Norops datzorum* and *N. salvini* appear more closely related to each other than to any of the outgroups, separated by p-distances of 15.8–16.7%. The nominal taxon *N. datzorum* is further split in two lineages. The barcoded male from La Fortuna, the only representative of the western lineage 1, is differentiated by a p-distance of 4.8% from the specimen SL 250 collected at the type locality, and by 4.6% from the third specimen collected a little further east. The p-distance between these two representatives of the eastern lineage 2 is a mere 0.2%. While only one substitutional step lies between their respective haplotypes, 26 steps are required to connect them to the Fortuna specimen – two more than necessary to connect representatives of the two DCLs found in *N. gruuo,* and 2.6 times the connection limit calculated for a 95% parsimony probability in this PN analysis. Not surprisingly, the two sampled individuals of *N. salvini,* both from Cerro Saguí, are very closely related with a p-distance of 0.4%, and two steps in the PN analysis. As shown in Figure 4.51, the 16S barcodes reveal genetic differentiation between specimens of *N. salvini* that have been collected at different localities lying further apart. While two individuals from Cerro Saguí share the same 16S haplotype (lineage 3), they are separated by a p-distance of 3%, respectively, from the specimen representing the population at Jurutungo (lineage 1) and that caught at Cerro Altrillería (lineage 2). Similarly, 2.6% lie between the representatives of the latter two lineages. In the PN analysis, the connection limit of 10 steps calculated for a 95% parsimony probability leaves the respective two specimens of each *N. gruuo, N. kemptoni,* and *N. pachypus* connected. In *N. salvini,* 17 steps lie between the lineages 1 and 2 as well as between 2 and 3, and 18 steps will connect lineage 1 to lineage 3 – almost as much as needed to connect the deeply divergent DCLs of *N. pseudopachypus.*

In summary, similar to what is observable in the species complexes dealt with in the preceding sections, the two highland species *Norops datzorum* and *N. salvini* comprise discrete genealogical lineages lined up along the continental divide of western Panama.

However distinct, their divergence is within the range of that between clades classified as DCLs in preceding analyses. Moreover, I could not find any profound morphological distinctions between the three lineages of *N. salvini,* or (except that the HW/HL ratio assumes marginally higher values in specimens from Fortuna) the two lineages of *N. datzorum.*

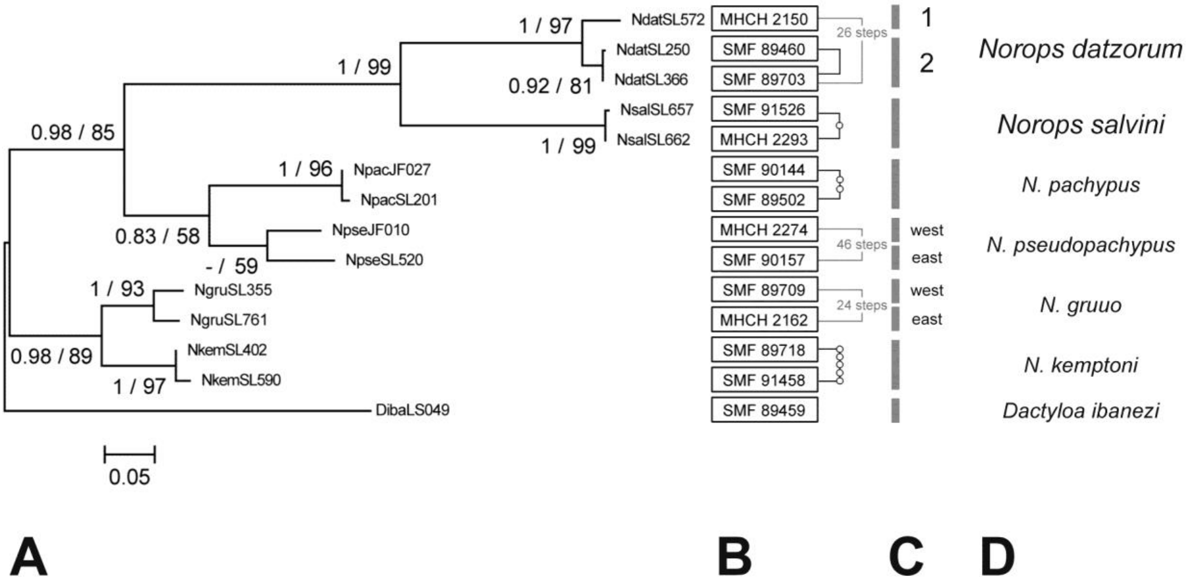


Figure 4.50: Results of COI analyses. (A) Consensus tree from ML analysis of COI barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the COI barcodes, numbered from west to east for *Norops datzorum.* (D) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding taxonomic analyses.

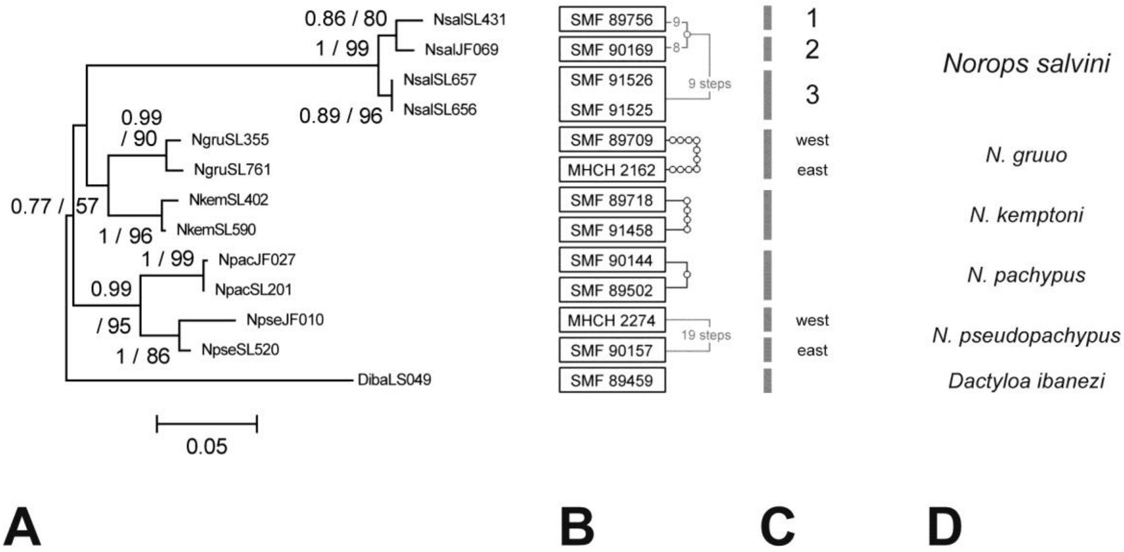
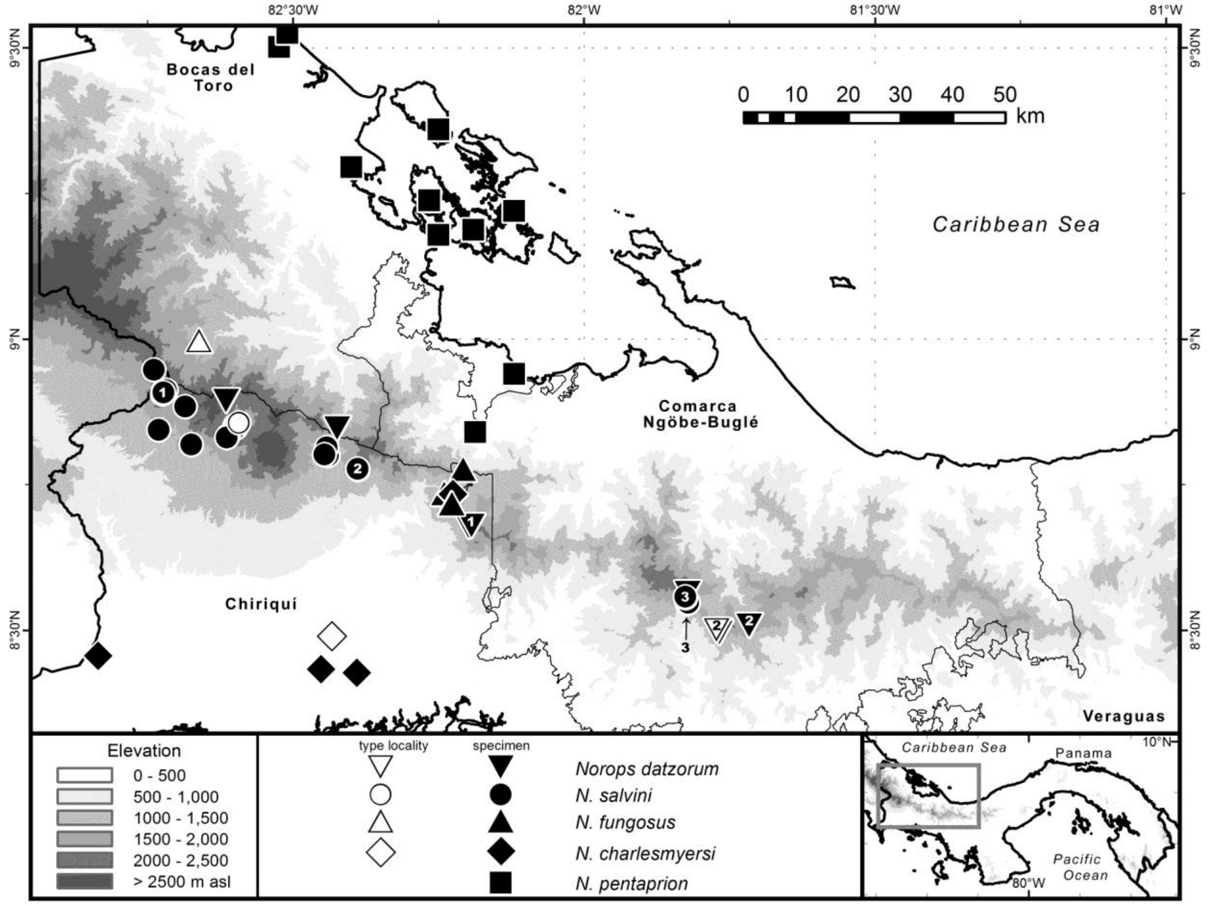


Figure 4.51: Results of 16S analyses. (A) Consensus tree from ML analysis; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the 16S barcodes, numbered from west to east for *Norops salvini.* (D) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding taxonomic analyses.

Figure 4.52 integrates the molecular results obtained for these two species with morphological key characteristics employed by Köhler (2010) to the *pentaprion* species group, adding those key characters for the remaining three species *N. fungosus, N. charlesmyersi,* and *N. pentaprion,* for which unfortunately no DNA sequences were obtained. Once again, the male dewlap is the paramount distinguishing feature that, without the aid of any other, allows to assign the proper name to a given male of this clade. In the case of the otherwise truely cryptic species pair *N. pentaprion* and *N. charlesmyersi,* the dewlap is the only characteristic allowing for a reliable species identification. Other than in the *N. kemptoni* complex, the hemipenes of these lizards are quite similar and bear little diagnostic value, having been described as bilobated for four species (Myers 1971b, Köhler 2010, Lotzkat et al. 2010a) and observed to be so for the remaining *N. salvini.* Apart from the male dewlap, the presence or absence of enlarged postcloacal scales in males and/or conspicuous serrated crests formed by the middorsal and/or ventral caudal scales help to identify these species, as well as other qualitative scalation characters such as the presence of enlarged middorsal rows, presence or absence of keeling on dorsals and ventrals, among others. Most conveniently, also the female dewlap can be regarded as a very reliable tool for species determination. Regardless of certain similarities to *N. salvini,* individuals of *N. datzorum* can immediately be distinguished from members of the *pentaprion* group by their always conspicuously multicarinate dorsal head scales, be they male or female, adult or juvenile, alive or preserved.

Based on morphology, *Norops datzorum* is considered a close relative of *N. cusuco, N. kreuzti,* and *N. laeviventris* (Köhler et al. 2007; Lotzkat et al. 2010a), from which it differs by its multicarinate dorsal head scales and in lacking wart-like protruding, whitish, enlarged scales interspersed between the otherwise homogeneous flank scales. I follow Savage (2002) and others in regarding the LCA *N. intermedius,* described by Peters (1863a: p. 143) based on an individual collected by Warszewicz in "Veragua", as a separate species rather than a synonym of *N. laeviventris* as seen by Köhler (2008). Mostly called by the former name, this species is known from many sites in central Costa Rica (Savage 2002). It was reported for the Boquete area by Slevin (1942) and listed for Panama by subsequent authors until Jaramillo et al. (2010). However, Slevin (1942: p. 464) noted that "the dewlap, in life, is a rich blood-orange", which would rule out the possibility that the underlying specimens CAS 79366–74 are representatives of *N. intermedius,* since that species is known to have a white dewlap (Taylor 1956; Savage 2002; Köhler 2008). Indeed, the CAS collection database (http://collections.calacademy.org/herp/) reveals that these specimens were re-identified as *Anolis vociferans* (= *N. salvini*) by Ernest E. Williams in 1989. Since Slevin's specimens are the only original records of *N. intermedius* known to me from Panama, I regard this taxon to be absent from the country. Regarding its type locality "Veragua", I must assume a simple mixup of locality and/or collector data in the original description (Peters 1863a). This does not seem too far-fetched considering that the same paper contains several anole descriptions based on material collected by C. Hoffmann in Costa Rica and others with clearly erroneous locality data (e.g., "Chili" for the Venezuelan endemic *Dactyloa tigrina*), as well as taking into account several cases of type specimens alledgedly collected by Warszewicz in Veragua but representing species that do not occur in or near Panama (Savage 1970: p. 279–281).



Map 4.10: Distribution of *Norops datzorum, N. salvini, N. fungosus, N. charlesmyersi,* and *N. pentaprion* in western Panama and immediately adjacent eastern Costa Rica. Based on specimens examined by Köhler (2007, 2010), Bienentreu et al. (2013), and myself, as well as the type series of *N. vociferans* as reported by Myers (1971b). Collection localities of barcoded specimens bear the number of the corresponding DCL.

An overview of the variability which colleagues and myself have found within the five species in western Panama is provided in Figures 4.53–4.57. More illustrations of external morphology have been published by Myers (1971b), Köhler (2007, 2010), and Köhler et al. (2007). Color plates were provided for *N. datzorum* by Köhler & Vargas (2010) and Lotzkat et al. (2010a), and for *N. salvini* by Bienentreu et al. (2013). Table 4.13 summarizes selected morphometric and pholidotic characters for specimens collected in western Panama. Likewise, Map 4.10 provides an overview of the distribution of the five species in and around my study area. For more information, see the species accounts in chapter 4.2.2.

Table 4.13: Selected measurements, proportions, and scale characters of *Norops datzorum, N. salvini, N. fungosus, N. charlesmyersi,* and *N. pentaprion.* Based exclusively on Panamanian specimens examined by Köhler (2010), Köhler et al. (2007), Bienentreu et al. (2013), and myself.

		Norops datzorum	***N. salvini***	***N. fungosus***	***N. charlesmyersi***	***N. pentaprion***
		♂ 6 **♀ 10**	**♂ 12** **♀ 16**	**♂ 2** **♀ 0**	**♂ 6** **♀ 5**	**♂ 6** **♀ 4**
SVL	♂	21–47 (39.3 ± 10.4)	36–61 (52.7 ± 6.3)	47–49	40–65 (54.2 ± 11.8)	41–65 (55.2 ± 10.6)
	♀	42–52 (47.0 ± 2.8)	33–66 (55.6 ± 7.6)		48–55 (51.8 ± 3.3)	49–59 (53.3 ± 4.7)
TL / SVL	♂	1.53–1.83 (1.67 ± 0.11)	1.22–1.45 (1.31 ± 0.07)	1.12–1.19	1.24–1.43 (1.33 ± 0.09)	1.17–1.31 (1.24 ± 0.05)
	♀	1.39–1.73 (1.61 ± 0.12)	1.12–1.37 (1.24 ± 0.07)		1.32–1.36 (1.34 ± 0.02)	1.21–1.25 (1.23 ± 0.02)
verDT / horDT	♂	1.13–1.61 (1.28 ± 0.17)	1.10–1.46 (1.30 ± 0.13)	1.05	1.10–1.42 (1.22 ± 0.12)	1.07–1.40 (1.20 ± 0.14)
	♀	1.10–1.38 (1.23 ± 0.09)	1.04–1.50 (1.29 ± 0.13)		0.75–1.25 (1.06 ± 0.22)	0.92–1.11 (1.04 ± 0.09)
HL / SVL	♂	0.27–0.31 (0.29 ± 0.01)	0.25–0.27 (0.26 ± 0.01)	0.26–0.26	0.26–0.27 (0.27 ± 0.00)	0.25–0.27 (0.26 ± 0.01)
	♀	0.25–0.28 (0.27 ± 0.01)	0.24–0.27 (0.26 ± 0.01)		0.24–0.28 (0.26 ± 0.02)	0.26–0.27 (0.26 ± 0.00)
HL / HW	♂	1.37–1.62 (1.49 ± 0.08)	1.38–1.59 (1.48 ± 0.06)	1.83–1.88	1.51–1.73 (1.65 ± 0.08)	1.55–1.73 (1.61 ± 0.08)
	♀	1.41–1.68 (1.55 ± 0.08)	1.38–1.62 (1.51 ± 0.06)		1.56–1.72 (1.64 ± 0.06)	1.52–1.68 (1.62 ± 0.07)
Shank length / SVL	♂	0.19–0.24 (0.21 ± 0.02)	0.15–0.19 (0.18 ± 0.01)	0.14–0.17	0.14–0.21 (0.19 ± 0.03)	0.16–0.20 (0.18 ± 0.02)
	♀	0.19–0.23 (0.2 ± 0.01)	0.16–0.19 (0.17 ± 0.01)		0.17–0.20 (0.19 ± 0.01)	0.16–0.20 (0.18 ± 0.01)
AGD / SVL	♂	0.41–0.44 (0.43 ± 0.01)	0.40–0.44 (0.42 ± 0.01)	0.47	0.35–0.43 (0.39 ± 0.02)	0.39–0.43 (0.41 ± 0.02)
	♀	0.40–0.46 (0.43 ± 0.02)	0.39–0.47 (0.43 ± 0.02)		0.38–0.44 (0.41 ± 0.02)	0.40–0.45 (0.42 ± 0.02)
Subdigital lamellae under phalanges II–IV of 4th toe		21–29 (25.3 ± 2.2)	25–34 (29.2 ± 2.0)	27	27–34 (30.7 ± 2.4)	29–32 (30.4 ± 1)
Number of scales between SS		0–2 (1.1 ± 0.8)	0–1 (0.5 ± 0.5)	2	0–1 (0.6 ± 0.5)	1–1 (1.0 ± 0.0)
Number of scales between IP and SS		1–3 (1.8 ± 0.6)	1–3 (1.6 ± 0.6)	1–2	0–3 (1.7 ± 0.9)	1–4 (2.3 ± 0.8)
Number of scales between SBO and SPL		0	0	0	0	0
Number of SPL to level below center of eye		6–8 (6.7 ± 0.6)	6–8 (7.0 ± 0.6)	7–8	7–11 (8.3 ± 1.3)	8–10 (8.8 ± 0.8)
Number of INL to level below center of eye		5–8 (6.6 ± 1.0)	5–8 (6.7 ± 0.7)	7–9	6–10 (8.2 ± 1.1)	8–10 (8.8 ± 0.8)
Total number of loreals		28–53 (39.4 ± 7.3)	12–39 (21.1 ± 5.9)	16–19	18–46 (26.1 ± 8.2)	17–32 (24.3 ± 4.6)
Number of horizontal loreal scale rows		4–7 (5.4 ± 0.7)	2–4 (2.9 ± 0.5)	3	3–5 (4.0 ± 0.8)	3–4 (3.7 ± 0.5)
Number of postrostrals		4–9 (5.9 ± 1.1)	5–9 (6.3 ± 1.1)	3–5	5–10 (6.9 ± 1.6)	6–7 (6.8 ± 0.5)
Number of postmentals		4–8 (5.8 ± 1.1)	4–9 (5.9 ± 1.7)	5	5–6 (5.9 ± 0.3)	6–6 (6.0 ± 0.0)
Number of scales between nasals		6–10 (7.9 ± 1.0)	5–7 (5.8 ± 0.7)	5	5–9 (7.2 ± 1.2)	5–8 (6.6 ± 1.1)
Number of scales between 2nd canthals		5–9 (7.4 ± 1.0)	4–7 (5.7 ± 0.9)	8	5–9 (6.7 ± 1.2)	7–9 (7.8 ± 1.0)
Number of scales between posterior canthals		6–12 (8.0 ± 1.6)	5–9 (7.1 ± 1.1)	7–8	7–12 (8.7 ± 1.6)	7–15 (9.6 ± 2.2)
Number of medial dorsal scales in one HL		36–58 (49.1 ± 6.0)	20–46 (37.4 ± 5.3)	52–58	44–70 (57.3 ± 7.5)	50–66 (58.4 ± 5.3)
Number of medial ventral scales in one HL		32–60 (45.1 ± 7.2)	20–58 (44.8 ± 7.2)	40–44	46–60 (52.0 ± 5.7)	36–58 (47.8 ± 7.0)
Number of scales around midbody		106–160 (133.4 ± 13.1)	106–142 (125.4 ± 9.4)	116	136–178 (162.2 ± 12.7)	134–164 (153.1 ± 11.4)
Number of dorsal scales between axilla and groin		60–94 (75.5 ± 9.4)	45–82 (64.6 ± 8.3)	92	66–102 (91.1 ± 10.0)	82–114 (94.2 ± 10.5)
Number of ventral scales between axilla and groin		52–81 (64.9 ± 8.3)	60–87 (71.3 ± 7.3)	77	66–96 (77.8 ± 10.1)	65–82 (72.0 ± 6.0)

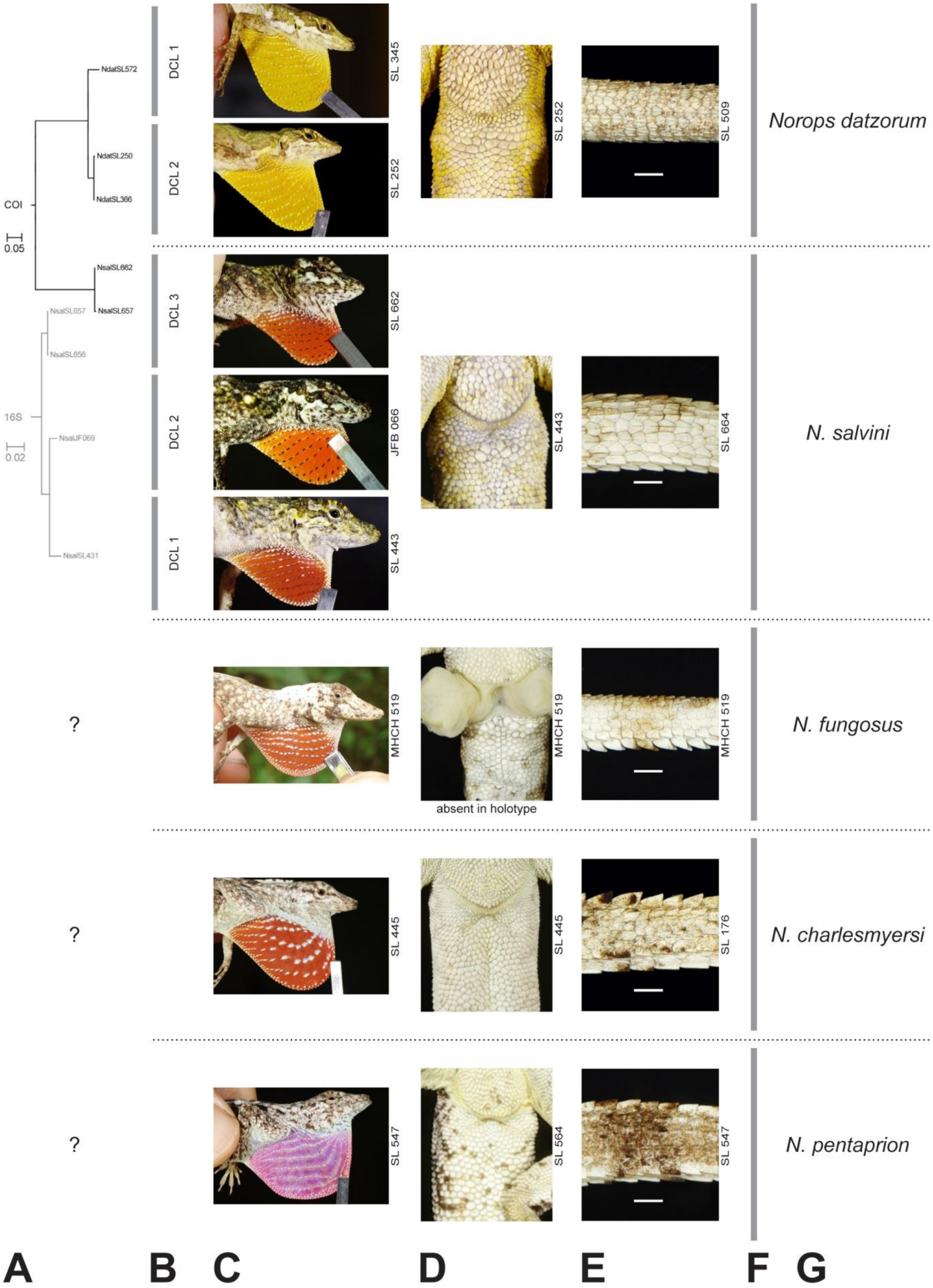


Figure 4.52: Integration of molecular results and morphological key features for *Norops datzorum, N. salvini,* and related species. (A) Details from Figures 4.50 and 4.51. (B) Lineages diagnosable through barcoding. (C) Dewlaps of collected males labelled with field numbers; photo of JFB specimen by JFB. (D) Presence or absence of enlarged postcloacal scales in males. (E) Presence or absence of a serrated middorsal and/or ventral caudal crest; scale bars equal 1 mm. (F) Lineages diagnosable with these three morphological key features. (G) Taxonomic identity of inferred CGLs.

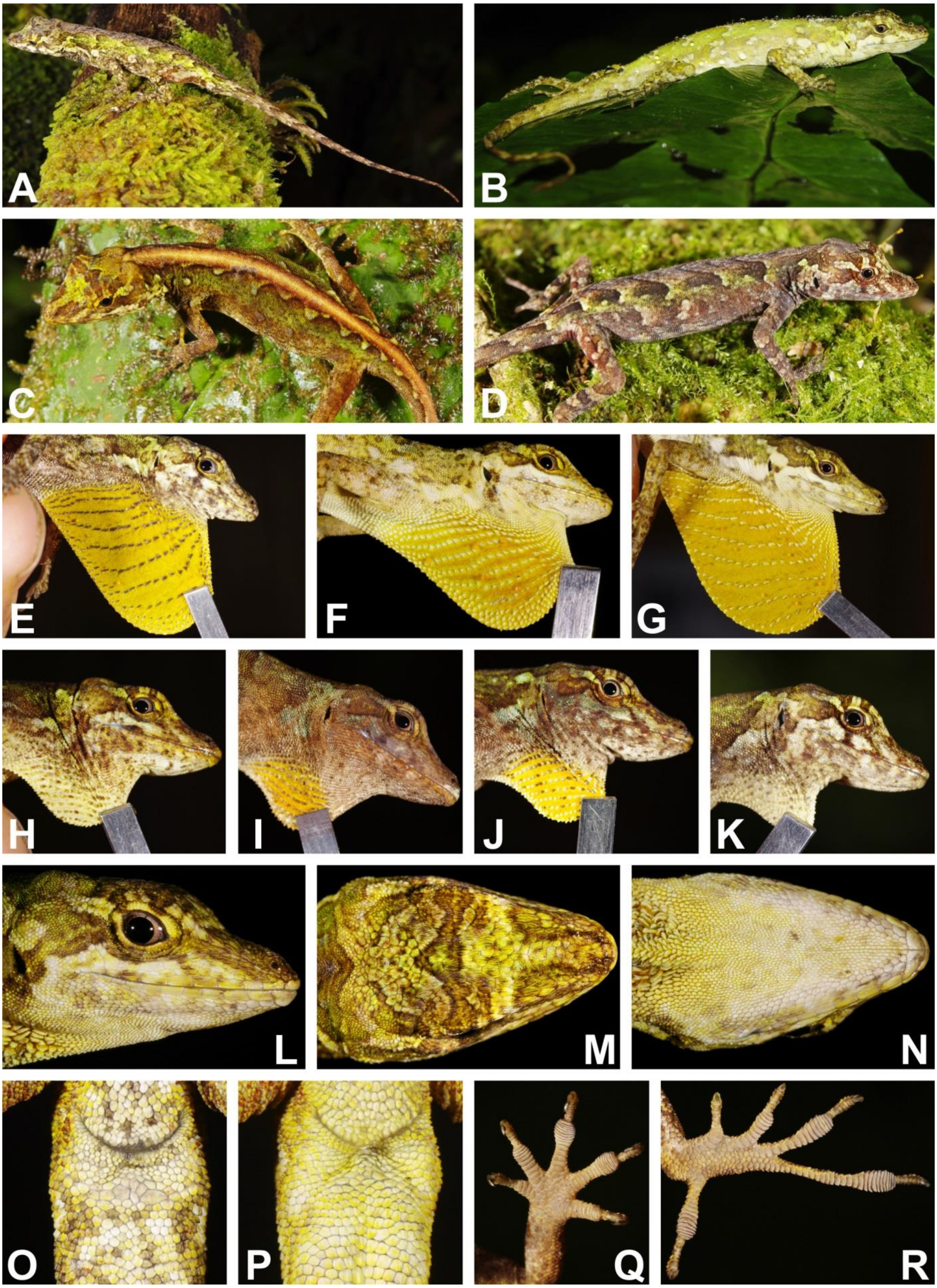


Figure 4.53: Individuals of *Norops datzorum.* (A) Adult male SMF 90101, (B) adult female MHCH 2149, and (C) adult female SMF 90100 from near the type locality at La Nevera; (D) adult female SMF 89703 from above Río Rey; (E–G) male dewlaps: (E) SMF 90101, (F) subadult SMF 89460 from La Nevera, and (G) adult SMF 89704 from La Fortuna; (H–K) female dewlaps: (H) SMF 90100, (I) SMF 90100 and (J) MHCH 2150 from La Fortuna, (K) SMF 89703; (L) lateral, (M) dorsal, and (N) ventral view of adult male SMF 89461 from La Nevera; (O) well-enlarged postcloacal scales of SMF 90101; (P) only slightly enlarged postcloacal scales of SMF 89704; ventral views of (Q) left hand and (R) left foot of female SMF 91456 from Cerro Saguí.

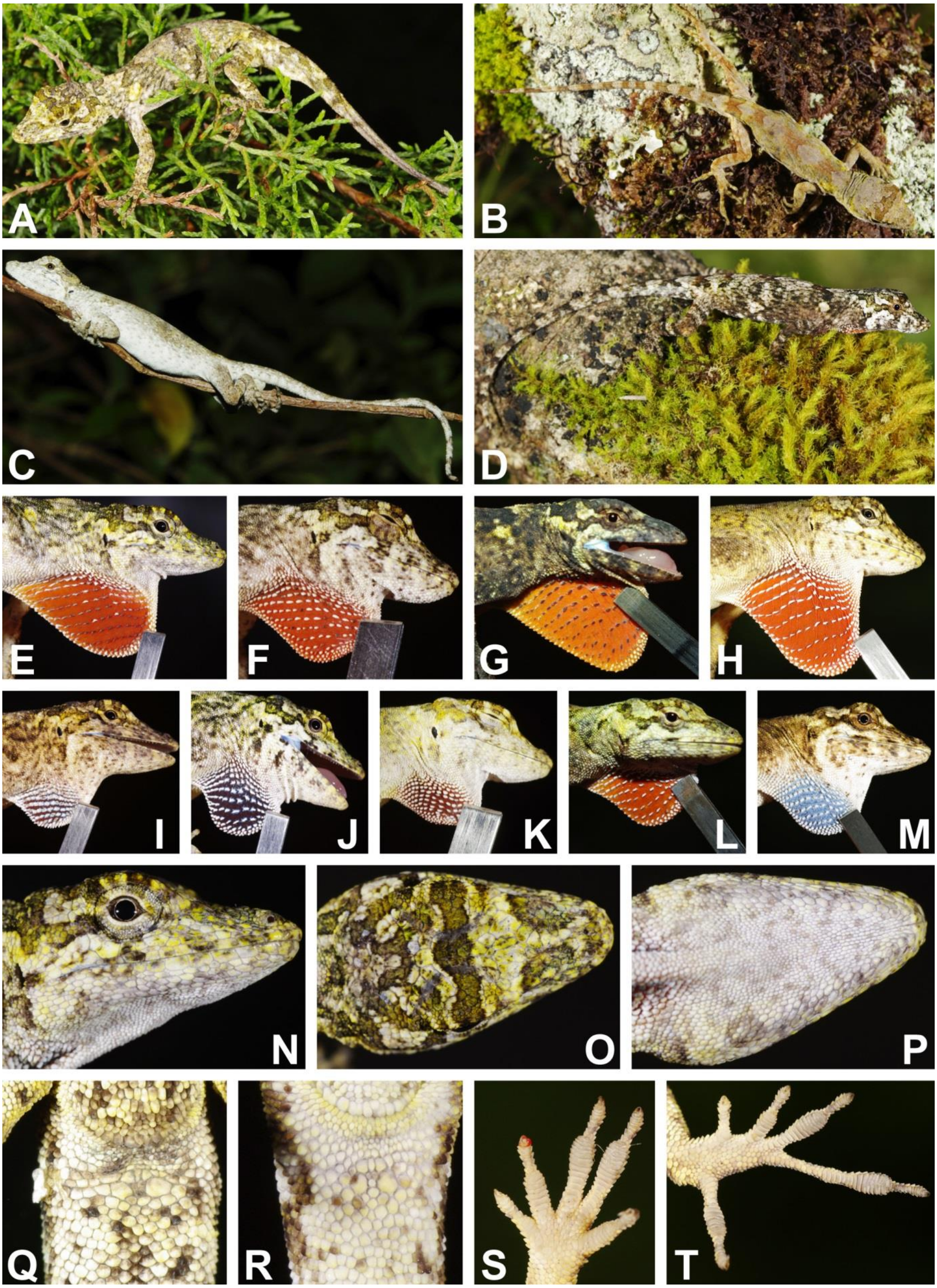


Figure 4.54: Individuals of *Norops salvini.* (A) Adult male SMF 89758 and (B) young female SMF 89757 from Jurutungo; (C) young male SMF 89756 from Jurutungo in sleeping position and (D) the next day; (E–H) male dewlaps: (E) SMF 89758, (F) SMF 89756, (G) MHCH 2287 from Cerro Altrillería, (H) SMF 91526 from Cerro Saguí; (I–M) female dewlaps: (I) SMF 89755, (J) MHCH 2291, and (K) SMF 89757 from Jurutungo, (L) SMF 90167 from Cerro Altrillería, and (M) SMF 91527 from Cerro Saguí; (N) lateral, (O) dorsal, and (P) ventral view of SMF 89758; enlarged postcloacal scales of (Q) MHCH 2293 from Cerro Saguí and (R) SMF 89756; ventral views of (S) left hand and (T) left foot of SMF 91525 from Ratón. Photos (G) and (L) by JFB. In part modified from Bienentreu et al. (2013).

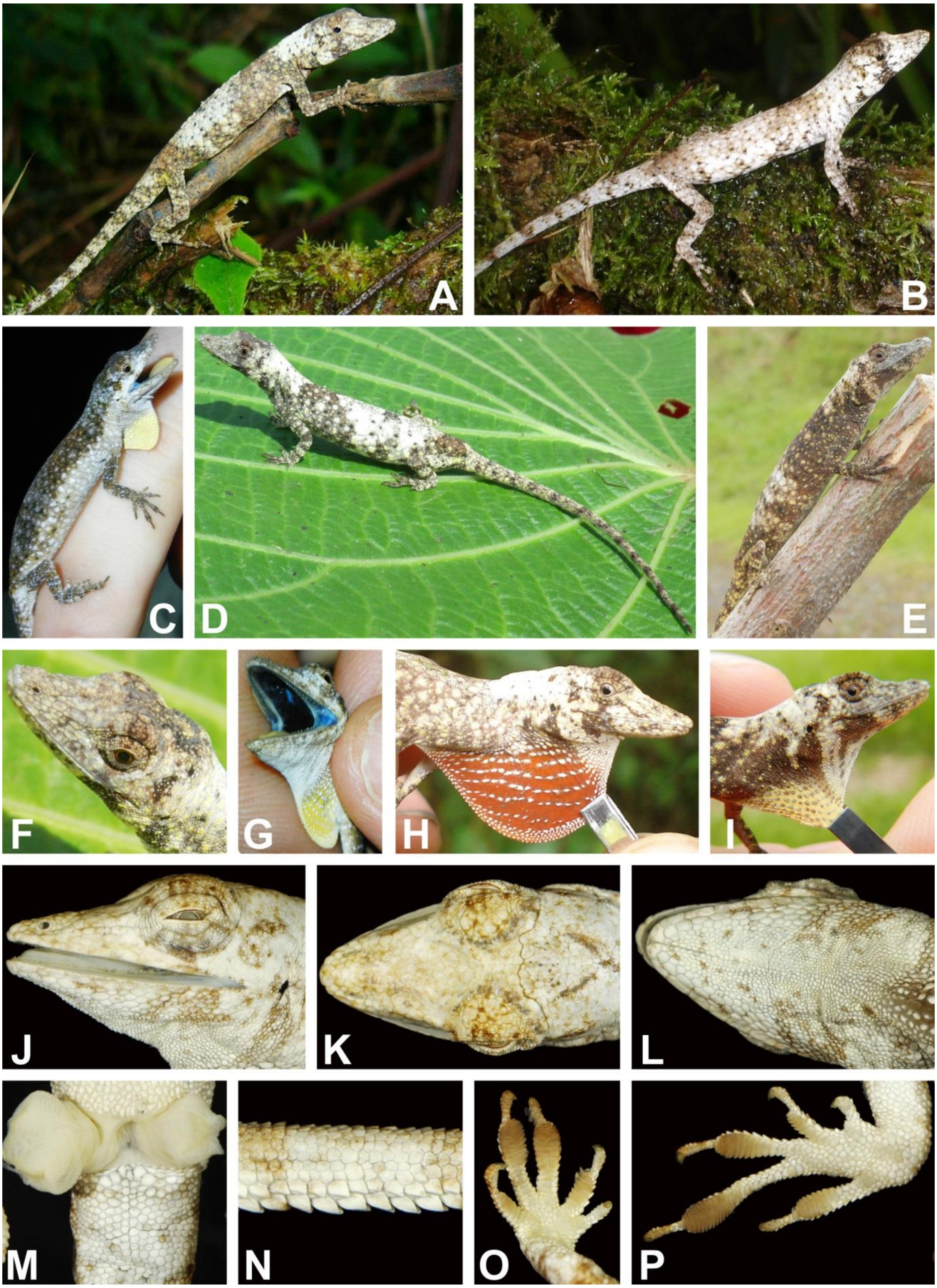


Figure 4.55: Individuals of *Norops fungosus* from La Fortuna. (A) Male SMF 86385; (B) female MHCH 509; (C–G) female MVUP 2095 in life: (C) when caught at night, (D–E) the next day at different stages of metachrosis, (F) detail of head with dark-rubbed parietal protuberances, (G) black mouth and throat lining and blue tissue in corners of mouth and white dewlap scales; (H) male dewlap, SMF 86385; (I) female dewlap, MVUP 2095, now with dark scales; (J–N) details of SMF 86385 after 7 years in preservative: (J) lateral, (K) dorsal, and (L) ventral views of head; (M) enlarged postcloacal scales; (N) lateral view of tail; ventral views of (O) right hand and (P) right foot. Photos (A, B, H) by AB, (C, E–G, I) by David Laurencio, (D) by John Phillips.

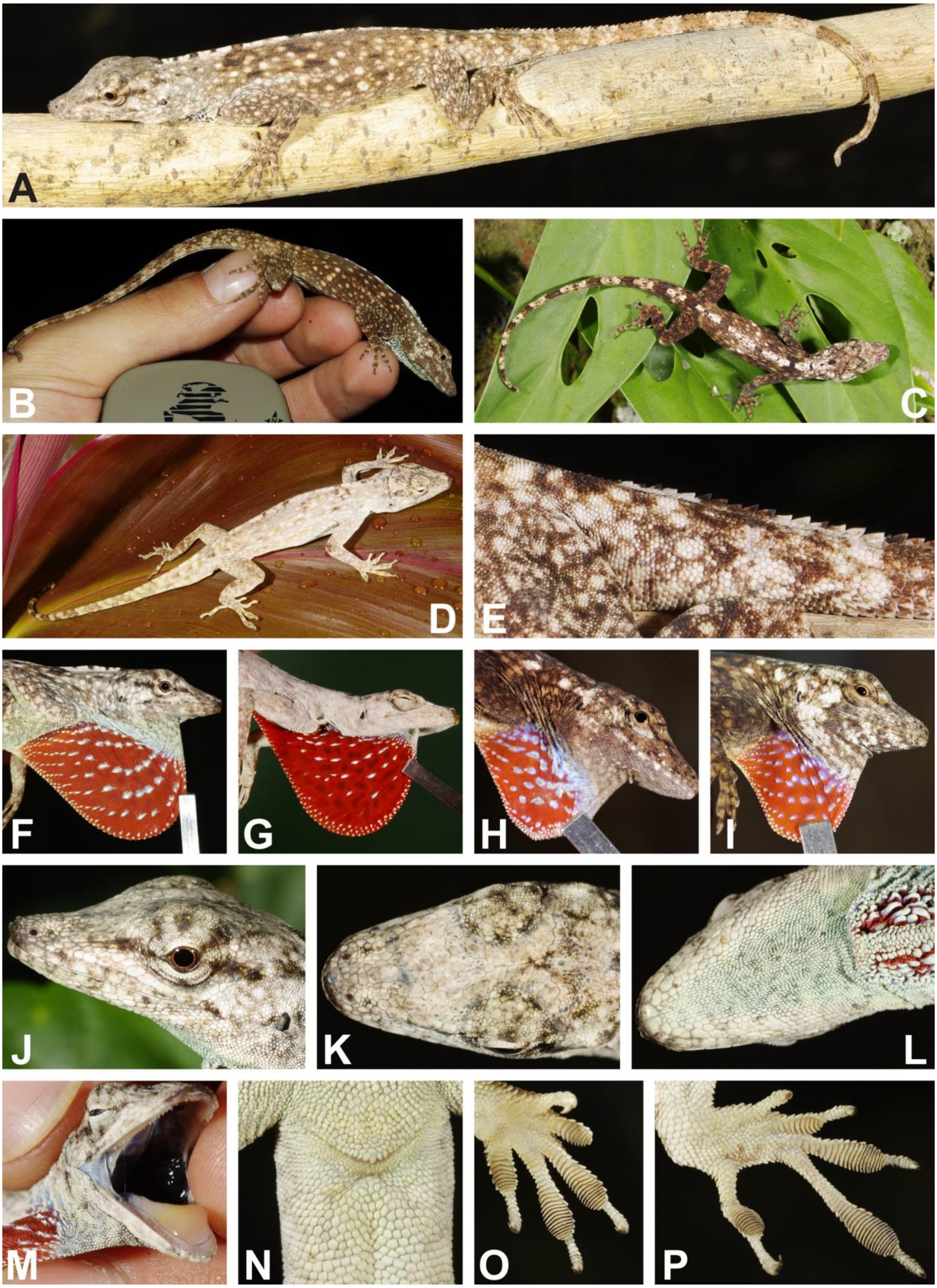


Figure 4.56: Individuals of *Norops charlesmyersi* from the type locality near Los Algarrobos, Chiriquí. (A) and (B) different stages of metachrosis in the adult male holotype SMF 89688; (C) juvenile MHCH 2138; (D) adult male paratype SMF 89508; (E) detail of base of tail of SMF 89688 showing serrated caudal crest; (F–I) dewlaps of (F) SMF 89688, (G) adult male paratype SMF 90053=MHCH 2137, (H) adult female SMF 90099, and (I) MHCH 2138; (J–P) details of SMF 89688: (J) lateral, (K) dorsal, and (L) ventral view of head; (M) black throat lining characteristic of the close relatives of *N. pentaprion;* (N) cloacal region without enlarged postcloacal scales; ventral views of (O) left hand and (P) left foot.

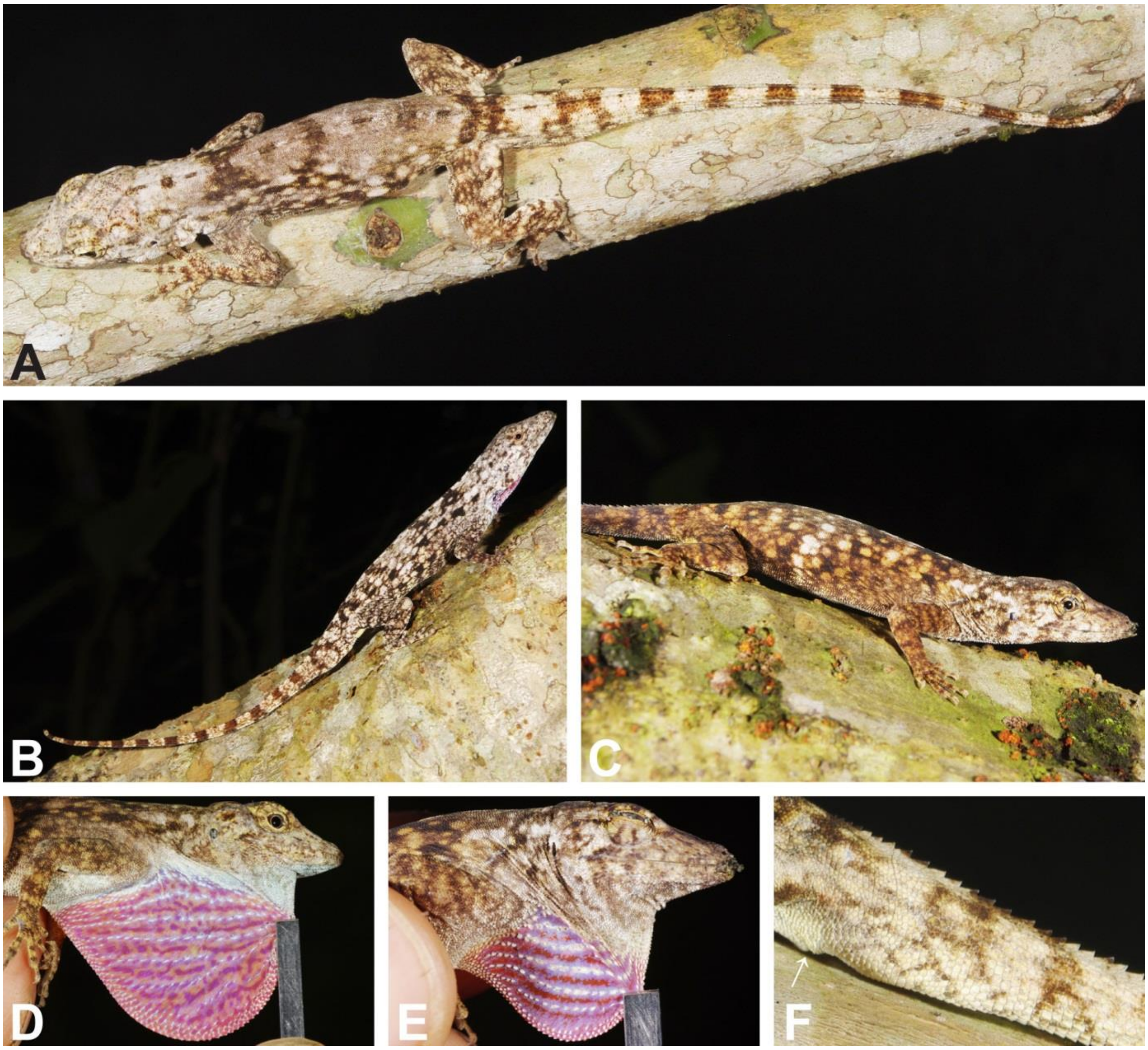


Figure 4.57: Individuals of *Norops pentaprion* from San San Pond Sak, Bocas del Toro. (A) Adult male MHCH 2254; (B) adult male SMF 90150; (C) adult female SMF 90151; (D) male dewlap of MHCH 2254; (E) female dewlap of SMF 90151; (F) detail of base of tail (arrow points to cloaca) of SMF 89688 showing serrated caudal crest.

4.1.7 Iguania, Dactyloidae: *Norops* lineages of primarily lowland distribution

In the preceding chapters 4.1.3–4.1.6, I have reviewed the taxonomy of all anole species known to be restricted in their vertical distribution along the Panamanian Cordillera Central to premontane and/or montane elevations. In the case of *Dactyloa* and the *Norops pentaprion* group, for the sake of completeness, I have included closely related species that also dwell at premontane elevations but have their primordial distribution in the lowlands. In the following five sections of this chapter, I briefly compare the results of my DNA barcoding with the current taxonomic arrangements of several clusters of *Norops* that are predominantly found in the lowlands of western Panama. Though some are revealed to reach higher in this study, most of these species do apparently not enter the montane life zones above approximately 1500 m asl. Since many of these "lowland lineages" are distributed way beyond Panama and comprehensive studies of their variation throughout their respective areals would require the examination of specimen numbers that by far exceed the scope of this study, the following reviews are kept shorter and result in less explicit taxonomies than the analyses presented above.

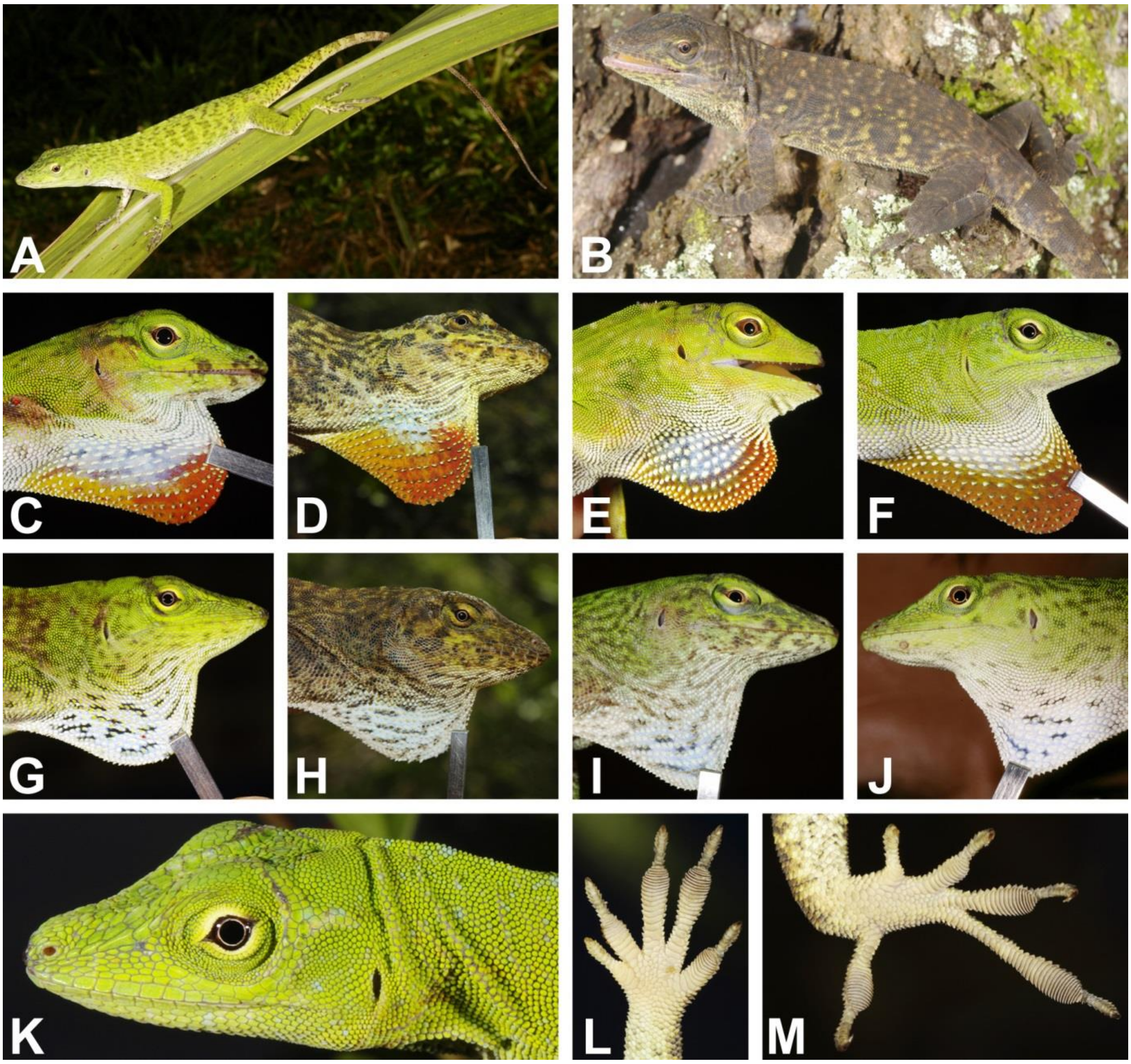


Figure 4.58: Individuals of *Norops biporcatus.* (A) Uncollected female from Los Algarrobos in green color phase; (B) adult male SMF 91447 from Guayabito in "angry" brown color phase; (C–F) male dewlaps: (D) SMF 89670 from Cerro Negro, (D) SMF 89669 from Buabidí, (E) young male SMF 91449 from Hacha, and (F) SMF 89671 from Los Algarrobos; (G–J) female dewlaps: (G) SMF 91446 from Alto Tólica, (H) MHCH 1321 from Buabidí, (I) MHCH 2111 from road to Almirante, and (J) uncollected female from Los Algarrobos; (K) head of SMF 89671; (L) left hand and (M) left foot of SMF 91447.

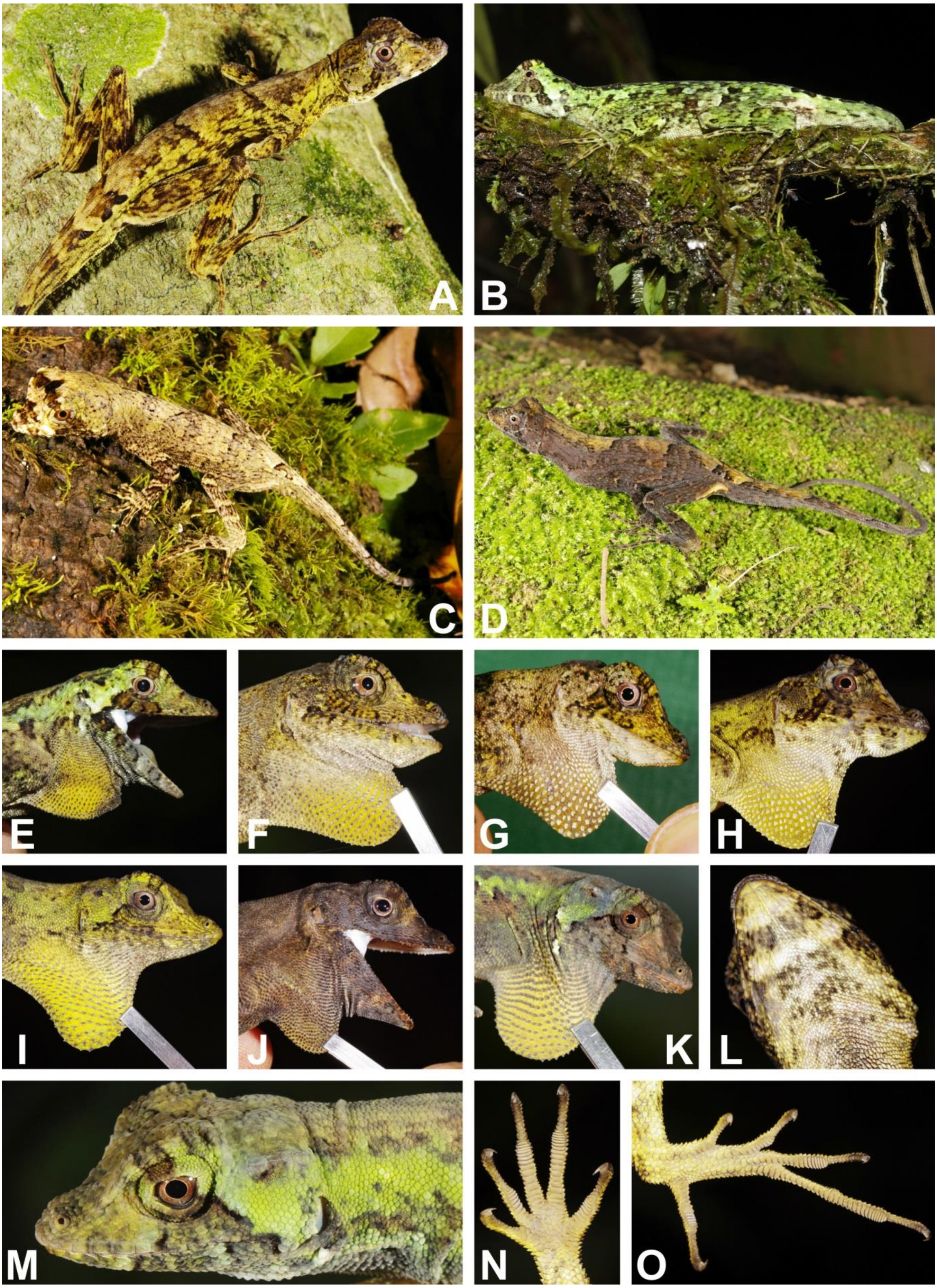


Figure 4.59: Individuals of *Norops capito.* (A) Adult male SMF 91451 from El Paredón; (B) male SMF 91450 from Changena trail in sleeping position; (C) juvenile SMF 89449 from La Fortuna; (D) male MHCH 2119 from La Fortuna; (E–I) male dewlaps: (E) SMF 91450, (F) SMF 90096 from headwaters of Río Chiriquí Malí, (G) SMF 89451 from La Fortuna, (H) SMF 91451, and (I) SMF 90097 from Potrerillos Arriba; (J–K) female dewlaps: (J) SMF 91452 from Changena trail and (K) MHCH 2117 from Potrerillos Arriba; (M) head of MHCH 2117; (N) left hand and (O) left foot of SMF 91451.

4.1.7.1 *Norops biporcatus* and *N. capito*

Two of the largest known species of *Norops* are distributed from Mexico south throughout Central America, and very easily identified: the short-legged, usually green *N. biporcatus* with well-dilated lamellar pads and the long-legged, usually brownish *N. capito* with narrow lamellar pads (Savage 2002; Köhler 2008). Although various populations of either species have been described as separate species in the past, both *N. biporcatus* and *N. capito* are currently regarded as single, wide-ranging species (Savage 2002; Köhler & Vesely 2003; Köhler et al. 2005; Köhler 2008). The morphological variation was described by Köhler & Vesely (2003) for the former species, and by Köhler et al. (2005) for the latter. I collected several specimens of both species, respectively, along both versants of the Cordillera Central. Analyzing the COI barcodes sequenced by the ColdCode project for some specimens of either species, I found certain individuals to be far less closely related to their nominal conspecifics than their external morphology would suggest. The manually refined final alignment of 19 sequences (three *N. biporcatus,* six *N. capito,* as well as one *N. aquaticus* and the nine anoles already employed as outgroups in the preceding chapters) contained 558 positions, of which, excluding the outgroups, 185 were variable and 131 parsimony-informative. T92+G+I was determined as the best-fitting substitution model. The alignments and distance matrices underlying the following results are provided in Appendix 5.7.

As shown in Figure 4.60, *Norops capito* is inferred to be more closely related to the *N. pachypus* and *N. kemptoni* complexes than to *N. aquaticus* and *N. biporcatus.* Five of the six sampled *N. capito,* collected over airline distances up to 175 km along the Caribbean slopes of the Serranía de Talamanca and the Pacific slopes of the Serranía de Tabasará (Map 4.11), appear closely related. Within their well-supported clade, henceforth called lineage 1, uncorrected p-distances range from 0.2–3.1%. In the PN analysis, the three individuals from the vicinities of the Fortuna dam are interconnected within the connection limit of 10 steps calculated for a 95% parsimony probability. Lowering the parsimony probability to 90% raises the connection limit to 14, within which the two vouchers from the western and eastern extremes are connected to each other and to the Fortuna specimens. The sixth individual of *N. capito,* from Potrerillos Arriba, is inferred as the sister taxon to the aforementioned clade. Despite the comparably short airline distance of about 33 km to the nearest Fortuna specimen, this only barcoded representative of lineage 2 is separated by p-distances of 11.7–13.3% from the representatives of lineage 1. According to the PN analysis, a minimum of 65 substitutional steps would be required to join it to the haplotype network of lineage 1. That is, the divergence in the COI barcode found within the nominal taxon *N. capito* is 34–77% higher than that found between the deeply divergent DCLs of *N. pseudopachypus,* for which individual p-distances of 7.5–9.4% have been calculated in chapter 4.1.4.1. From another point of view, the distance between *N. capito* lineages 1 and 2 is in the order of magnitude of those calculated from this alignment for the representatives of the species pairs *N. gruuo–N. kemptoni* (10.0–10.8%) and *N. pachypus–N. pseudopachypus* (12.0–13.8%).

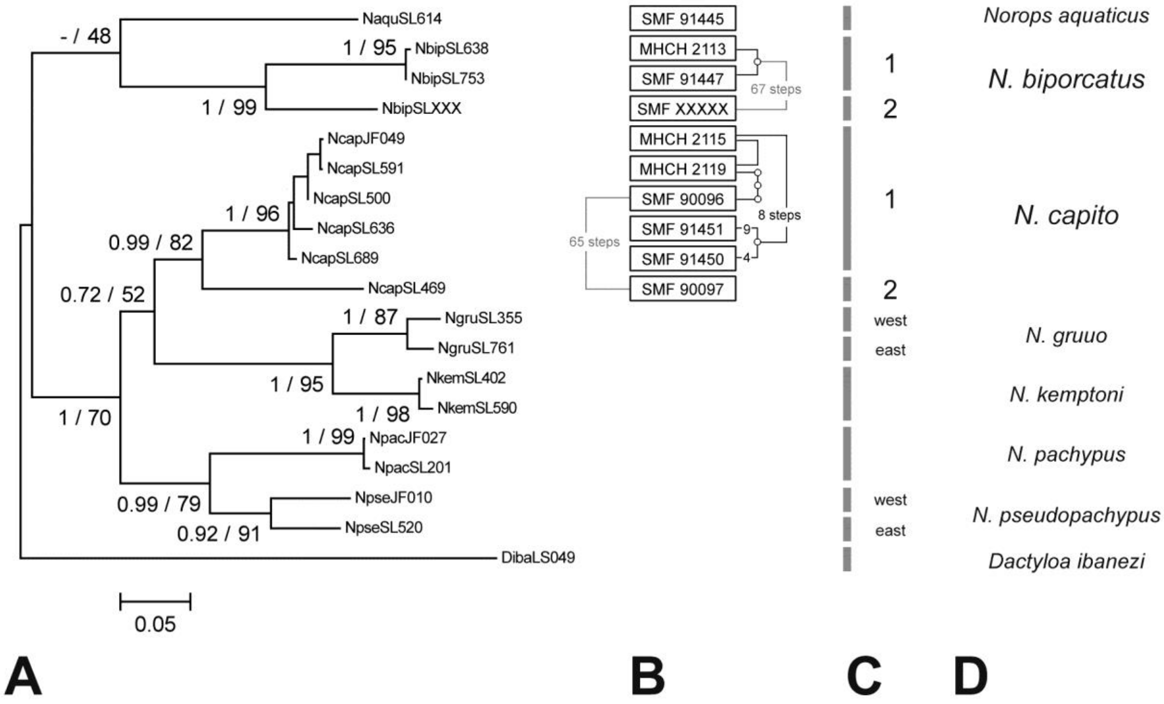
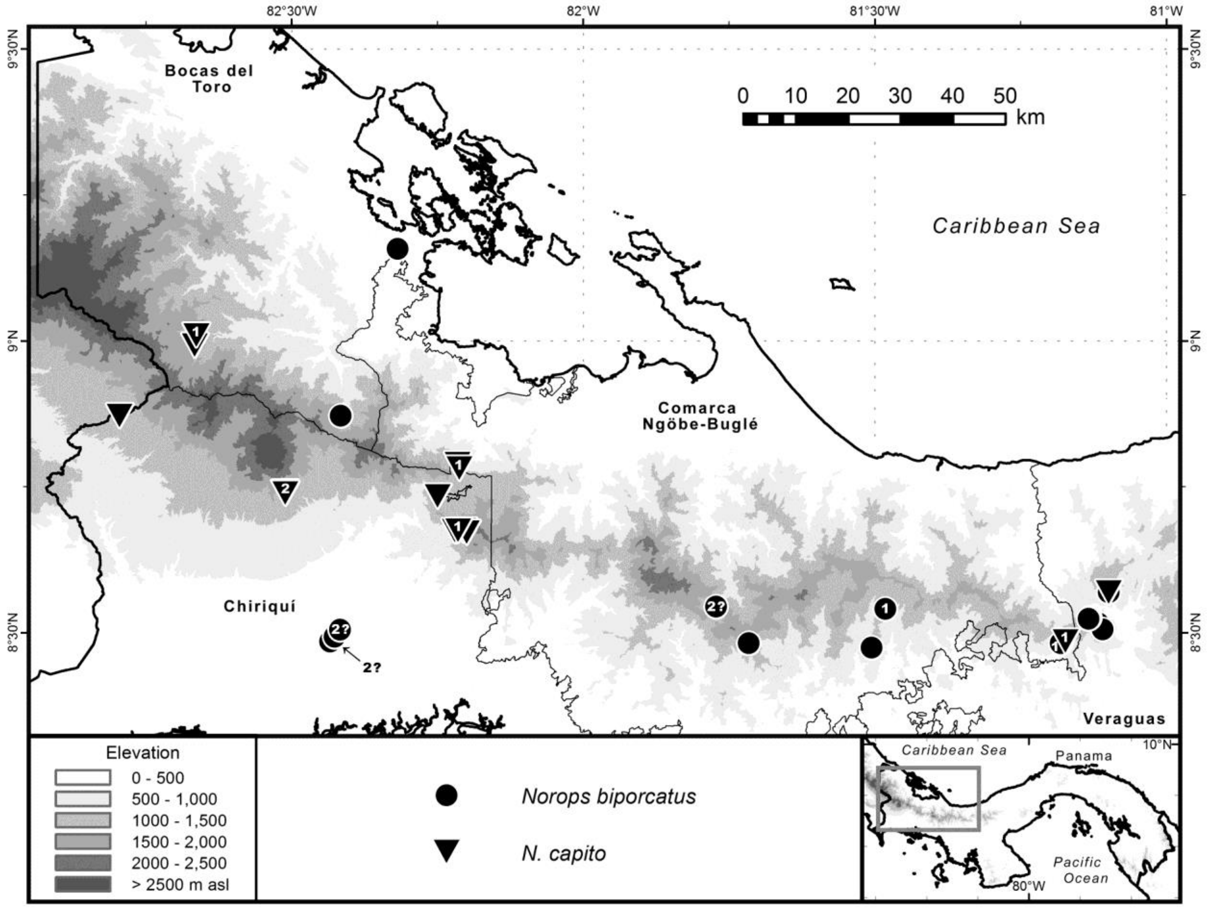


Figure 4.60: Results of COI analyses. (A) Consensus tree from ML analysis of COI barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the COI barcodes, numbered. (D) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding taxonomic analyses.

The sole barcoded *Norops aquaticus* and three *N. biporcatus* form the second principal species cluster in the ML tree above. A similar scenario as found in *N. capito* is revealed for *N. biporcatus,* within which two individuals from the Pacific slopes of the central and eastern Serranía de Tabasará are separated by just 0.4%, constituting lineage 1 within this nominal species. The third barcode represents lineage 2 at a p-distance of 12.4% to either specimen of lineage 1. In the PN analysis, two steps would connect the haplotypes of lineage 1, whereas 67 steps are required to connect this network to the haplotype of lineage 2. As with the two lineages revealed within *N. capito,* the divergence found between the two lineages of *N. biporcatus* is far more pronounced than any divergence found in the preceding chapters between lineages classified as DCLs, but rather in the range of those found between CGLs, or species. Most inconveniently, the provenance of the lineage 2 barcode is unknown, since the identity of the sequenced tissue sample is ambiguous. The most likely candidates for the sequence labelled herein NbipSLXXX are from Los Algarrobos (SL 175, 369).



Map 4.11: Examined specimens of *Norops biporcatus* and *N. capito* from western Panama. Collection sites of barcoded specimens bear the number of the corresponding lineage as defined in the text. Possible provenances of the single specimen of *N. biporcatus* lineage 2 with uncertain identity are marked with questionmarks.

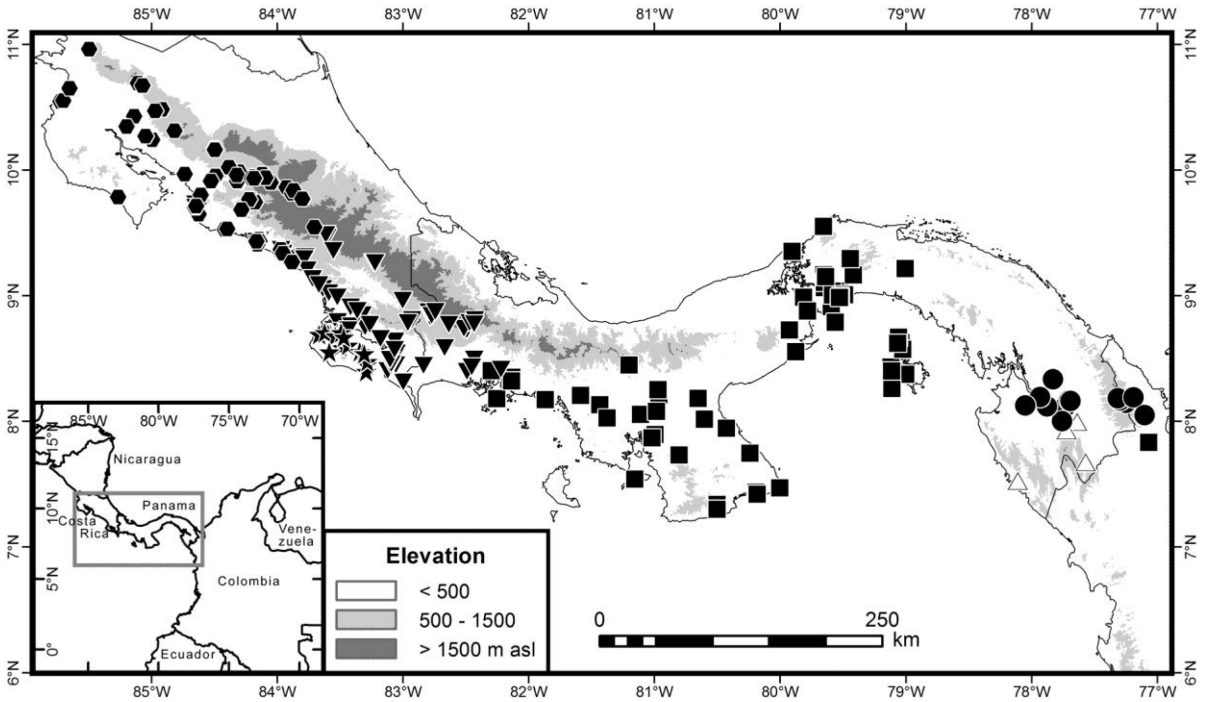
This assumption is somewhat supported by tentative morphological comparisons of the three *Norops biporcatus* collected around Los Algarrobos with all other morphologically examined specimens. The Los Algarrobos animals have, on average, lower or higher values in several scale counts (DHL, IP/SS, Canths, post Canths higher; PM lower) and body proportions (shank/SVL and HL/HW higher; SnL/HL and SnL/SVL lower) that often exceed the respective ranges exhibited in the other specimens. Yet, all of these characters still show overlaps between the lineages. However, since these preliminary comparisons are based on the merely assumed provenance of a COI barcode, and moreover the nominal species *N. biporcatus* is exceedingly widespread and has been collected in considerable numbers whereas my sample is very small, I classify the two lineages as UGLs pending further study.

For *Norops capito,* the case is slightly different. Adding the specimen SMF 85196 from near Río Sereno at the Costa Rican border to the two specimens caught at Potrerillos to make up the morphological sample of lineage 2, a tentative comparison with all other examined specimens that are referred to lineage 1 in view of their collection localities yields slightly more determined differences chiefly in pholidotic characters, though overlap remains in all cases. The lineage 2 specimens have on average higher values for 4toe and 4toepad. Their values are on average lower for 4toedist, post Canths, 2nd Canths, PM, PR, and SAM, as well as with minimal overlap for loreal rows and loreals. Especially the difference in loreal scale numbers (30–61, mean 45.5 ± 7.5 in lineage 1 vs. 27–33 in lineage 2) appears comparably clear-cut, presenting an overlap of only 3 scales caused by a single individual of lineage 1. Although the morphological differences between the two lineages of *N. capito* are more numerous and pronounced than those in *N. biporcatus,* I classify the two lineages as UGLs pending further study. Just as it is the case with *N. biporcatus,* the nominal taxon *N. capito* is very widespread and my samples of either lineage are small and geographically restricted. A sound taxonomical revision of the two respective lineages revealed herein would at least require material from all over Panama and Costa Rica, and is far beyond the scope of this study. For more information on the two species, see their respective species accounts in chapter 4.2.2, and Figures 4.58 and 4.59 for an outline of their morphological variation.

4.1.7.2 *Norops gaigei, N. tropidogaster,* and *N. polylepis*

[In part modified from Köhler et al. (2012b) who used the generic name *Anolis;* see Appendix 8 for original publication]

At low and premontane elevations along the Pacific versant of western Panama, among the most abundant and commonly found anoles are certain medium-sized (maximum SVL between 50 and 60 mm) *Norops* with a rather slender habitus, long legs (longest toe of adpressed hind limb reaching at least to center of eye, usually beyond eye), and a large, chiefly orange male dewlap. In western Panama, populations exhibiting these characteristics have traditionally been referred to as *N. polylepis,* while in more eastern portions of the country the name *N. tropidogaster* was commonly used (Köhler 2008; Jaramillo et al. 2010; Köhler et al. 2012b, and references therein). Recently, Köhler et al. (2012b) demonstrated that populations from western Panama to Colombia formerly regarded as representing the latter species comprise two profoundly different phenotypes, and revalidated the species *N. gaigei* for *tropidogaster*-like populations with a very small, unilobate hemipenis. Moreover, they revealed that *N. gaigei* ranges far into western Panama, and has often been confused with *N. polylepis.* The distribution of these species is shown in Map 4.12. Motivated by the manifold misidentifications that have occurred throughout Panama (see species accounts in chapter 4.2.2), I review the molecular and morphological distinctions between *N. gaigei, N. polylepis,* and *N. tropidogaster,* focusing on the former two species since both occur in my study area.



Map 4.12: Collection sites of selected long-legged lowland anoles inhabiting the Pacific versant of Lower Central America. Each symbol can represent one or more nearby localities. Circles: *Norops tropidogaster;* squares: *N. gaigei;* white triangles: localities of *N. tropidogaster*-like specimens not verified by Köhler et al. (2012b); black inverted triangles: *N. polylepis;* stars: *N. osa*; hexagons: *N. cupreus*. From Köhler et al. (2012b).

Since *Norops gaigei* and *N. tropidogaster* form a clade together with the long-legged anoles related to *N. lemurinus, N. limifrons,* and *N. lionotus* (see Fig. 4.1), the alignments used in this chapter for the analyses of 16S and COI barcodes include the latter groups. They are again analyzed specifically for those groups in chapters 4.1.7.4 and 4.1.7.5. The complete alignments and distance matrices underlying the following results, as well as separate distance matrices restricted to the respective focus groups, are provided in Appendix 5.7. The final 16S alignment comprised 35 taxa (the 9 anoles already employed as outgroups in preceding chapters, two *N. polylepis,* one *N. tropidogaster,* 7 *N. gaigei,* and 16 specimens related to *N. limifrons*) contained 536 positions, of which, excluding the outgroups, 79 were variable and 68 parsimony-informative. T92+G was determined as the best-fitting substitution model. The final COI alignment comprised 46 taxa (identical outgroups and *N. polylepis,* 10 *N. gaigei,* 15 specimens related to *N. limifrons,* three *N. lemurinus,* and 7 specimens related to *N. lionotus*) contained 561 positions, of which, excluding the outgroups, 209 were variable and 188 parsimony-informative. HKY+G+I was determined as the best-fitting substitution model.

Figure 4.61A shows the ML consensus tree obtained from the 16S barcodes. All analyzed *Norops gaigei* from Panama appear very closely related and form the sister group to the single barcoded *N. tropidogaster,* at uncorrected p-distances of 3.8–4.2%. Separated from these by individual p-distances between 8.8–9.7%, *N. polylepis* is rather distantly related to the aforementioned species pair. Indeed, this species has been shown to be the closest relative of the Costa Rican *N. cupreus* and *N. osa* (Köhler et al. 2010b, 2012a, b). In the PN analysis (not shown), the 95% parsimony probability connection limit of 9 steps leaves all respective haplotypes of *N. gaigei* (4 steps between GK 3116 and the shared haplotype of the remaining six) and *N. polylepis* (6 steps) interconnected.

A congruent picture is drawn in Fig. 4.61B for the COI barcodes, with the exception that no sequences were obtained for *N. tropidogaster*. For this fragment, p-distances between *N. gaigei* and *N. polylepis* range from 16.0–16.8%. In the PN analysis (not shown), the 7 haplotypes found in *N. gaigei* are connected by a maximum of three steps, while those of *N. polylepis* require 14 steps (the connection limit calculated for a 90% parsimony probability). In short, DNA barcoding confirms the distinctness of *N. gaigei, N. polylepis,* and *N. tropidogaster*.

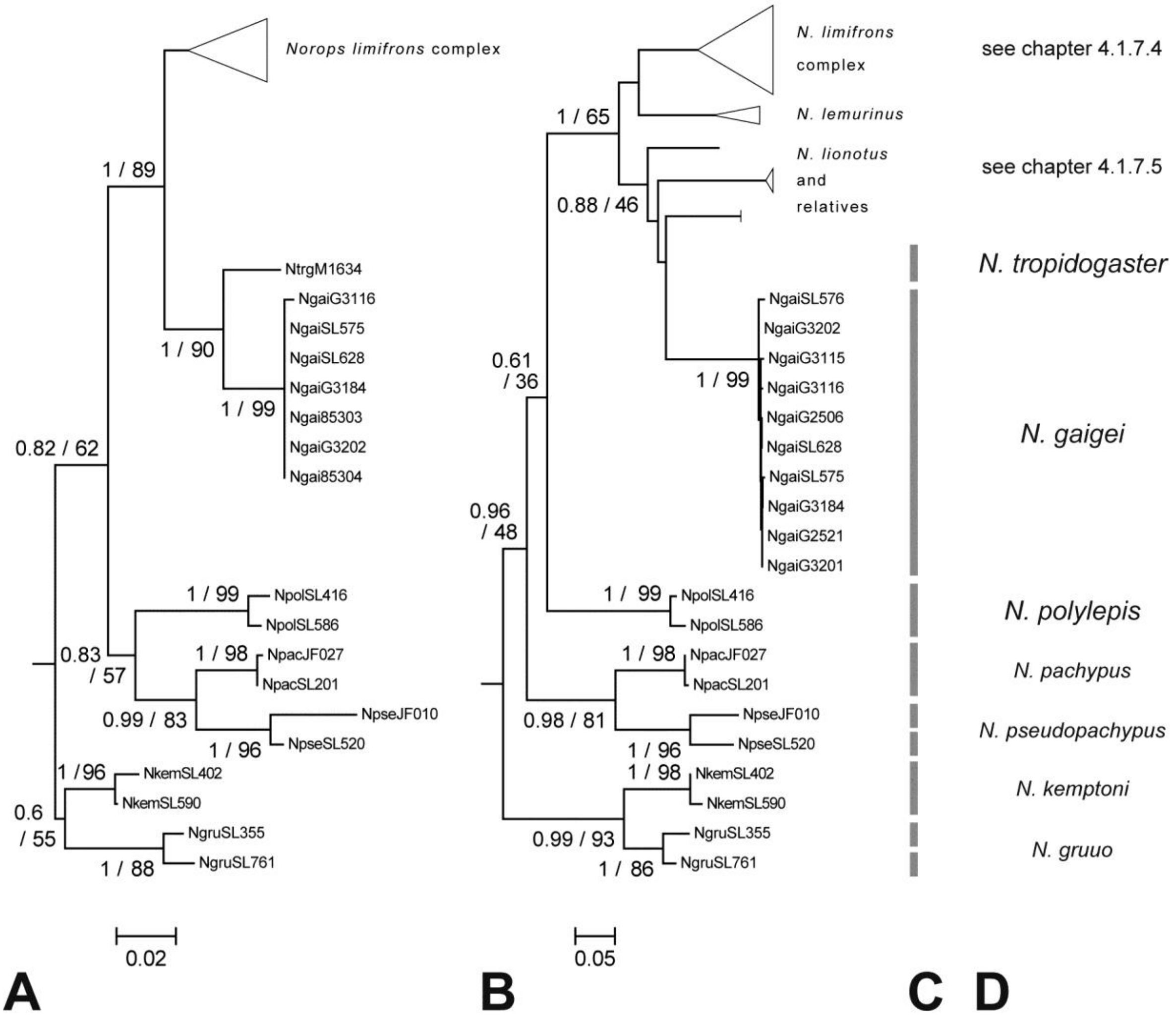


Figure 4.61: Results of DNA barcode analyses of *Norops gaigei, N. polylepis,* and *N. tropidogaster*. (A) Consensus tree from ML analysis of 16S barcodes. (B) Consensus tree from ML analysis of COI barcodes. (C) Lineages diagnosable through barcoding. (D) Taxonomic identity derived from morphology on the basis of preceding analyses and Köhler et al. (2012b). In (A) and (B), bootstrap values at selected nodes are preceded by posterior probabilities from correspondent BI analyses, and the outgroup *Dactyloa ibanezi* is not shown.

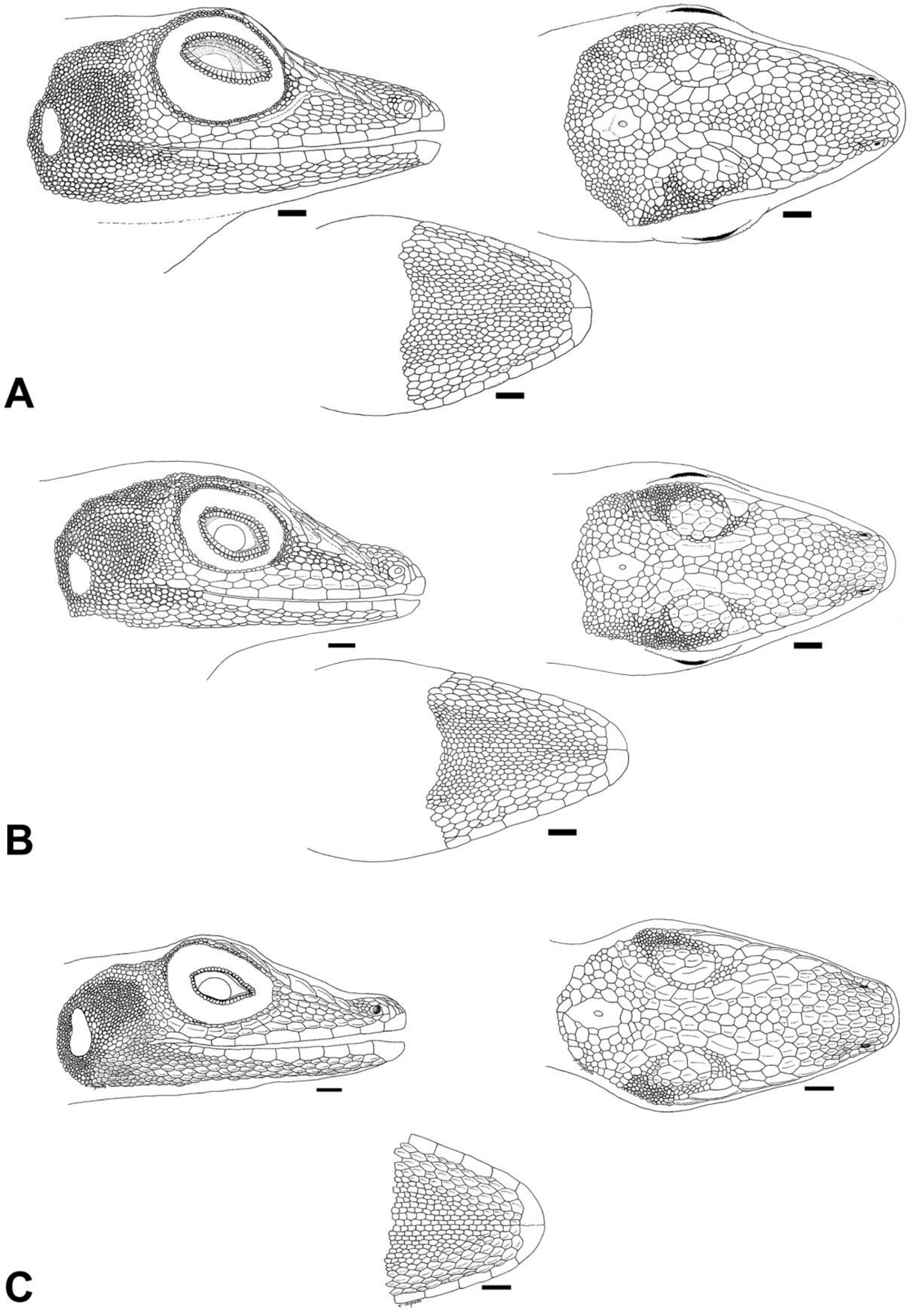


Figure 4.62: Lateral (upper left), dorsal (upper right), and ventral (lower middle) views of heads showing the head scalation of (A) *Norops tropidogaster* MHCH 1640; (B) *N. gaigei* SMF 91921 with lateral view of left side of head mirrored; (C) *N. polylepis* SMF 85206. All scale bars equal 1 mm. Drawings in (A, B) by Milan Vesely, modified from Köhler et al. (2012b), drawings in (C) by Lara Czupalla, modified from Köhler et al. (2010b).

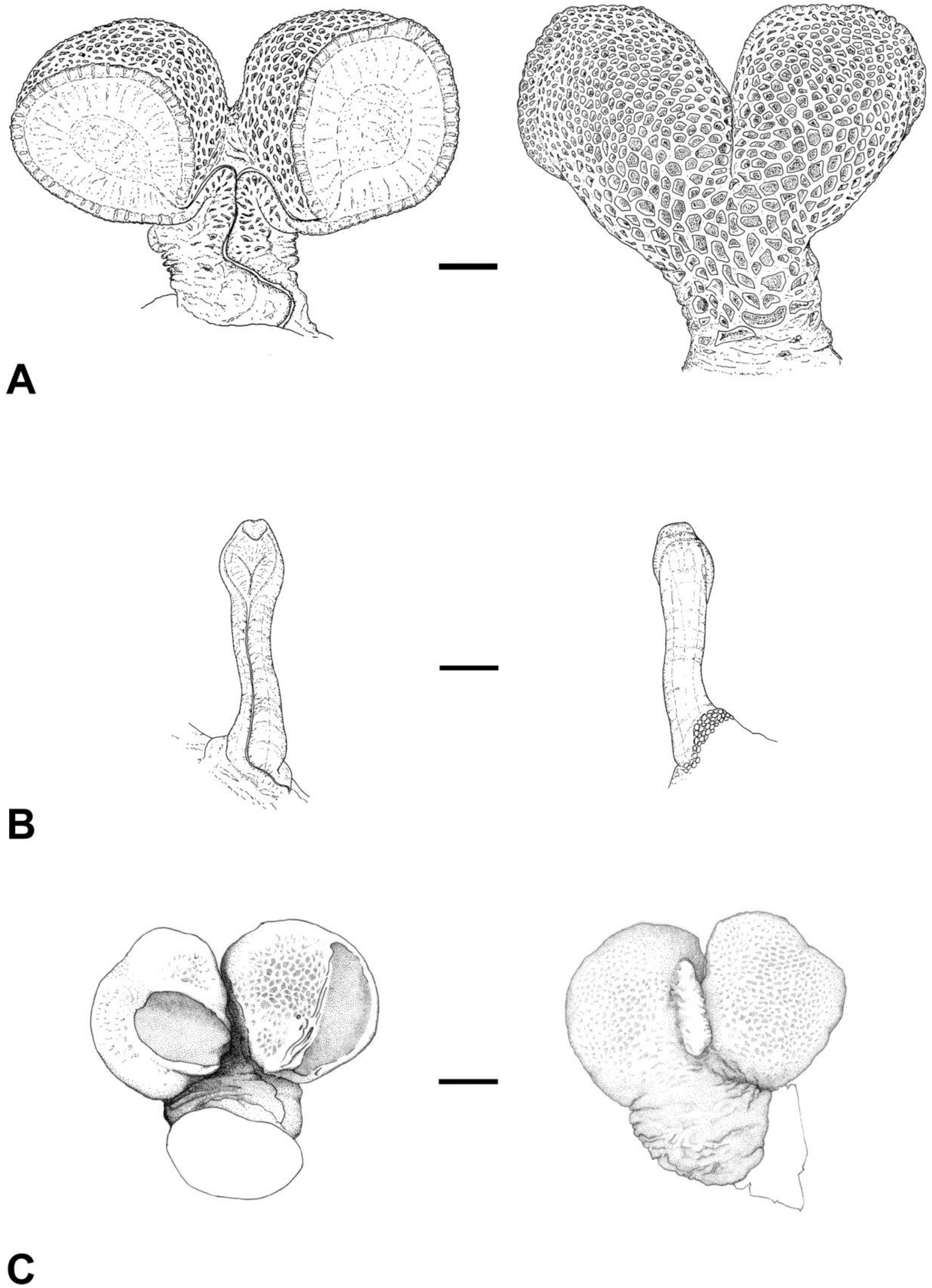


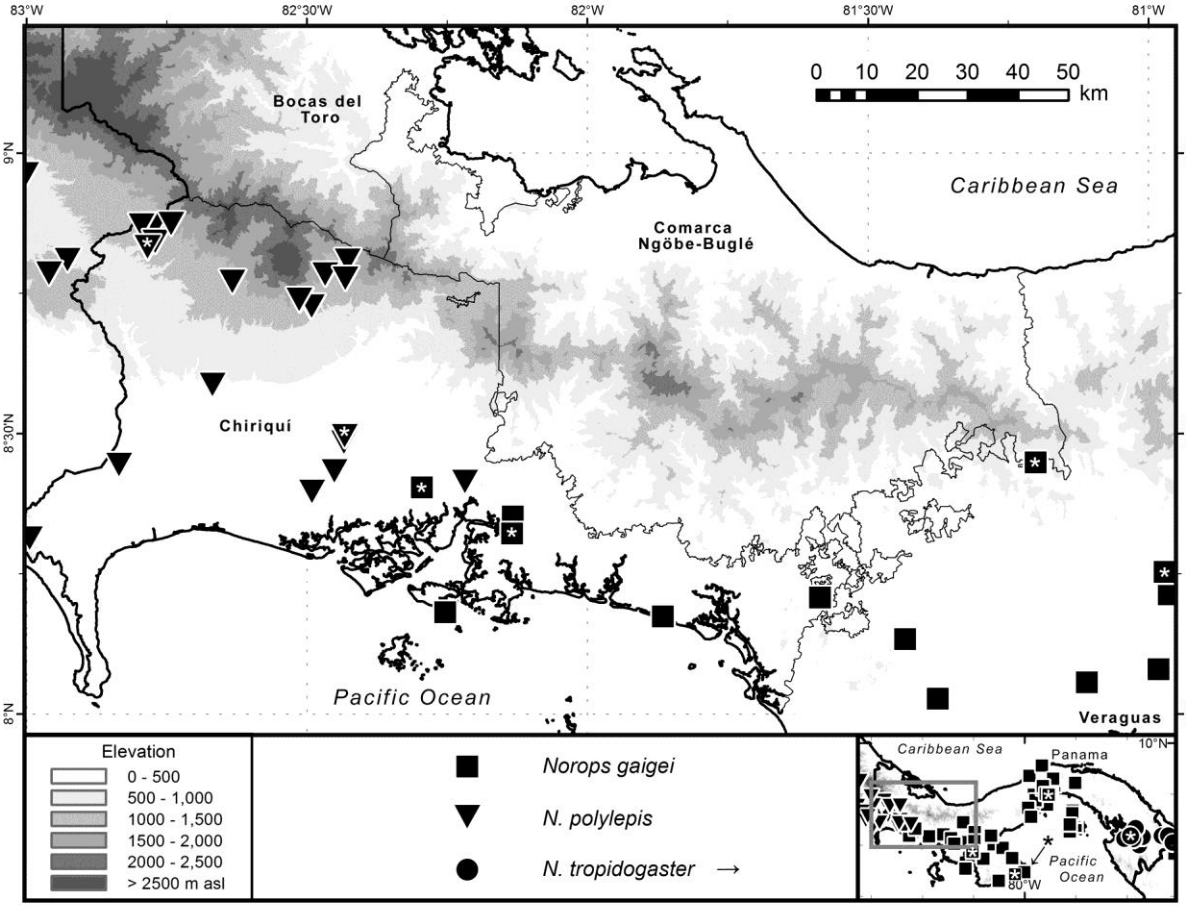
Figure 4.63: Hemipenes of (A) *Norops tropidogaster* MHCH 1645 (not SMF 91956 as erroneously stated by Köhler et al. 2012b); (B) *N. gaigei* SMF 91902; (C) *N. polylepis* MHCH 1024. Sulcate views left, asulcate views right. All scale bars equal 1 mm. Drawings in (A, B) by Milan Vesely, modified from Köhler et al. (2012b), drawings in (C) by Johannes Justus Köhler, modified from Köhler et al. (2010b).

Concerning morphology, these three species may appear very similar at first glance, which has been the cause for considerable taxonomic confusion throughout Panama in the past (see Köhler et al. 2012b, and species accounts in chapter 4.2.2). However, Köhler et al. (2012b) pointed out that the before almost invariably confounded *Norops gaigei* and *N. tropidogaster* are readily separable by a number of morphological characters. Among others, these include head scalation, enlarged postcloacal scales in males, dewlap coloration, and hemipenial morphology (see Figs. 1, 3, 4, 8, and 11 in Köhler et al. 2012b, or Figs. 4.62–4.64 of this work). According to these authors, *N. tropidogaster* is restricted to Colombia and extreme eastern Panama (Maps 4.12). In and around my study area, *N. gaigei* occurs instead, and has appeared in different works as *N. tropidogaster* or *N. polylepis.* This may seem surprising considering the marked morphological distinctions summarized in the following.

In terms of head scalation (Fig. 4.62), *Norops tropidogaster* is readily separated from the other two species, which in turn are difficult to discern from each other relying on these characteristics. Yet, two pholidotic characteristics immediately allow for distinguishing *N. gaigei* from *N. polylepis:* While the former has strongly keeled, imbricate, and mucronate midventral scales (Fig. 4.65K), those of the latter are smooth, at most subimbricate, and never mucronate (Fig. 4.66N). Second, all examined males of *N. gaigei* have a pair of greatly enlarged postcloacal scales (Fig. 4.65L, M), whereas male *N. polylepis* do have several only slightly enlarged scales posterior to the cloacal opening (Fig. 4.66O, P), but never exhibit the conspicuous single pair found in the former species.

The differences between the two species become more obvious when it gets to the male dewlap (Figs. 4.64–4.66): The large dewlap of *Norops gaigei* is yellow with a rather solid central portion of darker orange, and has 7–9 equally distributed gorgetal-sternal rows with 11–15 comparably large scales per row. In contrast, the dewlap of male *N. polylepis* must be called very large, and, despite of also being yellow with a basal orange portion, the orange pigmentation is more intense along the gorgetal-sternal rows in all Panamanian individuals that I have seen. Moreover, the 6–8 gorgetal-sternal rows consist of usually more than 25 comparably small scales per row, and appear more densely packed in the basal two-thirds of the dewlap, leaving a conspicuous gap to the disteromarginals.

Analogously to the "cryptic" species pair *Norops tropidogaster–N. gaigei,* the most striking difference between *N. gaigei* and *N. polylepis* is the hemipenis (Fig. 4.63). While the unilobate hemipenis of *N. gaigei* is the smallest and most delicate reproductive organ documented so far in anoles, that of *N. polylepis* is similarly bilobated, large, and voluminous as that of *N. tropidogaster.* Even without eversion of these organs, adult males of *N. polylepis* are readily distinguished from those of *N. gaigei* by having the base of their tails distinctly swollen and conspicuously bulging, while the basal portions of the tail narrow gradually even in the largest males of *N. gaigei,* just as they do in females of either species (Figs. 4.65; 4.66).



Map 4.13: Distribution of *Norops gaigei* and *N. polylepis* in western Panama and and immediately adjacent eastern Costa Rica (main map), as well as of *Norops gaigei* and *N. tropidogaster* in other portions of Panama and immediately adjacent Colombia. Based on specimens examined by Köhler et al. (2012b) and myself. Localities of specimens with DNA barcodes included in the molecular analyses are marked with an asterisk (*).

Molecular and morphological evidence is integrated in Figure 4.64. Without doubt, the three nominal taxa characterized above are inferred as CGLs and their current taxonomy confirmed. Again, at least male individuals of a given population can confidently be assigned to either species by employing just a few key characteristics. Moreover, in the case of *Norops gaigei* and *N. polylepis* in western Panama, even the reliable identification of females should be possible on the basis of their midventral scale surface. Based on examined specimens only, Map 4.13 shows the distribution in Panama of all three species dealt with in this chapter and details that of *N. gaigei* and *N. polylepis* in western Panama, clarifying that any *N. polylepis* or *N. tropidogaster* hitherto reported from Veraguas province or the Azuero Peninsula is referable to *N. gaigei* (that is, if not to a third species not considered in this chapter). Table 4.14 presents a synopsis of selected morphological characters of the two species occuring along my study area, while aspects of their variability are illustrated in Figures 4.65 and 4.66.

Table 4.14: Selected measurements, proportions, and scale characters of *Norops gaigei* and *N. polylepis*. Based exclusively on Panamanian specimens examined by Köhler et al. (2010b, 2012b) and myself.

		Norops gaigei	***N. polylepis***
		♂ 50 **♀ 21**	**♂ 31** **♀ 16**
SVL	♂	36–53 (45.7± 3.4)	43–54 (48.8 ± 3.2)
	♀	37–52 (44.1 ± 5.4)	30–53 (43.9 ± 5.1)
TL / SVL	♂	1.90–2.34 (2.13 ± 0.12)	1.85–2.19 (2.02 ± 0.10)
	♀	2.02–2.27 (2.13 ± 0.09)	1.80–2.03 (1.88 ± 0.08)
verDT / horDT	♂	1.05–1.47 (1.23 ± 0.11)	0.56–1.76 (1.38 ± 0.21)
	♀	1.06–1.31 (1.18 ± 0.08)	1.08–1.47 (1.28 ± 0.09)
HL / SVL	♂	0.26–0.3 (0.27 ± 0.01)	0.24–0.27 (0.26 ± 0.01)
	♀	0.25–0.29 (0.27 ± 0.01)	0.24–0.28 (0.26 ± 0.01)
HL / HW	♂	1.56–1.75 (1.66 ± 0.06)	1.53–1.71 (1.63 ± 0.05)
	♀	1.59–1.75 (1.65 ± 0.04)	1.51–1.73 (1.61 ± 0.06)
SnL / SVL	♂	0.11–0.13 (0.12 ± 0.01)	0.10–0.20 (0.14 ± 0.04)
	♀	0.11–0.14 (0.12 ± 0.01)	0.11–0.19 (0.12 ± 0.02)
Shank length / SVL	♂	0.28–0.32 (0.30 ± 0.01)	0.25–0.3 (0.27 ± 0.01)
	♀	0.27–0.33 (0.30 ± 0.02)	0.25–0.27 (0.26 ± 0.01)
AGD / SVL	♂	0.24–0.43 (0.38 ± 0.04)	0.36–0.43 (0.40 ± 0.01)
	♀	0.36–0.45 (0.39 ± 0.03)	0.40–0.45 (0.42 ± 0.02)
Subdigital lamellae under phalanges II–IV of 4th toe		20–28 (25.4 ± 1.6)	21–26 (24.0 ± 1.3)
Number of scales between SS		1–4 (2.1 ± 0.6)	1–4 (2.6 ± 0.7)
Number of scales between IP and SS		2–4 (3.0 ± 0.6)	2–5 (3.1 ± 0.9)
Number of scales between SBO and SPL		0–2 (1.0 ± 0.5)	0–1 (0.3 ± 0.5)
Number of SPL to level below center of eye		6–9 (7.3 ± 0.7)	6–8 (6.8 ± 0.7)
Number of INL to level below center of eye		6–9 (7.4 ± 0.6)	5–9 (7.0 ± 0.8)
Total number of loreals		32–51 (40.0 ± 4.4)	32–74 (48.7 ± 9.9)
Number of horizontal loreal scale rows		5–8 (6.2 ± 0.6)	4–10 (6.2 ± 1.6)
Number of postrostrals		6–9 (6.4 ± 0.8)	6–9 (7.1 ± 0.9)
Number of postmentals		5–7 (6.0 ± 0.5)	7–10 (7.8 ± 0.7)
Number of scales between nasals		5–9 (7.0 ± 1.0)	7–9 (7.9 ± 0.7)
Number of scales between 2nd canthals		9–14 (11 ± 1.1)	7–14 (10.0 ± 1.2)
Number of scales between posterior canthals		11–16 (13.2 ± 1.3)	10–16 (11.9 ± 1.5)
Number of medial dorsal scales in one HL		30–56 (38.7 ± 6.0)	35–53 (45.2 ± 4.6)
Number of medial ventral scales in one HL		27–48 (34.3 ± 4.2)	32–58 (43.1 ± 6.2)
Number of scales around midbody		94–138 (119.2 ± 8.4)	124–180 (150.0 ± 13.7)
Number of dorsal scales between axilla and groin		40–58 (48.8 ± 4.3)	56–90 (70.5 ± 7.7)
Number of ventral scales between axilla and groin		51–83 (62.8 ± 6.4)	49–76 (58.9 ± 5.5)

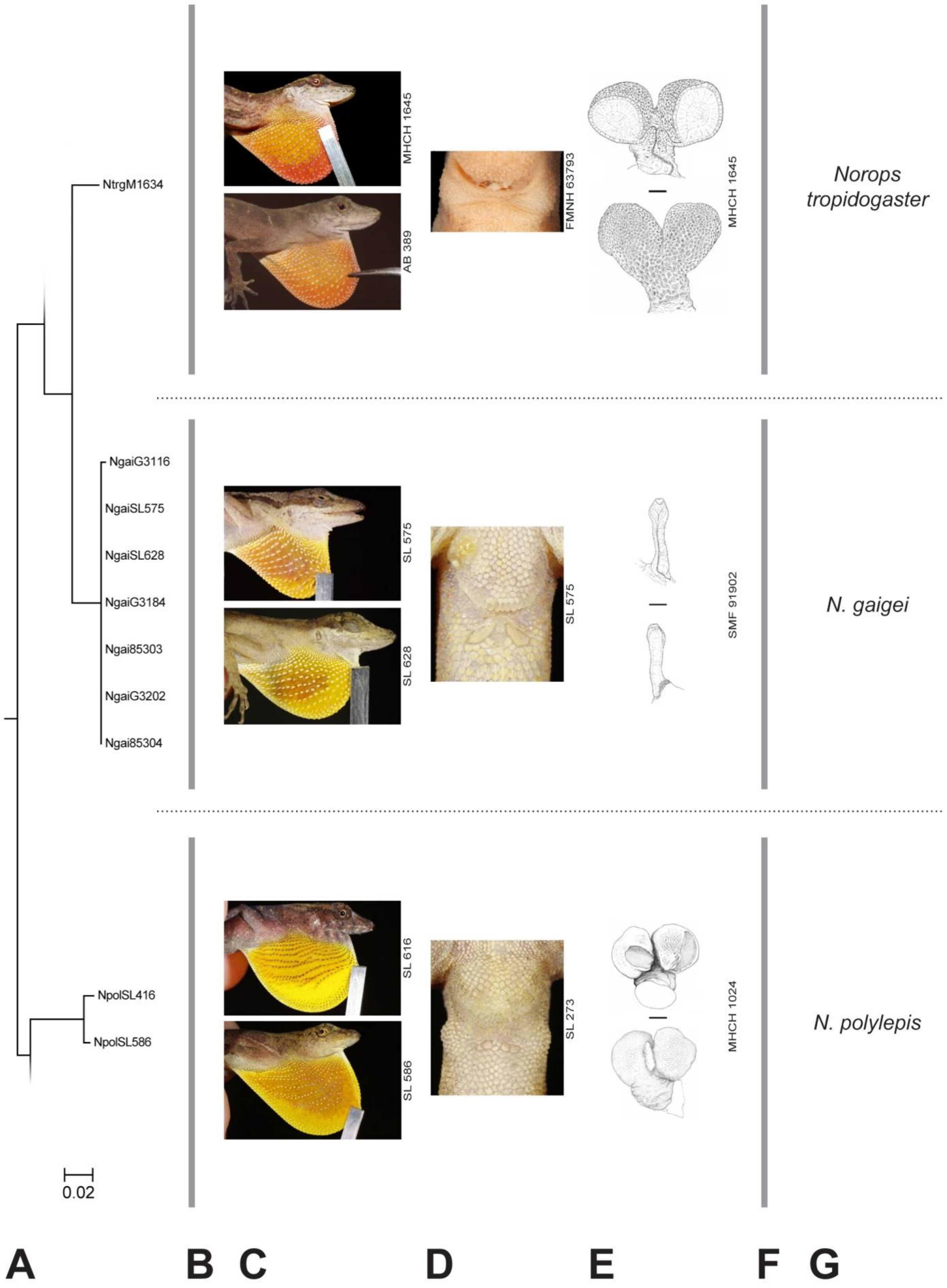


Figure 4.64: Integration of molecular and morphological lines of evidence for *Norops gaigei, N. polylepis,* and *N. tropidogaster.* (A) Detail from Figure 4.61A. (B) Lineages diagnosable through barcoding. (C) Dewlaps of collected males labelled with field numbers; photo of MHCH specimen by MP, of AB specimen by AB. (D) Presence or absence and quality of enlarged postcloacal scales in males; photo of FMNH specimen by GK. (E) Representative hemipenes from Fig. 4.63, sulcate view above asulcate view. (F) Lineages diagnosable through these three morphological key features. (G) Taxonomic identity of inferred CGLs.

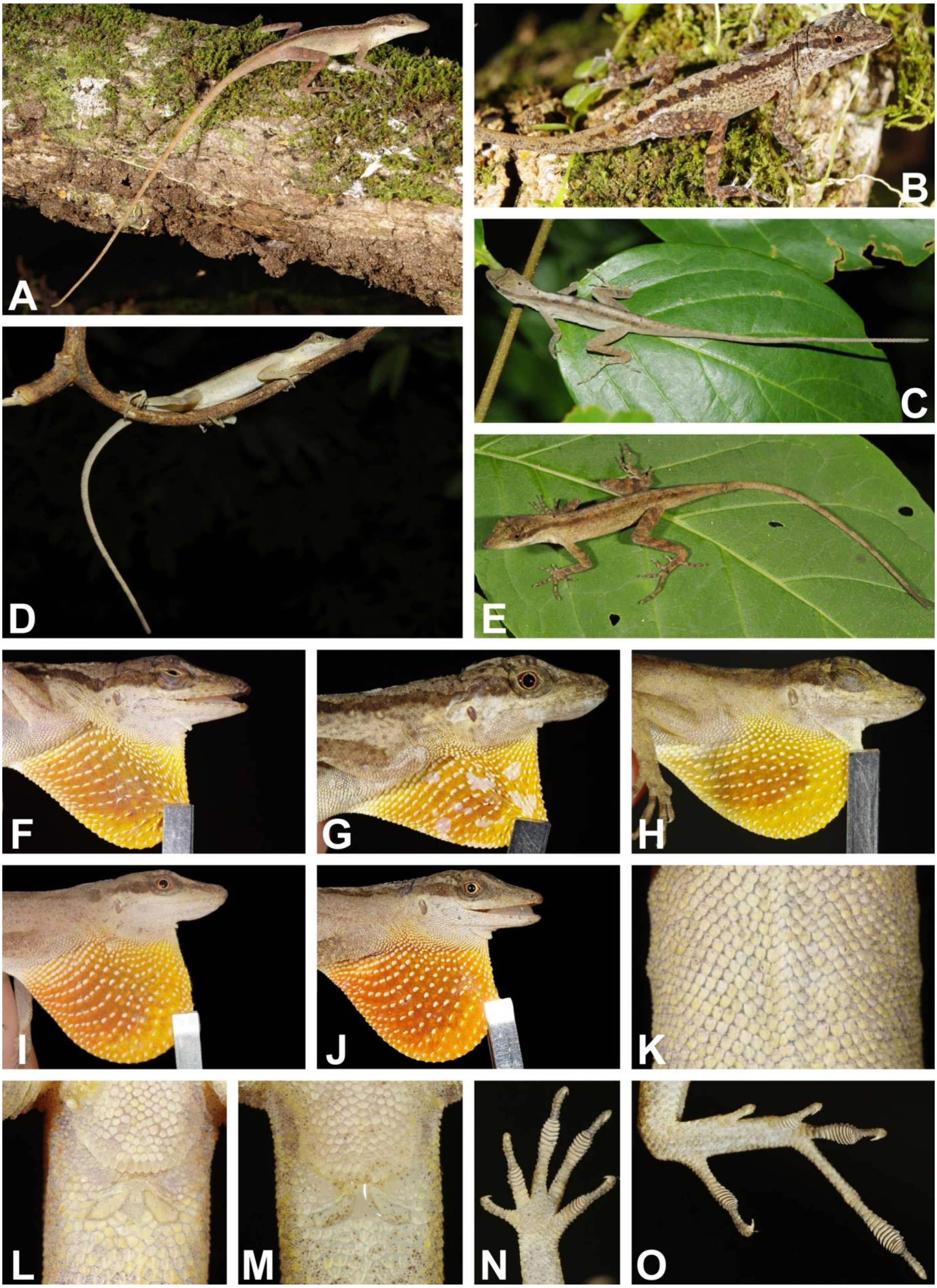


Figure 4.65: Individuals of *Norops gaigei* from western Panama, if not otherwise mentioned from Veraguas province. (A) Male SMF 91529, (B) male MHCH 2294, and (C) uncollected male from Finca La Providencia; (D) male SMF 91530 from Los Valles in sleeping position and (E) the next day; (F–J) male dewlaps of (F) SMF 91529, (G) MHCH 2294, (H) SMF 91530, (I) SMF 91902 from Santo Domingo, Los Santos province, and (J) SMF 91910 from Road Soná–El María; (K) keeled, imbricate midventral scales of SMF 91529; pairs of greatly enlarged postcloacal scales of (L) SMF 91529 and (M) SMF 91530; (N) left hand and (O) left foot of SMF 91530. Photos (I, J) by GK. Note slender tail bases in male individuals.

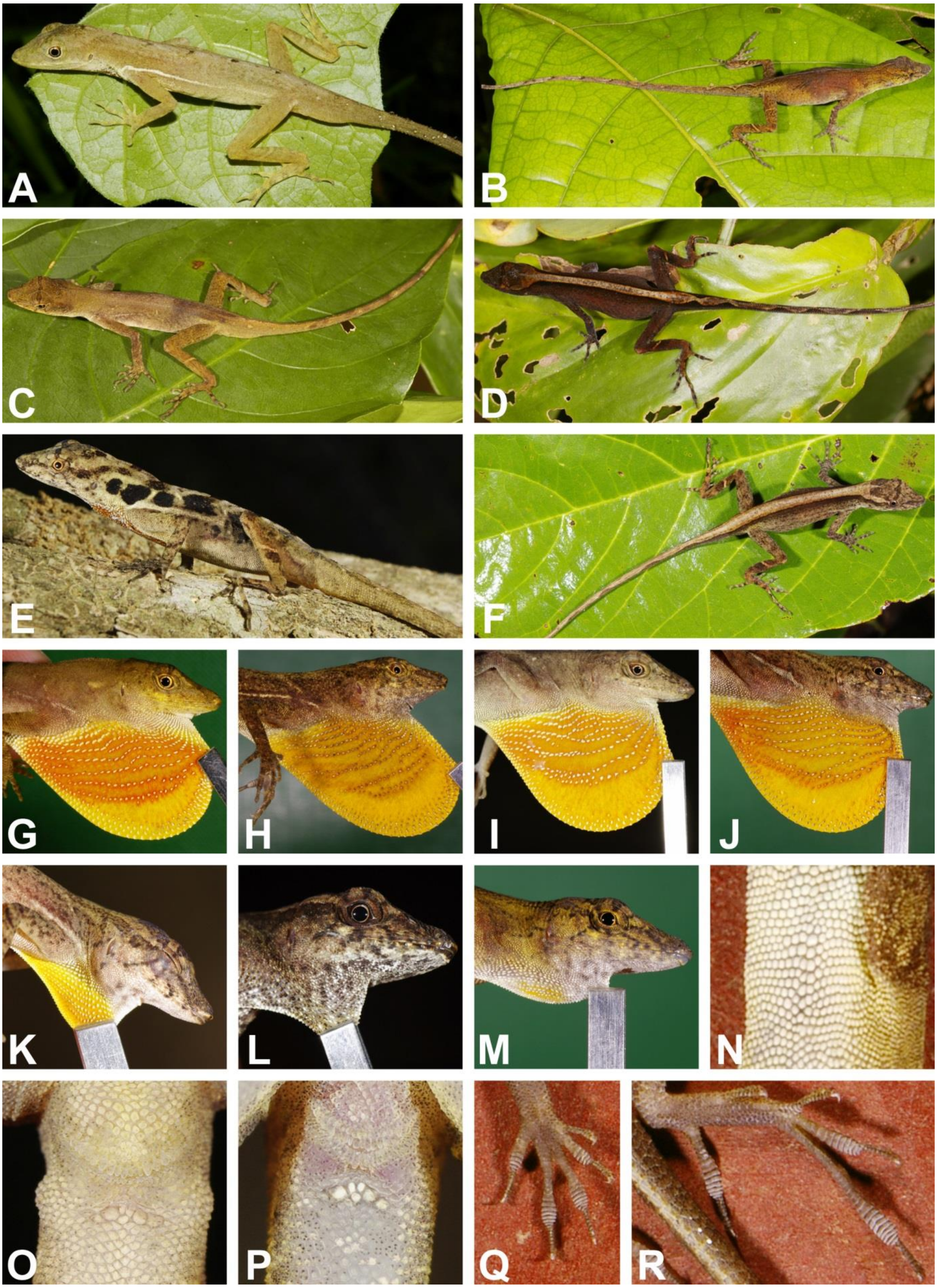


Figure 4.66: Individuals of *Norops polylepis* from Chiriquí province. (A) Male SMF 89514 and (B) female MHCH 2259 from Volante; (C) male MHCH 2157 and (B) female SMF 89511 from Hacienda Café de Eleta; (E) male SMF 89748 from Cabecera de Cochea; (F) female MHCH 2262 from Santa Clara; (G–K) male dewlaps of (G) MHCH 2157, (H) SMF 89509, also from Hacienda Café de Eleta, (I) SMF 89747 from Cabecera de Cochea, (J) SMF 89514, and (K) juvenile male MHCH 2255 from Los Algarrobos; rudimentary female dewlaps of (L) MHCH 2262 and (M) MHCH 2259; (N) smooth, at most subimbricate, and non-mucronate midventral scales of SMF 89513 from Los Algarrobos; enlarged postcloacal scales of (O) SMF 89747 and (P) MHCH 2255; (Q) left hand and (R) left foot of SMF 89513. Note bulging tail bases in male individuals.

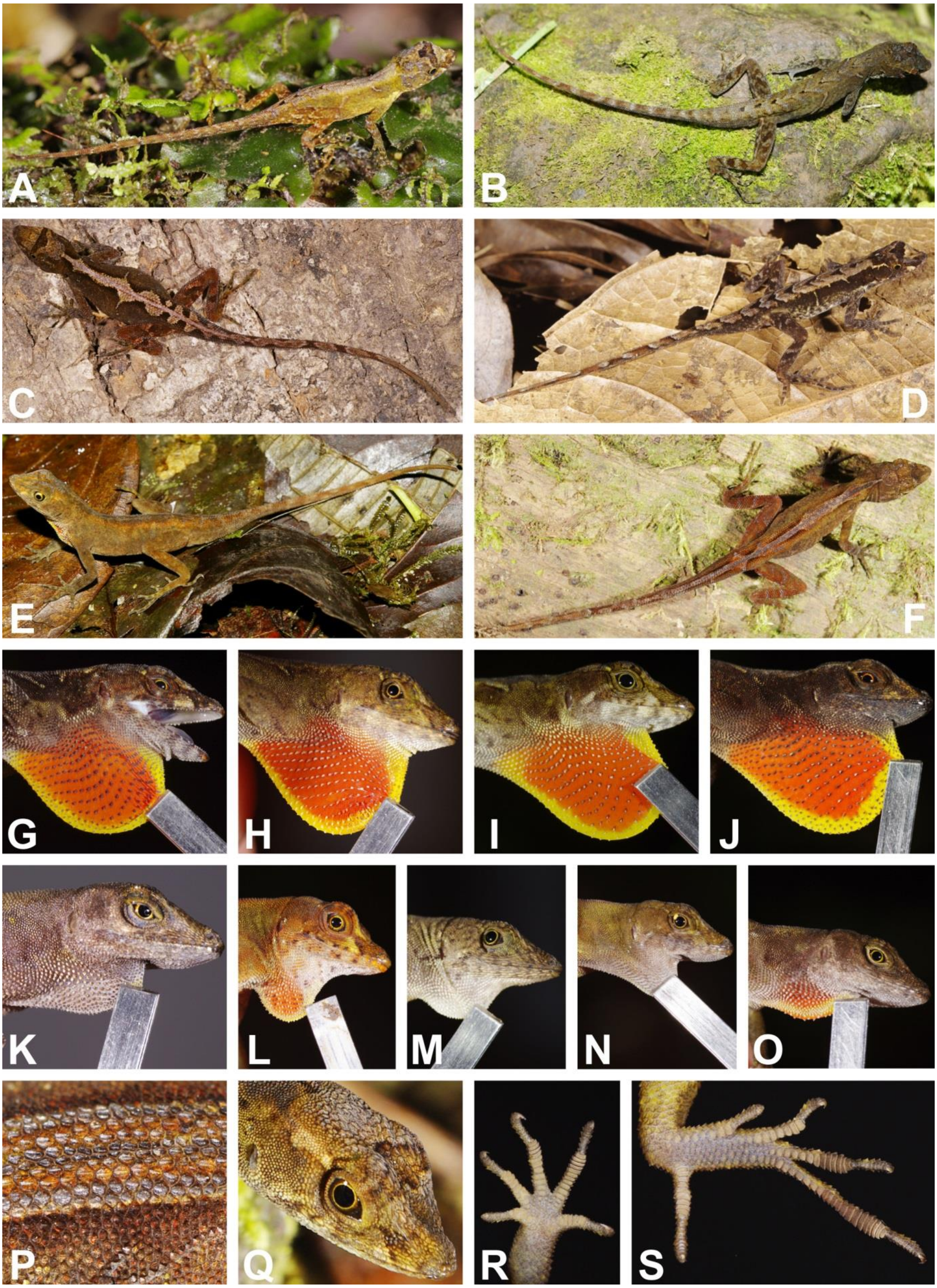


Figure 4.67: Individuals of *Norops humilis.* (A) Juvenile SMF 91473 from Changena trail; (B) male SMF 90105 from headwaters of Río Chiriquí Malí; (C) female SMF 89477 and (D) male MHCH 2176 from La Fortuna; (E) male SMF 89472 from Cerro Mariposa; (F) female SMF 89715 from Cerro Negro; (G–J) male dewlaps: (G) SMF 91471 from Willie Mazú, (H) SMF 91466 from La Fortuna, (I) MHCH 2182 from Río Flor, and (J) SMF 89714 from Cerro Negro; (K–O) female dewlaps: (K) MHCH 2172 from road ro Almirante, (L) MHCH 2173 and (M) MHCH 2178 from La Fortuna, (N) SMF 91469 from Río Hacha, and (O) SMF 89715; (P) detail of middorsum at midbody of SMF 91472 showing 10 rows of distinctly enlarged, keeled middorsal scales; (Q) dorsolateral view of head of MHCH 2175; (R) left hand and (S) left foot of MHCH 2180.

4.1.7.3 *Norops humilis*

Norops humilis (Figure 4.67) is a small, long-legged anole that inhabits the forest ground (Savage 2002; Köhler 2008). Peters (1863a) described *Anolis humilis* from "Veragua", that is, most probably from somewhere in western Panama (see chapter 1.3). As detailed by Köhler et al. (2003, 2006), different populations related to *N. humilis* as delimited by these authors and herein from throughout Nuclear and Lower Central America have at some point in time been described as independent species. Most of these nomina were again sunk into synonymy, to remain there or become resurrected again. In the last decade, Köhler et al. (2003) revalidated the name *N. quaggulus* (Cope 1885) for Caribbean populations from eastern Honduras to northern Costa Rica that have a bilobed, uncalyculate hemipenis with short and stout lobes, thereby restricting the name *N. humilis* to populations from more southern Costa Rica and Panama that have a strongly calyculate, bilobed hemipenis with elongate lobes. They further concluded that *N. humilis marsupialis* (Taylor 1956) from Pacific Costa Rica should remain in the synonymy of *N. humilis.* Köhler et al. (2006) reconfirmed the validity of the aforementioned two species and the more northerly found *N. uniformis* on the basis of more specimens, and presented detailed distribution maps. Interestingly, they found one male representing the hemipenial morph of *N. quaggulus* in Limón province of Caribbean Costa Rica, next to the Panamanian border. The fact that Johannes J. Köhler found additional males referable to that species at nearby localities during his PhD field work (J.J. Köhler, pers. comm.) render the presence of short-lobed "*N. humilis*" in western Panama possible. In the following, I briefly examine the molecular and morphological distinctions among the material from the Cordillera Central and adjacent lowlands examined by myself.

The complete alignments and distance matrices underlying the following results are provided in Appendix 5.7. The final 16S alignment comprised 15 taxa (the nine anoles already employed as outgroups in preceding chapters, and six *N. humilis*) contained 546 positions, of which, excluding outgroups, 29 were variable and 9 parsimony-informative. The final COI alignment comprised 18 taxa (identical outgroups and 9 *N. humilis*) contained 554 positions, of which, excluding the outgroups, 86 were variable and 72 parsimony-informative. T92+G was determined as the best-fitting substitution model for both fragments.

The COI barcodes of anoles identified as *Norops humilis* can be split into up to five lineages that numbered from west to east in Figure 4.68. Lineage 4 comprises individuals from northern and southern vicinities of the Fortuna reservoir and is thus assumed to include the specimens LACM 150384–86 (collected close to the lake) that represented *N. humilis* in the molecular analyses of Köhler et al. (2003). Individual uncorrected p-distances between members of different lineages range from 4.8–9.4%. In the PN analysis, the individuals within each lineage are connected by 0–2 steps. To interconnect all lineages, the connection limit of 10 steps calculated for a 95% parsimony probability has to be more than tripled.

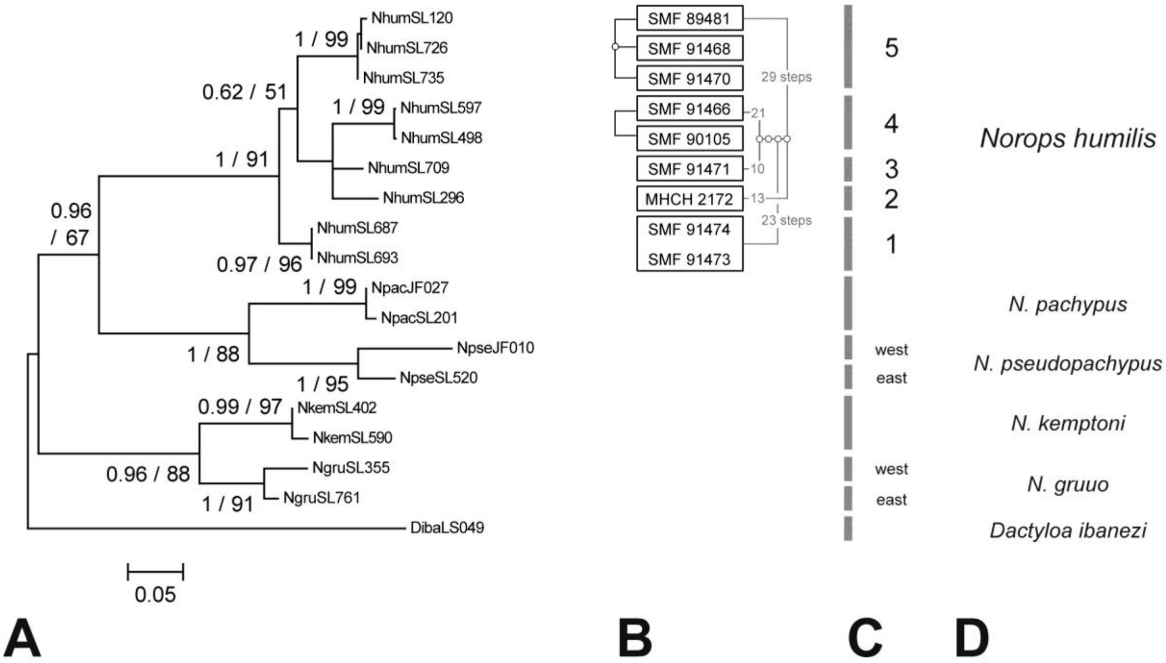


Figure 4.68: Results of COI analyses. (A) Consensus tree from ML analysis of COI barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the COI barcodes, numbered from west to east. (D) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding taxonomic analyses.

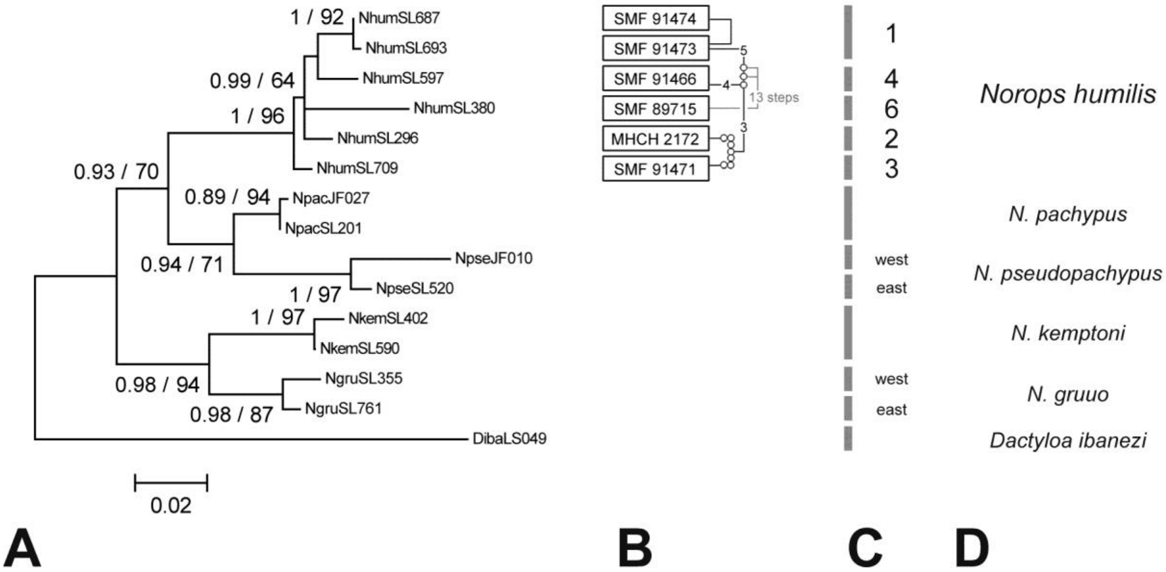
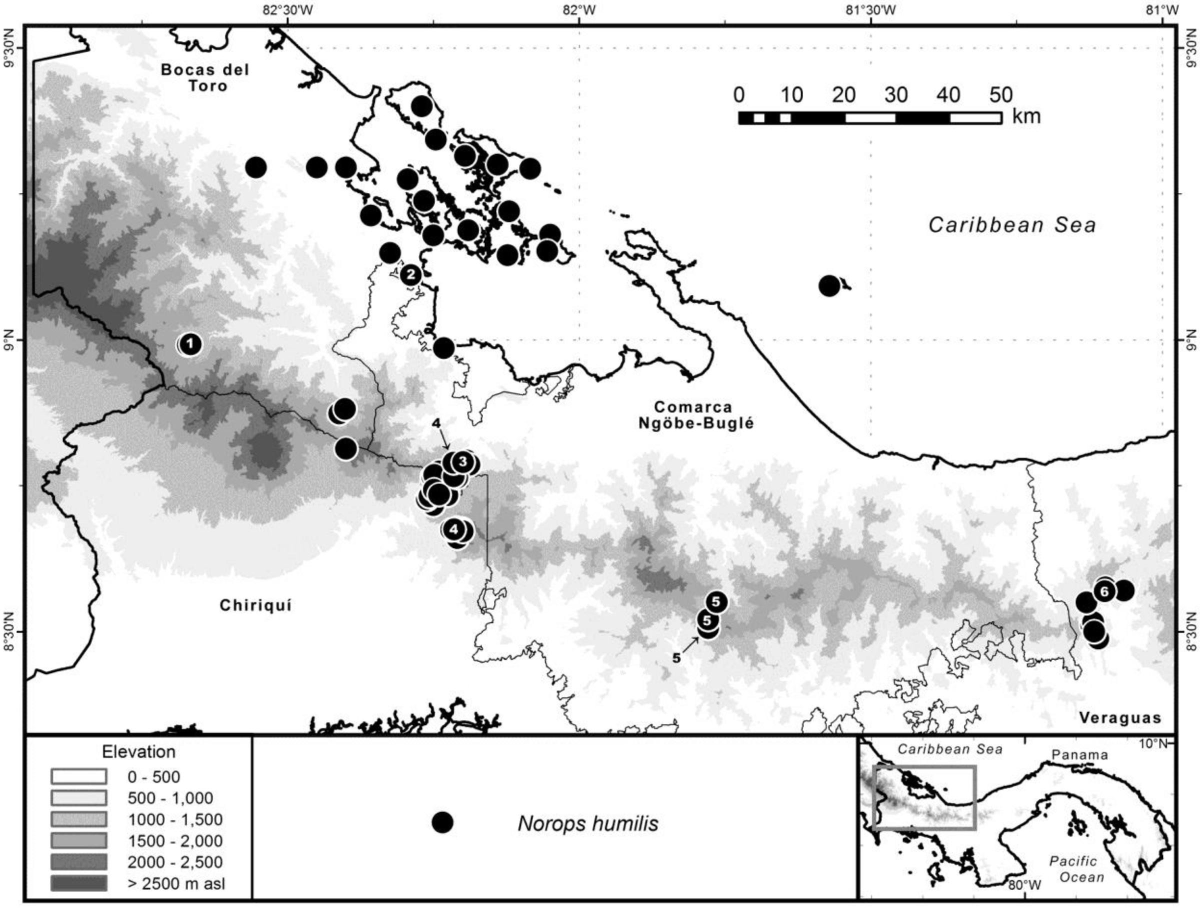


Figure 4.69: Results of 16S analyses. (A) Consensus tree from ML analysis; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through the 16S barcodes, with 1–4 corresponding to those diagnosed in Fig. 4.68. (D) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding taxonomic analyses.

As shown in Figure 4.69, lineages 1–4 are also represented by 16S barcodes, as well sixth from Cerro Negro, Veraguas. For this fragment, individual p-distances between members of different lineages range from 1.9–3.2%. In the PN analysis, the connection limit of 14 steps calculated for a 90% parsimony probability unites in a single network all lineages except lineage 6, that is separated by a minimum of 18 steps from lineages 1 and 4.



Map 4.14: Distribution of *Norops humilis* in western Panama. Based on specimens examined by Köhler et al. (2003, 2006) and myself. Collection localities of barcoded specimens bear the number of the corresponding lineage.

The geographic provenance of the barcoded specimens is plotted along with that of my examined material (mostly from along the Cordillera) and the specimens examined by Köhler et al. (2003, 2006; the majority of plotted records from La Fortuna and the lowlands) in Map 4.14. In a tentative screening of standard characters of external morphology, all six lineages appear largely congruent in their variation. Even whithout taking into account metachrosis, the populations identified as *Norops humilis* from all over my study area are very variable in their coloration and pattern, in a way that any individual pictured in Fig. 4.67 could pertain to any of the lineages 3–6 of which several male and female individuals were examined, respectively. This also applies to the female dewlap which varies from white to red with a light-colored margin. However, the moderately large dewlap is invariably bright red with a yellow margin in all males of these four lineages. Moreover, all barcoded and syntopical adult males of these lineages have the long-lobed, calyculate hemipenis considered typical for *N. humilis* (Köhler et al. 2003, 2006). As shown in Map 4.14, the samples of the other two lineages were collected closer to the Costa Rican border and either might represent the short-lobed hemipenial morph. Unfortunately, lineage 1 is represented by just two juveniles in my sample, and lineage 2 by a single female, preventing the examination of hemipenes as the feature most profoundly distinguishing *N. humilis* from *N. quaggulus.* A thorough analysis of morphological characters as warranted by the complex genealogical structure found in my barcode sample should involve more material especially of lineages 1 and 2, and a more detailed examination of hemipenial morphology. Moreover, the phylogenetic relationships inferred from the two barcodes are weakly supported and partly contradictory, rendering the employment of further genetic markers, preferably of nuclear genes, desirable. These voluminous tasks are definitely beyond the scope of the present work. In consequence, I classify lineages 1–6 as UGLs pending further study.

4.1.7.4 The *Norops limifrons* complex

Especially in secondary vegetation, the small, long-legged, and very slender anoles related to *Norops limifrons* can be found in high densities all along the Cordillera Central. Cope (1862b) described *Anolis limifrons* from "Veragua", which can rather confidently interpreted as "Cocuyos de Veraguas", since that more precise locality has been stated by Cope for various type specimens that also had been collected by R. W. Mitchell (see chapter 1.3 and Map 1.13). As detailed and discussed by Savage (2002) and Köhler & Sunyer (2008), many names have been created for *limifrons*-like populations throughout Central America thereafter, most of which have been considered synonyms of *N. limifrons* during the last decades. Having examined more than 1400 specimens referable to that species, Köhler & Sunyer (2008) restricted the name *N. limifrons* to populations from Honduras to central Panama that have a chiefly white dewlap and a small, unilobed hemipenis, referring to its synonymy virtually all hitherto described species from that region. Simultaneously, they described the populations from Bocas del Toro that have a chiefly white dewlap but a large, bilobed hemipenis as *A. cryptolimifrons,* and those from central and eastern Panama with a yellow-orange dewlap and a large, bilobed hemipenis as *A. apletophallus.* In the spring of 2009, RdL, AH, and myself accompanied JJK on a targeted fine-scale sampling trip to the lowlands of Bocas del Toro in search for contact and presumed hybridization zones between unilobed *N. limifrons* and bilobed *N. cryptolimifrons.* Since anoles identified as members of the *N. limifrons* complex occur all along my study area, I obtained COI barcodes for specimens from different localities through collaboration with the ColdCode project. For the following analyses, these are complemented with 16S sequences provided by JJK. Alignment specifications are given in chapter 4.1.7.2. The distance matrices restricted to *N. limifrons* and its close relatives underlying the following results are provided in Appendix 5.7.

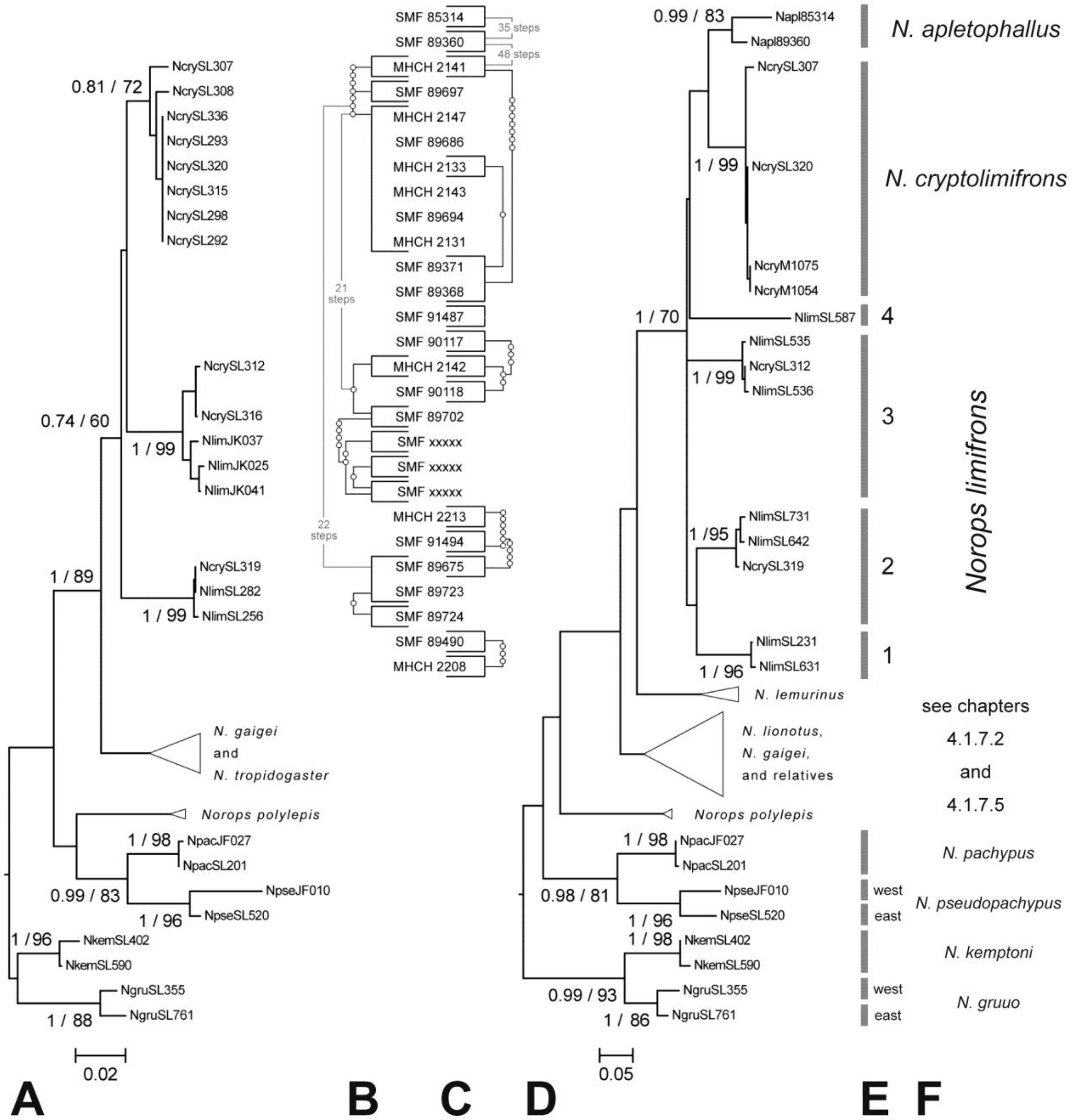
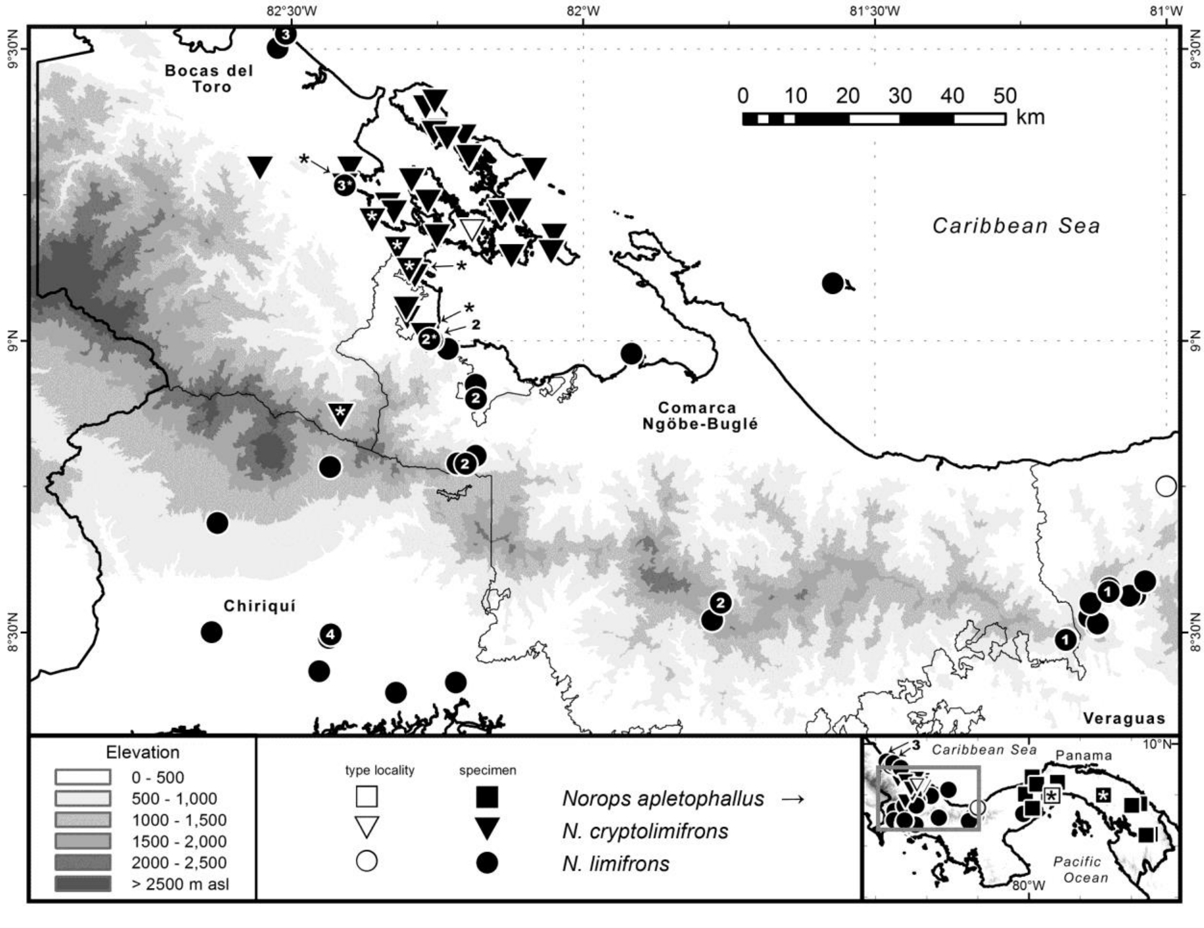


Figure 4.70: Results of DNA barcode analyses of the *Norops limifrons* complex. (A) Consensus tree from ML analysis of 16S barcodes. (B) Parsimony network of 16S barcodes with a 95% parsimony probability resulting in a connection limit of 9 steps drawn on the left side, and (C) Parsimony network of COI barcodes with a 95% parsimony probability resulting in a connection limit of 10 steps drawn on the right side of the correspondent collection numbers. (D) Consensus tree from ML analysis of COI barcodes. (E) Lineages diagnosable through barcoding. (F) Taxonomic identity derived from morphology on the basis of available literature or, in the case of the outgroups, from preceding analyses. In (A) and (D), bootstrap values shown at selected nodes are preceded by posterior probabilities from correspondent BI analyses, and the outgroup *Dactyloa ibanezi* is not shown. In (B) and (C), additional connections acheived by manually increasing the connection limit are indicated by the number of necessary steps.

Figure 4.70 aligns the ML consensus trees from the analyses of 16 16S and 15 COI sequences with the corresponding haplotype networks. Among the 16S barcodes exclusively coming from Bocas del Toro and interspersed areas of the Comarca Ngöbe-Buglé, three lineages are evident: One is readily identified as *Norops cryptolimifrons* in view of the large, bilobed hemipenes exhibited by all its male members. The remaining two lineages represent populations east and west of this species' collection sites with small, unilobed hemipenes. Yet, their barcoded males collected in close vicinities to those of *N. cryptolimifrons* (MHCH 2142 and SMF 89702 of the western, and SMF 89675 of the eastern lineage, all labelled with the abbreviation "Ncry" according to their phenotype) have the hemipenial morph of that species. Individual uncorrected p-distances within the three lineages range from 0.0–1.5%, those between individuals of different lineages from 4.0–6.5%. In the PN analysis, all haplotypes within a given lineage are connected well before the connection limit of 9 steps calculated for a 95% parsimony probability, while connections between lineages require more than 22 steps.



Map 4.15: Distribution of the members of the *Norops limifrons* complex in western Panama (main map) and the entire country (overview map). Based on specimens examined by Köhler & Sunyer (2008: only selected localities shown for *N. apletophallus*) and myself. Collection localities of barcoded specimens are marked with an asterisk for *N. apletophallus* and *N. cryptolimifrons,* or with the number of the corresponding lineage for *N. limifrons*. At the contact zones of the latter two species, an asterisk following the lineage number denotes male specimens exhibiting the bilobed hemipenial phenotype of *N. cryptolimifrons* while their barcodes cluster with the specified lineage of *N. limifrons.*

The same three lineages, including two of the three specimens whose mtDNA contradicts their respective hemipenial phenotype, are also represented by COI barcodes, which moreover reveal three additional lineages. One of these is represented by two specimens from central and eastern Panama, and includes a female paratype of *N. apletophallus*. The other two novel lineages again comprise animals from populations with small, unilobate hemipenes. Map 4.15 shows the provenance of all barcoded representatives along with their lineage affiliation. Individual p-distances within the COI lineages range from 0.0–1.6% in the five lineages from western Panama, and reach 6.7% in that referred to *N. apletophallus.* Individual p-distances between members of different lineages range from 8.6–13.7%. In the corresponding PN analysis, all lineages except *N. apletophallus* form independent haplotype networks already below the connection limit of 10 steps calculated for a 95% parsimony probability. The two haplotypes from eastern and central Panama are separated by 35 steps, while connections between lineages require a minimum of 48 steps.

Figure 4.71 integrates these molecular results with two primordial morphological characteristics, that is, male dewlap and hemipenis. Two of the six inferred genealogical lineages are readily referable to *Norops apletophallus* and *N. cryptolimifrons* based on male morphology. Members of any of the remaining four lineages, which are roughly numbered according to their distance to the type locality of *N. limifrons,* were all identified as pertaining to this nominal taxon employing the most recently published keys (Köhler 2008; Köhler & Sunyer 2008), which rely on dewlap coloration and hemipenis morphology. However, slight differences in dewlap coloration, especially regarding the ubication and extent of yellow-pigmented areas, seem to exist among the pictured individuals. Nevertheless, I also observed a certain variation in these characteristics within a given lineage. The hemipenis of lineage 2 has been pictured by Köhler & Sunyer (2008), and I everted very similar organs in males of lineages 1 and 3. Unfortunately, I have not seen dewlaps in life or hemipenes of lineage 4. All in all, notwithstanding their genetic distinctiveness, these four lineages are of almost identical appearance not only at first sight. Since a profound morphological analysis of the numerous specimens allied to *N. limifrons* that are available to me is far beyond the scope of the present work, for now I classify the four lineages as UGLs. Their relationships, distinctions, and evolutionary history, as well as the phenomenon of apparent hybridization between *N. cryptolimifrons* and *N. limifrons* UGLs 2 and 3, are the subject of the PhD thesis of JJK (Köhler, J.J., in prep.) and ongoing studies at the herpetology department of Senckenberg Forschungsinstitut Frankfurt. Figures 4.72 and 4.73 give an outline of the morphological variation I documented for the two nominal species occurring in my study area.

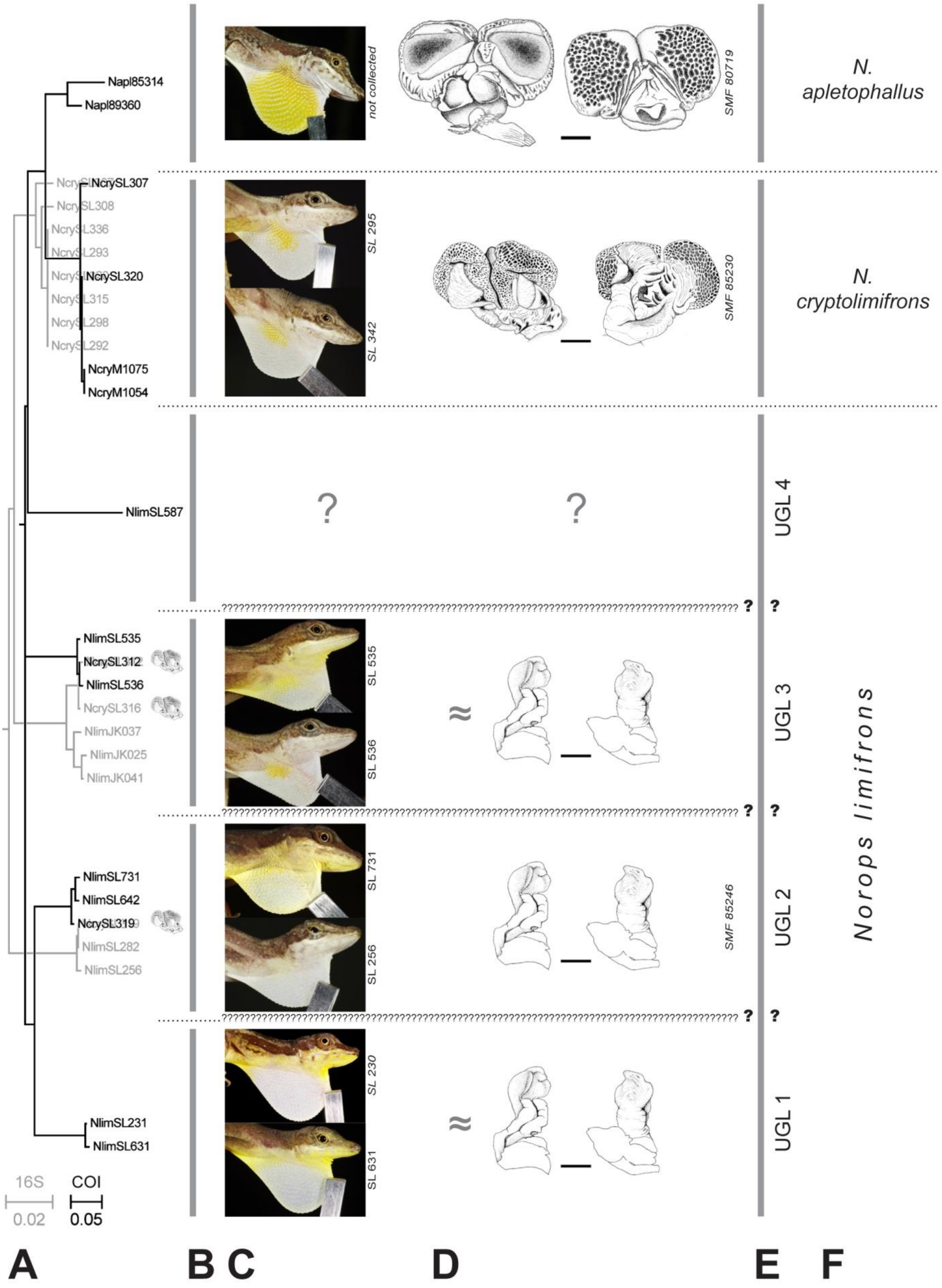


Figure 4.71: Integration of molecular and fragmentary morphological results for the *N. limifrons* complex. (A) Details from Figure 4.70A and D. (B) Lineages diagnosable through barcoding. (C) Dewlaps of collected or syntopical males, field numbers of the latter in *italics.* (D) Representative hemipenes labelled with collection numbers, and approximate hemipenial morphology for lineages for which I have seen everted hemipenes; sulcate views left, asulcate views right. (E) Lineages diagnosable through these two morphological key features. (G) Taxonomic identity of inferred CGLs. All scale bars equal 1 mm. Hemipenis drawings by Johannes Justus Köhler, modified from Köhler & Sunyer (2008).

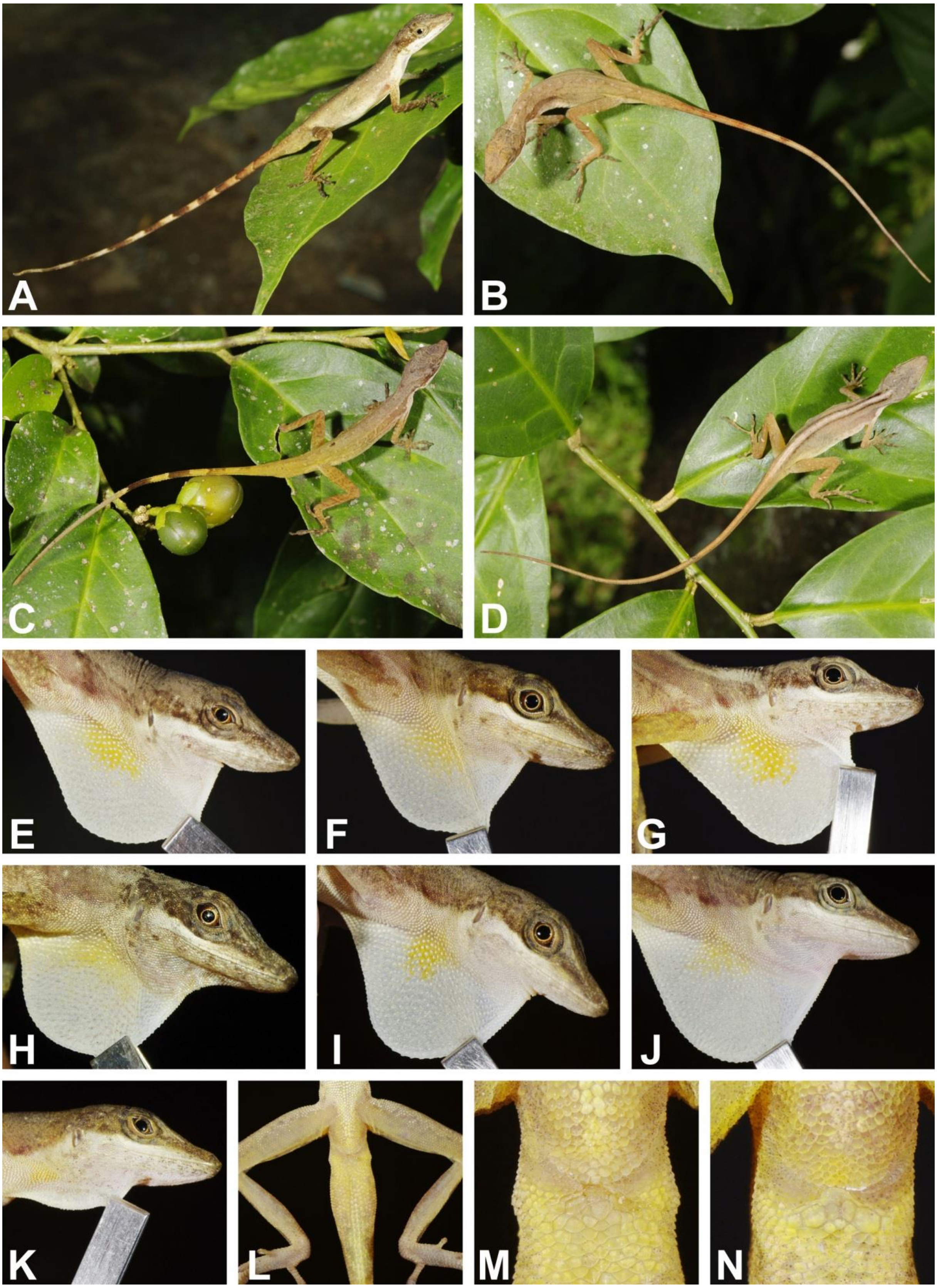


Figure 4.72: Individuals of *Norops cryptolimifrons* collected along the road to Almirante. (A) Male MHCH 2133 and (B) female SMF 89679 from km 15.5; (C) male SMF 89693 from km 35.5; (D) female SMF 89689 from km 24.5; (E–G) male dewlaps: (E) SMF 90682 from km 15.5, (F) SMF 89693, and (G) SMF 89683 from km 23; (H–J) dewlaps of males with *N. cryptolimifrons* phenotype but mtDNA haplotypes of different *N. limifrons* UGLs: (H) SMF 89675 from km 13.5 clustering with UGL 2, (I) MHCH 2142 and (J) SMF 89701 from km 63 clustering with UGL 3; (K) female dewlap of MHCH 2140 from km 43; (L) cloacal area and base of tail of male SMF 89697 from km 53; enlarged postcloacal scales (M) SMF 89697 and (N) MHCH 2132 from km 33. Note bulging tail bases in male individuals.

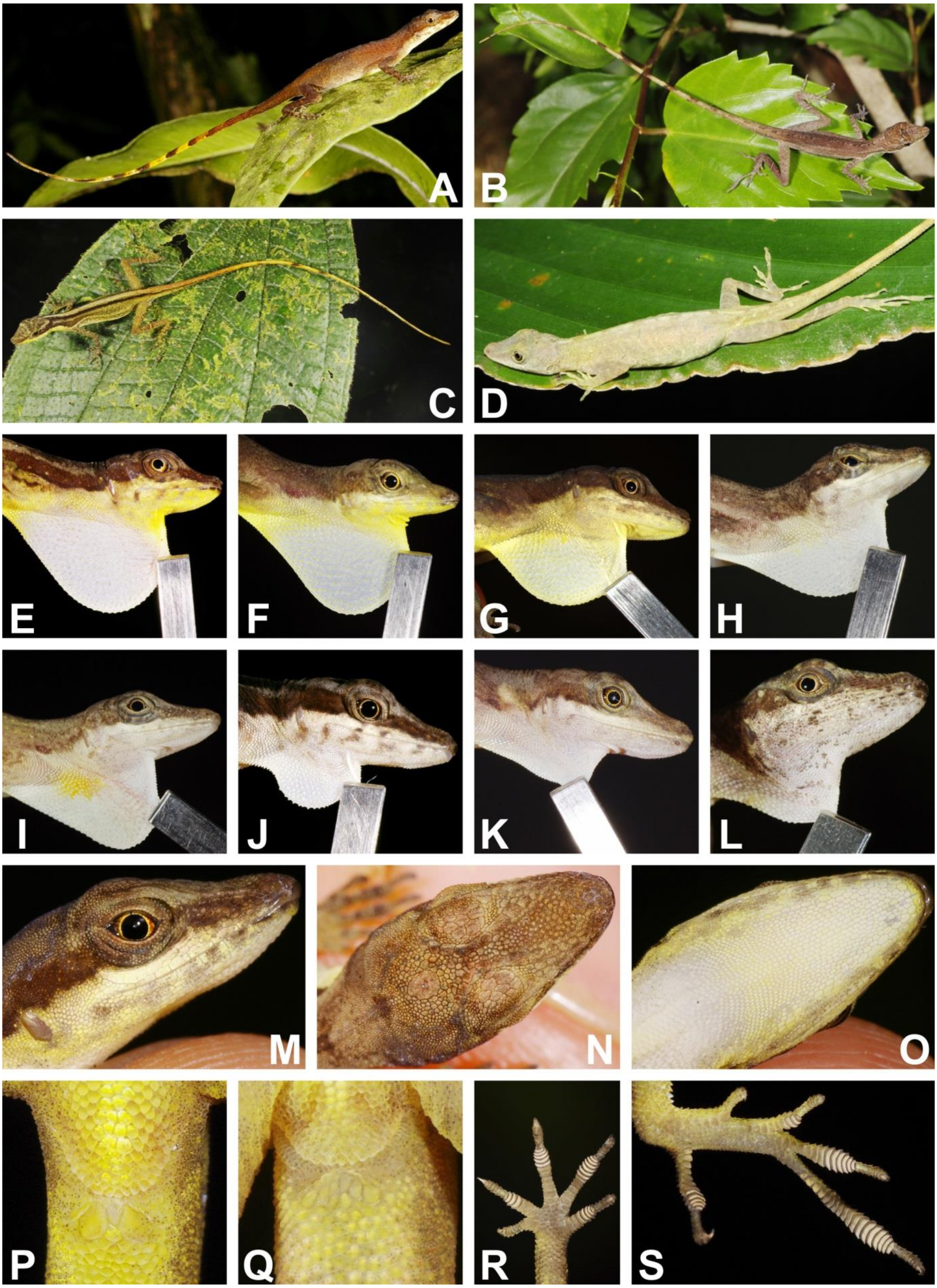


Figure 4.73: Individuals of *Norops limifrons* from western Panama. (A) uncollected individual from Cerro Negro; (B) male SMF 89723 from Bocas del Toro near Chiriquí Grande; (C) female SMF 91494 from Willie Mazú; (D) female SMF 91487 from Los Algarrobos; (E–I) male dewlaps: (E) SMF 89489 from Cerro Negro, (F) MHCH 2208 from El Paredón, (G) MHCH 2213 from Río Hacha, (H) SMF 89723, and (I) SMF 90118 from San San Pond Sak; (J–L) female dewlaps: (J) SMF 89490 from Cerro Negro, (K) SMF 89724 from km 13 of road to Almirante, and (L) SMF 91487; (M) lateral, (N) dorsal, and (O) ventral view of head of SMF 2198 from Cerro Mariposa; enlarged postcloacal scales of (P) MHCH 2208 and (Q) SMF 90117 from San San Pond Sak; (R) hand and (S) left foot of SMF 91489 from El Paredón. Note slender tail bases in male individuals.

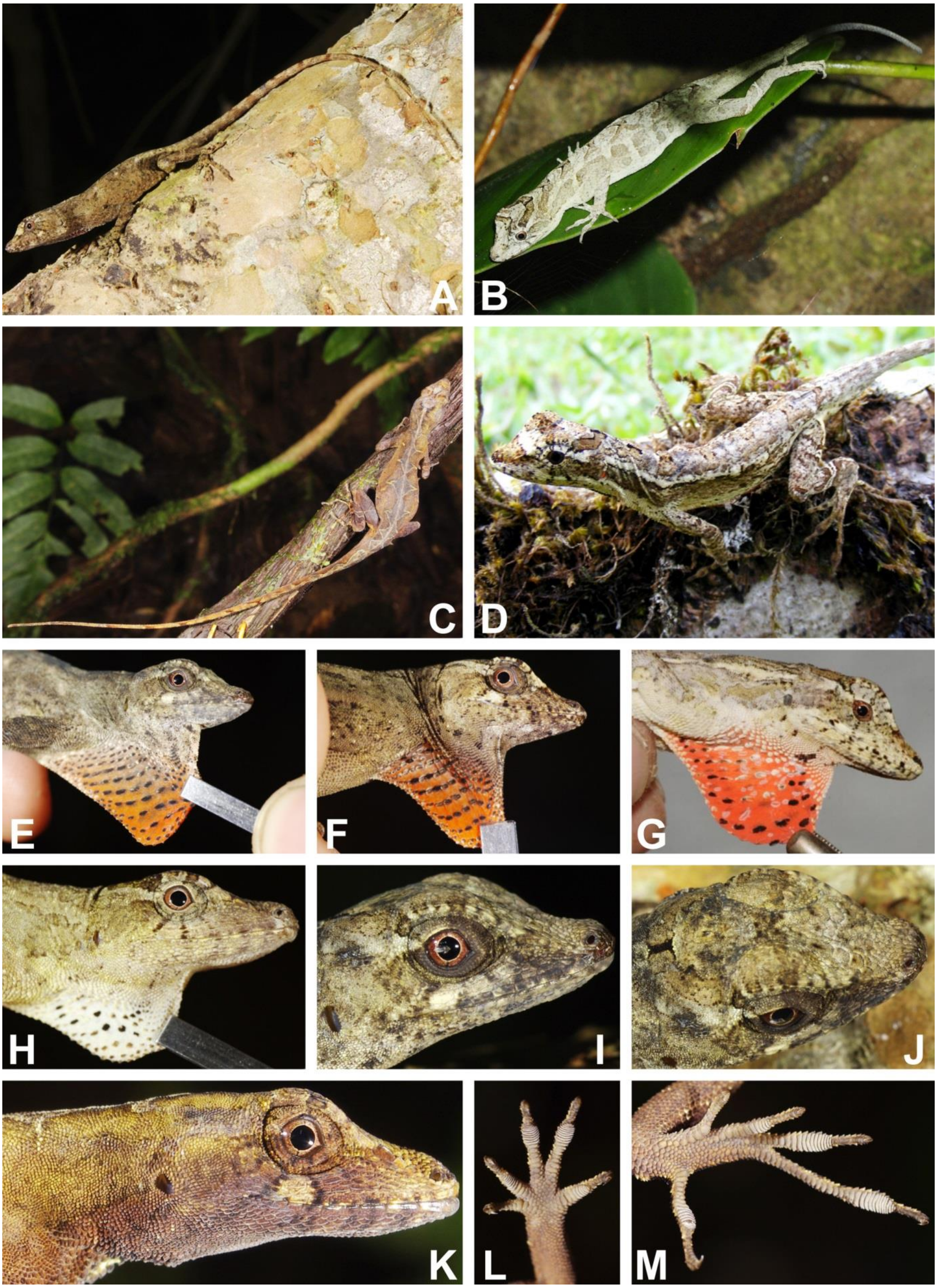


Figure 4.74: Individuals of *Norops lemurinus* from western Panama. (A) Young male SMF 90114 from San San Pond Sak; (B) female SMF 90115 from San San Pond Sak in sleeping position; (C) female SMF 91486 from Río Hacha; (D) male SMF 89496 from Cerro Mariposa; (E–G) male dewlaps of (E) adult MHCH 2197 from San San Pond Sak, (F) SMF 90114, and (G) SMF 89496; (H) female dewlap of SMF 91486; (I) lateral and (J) dorsal view of head of MHCH 2197; (K) detail of SMF 91486 showing small, granular scales anterior and posterior to ear; (L) left hand and (M) left foot of SMF 91486.

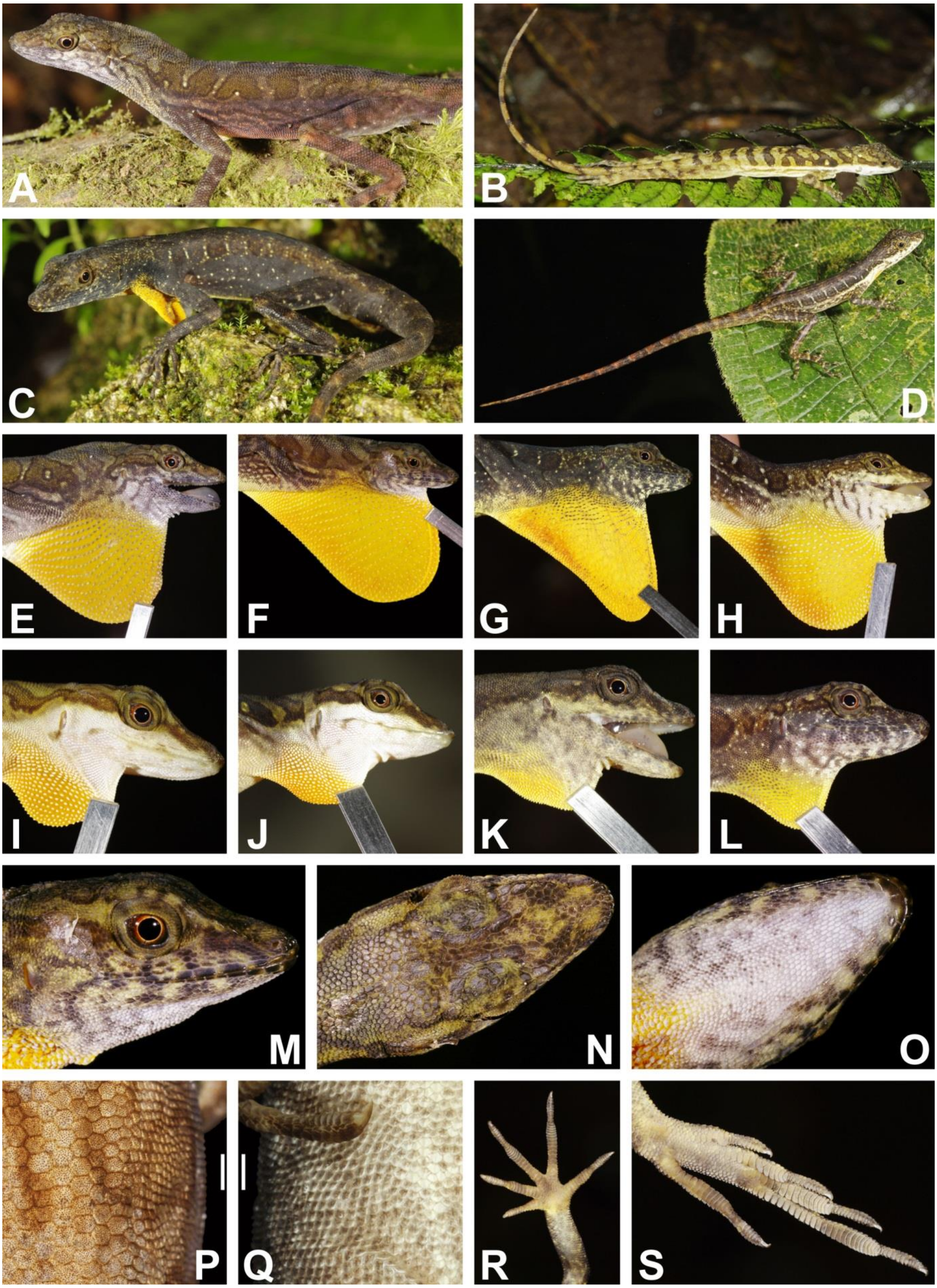


Figure 4.75: Individuals of *Norops lionotus* from western Panama. (A) Male MHCH 2218 from Cerro Negro; (B) female MHCH 2221 from Cerro Mariposa in sleeping position, photo rotated 90° clockwise; (C) male SMF 91496 from Río Hacha; (D) male juvenile MHCH 2219 from Willie Mazú; (E–H) male dewlaps: (E) MHCH 2218, (F) SMF 89495 from Río Chilagres, (G) SMF 91496, (H) subadult SMF 91495 from headwaters of Río Chiriquí Malí; (I–L) female dewlaps: (I) SMF 89726 from Cerro Negro, (J) MHCH 2221, (K) SMF 91497 from Río Hacha, (L) SMF 91498 from Willie Mazú; (M) lateral, (N) dorsal, and (O) ventral view of head of SMF 89495; details of right half of (P) dorsum and (Q) venter of MHCH 2218 at midbody, scale bars equal 1 mm; (R) left hand and (S) left foot of SMF 91496.

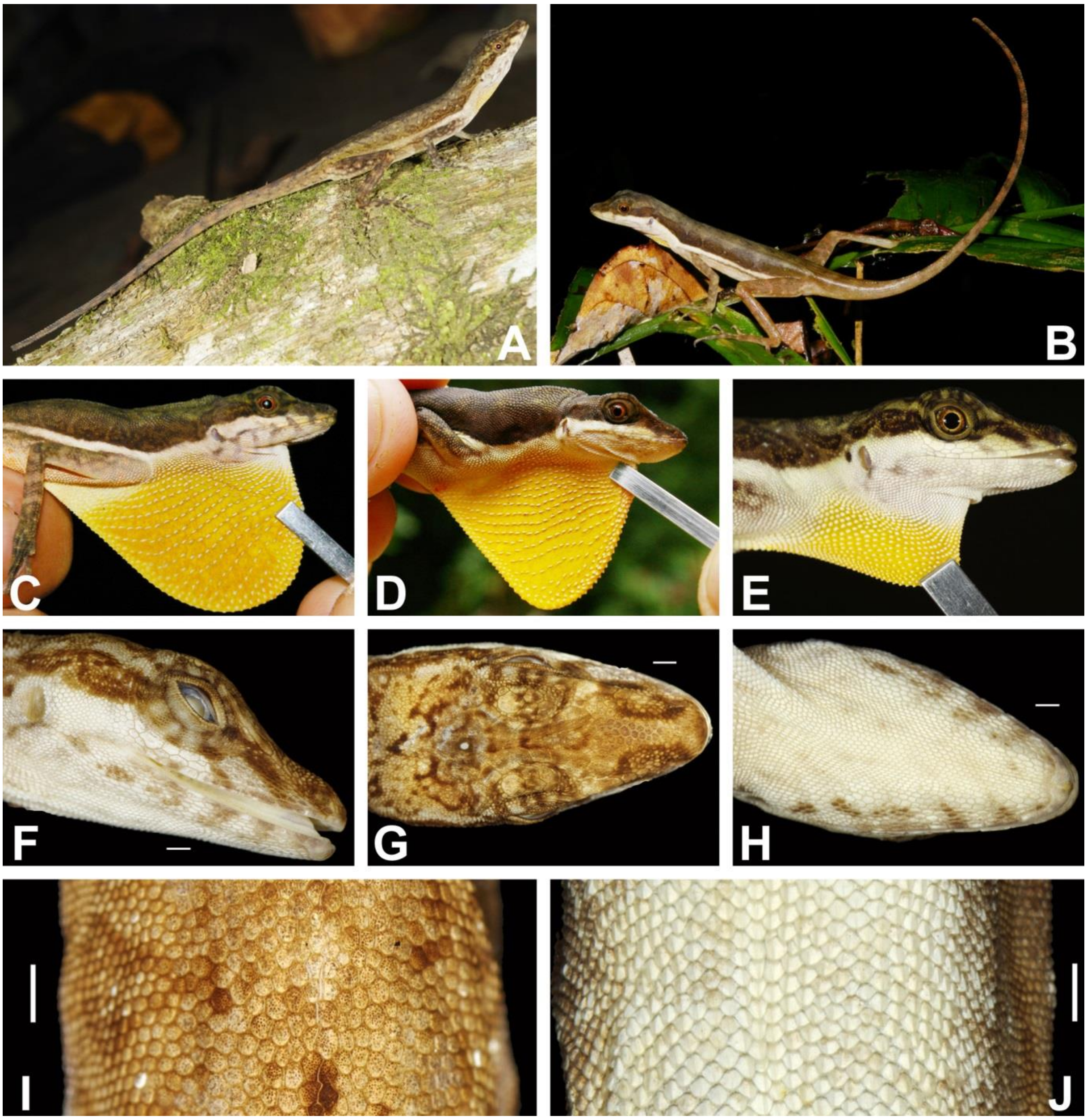


Figure 4.76: Individuals of *Norops oxylophus.* (A) Female SMF 90120 from San San Pond Sak; (B) adult male from Dos Bocas de Bartola, Nicaragua; (C) dewlap of male from Boca de San Carlos, Nicaragua; (D) dewlap of male shown in (B); (E) dewlap of female SMF 90120; (F–J) details of preserved SMF 90120, scale bars equal 1 mm: (F) lateral, (G) dorsal, and (H) ventral view of head, (I) dorsum and (J) venter at midbody.

4.1.7.5 *Norops lemurinus, Norops lionotus,* and *N. oxylophus*

The last set of anoles dealt with herein comprises medium-sized, long-legged animals whose populations in western Panama have been referred to as *Norops lemurinus* and *N. lionotus* (Köhler 2008; Jaramillo et al. 2010). Both species were described by Cope (1861c), who explicitly stated "Cocuyas de Veraguas, New Grenada" as the type locality for the latter, which can also be assumed for the former given that all types were collected by R. W. Mitchell and apparently received simultaneously by Cope. Both nominal taxa occur at low and premontane elevations at least along the Caribbean versant of the Cordillera Central. In the following, I briefly report on novel findings resulting from the analysis of COI barcodes obtained from a few individuals. Alignment specifications are given in chapter 4.1.7.2, distance matrices restricted to the individuals dealt with in this chapter in Appendix 5.7.

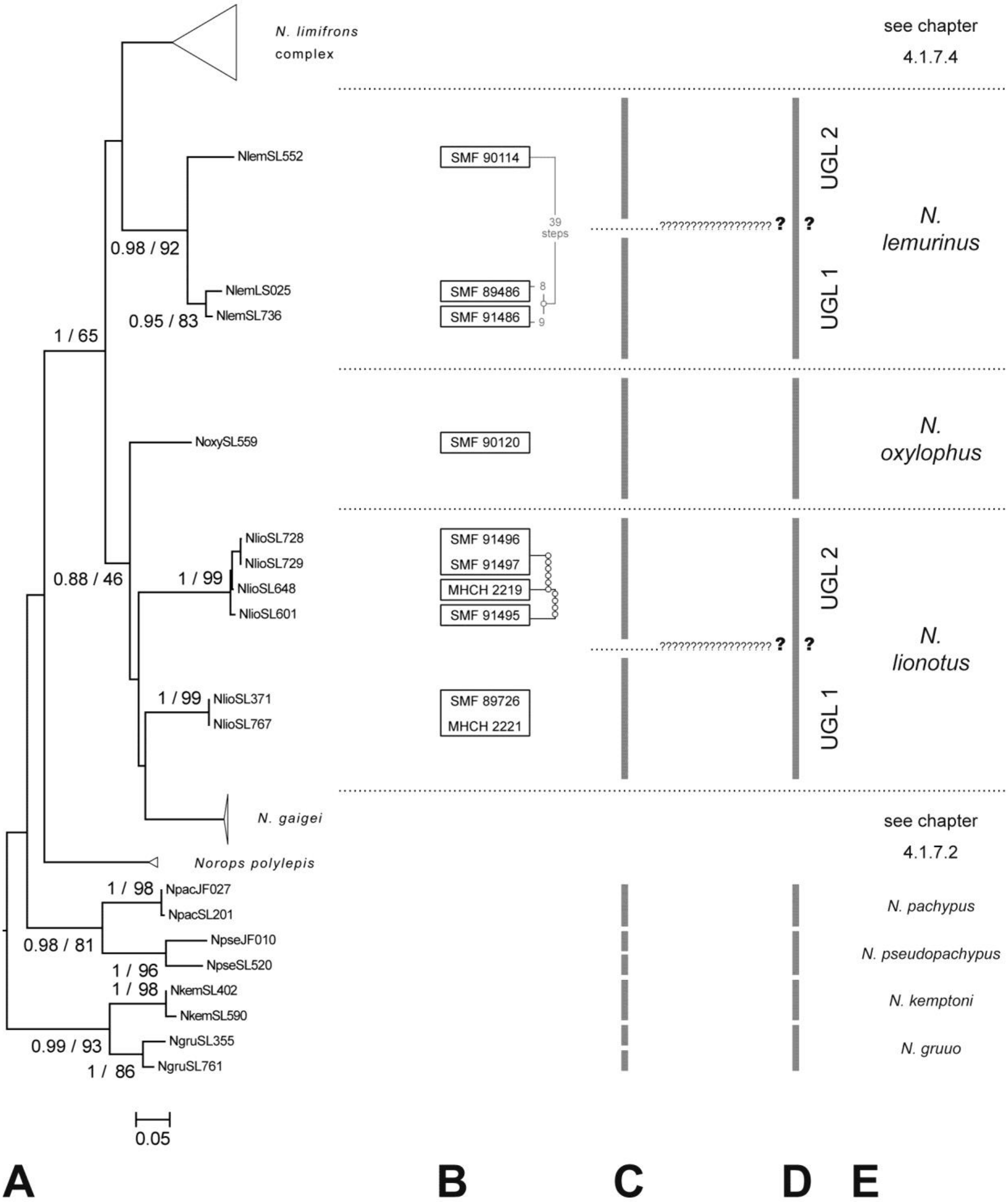
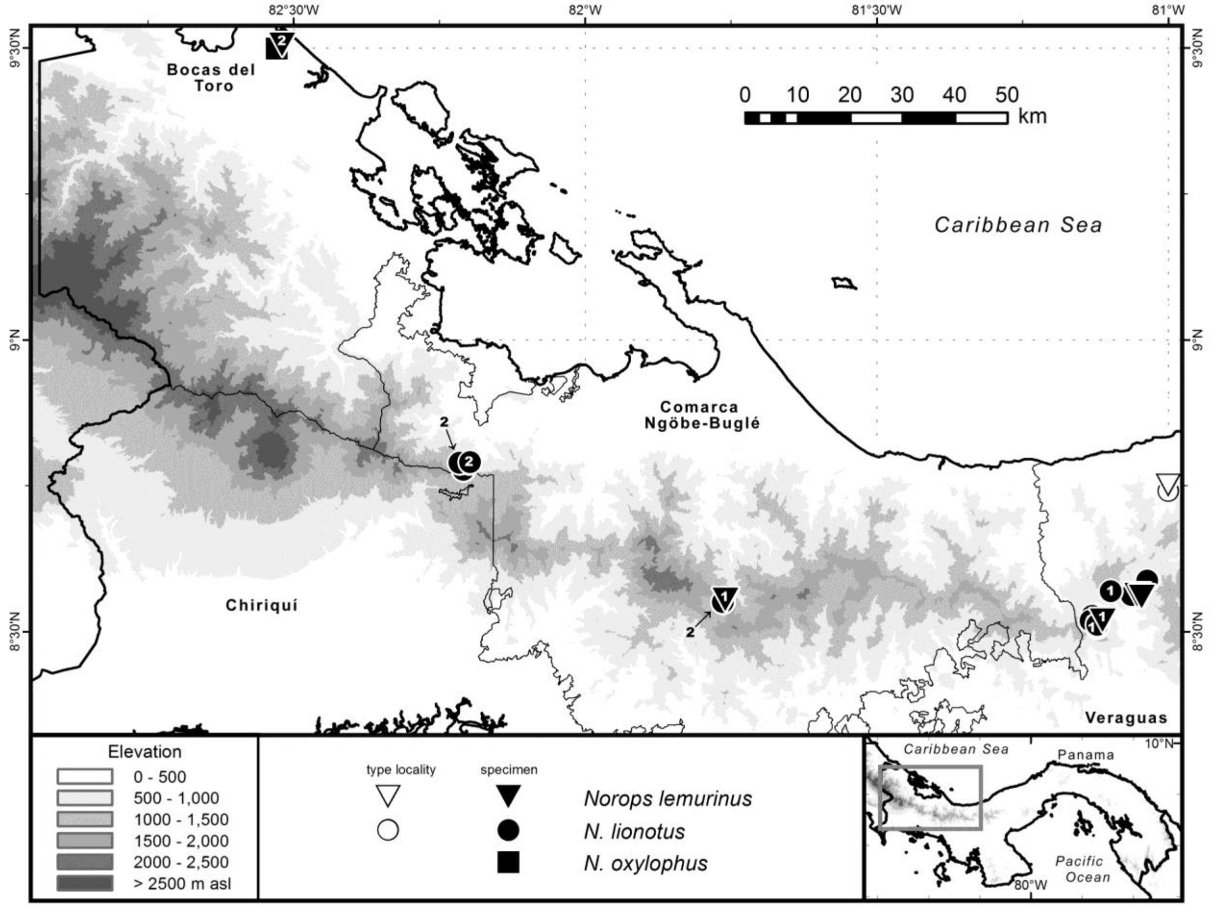


Figure 4.77: Integration of molecular and provisional morphological results for *Norops lemurinus, N. lionotus,* and *N. oxylophus.* (A) Consensus tree from ML analysis of COI barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from correspondent BI analysis, and the outgroup *Dactyloa ibanezi* is not shown. (B) Parsimony network of COI barcodes with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. (C) Lineages diagnosable through barcoding. (D) Lineages diagnosable through morphological key features as detailed by Savage (2002) and in the text. (E) Taxonomic identity of inferred CGLs.

Figure 4.77A shows the ML consensus tree of the 10 barcoded individuals, whose collection sites are plotted in Map 4.16. The three individuals readily identified as *Norops lemurinus* based on their morphology represent two distinct genealogical lineages, whereas the seven animals morphologically referable to *N. lionotus* using the key of Köhler (2008) split into three distinct clusters. For *N. lemurinus,* the specimen from San San Pond Sak representing lineage 2 is separated by 8.6% uncorrected p-distance from the lineage 1 individuals collected along the Serranía de Tabasará, which are separated by a p-distance of 3.4%. In the corresponding PN analysis (Fig. 4.77B), 17 steps or 1.7 times the connection limit calculated for a 95% parsimony probability lie between the lineage 2 individuals, while 47 and 49 steps, respectively, connect their haplotypes to that of the lineage 1 individual. In the case of *N. lionotus,* the two individuals from Veraguas representative of lineage 1 share a common haplotype. The same holds for two specimens collected at Río Hacha, which form a network with specimens from near the Fortuna depression within the 95% parsimony probability connection limit. At a manually increased connection limit of 50 steps which would connect the lineages of *N. lemurinus* or the outgroup DCLs of *N. pseudopachypus* (network not shown), the three lineages still remain unconnected. While individual p-distances between members of lineage 2 at most assume 2.1%, those between members of different lineages range from 12.0–16.7% In summary, while the two lineages found within *N. lemurinus* are about as divergent as the DCLs of *N. pseudopachypus,* the lineages revealed within what would currently be identified as *N. lionotus* exhibit a far deeper divergences than any set of lineages classified as DCLs in the preceding chapters.

Figure 4.77D sketches the results of my provisional morphological comparisons. In a preliminary screening of external morphology, I could not detect any profound, non-overlapping distinctions between the respective lineages 1 and 2 of both nominal taxa, and in consequence classify these four lineages as UGLs pending further study. The case is different with "*Norops lionotus* lineage 3", although it is represented by a single female in my sample. This specimen has a greater HL/SVL ratio than any *N. lionotus* collected farther east (1.70 vs. 1.47–1.66, mean 1.57 ± 0.056, in combined lineages 1 and 2). Most notably, this specimen exhibits a striking difference in the state and relative size of the middorsal and midventral scales (compare Figs. 4.75P and Q with 4.76I and J). While in *N. lionotus* lineage 1 and 2 the 10–14 rows of enlarged middorsals are composed of flat, smooth, and juxtaposed scales that are distinctly larger than the midventrals at least along the median rows, the lineage 3 female has 17 rows of less contrastingly enlarged, keeled, and rather subimbricate scales that are roughly equal in size to the midventrals. This characteristic has been noted and illustrated by Williams (1984: Figures 8 and 9, and Table 1) to distinguish *N. lionotus* from *N. oxylophus*

(Cope 1876). The validity of the latter taxon has been rejected, among others, by Köhler (2001, 2008) based on the results of Obermeier (1998), but tentatively accepted by Williams (1984), Savage (2002), and Jaramillo et al. (2010).



Map 4.16: Distribution of *Norops lemurinus, N. lionotus,* and *N. oxylophus* along the study area. Based on specimens examined by myself and the type localities of the former two taxa (Cope 1861c).

Weighing the small and geographically widely scattered Panamanian sample analyzed by Obermeier (1998) against the profound genetic distinctiveness of my lineage 3 specimen and the corresponding differences in dorsal scalation, I feel bound to accept the position of the latter authors. In consequence, I recognize *Norops oxylophus* as a valid species and assign this name to my lineage 3, which is accordingly classified as a CGL. This notion is supported by a preliminary screening of specimens form Costa Rica and Nicaragua that are catalogued as *N. lionotus* in the collection of SMF. The phylogenetic relationships, classification, and biogeography of *N. lionotus* and relatives are the subject of ongoing studies by GK, JFB, and myself. The three nominal species accepted herein for western Panama are illustrated in Figures 4.74–4.76 and further characterized in their respective species accounts.

4.1.8 Caenophidia, Dipsadidae: The genera *Dipsas* and *Sibon*

The closely related genera *Dipsas* and *Sibon* comprise more than four dozens of small to moderate-sized, chiefly nocturnal snakes distributed in Central and South America (Köhler 2008; Sheehy 2012; Uetz & Hošek 2014). Although the members of these genera are collectively accepted as gastropod specialists and thus called snail-eaters, several species have been shown to prey largely on other soft-bodied prey such as amphibian eggs or earthworms (Savage 2002; Sheehy 2012; Ray et al. 2012). Jaramillo et al. (2010) listed five species for each genus as present in Panama: *Dipsas articulata, D. nicholsi, D. temporalis, D. tenuissima,* and *D. viguieri,* as well as *S. annulatus, S. argus, S. lamari, S. longifrenis,* and *S. nebulatus.*

In the course of our joint field work from 2008–2010, my coworkers and I collected numerous representatives of both genera throughout my study area. The examination of these specimens revealed two hitherto undescribed species as well as unreported variation in known species. In the following, I report on the results obtained from the analysis of this and other comparative material. First, I provide a molecular glance on my snake sample. In the subsequent chapters, I present the descriptions of *Sibon perissostichon* Köhler, Lotzkat and Hertz 2010 (chapter 4.1.8.1) and *S. noalamina* Lotzkat, Hertz and Köhler 2012 (chapter 4.1.8.2). The latter includes a summary of morphological data for the species of *Sibon* occurring in my study area and LCA. Additional data for the Central American species of *Sibon* and *Dipsas* was taken from Köhler (2008), McCranie (2006a, 2011), Peters (1960), Rovito et al. (2012), Savage (2002), Savage and McDiarmid (1992), and Solórzano (2002, 2004). More information on the members of these genera occurring in my study area, including the morphological and distributional novelties revealed by the examined material, is found in their respective species accounts in chapter 4.2.2.

The manually refined final COI alignment of 49 sequences (*Sphenodon punctatus* NC_004815.1 as well as the *Dactyloa ibanezi, Norops pachypus,* and *N. pseudopachypus* already used in preceding analyes as outgoups; one boid, four viperids, 6 colubrids, and 32 dipsadids, the latter including 9 representatives of *Dipsas* and *Sibon*) contained 562 positions, of which, excluding the non-snake outgroups, 228 were variable and 214 parsimony-informative. TN93+G+I was determined as the best-fitting substitution model. For the 16S barcodes, the final alignment of 46 taxa (identical non-snake outgroups; one colubrid and 39 dipsadid snakes, the latter including 14 *Dipsas* and *Sibon*) contained 587 positions, of which, excluding the outgroups, 99 were variable and 70 parsimony-informative. TN93+G was determined as the best-fitting substitution model. The alignments and the corresponding complete distance matrices underlying the following results are provided in Appendix 5.8.

Table 4.15 shows the uncorrected p-distances calculated for the COI barcodes of the sampled representatives of *Dipsas* and *Sibon*. Between the five nominal species of these genera for which barcodes have been generated, distances range from 9.3–13.3%, and from 0.0–3.0% within nominal taxa. Uncorrected p-distances of these snail-eaters to members of other dipsadid genera are between 9.8–18.5%, those to colubrids between 15.3–19.0%, to viperids 18.0–22.3%, and 19.8–21.4% to the only barcoded boid. All nominal species including the newly described *S. noalamina* appear well separated in the ML tree that is shown in Figure 4.78A. In the PN analysis (Fig. 4.78B), a joint haplotype network of *S. annulatus* is achieved within the 95% parsimony probability connection limit of 10 steps, whereas 18 steps are required to interconnect the two haplotypes of *S. noalamina*.

Table 4.15: Uncorrected p-distances between COI barcodes of sampled specimens of *Dipsas* and *Sibon*. Individual p-distances in lower-left, mean distances between species in upper-right matrix. Mean distances within a lineage are in **bold** face.

			Sibon annulatus		***S. longifrenis***	***S. nebulatus***		***S. noalamina***		***D. temporalis***
		JFB 035	SL 144	SL 625	SL 756	SL 227	LSt 015	SL 494	SL 775	SL 770
Sibon annulatus	JFB 035									
	SL 144	0.012	**0.014**		0.097	0.106		0.105		0.116
	SL 625	0.014	0.016							
S. longifrenis	SL 756	0.100	0.098	0.093		0.114		0.108		0.101
S. nebulatus	SL 227	0.105	0.105	0.107	0.114			0.129		0.123
S. noalamina	LSt 015	0.107	0.105	0.110	0.100	0.121				
	SL 494	0.105	0.102	0.107	0.112	0.133	0.030	**0.020**		0.101
	SL 775	0.105	0.102	0.107	0.112	0.133	0.030	0.000		
Dipsas temporalis	SL 770	0.119	0.112	0.116	0.101	0.123	0.093	0.105	0.105	

Table 4.16 shows the uncorrected p-distances calculated for the 16S barcodes of the sampled representatives of *Dipsas* and *Sibon*. Between their sampled nominal species, distances range from 3.3–6.2%, and from 0.0–1.4% within nominal taxa. Uncorrected p-distances of these snail-eaters to members of other dipsadid genera range from 3.5–7.2%,

those to the only sequenced colubrid *Oxybelis brevirostris* between 7.8–9.3%. All nominal species including *S. noalamina* appear well separated in the ML tree (4.79A). Moreover, all sampled haplotypes within each species are connected within the 95% parsimony probability connection limit of 10 steps in the PN analysis (Fig. 4.79B).

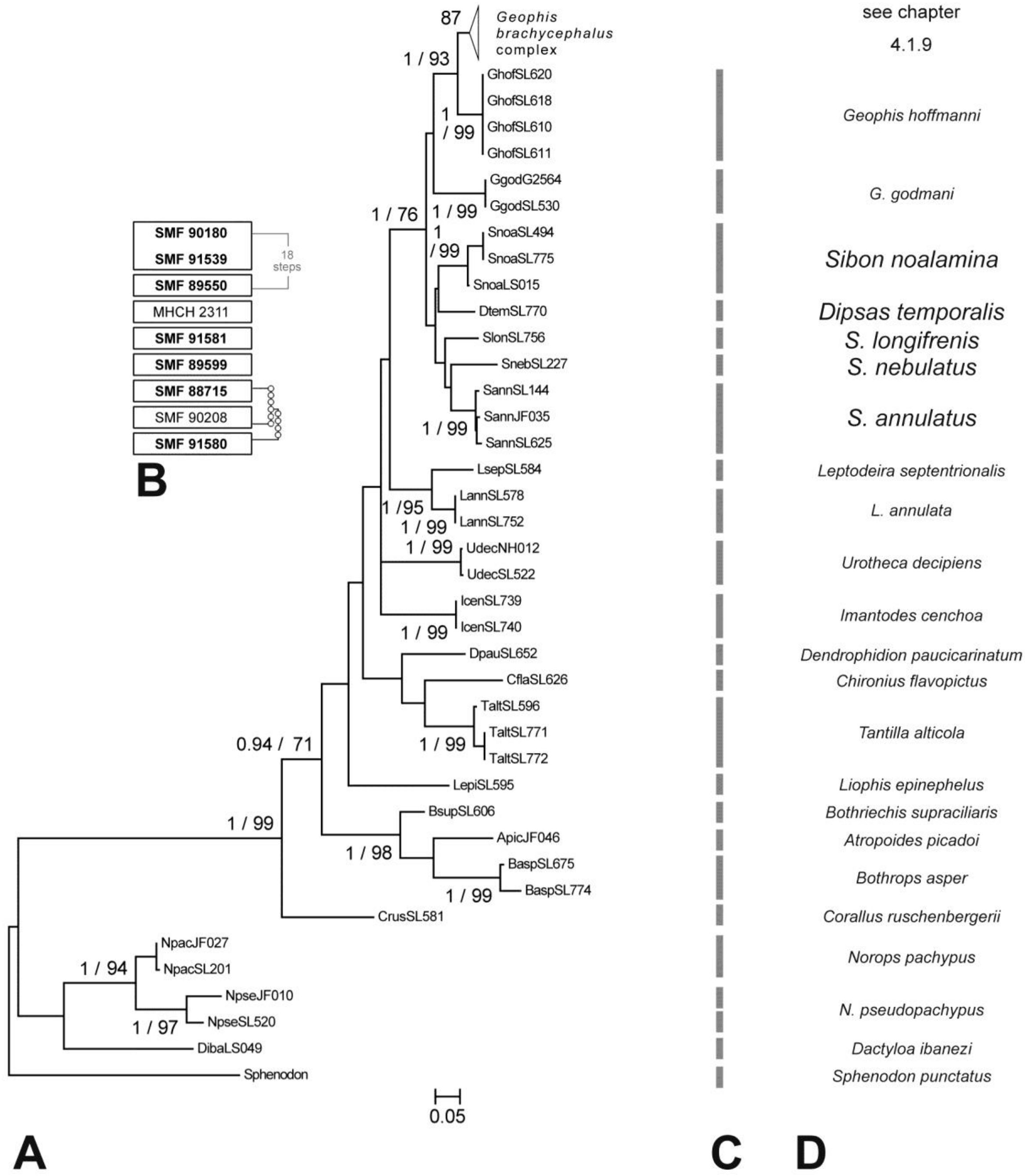


Figure 4.78: Results of analyses of the COI barcodes obtained from snake specimens. (A) Tree with the highest likelihood from ML analysis of COI barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network for the specimens of *Dipsas* and *Sibon* with a 95% parsimony probability resulting in a connection limit of 10 steps drawn with haplotype symbols; additional connections indicated by the number of necessary steps. Collection numbers in **bold** face indicate individuals for which also 16S barcodes are available. (C) Lineages diagnosable through the COI barcodes. (D) Taxonomic identity derived from morphology on the basis of available literature or own taxonomic analyses.

Table 4.16: Uncorrected p-distances between 16S barcodes of sampled specimens of *Dipsas* and *Sibon*. Individual p-distances in lower-left, mean distances between species in upper-right matrix. Mean distances within a lineage are in **bold** face.

		Sibon annulatus						***S. longifrenis***	***S. nebulatus***		***S. noalamina***			***Dipsas temporalis***	
		SL 700	SL 144	SL 379	SL 625	SL 769	SL 496	SL 756	LSt 055	SL 227	LSt 015	SL 494	SL 775	LSt 110	SL 382
Sibon annulatus	SL 700				**0.007**			0.059	0.049			0.054			0.042
	SL 144	0.013													
	SL 379	0.013	0.008												
	SL 625	0.014	0.008	0.000											
	SL 769	0.013	0.008	0.000	0.000										
	SL 496	0.010	0.004	0.004	0.004	0.004									
S. longifrenis	SL 756	0.052	0.062	0.060	0.062	0.060	0.058		0.041			0.056			0.050
S. nebulatus	LSt 055	0.048	0.056	0.052	0.054	0.052	0.052	0.044	**0.006**			0.047			0.040
	SL 227	0.042	0.050	0.046	0.048	0.046	0.046	0.039							
S. noalamina	LSt 015	0.052	0.056	0.048	0.048	0.048	0.052	0.054	0.048	0.044		**0.006**			0.037
	SL 494	0.054	0.061	0.054	0.054	0.054	0.058	0.058	0.048	0.048	0.010				
	SL 775	0.054	0.061	0.054	0.054	0.054	0.058	0.058	0.048	0.048	0.010	0.000			
Dipsas temporalis	LSt 110	0.037	0.046	0.042	0.044	0.042	0.042	0.050	0.042	0.039	0.033	0.038	0.038		
	SL 382	0.037	0.046	0.042	0.044	0.042	0.042	0.050	0.042	0.039	0.033	0.038	0.038	0.000	

Recently, Sheehy (2012) provided a molecular phylogeny of the Dipsadinae that revealed several nominal taxa of *Dipsas* and *Sibon* to comprise separate lineages so deeply divergent that they should warrant recognition as separate species. Since among these nomina were *D. temporalis* (accordingly already called "*Dipsas* sp." by Ray et al. 2012), *S. annulatus,* and *S. nebulatus,* it should be noted that each of these nominal taxa is represented by a sole lineage in my sample, i.e., that the respective specimens of *D. temporalis* (from Cerro Negro and Cerro Mariposa), *S. annulatus* (from throughout my study area, see Map 4.17), and *S. nebulatus* (from Veraguas and Chiriquí, see Map 4.17) barcoded for the present study are clearly conspecific. The interesting question to which of the lineages revealed by Sheehy (2012) my sampled *S. annulatus* and *S. nebulatus* pertain is the subject of ongoing studies. Moreover, Sheehy (2012) inferred the holotype of the morphologically well-diagnosable *S. perissostichon,* for which my barcoding attempts failed, as the sister taxon to *S. annulatus* from Costa Rica and Nicaragua. The morphologically unquestionable new species *S. noalamina* described below (chapter 4.1.8.2) is perfectly supported by DNA barcoding.

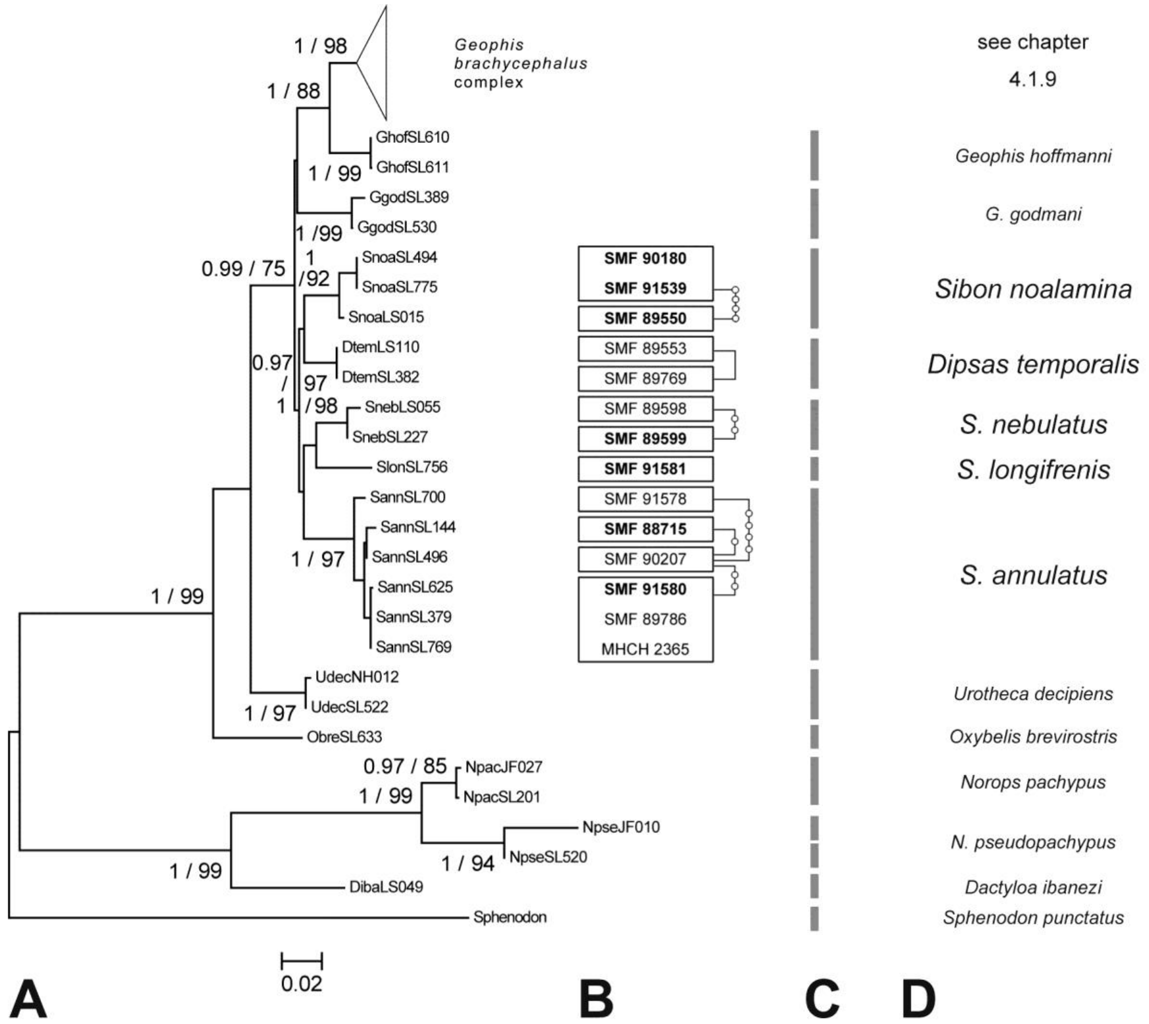


Figure 4.79: Results of analyses of the 16S barcodes obtained from snake specimens. (A) Consensus tree from ML analysis of 16S barcodes; bootstrap values shown at selected nodes are preceded by posterior probabilities from BI analysis. (B) Parsimony network for the specimens of *Dipsas* and *Sibon* with a 95% parsimony probability resulting in a connection limit of 10 steps. Collection numbers in **bold** face indicate individuals for which also COI barcodes are available. (C) Lineages diagnosable through the 16S barcodes. (D) Taxonomic identity derived from morphology on the basis of available literature or own taxonomic analyses.

4.1.8.1 *Sibon perissostichon* – a new species of *Sibon* from western Panama

[Modified from Köhler et al. (2010a); see Appendix 8 for original publication]

Abstract: We describe a new species of *Sibon* from the Reserva Forestal La Fortuna, Chiriquí Province, Panama. The new species is distinguished from all species presently assigned to *Sibon* by having 17 rows of dorsal scales at midbody and 15 rows one head length anterior to

cloaca (versus 13 or 15 rows of dorsal scales at midbody without reduction on posterior portion of body in all other species of *Sibon*), and dorsal scale rows that change orientation from the sides of body towards middorsum (versus maintaining more or less the same orientation).

Key words: Colubridae, new species, Panama, *Sibon,* Squamata.

On the evening of 14.05.2008, in the company of AH and NH, I found a female specimen of *Sibon* that differs differs strikingly from all its congeners in the number and arrangement of dorsal scale rows. Comparisons with the known species of *Sibon* from Central America demonstrated that this specimen represents an undescribed species. The core of the species description is provided below. An exclusive list of the material examined for this description by GK is provided in the Appendix of the original publication.

Sibon perissostichon Köhler, Lotzkat and Hertz 2010

Figures 4.80A; 4.81; 4.84; 4.112A; Maps 4.17; 4.168.

Holotype. SMF 88716 (Figs. 4.80A; 4.81; 4.84; 4.112A), adult female as judged by the shape of the base of the tail, collected near Lost & Found Ecohostel, Reserva Forestal La Fortuna, 8.67443°N, 82.21611°W, 1434 m asl, by Sebastian Lotzkat on 14 May 2008. Original field number SL 145.

Diagnosis. *Sibon perissostichon* can be distinguished from its congeners by having 17 rows of dorsal scales at midbody and 15 rows one head length anterior to cloaca (versus 13 or 15 rows of dorsal scales at midbody without reduction on posterior portion of body in all other species of *Sibon* except *S. nebulatus,* which occasionally has reductions from 15 to 13 according to Peters 1960), and dorsal scale rows that change orientation from the sides of body towards middorsum (versus maintaining more or less the same orientation).

Additionally, *Sibon perissostichon* differs from its congeners by the following characteristics: Ventrals 186 in *S. perissostichon* vs. 171–185 in female *S. annulatus* from Panama. Light interspaces between dark bands on body Sayal Brown (223C) in S. *perissostichon* vs. interspaces orange to red-orange middorsally, grading to cream laterally in *S. anthracops*. Enlarged penultimate supralabial not in contact with eye in *S. perissostichon* vs. this scale usually in contact with eye in *S. argus* and *S. longifrenis*. Also, dark dorsal bands or spots reach well onto venter or even across venter in *S. perissostichon* vs. dark dorsal bands or spots reach at most to outer edges of ventrals, although dark shading may be present on venter in *S. argus* and *S. longifrenis*. One anterior temporal present in *S. perissostichon* vs. no such scale in *S. carri*. Therefore, penultimate supralabial not in contact with parietal in *S. perissostichon* vs. these scales in contact in *S. carri*. Bands solid dark brown, darker than interspaces in *S. perissostichon* vs. bands dark brown ventrally, their centers paler brown, paler than interspaces in *S. dimidiatus*. Dorsal surface of head with black markings, ground color of body brown, postmental single in *S. perissostichon* vs. dorsal surface of head with green or yellow as well as red and black markings, ground color of body green, and postmental divided in *S. lamari*. Ventrals 186, loreal in contact with eye in *S. perissostichon* vs. ventrals 155, loreal separated from eye in only known female specimen of *S. linearis*. Dark dorsal bands present, reaching well onto venter or even across venter in *S. perissostichon* vs. usually no dark dorsal bands and venter immaculate in *S. manzanaresi* and *S. sanniolus*. Ventrals 186, subcaudals 108, bands solid dark brown, darker than interspaces in *S. perissostichon* vs. ventrals 168–171 in females, subcaudals 95–100 in females, bands dark brown ventrally but their centers paler than interspaces in *S. miskitus*. Postmental present, therefore, first infralabials not in contact with each other in *S. perissostichon* vs. no postmental, first infralabials in contact with each other, in *S. nebulatus*.

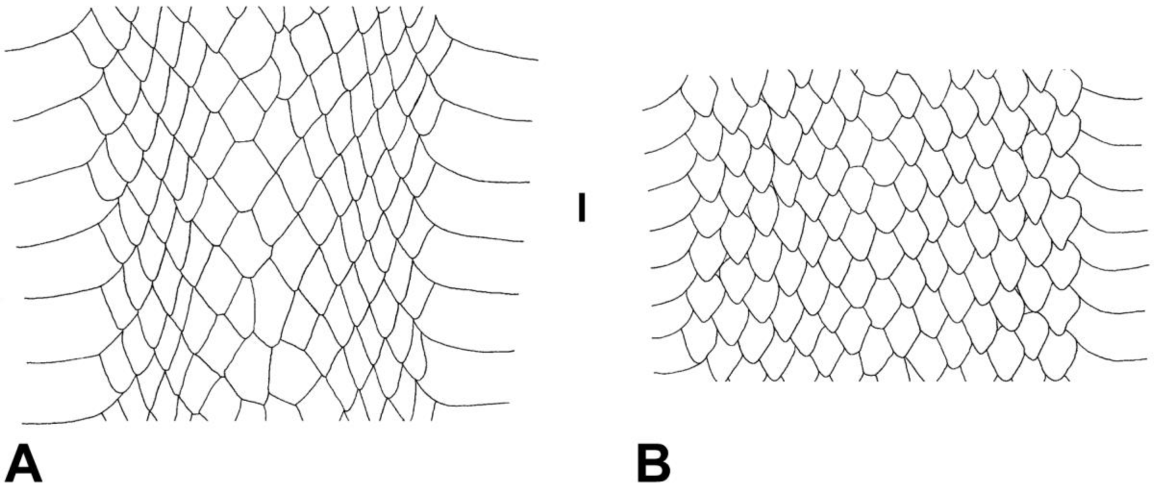


Figure 4.80: Scalation at midbody of (A) *Sibon perissostichon* (SMF 88716) and (B) *S. annulatus* (SMF 88715). Scale bar equals 1 mm. Drawing by Andreas Hertz.

Description of the holotype. Adult female (Figs. 4.80A, 4.81, 4.84; 4.112A); SVL 458 mm, TL 210 mm; HL 15.0 mm; HW 9.0 mm; SL 4.2 mm. Head very distinct from neck; snout short, blunt in dorsal and lateral outline; rostral wider (2.6 mm) than high (2.0 mm), not extending posteriorly between internasals, its length visible from above one quarter length of median internasal suture (1.2 mm); internasals shorter (1.5 mm) than wide (2.0 mm), two-thirds length of prefrontal suture (2.6 mm); prefrontals longer (2.6 mm) than wide (2.2 mm), their median suture two-thirds length of frontal; prefrontals bordering eye above loreal; frontal longer (4.1 mm) than wide (3.5 mm), widest anteriorly, length two-thirds that of parietal, in contact with prefrontals, supraoculars, and parietals; supraoculars longer (3.6 mm) than wide (1.6 mm), nearly as long as frontal; parietals longer (5.9 mm) than wide (3.8 mm), widest anteriorly, their median suture (4.4 mm) slightly longer than frontal; parietals in contact with frontal, supraoculars, upper postoculars, anterior and posterior temporals, and eight nuchal scales; nasal divided, in contact with first two supralabials, loreal, prefrontal, internasal, and rostral; loreal single, longer (1.6 mm) than high (0.7 mm), its length less than one-half length of snout (tip of snout to anterior edge of eye) and one-half length of eye (3.3 mm); preoculars absent; postoculars three (right) and two (left); temporals 1+3, anterior one above fifth supralabial, lowest posterior one above sixth supralabial; supralabials six, with third and fourth/fourth bordering eye (enlarged penultimate supralabial separated from eye by lower postocular); pupil vertically elliptical; eye length two times length of loreal; infralabials seven, first pair separated posterior to mental by a single, triangular postmental, first infralabial in contact with postmental, infralabials 2–5 in contact with anterior chin shields; anterior chin shields paired, longer (5.6 mm) than wide (1.6 mm), longer than posterior chin shields; posterior chin shields longer (3.4 mm) than wide (2.5 mm), paired, in broad contact medially; mental groove present; ventrals 186; cloacal scute single; subcaudals 108, divided except for third and forth pairs that are fused; ventrals plus subcaudals 294; dorsal scales smooth, in 15–17–15 rows, without apical pits or supracloacal ridges; dorsal scale rows changing orientation from the sides of body towards middorsum; vertebral row not enlarged.

Color in life. Dorsal ground color Sayal Brown (223C) with Sepia (119) blotches reaching onto venter, mostly continuous across venter, some ventrally offset; ventral surface between dark blotches dirty white, suffused with Buff (124) and mottled with Sepia (119); dorsal surface of head Verona Brown (223B) with Jet Black (89) blotches; ventral surface of head dirty white with Raw Umber (223) mottling and Jet Black (89) chin shields and first ventral scale; iris Mars Brown (223A). Color in preservative (70% ethanol) similar to color in life.

Etymology. The name *perissostichon* is a noun in aposition and is derived from the Greek words *perissos* (beyond the regular number or size) and *stichos* (row, line), referring to the high number of dorsal scale rows in this species.

Natural history notes. See species account in chapter 4.2.2.

Geographic distribution. Known only from the type locality (Maps 4.17 and 4.168).

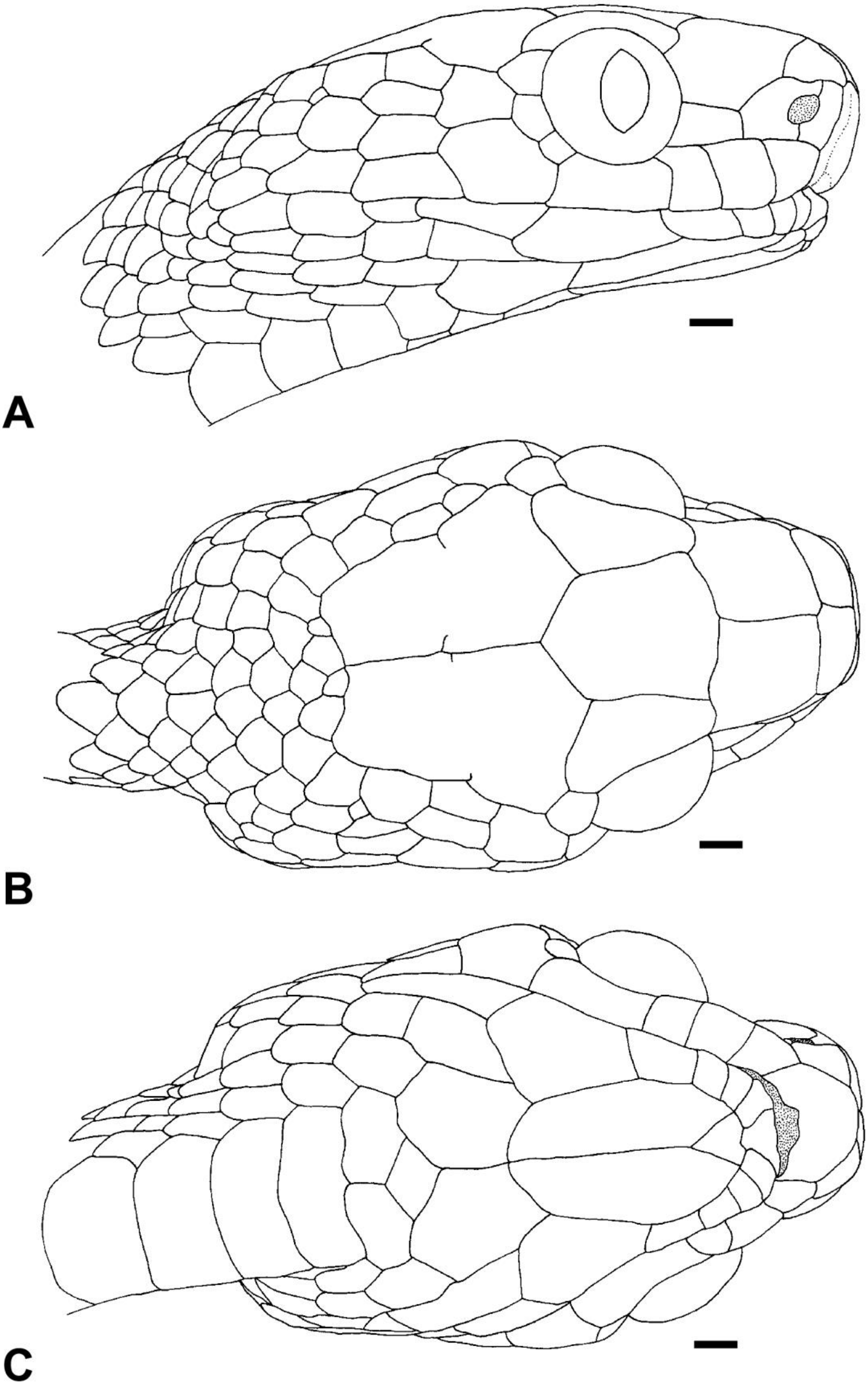


Figure 4.81: Head of holotype (SMF 88716) of *Sibon perissostichon* in (A) lateral, (B) dorsal, and (C) ventral view. Scale bars equal 1 mm.

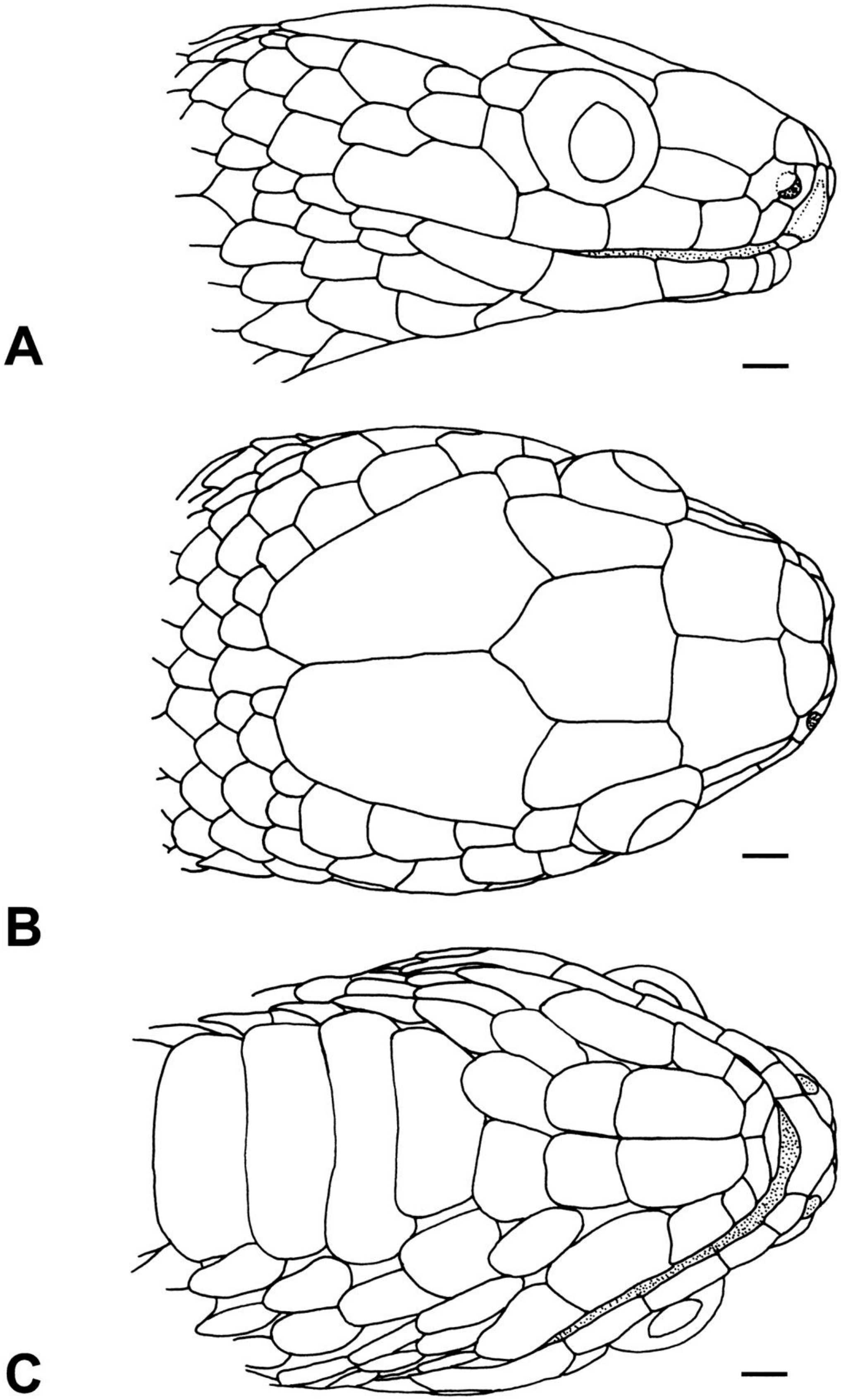


Figure 4.82: Head of holotype (SMF 91539) of *Sibon noalamina* in (A) lateral, (B) dorsal, and (C) ventral view. Scale bars equal 1 mm.

4.1.8.2 *Sibon noalamina* – another new species of *Sibon* from western Panama, with comments on other species of the genus in this area

[Modified from Lotzkat et al. (2012d); see Appendix 8 for original publication]

Abstract: We describe *Sibon noalamina* sp. nov. from the Caribbean versant of the Cordillera Central, in the Comarca Ngöbe-Buglé and the province of Veraguas of western Panama. Due to its coral snake-like, bicolored pattern, the new species superficially resembles *Sibon anthracops, Dipsas articulata, D. bicolor, D. temporalis,* and *D. viguieri.* It differs from these species, and from all its congeners, by having only five supralabials, by the unique shape of the posterior supralabial, and by a slight keeling on some dorsal rows in adults. We provide morphological data as well as an updated key to the Lower Central American species of *Sibon*.

Key words: snail-eater, *Dipsas*, Chiriquí, Comarca Ngöbe-Buglé, Bocas del Toro, Veraguas, conservation, distribution extension, morphology.

In May 2008, AH and myself found a hatchling snail-eater in the cloud forest on Cerro Mariposa, which we tentatively identified as *Dipsas articulata* based on its general appearance. In October 2009 we collected a similar specimen at the headwaters of Río Chiriquí Malí, which I catalogued under the same name. At the same locality, towards the end of our very last night sampling in Panama, AH spotted an adult specimen of *Sibon* that differs profoundly from all its congeners in the number and condition of its supralabial scales and other characters. Only in the course of closer examination of my snake material in the laboratory it became clear that the aforementioned two juveniles are conspecific with this adult specimen. Comparisons with the known species of *Dipsas* and *Sibon* from Central America confirmed that these specimens represent an undescribed species. The core of the species description is provided below. Scale dimensions were only taken from the holotype. An exclusive list of the material examined for this description by GK and myself is provided in the Appendix of the original publication.

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Figures 4.82; 4.83; 4.85; 4.111H; Maps 4.17; 4.167.

Holotype. SMF 91539 (original field number SL 775; Figs. 4.82, 4.83, 4.85A–C; 4.111H), adult male as indicated by everted hemipenes, from headwaters of Río Chiriquí Malí, approximately 6.4 km NNE Fortuna dam (8.7891°N, 82.2155°W, 1050 m asl), Bosque Protector Palo Seco, Comarca Ngöbe-Buglé (formerly province of Bocas del Toro), Panama; collected by Andreas Hertz and Sebastian Lotzkat on 10 August 2010.

Paratypes. SMF 90180 (original field number SL 494; Fig 4.85D), juvenile male, same locality as holotype; collected by AH and SL on 29 October 2009; SMF 89550 (original field number LSt 015; Fig 4.85E), juvenile, from Cerro Mariposa near Alto de Piedra, approx. 3.5 km W of Santa Fé, 8.5001°N, 81.1170°W, 1260 m, province of Veraguas, Panama; collected by SL and AH on 28 May 2008.

Diagnosis. *Sibon noalamina* differs from all described species of *Sibon,* and in fact from all other Central American snail-eaters, in its slight keeling on the third to fifth dorsal row at midbody in adults, and, most obviously, in having only five supralabials, with the fifth and ultimate one being the only supralabial posterior to the orbit (versus two supralabials posterior to orbit in all other species of *Sibon*) and exhibiting a peculiar shape: Its anterior portion is almost twice as high as the remaining supralabials, resembling the enlarged penultimate supralabial of other *Sibon*. Then it decreases in height towards the posterior portion that is about as high as the third supralabial, resembling the ultimate, usually moderately-sized, supralabial of other *Sibon*.

Additionally, its contrasting color pattern of complete dark rings on light background distinguishes *Sibon noalamina* from all Lower Central American *Sibon* except *S. anthracops,* from which it differs by having 15 dorsal rows throughout the body (vs. 13 in *S. anthracops*). At first sight, especially the more contrastingly colored juveniles of the new species might be confused with the coral snake-mimics *Dipsas articulata, D. bicolor, D. temporalis,* or *D. viguieri.* From these, *S. noalamina* is distinguished by the presence of a mental groove (lacking in the genus *Dipsas*), lower ventral counts (164–177 vs. 196–217 in *D. articulata*, 186–199 in *D. bicolor,* 170–208 in *D. temporalis,* and 190–203 in *D. viguieri*), the unique supralabial condition (5 supralabials with only the ultimate, peculiarly shaped one posterior to orbit versus 9–10 supralabials in *D. articulata,* 10–11 in *D. bicolor,* 7–8 in *D. temporalis,* and 9–10 in *D. viguieri,* all shaped similarly, with typically three or more, rarely just two, posterior to orbit), and fewer infralabials (6–7 infralabials versus 11–12 in *D. articulata,* 10–11 in *D. bicolor,* 8–13 in *D. temporalis,* and 9–11 in *D. viguieri*). Furthermore, *S. noalamina* differs from *D. temporalis* in retaining the contrast between light and dark rings throughout body and tail (Fig. 4.85), whereas in *D. temporalis* the light portions grade into medium to dark brown posteriorly (Fig. 4.86).

Description of the holotype. Adult male (Figs. 4.82; 4.83; 4.85A–C; 4.111H), as indicated by everted hemipenes; SVL 385 mm, TL 161 mm (but tail incomplete); TOL 546 mm; HL 12.4 mm; HW 8.2 mm; SL 3.5 mm. Head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral wider (2.1 mm) than high (1.3 mm), not extending posteriorly between internasals, its length visible from above one fifth length of median internasal suture (1.0 mm); internasals shorter (1.1 mm) than wide (1.7 mm), their length between one half and two-thirds length of prefrontal suture (1.9 mm); prefrontals shorter (2.5 mm) than wide (2.8 mm), their median suture (2.1 mm) about three-fifths length of frontal; prefrontals bordering eye above loreal; frontal longer (3.6 mm) than wide (3.0 mm), widest anteriorly, length almost two-thirds that of parietal, in contact with prefrontals, supraoculars, and parietals; supraoculars longer (3.4 mm) than wide (1.7 mm), nearly as long as frontal; parietals longer (5.8 mm) than wide (3.8 mm), widest anteriorly, their median suture (4.1 mm) slightly longer than frontal; parietals in contact with frontal, supraoculars, upper postoculars, anterior and posterior temporals, and nine nuchal scales; nasal divided, in contact with first two supralabials, loreal, prefrontal, internasal, and rostral; loreal single, longer (1.9 mm) than high (1.0 mm), its length more than one-half length of snout, and two-thirds length of eye (2.8 mm); preoculars absent; postoculars 2; temporals 1+2/2+2, all above fifth supralabial; supralabials five, with third and fourth bordering eye (enlarged anterior portion of ultimate supralabial separated from eye by lower postocular); fifth and ultimate supralabial conspicuously long (3.9 mm), longer than combined lengths of third and fourth supralabials, with a higher (1.7 mm) anterior and a lower (1.2 mm) posterior portion; pupil vertically elliptical; eye length one and a half times length of loreal; infralabials 6, first pair in contact behind mental; no postmental; infralabials 1–4 in contact with anterior chin shields; anterior chin shields paired, longer (2.8 mm) than wide (1.3 mm), longer than posterior chin shields; posterior chin shields longer (1.9 mm) than wide (1.4 mm), paired, in broad contact medially; mental groove present; ventrals 170; cloacal scute single; subcaudals 80 (but tail incomplete), divided; ventrals plus subcaudals 250 (but tail incomplete); dorsal scales mostly smooth, but slightly keeled on dorsal rows 3–5 around midbody, striate, in 15–15–15 rows, without apical pits or supracloacal ridges; vertebral row slightly enlarged.

The fully everted hemipenis (Fig. 4.83) is a stout unilobed capitate organ; the capitulum is covered by calyces bearing spinules; no naked pocket; the sulcus spermaticus is bordered by well-developed sulcal lips, bifurcates at the base of apex with the branches continuing onto the apex; truncus with two series of large recurved spines.

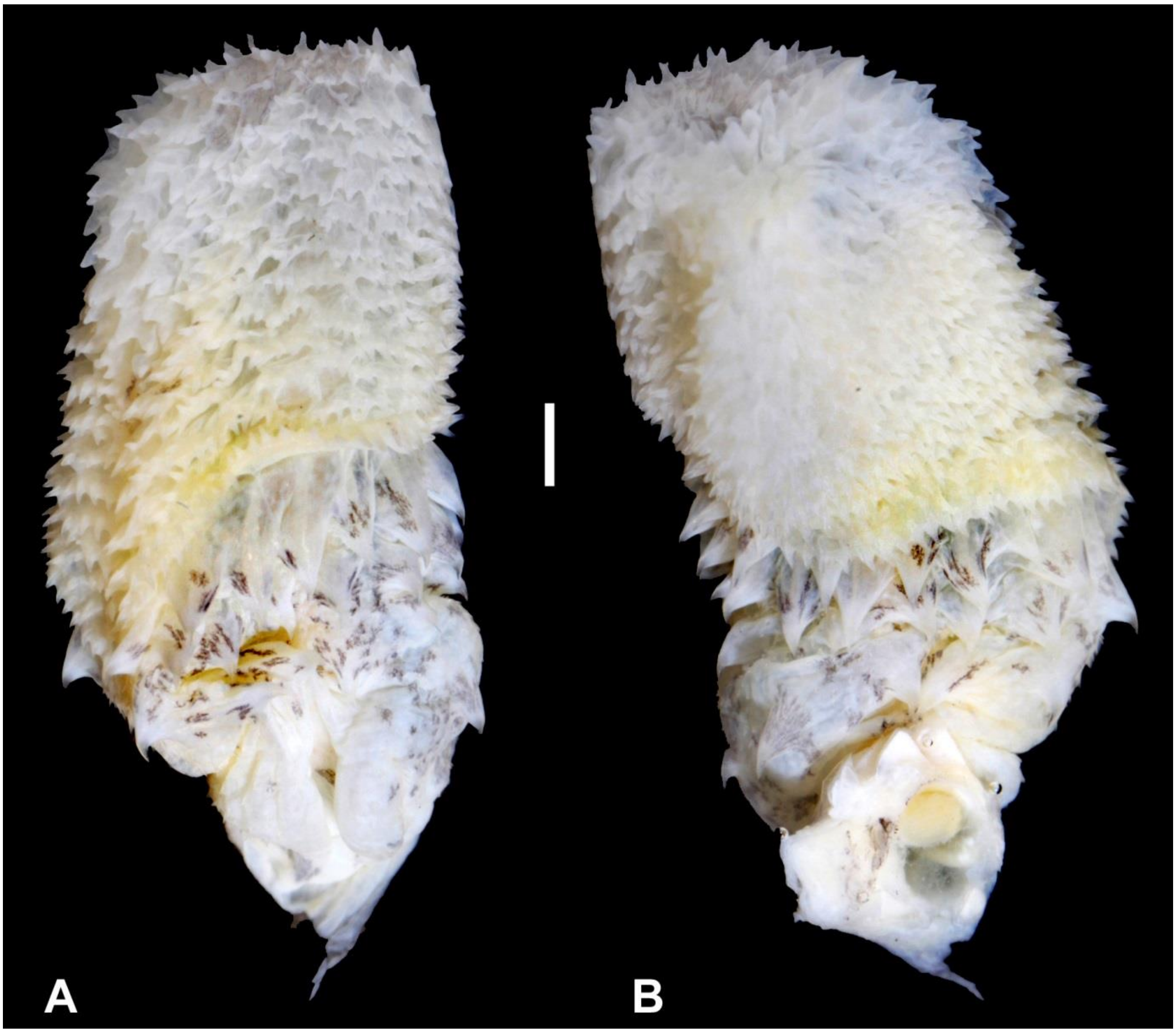


Figure 4.83: Hemipenis of Holotype (SMF 91539) of *Sibon noalamina* in (A) sulcate and (B) asulcate view. Scale bar equals 1 mm. Photos by GK.

Coloration in life. Dorsal, lateral, and ventral surfaces of body and tail Pale Horn Color (92); body with 14, tail with eight broad Sepia (219) rings, body rings extending over 6–12 middorsal scales, narrowing towards and on venter; interspaces between these rings extending over 3–6 middorsal scales, speckled with Sepia (219) except for narrow portions immediately adjacent to the dark rings; tip of (incomplete) tail Sepia (119); dorsal and lateral surfaces of head Pale Horn Color (92), grading into Flesh Ocher (132D) anteriorly, heavily mottled with Sepia (219); parietals, frontal, and central portions of prefrontals almost completely Sepia (219), as well as the middorsal scales of the first two transverse rows of dorsals posterior to parietals, connecting Sepia (219) coloration to first body ring; ventral surface of head Pale Horn Color (92) mottled with Sepia (219), especially on infralabials; iris Sepia (119). Color after ten months in preservative (70% ethanol) is similar to that in life, apart from that all yellow and orange shades have faded.

Variation. The juvenile paratypes (SMF 89550, Fig. 4.83E; and SMF 90180, Fig. 4.83D) agree well with the holotype in terms of general morphology and pholidosis (even in their tails being incomplete), differing mostly in their lack of any keels on dorsal rows 3–5 and in their somewhat more contrasting coloration. Scale counts that differ from that of the holotype are as follows: ventrals 164 (SMF 89550), 177 (SMF 90180); subcaudals 93, 96 (both tails are incomplete); ventrals plus subcaudals 257, 273 (but both tails are incomplete); temporals 1+2/1+2 in both, anterior temporals of both sides entering orbit between upper and lower postoculars (SMF 89550); parietals bordered posteriorly by 8 nuchal scales in both; infralabials 6/7, 1–5 in contact with first chin shield on left side (SMF 89550). Body measurements of the juvenile specimens are SVL 178 mm, TL 68 mm (SMF 89550), SVL 161 mm, TL 64 mm (SMF 90180). For variation in coloration see species account in chapter 4.2.2.

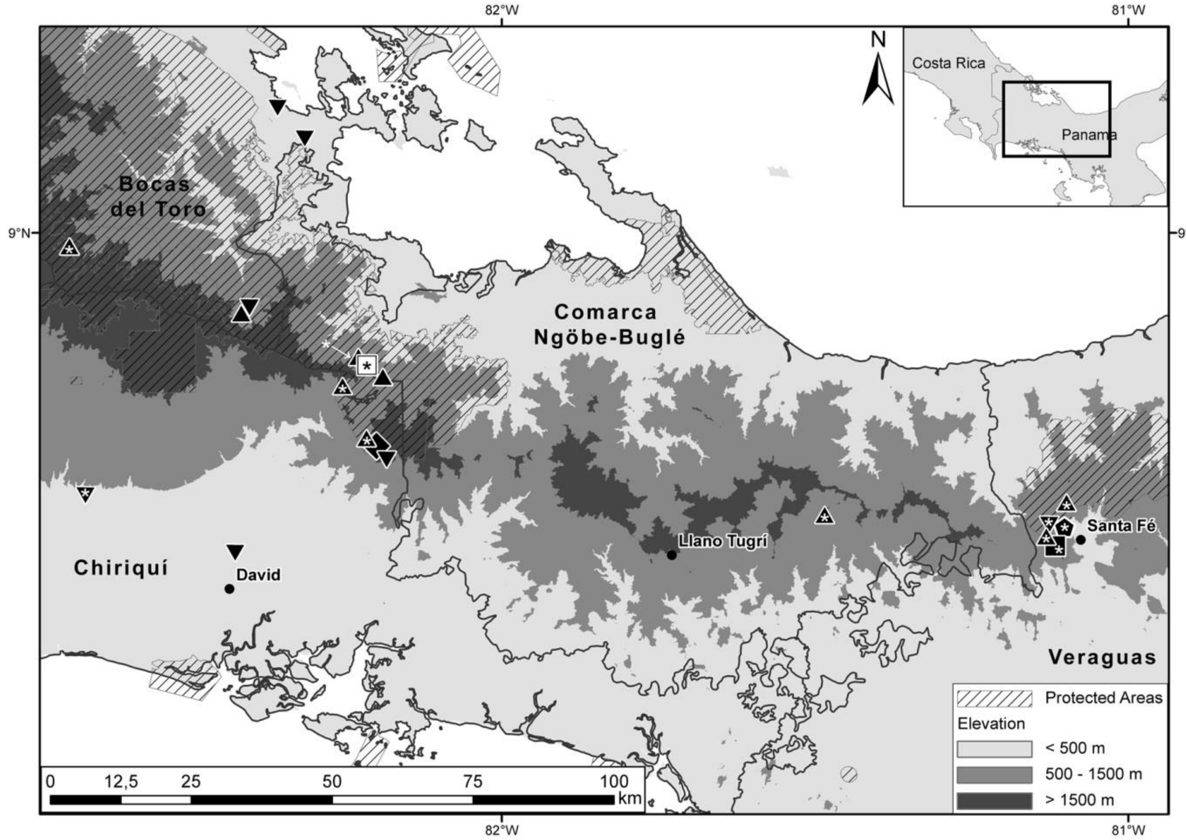
Etymology. The specific epithet is a contraction of the exclamation "no a la mina!", Spanish for "no to the mine", in the sense of "no mining". This affirmation was and is used by members of the indigenous Ngöbe communities living in the Serranía de Tabasará in the course of their protests against mining interests aiming to exploit their territory, especially around Cerro Colorado. The specific name is given in recognition and support of the Ngöbe’s struggle to protect their territory and environment, which is home to the new species described herein and many others dealt with in this work, from profit-driven destructive interventions.

Natural history notes. See species account in chapter 4.2.2.

Geographic distribution. See Maps 4.17 and 4.167, and species account in chapter 4.2.2.

The new species has the lowest number of supralabials of all described *Sibon*. Moreover, the condition of the ultimate supralabial as well as the slight but discernible keeling on some lateral rows of dorsal scales are unique among the members of this genus. These characters readily distinguish *S. noalamina* from all congeners, rendering the species well separated morphologically. While its coral snake-like color pattern already distinguishes the new species from any Lower Central American Sibon except *S. anthracops* (from which it differs significantly in dorsal scale row number), it might lead to mistaking especially juvenile specimens for bicolored coral snake-mimics of the genus *Dipsas,* most probably the sympatric *D. articulata* (Figs. 4.86A–C). Although this may seem trivial, such confusion has already occurred: The juvenile paratype SMF 89550 was tentatively identified *D. articulata* in my field notes and has accordingly appeared as such in a Diploma thesis (Stadler 2010) and a book (Köhler 2008: p. 219: Fig. 592).

The collection localities of our Panamanian specimens are shown in Map 4.17, the resulting distribution extensions are detailed in the respective species accounts (chapter 4.2.2).



Map 4.17: Collection localities of examined specimens of *Sibon noalamina* (squares, hollow symbol represents type locality), *S. annulatus* (upright triangles), *S. longifrenis* (pentagon), *S. nebulatus* (inverted triangles), and *S. perissostichon* (diamond), as well as protected areas (hatched) in western Panama. One symbol may represent several specimens from nearby. At the localities for *S. noalamina* and *S. perissostichon,* the symbols of other species found at the same general locality are offset for better visibility. The provenances of barcoded individuals are marked with asterisks. Modified from original map created by AH for Lotzkat et al. (2012d).

Table 4.17 summarizes the morphological variation among our Panamanian sample of *Sibon.* Among the corresponding morphological novelties detailed in the species accounts, some concerning *S. annulatus* are of taxonomic significance as follows: In one of our specimens (SMF 90208) of *S. annulatus,* the enlarged penultimate supralabial contacts the eye on both sides. This condition has previously been considered to be restricted to *S. argus* and *S. longifrenis* (Savage & McDiarmid 1992; Savage 2002; Köhler 2008). On the other hand, the presence of a pair of postmentals separating the first pair of infralabials has been considered typical for *S. annulatus* (Savage & McDiarmid 1992; Savage 2002; Köhler 2008). However, as already suggested by Köhler et al. (2010a), this is definitely not the case among Panamanian specimens: only two (SMF 90208 and SMF 91578) of our 19 Panamanian specimens exhibit this condition, whereas the remaining 17 have a single postmental. Based on its single postmental, one of these specimens (SMF 85077) was erroneously labeled as a representative of *S. dimidiatus* by Köhler (2008: p. 278: Fig. 752). Since I was unable to find any substantiated record of that species from Panama, I agree with Jaramillo et al. (2010) in regarding *S. dimidiatus* as absent from Panama.

Table 4.17: Selected measurements and scale counts of Panamanian specimens of *Sibon* examined for this study. Imperfect values owing to incomplete tails are in *italics.*

	Sibon annulatus N = 19	***S. longifrenis*** N = 1	***S. nebulatus*** N = 7	***S. noalamina*** N = 3	***S. perissostichon*** N = 1
SVL	139–427	279	267–612	161–385	458
TL	64–221	138	87–197	64–161	210
TOL	203–648	417	354–809	*225–546*	671
TOL max ♂	648		809	*546*	
TOL max ♀	536	417	695		671
Ventrals	171–188 (182.4 ± 5.0)	147	179–195 (184.4 ± 5.7)	164–177	186
♂	180–188 (184.7 ± 2.1) n = 11		184–195 n = 2	170–177 n = 2	
♀	171–185 (178.0 ± 5.9) n = 4	147	179–188 (183.3 ± 4.0) n = 4		186
Subcaudals	103–130 (118.2 ± 7.3)	101	80–94 (88.4 ± 4.9)	*80–96*	108
♂	113–130 (120.9 ± 4.9) n = 10		87–94 n = 2	*80–96* n = 2	
♀	107–124 (117.0 ± 7.2) n = 4	101	80–93 (88.3 ± 5.7) n = 4		108
Ventrals + Subcaudals	278–312 (301.1 ± 9.6)	248	261–289 (272.9 ± 9.8)	*250–273* n = 2	294
♂	299–312 (305.5 ± 4.0) n = 10		271–289 n = 2	*250–273* n = 2	
♀	278–304 (295.0 ± 12.0) n = 4	248	261–279 (271.5 ± 8.6) n = 4		294
Dorsals at midbody	15	15	15	15	17
Postoculars	0–2	2	1–2	2	2–3
Anterior Temporals	1–2	1	1	1–2	1
Posterior Temporals	2–3	2	1–2	2	3
Supralabials	6–8	7	7–8	5	6
S contacting eye	1–3	2	2	2	1–2
Infralabials	6–8	7	8–9	6–7	7

The two new species raise the number of *Sibon* species in Panama from the five reported by Jaramillo et al. (2010) to seven. Together with *S. anthracops* and *S. dimidiatus* that occur in Costa Rica, there are 9 species of the genus that occur in Lower Central America. Their morphological key characters are summarized in Table 4.18, which, together with the following key, should provide a sound basis for the identification of any member of the genus encountered in Panama or Costa Rica.

Table 4.18: Selected measurements and scale counts of the nine species of *Sibon* known to occur in Lower Central America (Costa Rica and Panama), combining data from Köhler (2008), McCranie (2011), Savage (2002), and Solórzano (2004) with that of the examined specimens listed in the appendix. Values from examined specimens that expand the hitherto documented variation are in **bold** face, imperfect values owing to incomplete tails are in *italics*.

	Sibon annulatus	***S. anthracops***	***S. argus***	***S. dimidiatus***	***S. lamari***	***S. longifrenis***	***S. nebulatus***	***S. noalamina***	***S. perissostichon***
TOL max	**648**	664	*690*	ca. 800	589	700	1013	546	671
♂	**648**	664		751		578	738	546	
♀	557	475		ca. 800		541	709		671
Ventrals	161–193	162–188	181–201	171–200	162–171	**147**–173	159–200	164–177	186
♂	170–193	166–187	181–201	184–200	162–163	166–173	159–200	170–177	
♀	161–186	162–186	186–192	171–196	168–171	**147**–168	161–193		186
Subcaudals	103–135	69–91	112–121	100–126	77–119	80–106	64–114	*80–96*	108
♂	108–133	80–91	112–121	113–126	77–108	95–106	75–114	*80–96*	
♀	107–124	69–83	*95–108*	100–122	112–119	80–**101**	64–100		108
V + SC	277–318	231–271	294–322	281–323		231–275	247–**289**	*250–273*	294
♂	278–318	248–271	294–322	303–323		263–275	262–**289**	*250–273*	
♀	277–**304**	231–269	*281–300*	271–317		231–263	247–**279**		294
Dorsal scale rows	15–15–15	13–13–13 (13–15–13)	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–15–15	15–17–15
Postmentals	1–2	0	0	1–2	1–2	0–1	0	0	1
Postoculars	**0**–3	2–3	2–3	1–2	2	1–3	1–4	2	2–3
Tant	1–2	1–2	1–2	1–2	1	1–2	1	1–2	1
Tpost	1–3	2–3	2–3	2–3	2–3	1–3	1–2	2	3
SPL	**6**–9	6–8	6–9	7–9	7–8	7–9	5–9	5	6
INL	**6**–10	7–9	6–9	7–12	8–10	6–9	6–10	6–7	7

Key to the Lower Central American species of *Sibon*

1. Seventeen rows of dorsal scales at midbody and 15 rows one head length anterior to cloaca; dorsal rows running obliquely towards middorsum .... ***Sibon perissostichon*** (Figs. 4.80A; 4.81; 4.84; 4.112A)

Dorsal scale rows 13 or 15 at midbody, usually without reduction, oriented longitudinally **2**

2. Thirteen dorsal rows, both at midbody and one head length anterior to cloaca (very rarely 15 rows at midbody, but then 13 both one head length posterior to head and anterior to cloaca); coral snake-like pattern of alternating light and dark rings ....***S. anthracops***

Fifteen dorsal rows, both at midbody and one head length anterior to cloaca **3**

3. Five supralabials; only one supralabial posterior to orbit, with a higher anterior and a lower posterior portion; coral snake-like pattern of alternating light and dark rings ....***S. noalamina*** (Figs. 4.82; 4.83; 4.85; 4.111H)

Six or (in most cases) more supralabials, two supralabials posterior to orbit, with the penultimate one greatly enlarged; coloration variable involving bands or blotches, but no conspicuous coral snake-like pattern of alternating light and dark rings... **4**

4. Enlarged penultimate supralabial usually in contact with eye; dorsal ground color greenish, with an ocellated or blotched rather than a banded or striped pattern; these dark dorsal markings reach at most to outer edges of ventrals, although dark shading or mottling may be present on venter **5**

Enlarged penultimate supralabial usually not in contact with eye; dorsal color pattern banded or striped rather than ocellate or blotched; these dark dorsal markings reach well onto venter or even across venter **6**

5. 181–201 ventrals; 112–121 subcaudals; body very slender; head blunt and very distinct from neck; eyes conspicuously large and protuberant ....***S. argus*** (Fig. 4.111D)

147–173 ventrals; 80–106 subcaudals; body rather stout; snout acuminate, head gradually narrowing towards neck; eyes not conspicuously large, not protuberant ....***Sibon longifrenis*** (Figs. 4.87D, E; 4.111F)

6. First infralabials in contact with each other behind the mental .... ***Sibon nebulatus*** (Figs. 4.87F–H; 4.111G)

First infralabials separated from each other by one or two postmentals behind the mental **7**

7. Bands dark brown ventrally; laterally, their centers are of a paler brown, which is paler than their borders or the interspaces between the bands; usually a single postmental .... ***Sibon dimidiatus***

Bands dark brown ventrally and laterally, their centers not paler brown than their borders laterally, and darker than interspaces; one or two postmentals present **8**

8. Dorsal surface of head with comparatively small, white or yellow as well as green, red, and black markings; ground color of body green; 162–171 ventrals; 77–119 subcaudals ....***Sibon lamari*** (Fig. 4.111E)

Dorsal surface of head with comparatively large, usually somewhat symmetrical, dark brown markings on a light to reddish brown ground color; ground color of body usually olive to pale brown; 161–193 ventrals; 103–135 subcaudals ....***Sibon annulatus*** (Figs. 4.80B; 4.87A–C; 4.111C)

Figure 4.84: Holotype (SMF 88716) of *Sibon perissostichon* from Reserva Forestal La Fortuna. (A–C) Different aspects photographed the day after capture; (D) entire specimen at the time and place of encounter.

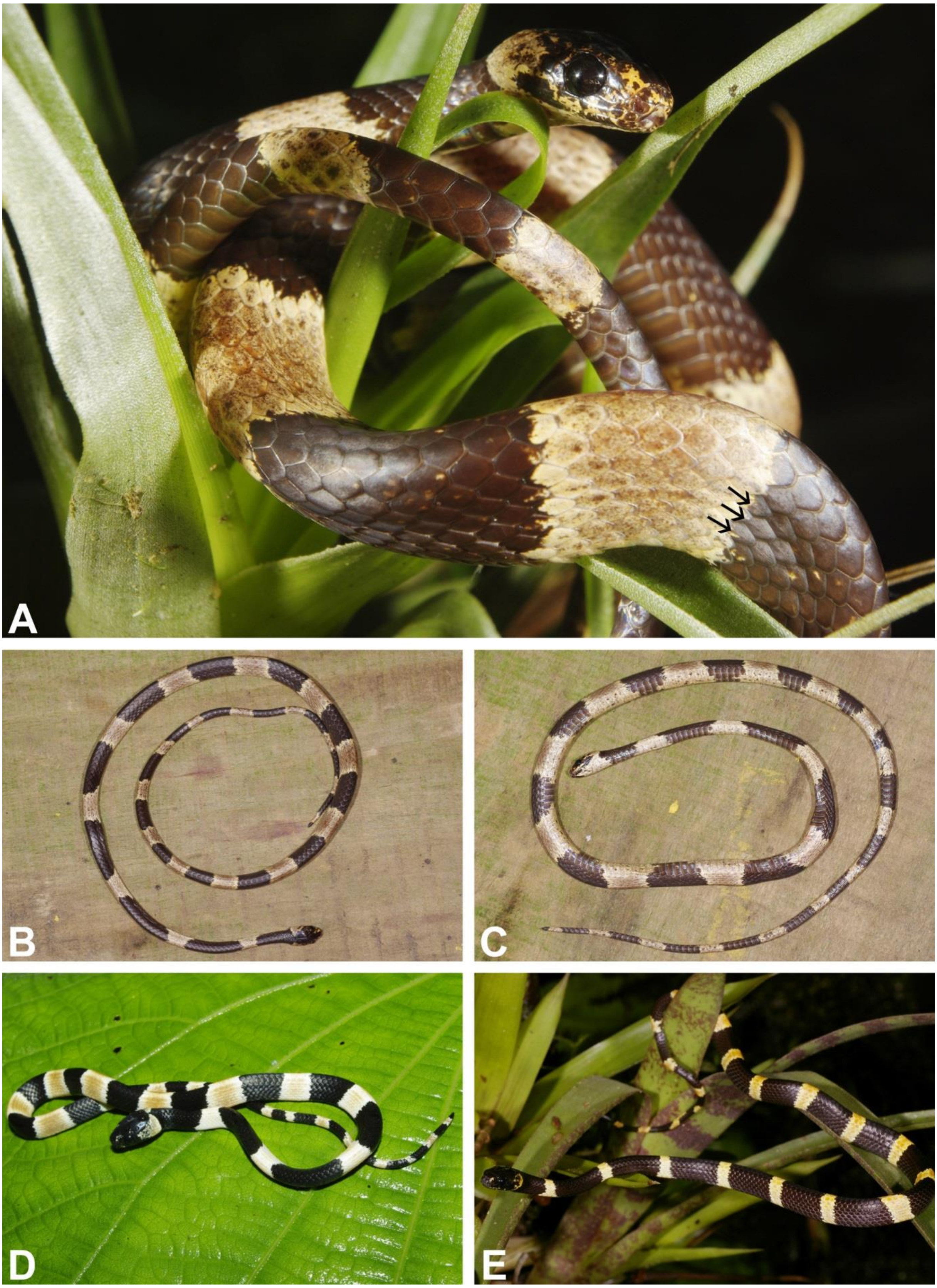


Figure 4.85: Type series of *Sibon noalamina:* (A) Holotype (SMF 91539) in life (arrows indicate dorsal rows 3–5 next to visible keels); (B) dorsolateral and (C) ventrolateral views of euthanized holotype prior to eversion of hemipenes and preservation; (D) juvenile paratype SMF 90180 from type locality at th time and place of encounter; (E) juvenile paratype SMF 89550 from Veraguas.

Figure 4.86: Individuals of *Dipsas* from around Santa Fé, Veraguas. (A–C) *D. articulata,* male SMF 89952 from Cerro Negro: (A) entire specimen, (B) dorsal and (C) lateral view of head; (D–H) *D. temporalis:* (D) male SMF 90036 and (E) juvenile SMF 89769 from Cerro Negro, (F) male juvenile MHCH 2311 from Cerro Mariposa, (G) dorsal and (H) lateral view of head of SMF 89769.

Figure 4.87: Individuals of *Sibon* from western Panama. (A–C) *S. annulatus:* (A) female SMF 91578 from Río Changena, (B) male SMF 88715 from Reserva Forestal La Fortuna, (C) lateral view of head of male SMF 90207 from headwaters of Río Chiriquí Malí; (D–E) *S. longifrenis,* female SMF 91581 from Cerro Mariposa: (D) lateral view of head and (E) entire specimen; (F–H) *S. nebulatus:* (F) female SMF 89787 from km 43 of road to Almirante, (G) male SMF 90209 from Reserva Forestal La Fortuna, (H) lateral view of head of female SMF 89599 from Volante.

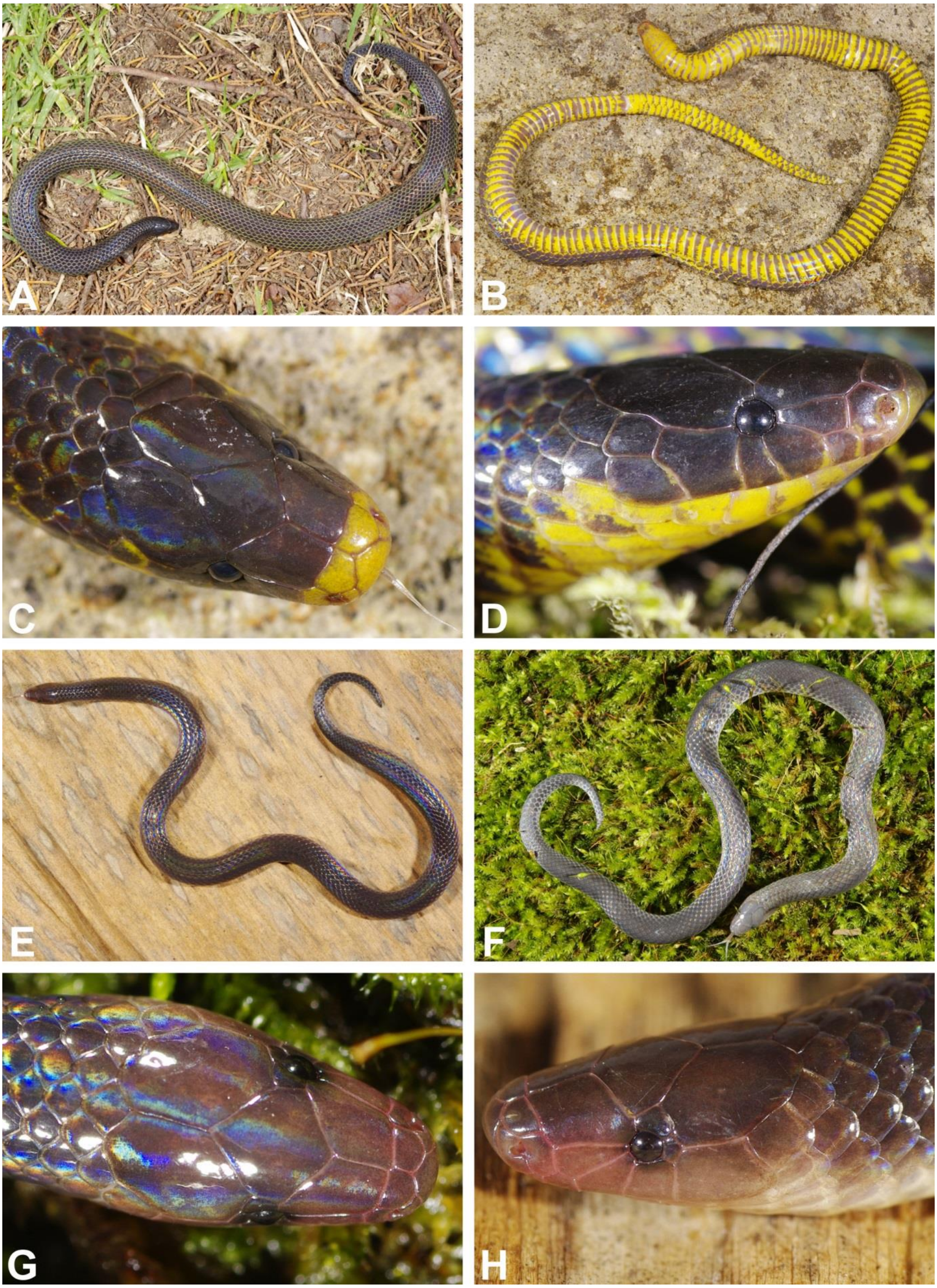


Figure 4.88: Individuals of *Geophis godmani* and *G. hoffmanni* from the Serranía de Talamanca in Chiriquí province. (A–D) *Geophis godmani* from Jurutungo: (A) female MHCH 2317, (B) ventral view of male SMF 89565, (C) dorsal view of head of SMF 89565, and (D) lateral view of head of MHCH-2137; note variability in yellow snout coloration. (E–F) *G. hoffmanni* from Santa Clara: (E) female SMF 91548, (F) male SMF 91550 shortly before shedding skin, (G) dorsal and (H) lateral view of head of SMF 91548, showing presence of only five supralabials as well as post- and supraocular scales excluding parietal from orbit.

Figure 4.89: Individuals of the *Geophis brachycephalus* complex from western Panama. (A, B) *Geophis brachycephalus* male SMF 90181 from headwaters of Río Chiriquí Malí; (C, D) *Geophis* sp. male SMF 91546 from Lost & Found Ecohostel, RFLF; (E, F) *G. talamancae* female SMF 89567 from road to Jurutungo; (G, H) *G. tectus* male SMF 91551 from Willie Mazú, about to shed skin. Note presence of six supralabials, keeling at least on middorsal scales, as well as pre- and postocular scales excluding parietal from orbit in all individuals.

4.1.9 Caenophidia, Dipsadidae: The genus *Geophis*

The genus *Geophis* contains 48 currently recognized species of small, usually inconspicuously colored, semifossorial snakes that are distributed from Mexico throughout Central America to Colombia (Savage 2002; Myers 2003; Köhler 2008; Uetz & Hošek 2014). Jaramillo et al. (2010) listed 7 species to occur in Panama: *G. bellus, G. brachycephalus, G. championi, G. godmani, G. hoffmanni, G. talamancae,* and *G. tectus.* With the exception of *G. bellus,* all species are known from the Cordillera Central. The according to current knowledge (Savage 2002; Köhler 2008; Uetz & Hošek 2014) wide-ranging species *G. hoffmanni* was described from Costa Rica by Peters (1859; as *Colobognathus*). Twelve years later, Cope (1871) described *G. brachycephalus* (also as *Colobognathus*) from "near San José" in the same country. Boulenger (1894) added *G. godmani* from "Irazú, Costa Rica" and *G. championi* from "Chiriquí, Panama" (narrowed to Boquete by Savage & Watling 2008) to the genus. A monumental revision for the whole genus was provided by Downs (1967), who defined seven species groups, two of which have members in Panama (the *G. championi* group with its namesake and *G. godmani*, and the *G. sieboldi* group with the remaining two Panamanian species known at the time, nowadays including the remaining five Panamanian species). Moreover, he revealed the second known specimen for *G. championi,* a species with smooth dorsals, from Boquete, and reconfirmed that the polychromatic populations with keeled dorsals from Finca Lérida and Boquete of which large series had previously been collected (Slevin 1942; Dunn 1947) were referable to *G. brachycephalus.* Lips & Savage (1994) described *G. talamancae* based on a single specimen from the Las Tablas area in southern Pacific Costa Rica, close to the Panamanian border. Also on the basis of a single type, Myers (2003) described *G. bellus* from "near Altos de Pacora" in Panama province east of the Canal. Moreover, he pointed out that among populations commonly referred to as *G. brachycephalus* from the Fortuna area and Caribbean slopes of the Serranía de Talamanca, several individuals stand out from the what was considered typical for that species by having higher segmental counts as well as a unilobed instead of a slightly bilobed hemipenis. In consequence, he tentatively referred nine specimens to *Geophis, species inquirenda.* In their revision of the *G. sieboldi* group, Savage & Watling (2008) presented an in-depth analysis of populations from LCA traditionally referred to as *G. brachycephalus.* Chiefly based on counts of ventrals, subcaudals, and total segmentals (V + SC), they referred the bulk of the Lérida and Boquete collections to *G. talamancae,* thus greatly extending the variation known for this species, and its known distribution into Panama. Furthermore, they referred four of Myers' (2003) *species inquirenda* to *G. brachycephalus* and described the remaining five, together with some others (including two from the large Boquete sample and two from Cerro Horqueta north of Boquete) as a new species, *G. tectus.*

In the course of my field work in western Panama, I have collected 22 specimens of *Geophis.* Together with two specimens collected by JFB, two collected by AB and MP, four collected by NH, four collected by AH, and three MVUP specimens as well as the holotype and a paratype of *Geophis tectus* (MCZ 19325 and 19326) which I have examined, my sample from the Cordillera Central consists of 39 specimens. These are complemented with one representative each of *G. godmani, G. hoffmanni,* and *G. brachycephalus* which GK collected in Costa Rica. Among the Panamanian specimens collected by myself, five specimens have smooth dorsal scales. Due to the lack of a postocular, their parietals are in contact with the orbits. These characteristics and their yellow ventral coloration render them easily identifiable as *G. godmani.* The remaining 34 examined specimens from Panama have keeled dorsals at least on the posterior part of their bodies, lack yellow ventral pigmentation, and possess a supraocular excluding the parietal from the orbit, i.e., are referable to the *G. sieboldi* group. Among these, four small individuals that I collected at Santa Clara are distinguished by having only five supralabials, and readily identified as *G. hoffmanni.* The remaining 30 specimens agree in having six supralabials and are referable to the *G. brachycephalus* complex. Lamentably, of the 28 non-type specimens, as many as 12 could not be confidently assigned to any of the three species known from western Panama using the key and descriptions provided by Savage & Watling (2008). The situation is especially confusing among the 15 individuals collected at La Fortuna, for 9 of which the taxonomic allocation is unclear. Forced by these uncertainties, I obtained barcodes from 24 Panamanian and two Costa Rican specimens. The 23 16S sequences generated by myself were complemented with 16 COI barcodes provided by the ColdCode project, and with 15 cyt-b sequences generated by Luis Canseco in the course of his PhD studies on the phylogenetics of *Geophis.*

The alignments and distance matrices underlying the following results are provided in Appendix 5.9. For the 16S barcodes, the manually refined final alignment of 24 taxa (a *Sibon nebulatus* as outgroup and 23 *Geophis*) contained 523 positions, of which, excluding the outgroup, 48 were variable and 38 parsimony-informative. TN93+I was determined as the best-fitting substitution model. The final COI alignment of 17 sequences (same outgroup and 16 *Geophis*) contained 565 positions, of which, excluding the outgroup, 90 were variable and 87 parsimony-informative. HKY+G was determined as the best-fitting substitution model. The final cyt-b alignment of 15 sequences (*Geophis godmani* serving as outgroup) contained 1095 positions, of which, including all sequences, 252 were variable and 121 parsimony-informative. HKY+G was determined as the best-fitting substitution model.

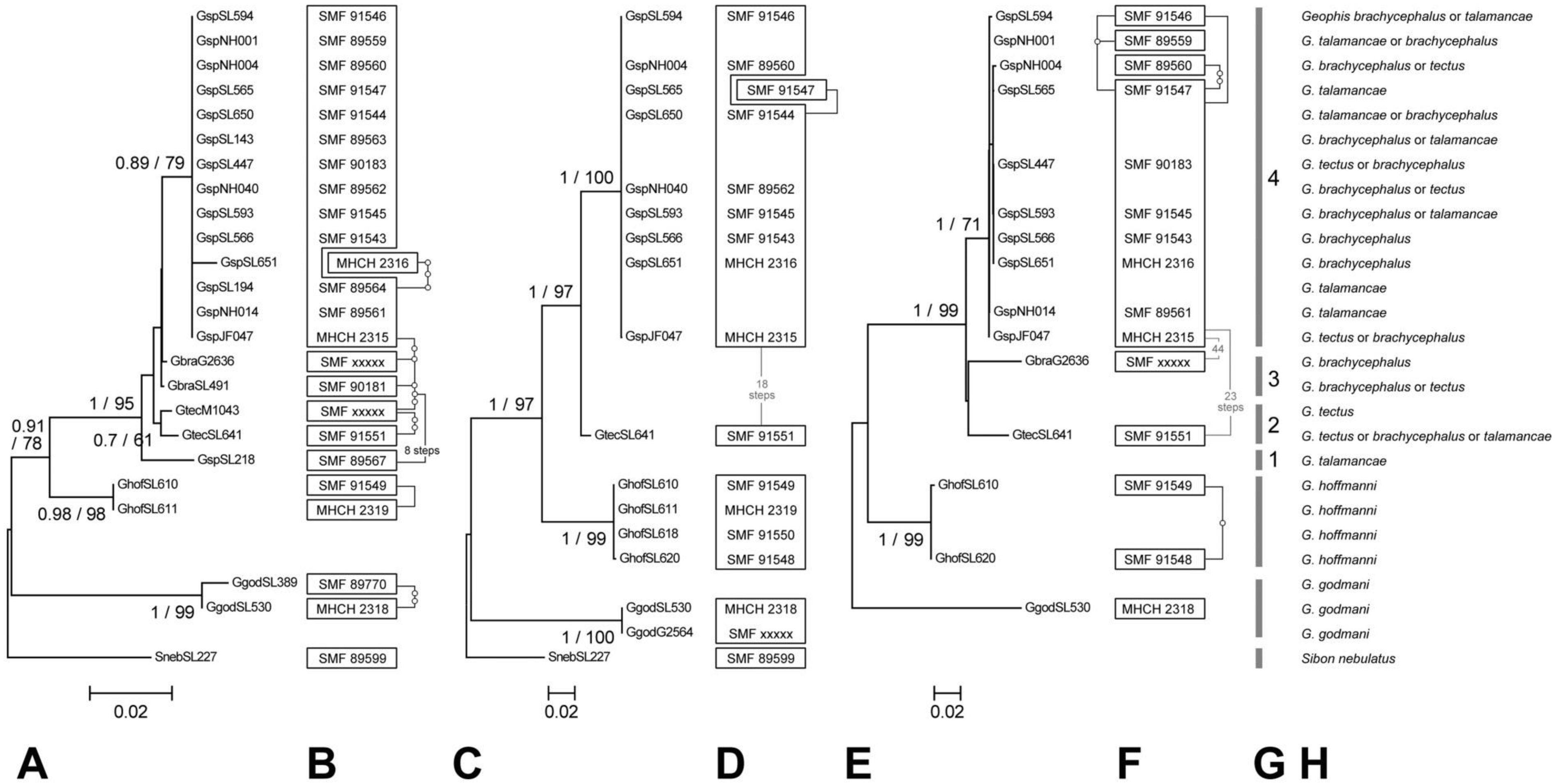


Figure 4.90: Results of molecular analyses for the genus *Geophis*. (A) ML consensus tree of 16S barcodes. (B) Parsimony network of 16S barcodes with a 95% parsimony probability resulting in a connection limit of 9 steps. (C) ML consensus tree of COI barcodes. (D) Parsimony network of COI barcodes with a 95% parsimony probability resulting in a connection limit of 10 steps. (E) ML consensus tree of cyt-b sequences. (F) Parsimony network of cyt-b sequences with a 95% parsimony probability resulting in a connection limit of 14 steps. (G) lineages diagnosable through DNA. (H) Taxonomic identity derived from morphology on the basis of the keys and information presented by Köhler (2008) and Savage & Watling (2008). In (A, C, E), bootstrap values shown at selected nodes are preceded by posterior probabilities from correspondent BI analyses. In (B, D, F), additional connections acheived by manually increasing the connection limit are indicated by the number of necessary steps, in gray or black as specified in the text.

Table 4.19: Uncorrected p-distances between the 16S barcodes of the lineages identified within *Geophis*. Mean p-distances between lineages in lower-left, ranges of individual p-distances for the *G. brachycephalus* complex in upper-right matrix. Mean distances within a lineage are in **bold** face.

	Sibon nebulatus	***Geophis godmani***	***G. hoffmanni***	***G. brachycephalus* complex**			
				1	**2**	**3**	**4**
Sibon nebulatus	–						
Geophis godmani	0.057	**0.0058**					
G. hoffmanni	0.048	0.050	**0.0**				
***G. brachycephalus* complex 1**	0.052	0.062	0.043	–	0.021–0.021	0.017–0.021	0.019–0.027
***G. brachycephalus* complex 2**	0.050	0.059	0.038	0.021	**0.0064**	0.006–0.015	0.011–0.018
***G. brachycephalus* complex 3**	0.050	0.054	0.037	0.019	0.011	**0.0039**	0.006–0.012
***G. brachycephalus* complex 4**	0.049	0.061	0.039	0.020	0.011	0.006	**0.0009**

Table 4.20: Uncorrected p-distances between the COI barcodes of the lineages identified within *Geophis*. Mean p-distances between lineages in lower-left, ranges of individual p-distances for the *G. brachycephalus* complex in upper-right matrix. Mean distances within a lineage are in **bold** face.

	Sibon nebulatus	***Geophis godmani***	***G. hoffmanni***	***G. brachycephalus* complex**			
				1	**2**	**3**	**4**
Sibon nebulatus	–						
Geophis godmani	0.129	**0.0**					
G. hoffmanni	0.118	0.123	**0.0**				
***G. brachycephalus* complex 1**	–	–	–	–	–	–	–
***G. brachycephalus* complex 2**	0.116	0.114	0.066	–	**0.0**	–	0.031–0.033
***G. brachycephalus* complex 3**	–	–	–	–	–	–	–
***G. brachycephalus* complex 4**	0.128	0.123	0.076	–	0.032	–	**0.0**

Table 4.21: Uncorrected p-distances between the cyt-b fragments of the lineages identified within *Geophis*. Mean p-distances between lineages in lower-left, ranges of individual p-distances for the *G. brachycephalus* complex in upper-right matrix. Mean distances within a lineage are in **bold** face.

	Sibon nebulatus	***Geophis godmani***	***G. hoffmanni***	***G. brachycephalus* complex**			
				1	**2**	**3**	**4**
Sibon nebulatus	–						
Geophis godmani	–	–					
G. hoffmanni	–	0.132	**0.0023**				
***G. brachycephalus* complex 1**	–	–	–	–	–	–	–
***G. brachycephalus* complex 2**	–	0.165	0.109	–	–	0.063–0.063	0.031–0.055
***G. brachycephalus* complex 3**	–	0.163	0.127	–	0.063	–	0.055–0.060
***G. brachycephalus* complex 4**	–	0.152	0.108	–	0.045	0.056	**0.0010**

The results of the phylogenetic analyses are shown in Figure 4.90, while Tables 4.19–4.21 present condensed distance matrices for the three gene fragments. *Geophis godmani* and *G.*

hoffmanni appear well separated from the *G. brachycephalus* complex in all trees, the former species apparently not being much more closely related to the other *Geophis* than the outgroup *Sibon nebulatus* in the analyses of 16S and COI. Regarding the 16S barcodes (Fig. 4.90A and B; Tab. 4.19), the p-distances between *Sibon, G. godmani, G. hoffmanni,* and the *G. brachycephalus* complex are in the range of interspecific distances inferred for *Dipsas* and *Sibon* in the previous chapter. Between the four lineages diagnosable within the *G. brachycephalus* complex, roughly numbered from west to east in Fig. 4.90, the divergences in the 16S fragment are much shallower, with individual p-distances between lineages of just 0.6–2.7%, that is, comparable to intraspecific distances calculated for certain pairs of individuals of *S. anulatus* or *S. noalamina* in chapter 4.1.8. In the corresponding PN analysis, lineages 2–4 form a joint haplotype network within the connection limit of 9 steps calculated for a 95% parsimony probability, and lineage 1 joins this network when the connection limit is increased to 10 steps. As it was to be expected, the COI barcodes, which unfortunately are lacking for lineages 1 and 3 of the *G. brachycephalus* complex, exhibit deeper divergences and higher distances (Fig. 4.90C and D; Tab. 4.20). Yet, the p-distances of 3.1–3.3% found within the *G. brachycephalus* complex are again much lower than interspecific distances calculated for lizards or snakes in the preceding chapters. In the corresponding PN analysis, the single individual of lineage 2 would connect to the network of lineage 4 via 18 substitutional steps, almost twice the connection limit of 10 steps calculated for a 95% parsimony probability. The cyt-b fragment (Fig. 4.90E and F; Tab. 4.21) offers the deepest divergences and largest distances. Still, the individual p-distances between the three sampled lineages of the *G. brachycephalus* complex are at most half as large as those calculated between any member of this complex and the closely related *G. hoffmanni.*

The low values of the uncorrected p-distances of both 16S and COI barcodes within the *Geophis brachycephalus* complex presented above sharply contrast with all interspecific p-distances calculated for any lizard or snake alignment in the previous chapters. In fact, they are definitely in the range of distances calculated in previous chapters for specimen pairs classified as conspecific, and even below the values determined between obviously divergent DCLs. Nevertheless, the p-distances between the cyt-b sequences of the three analyzed lineages of the *G. brachycephalus* complex are 2–4 times higher than those found by Fritz et al. (2012) between closely related species of *Trachemys,* and in the order of magnitude of those that have been found between several well-diagnosable species of *Geophis* by Luis Canseco (pers. comm.). Thus, I must assume that within the *G. brachycephalus* complex, or even the genus *Geophis* as a whole, genetic differentiation at least in mitochondrial DNA is far less pronounced than in other dipsadid snakes, or the lizard groups which I analyzed above. I thus continue to recognize the lineages 2–4 of the *G. brachycephalus* complex as distinct genealogical clusters. Considering that lineage 1, though lacking COI and cyt-b support, is the most divergent lineage in the 16S analysis, I likewise recognize it as a lineage of equal rank. In conclusion, I have identified four genealogical lineages within members of the *G. brachycephalus* complex among my sample, whose close genetic relationship is reflected by their morphological resemblance. Next, I try to determine which of the three available names is properly assigned to which lineage.

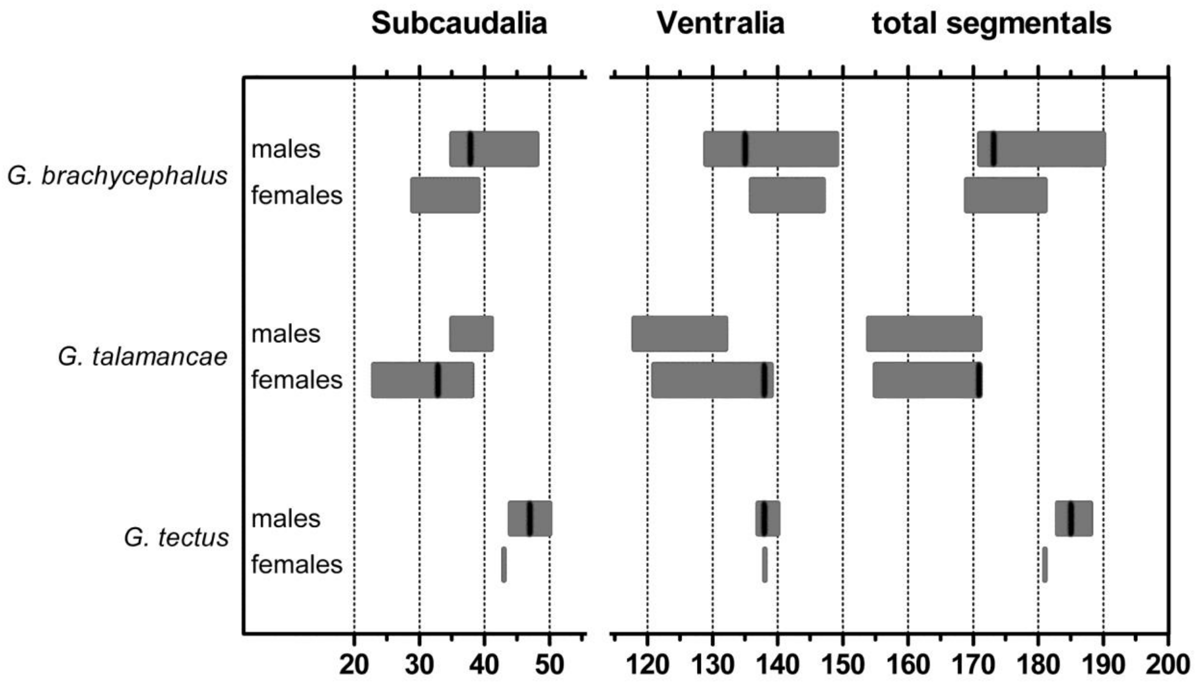


Figure 4.91: Segmental scale counts of the three species of the *Geophis brachycephalus* complex known to occur in Panama, as reported by Savage & Watling (2008). Black bars mark the values of each species' holotype as reported by these authors for *G. talamancae* and *G. tectus,* and by Downs (1967) for *G. brachycephalus.*

Figure 4.91 summarizes the diagnostic segmental counts of the three nominal species as presented by Savage & Watling (2008). According to the results of these authors, *Geophis talamancae* and *G. tectus* are separable from each other by their non-overlapping numbers of subcaudals and total segmentals, while between these two species and *G. brachycephalus* there may be certain overlaps depending on gender. In any case, *G. talamancae* was revealed by Savage & Watling (2008) to have comparably low subcaudal and ventral counts, resulting in total segmental counts of 171 or fewer which only slightly overlap with those of *G. brachycephalus.* In view of the very low counts of the sole barcoded individual of lineage 1, SL 218 (132 V + 33 SC = 165), I assign the name *G. talamancae* to my lineage 1. This conclusion is further supported by the fact that I collected this specimen at an elevation of 1834 m at Jurutungo, only a few kilometers from the type locality of this taxon (Finca Jaguar, 1800 m), and, since its segmental counts closely match those of the holotype, could easily identify it using the key of Köhler (2008) already before the revision by Savage & Watling was available to me. As shown in Figure 4.92, I also assign JFB 055 from Las Nubes and MVUP 963 from Bajo Mono to *Geophis talamancae,* based on their low counts especially of subcaudals and total segmentals.

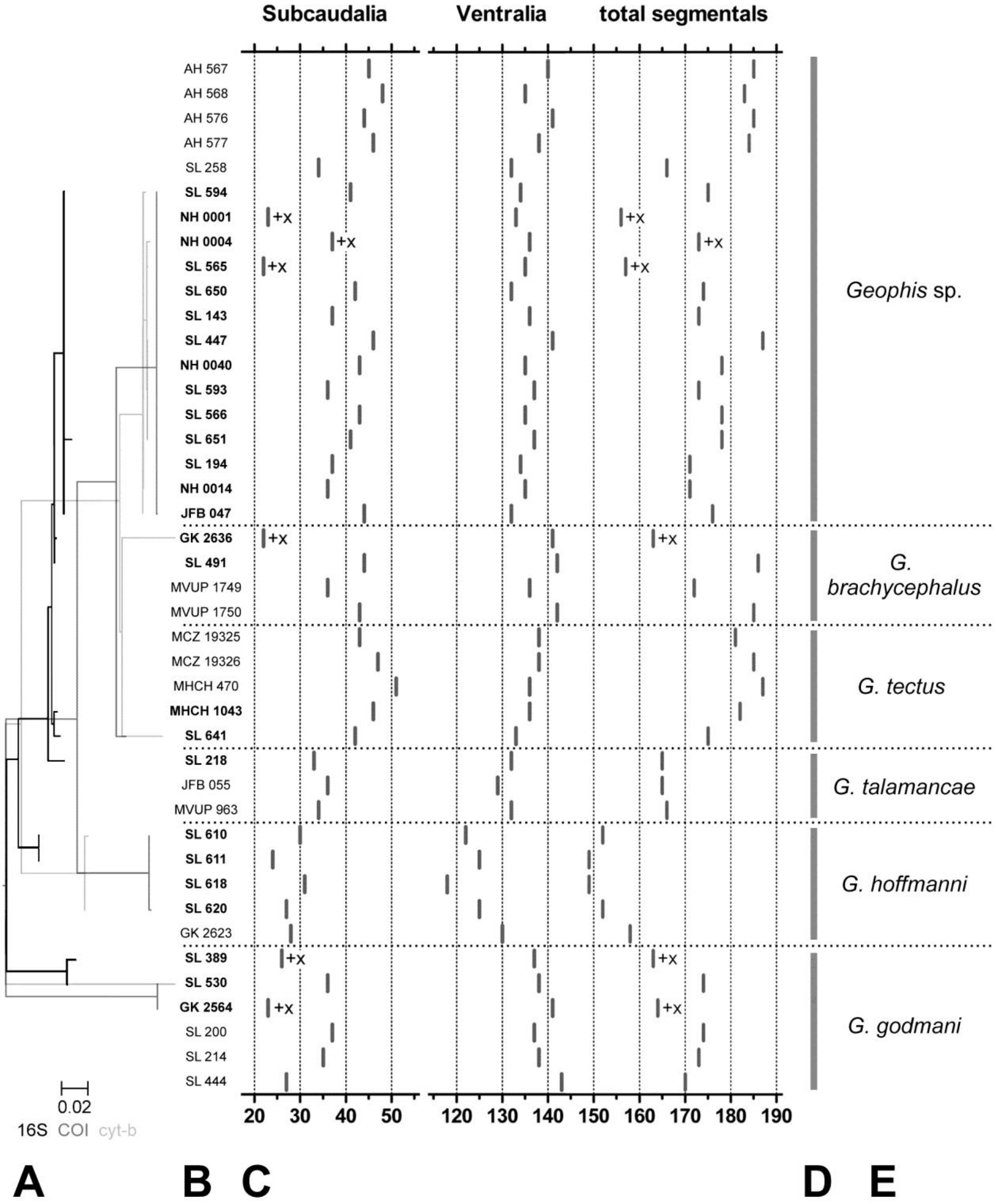
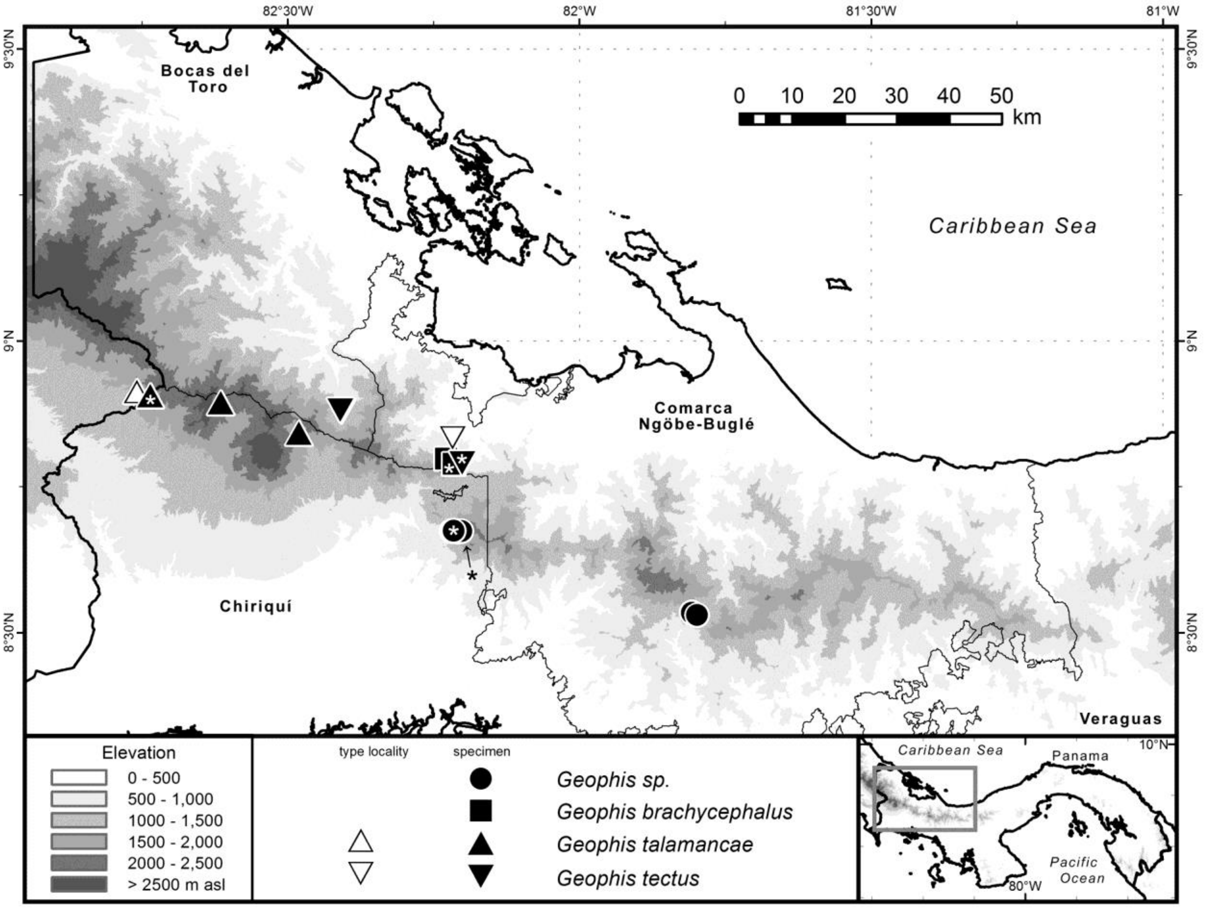


Figure 4.92: Integration of molecular and morphological results for the examined specimens of the genus *Geophis.* (A) Overlay of the ML trees shown in Fig. 4.90. (B) Field or collection numbers of examined specimens, in **bold** face if included in the molecular analyses. (C) Segmental counts of examined specimens; imperfect values owing to incomplete tails are marked with "+x". (D) Delimitation of specimen assignment to lineages inferred from mtDNA in Fig. 4.90. (E) Taxonomic identity of inferred CGLs.



Map 4.18: Collection localities of examined specimens of the *Geophis brachycephalus* complex. The provenances of individuals included in the molecular analyses are marked with an asterisk.

Regarding lineage 3, the barcoded specimen GK 2636 is from central Costa Rica and shares its high ventral count with the other barcoded specimen, SL 491 from the Caribbean slope just west of La Fortuna. Taking into account the large geographic but comparatively small genetic distance between the two specimens, at this point I see no other option but to assume their pertinence to the same species. Since the latter specimen has a slightly bilobed hemipenis, the name *G. brachycephalus* is assignable to my lineage 3. Relying more on the key of Savage & Watling (2008) than on the close proximity of their collection sites to that of SL 491, I regard MVUP 1749 and 1750 to represent this species, too.

One of the two barcoded specimens of lineage 2 (MHCH 1043) stands out in having high segmental counts similar to those of the examined holo- and paratype of *G. tectus.* Further supported by the biogeographical proximity (about 20 airline km along the same versant) of its collection site to the species' type locality La Loma, I conclude that my lineage 2 represents *G. tectus,* assuming that the comparably low segmental counts of SL 641 represent hitherto unreported variability of this species. I further assign to this nominal taxon the specimen MHCH 470, collected a little lower along Sendero El Pianista than MHCH 1043, since it has the highest subcaudal and total segmental counts of all examined specimens.

Now that the three names available within the *Geophis brachycephalus* complex have been assigned to my mtDNA lineages 1–3, no name is left for the fourth lineage comprising the specimens from Lost & Found Ecohostel, Río Hornito, and Cerro Pata de Macho at RFLF. As noted above and indicated in Fig. 4.90, any of these animals may closely resemble one, two, or three of the hitherto named species of the *G. brachycephalus* complex, depending on the character contemplated. Their segmental counts seem to somewhat cover the ranges of *G. brachycephalus* and *G. tectus,* while in all examined males of this lineage that have their organs everted, the hemipenis is slightly bilobed as in *G. brachycephalus* and *G. talamancae.* Without realizing their genetic distinctness, I would have distributed my sample from La Fortuna specimen by specimen among the three named species. Yet, the order of magnitude of mtDNA divergence found for the Fortuna population is comparable to those of the three nominal taxa included in my analyses. If the three lineages for which names are available merit their recognition at the species level, then equally does the lineage from La Fortuna. Another possible consequence would be sinking both *G. talamancae* and *G. tectus* into the synonymy of *G. brachycephalus.* For the latter action, I consider both my molecular and morphological samples too small, and my analyses too preliminary, especially when regarding the fact that the large samples from Boquete and surroundings are absent from my barcode alignments. Thus, in the light of the data available to me, I conclude that the population sampled at La Fortuna represents an undescribed species, which I refer to as *Geophis* sp. throughout the following. I assign to this lineage my only non-barcoded specimen from Fortuna (SL 258) as well as, most tentatively, four males (AH 567, 568, 576, and 577) that were recently collected by Andreas Hertz near Ratón.

Apart from the tentative allocation of these four specimens, the question to which of the genealogical lineages revealed herein the large samples from Boquete and surroundings that were largely assigned to *G. talamancae* by Savage & Watling (2008) would pertain remains unsolved, yet crucial for a robust phylogenetic notion of the *G. brachycephalus* complex. At any rate, the taxonomy and biogeography of the *G. brachycephalus* complex remain unsatisfactorily resolved, necessitating a thorough integrative taxonomic approach involving larger and geographically more inclusive samples than that analyzed in the present work, as well as the inspection of more morphological characters than analyzed herein or by Savage & Watling (2008). While the latter authors already showed the extent of keeling on the D scales to be of little diagnostic value, I came to an equivalent conclusion regarding apical pits, having found all members of this complex in my sample to share 2 shallow, subapically located APs, which are not easy to discern but no matter of imagination either. Since characters of external morphology that allow for unarbitrarily identifying a given member of the *G. brachycephalus* complex are sorely needed, any future revisor should optimally make the effort to test whether any of the head scalation characters traditionally employed in *Geophis* systematics but not mentioned by Savage & Watling (2008), such as relative suture lengths which were much used by Downs (1967), bears diagnostic value. Until then, the assignment of a given specimen to either of the four lineages recognized herein will often remain guesswork to a certain extent. More information on the *Geophis* which inhabit my study area is provided in their respective species accounts in chapter 4.2.2.

4.1.10 Summary of unnamed lineages and genetic distances reported in this study

All unnamed lineages that I have identified throughouth the preceding chapters 4.1.1–4.1.9 are summarized by nominal species in Table 4.22, along with their classification, diagnostic characters, and approximate known geographical distribution. Of the 37 genealogical lineages listed, I confidently regard four to represent undescribed species and treat them as separate species in the following, although for two of these I cannot present sound morphological or molecular evidence. I have classified 15 mtDNA lineages within 7 nominal anole species (1 *Dactyloa,* 6 *Norops*) as DCLs which do not exhibit consistent differences to the other lineage(s) within their respective nominal taxon. Last, 18 UGLs identified within 6 species of *Norops* await confirmation or rejection of their possible specific distinctness through sound analyses of their morphology that are yet to be performed.

Table 4.22: Unnamed lineages identified in this study.

Nominal species	Lineage	Genetic distinction	Morphological distinction	Distribution
Celestus sp.	undescribed species (UGL)	?	loreals, lamellae, etc.	RFLF: Lost & Found Ecohostel
Lepidoblepharis sp. 1	undescribed species (CGL)	16S	lamellae, SC, escutcheon, etc.	Cerro Negro, Veraguas, and Donoso, Colón
Lepidoblepharis sp. 2	undescribed species (CGL)	16S	lamellae, SC, escutcheon, etc.	eastern Panama
Dactyloa casildae	DCL east	16S, COI	–	Central Serranía de Tabasará
D. casildae	DCL west	16S, COI	–	Fortuna depression and surroundings
Norops benedikti	DCL east	16S, COI	–	Senderos Pianista and Culebra, Bajo Mono, Alto Chiquero
N. benedikti	DCL west	16S, COI	–	N and S slopes of Cerro Pando
N. pseudopachypus	DCL east	16S, COI	–	central Serranía de Tabasará

Table 4.22: continued.

Nominal species	Lineage	Genetic distinction	Morphological distinction	Distribution
N. pseudopachypus	DCL west	16S, COI	–	RFLF
N. gruuo	DCL east	16S, COI	slight but overlapping	Cerro Mariposa
N. gruuo	DCL west	16S, COI	slight but overlapping	central Serranía de Tabasará
N. kemptoni	DCL east	16S, COI	–	Costa Rica to SE slopes of Volcán Barú
N. kemptoni	DCL west	16S, COI	–	E slopes of Volcán Barú to RFLF
N. datzorum	DCL 1	COI	slight but overlapping	RFLF: Cerro Pata de Macho
N. datzorum	DCL 2	COI	slight but overlapping	central Serranía de Tabasará
N. salvini	DCL 1	16S	–	Jurutungo
N. salvini	DCL 2	16S	–	Cerro Altrillería
N. salvini	DCL 3	16S	–	Cerro Saguí
N. biporcatus	UGL 1	COI	?	central and eastern Tabasará
N. biporcatus	UGL 2	COI	?	unknown; probably Los Algarrobos
N. capito	UGL 1	COI	?	Serranía de Tabasará and Caribbean slopes of Serranía de Talamanca
N. capito	UGL 2	COI	?	Potrerillos Arriba and probably Pacific slopes W of Volcán Barú
N. humilis	UGL 1	16S, COI	?	Río Changena
N. humilis	UGL 2	16S, COI	?	road to Almirante, km 33
N. humilis	UGL 3	16S, COI	?	Willie Mazú
N. humilis	UGL 4	16S, COI	?	headwaters of Río Chiriquí Malí and RFLF
N. humilis	UGL 5	COI	?	central Serranía de Tabasará
N. humilis	UGL 6	16S	?	Cerro Negro
N. limifrons	UGL 1	COI	?	eastern Serranía de Tabasará
N. limifrons	UGL 2	16S, COI	?	road to Almirante east of km 13.5, RFLF, central Serranía de Tabasará
N. limifrons	UGL 3	16S, COI	?	road to Almirante west of km 63, San San Pond Sak, Costa Rica
N. limifrons	UGL 4	COI	?	Los Algarrobos
N. lemurinus	UGL 1	COI	?	central and E Serranía de Tabasará
N. lemurinus	UGL 2	COI	?	San San Pond Sak
N. lionotus	UGL 1	COI	?	eastern Serranía de Tabasará
N. lionotus	UGL 2	COI	?	near Fortuna depression to Central Serranía de Tabasará
Geophis sp.	undescribed species (UGL)	16S, COI, cyt-b	?	RFLF: Lost & Found Ecohostel and Cerro Pata de Macho to Cerro Saguí

The following Table 4.23 summarizes the ranges of mean uncorrected p-distances calculated within and between species of six major reptile families from the alignments provided in Appendices 5.1 (Gymnophthalmidae) and 5.2–5.9 (other families). While the mean p-distances between DCLs of the same nominal species are included in the intraspecific ranges, those calculated between UGLs of the same nominal taxon are not included at all. Yet, distances between UGLs of a given species and members of another species are considered in the latter three columns. For interspecific distances, inspired by Nagy et al. (2012) I separately present the ranges found between closely related species (that is, very similar and often cryptic taxa many of which were only recently recognized and described, e.g., the respective members of the *Norops pachypus, N. kemptoni, N. limifrons,* or *Geophis brachycephalus* complexes), between "good" species within the same genus (i.e., species pairs that are well distinguishable from each other morphologically and not members of the same species complex, as for instance *N. pachypus* and *N. kemptoni* or *G. brachycephalus* and *G. godmani*), and between representatives of different genera.

Table 4.23: Mean uncorrected p-distances calculated in this study from 16S and COI barcodes of LCA specimens representing six reptile families. Taken from the distance matrices provided in Appendix 5.

Family	within species	between closely related species	between "good" congeneric species	between species of different genera
Sphaerodactylidae	16S: 0.029 COI: –	16S: 0.106 COI: –	16S: 0.114–0.126 COI: –	16S: – COI: –
Dactyloidae	16S: 0–0.038 COI: 0–0.083	16S: 0.027–0.069 COI: 0.088–0.148	16S: 0.050–0.117 COI: 0.12–0.223	16S: 0.110–0.149 COI: 0.173–0.239
Gymnophthalmidae	16S: – COI: 0–0.035	16S: – COI: –	16S: – COI: –	16S: – COI: 0.180–0.215
Colubridae	16S: – COI: 0.015	16S: – COI: –	16S: – COI: –	16S: – COI: 0.151–0.179
Dipsadidae	16S: 0–0.007 COI: 0–0.020	16S: 0.006–0.021 COI: 0.032–0.093	16S: 0.037–0.062 COI: 0.066–0.129	16S: 0.035–0.077 COI: 0.101–0.184
Viperidae	16S: – COI: 0.043	16S: – COI: –	16S: – COI: –	16S: – COI: 0.135–0.147

As noted in the preceding chapters, uncorrected p-distances in the COI barcode are invariably higher than those in the 16S barcode. In the latter gene fragment, even after excluding from the intraspecific distances those calculated between nominally conspecific UGLs which might be shown to merit recognition at the species level in the future, the ranges of p-distances calculated between conspecifics overlap with those calculated between representatives of closely related species in Dactyloidae and Dipsadidae. As shown by Nagy et al. (2012) for reptiles from Madagascar, mean p-distances typically found within and between species vary greatly among the families studied, in a way that, e.g., the 16S and COI distances found between "good" dactyloid species are almost twice as large as those calculated between "good" dipsadid species.

4.1.11 Summary of taxonomical changes since 2010

Similar to Table 1 of Jaramillo et al. (2010), the following Table 4.24 summarizes all taxonomical changes at the species level applicable to Panamanian reptile populations that have been formally published since the last summary of the Panamanian herpetofauna by Jaramillo et al. (2010). That is, it includes the new species described by our group or other colleagues as well as reallocations of known species to other genera that are traceable in scientific publications up to November 2013.

The only exception not appearing in Table 4.24 is the generic nomenclature of anoles, for which I follow Nicholson et al. (2012) in regarding the alpha- and beta- anoles of Panama, which have collectively been referred to the genus *Anolis* by most previous authors, as representing two different genera, namely *Dactyloa* and *Norops.* The latter generic name is applied to all Panamanian anoles except for the 10 species recounted in chapter 4.1.3. Changes that are of purely biogeographical nature are only included if they represent new distributional records at the country level, that is, names to be added to the list of the Panamanian reptile fauna.

Table 4.24: Summary of taxonomical additions and changes at the species level since the treatment by Jaramillo et al. (2010).

Current taxonomy	Reference	Explanation
Trachemys grayi	Fritz et al. (2012)	new combination comprising former subspecies of *Trachemys venusta* (*T. v. grayi, T. v. panamensis*) and *T. emolli*
Cryptochelys angustipons	Iverson et al. (2013)	transferred from the genus *Kinosternon* to *Cryptochelys* gen. nov.
Cryptochelys leucostoma	Iverson et al. (2013)	transferred from the genus *Kinosternon* to *Cryptochelys* gen. nov.
Amphisbaena varia	Gans (2005)	former subspecies removed from the synonymy of *A. fuliginosa*
Dactyloa ginaelisae	Lotzkat et al. (2013) this study: chapter 4.1.3	description of new species comprising populations formerly referred to as *D. microtus*
Dactyloa ibanezi	Poe et al. (2009)	description of new species comprising populations from western Panama formerly referred to as *D. chocorum* (see chapter 4.1.3)
Norops benedikti	Lotzkat et al. (2011) this study: chapter 4.1.4	description of new species comprising populations formerly referred to as *N. pachypus*
Norops charlesmyersi	Köhler (2010)	description of new species comprising populations formerly referred to as *N. pentaprion* (see chapter 4.1.6)
Norops gaigei	Köhler et al. (2012b)	name revalidated: populations from central and western Panama removed from the synonymy of *N. tropidogaster* (see chapter 4.1.7.2)
Marisora unimarginata	Hedges & Conn (2012)	transferred from the genus *Mabuya* to *Marisora* gen. nov.
Scincella cherriei	Linkem et al. (2011)	transferred from the genus *Sphenomorphus* to *Scincella*
Scincella rara	Linkem et al. (2011)	transferred from the genus *Sphenomorphus* to *Scincella* other than stated by Linkem et al. (2011), the specific epithet now should read "*rara*" since it is an adjective fide Myers & Donnelly (1991)
Potamites apodemus	Lotzkat et al. (2012a)	distribution extended into western Panama, first country record
Ameiva praesignis	Ugueto & Harvey (2011)	former subspecies removed from the synonymy of *A. ameiva*
Holcosus festivus	Harvey et al. (2012)	transferred from the genus *Ameiva* to the resurrected *Holcosus*
Holcosus leptophrys	Harvey et al. (2012)	transferred from the genus *Ameiva* to the resurrected *Holcosus*
Holcosus quadrilineatus	Harvey et al. (2012)	transferred from the genus *Ameiva* to the resurrected *Holcosus*
Coluber mentovarius	Utiger et al. (2005)	transferred from the genus *Masticophis* to *Coluber*
Dendrophidion apharocybe	Cadle (2012a)	description of new species: Atlantic versant populations from Honduras to Panama removed from synonymy of *D. vinitor*
Dendrophidion clarkii	McCranie (2011); Cadle & Savage (2012)	name revalidated: all Panamanian populations removed from synonymy of *D. nuchale*

Table 4.24: continued.

Current taxonomy	Reference	Explanation
Phrynonax poecilonotus	Jadin et al. (2013)	transferred from the suspended genus *Pseustes* to the resurrected *Phrynonax*
Tantilla armillata	Savage (2002); Knight et al. (2012)	certain populations from western Panama removed from synonymy of *T. melanocephala*
Erythrolamprus epinephelus	Grazziotin et al. (2012)	transferred from the genus *Liophis* to *Erythrolamprus*
Lygophis lineatus	Zaher et al. (2009); Grazziotin et al. (2012)	transferred from the genus *Liophis* to *Lygophis*
Oxyrhopus petolarius	Savage (2011)	"*petolarius*" demonstrated to be the correct specific epithet instead of "*petola*"
Rhadinella godmani	Myers (2011)	transferred from the genus *Rhadinaea* to the resurrected *Rhadinella*
Sibon noalamina	Lotzkat et al. (2012d) this study: chapter 4.1.8.2	description of new species
Sibon perissostichon	Köhler et al. (2010a) this study: chapter 4.1.8.1	description of new species
Cerrophidion sasai	Jadin et al. (2012)	description of new species: Costa Rican populations removed from synonymy of *C. godmani;* must logically apply to Panamanian populations, too
Porthidium volcanicum	Dwyer & van den Burgh (2012)	distribution extended into western Panama, first country record

While it can take some time until new species discoveries and distribution extensions are included in faunal lists, it usually takes much longer until names of species whose occurrence is neither substantiated by traceable records nor supported by the current notion of their distribution are finally deleted from such lists. In the subsequent Table 4.25, I recount the species listed by Jaramillo et al. (2010) and Uetz & Hošek (2014; even if already stated as absent from the country by Jaramillo et al. 2010) which to my knowledge should be deleted from the list of Panamanian reptiles.

Table 4.25: Reptile species recently listed but herein considered absent from Panama.

Current taxonomy	Reference	Explanation
Trachemys scripta	Jaramillo et al. (2010)	listed by Rhodin et al. (2010) as introduced and by Uetz & Hošek (2014); not in Panama according to Jaramillo et al. (2010)
Trachemys venusta	Fritz et al. (2012)	listed by Rhodin et al. (2010), Jaramillo et al. (2010), and Uetz & Hošek (2014); Panamanian populations of *Trachemys* are referable to *T. grayi* according to Fritz et al. (2012)

Table 4.25: continued.

Current taxonomy	Reference	Explanation
Amphisbaena alba	Köhler (2008)	listed by Uetz & Hošek (2014) and without any further information by Jaramillo et al. (2010); occurrence in Panama questionable according to Köhler (2008), who specified the distribution as "Tropical South America east of the Andes"; I regard this species as absent from Panama
Coleonyx mitratus	Köhler (2008)	listed by Uetz & Hošek (2014) and without any further information by Jaramillo et al. (2010); "Guatemala to Costa Rica", but not in Panama according to Köhler (2008); I regard this species as absent from Panama
Gonatodes annularis	Avila-Pires (1995); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); not in Panama according to Jaramillo et al. (2010)
Norops intermedius	this study: chapter 4.1.6	listed by Uetz & Hošek (2014) and Jaramillo et al. (2010); I regard this LCA species as absent from Panama
Norops laeviventris	Savage (2002) this study: chapter 4.1.6	listed by Köhler (2008) and Uetz & Hošek (2014); I regard this species to be different from *N. intermedius* (see above) and not ranging into LCA, that is, absent from Panama
Echinosaura horrida	Fritts et al. (2002) Köhler (2008) Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); distribution restricted to South America by Fritts et al. (2002) who removed from its synonymy the former subspecies *E. palmeri* and *E. panamensis,* both of which occur in Panama
Tupinambis teguixin	Köhler (2008) Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); not listed by any recent author; I regard this species as absent from Panama
Drymarchon corais	Wüster et al. (2001)	listed by Uetz & Hošek (2014); in Panama, *D. melanurus,* a former subspecies removed from the synonymy of *D. corais,* occurs instead
Phrynonax shropshirei	Savage (2002); Köhler (2008); Jaramillo et al. (2010) Jadin et al. (2013)	listed by Uetz & Hošek (2014); considered a synonym of *P. poecilonotus* by most recent authors; recognized as valid species and transferred from *Pseustes* to *Phrynonax* by Jadin et al. (2010), but without comment on distribution, inclusion in their analyses, or discussion of status
Scaphiodontophis annulatus	McCranie (2006b); Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014) with a question mark; in Panama, *S. venustissimus,* a former subspecies removed from the synonymy of *S. annulatus,* occurs instead
Stenorrhina freminvillii	Savage (2002); Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014) as *S. freminvillei;* records from Panama based on misidentifications according to Savage (2002); I regard this species as absent from Panama
Tantilla semicincta	Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014) with a question mark; not listed by any recent author; I regard this species as absent from Panama

Table 4.25: continued.

Current taxonomy	Reference	Explanation
Atractus crassicaudatus	Myers (2003)	listed by Uetz & Hošek (2014), probably based on Dunn & Bailey (1939), Auth (1994), and Ibáñez et al. (1995; 2001); the head-only specimen reported by Dunn & Bailey (1939) and Ibáñez et al. (1995) became the holotype of *A. imperfectus* Myers 2003
Conophis lineatus	Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014) with a question mark; not listed by any recent author; I regard this species as absent from Panama
Leptodeira nigrofasciata	Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); not listed by any recent author; I regard this species as absent from Panama
Rhadinella serperaster	Savage (2002); Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); not listed by any recent author; I regard this species as absent from Panama
Porthidium ophryomegas	Savage (2002); Campbell & Lamar (2004); Köhler (2008); Jaramillo et al. (2010)	listed by Uetz & Hošek (2014); not listed by any recent author; I regard this species as absent from Panama
Epictia magnamaculata	Adalsteinsson et al. (2009); Jaramillo et al. (2010)	former subspecies removed from the synonymy of *E. goudotii;* listed by Uetz & Hošek (2014); not listed by any recent author; I regard this species as absent from Panama

4.2 Diversity

Having dealt with some taxonomic issues in the preceding section, I now sum up the reptile diversity of my study area. In chapter 4.2.1, I present a synopsis of the reptile species occurring in Panama, its Cordillera Central, and my study area. Each species considered present in my study area is further dealt with in its species account in chapter 4.2.2.

4.2.1 The reptile fauna of the Serranías de Talamanca and Tabasará

Since the treatment by Jaramillo et al. (2010) listing 248 reptile species, several additional species have been described or reported for the first time from Panama (Tab. 4.24), whereas three species listed by these authors should to my knowledge be regarded absent from the country (Tab. 4.25), leaving a total of 258 species whose presence in Panama is documented in works published until December 2013. Taking into account the four undescribed species recounted in Table 4.22 and two unpublished country records (*Lepidophyma reticulatum,* Batista et al. in prep. b; and *Norops oxylophus,* chapter 4.1.7.5), the number of reptile species documented to occur in the country rises to 264. Finally, I must regard the occurrence of *Dendrophidion crybelum* Cadle 2012 in Panama as plausible. Including the latter species, my count of Panamanian reptiles is 265 species, that is, 17 species (or about 7%) more than listed by Jaramillo et al. (2010). Of these, 39 are only known from Panama, i.e., national endemics. In view of their ranges extending close to the border between Costa Rica and Panama, I regard the presence of four additional species in Panama as possible.

From along the course of the Cordillera Central, 189 species have to my knowledge been documented, and I regard the occurrence of five additional species along this mountain chain as plausible. The resulting 194 species for the Cordillera Central represent an increment of 39 species (or 25%) from the 155 species listed by Jaramillo et al. (2010), and comprise about 73% of Panama's reptile fauna and 27 national endemics (69%). Fifteen more species possibly range into this ecoregion.

From within my study area, I could trace records of 160 reptile species and regard the occurrence of 20 additional species as plausible. Thus, the reptile fauna of the Serranías de Talamanca and Tabasará as reported herein comprises 180 species, holding almost 68% of the Panamanian and 93% of the Cordillera Central's species, and 21 national endemics (54%). Apart from these, 27 others possibly occur in my study area. Table 4.26 presents my updated list of the reptile species occurring in Panama, its Cordillera Central, and my study area.

Table 4.26: Reptile species of Panama, its Cordillera Central, and the study area comprising the Serranías de Talamanca and Tabasará west of 81°W. X = presence documented; (x) = presence plausible; x? = presence possible. Occurrences (documented or plausible) not reported by Jaramillo et al. (2010) are in **bold** face. Species endemic to Panama are marked with an asterisk (*).

Taxon	Panama	Cordillera Central	study area	Taxon	Panama	Cordillera Central	study area
Class Reptilia				*D. monotropis*	X	x?	x?
Subclass Anapsida				*D. montisilvestris**	X		
Order Testudines				*Mesaspis monticola*	X	X	X
Suborder Cryptodira				**Infraorder Gekkota**			
Family Cheloniidae				**Family Gekkonidae**			
Caretta caretta	X			*Hemidactylus brooki*	X		
Chelonia mydas	X			*H. frenatus*	X	X	X
Eretmochelys imbricata	X			*H. mabouia*	**X**		
Lepidochelys olivacea	X			*H. turcicus*	**X**		
Family Chelydridae				*Lepidodactylus lugubris*	X	**X**	x?
Chelydra acutirostris	X	x?	x?	**Family Phyllodactylidae**			
Family Dermochelyidae				*Thecadactylus rapicauda*	X	X	(x)
Dermochelys coriacea	X			**Family Sphaerodactylidae**			
Family Emydidae				*Gonatodes albogularis*	X	X	X
Trachemys grayi	X	**X**	X	*Lepidoblepharis sanctaemartae*	X	**X**	
Family Geoemydidae				*L. xanthostigma*	X	X	X
Rhinoclemmys annulata	X	X	(x)	*Lepidoblepharis* sp. 1*	**X**	**X**	X
R. funerea	X	x?	x?	*Lepidoblepharis* sp. 2*	**X**		
R. melanosterna	X			*Sphaerodactylus argus*	X		
Family Kinosternidae				*S. graptolaemus*	X	x?	x?
Cryptochelys angustipons	X			*S. homolepis*	X	**X**	X
C. leucostoma	X	**(x)**	(x)	*S. lineolatus*	X	X	x?
Kinosternon scorpioides	X	X	(x)	**Infraorder Iguania**			
Family Testudinidae				**Family Corytophanidae**			
Chelonoidis carbonaria	X			*Basiliscus basiliscus*	X	X	X
Subclass Archosauria				*B. galeritus*	X		
Order Crocodylia				*B. plumifrons*	X	**X**	X
Suborder Eusuchia				*B. vittatus*	X	**X**	X
Family Alligatoridae				*Corytophanes cristatus*	X	X	X
Caiman crocodilus	X	**(x)**	(x)	**Family Dactyloidae**			
Family Crocodylidae				*Dactyloa casildae**	X	X	X
Crocodylus acutus	X			*D. chloris*	X		
Subclass Lepidosauria				*D. chocorum*	X		
Order Squamata				*D. frenata*	X	X	X
Suborder Amphisbaenia				*D. ginaelisae**	**X**	**X**	X
Family Amphisbaenidae				*D. ibanezi*	**X**	**X**	X
Amphisbaena spurrelli	X			*D. insignis*	X	X	X
A. varia	X	X	x?	*D. kunayalae**	X	X	X
Suborder "Sauria"				*D. latifrons*	X		
Infraorder Anguimorpha				*D. microtus*	X	X	X
Family Anguidae				*Norops apletophallus**	X	X	
*Celestus adercus**	X	X	x?	*N. aquaticus*	X	X	X
Celestus sp.*	**X**	**X**	X	*N. auratus*	X	X	X
Coloptychon rhombifer	X	x?	x?	*N. benedikti*	**X**	**X**	X
Diploglossus bilobatus	X	X	X	*N. biporcatus*	X	X	X

Table 4.26: continued.

Taxon	Panama	Cordillera Central	study area	Taxon	Panama	Cordillera Central	study area
N. capito	X	X	X	**Family Gymnophthalmidae**			
N. carpenteri	X	**X**	X	*Anadia ocellata*	X	X	X
N. charlesmyersi	**X**	**X**	X	*A. vittata*	X		
N. cryptolimifrons	X	**X**	X	*Bachia blairi*	X	**X**	X
N. datzorum	X	X	X	*B. pallidiceps*	X		
*N. fortunensis**	X	X	X	*Cercosaura vertebralis*	X		
N. fungosus	X	X	X	*Echinosaura palmeri*	X		
N. cf. fuscoauratus	**X**			*E. panamensis**	X	X	X
N. gaigei	**X**	**X**	**X**	*Gymnophthalmus speciosus*	X	X	X
*N. gruuo**	X	X	X	*Leposoma rugiceps*	X	X	x?
N. humilis	X	X	X	*L. southi*	X	X	X
N. kemptoni	X	X	X	*Potamites apodemus*	**X**	**X**	X
N. lemurinus	X	X	X	*Ptychoglossus festae*	X	X	X
N. limifrons	X	X	X	*P. myersi**	X		
*N. lionotus**	X	X	X	*P. plicatus*	X	X	X
*N. magnaphallus**	X	X	X	**Family Teiidae**			
N. oxylophus	**X**	x?	x?	*Ameiva praesignis*	X	X	X
N. pachypus	X	X	X	*Cnemidophorus duellmani*	X		
N. pentaprion	X	X	X	*Holcosus festivus*	X	X	X
N. poecilopus	X			*H. leptophrys*	X	X	X
N. polylepis	X	X	X	*H. quadrilineatus*	X	X	X
*N. pseudokemptoni**	X	X	X	**Suborder Serpentes**			
*N. pseudopachypus**	X	X	X	**Infraorder Caenophidia**			
N. salvini	X	X	X	**Family Colubridae**			
N. tropidogaster	X			*Chironius exoletus*	X	X	X
N. vittigerus	X	X	X	*C. flavopictus*	X	X	X
N. woodi	X	X	X	*C. grandisquamis*	X	X	X
Family Hoplocercidae				*Coluber mentovarius*	X		
Enyalioides heterolepis	X	X	X	*Dendrophidion apharocybe*	X	X	X
Morunasaurus groi	X	X		*D. clarkii*	X	X	X
Family Iguanidae				*D. crybelum*	**(x)**	**(x)**	(x)
Ctenosaura similis	X			*D. paucicarinatum*	X	X	X
Iguana iguana	X	X	(x)	*D. percarinatum*	X	X	X
Family Phrynosomatidae				*Drymarchon melanurus*	X	X	X
Sceloporus malachiticus	X	X	X	*Drymobius margaritiferus*	X	X	X
Family Polychrotidae				*D. melanotropis*	x?	x?	x?
Polychrus gutturosus	X	X	X	*D. rhombifer*	X	X	X
Infraorder Scinciformata				*Lampropeltis triangulum*	X	X	X
Family Mabuyidae				*Leptophis ahaetulla*	X	X	X
Marisora unimarginata	X	X	X	*L. depressirostris*	X	X	X
Family Sphenomorphidae				*L. nebulosus*	X	**X**	(x)
Scincella cherriei	X	**X**	X	*L. riveti*	X	X	(x)
*S. rara**	X	X	X	*Mastigodryas melanolomus*	X	X	X
Family Xantusiidae				*M. pleei*	X	**X**	x?
Lepidophyma flavimaculatum	X	X	(x)	*Oxybelis aeneus*	X	X	X
L. reticulatum	**X**	**X**	X	*O. brevirostris*	X	X	X
Infraorder Teiformata				*O. fulgidus*	X	X	X

Table 4.26: continued.

Taxon	Panama	Cordillera Central	study area	Taxon	Panama	Cordillera Central	study area
Phrynonax poecilonotus	X	X	X	*H. dunni**	X	X	X
Rhinobothryum bovallii	X	X	X	*Imantodes cenchoa*	X	X	X
Scaphiodontophis venustissimus	X	**X**	(x)	*I. gemmistratus*	X	**X**	(x)
Spilotes pullatus	X	X	X	*I. inornatus*	X	X	X
Stenorrhina degenhardtii	X	X	X	*I. phantasma**	X		
*Tantilla albiceps**	X			*Leptodeira annulata*	X	X	X
T. alticola	X	X	X	*L. rubricata*	X		
T. armillata	**X**	**X**	(x)	*L. septentrionalis*	X	X	X
T. melanocephala	X			*Lygophis lineatus*	X	x?	x?
T. reticulata	X	**X**	X	*Ninia atrata*	X		
T. ruficeps	X	X	X	*N. celata*	X	X	X
T. schistosa	X	X	X	*N. maculata*	X	X	X
T. supracincta	X	X	(x)	*N. psephota*	X	X	X
Family Dipsadidae				*N. sebae*	X	x?	x?
Amastridium veliferum	X	X	X	*Nothopsis rugosus*	X	X	X
Atractus clarki	X			*Oxyrhopus petolarius*	X	**X**	X
*A. darienensis**	X			*Phimophis guianensis*	X	x?	x?
*A. depressiocellus**	X			*Pliocercus euryzonus*	X	X	X
*A. hostilitractus**	X			*Pseudoboa neuwiedii*	X	**X**	X
*A. imperfectus**	X			*Rhadinaea calligaster*	X	X	X
Clelia clelia	X	X	X	*R. decorata*	X	X	X
C. equatoriana	X	**X**	X	*R. pulveriventris*	X	X	X
C. scytalina	X	X	X	*R. sargenti**	X	**X**	X
Coniophanes bipunctatus	X			*R. vermiculaticeps**	X	X	X
C. fissidens	X	X	X	*Rhadinella godmani*	X	X	X
*C. joanae**	X			*Sibon annulatus*	X	X	X
Diaphorolepis wagneri	X			*S. argus*	X	X	X
Dipsas articulata	X	X	X	*S. lamari*	X	**(x)**	(x)
*D. nicholsi**	X	**X**	x?	*S. longifrenis*	X	**X**	X
D. temporalis	X	**X**	X	*S. nebulatus*	X	X	X
D. tenuissima	X	x?	x?	*S. noalamina**	**X**	**X**	X
*D. viguieri**	X			*S. perissostichon**	**X**	**X**	X
Enuliophis sclateri	X	X	X	*Siphlophis cervinus*	X		
Enulius flavitorques	X	X	X	*S. compressus*	X		
Erythrolamprus bizona	X	X	X	*Tretanorhinus mocquardi**	X		
E. epinephelus	X	X	X	*T. nigroluteus*	X		
E. mimus	X	X	(x)	*Trimetopon barbouri**	X	X	x?
*Geophis bellus**	X	**X**	x?	*T. pliolepis*	X	X	X
G. brachycephalus	X	X	X	*T. slevini*	X	X	X
*G. championi**	X	X	X	*Urotheca decipiens*	X	X	X
G. downsi	x?	x?	x?	*U. fulviceps*	X	x?	x?
G. godmani	X	X	X	*U. guentheri*	X	X	X
G. hoffmanni	X	X	X	*U. myersi*	x?	x?	x?
G. talamancae	X	X	X	*U. pachyura*	X	X	X
*G. tectus**	X	X	X	*Xenodon rabdocephalus*	X	X	X
Geophis sp.*	**X**	**X**	X	**Family Elapidae**			
Hydromorphus concolor	X	X	X	*Hydrophis platurus*	X		

Table 4.26: continued.

Taxon	Panama	Cordillera Central	study area	Taxon	Panama	Cordillera Central	study area
Micrurus alleni	X	X	X	*Corallus annulatus*	X	**X**	(x)
M. ancoralis	X			*C. ruschenbergerii*	X	x?	x?
M. clarki	X	**X**	X	*Epicrates maurus*	X	X	(x)
M. dissoleucus	X			*Ungaliophis panamensis*	X	X	(x)
M. dumerilii	X			**Family Tropidophiidae**			
M. mipartitus	X	X	X	*Trachyboa boulengeri*	X		
M. mosquitensis	X	**(x)**	**(x)**	**Infraorder "Scolecophidia"**			
M. multifasciatus	X	X	X	**Family Anomalepididae**			
M. nigrocinctus	X	X	X	*Anomalepis mexicanus*	X	x?	x?
*M. stewarti**	X	X	x?	*Helminthophis frontalis*	X	X	X
Family Viperidae				*Liotyphlops albirostris*	X	X	x?
Atropoides mexicanus	X	X	X	**Family Leptotyphlopidae**			
A. picadoi	X	X	X	*Epictia goudotii*	X		
Bothriechis lateralis	X	X	X	*Trilepida macrolepis*	X		
B. nigroviridis	X	X	X				
B. schlegelii	X	X	X	**Total Lizards**	**99**	**75**	**68**
B. supraciliaris	X	X	X	documented	99	75	65
Bothrops asper	X	X	X	plausible			3
B. punctatus	X			possible		4	8
Cerrophidion sasai	X	X	X				
Lachesis acrochorda	X			**Total Snakes**	**148**	**113**	**107**
L. melanocephala	X	X	X	documented	147	110	94
L. stenophrys	X	X	X	plausible	1	3	13
Porthidium lansbergii	X	**X**	X	possible	4	9	16
P. nasutum	X	X	X				
P. porrasi	x?			**Total Reptilia**	**265**	**194**	**180**
P. volcanicum	**X**	**X**	X	documented	264	189	160
Infraorder "Macrostomata"				plausible	1	5	20
Family Boidae				possible	4	15	27
Boa constrictor	X	X	X				

In terms of relative species richness, Panama holds 34.9 species per 10000 km^2, and has a Species Richness Index (SRI; Wilson & Johnson 2010) of 286, i.e., one species per every 286 km^2. The study area appears more densely packed with species, amounting to 178.8 species per 10000 km^2 and a SRI of 56.

Table 4.27 breaks down the numbers of families, genera, and species for the reptilian orders and squamate suborders for Panama and the study area. The 265 reptile species herein reported to occur in Panama are distributed among 33 families and 109 genera. With 180 species in 25 families and 81 genera, about three quarters of the families and genera, respectively, and a little more than two-thirds of the species known from Panama occur in the mountainous areas of the Serranías de Talamanca and Tabasará. While snakes show the highest representativeness at the species level, lizards are the only reptile group of which every single family known from Panama has at least one species in my study area.

Table 4.27: Numbers of families, genera, and species reported herein from Panama and the study area, per order and squamate suborders. The study area's percentage of the corresponding Panamanian taxon richness is given in parentheses.

	Panama			**study area**		
Taxon	**Families**	**Genera**	**Species**	**Families**	**Genera**	**Species**
Order Testudines	7	11	14	3 (42.9%)	4 (36.4%)	4 (28.6%)
Order Crocodylia	2	2	2	1 (50%)	1 (50%)	1 (50%)
Order Squamata	24	96	249	21 (87.5%)	76 (79.2%)	175 (70.3%)
Suborder Amphisbaenia	1	1	2	0?	0?	0?
Suborder "Sauria"	15	34	99	15 (100%)	28 (82.4%)	68 (68.7%)
Suborder Serpentes	8	61	148	6 (75%)	48 (78.7%)	107 (72.3%)
Total Reptilia	**33**	**109**	**265**	**25** (75.8%)	**81** (74.3%)	**180** (67.9%)

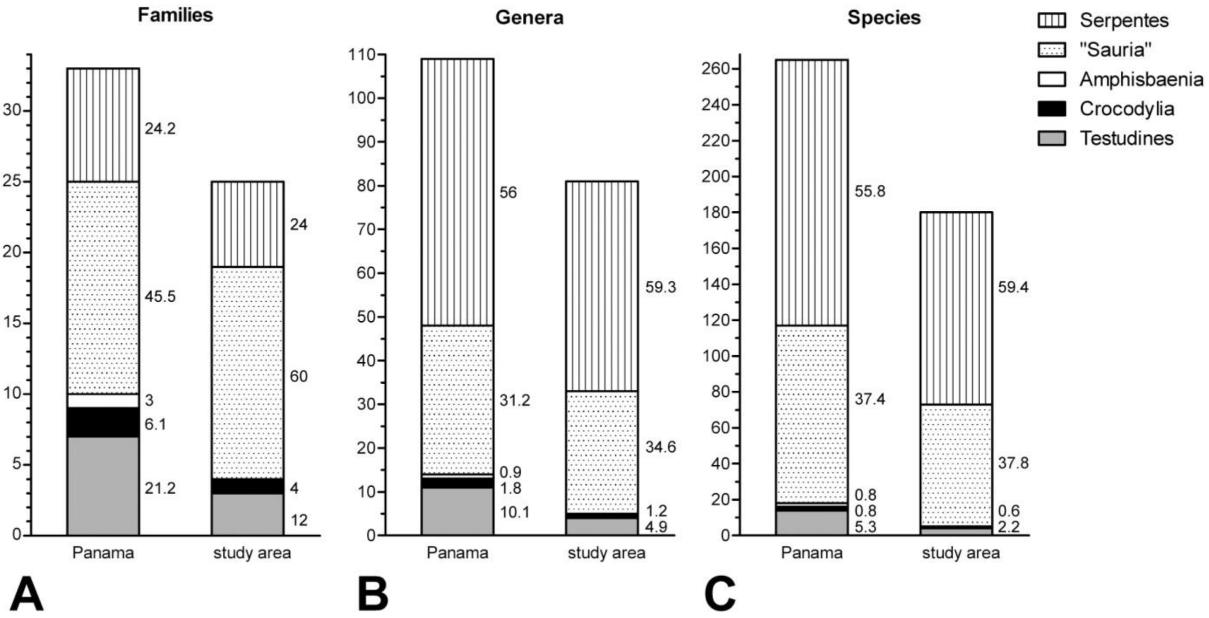


Figure 4.93: Composition of the reptile faunas reported herein for Panama (left) and the study area (right) at the (A) family, (B) genus, and (C) species level. Bar and bar segment heights correspond to absolute numbers of taxa, the corresponding percentages of the respective total fauna are given next to each bar segment.

In a similar fashion, Table 4.28 presents a synopsis of the genera and species numbers per family, again for Panama and the study area. The most species-rich families in Panama as well as in my study area are Dipsadidae, Dactyloidae, and Colubridae, followed by Viperidae, Gymnophthalmidae, and Elapidae. Finally, Figure 4.93 visualizes the relative contributions of the different orders and suborders to the respective faunas of Panama and the study area at the family, genus, and species levels.

Table 4.28: Numbers of genera and species per family reported herein from Panama and the study area. The study area's percentage of the corresponding Panamanian taxon richness is given in parentheses.

Family	Panama		study area	
	Genera	**Species**	**Genera**	**Species**
Order Testudines				
Cheloniidae	4	4	0	0
Chelydridae	1	1	0?	0?
Dermochelyidae	1	1	0	0
Emydidae	1	1	1 (100%)	1 (100%)
Geoemydidae	1	3	1 (100%)	1 (33.3%)
Kinosternidae	2	3	2 (100%)	2 (66.7%)
Testudinidae	1	1	0	0
Order Crocodylia				
Alligatoridae	1	1	1 (100%)	1 (100%)
Crocodylidae	1	1	0	0
Order Squamata				
Amphisbaenidae	1	2	0?	0?
Anguidae	4	7	3 (75%)	3 (42.9%)
Gekkonidae	2	5	1 (50%)	1 (20%)
Phyllodactylidae	1	1	1 (100%)	1 (100%)
Sphaerodactylidae	3	9	3 (100%)	4 (44.4%)
Corytophanidae	2	5	2 (100%)	4 (80%)
Dactyloidae	2	42	2 (100%)	34 (81%)
Hoplocercidae	2	2	1 (50%)	1 (50%)
Iguanidae	2	2	1 (50%)	1 (50%)
Phrynosomatidae	1	1	1 (100%)	1 (100%)
Polychrotidae	1	1	1 (100%)	1 (100%)
Mabuyidae	1	1	1 (100%)	1 (100%)
Sphenomorphidae	1	2	1 (100%)	2 (100%)
Xantusiidae	1	2	1 (100%)	2 (100%)
Gymnophthalmidae	8	14	7 (87.5%)	8 (57.1%)
Teiidae	3	5	2 (66.7%)	4 (80%)
Colubridae	15	35	14 (93.3%)	31 (88.6%)
Dipsadidae	28	76	22 (78.6%)	52 (68.4%)
Elapidae	2	11	1 (50%)	6 (54.5%)
Viperidae	6	15	6 (100%)	13 (86.7%)
Boidae	4	5	4 (100%)	4 (80%)
Tropidophiidae	1	1	0	0
Anomalepididae	3	3	1 (33.3%)	1 (33.3%)
Leptotyphlopidae	2	2	0	0

Each of the 180 species revealed herein to be present in my study area has a species account and distribution map in the subsequent chapter 4.2.2. For the 27 species whose occurrence in the study area I consider possible, I provide distribution maps in Appendix 7 and shortly mention the possibility of their occurrence in the species accounts of closely related or similar species.

4.2.2 Species accounts

The following species accounts for the 180 species whose presence in my study area I found documented or plausible are arranged in the same order of taxa as the tables in the preceding chapter. For the 27 additional species of possible presence that are briefly mentioned in the accounts of closely related species (or, if there are no congeneric species in my study area, between accounts according to their position in Table 4.26), distribution maps are given in Appendix 7. Some of these 27 species, as well as all species pictured within this work and additional species occurring in western Panama, are also pictured in Appendix 9.

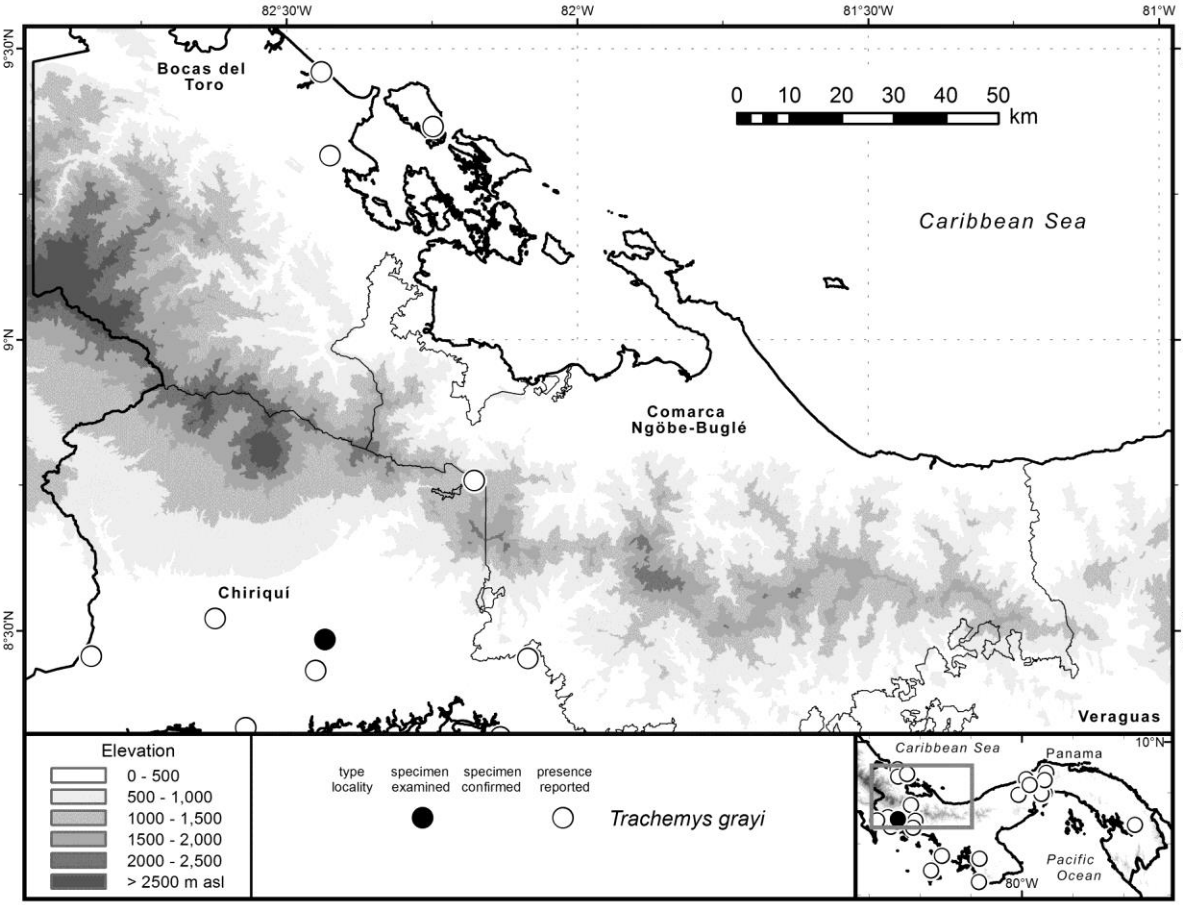
Class Reptilia Laurenti 1768
Subclass Anapsida Williston 1917
Order Testudines Batsch 1788
Suborder Cryptodira Cope 1869

Family Emydidae Rafinesque 1815

***Trachemys grayi* (Bocourt 1868)**
(Red-eared) Slider, Meso-American Slider; Tortuga resbaladora, Tortuga de oreja roja, Jicotea
Figure 4.94A; Map 4.19.
Chrysemys ornata: Savage (2002).
Pseudemys ornata: Breder (1946).
Pseudemys scripta ornata: Myers & Rand (1969).
Trachemys emolli: Sasa et al. (2010); Wilson & Johnson (2010).
Trachemys ornata: McDiarmid & Savage (2005).
Trachemys scripta: Rand & Myers (1990); Auth (1994); de la Riva (1997); Ibáñez et al. (1997, 2001); Young et al. (1999); Köhler (2001, 2008: in part.); ANAM (2004; 2005a; 2009); Martínez & Rodriguez (2005); Rodriguez et al. (2005); Ibáñez (2006); Fundación PA.NA.M.A. (2007); Sunyer (2009); Lotzkat & Hertz (2011); Batista & Ponce (2011); among many others.
Trachemys venusta: Ernst & Seidel (2006: in part.); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010: in part.).

Holotype. Exact specimen assignment unclear, from "l'embouchure du Nagualate, dans le Pacifique (Guatemala)" (Ernst & Seidel 2006).

Geographic distribution. Mexico to Panama and possibly Colombia, 0–1050 m asl. In Panama, throughout the lowlands, including those of Bocas del Toro, Chiriquí, Veraguas, and the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from Quebrada Bijau, RFLF, approx. 1050 m asl.



Map 4.19: Distribution of *Trachemys grayi.*

Diagnosis. A medium-sized to large turtle (maximum carapace length 600 mm) that is readily identified by its contrasting yellow and dark stripes covering the lateral and ventral surfaces of head and neck, with at least one dark stripe running horizontally through the eye. It further differs from *Rhinoclemmys annulata* by lacking the prominent middorsal keel on the carapace in adults and by having the ventral surfaces of head and neck striped (vs. blotched or spotted), and from members of the family Kinosternidae by lacking two movable plastral hinges.

Description. Carapace length to 600 mm; carapace with 6 vertebral scutes and 4 laterals per side, the latter decreasing in size posteriorly; plastron with 12 scutes; middorsal keel in juveniles, but reduced or absent in adults; extensive finger and toe webbing; notched beak on the upper jaw; broad alveolar surface of upper jaw with a distinct ridge.

Coloration in life. Carapace usually greenish or olive gray, with ocelli at least on the L scutes, which may become indistinct as adult specimens become darker and darker; plastron yellow with dark markings; juveniles generally more contrastingly colored than adults.

Natural history notes. Aquatic, diurnal and nocturnal, omnivorous. The animal pictured in Fig. 4.94A was accidentally caught in a pond while fishing with a small piece of fish as bait during a sunny afternoon.

Remarks. The species is included in the reptile fauna of the study area based on the specimen MVUP 1405, collected on 28.08.1990 at "Qda. Bijau, Gualaca, Chiriquí". The SRTM altitude of 1052 m asl for my georeference of this locality is slightly above the upper elevational limit of 1000 m given by Köhler (2008).

The populations referred herein to *Trachemys grayi* have been treated under different generic, specific, and subspecific names by different authors (see Savage 2002, Köhler 2008, and Savage & Bolaños 2009 for examples), but were called *T. scripta* by most authors preceding Jaramillo et al. (2010). According to the latter authors and Rhodin et al. (2010), *T. venusta* is the species naturally occurring in Panama. Fritz et al. (2012) revealed *T. venusta* to be polyphyletic and referred *T. emolli, T. venusta grayi,* and *T. venusta panamensis* to *T. grayi.* Consequently, the latter name is now applicable to all populations naturally occurring in Costa Rica and Panama, and N to Mexico at least along the Pacific versant.

To my knowledge, it remains unclear whether *T. grayi* ranges into Colombia. However, I tentatively assume herein that the Colombian populations referred to *T. venusta* in the past (e.g., Ernst & Seidel 2006; Rhodin et al. 2010) represent *T. grayi* rather than any other of the other taxa considered subspecies of *T. venusta* before Fritz et al. (2012). Although *T. scripta* is listed for Panama by Rhodin et al. (2010, as introduced) and Uetz & Hošek (2014), since it does not appear in the list of Jaramillo et al. (2010) I prefer not to include that species in the Panamanian reptile fauna until the presence of populations of *T. scripta* in the country is actually documented.

The presence of another aquatic turtle attaining medium to large size, the Snapping Turtle *Chelydra acutirostris* Peters 1862, in my study area is rendered possible by its distribution along the Caribbean lowlands of western Panama (also rendering its occurrence in the Comarca Ngöbe-Buglé and Veraguas plausible; see distribution map in Appendix 7) and its upper elevational limit reported as 1160 m asl (Savage 2002; Köhler 2008). It is unmistakeably distinguished from all other Panamanian turtles by its large head with a strongly hooked beak, its reduced cruciform plastron comprising only 9 plates, and its tail which is at least as long as the carapace.

Family Geoemydidae Theobald 1868

Rhinoclemmys annulata (Gray 1860)

Brown Wood Turtle; Tortuga de bosque, Tortuga negra, Tortuga terrestre café

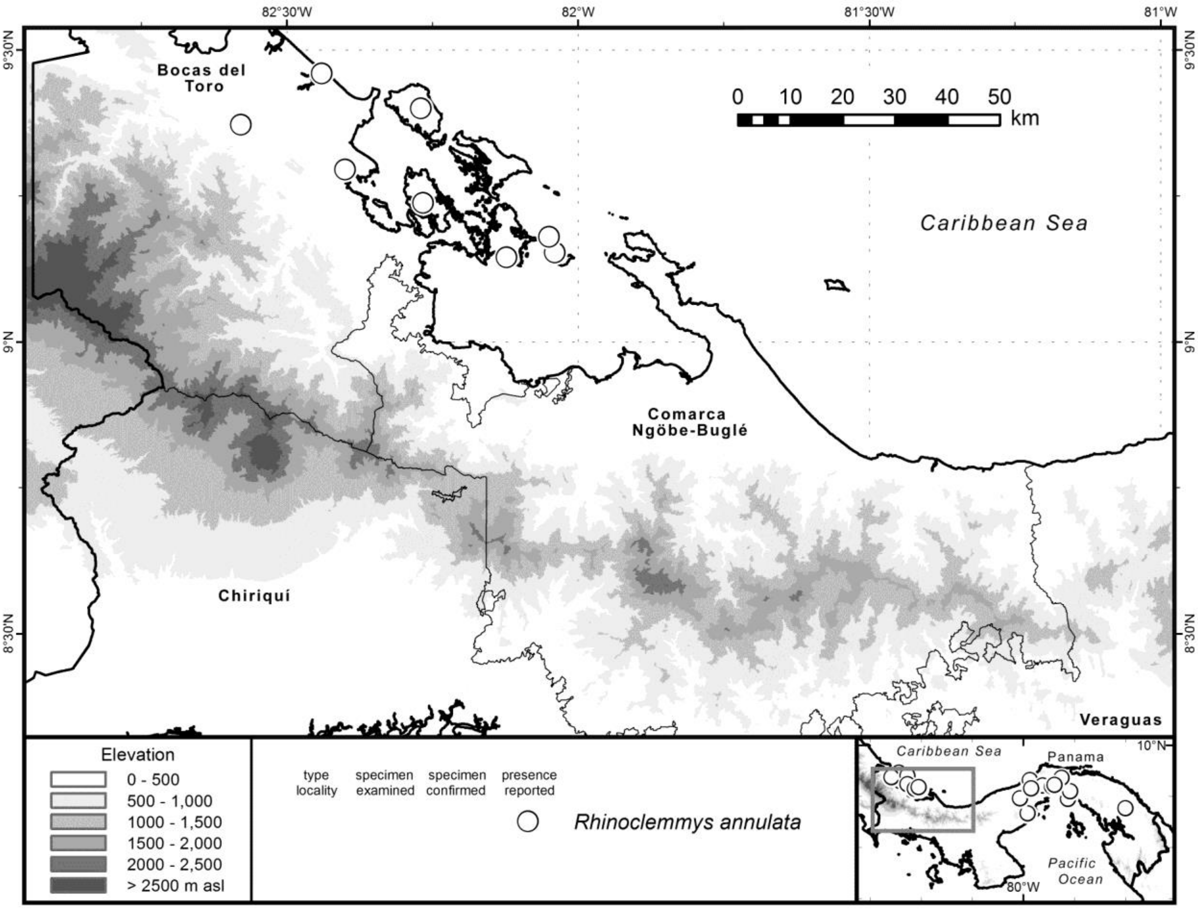
Figure 4.94B; Map 4.20.

Geomyda annulata: Breder (1946).

Geoemyda annulata: Wettstein (1934); Evans (1947); Myers & Rand (1969).

Syntypes. BMNH 1946.1.22.56 and 1947.3.5.58–59, from Esmeraldas, Ecuador.

Geographic distribution. Eastern Honduras to northern Ecuador, 0–920 m asl. In Panama, along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, as well as on both versants of central Panama, and Pacific eastern Panama. In the Cordillera Central, reported from PNAC around 850 m asl.



Map 4.20: Distribution of *Rhinoclemmys annulata.*

Diagnosis. A medium-sized turtle (maximum carapace length around 200 mm) that is readily identified by its single, broad, light-colored middorsal keel on the carapace that is prominent also in adults. It further differs from *Rhinoclemmys funerea* and *Trachemys grayi* by lacking extensive toe webbing, and from the latter by having five instead of six vertebral scutes, as well as from members of the family Kinosternidae by lacking two movable plastral hinges.

Description. Carapace length to 204 mm; carapace with 5 vertebral scutes and 4 laterals per side, the latter decreasing in size posteriorly; plastron with 12 scutes; middorsal keel broad and prominent in juveniles as well as in adults; extensive finger webbing, toe webbing reduced or absent; hooked, unnotched beak on the upper jaw.

Coloration in life. Carapace brown to black, middorsal keel of lighter color; plastron dark in the center, with lighter margins; head and neck with covered with dark blotches arranged in irregular stripes, but no contrasting dark stripe running horizontally through the eye.

Natural history notes. Terrestrial, diurnal, and herbivorous. The individuals I have seen in southeastern Nicaragua had ticks attached to their carapace.

Remarks. Together with the upper elevational limit of 920 m asl given by Savage (2002) for Costa Rica, the Panamanian records of *Rhinoclemmys annulata* from premontane elevations up to 850 m (Jaramillo et al. 2010) including PNAC (Ibáñez et al. 1996) render the species' presence in my study area plausible. I further regard the presence of its congener *Rhinoclemmys funerea* (Cope 1876) in my study area as possible in view of its distribution along the Caribbean lowlands of western Panama (also rendering its occurrence in the Comarca Ngöbe-Buglé and Veraguas plausible; see distribution map in Appendix 7) and its upper elevational limit reported as 600 m (Köhler 2008).

Family Kinosternidae Agassiz 1857

Cryptochelys leucostoma (Duméril & Bibron 1851)

White-lipped Mud Turtle; Galápago ediondo

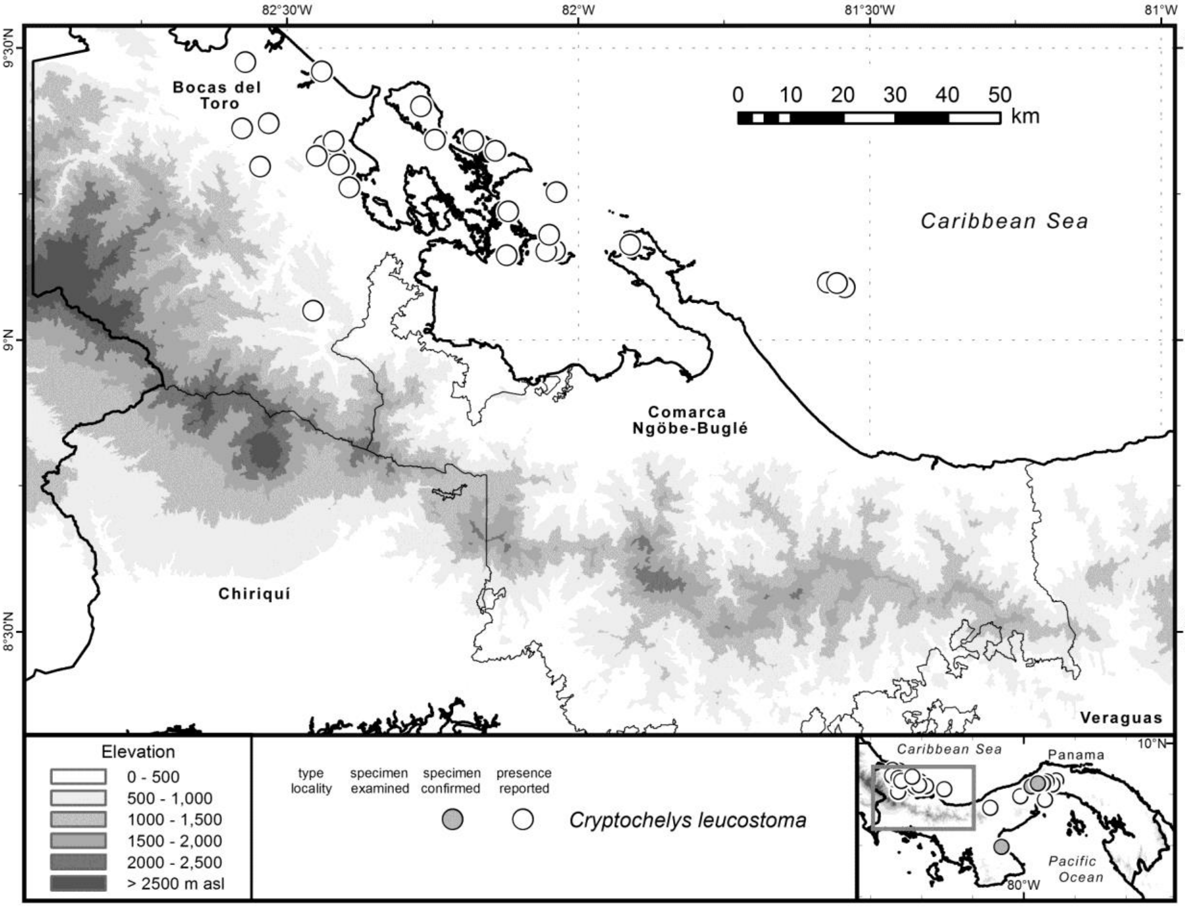
Figure 4.94C; Map 4.21.

Kinosternon leucostomum: Wettstein (1934); Myers & Rand (1969); Peters and Donoso-Barros (1970); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1997, 2001); Young et al. (1999); Köhler (2001, 2008); Savage (2002); ANAM (2004, 2009b); McDiarmid & Savage (2005); Fundación PA.NA.M.A. (2007); Savage & Bolaños (2009); Sunyer (2009); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); among many others.

Lectotype. MNHN 8311, from New Orleans (in error), Mexique; Río Usumacinta.

Geographic distribution. Mexico to Peru, 0–1500 m asl. In Panama, along both versants throughout the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and

Veraguas. In the Cordillera Central, reported from the upper Río Changuinola drainage up to ca. 230 m asl.



Map 4.21: Distribution of *Cryptochelys leucostoma.*

Diagnosis. A small turtle (maximum carapace length 174 mm) that is immediately recognized as a member of the family Kinosternidae by its plastron composed of only 11 plates and having two movable hinges. It differs from *Cryptochelys angustipons* by having a fully developed plastron covering most or all of the soft parts when closed (vs. reduced plastron leaving a lot of the soft parts uncovered), and from *Kinosternon scorpioides* by having a unicarinate (vs. bi- or usually tricarinate) carapace and the axillary scute separated from the inguinal scute (vs. in contact).

Description. Carapace length to 174 mm; carapace with 5 vertebral scutes and 4 laterals per side; plastron with 11 scutes and two movable hinges; single middorsal keel low, may disappear in adults; extensive finger and toe webbing; hooked beak on the upper jaw; one or more pairs of chin and throat barbles.

Coloration in life. Carapace dark brown; plastron yellowish light brown; head dark brown dorsally, with a yellow postorbital stripe spotted with lighter yellow, bordered below by a dark brown postorbital stripe; beak dirty white to yellow.

Natural history notes. Aquatic, nocturnal, and omnivorous.

Remarks. Together with the upper elevational limit of 1200 m asl given by Savage (2002) for Costa Rica, the Panamanian records of *Cryptochelys leucostoma* from premontane elevations up to 850 m (Jaramillo et al. 2010) and especially the specimen CHP 6312 from Guayabal, my georeference for which yields a SRTM elevation of 234 m, render the species' presence in my study area plausible.

Cryptochelys leucostoma is the type species of the genus *Cryptochelys* Iverson, Le & Ingram 2013. The widespread species has been treated as *Kinosternon leucostomum* by most former authors.

Kinosternon scorpioides **(Linnaeus 1766)**

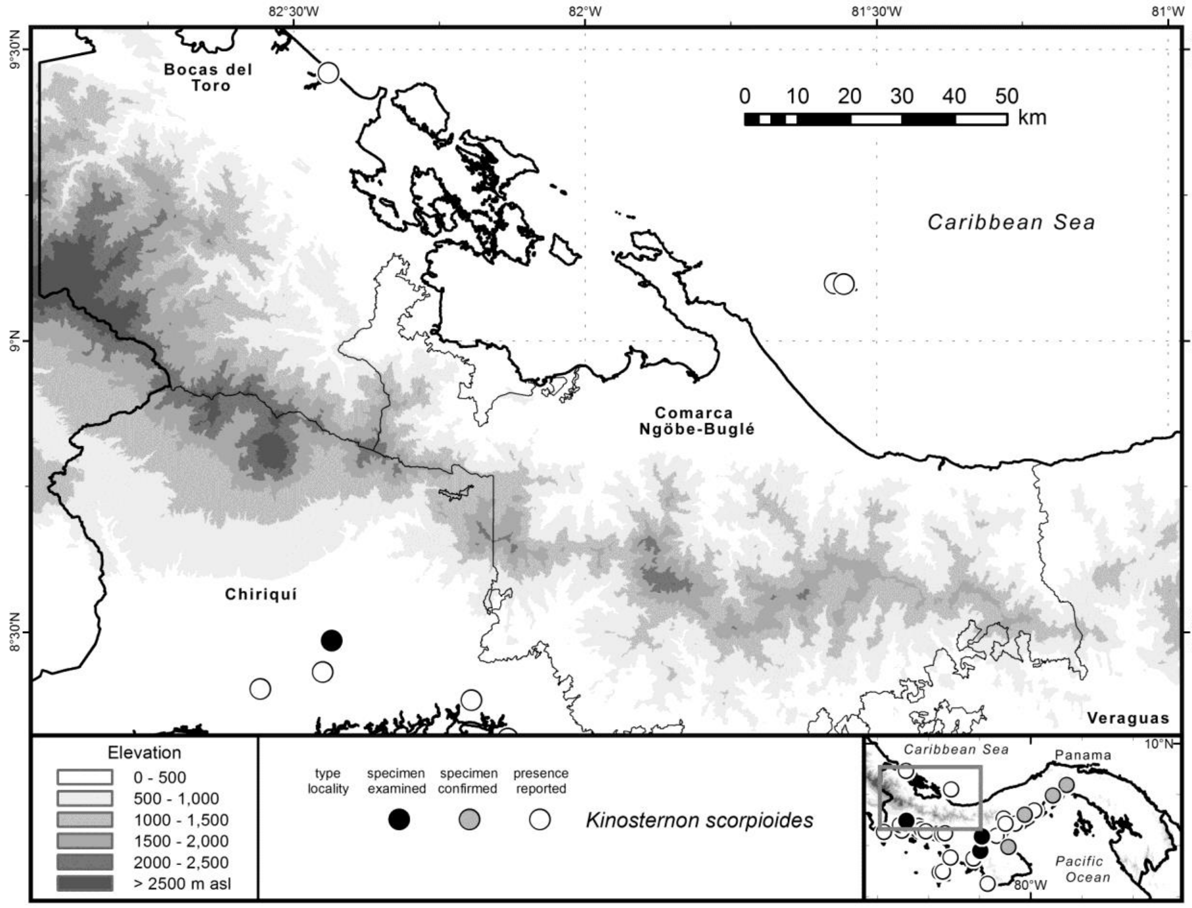
Scorpion Mud Turtle; Galápago, Tortuga de ciénagas, Tortuga candado

Figure 4.94D; Map 4.22.

Kinosternon cruentatum: Dunn (1933); Wettstein (1934); Swanson (1945).

Kinosternon panamensis: Busack (1966).

Holotype. Exact specimen assignment unclear, from Surinam.



Map 4.22: Distribution of *Kinosternon scorpioides.*

Geographic distribution. Mexico to Peru, Brazil, Bolivia, and Argentina, 0–1500 m asl. In Panama, along the Pacific versant throughout the country, including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas; singular records from Bocas del Toro on the Caribbean versant, which it probably inhabits in central and eastern Panama. In the Cordillera Central, reported from El Valle de Antón and PNAC up to 850 m asl.

Diagnosis. A medium-sized turtle (maximum carapace length 270 mm) that is immediately recognized as a member of the family Kinosternidae by its plastron composed of only 11 plates and having two movable hinges. It differs from the other Panamanian members of this family by having three, sometimes two, keels on the carapace (vs. unicarinate or flattened).

Description. Carapace length to 270 mm; carapace with 5 vertebral scutes and 4 laterals per side; plastron with 11 scutes and two movable hinges; one middorsal and two L keels on carapace, the former may disappear in adults; extensive finger and toe webbing; strongly hooked beak on the upper jaw in adults; 2–3 pairs of chin and throat barbles.

Coloration in life. Carapace medium to very dark brown; plastron almost uniform yellow or with centers of scutes dark brown; D and L surfaces of head and neck dark brown, D surfaces of neck as well as L surfaces of head and neck mottled with orange; head and neck becoming almost uniformly dark brown in large specimens; beak yellow with dark brown mottling.

Natural history notes. Aquatic and omnivorous. We found individuals of this species in still ponds and slow-moving creeks on open pastures, rather fast-flowing rivers with gallery forest, as well as one specimen (SMF 89574) dead on a road through recently burnt pasture and cropland. When released, the animals usually dived away quickly, and one could be observed digging itself into the mud of the streambed.

Remarks. Together with the upper elevational limit of 1425 m asl given by Savage (2002) for Costa Rica, the Panamanian records of *Kinosternon scorpioides* from premontane elevations up to 800 m (Jaramillo et al. 2010) and especially the records from PNAC (Ibáñez et al. 1996; my georeference for their localitie yields a SRTM elevation of 847 m) and Valle de Antón (Dunn 1933) render the species' presence in my study area plausible. The records from San San Pond Sak (ANAM 2004) and Isla Escudo de Veraguas (USNM 148253, 525744 fide HerpNet) require verification in view of the distribution as described by Savage (2002) and Jaramillo (2010). However, I retain these distributional points since both ANAM (2004) and the USNM catalogue also list *Cryptochelys leucostoma,* the most probable candidate for misidentifications, from the same respective localities, and the distribution map given by Köhler (2008) lets the records appear possible.

Subclass Archosauria Cope 1869

Order Crocodylia Gmelin 1789

Suborder Eusuchia Huxley 1875

Family Alligatoridae Cuvier 1807

***Caiman crocodilus* (Linnaeus 1758)**

Spectacled Caiman, Common Caiman; Caimán, Lagarto, Baba, Babilla, Babillo

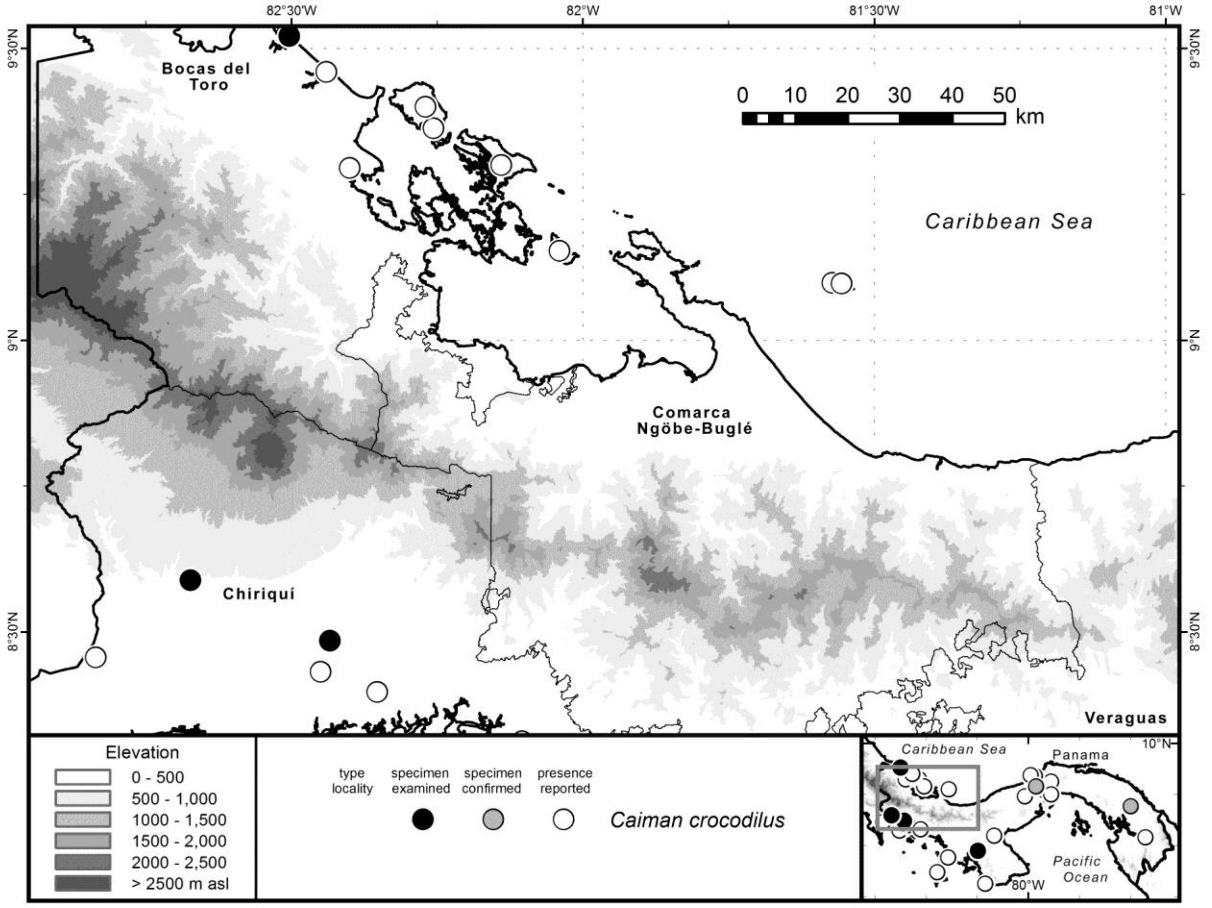
Figure 4.94E; Map 4.23.

Caiman fuscus: Swanson (1945); Breder (1946); Evans (1947).

Jacaretinga crocodilus fuscus: Wettstein (1934).

Lectotype. At ZMUU, from unknown locality.

Geographic distribution. Mexico to Peru, Brazil, and probably northern Bolivia, 0–430 m asl. In Panama, throughout the lowlands. In the Cordillera Central, approaching premontane elevations at least in Chiriquí (see remarks).



Map 4.23: Distribution of *Caiman crocodilus.*

Diagnosis. A medium-sized crocodilian (maximum TOL 2750 mm) that is readily distinguished from the only other Panamanian member of this order, *Crocodylus acutus,* by having an elevated transverse ridge just anterior to eyes and no teeth of the lower jaw visible when the mouth is closed (vs. no such ridge and 3rd mandibular tooth visible when mouth is closed in *C. acutus*).

Description. TOL to 2750 mm; upper eyelids with an elevated tubercle; 18 or 19 transverse and 8 to 13 longitudinal rows of D scutes; V scutes in 20–27 transverse rows.

Coloration in life. D surfaces of larger individuals almost unicolor dark to olive brown, grading into cream color towards the venter; D and L surfaces of younger individuals with yellow and dark crossbands, which may be retained on the L tail surfaces in larger specimens.

Natural history notes. Nocturnal and carnivorous.

Remarks. I observed the characteristic red eye glare of several *Caiman crocodilus* in the Río Escárrea near Volante (WP 89) at about 430 m asl. This locality extends the upper elevational limit of 300 m as given by Wilson & Johnson (2010; though I assume a confusion with the upper limit for *Crocodylus acutus,* which is given as 650 m). Moreover, it is situated at less than 1 km from my study area, rendering the occurrence of this species therein plausible.

Subclass Lepidosauria Haeckel 1866

Order Squamata Oppel 1811

I regard the presence of the amphisbaenid ***Amphisbaena varia*** **Laurenti 1768** in my study area as possible in view of its distribution extending W to PNGDOTH and Donoso district (also rendering its occurrence in Veraguas possible; see distribution map in Appendix 7) and its upper elevational limit in Panama reported as 850 m asl (Jaramillo et al. 2010). The species was called *A. fuliginosa* by most authors before 2010 and is readily distinguished from all other reptiles of western Panama by having the limbless body as well as the very short, thick tail covered with complete whorls of rectangular scales.

Suborder "Sauria" Macartney 1802

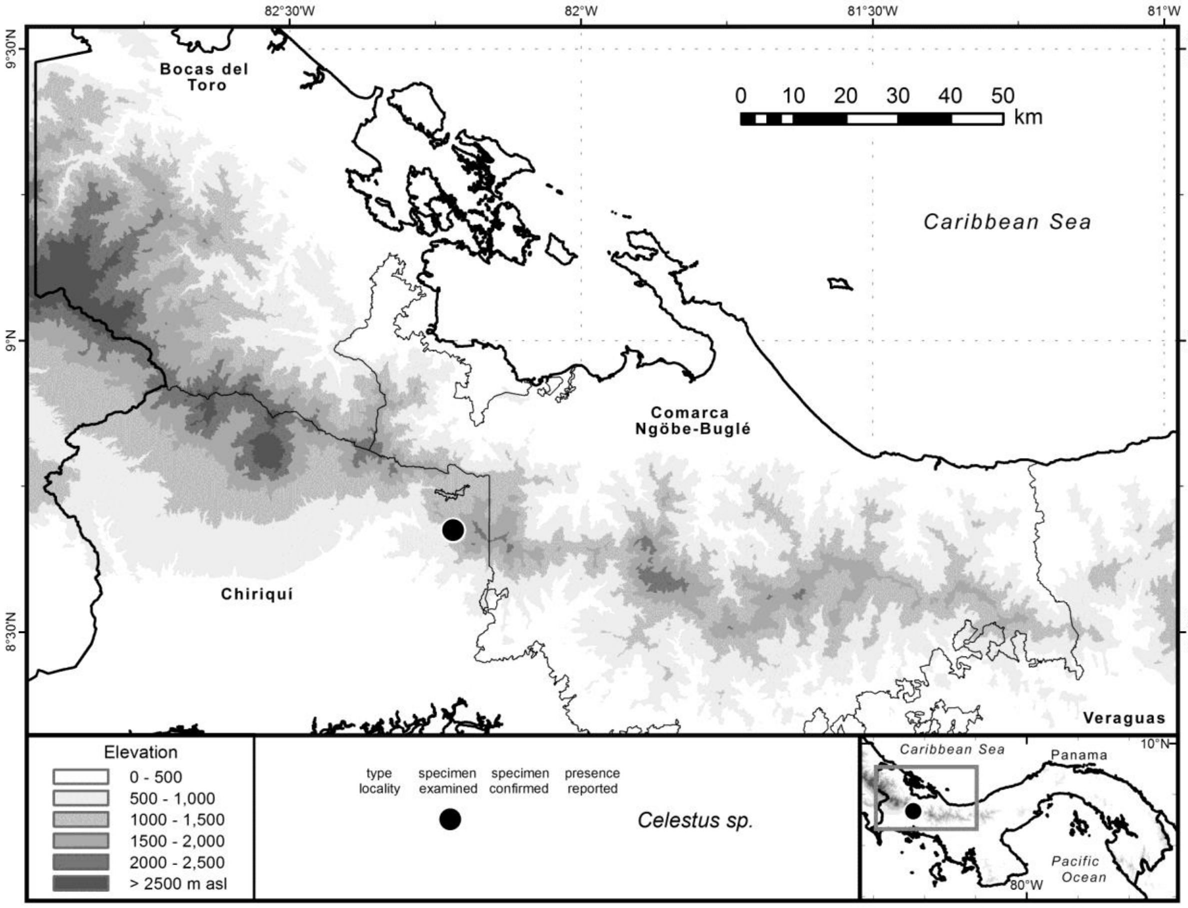
Infraorder Anguimorpha Fürbringer 1902

Family Anguidae Gray 1825

***Celestus* sp.**

Figures 4.2; 4.94F; Map 4.24.

Geographic distribution. Only known from the grounds of the Lost & Found Ecohostel (8.67462°N, 82.21958°W, 1250 m asl), RFLF, Chiriquí, Panama.



Map 4.24: Distribution of *Celestus* sp.

Diagnosis. A presumably medium-sized (only known specimen is a small juvenile), skink-like lizard that is immediately recognized as a member of the family Anguidae, and thus distinguished from the superficially similar species of *Gymnophthalmus, Marisora,* and *Scincella,* by the presence of two pairs of internasals separating the rostral from the first unpaired dorsal head plate (vs. fewer than two pairs of internasals in members of the non-anguid genera). Among the anguids known from the Cordillera Central and its surroundings, it differs from *Coloptychon rhombifer* and *Mesaspis monticola* in lacking a distinct lateral fold (vs. presence of a longitudinal lateral fold of granular scales separating the enlarged dorsals from the ventrals), and from *Diploglossus bilobatus* and *D. monotropis* in having the claws exposed (Fig. 4.2I–L; vs. claws enclosed in a claw sheath). *Celestus* sp. can readily be distinguished from the only congeneric Panamanian species, *C. adercus,* by the presence of two loreals (vs. three), 33 SAM (vs. 31), 72 transverse rows of dorsals (vs. 79), 77 transverse rows of ventrals (vs. 86), and 10 precloacal scales (vs. 8). See chapter 4.1.1 for the distinctions from other Central American *Celestus*.

Description. SVL in the only known juvenile specimen 35 mm, TL of incomplete tail 15 mm; cycloid body scales striate but unkeeled; cycloid caudal scales striate and, except on base of tail, markedly unicarinate; 4toe 24; 4finger 19. For a detailed description of pholidosis and morphometrics, see chapter 4.1.1.

Coloration in life. D ground color of head, body, and anterior portion of tail Warm Sepia (221A) with Tawny Olive (223D) dots partly bordered by Sepia (119); lips Beige (219D); D and L head scale borders Sepia (119); D surfaces of limbs Sepia (119); tail grading into Dark Neutral Gray (83) posteriorly; V surfaces of head and body Pistachio (161); V surfaces of tail grading from Pistachio (161) to Dark Neutral Gray (83); soles of hands and feet Grayish Horn Color (91); iris True Cinnamon (139) (Figs. 4.2A–E).

Coloration in preservative. After 42 months of preservation in 70% ethanol, D surface of head brown, with plate sutures outlined by darker brown; L surfaces of head grading from brown to bluish light gray ventrally, with dark brown sutures; D and L surfaces of body and tail brown with scattered light spots with dark anterior borders; light spots loosely aggregated to form a subtle pattern of irregular and interrupted transverse stripes dorsolaterally, and more densely arranged to form a reticulum suggesting a diffuse, broad longitudinal band ventrolaterally; D and L surfaces of limbs brown with dark scale borders, on upper arm also with light spots; V surfaces of head, body, and limbs bluish light gray to dirty white, almost free of dark pigmentation, grading into slightly darker gray under tail (Figs. 4.2F–L).

Natural history notes. The neonate specimen (umbilical opening not yet closed) was caught on 30.09.2009 around noon while it was active on the concrete stairs leading from the dormitory to the kitchen of Lost & Found Ecohostel.

Conservation. *Celestus* sp. is known from a single locality and a single specimen, which was discovered while moving through an anthropogenic structure. That is, virtually nothing is known about the distribution, population, and natural history of this species, or any other aspect of its biology. Thus, I see no other option but to place it in the IUCN category "Data Deficient" (DD). Nevertheless, I calculated the EVS for *Celestus* sp. as 6 (range) + 3 (persecution) + 5 (ecological distribution) = 14, indicating a high vulnerability.

Remarks. The juvenile individual is the second specimen of the genus *Celestus* collected in Panama. The diversity of this genus along the Talamancan Highlands is still unsatisfactorily understood, with both *C. orobius* and *C. adercus* also represented by a single voucher specimen, respectively (Savage 2002; Savage et al. 2008), and possibly undescribed forms reported from Boruca (Savage 2002: p. 527) and Las Cruces (J.M. Savage, pers. comm. May and September 2012) in southern Pacific Costa Rica.

I regard the presence of another species of this genus, *Celestus adercus* Savage, Lips & Ibañez 2008, in Veraguas and my study area as possible in view of the proximity of its type locality at PNGDOTH to the Santa Fé area (see distribution map in Appendix 7).

Diploglossus bilobatus **(O'Shaughnessy 1874)**

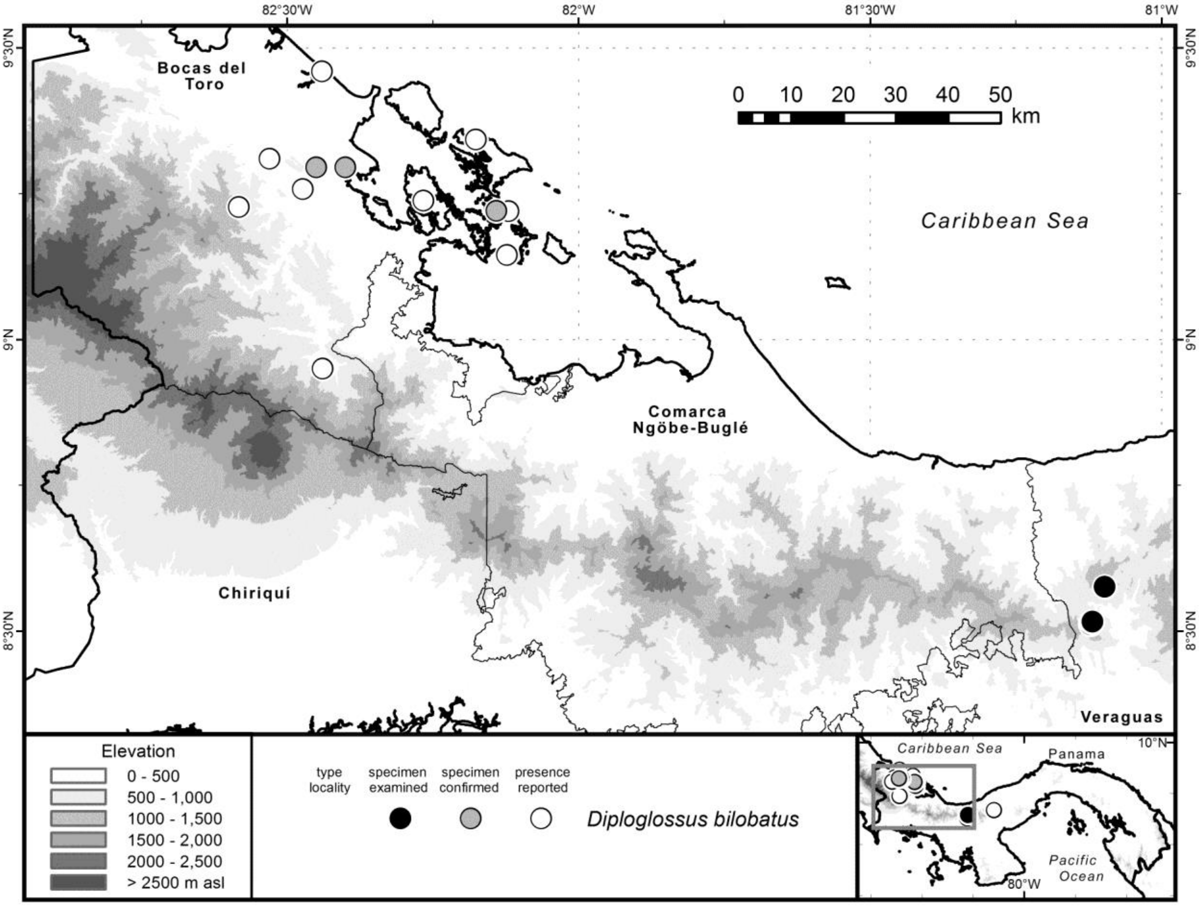
O'Shaughnessy's Galliwasp, Talamancan Galliwasp

Figures 4.94G, H; Map 4.25.

Diploglossus bilabatus: Martínez et al. (1995).

Holotype. BMNH 1946.8.7.91 from Costa Rica.

Geographic distribution. Nicaragua to Panama, 0–1360 m asl. In Panama, at low and premontane elevations chiefly along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, Veraguas, Colón, and Coclé. In the Cordillera Central, reported from the Caribbean versant of the Serranía de Talamanca in Bocas del Toro, the Santa Fé area, and PNGDOTH, up to 1000 m asl.



Map 4.25: Distribution of *Diploglossus bilobatus.*

Diagnosis. A medium-sized (maximum SVL 99 mm) skink-like lizard that is immediately recognized as a member of the family Anguidae, and thus distinguished from the superficially similar species of *Gymnophthalmus, Marisora,* and *Scincella,* by the presence of two pairs of internasals separating the rostral from the first unpaired dorsal head plate (vs. fewer than two pairs of internasals in members of the non-anguid genera). Among the anguids known from the Cordillera Central and its surroundings, it differs from *Coloptychon rhombifer* and *Mesaspis monticola* in lacking a distinct lateral fold (vs. presence of a longitudinal lateral fold of granular scales separating the enlarged dorsals from the ventrals), and from *C. adercus* and *Celestus* sp. by the presence of a claw sheath enclosing the claw except for its very tip (vs. claws exposed due to absence of claw sheath). *Diploglossus bilobatus* is readily distinguished from the much larger and more colorful *D. monotropis* by lacking pronounced keels on the striate dorsals, and by exhibiting a single large prefrontal plate (vs. two PF and one FN).

Description. TOL to 240 mm; SVL to 99 mm; a single, large prefrontal (i.e., PF and FN fused into a single plate); two superposed postnasals; nasal in contact with rostral; nostril pierced in the posterior portion of the nasal; SAM 36–41; 4toe 11–16; 4finger 7–9*; D, L, V, and caudals cycloid; D and L striate (smooth in juveniles), in some examples weakly keeled.

Coloration in life. Juveniles chiefly dark brown or black, with yellow snout and light gray V surfaces; adults with gray, bronze, or brown dorsum with dense dark mottling, separated by a dorsolateral dark line from the lighter-colored flanks that may bear transverse bars, ocelli, or blotches and are gray to brown in females and green in males.

Lotzkat et al. (2010b; original publication provided in Appendix 8) found coloration to be quite variable among their sample: "One of the adult females (SMF 89548) from Cerro Mariposa, Veraguas, was recorded as follows: D scales Verona Brown (223B), edged by Sepia (219); a Cream Color (54) dorsolateral stripe present, L surfaces of body Cinnamon-Drab (219C), grading ventrally into Light Russet Vinaceous (221D); venter Light Russet Vinaceous (221D); D surface of head Verona Brown (223B); L surfaces of head and neck Light Drab (119C), with Chamois (123D) bars on lips and neck; upper surfaces of limbs Raw Umber (223); D surface of tail Sepia (119) with Light Drab (119C) scale centres; V surfaces of head and neck Pale Neutral Gray (86) with Chamois (123D) flecks on chin; V surface of tail Light Neutral Gray (85); V surfaces of hands and feet Plumbeous (78). The other three adult females from Cerro Mariposa exhibited a different coloration. As a representative example, one of them (SMF 89547) was recorded as follows: D scales Verona Brown (223B), edged by Sepia (119); a Clay Color (123B) dorsolateral line present; L surfaces of body Mars Brown (223A), grading into Kingfisher Rufous (240) ventrally; venter Kingfisher Rufous (240); D surface of head Raw Umber (123), L surfaces of head and neck Olive-Green (Auxiliary) (48) with Chamois (123D) bars on lips and Sulfur Yellow (157) flecks on neck; upper surfaces of limbs Raw Umber (223); D surface of tail Sepia (119) with Dark Drab (119B) pigment in scale centres; V surfaces of head and neck Light Drab (119C) with Chamois (123D) flecks on chin; V surfaces of hands and feet Sepia (119). The juvenile collected on Cerro Mariposa was recorded as follows: D ground color Jet Black (89), grading into Spectrum Yellow (55) towards tip of snout; venter mainly transparent, however with a suggestion of Dark Neutral Gray (83); V surface of tail uniform Dark Neutral Gray (83); L surfaces speckled with Apple Green (61). The juvenile from nearby Cerro Negro has a lower number of rather bluish-white speckles on the flanks and shows suggestions of the D reticulum present in the adults. The juvenile from Isla Popa exhibits a conspicuous reddish flank coloration posterior to the forelimbs. All three juveniles share the bright yellow snout but differ from each other in the extent of this coloration posteriorly onto the dorsum. Since all our adult specimens are females, the differences observed among them are clearly due to individual variation. As suspected by Myers (1973), coloration obviously changes drastically during ontogenesis."

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that the formerly yellow snouts of juveniles are cream and the reddish D hues have faded; the venters of the females retain a suggestion of salmon color.

Natural history notes. This terrestrial lizard seems to be active both at day- and nighttimes. Lotzkat et al. (2010b) encountered four adult females on 12.05.2008 under logs and boards between 20:15 and 20:40 and spotted two more adult specimens darting through the leaf litter along a forest trail between 01:00 and 01:30 in the same night. The first juvenile specimen from Cerro Mariposa was found crossing a forest trail around noon on a sunny day. On Cerro Negro, the juvenile moved about through the leaf litter at night. After the publication of Lotzkat et al. (2010b), a second juvenile from Cerro Mariposa (MHCH 2310; Fig. 4.94H) was found active in the leaf litter at 16:15. Lotzkat at al. (2010b) further noted that only two of their seven specimens possess complete tails (tail complete in MHCH 2310), and suspected the observability of *Diploglossus bilobatus* to be somewhat correlated to precipitation.

Remarks. Lotzkat et al. (2010b) stated their as well as preceding records (Martínez & Rodriguez 1994; Martínez et al. 1995) from around Santa Fé to constitute the easternmost records of *Diploglossus bilobatus,* being unaware of the unpublished specimens CHP 4870 (collected at "El Copé") and 5848 (collected at "Camino pedregoso, El Copé", PNGDOTH) from about 57 airline km E of Cerro Negro. These records from PNGDOTH render the occurrence of *D. bilobatus* in Colón province plausible. The juvenile SMF 89951, collected by AC on Cerro Negro at 1000 m asl (not 1063 m as reported by Lotzkat et al. 2010b), raises the upper elevational limit reported for Panama from 850 m (Jaramillo et al. 2010).

Contrary to the statement in Savage (2002: p. 530), none of the adult females from Panama which I examined has "flanks with a definite greenish cast", a condition I regard to be restricted to adult males. Lotzkat et al. (2010b) noted variation in certain pholidotic characters among their Panamanian material: "as in the material examined by Myers (1973), several of our specimens exhibit, either on one (SMF 89549; MHCH 2309) or both (SMF 89548) sides of the head, a single first (anterior) loreal touching the posterior internasal rather than the two superposed first loreals (with the upper one touching the prefrontal) commonly found in this species. One specimen (SMF 89547) shows five, another one (SMF 89951) seven instead of the usual six supralabials to the level below the centre of eye on one side of the head. Three specimens (SMF 85002, 89549; MHCH 2309) have five instead of the usual six infralabials to the level below the centre of eye on one side of the head. The number of longitudinal scale rows at midbody ranges from 36 (SMF 89951) to 42 (SMF 89546; [re-examination showed 40]). While D and L trunk scales of the juvenile specimens are smooth, those of the adult specimens have 8–12 striae. In contrast to the specimens described by Taylor (1956) and Myers (1973), none of our specimens has any discernible median keels on these scales."

I regard the presence of another *Diploglossus,* the large and colorful *D. monotropis* (Kuhl 1820), in my study area as possible in view of its distribution along the Caribbean lowlands of Panama (also rendering its occurrence in the Comarca Ngöbe-Buglé and Veraguas plausible; see distribution map in Appendix 7) as well as its upper elevational limit reported as 500 m asl for Panama (Jaramillo et al. 2010) and 1000 m for the species as a whole (Köhler 2008).

Mesaspis monticola **(Cope 1877)**

Cope's Alligator Lizard; Dragón, Lagartija de altura

Figures 4.95A, B; Map 4.26.

Barisia monticola: Walters (1953).

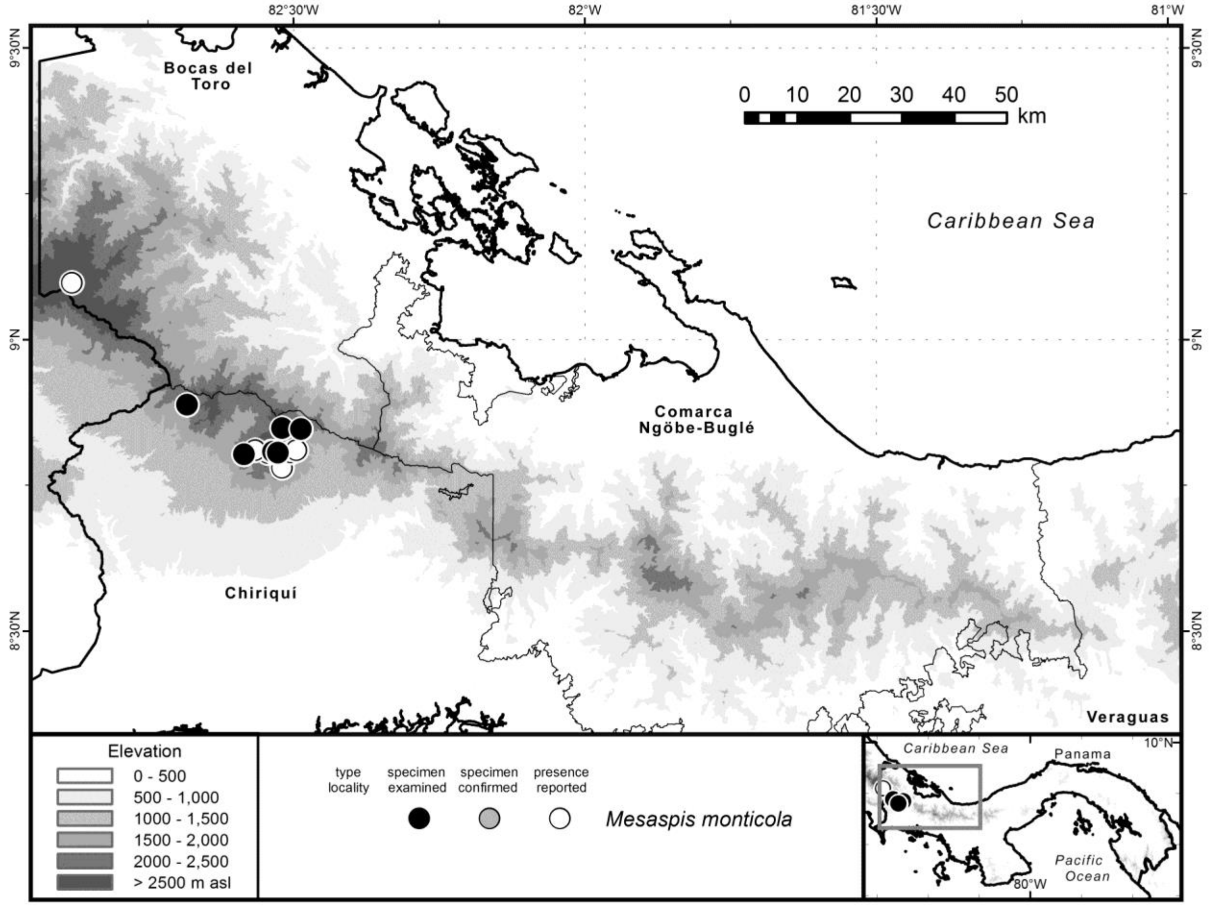
Gerrhonotus alfaroi: Wettstein (1934).

Gerrhonotus monticola: Slevin (1942).

Holotype. From the summit of Pico Blanco (elevation 11500 ft) in the Eastern Cordillera of Costa Rica (= surnmit of Cerro Utyum, Cantón de Talamanca, Provincia de Limón fide Savage 1970, 1974); collected by W.M. Gabb.

Geographic distribution. Endemic to the Talamancan Highlands of Costa Rica and western Panama, 1340–3820 m asl. In Panama, reported from the Cordillera de Talamanca in Bocas del Toro and Chiriquí as far east as the Boquete area, 1850–3420 m asl.

Diagnosis. A medium-sized (maximum SVL 88 mm) lizard that is immediately recognized as a member of the family Anguidae, and thus distinguished from the superficially similar species of *Leposoma* and *Ptychoglossus,* by the presence of two pairs of internasals separating the rostral from the first unpaired dorsal head plate (vs. fewer than two pairs of internasals in members of the non-anguid genera). Among the anguids known from the Cordillera Central and its surroundings, it differs from all species except *Coloptychon rhombifer* in having a distinct longitudinal lateral fold of granular scales separating the enlarged dorsals from the ventrals (vs. no such fold), and from the much larger *C. rhombifer* by the presence of 3–4 pairs of enlarged chin shields (vs. five pairs) as well as by the lack of conspicuous dark crossbands on body and tail.



Map 4.26: Distribution of *Mesaspis monticola*.

Description. TOL to 236 mm; SVL to 88 mm; two pairs of IN; 1 large FN separating 2 lateral PF (which are absent in the examined specimen SMF 90199); D rectangular, in 16 longitudinal rows at MB, middorsal rows markedly keeled; longitudinal fold with much smaller granular L extending from ear to groin; V cycloid, smooth, in 12 longitudinal rows at MB; SAM 32–38*; 4toe 14–16*; 4finger 9–13*.

Coloration in life. Females and juveniles with light to medium brown dorsum and darker brown flanks, both with longitudinal series of dark blotches, V surfaces rather homegeneously light-colored; adult males with very dark D and L surfaces heavily mottled with green, and grayish V surfaces with dark mottling.

The adult female SMF 90199 (Fig. 4.95B) was recorded as follows: D surfaces of head, body and tail Light Drab (119C) grading into Hair Brown (119A) towards tip of tail; body and base of tail with a series of Sepia (119) middorsal blotches; a series of Sepia (119) dorsolateral blotches suggesting a stripe extending from eye onto tail; L surfaces of body and tail below these blotches, and D and L surfaces of limbs Walnut Brown (221B), grading into Hair Brown (119A) on posterior portion of tail; V surfaces of body, tail and limbs Flesh Ocher (132D) with a suggestion of Orange Rufous (132C), grading into Mikado Brown (121C) posteriorly on tail; regenerated tip of tail Hair Brown (119A); L surface of head Light Drab (119C) with a few Sepia (119) blotches; V surface of head Light Sky Blue (168D) with a suggestion of Opaline Green (162D); iris Glaucous (79). Photos of the juvenile specimen SMF 90198 show that its D and L surfaces were much darker, and the latter much more densely mottled, than those of the adult female described above.

Coloration in preservative. After 4 years of preservation in 70% ethanol, the coloration is similar to that in life, apart from that all reddish tonalities (especially on the venter of adult specimens) have faded and the venters have a bluish hue.

Natural history notes. Terrestrial and diurnal. At Refugio Las Rocas (WP 158, 2420 m asl) along Sendero Los Quetzales as well as Area de acampar Los Fogones (WP 201, 3321 m) along the road to the summit of Volcán Barú, I observed adult individuals of *Mesaspis monticola* basking on moss cushions or dead organic material during the morning hours. In the crater of Volcán Barú (WP 204, 2972 m), several individuals were seen active in the early afternoon, with one adult female moving through the high grass about 1 m above ground. The female SMF 90199 caught at this place carried 6 eggs.

Remarks. Together with *Sceloporus malachiticus,* this species is one of the highest-ranging reptiles in Panama, where it has been recorded from elevations up to 3420 m asl (Walters 1953; Jaramillo et al. 2010). The examined specimens SMF 85439–40 from Alto Chiquero at 1850 m set a new lower elevational limit for Panama (from 2130 m reported by Jaramillo et al. 2010). The specimen MVUP 1855 from Cerro Itamut is the hitherto only record from Bocas del Toro. The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible.

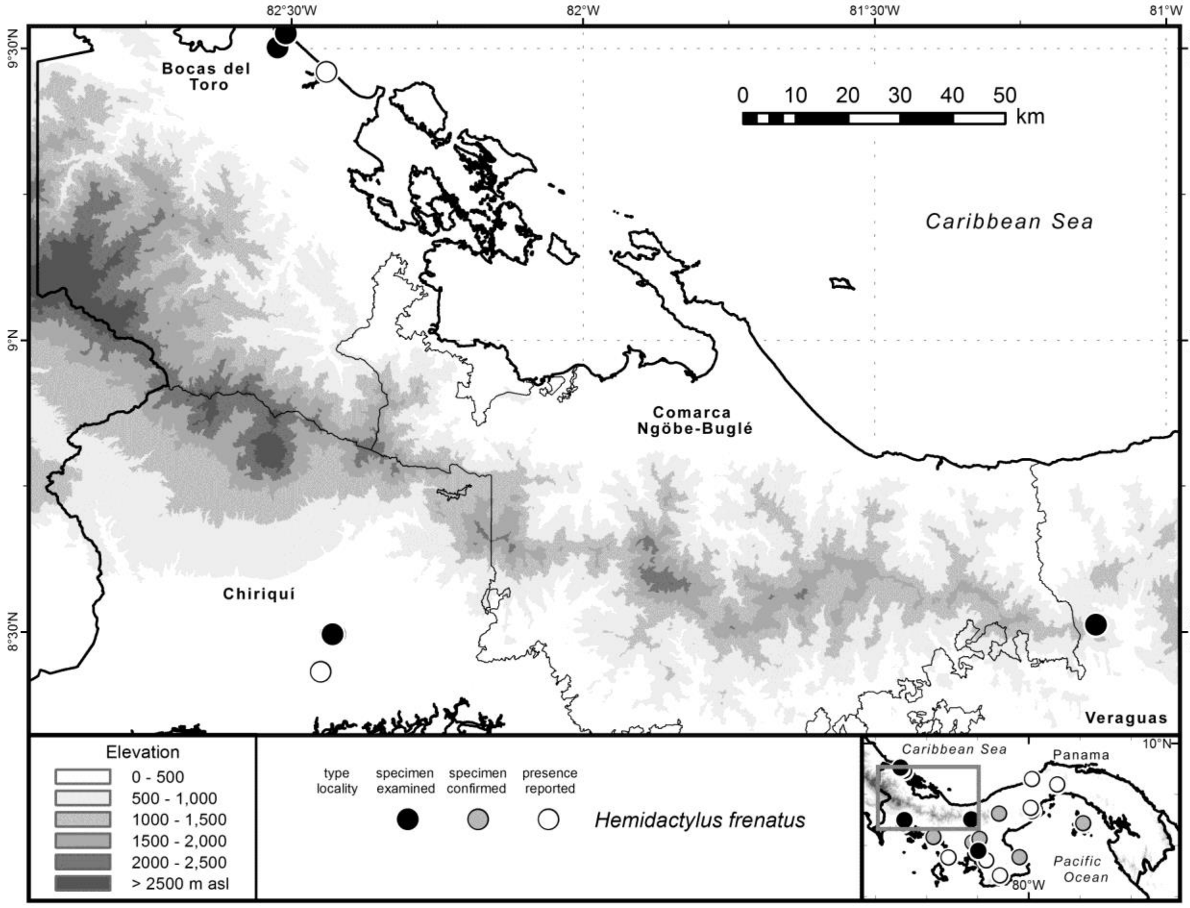
I regard the presence of another anguid with a distinct L fold, *Coloptychon rhombifer* (Peters 1876), in my study area as possible in view of its distribution in E Pacific Costa Rica and reported presence in western Panama (though I could not trace any point record; see distribution map in Appendix 7), as well as its upper elevational limit reported as 500 m (Savage 2002; Köhler 2008).

Infraorder Gekkota Camp 1923

Family Gekkonidae Gray 1825

Hemidactylus frenatus Schlegel 1836

Common House Gecko, (South) Asian House Gecko; Gueco asiático, Gueco de paréd, Limpia casa, Limpiacasas
Figure 4.95C; Map 4.27.
Syntypes. At MNHN, from Timor and Java.



Map 4.27: Distribution of *Hemidactylus frenatus*.

Geographic distribution. Native to SE Asia, introduced in tropical regions worldwide, including Central America from Mexico to Panama, 0–1230 m asl. In Panama, throughout the lowlands, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and in certain places at premontane elevations. In the Cordillera Central, reported from PNAC, PNGDOTH, and Cerro Mariposa, up to ca. 1000 m asl.

Diagnosis. A medium-sized gecko (maximum SVL 65 mm) of that is very similar in general appearance to *Lepidodactylus lugubris,* from which it differs in having claws on all fingers and toes, all but the terminal and basal subdigital lamellae divided, two pairs of greatly enlarged chin shields, and by its conspicuously enlarged median subcaudals (vs. first finger and toe without claw, only some distal lamellae divided, no greatly enlarged chin shields, and no enlarged median subcaudals). The species can readily be distinguished from the much larger *Thecadactylus rapicauda* by the absence a fleshy web between fingers and toes, and by its non-retractile claws that protrude distally from the dilated lamellar pads (vs. extensive finger and toe webbing and retractile claws that barely protrude from between the divided distal lamellae).

Description. TOL to 140 mm; SVL to 65 mm; D granular, with interspersed enlarged tubercles; V cycloid, smooth; D caudal scales granular, with interspersed denticulate tubercles; SC cycloid, smooth, median series conspicuously enlarged; males with a continuous series of femoral and precloacal pores; two pairs of chin shields (sublabials) in broad contact with the infralabials; 4toe 9–11; 4finger 7*.

The hemipenis of *Hemidactylus frenatus* is a small, rather slender, bilobed organ; lobes about the diameter of, and a little shorter than, truncus.

Coloration in life. In the course of metachrosis, the D and L ground color of any individual may vary from almost white to medium brown. Darker brown or gray spots, dashes, bars, blotches, or reticula may be present. The V surfaces are invariably lighter colored. The adult male SMF 89568 was recorded in the light phase as follows: D ground color Grayish Horn Color (91), irregularly suffused with Smoke Gray (44); V surfaces dirty white with shadings of Sulfur Yellow (157) on venter and Chamois (123D) on median SC and around cloaca; soles of hands and feet Pale Pinkish Buff (121D), lamellae dirty white; iris Sayal Brown (223C).

Coloration in preservative. After 4–6 years in 70% ethanol, D surfaces light gray to brown with only faint suggestions of darker markings; V surfaces dirty white, with a suggestion of salmon color in some specimens.

Natural history notes. Nocturnal, occurring in high densities in most lowland settlements in western Panama.

Remarks. The presence of *Hemidactylus frenatus* in my study area is based on the juvenile specimen MHCH 2322 (original field number LSt 122), found by LS and NH in a funnel trap on Cerro Mariposa around 1000 m asl, about 400 m (airline) from the next inhabited house. Assuming that it had been taken there from the lowlands within the very trap (which, considering the study periods of LS and NH at Cerro Mariposa, would mean that the animal had stayed unnoticed for at least four days in the trap, or returned to it), Stadler (2010) neither included nor mentioned this specimen in his inventory of Cerro Mariposa. However, in the case that his assumption was right, the presence of *H. frenatus* in my study area is rendered plausible by the records from PNAC (Ibáñez et al. 1996) and PNGDOTH (Jadin et al. 2010b), together with the maximum elevations of 820 m given for Panama (Jaramillo et al. 2010) and 1230 m given for Costa Rica (Savage 2002).Many locals in western Panama recall that the "white gecko" (*Hemidactylus frenatus*) replaced the "red-headed" gecko (*Gonatodes albogularis*) from their houses, claiming the former to also prey upon the latter. Apart from these plausible memories, several popular beliefs about *H. frenatus* exist, most dealing with the alledged venomousness of this species and especially its tail, which is said to be fired off. Many Chiricanos claim to know of cases of multiple envenomation in their circles of friends after a *H. frenatus* had fallen into a cooking pot or similar. On the other hand, many Panamanians recognize that the species benefits their households by decimating insects.

I regard the presence of the very similar, likewise introduced gekkonid *Lepidodactylus lugubris* (Duméril & Bobron 1836) in my study area as possible in view of its occurrence throughout the lowlands of western Panama (also rendering its presence in the Comarca Ngöbe-Buglé and Chiriquí plausible; see distribution map in Appendix 7) and its upper elevational limit reported as 700 m (Köhler 2008).

Family Phyllodactylidae Gamble, Bauer, Greenbaum & Jackman 2008

***Thecadactylus rapicauda* (Houttuyn 1782)**

Turnip-tailed Gecko, Turniptail Gecko; Gueco gigante

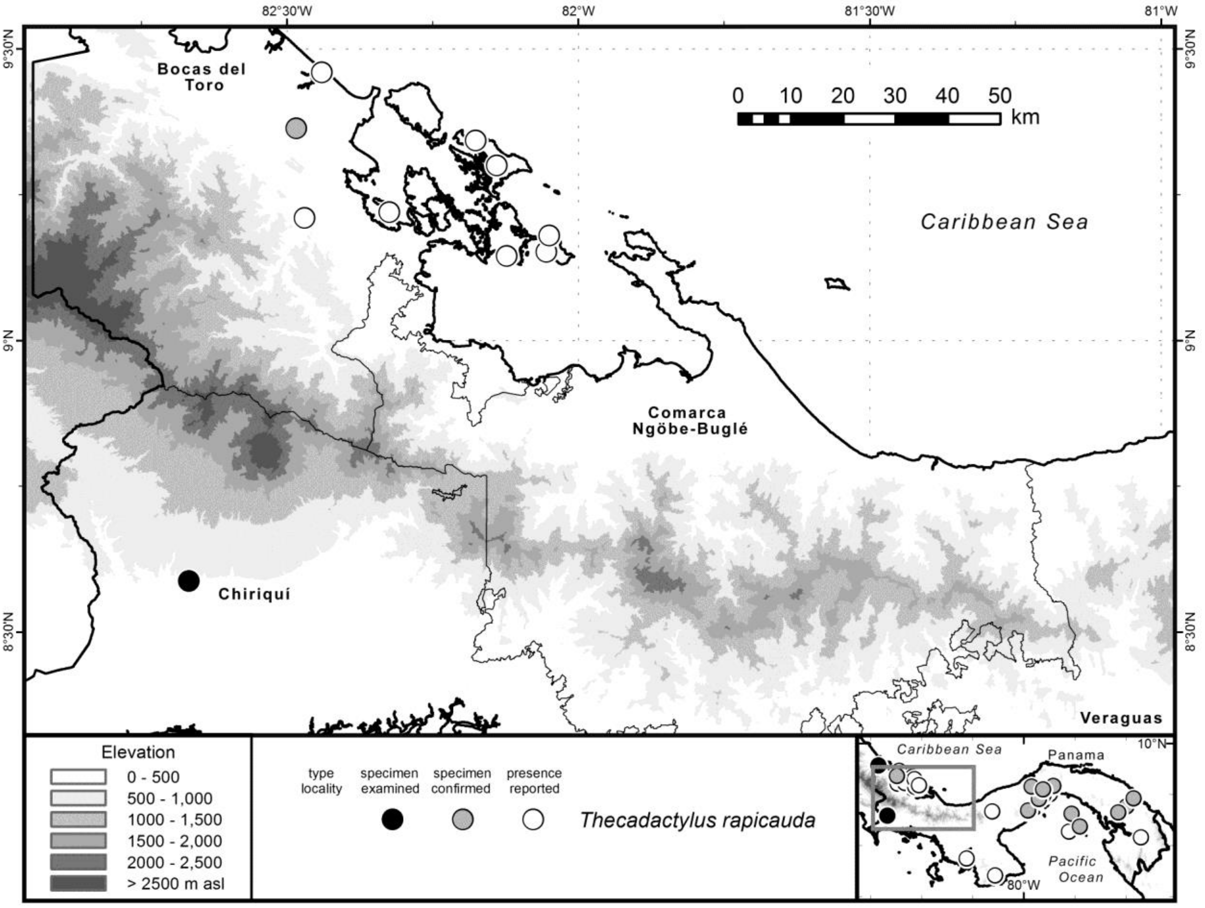
Figure 4.95D; Map 4.28.

Thecadactylus rapicaudus: Barbour (1906); Swanson (1945); Breder (1946); Cochran (1946); Martínez et al. (1999).

Thecodactylus rapicaudus: Cope (1899).

Neotype. RMNH 16267, from Surinam (holotype probably lost, from American Islands).

Geographic distribution. Mexico through Central America to western Ecuador, Colombia, the Guayanas, and northern Brazil, 0–1050 m asl. In Panama, throughout the lowlands including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and several premontane sites. In the Cordillera Central, reported from PNAC, PNGDOTH, the Río Changuinola drainage, and Volante, up to ca. 990 m asl.



Map 4.28: Distribution of *Thecadactylus rapicauda*.

Diagnosis. This largest Panamanian gecko (maximum SVL 126 mm) is most similar in general appearance to the much smaller *Hemidactylus frenatus* and *Lepidodactylus lugubris,* from which it differs by its extensive fleshy finger and toe webbing (vs. no web), its retractile claws that barely protrude from between the divided distal lamellae and are not visible from above (vs. non-retractile claws that protrude distally from the dilated lamellar pads, thus being well visible from above), its much higher number of finger and toe lamellae (18 or more vs. 15 or less), and the lack of denticulate tubercles on the tail (vs. tubercles present).

Description. TOL to 225 mm; SVL to 126 mm; D and L sclaes of body and tail granular, without enlarged tubercles; V cycloid, smooth; SC cycloid, smooth, without enlarged median series; a pair of large postcloacal tubercles; tail abruptly becoming very stout posterior to base; SAM 146–147*; 4toe 18–25; 4finger 23*.

The hemipenis of *Thecadactylus rapicauda* is a medium-sized, bilobed organ with short and stout truncus and lobes (based on a photo of the Venezuelan specimen SL 045).

Coloration in life. D and L surfaces of body and tail light gray to medium brown; head and body spotted and mottled with darker brown to almost black as well as lighter gray to almost white; tail similarly mottled or with irregular longitudinal stripes of dark brown to almost black; V surfaces ranging from dirty white to yellow, sparsely mottled with brown under tail;

a light postorbital stripe usually present. In the course of metachrosis, the D and L ground color of any individual may vary from almost white to medium brown, and the darker markings become more or less contrasting.

Coloration in preservative. After 6 years in 70% ethanol, D surfaces light grayish brown with darker brown markings; V surfaces dirty white to light gray with brown spotting.

Natural history notes. Nocturnal. The only individual which I encountered in Panama (SMF 89601) was active on a branch about 2 m above ground at 21:36.

Remarks. The specimen SMF 89601 from Volante (WP 88) was collected less than 1 km from my study area. This record, as well as the specimens CHP 6213 (from El Guayabal, Río Changuinola, less than 5 km from study area) and CHP 6024 (PNGDOTH), together with the records from PNAC (Ibáñez et al. 1996) and the upper elevational limit of 1052 m asl in Costa Rica (Savage 2002) render the occurrence of this species in the study area plausible. My georeference for CHP 6024 yields a SRTM elevation of 986 m, which is well above the highest elevation of 850 m reported from Panama (Jaramillo et al. 2010).

Family Sphaerodactylidae Underwood 1954

Gonatodes albogularis (Duméril & Bibron 1836)

Yellow-headed Gecko; Gueco cabecirrojo, Gueco cabecinaranja

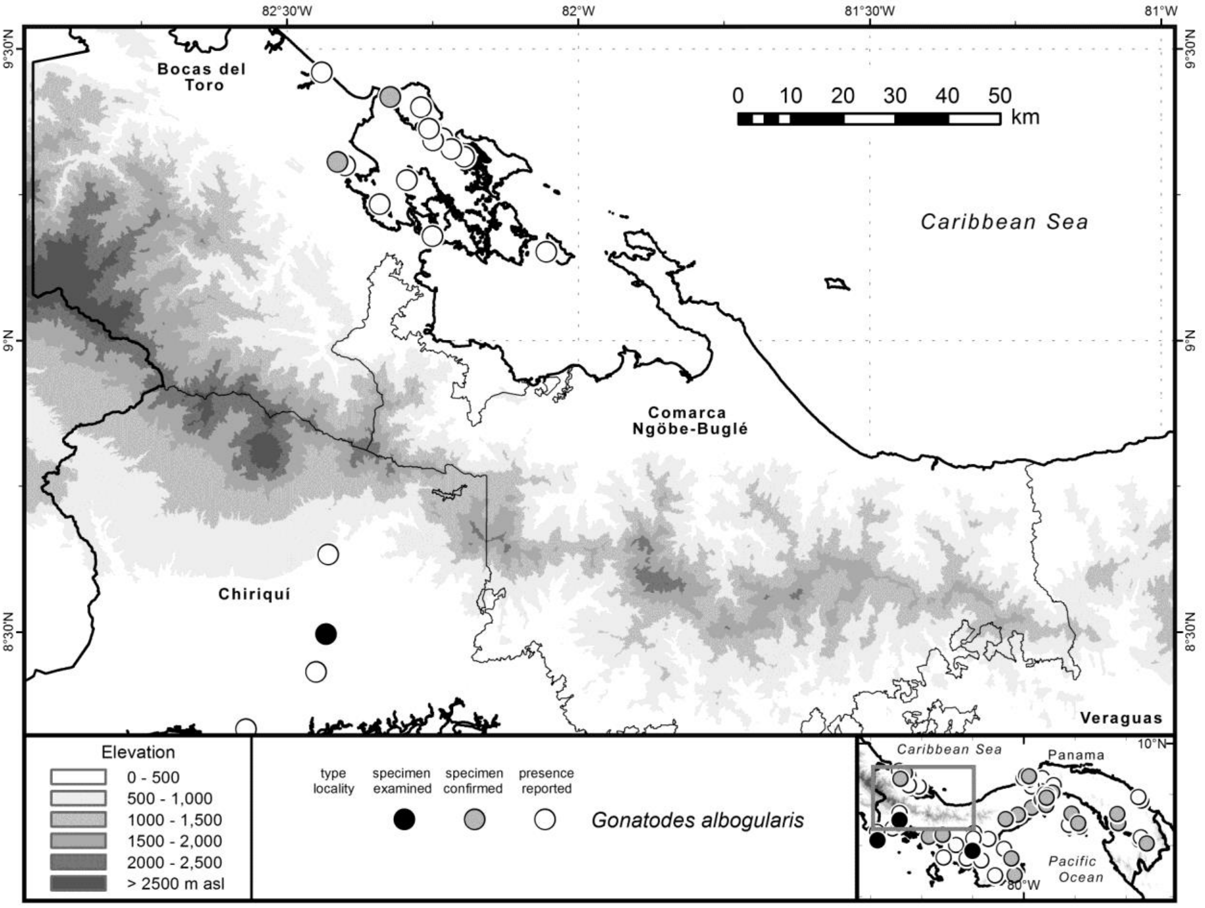
Figures 4.95E, F; Map 4.29.

Gonatodes caudiscutatus: Barbour (1906).

Gonatodes fuscus: Barbour (1906); Swanson (1945); Breder (1946); Cochran (1946); Evans (1947); Taylor (1956).

Syntypes. MNHN 1776, from Martinique.

Geographic distribution. Mexico to Colombia and Venezuela, Antilles, Florida (introduced), 0–1000 m asl. In Panama, throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC, El Valle de Antón, and El Francés, up to 600 m asl.



Map 4.29: Distribution of *Gonatodes albogularis*.

Diagnosis. A small gecko (maximum SVL 48 mm) that is readily distinguished from members of the families Gekkonidae and Phyllodactylidae by its round pupils and the absence of dilated lamellar pads under fingers and toes. It differs from members of *Lepidoblepharis* and *Sphaerodactylus* in having exposed claws, with only the basalmost portion envolved in one ventral and one dorsal scale (vs. retractile claws mostly enclosed in an ungual sheath).

Description. TOL to 113 mm; SVL to 48 mm; D and L sclaes of body and tail granular, without enlarged tubercles; V cycloid, smooth; SC cycloid, smooth, with enlarged median series; males with V and femoral escutcheon scales; 4toe 18–22; 4finger 15–16*.

Coloration in life. *Gonatodes albogularis* exhibits a marked sexual dichromatism. Adult males (Fig. 4.95E): D and L surfaces of body, limbs, and tail dark bluish gray to almost black, with more or less densely arranged lighter or darker spots on body, limbs, and base of tail; tip of tail dirty white; head and neck orange, with darker spots; dark-edged light blotches suggesting a labial stripe and (usually) a fragmentary collar anterior to shoulders. Females (Fig. 4.95F): D and L surfaces of body, limbs, and tail light gray to brown, with dense light and dark mottling. Juveniles similar to females; V surfaces dirty white to light brown in all.

Coloration in preservative. After 4 years in 70% ethanol, the coloration of the female SMF 91553 is very similar to that in life, while in the male SMF 91552 all bluish hues on body and blue blotches on head have faded to gray, and the orange head to brown, grading into white spotted with brown on neck and under head.

Natural history notes. Diurnal, terrestrial and arboreal. Found in a variety of habitats including beach vegetation, forests, and settlements.

Remarks. Since this village stretches well into it, I regard the specimens MVUP 398–9 from El Francés to document the presence of *Gonatodes albogularis* in my study area. This notion is supported by the records from PNAC (Ibáñez et al. 1996), and El Valle de Antón (FMNH 177013) as well as by and the upper elevational limits given as 850 m asl for Panama (Jaramillo et al. 2010), 530 m in Costa Rica (Savage 2002), 800 m in Nicaragua (Sunyer 2009), and 1000 m in general (Köhler 2008).

***Lepidoblepharis xanthostigma* (Noble 1916)**

Costa Rica Scaly-eyed Gecko, Litter Gecko; Gueco de hojarasca, Morachito de suelo

Figures 4.3G, H; 4.4D; 4.5D; 4.6D; 4.9; 4.11; 4.95G; Maps 4.1; 4.30.

Lathrogecko xanthostigma: Noble (1916, 1923).

Lepidoblepharis peraccae: Breder (1946).

Lepidoblepharis sp.: Martínez & Rodriguez (1994, possibly); Martínez et al. (1995, possibly).

Holotype. MCZ 11658, female, from Zent, near Puerto Limón, Costa Rica.

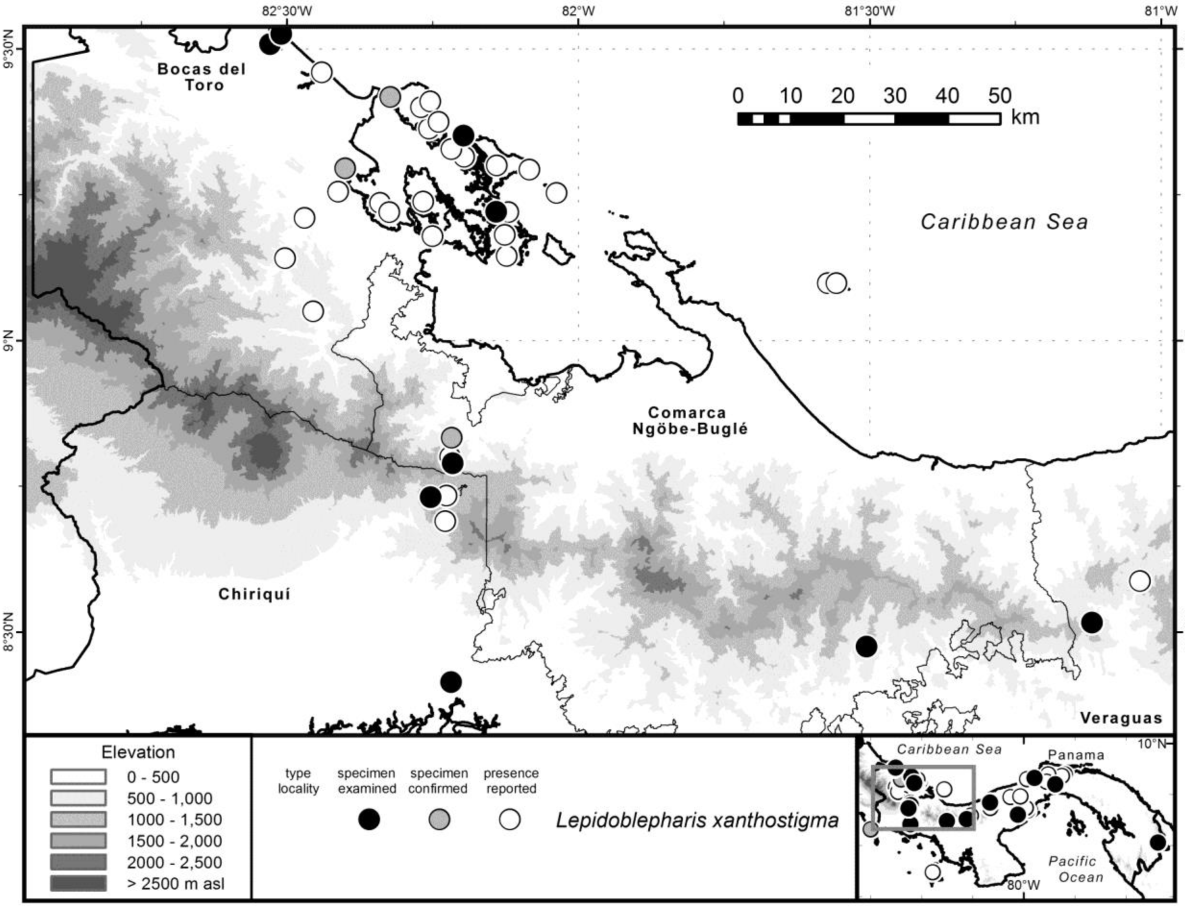
Geographic distribution. Nicaragua to Colombia, 0–1360 m asl. In Panama, throughout the country including low and premontane elevations Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from both versants up to 1300 m asl.

Diagnosis. A very small gecko (maximum SVL 35 mm) that is readily distinguished from members of the families Gekkonidae and Phyllodactylidae by its round pupils and the absence of dilated lamellar pads under fingers and toes. It differs from members of *Gonatodes* and *Sphaerodactylus* in having the retractile claws mostly enclosed in a symmetrical ungual sheath composed of six scales (vs. exposed claws and no ungual sheath in *Gonatodes,* and asymmetrical ungual sheath with a large, circular, terminal subdigital scale in *Sphaerodactylus*). It differs from all other Panamanian *Lepidoblepharis* in having 12 or more lamellae under the 4th toe, and 10 or more under the 4th finger (vs. 4toe 9 or fewer, 4finger 8 or fewer). A detailed key to Panamanian *Lepidoblepharis* as well as other pholidotic characters are provided in chapter 4.1.2.

Description. TOL to 84 mm; SVL to 35 mm; D and L scales of head, body, and tail granular and more or less raised or pointed; V and SC cycloid, smooth; median SC greatly enlarged; males with 36–90 V and usually also subfemoral (0–7 per thigh) escutcheon scales; PR 2–6;

PM 3–6; mental with 0–2 short lateral clefts in posterior border; SAM 62–88; 4toe 12–16; 4finger 10–12. See chapter 4.1.2 for detailed morphological data.

The hemipenis of *Lepidoblepharis xanthostigma* is a small organ with two short, stout lobes; truncus and lobes finely calyculate.



Map 4.30: Distribution of *Lepidoblepharis xanthostigma*.

Coloration in life. The coloration of *Lepidoblepharis xanthostigma* is quite variable (see Fig. 4.11 for examples): the light to dark brown D and L surfaces can be variably spotted, mottled, or striped with lighter and darker color; two dorsolateral light stripes and/or a light nuchal collar composed of two crescent-shaped markings may be present; the tail is reddish in some specimens; V surfaces usually lighter and more unicolor, except for escutcheon scales which are white. Juveniles seem to be more contrastingly mottled than adults. The adult male SMF 89576 (Fig. 4.11A) was recorded as follows: D and L ground color Raw Umber (223) with black flecks and a black dorsolateral stripe; a Buff (24) dorsolateral line extending from shoulders to middle of tail; V surfaces of head, neck and body Cinnamon Brown (33), with a dirty white V escutcheon; chin mottled with black; V surface of tail Fawn Color (25), with flecks of Raw Umber (223); D surface of limbs as well as soles of hands and feet Raw Umber (223).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that all reddish shades have faded.

Natural history notes. Mostly diurnal, but also found active at night; chiefly terrestrial. I found most collected specimens at night while they were fleeing on the ground, actively moving about with no obvious hurry, or under fallen logs. The habitats ranged from pristine forest to open secondary vegetation.

Remarks. Panamanian *Lepidoblepharis* with granular dorsals that would be referred to this species using the key of Köhler (2008) comprise three different species delineated in chapter 4.1.2. Savage (2002) gives the maximum SVL as 45 mm, which I consider a very large value since it is close to that of *Gonatodes albogularis*. I thus use the maximum values obtained from my examined specimens.

Lotzkat et al. (2010c) provided the first record of a voucher specimen of *Lepidoblepharis xanthostigma* from Veraguas province. One of their specimens, SMF 89963, also reported by Carrizo (2010), is actually a representative of *Lepidoblepharis* sp. 1.

***Lepidoblepharis* sp. 1**

Scaly-eyed Gecko, Litter Gecko; Gueco de hojarasca

Figures 4.3C, D; 4.4B; 4.5D; 4.6B; 4.9; 4.10; 4.95H; Maps 4.1; 4.31.

Lepidoblepharis sp.: Martínez & Rodriguez (1994: possibly); Martínez et al. (1995: possibly).

Lepidoblepharis xanthostigma: Carrizo (2010: in part.); Lotzkat et al. (2010c: in part.).

Geographic distribution. Endemic to western Panama, hitherto only known from Colón and Veraguas, 100–700 m asl. In the Cordillera Central, recorded from Cerro Negro at 700 m asl.

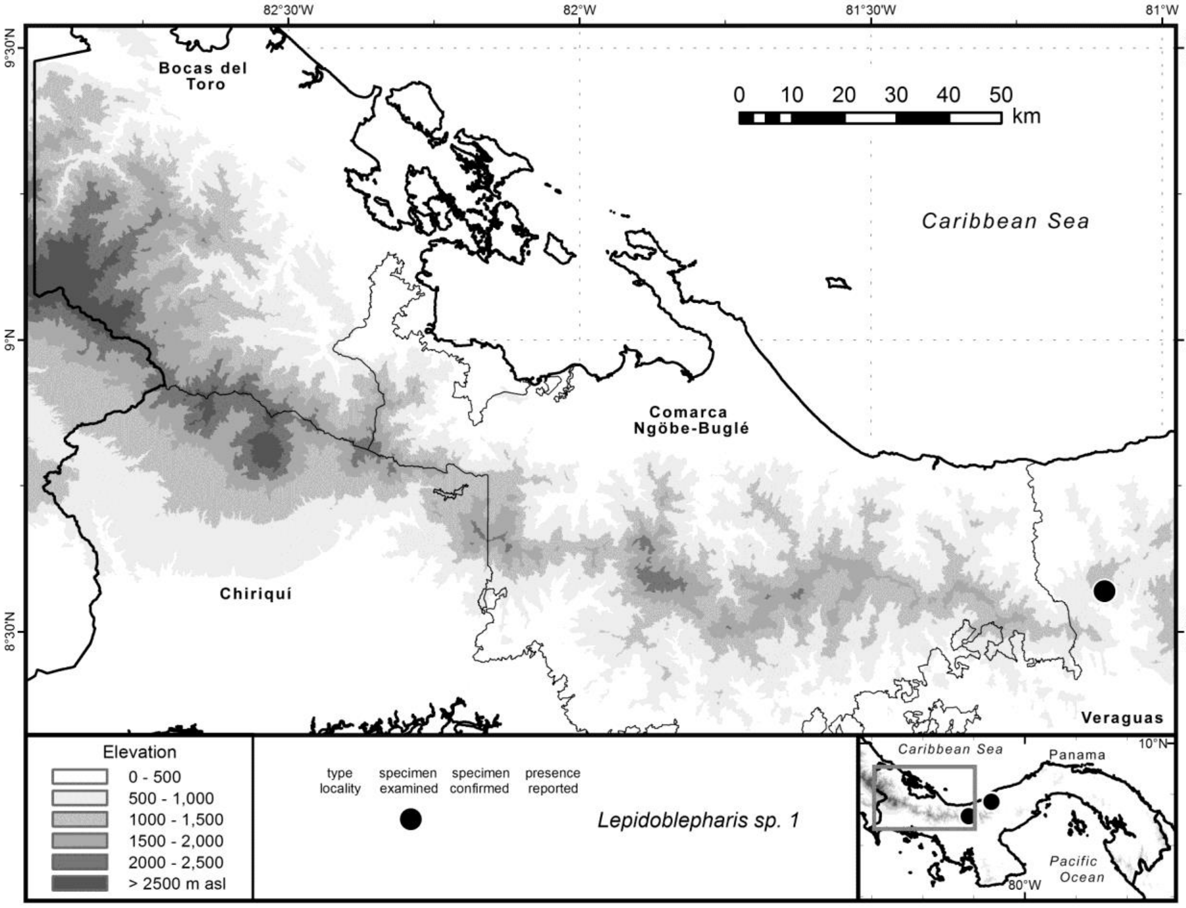
Diagnosis. A small gecko (maximum SVL 27 mm) that is readily distinguished from members of the families Gekkonidae and Phyllodactylidae by its round pupils and the absence of dilated lamellar pads under fingers and toes. It differs from members of *Gonatodes* and *Sphaerodactylus* in having the retractile claws mostly enclosed in a symmetrical ungual sheath composed of six scales (vs. exposed claws and no ungual sheath in *Gonatodes,* and asymmetrical ungual sheath with a large, circular, terminal subdigital scale in *Sphaerodactylus*). It differs from all other Panamanian *Lepidoblepharis* in having 1–3 subdigital lamellae per digit greatly enlarged, i.e., each up to 4 times as long as the distal one(s) (vs. proximal subdigital lamellae at most twice as long as the distal ones). A detailed key to Panamanian *Lepidoblepharis* is provided in chapter 4.1.2.

Description. TOL to 58 mm; SVL to 27 mm; D and L scales of head, body, and tail granular and more or less raised or pointed; V and SC cycloid, smooth; median SC slightly enlarged; males with 61–68 V but no subfemoral escutcheon scales; PR 3–5; PM 5–7 mental with 2 pronounced paramedian clefts in posterior border; SAM 71–84; 4toe 6–8; 4finger 4–5. See chapter 4.1.2 for detailed morphological data.

The hemipenis of *Lepidoblepharis* sp. 1 is a small organ with two short, stout lobes; truncus and lobes finely calyculate; a small third lobule with spinulate calyces at base of truncus not connected to sulcus spermaticus.

Coloration in life. D and L surfaces reddish brown with bluish-gray as well as dark brown spots; two light-colored, crescent-shaped nuchal markings usually present and very conspicuous; two light dorsolateral stripes may be present on body and tail; lips with light and dark transverse bars passing into a contrasting reticulum under chin and towards chest.

Coloration in preservative. After 3–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, except that the reddish shades have mostly faded, leaving the specimens with a medium, possibly rusty, brown overall coloration (Figs. 4.10D–N).



Map 4.31: Distribution of *Lepidoblepharis* sp. 1.

Natural history notes. Diurnal and nocturnal, terrestrial. The male SMF 89963 was encountered active in the leaf litter between the buttress roots of a tree next close to our camp at 700 m asl on 28.07.2008 at 23:30, different to what was reported by Carrizo (2010).

Conservation. This species has only been recorded from three localities which lie at a maximum distance of 60 airline km from each other. Since they are situated almost exactly along a straight line, the calculation of the extent of occurrence from a minimum convex polygon does yield a value (6.55 km^2), but does not really make sense. However, based on current knowledge I have to assume a very restricted distributional range for *Lepidoblepharis* sp. 1. If one, for example, includes the entire terrestrial surface from the Caribbean coastline to the Pacific foothills of the Cordillera Central between the longitudes of the western- and easternmost collection sites of the species, the resulting area would still amount to less than 5000 km^2. Taking into account the deforestation I observed in the area as well as the mining activities in the Donoso district of Colón province around the eastern collection localities, both of which entail a decline in area, extent, and/or quality the obviously preferred forest habitats, *Lepidoblepharis* sp. 1 clearly qualifies for the IUCN category EN according to criteria B1ab(iii). I calculated the EVS for this species as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability.

Remarks. Both around Santa Fé, Veraguas, and Donoso, Colón, *Lepidoblepharis* sp. 1 occurs in sympatry with *L. xanthostigma,* as which it has been identified by Carrizo (2010) and Lotzkat et al. (2010c) based on the key of Köhler (2008). In their pioneering inventories from the Santa Fé area, Martínez & Rodriguez (1994) and Martínez et al. (1995) reported the presence of *Lepidoblepharis* sp., which they considered to resemble *L. xanthostigma.* Their specimens might have included individuals of *Lepidoblepharis* sp. 1. However, since the respective voucher specimens were lost (V. Martínez, pers. comm.), this assumption will forever remain speculative. Since the collection site at Cerro Negro is less than 8 km from the border between Verguas and the Comarca Ngöbe-Buglé, I consider the occurrence of *Lepidoblepharis* sp. 1 in the Comarca possible.

***Sphaerodactylus homolepis* Cope 1886**

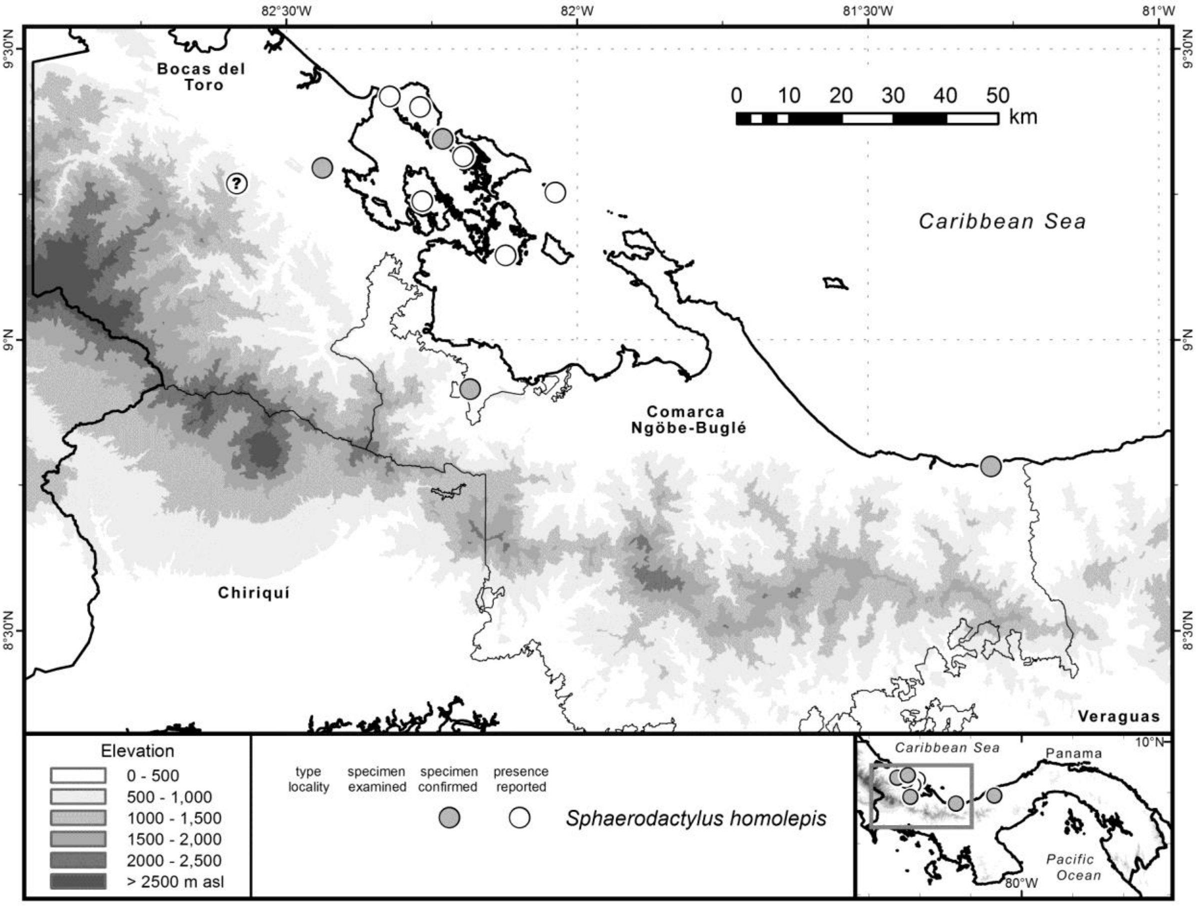
Caribbean Least Gecko, Yellow-headed Dwarf Gecko; Limpiacasa, Gueco enano.

Figure 4.96A; Map 4.32.

Sphaerodactylus imbricatus: Taylor (1956: in part.).

Holotype. USNM 14207, from Nicaragua (restricted to between El Castillo and San Juan del Norte, along the Río San Juan and its tributaries; Harris & Kluge 1984).

Geographic distribution. Southern Nicaragua to west-central Panama, 0–745 m asl. In Panama, along the Caribbean versant west of the Canal including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from Punta de Peña and probably also from around 610 m asl in the PILA (see remarks).



Map 4.32: Distribution of *Sphaerodactylus homolepis*.

Diagnosis. A very small gecko (maximum SVL 33 mm) readily distinguished from members of the families Gekkonidae and Phyllodactylidae by its round pupils and the absence of dilated lamellar pads under fingers and toes. It differs from members of *Gonatodes* and *Lepidoblepharis* in having the retractile claws mostly enclosed in an asymmetrical ungual sheath with a large, circular, pilose, terminal subdigital scale sheath (vs. exposed claws and no ungual sheath in *Gonatodes,* and symmetrical ungual sheath composed of six scales without a large, circular terminal scale in *Lepidoblepharis*). It differs from *S. graptolaemus* which only occurs on the Pacific versant of western Panama in lacking a striped or reticulate dorsal pattern and a series of homogeneously enlarged median subcaudals, and from *S. lineolatus* in lacking a striped dorsal pattern as well as in having the parietal scales keeled (vs. usually not keeled) and the subcaudals arranged alternately without a definite median row (vs. a median sequence of one very small, one large, and two small scales).

Description. TOL to 69 mm; SVL to 33 mm; D and L body scales granular, keeled; V cycloid, smooth; caudal scales cycloid, smooth, subcaudals largest; males with a V escutcheon of 38–79 scales; SAM 67–87; 4toe 10–12 (partially from Harris & Kluge 1984).

Coloration in life. Juveniles light-colored with dark crossbands that may be retained though less contrasting in adults or, like females, with dark spots; head and tail of adult males striped, reticulated, or spotted with bright yellow; V surfaces yellow.

Natural history notes. Probably diurnal and terrestrial.

Remarks. The presence of this species in my study area is documented by several USNM specimens (see below) from Punta de Peña, Bocas del Toro. The specimen MVUP 1530 from PILA in Bocas del Toro at about 610 m asl is catalogued as *Sphaerodactylus graptolaemus.* Since this species is restricted to the Pacific versant of eastern Costa Rica and extreme western Panama (Savage 2002; Köhler 2008), the specimen must have been misidentified and is much more likely a representative of *S. homolepis,* and treated as such herein. The corresponding point in Map 4.32 is marked with a question mark.

Elizondo et al. (2007) reported *Sphaerodactylus homolepis* from the Reserva Forestal La Tronosa, Los Santos province, in the southernmost portion of the Azuero peninsula. In view of the distribution of *S. homolepis* as documented by Harris & Kluge (1984), I regard this locality record as erroneous based on a misidentification. Likewise, I assume a misidentification in the opposite direction for the specimens USNM 38701 and 38704 from Punta de Peña, Bocas del Toro, which are catalogued as *S. lineatus* but interspersed in a series (USNM 38699–38706) of *S. homolepis.*

I regard the presence of two more species of *Sphaerodactylus,* namely *S. graptolaemus* Harris & Kluge 1984 and *S. lineolatus* Lichtenstein & von Martens 1856, in my study area as possible in view their respective documented distributions (see maps in Appendix 7): The former species is known from lowland Chiriquí and up to 700 m in adjacent Pacific Costa Rica, while the latter ranges throughout E and central Panama W to lowland Veraguas and the Islas Secas of Chiriquí, as well as W to PNGDOTH and up to 850 m along the Cordillera Central (Harris & Kluge 1984; Savage 2002; Köhler 2008; Jaramillo et al. 2010).

Infraorder Iguania Cope 1864

Family Corytophanidae Fitzinger 1843

Basiliscus basiliscus (Linnaeus 1758)

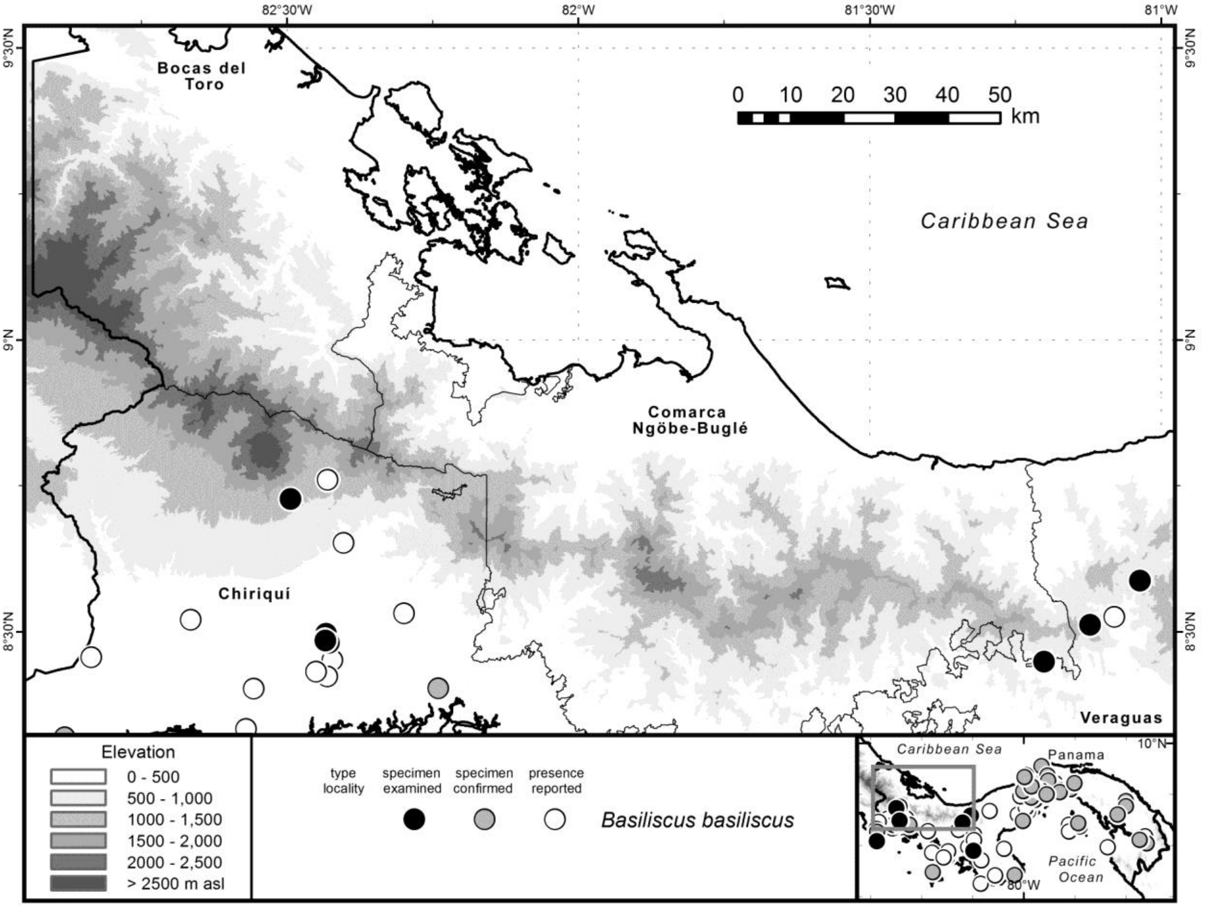
Common Basilisk, Jesus Christ Lizard; Lagarto jesucristo, Basilisco, Moracho (sierra)

Figure 4.96B; Map 4.33.

Basiliscus americanus: Barbour (1906).

Holotype. Unknown, from America australi.

Geographic distribution. Nicaragua to Colombia and Venezuela, 0–1200 m asl. In Panama, along the Pacific versant of western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and throughout central and eastern Panama on both versants. In the Cordillera Central, recorded from the Pacific versant up to 1140 m asl.



Map 4.33: Distribution of *Basiliscus basiliscus*.

Diagnosis. A large lizard (maximum SVL 240 mm) that is immediately recognized as a member of the genus *Basiliscus* by the presence of scaly fringes along the outer toes and knob-like keels on the subdigital lamellae. *Basiliscus basiliscus* differs from the very similar *B. vittatus* in having smooth ventrals and 3–4 chin shields (SBL) in broad contact with the infralabials (vs. keeled V and 1–2 SBL in contact with INL), and from *B. plumifrons* by its coloration which is predominantly brown (vs. green at least in adults) and shows longitudinal light lateral stripes (vs. spots or blotches), as well as by its occipital scales which are larger than the supraoculars and well differentiated from the much smaller posteriorly adjacent scales (vs. about the same size as the SPO and gradually becoming smaller posteriorly).

Description. TOL to 900 mm; SVL to 240 mm; D keeled, V smooth; adults with a single head crest (small in females, merely suggested in juveniles), in adult males with a posteriorly directed processus; adult males with a prominent, fin-like D crest supported by neural spines that is discontinuous with a lower caudal crest; females and juveniles with a serrated middorsal ridge.

Coloration in life. D and L surfaces gray to brown, with a light postorbital and supralabial stripe extending posteriorly onto body; body and tail with irregular, darker or lighter crossbands; venter dirty white to yellow.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that all yellow shades have faded.

Natural history notes. Diurnal, semiarboreal, and semiaquatic. Found in the immediate surroundings of water bodies into which they escape either by diving or running bipedally over the water. I found most individuals while they were sleeping on branches up to 4 m over the water surface. On 01.12.2009, I observed a female depositing five eggs in the soil between two large rocks next to the Río Majagua near Los Algarrobos (WP 167).

Remarks. In view of the distribution of *Basiliscus basiliscus* as outlined by recent authors (e.g., Savage 2002; Köhler 2008), I regard all records of this species from Bocas del Toro (e.g., ANAM 2004; UMNH 11035–11044; USNM 292066; and MCZ 22334 as *B. americanus*) to be based on misidentified individuals of the superficially similar *B. vittatus*.

Rogelio Moreno, at that time chief general of the Ngöbe, informed me that people of his nation use to eat "morachos" (a general term for *Basiliscus* lizards; on the Pacific versant where we met R. Moreno, these should be attributable to *B. basiliscus*) to cure anorexia, but would also consume them without suffering loss of appetite. He further stated that the teeth of young morachos would be a good cure for warts on the skin.

Basiliscus plumifrons Cope 1876

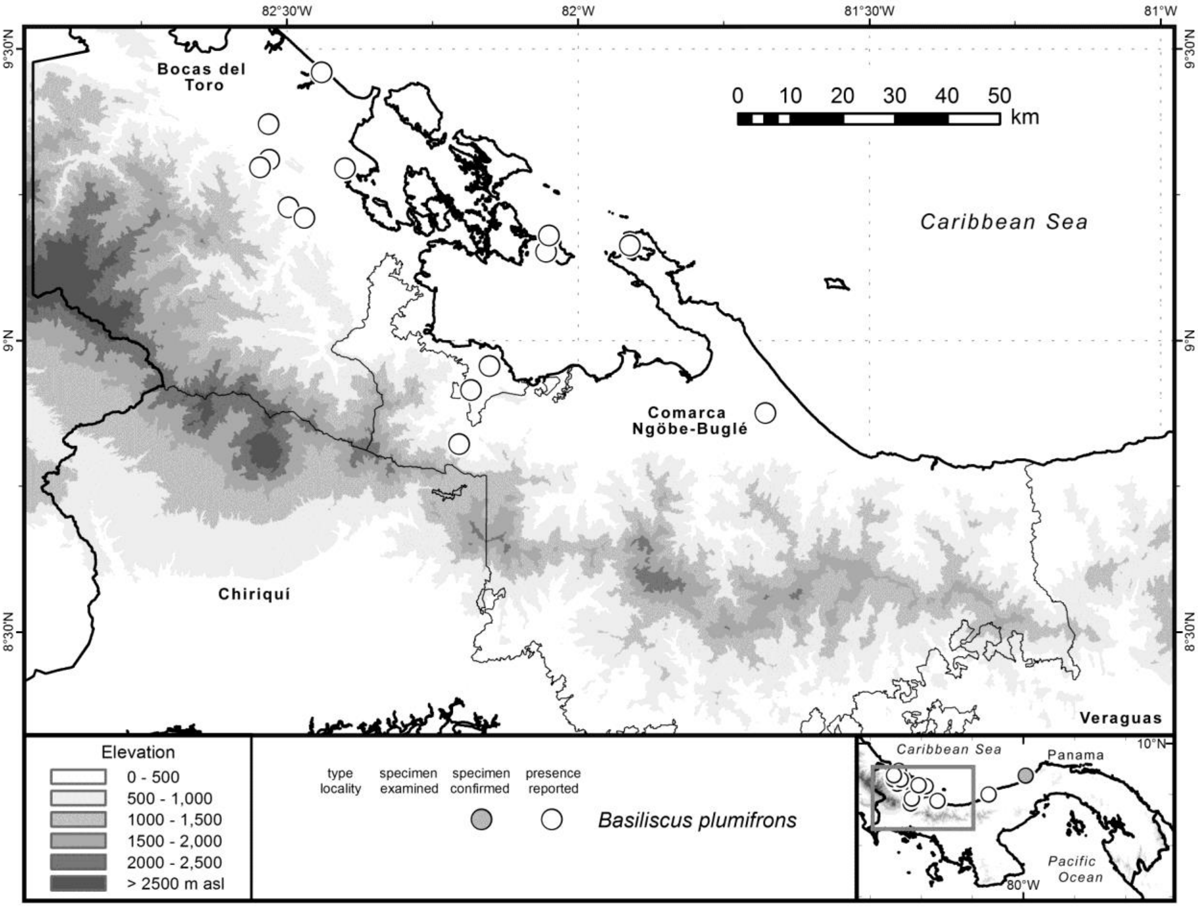
Green Basilisk, Jesus Christ Lizard; Lagarto jesucristo; Basilisco, Basilisco verde

Figure 4.96C; Map 4.34.

Holotype. UMNH 40735, from Sipurio, Costa Rica.

Geographic distribution. Eastern Honduras to central Panama, 0–1240 m asl. In Panama, along the Caribbean versant west of the Canal, including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from along the road to Chiriquí Grande and the Río Changuinola drainage, up to 650 m asl.

Diagnosis. A large lizard (maximum SVL 250 mm) that is immediately recognized as a member of the genus *Basiliscus* by the presence of scaly fringes along the outer toes and knob-like keels on the subdigital lamellae. *Basiliscus plumifrons* differs from the largely sympatric *B. vittatus* in having smooth ventrals and 3–4 chin shields (SBL) in broad contact with the infralabials (vs. keeled V and 1–2 SBL in contact with INL), and from *B. basiliscus* by its coloration which is, at least in adults, predominantly green (vs. brown) and shows lateral series of spots or blotches (vs. light longitudinal lateral stripes), as well as by its occipital scales which are about the same size as the supraoculars and gradually grade into smaller scales posteriorly (vs. larger than the supraoculars and well differentiated from the much smaller posteriorly adjacent scales).



Map 4.34: Distribution of *Basiliscus plumifrons*.

Description. TOL to 920 mm; SVL to 250 mm; D keeled, V smooth; head crest bilobed (small anterior and large posterior flap) in adult males, single in females and juveniles; adult males with a prominent, fin-like D crest supported by neural spines that is discontinuous with a sometimes equally high caudal crest; females and juveniles with a serrated middorsal ridge.

Coloration in life. D and L surfaces bright to bluish green (may turn very dark olive due to metachrosis) with L series of light spots and sometimes irregular middorsal transverse bars; posterior portion of tail with dark crossbands; body and tail with irregular, darker or lighter crossbands; venter light green; small juveniles brown with a green head.

Coloration in preservative. Similar to that in life. Some specimens at SMF still exhibit greenish and/or bluish hues after several decades in 70% ethanol.

Natural history notes. Diurnal, semiarboreal, and semiaquatic.

Remarks. The presence of *Basiliscus plumifrons* in my study area is documented by the specimens USNM 38685–7 from Punta de Peña, Bocas del Toro, as well as by a photographed specimen from the Celestine creek, Comarca Ngöbe-Buglé, at 650 m asl (Batista et al. in prep. b). Further records provided by Batista et al. (in prep. b) as well as the specimen MCZ 19485 from Fort Sherman, Colón, which was examined by GK, extend this lizard's distribution east to the Panama Canal.

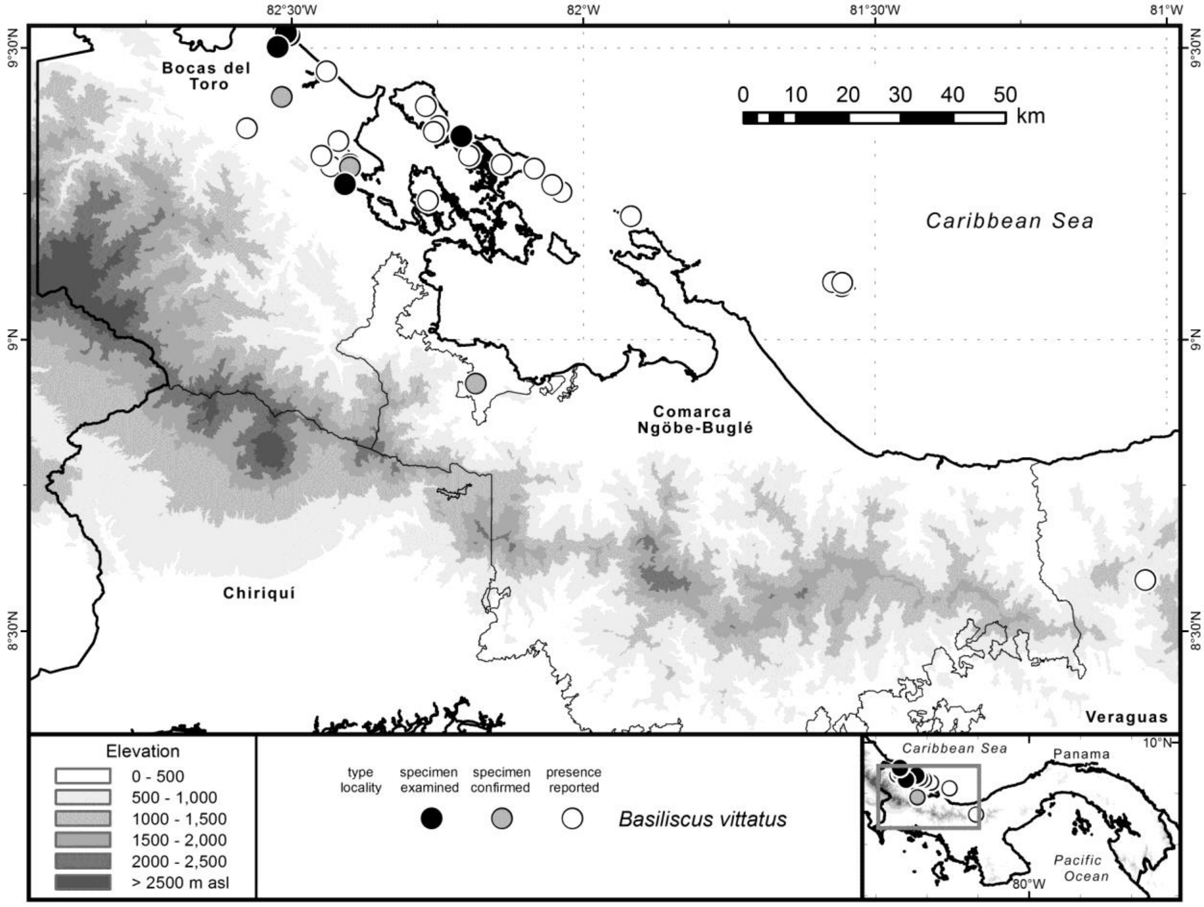
Given the distribution of the disjunct population in the Golfo Dulce region of southern Pacific Costa Rica (Savage 2002), the presence of *Basiliscus plumifrons* in adjacent western Panama, especially on and around the Peninsula de Burica, can be expected.

Basiliscus vittatus Wiegmann 1828

Striped Basilisk, Brown Basilisk, Jesus Christ Lizard; Lagarto jesucristo; Basilisco, Moracho rayado

Figure 4.96D; Map 4.35.

Holotype. At ZMB, from Mexico.



Map 4.35: Distribution of *Basiliscus vittatus*.

Geographic distribution. Mexico to western Panama, 0–1500 m asl. In Panama, along the Pacific versant in Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Talamancan foothills and the Santa Fé area up to around 735 m asl.

Diagnosis. A large lizard (maximum SVL 170 mm) that is immediately recognized as a member of the genus *Basiliscus* by the presence of scaly fringes along the outer toes and knob-like keels on the subdigital lamellae. *Basiliscus vittatus* differs from *B. basiliscus* and *B. plumifrons* in having keeled ventrals and 1–2 chin shields (SBL) in broad contact with the infralabials (vs. smooth ventrals and 3–4 SBL in contact with INL). It further differs from the largely sympatric *B. plumifrons* by its coloration which is predominantly brown (vs. green at least in adults) and shows a distinct light longitudinal lateral stripe extending posteriorly from the eye (vs. series of light lateral spots or blotches).

Description. TOL to 590 mm; SVL to 170 mm; D keeled, V keeled; head crest single and triangular in adult males, small in females, merely suggested in juveniles; adult males with a low D crest supported by neural spines that is continuous with a caudal ridge of serrated scales; females and juveniles with a serrated caudal ridge.

Coloration in life. D and L surfaces gray to brown, with a light postorbital and supralabial stripe extending posteriorly onto body; body and tail with irregular darker and lighter brown crossbands that are most contrasting in juveniles; venter tan.

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that yellowish shades have faded.

Natural history notes. Diurnal and semiarboreal, though more often found on the ground and/or at a greater distance to the next water body than its congeners.

Remarks. I regard all records of *Basiliscus basiliscus* from Bocas del Toro (see remarks for that species) to actually represent *B. vittatus*. The record from the Cerros Narices and La Anselma N of Santa Fé (Martínez et al. 1995, voucher specimens lost according to V. Martínez, pers. comm.) is the easternmost locality record for this species and could be the highest Panamanian record as deduced from the mean value (735 m asl) of the given altitudinal range. This record is from the same general area where I collected the *B. basiliscus* specimen SMF 89530, pointing out a possible contact zone between the two species.

Corytophanes cristatus (Merrem 1820)

Casque-headed Lizard; Lagartija crestada; Perro zompopo, Camaleón

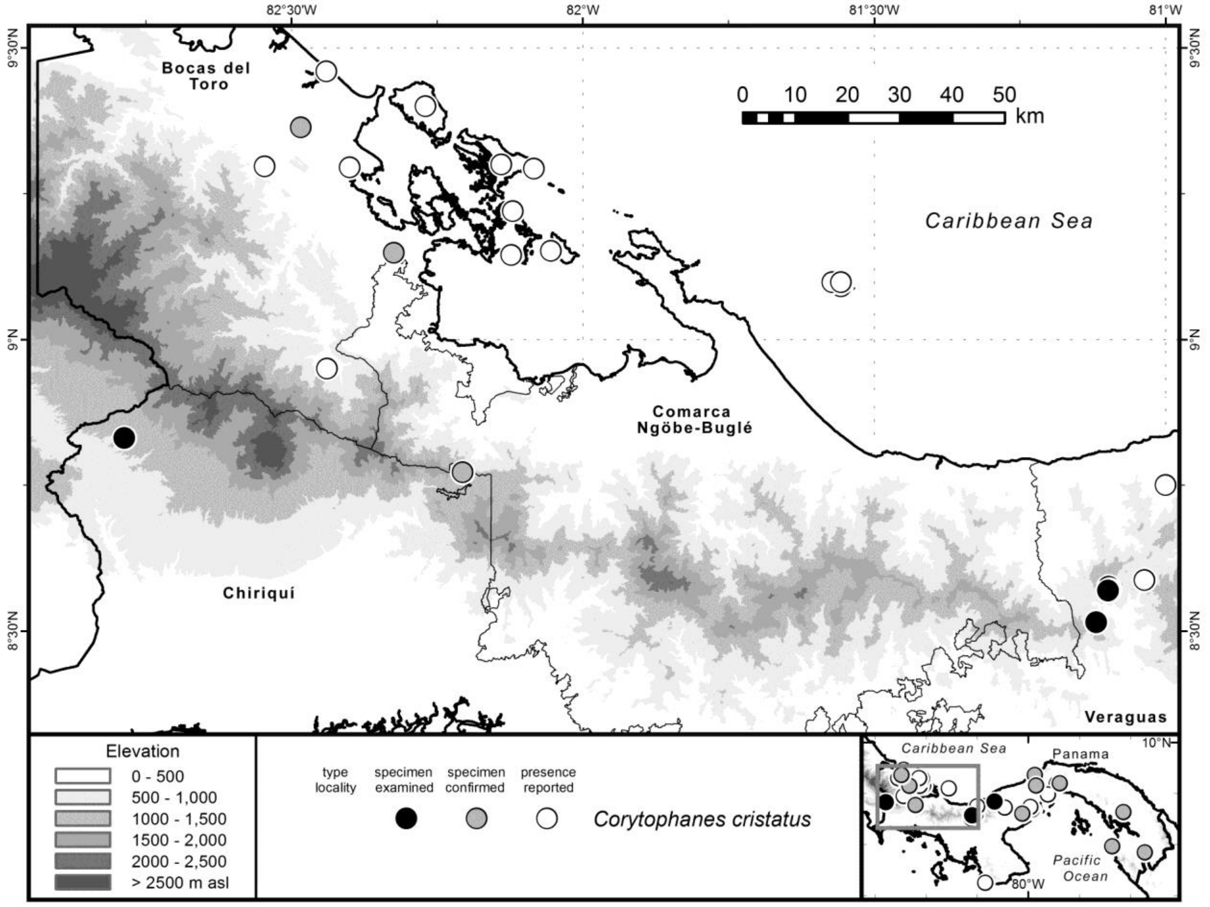
Figure 4.96E; Map 4.36.

Corythophanes cristatus: Barbour (1923).

Coritophanes cristatus: Martínez & Rodriguez (1994).

Holotype. unknown, from Ceylon (in error); restricted to Orizaba, Veracruz, Mexico.

Geographic distribution. Mexico to Colombia, 0–1640 m asl. In Panama, throughout the country including Chiriquí, Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from several localities along both versants, up to 1110 m asl.



Map 4.36: Distribution of *Corytophanes cristatus*.

Diagnosis. This largest (maximum SVL 120 mm) and only Panamanian representative of the genus *Corytophanes* cannot be confused with any other Panamanian lizard due to its prominent cephalic crest extending well beyond the head and bearing a margin of conspicuously serrate scales that continues as a dorsal crest posteriorly to the base of the tail, and its downwards directed corners of the mouth.

Description. TOL to 360 mm; SVL to 120 mm; D smooth, V strongly keeled; head casque made up by two elevated ridges that join to form the cephalic crest; serrate middorsal and midgular crests, but no caudal crest; SAM 81–111*; 4toe 27–36.

The hemipenis of *Corytophanes cristatus* is a large, stout, bilobed organ with a well-developed asulcate processus and short, calyculate lobes.

Coloration in life. *Corytophanes cristatus* is very variable in coloration and capable of considerable metachrosis. D and L ground color ranging from light gray over orange, green, and brown to blackish olive, with crossbands, blotches, or mottling in any of these colors; tail usually crossbanded; V surfaces lighter and more uniformly colored.

The juvenile SMF 89542 was recorded by LS as follows (translated from Stadler 2010): D ground color Drab (27) with irregular tranverse Dark Brownish Olive (129) crossbands and Dark Drab (119B) blotches especially on anterior flanks; casque Grayish Horn Color (91) and Flesh Color (5), grading into Drab (27) laterally; cephalic crest and D ridge Grayish Horn Color (91); posterior dorsum and base of tail Trogon Yellow (153); tail posteriorly to base crossbanded with Dark Brownish Olive (129), Dark Drab (119B), and Grayish Horn Color (91), becoming darker towards tip of tail; D surfaces of limbs Sepia (219) gefärbt mottled with Dark Drab (119B) Flecken; L surfaces of head Drab (27) suffused with Flesh Color (5) grading into Pale Pinkish Buff (121D) mottled with Dark Drab (119B) towards snout; V ground color Drab (27) with a suggestion of Pale Pinkish Buff (121D) Schimmer; chin and gular region with parallel Dark Drab (119B) longitudinal stripes; V surfaces of limbs mottled with Dark Drab (119B), Sepia (219), and Pale Pinkish Buff (121D).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is generally similar to that in life, though several specimens have assumed bluish and/or orangish hues on different surfaces.

Natural history notes. Diurnal and arboreal, mostly perched on vertical structures except when sleeping. Naturally motionless, but capable of running surprisingly fast on the hind legs for short distances. All individuals were encountered in closed forests while they were sleeping 0.5–3 m above ground.

Remarks. The specimens MHCH 2306–7 and SMF 91537 from 1110 m asl at Santa Clara extend the upper elevational limit for Panama given as 850 m (Jaramillo et al. 2010).

Family Dactyloidae Fitzinger 1843

Dactyloa casildae (Arosemena, Ibáñez and de Sousa 1992)

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

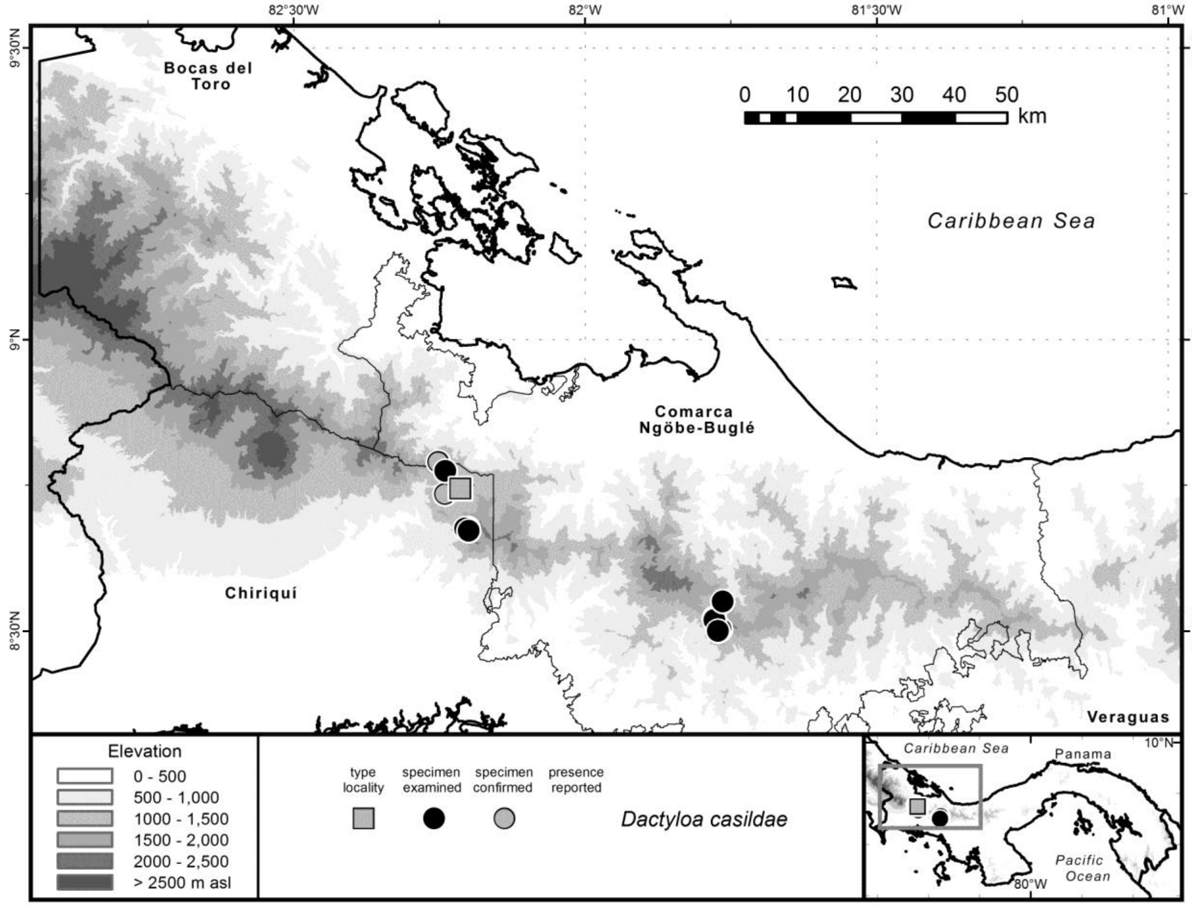
Casilda's (Giant) Anole; Anolis (gigante) de Casilda

Figures 4.12; 4.21; 4.22; 4.28A–C; 4.29A–D; 4.96F; Maps 4.3; 4.37.

Anolis casildae: Arosemena et al. (1992); Auth (1994); Young et al. (1999); Hofer & Bersier (2001); Ibáñez et al. (2001); Nicholson et al. (2001, 2005); Fundación PA.NA.M.A. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Carrizo (2010); Chun (2010); Jaramillo et al. (2010); Stadler (2010); Wilson & Johnson (2010); Castañeda & de Queiroz (2011); Uetz & Hošek (2014).

Holotype. MVUP 755, male, from Quebrada Frank, 1100 m, 8°44'N, 82°13'W, Reserva Forestal de Fortuna, Chiriquí province, Panama.

Geographic distribution. Endemic to Panama in, 990–1720 m asl. Only recorded from Chiriquí and the Comarca Ngöbe-Buglé (possibly also present in Bocas del Toro), between the general Fortuna area at Cerro Guayabo (RFLF, Chiriquí) and nearby BPPS (Comarca Ngöbe-Buglé) over 60 airline km east to Cerro Santiago, 990–1720 m asl.



Map 4.37: Distribution of *Dactyloa casildae*.

Diagnosis. A large species (maximum SVL 114 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this clade found in western Panama (*D. frenata, D. ginaelisae, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus*). *Dactyloa casildae* can readily be distinguished from these six species by its coloration (described below, shown in Figs. 4.12, 4.21, 4.22, and 4.96F), and from all except *D. ibanezi* by its very long tail (more than 2.5 times SVL). Moreover, *D. casildae* differs from *D. ginaelisae, D. insignis, D. kunayalae,* and *D. microtus* in having long legs (tip of 4th toe of adpressed hind limb reaching to eye or beyond, usually to nostril or beyond, in *D. casildae* vs.

at most to posterior border of eye), and from *D. ginaelisae, D. insignis* and *D. microtus* in having more horizontal loreal rows (6 or more in *D. casildae* vs. 5 or fewer). Additionally, *D. casildae* has more subdigital lamellae under the 4th toe (42 or more in *D. casildae* vs. 41 or fewer) as well as under the 4th finger (29 or more in *D. casildae* vs. 28 or fewer) than *D. ibanezi* and *D. kunayalae*.

Description. TOL to 446 mm; SVL to 114 mm in males, to 99 mm in females; tail very long, about 2.5–3 times SVL, compressed (only very slightly in many individuals), without D crest; legs long, tip of 4th toe of adpressed hind limb reaching at least to eye, in most individuals well beyond eye, and in some even beyond snout; internasals, canthals, and loreals keeled; scales of frontal and prefrontal area mostly keeled, some rugose or almost smooth (especially in juveniles); IP distinct, surrounded by smaller, keeled scales; parietal eye distinct; scales of SS enlarged, keeled; scales of supraorbital disk distinctly enlarged, keeled; a very elongate (in several specimens two, rarely three, accordingly shorter scales), keeled anterior superciliary scale, more than half as long (in some specimens almost as long) as horizontal eye diameter, usually followed by up to three similarly keeled but much shorter scales; anterior sublabials slightly enlarged, but never as high as INL, keeled; temporal arch weakly defined, with enlarged scales usually only in its anterior portion; ear opening large, higher than SPL and INL together, at least as high as eye, much larger than IP; nuchal and D crests present in males; 2 rows of keeled middorsal scales slightly enlarged only in few specimens; other D scales as well as L scales granular, conical to keeled; V larger than largest D, smooth; scales on anterodorsal surface of thigh mostly unicarinate, some bi- or tricarinate; scales on D surface of forearm unicarinate, becoming multicarinate towards wrist; 4th toe with well-developed dilated pad, about three times width of distal phalanx; male dewlap very large, extending posteriorly to halfway between axilla and groin in large specimens, with well-demarcated gorgetal-sternal scale rows of densely arranged scales and widely spaced scales in the broad interspaces between the rows; female dewlap moderate, extending posteriorly to slightly beyond axilla, with more diffuse gorgetal-sternal rows owing to the less widely spaced scales in their interspaces.

The completely everted hemipenis of SMF 91454 (Figs. 4.28A–C) is a small, bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; an asulcate ridge present; a knob-like processus present on asulcate side of truncus; lobes finely calyculate, truncus with transverse folds.

Coloration in life. D and L surfaces green to bluish green, either almost unicolor, or with brown, blue, and yellow spots or blotches, or additionally with oblique transverse bands that may appear solid or composed of blotches; some females of the unicolor and spotted variants with a dark-bordered light middorsal stripe; blue and yellow mottling usually most contrasting around chin, gular area, throat, and shoulders; light and dark lip bars often present; usually a postorbital stripe with dark borders; postorbital stripes of both sides often vaguely connected by a diffuse nuchal band; a less prominent preorbital stripe extending to snout in many specimens; tail with dark mottling suggesting diffuse crossbands; V surfaces unicolor yellow or yellowish green, in some individuals with dark mottling; iris brown; male dewlap cream-colored with gorgetal-sternal rows of yellow scales and interspersed blue or green scales, scales in interspaces between gorgetal-sternal rows widely spaced; female dewlap with contrasting yellow and green or blue mottling suggesting longitudinal stripes or a reticulate pattern, with only weakly demarcated gorgetal-sternal rows (Figs. 4.12; 4.21; 4.22; 4.96F). Apart from the extremely variable color pattern, *Dactyloa casildae* is capable of considerable metachrosis (compare Figs. 4.21A and I, or E and F). While the description above refers to the colorful or green phase usually shown while the animal is sleeping, the dark or brown phase, typically assumed when the animal is handled, can cause all colors to turn dark brown, making most or all elements of a possible spotted or banded pattern disappear. Specimens spotted at daytime showed either of the color phases. Color photographs of *D. casildae* have been published by Köhler (2003, 2008), Hamad (2009), Fläschendräger & Wijffels (2009), and Chun (2010).

The coloration in life of a subadult male (MHCH 2121, Figs. 4.21B, J) was recorded as follows: D and L ground color Apple Green (61); body with a series of broad transverse Greenish Olive (49) bands, interrupted by a Buff-Yellow (52) reticulate mottling covering D and L surfaces of body, and mottled with Dark Grayish Brown (20); D surface of head densely mottled with Buff (124) and Sepia (219); L and V surfaces of head Robin's Egg Blue (93) mottled with Spectrum Yellow (55); a Sulphur Yellow (57) postorbital stripe bordered by Sepia (219) extending from eye to above ear opening; chin region with a Sulfur Yellow (157) reticulate mottling bordered by Sepia (119); D surfaces of limbs and base of tail with Greenish Olive (49) mottling forming transverse bands; posterior portion of tail Citrine (51) with mostly ill-defined Sepia (219) transverse bands; V surface of body Cream Color (54) mottled with Citrine (51) and a suggestion of Lime Green (59); V surfaces of limbs and base of tail Citrine (51) mottled with Cream Color (54) and Lime Green (59); iris Clay Color (26); dewlap with a continuum of the chin coloration anteriorly, grading into Pale Horn Color (92) longitudinal lines of scales suffused with Leaf Green (146); skin between these lines Lime Green (59) with solitary Leaf Green (146) scales; dewlap margin Cream Color (54).

The coloration in life of an adult male (SMF 89455) was recorded as follows (translated from Hamad 2009): D surfaces with alternating crossbands from anterior head to tip of tail; transverse bands Yellowish Olive-Green (50), alternating with Olive-Yellow (52) bands with Straw Yellow (56) mottling, which grade into Turquoise Blue (65) and Straw Yellow (56) laterally; D surface of head Spectrum Yellow (55), Greenish Olive (49), and Paris Green (63); L surfaces of head Spectrum Yellow (55), Turquoise Blue (65), and Sulphur Yellow (57), extending over V surfaces of head and body posteriorly to midventer; then grading into Beige (219D) that continues to V surface of base of tail; tail thereafter with Sepia (219) and Raw Umber (23) crossbands; dewlap Cream (84) with longitudinal Orange-Yellow (18) stripes and Cerulean Blue (67) scales.

Coloration in preservative. After 21–48 months of preservation in 70% ethanol, all green and blue elements have turned to brown or, especially around head, to bluish gray; yellow throat markings are dirty white to yellowish brown (Figs. 4.29A–D). After 10 years (SMF 85370), also the bluish shades have vanished almost completely.

Natural history notes. All collected specimens were encountered at night while they were sleeping on branches, lianas, or leaves 0.3–4 m above ground. Hamad (2009) spotted individuals of this species sleeping as high as 8 m above the Río Hornito at RFLF. The only two individuals seen at daytime were perched head down on treetrunks 1.5 and 5 m above ground, respectively. During some surveys, *Dactyloa casildae* appeared very abundant at certain localities both at RFLF and Cerro Santiago in the Comarca Ngöbe-Buglé, with many sleeping individuals encountered very close to each other in some nights. In these surroundings, we also found this species to occur syntopically with *D. ginaelisae,* and in one case even to share a sleeping branch with that species. At the lowest collection site at Río Hacha, we found *D. casildae* to occur in syntopy with *D. kunayalae.*

Our automatized temperature recordings at collection localities of *Dactyloa casildae* (990–1560 m asl) range between 12.6–23.1°C. According to my combined dataset of 41 georeferenced occurrences, the species inhabits PMWF and LMWF, with temperatures between 11.8–27.4°C, mean annual temperatures of 17.8–21.2°C and a total annual precipitation of 2385–3376 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Dactyloa casildae,* and assigned the species to the IUCN category NT. I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of just 426 km^2 and the continuing deforestation we observed in the region qualify *D. casilde* for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. Our records expand the known range about 56 km southeastwards and 320 m uphill from previously reported localities (Nicholson et al. 2001; Chun 2010). Hofer and Bersier (2001) and consequently Nicholson et al. (2001) stated the westernmost specimens from BPPS to come from Bocas del Toro province. However, the region in question (Map 4.2: loc. 27) is presently situated within the Comarca Ngöbe-Buglé. As far as I know, *Dactyloa casildae* has not been reported from Bocas del Toro yet. However, I regard the species' presence in Bocas del Toro as possible in view of the suitable forest habitat covering the Caribbean slopes of the eastern Talamanca throughout the ca. 14 airline km between the collection site of SMF 90098 (or about 11 km between my georeference for the records of Hofer & Bersier 2001 and Nicholson et al. 2001) and the provincial border.

Based on a sample of eight specimens, Nicholson et al. (2001) restricted the color morphs without transverse bands to females. Among my sample, there are also male specimens which exhibit a non-banded pattern (Figs. 4.21G; 4.22E), just like the specimen LACM FS 1084 pictured by Chun (2010: Fig. 4). Likewise, the middorsal stripe (Fig. 4.21C) is not present in all specimens, not even in all females, that lack transverse bands (Fig. 4.21D). One of my adult male specimens (SMF 89673, Figs. 4.21A, I, Q) has no enlarged postcloacal scales. The same is true for the young male MHCH 2121 (Figs. 4.21B, J; 4.29A, B), that was erroneously pictured as a female by Köhler (2008: p. 99: Fig. 197) and could only be confidently sexed by verifying the presence of testes through an incision in the flanks. Considering the lack of postcloacal scales in some males, we assume that those allegedly female specimens having a chiefly white dewlap similar to the male dewlap (Nicholson et al. 2001) are actually males lacking enlarged postcloacal scales, whereas the female dewlap in reality always is contrastingly mottled.

A preliminary analysis of its COI barcode (GenBank accession number JN112726.1) revealed the specimen JMS 214 from RFLF "near STRI-Fortuna Biological Station" to be closely related to my barcoded representatives of *Dactyloa casildae* DCL west, with uncorrected p-distances of 5.0% to SMF 89454 (SL 243) and 0.0% to SMF 90134 (JFB 43; see Appendix 5.3 for alignment and distance matrix).

Dactyloa frenata **(Cope 1899)**

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Giant Anole; Anolis gigante

Figures 4.12; 4.23; 4.28D–F; 4.29E–G; 4.96G; Maps 4.3; 4.38.

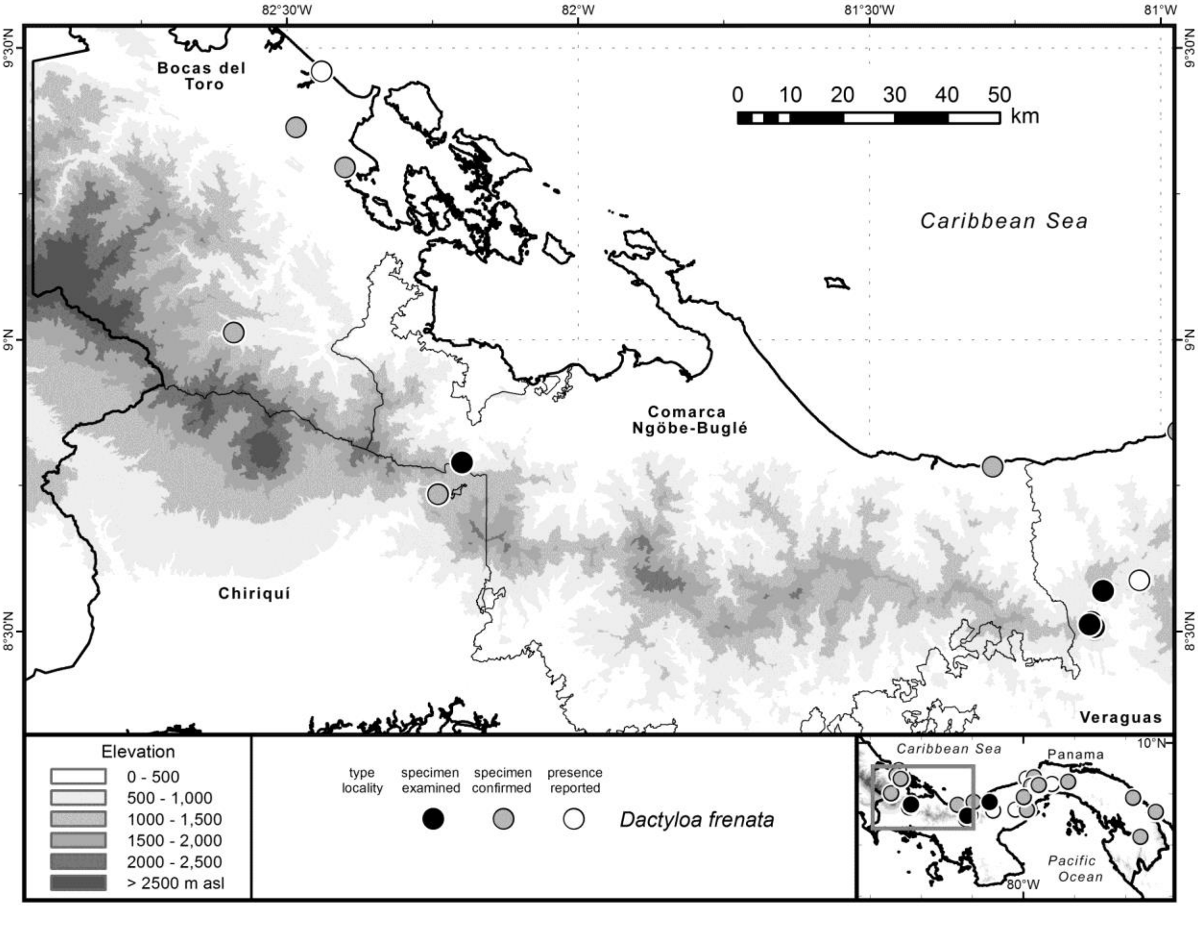
Anolis frenatus: Cope (1899); Dunn (1937a); Breder (1946); Evans (1947); Peters & Donoso-Barros (1970); Myers (1971); Scott et al. (1976); Myers (1977); Savage and Talbot (1978);

Rand & Myers (1990); Arosemena et al. (1992); Auth (1994); Martínez & Rodríguez (1994); Martínez et al. (1995); Ibáñez et al. (1995, 1996, 1997); Young et al. (1999); Ibáñez et al. (2001); Poe (2004); Nicholson et al. (2005); Fundación PA.NA.M.A. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Ugueto et al. (2009); Carrizo (2010); Jaramillo et al. (2010); Lotzkat et al. (2010b); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Castañeda & de Queiroz (2011); Uetz & Hošek (2014).

Anolis purpurescens: Taylor (1956) and references therein.

Holotype. Lost, from Colombia, but exact location uncertain (Savage & Talbot 1978).

Geographic distribution. Costa Rica to Colombia, 2–1170 m asl. In Panama, along the Caribbean versant of extreme western Panama and both versants from the Fortuna depression eastwards, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from several sites up to ca. 1170 m asl.



Map 4.38: Distribution of *Dactyloa frenata*.

Diagnosis. A large species (maximum SVL 143 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this clade found in western Panama (*D. casildae, D. ginaelisae, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus*). *Dactyloa frenata* can readily be distinguished from these six species by the presence of a pronounced light interorbital bar with dark anterior and posterior borders, and by its unique color pattern on dorsum and flanks consisting of dark blotches or ocelli arranged to form oblique bands (Fig. 4.23; 4.96G). Moreover, *D. frenata* has 9 or more SPL (vs. usually 8 or fewer) to the level below center of eye. In addition, *D. frenata* differs from *D. ginaelisae, D. insignis, D. kunayalae,* and *D. microtus* in having long legs (tip of 4th toe of adpressed hind limb reaching to eye or beyond in *D. frenata*), and from *D. ginaelisae, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus* in having the suboculars separated from the SPL by at least one scale row (vs. SBO and SPL in contact).

Description. TOL to 430 mm; SVL to 143 mm in males, to 118 mm in females; tail long, about two times SVL, compressed, without D crest; legs long, tip of 4th toe of adpressed hind limb reaching to eye or beyond; internasals, canthals, and loreals keeled; scales of frontal and prefrontal area mostly smooth, some weakly keeled; IP distinct, surrounded by smaller, mostly smooth, scales; parietal eye distinct; scales of SS not distinctly enlarged, keeled; scales of supraorbital disk only slightly enlarged, keeled; an elongate, keeled anterior superciliary scale, at least half as long as horizontal eye diameter, often followed by one or two similarly keeled, but much shorter scales; anterior sublabials not distinctly enlarged, keeled; scales of temporal arch slightly larger than those above and below; ear opening large, higher than SPL and INL together, at least as high as eye, much larger than IP; nuchal and D crests pronounced in males, weakly developed in female; 2–4 rows of keeled middorsal scales slightly enlarged; other D scales as well as L scales granular, smooth to slightly keeled; V slightly larger than largest D, smooth to very slightly keeled; scales on anterodorsal surface of thigh mostly unicarinate, some bi- or tricarinate; scales on D surface of forearm unicarinate, becoming multicarinate towards wrist; 4th toe with well-developed dilated pad, about three times width of distal phalanx; male dewlap very large, extending posteriorly to almost one-half of the distance between axilla and groin in large specimens; female dewlap moderate, extending posteriorly to slightly beyond axilla; dewlap in both sexes with well-demarcated gorgetal-sternal scale rows and scattered scales in their interspaces.

The completely everted hemipenis of SMF 89467 (Figs. 4.28D–F) is a small, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; a small asulcate ridge present; lobes finely calyculate, truncus with transverse folds.

Coloration in life. D and L surfaces green, usually involving brownish, yellowish, or bluish tonalities; series of darker green to dark brown blotches or ocelli form oblique transverse bands on dorsum, flanks, limbs, and anterior portion of tail; posterior portion of tail with dark crossbands; alternating yellow and dark stripes radiate more or less distinctly from eye, the upper ones meeting on D surface of head to form a pronounced light-colored interorbital bar usually with dark anterior and posterior borders; V surfaces largely unicolor cream or gray, becoming lighter towards head; iris brown; male dewlap white, female dewlap brown (Figs. 4.12; 4.23; 4.96G). We did not observe metachrosis in *Dactyloa frenata*. Color photographs of *D. frenata* have been published by Savage (2002), Köhler (2003, 2008), Fläschendräger & Wijffels (2009), Stadler (2010), Carrizo (2010), and Uetz & Hošek (2014), among others.

The coloration in life of an adult male (SMF 89467, Figs. 4.23A, E) was recorded as follows (translated from Stadler 2010): D surfaces of body, limbs, and anterior portion of tail Opaline Green (162D) with numerous Parrot Green (60) ocelli, partly bordered by Straw Yellow (56) and Spectrum Yellow (55), which are arranged in a pattern of transverse bands; middle portion of tail Sepia (119), posterior portion Olive-Yellow (52); anterior D surface of head with a heterogeneous pattern of Salmon Color (6), Olive-Gray (42), and Cyan (164); a Salmon Color (6) interorbital bar bordered anteriorly and posteriorly by Greenish Olive (59) stripes; posterior D surface of head with a random pattern of Flesh Color (5), Paris Green (63), and Salmon Color (6) scales; L surfaces of head from snout to posterior border of orbit Olive Gray (42), those posterior to orbit Cyan (164); Spectrum Yellow (55) and Grayish Olive (43) stripes extending from eyes radially in all directions; V surfaces largely dirty white, grading into Spectrum Yellow (53) laterally; V surfaces of hind limbs and anterior portion of tail Straw Yellow (53), those of middle and posterior portions of tail Sepia (119) and Olive-Yellow (52), respectively; dewlap Cream Color (54) with Sulphur Yellow (157) scales on the upper and Glaucous (80) scales in the lower half; margin dirty white anteriorly and Cream Color (54) posteriorly; iris Antique Brown (37).

Coloration in preservative. After 21–45 months of preservation in 70% ethanol, the greenish tonalities have turned to brown, gray, or bluish gray (the latter especially on head and flanks), venters are cream-colored (Figs. 4.29E–G).

Natural history notes. All specimens were encountered at night while they were sleeping on branches or lianas 1.5–4 m above ground. Around our collection sites of *Dactyloa frenata*, this species shares its habitat with *D. ibanezi, D. insignis,* and *D. kunayalae.*

Our automized temperature recordings at collection localities of *Dactyloa frenata* (700–900 m asl) range between 16.1–26.2°C. According to my combined dataset of 75 georeferenced occurrences, the species inhabits LMF, LWF, PMMF, and PMWF, with temperatures between 15.2–32.4°C, mean annual temperatures of 21.2–26.8°C and a total annual precipitation of 1735–4417 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 8 for *Dactyloa frenata,* and assigned the species to the IUCN category LC. I calculated the species' EVS as 1 (range) + 3 (persecution) + 4 (ecological distribution) = 8, indicating a low vulnerability. Its extent of occurrence of more than 49000 km^2 does not qualify *D. frenata* for any of the "Threatened" categories. In view of the continuing deforestation we observed in the region, we place the species in the category NT according to IUCN (2001) criterion B1b(iii).

Remarks. The adult male in my sample raised the upper vertical limit for this species to 900 m asl (Stadler 2010), and Sasa et al. (2010) raised it further to 1020 m. My georeference for the specimen JMS 192 from "Panama, Chiriquí, near STRI-Fortuna Biological Station" (Castañeda & de Queiroz 2011) yields a SRTM elevation of 1167 m, which is the highest elevation reported for this species. As confirmed by Ugueto et al. (2009), *Dactyloa frenata* definitely does not occur in Venezuela.

A preliminary analysis of its COI barcode (GenBank accession number JN112745.1) revealed the specimen JMS 192 from RFLF "near STRI-Fortuna Biological Station" to be closely related to my barcoded representatives of *Dactyloa frenata,* with uncorrected p-distances of 3.7% to SMF 91460 (SL 706) from nearby Willie Mazú and 0.5% to SMF 89467 (LSt 94) from Cerro Mariposa (see Appendix 5.3 for alignment and distance matrix).

Dactyloa ginaelisae Lotzkat, Hertz, Bienentreu and Köhler 2013

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Gina Elisa's (Giant) Anole, Gina Elisa's False Chameleon; Anolis (gigante) de Gina Elisa, Camaleón falso de Gina Elisa

Figures 4.12; 4.19; 4.20; 4.28G–I; 4.29R–S; 4.96H; Maps 4.5; 4.39.

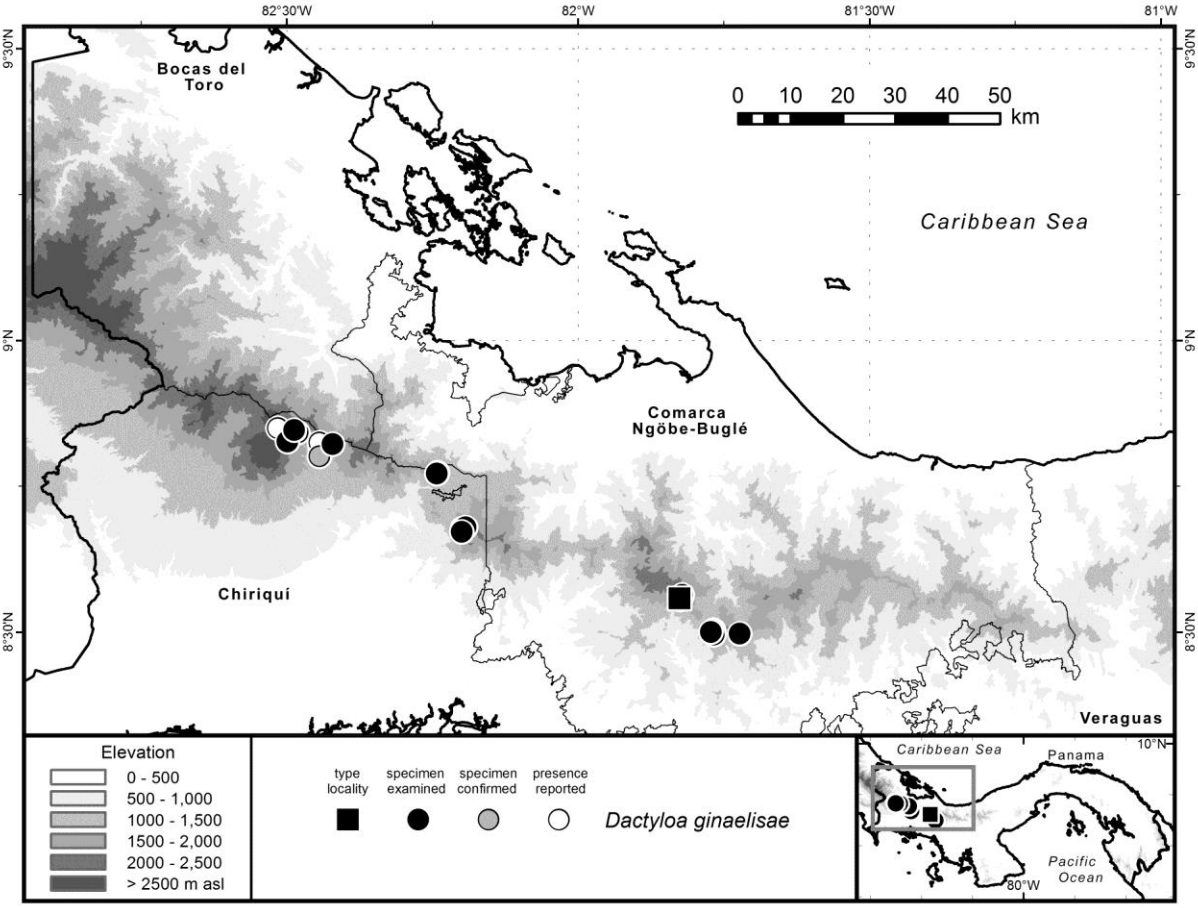
Anolis microtus: Dunn (1937a: in part.); Slevin (1942); Taylor (1956: in part.); Peters & Donoso-Barros (1970: in part.); Savage & Talbot (1978: in part.); Arosemena et al. (1992: in part.); Auth (1994: in part.); Young et al. (1999); Ibáñez et al. (2001); Fundación PA.NA.M.A. (2007); Köhler et al. (2008); Fläschendräger & Wijffels (2009: in part.); Hamad (2009: in part.); Lotzkat et al. (2010a); Jaramillo et al. (2010); Stadler (2010); Wilson & Johnson (2010: in part.); Castañeda & de Queiroz (2011: in part.); Uetz & Hošek (2014: photo).

Dactyloa microtus: Savage and Guyer (1989: in part.); Savage (2002: in part.); Köhler (2003, 2008: in part.).

Anolis ginaelisae: Uetz & Hošek (2014).

Holotype. SMF 91504 (Figs. 4.12; 4.19; 4.20S–T), male, from the banks of Quebrada Juglí, 8.5576°N, 81.8262°W, 1710 m asl, Corregimiento de Piedra Roja, Distrito de Kankintú, Comarca Ngöbe-Buglé, Panama.

Geographic distribution. Endemic to the Cordillera Central of western Panama, where it has been recorded on both versants from Volcán Barú in Chiriquí province (probably also present in Bocas del Toro) along 95 airline km to the eastern slopes of Cerro Santiago in the Comarca Ngöbe-Buglé, at 1370–2130 m asl.



Map 4.39: Distribution of *Dactyloa ginaelisae*.

Diagnosis. A large species (maximum SVL 112 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this genus found in western Panama (*D. casildae, D. frenata, D. ibanezi, D. insignis, D. kunayalae,* and *D. microtus*). *Dactyloa ginaelisae* can readily be distinguished from these six species by its color pattern described below and shown in Figs. 4.12, 4.19, 4.20, 4.29R–S, and 4.96H. It further differs from all mentioned species except *D. microtus* by its low numbers of horizontal loreal rows (4 or fewer in *D. ginaelisae* vs. 5 or more), total loreal scales (25 or fewer in *D. ginaelisae* vs. 39 or more), and scales around midbody (100 or usually much fewer in *D. ginaelisae* vs. 110 or more). Moreover, *D. ginaelisae* differs from *D. casildae, D. frenata,* and *D. ibanezi* in having short legs (tip of 4th toe of adpressed hind limb reaching to a point between tympanum and eye, very rarely to posterior border of eye, in *D. ginaelisae* vs. beyond eye; shank length/SVL = 0.22 or less in *D. ginaelisae* vs. 0.25 or more). Among the short-legged species of *Dactyloa* in western Panama, *D. ginaelisae* further differs from *D. insignis* in having fewer subdigital lamellae under the 4th toe (50 or fewer in *D. ginaelisae* vs.

52 or more) as well as under the 4th finger (36 or fewer in *D. ginaelisae* vs. 40), and from *D. kunayalae* in having more subdigital lamellae under the 4th toe (41 or more in *D. ginaelisae* vs. 35 or fewer) as well as under the 4th finger (29 or more in *D. ginaelisae* vs. 25 or fewer). *Dactyloa ginaelisae* is very similar to *D. microtus,* from which it differs in having longer legs (tip of 4th toe of adpressed hind limb reaching to a point between tympanum and eye in *D. ginaelisae* vs. to a point between shoulder and tympanum in *D. microtus;* shank length/SVL = 0.19 or more in *D. ginaelisae* vs. 0.183 or less) and by its conspicuous and clear-cut coloration pattern between eye and shoulder (a prominent light stripe extending from supralabials posteriorly above or a across the ear before bending down towards shoulder, delineating a dark preaxillary blotch above and posteriorly, and paralleled above by a dark postorbital stripe with darker borders that extends at least to a level above the preaxillary blotch in *D. ginaelisae* vs. light postsupralabial and dark postorbital stripe oriented more ventrally and losing their conspicuousness around ear).

Description. TOL to 362 mm; SVL to 112 mm in males, to 108 mm in females; tail long, about 1.7–2.4 times SVL, compressed, with a low D crest on the anterior portion; legs short, tip of 4th toe of adpressed hind limb reaching to a point between anterior border of tympanum and posterior border of eye; D and L head scales generally large; internasals, canthals, and loreals rugose to wrinkled; scales of frontal and prefrontal area mostly rugose to wrinkled; IP indistinct in most specimens, if discernable, then usually surrounded by scales of both smaller and equal size; scales of parietal area generally rugose to wrinkled; parietal eye indistinct in most specimens; scales of SS distinctly enlarged, rugose; scales of supraorbital disk conspicuously enlarged, rugose; one or sometimes two usually only slightly elongate, keeled anterior superciliary scale(s), one-4th to half as long as horizontal eye diameter, usually followed by several similarly keeled, but much shorter scales; one, two, or more anterior sublabials greatly enlarged, higher than INL; scales of temporal arch usually larger than those above and below; ear opening small, by far not as high as eye, less high than SPL and INL together, usually about as high as SPL; low nuchal and D crests present; two rows of middorsal scales strongly keeled and projecting upwards, but not laterally enlarged; other D scales as well as L scales elevated and rugose to wrinkled in adults, smooth in very small juveniles, with very small granules more or less densely filling the interspaces between them; V not or only slightly larger than largest D, smooth; scales on anterodorsal surface of thigh multicarinate; scales on D surface of forearm multicarinate; 4th toe with well-developed dilated pad, about three times width of distal phalanx; male dewlap large, extending posteriorly to between one-4th and one-third of the distance between axilla and groin in large specimens, with well-demarcated gorgetal-sternal scale rows of densely arranged scales and widely spaced scales in the broad interspaces between the rows; female dewlap moderate, extending posteriorly to slightly beyond axilla, with more diffuse gorgetal-sternal rows owing to the less widely spaced scales in their interspaces.

The completely everted hemipenis of SMF 89498 (Figs. 4.28G–I) is a medium-sized, bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; large asulcate processus and ridge present; a knob-like processus present on each L side of truncus just below base of apex; lobes finely calyculate, truncus with transverse folds.

Coloration in life. *Dactyloa ginaelisae* exhibits a very variable coloration. Among the typical pattern elements are dark crossbands around the tail and, mostly with light centers, on D surfaces of limbs and digits; a light stripe extending posteriorly from below the eye over the ear opening before bending down towards shoulder, paralleled above by a dark postorbital stripe with darker borders; a dark preaxillary blotch between tympanum and shoulder. Otherwise, D and L surfaces with spots, blotches, reticula, or solid bars or chevrons that are lighter and/or darker than ground color; V surfaces usually comparably unicolor white or yellow; ground and marking colors of D and L surfaces ranging from bright white over different shades of yellow, green, blue, and brown to black; iris gray to blue; male dewlap light salmon color; female dewlap pinkish to salmon color, in some individuals with dark blotches (Figs. 4.12; 4.19; 4.20; 4.96H). Apart from its highly variable pattern, this species is capable of overwhelming metachrosis (compare Figs. 4.20B and C, D and E) as already noticed by Dunn (1937a). The green phase, usually shown while the animal is sleeping, can culminate in restricting all colors to white, green, and blue, lightening up to invisibility some or all of the otherwise contrasting markings. Similarly, the dark or brown phase, often assumed when the animal is handled, can cause the whole animal to appear solid dark brown at its climax. In between, most coloration pattern elements of a given individual can apparently assume almost every color from the palette of this species. The only individual spotted at daytime was in the brown phase and showed no green at all. Color photographs of *D. ginaelisae* have been published by Köhler (2008), Köhler et al. (2008), Fläschendräger & Wijffels (2009), Hamad (2009), and Uetz & Hošek (2014) under the name *Anolis* or *Dactyloa microtus*.

The coloration in life of an adult female (SMF 89501, Figs. 4.20B–C, M–P) was recorded in the brown phase as follows: D and L ground color of body and limbs Straw Yellow (56) suffused with Tawny Olive (223D); D and L surfaces of body and limbs with Jet Black (89) irregular, sometimes broken, lines forming a reticulum suggesting transverse bands that enclose Robin Rufous (340) blotches, are suffused with Emerald Green (163) spots and disintegrate into mottles lateroventrally; D surface of head Light Russet Vinaceous (221D) with a reticulum of Sepia (219) bordered by shadings of Brick Red (132A) and Leaf Green (146); V surface of head Cream Color (54) with Tawny (38) shadings and Maroon (31) mottling posteriorly; a Buff (124) supralabial stripe originating anterior to eye with shadings of Paris Green (63) (also present on borders of infralabials) and grading to dirty white posterior to eye continues bordered by Sepia (119) above ear to level above shoulder; a Brick Red (132A) postorbital stripe bordered by Sepia (119) almost reaching to above shoulder; an elongate blotch of the same color behind ear opening; tail Drab-Gray (119D) with Walnut Brown (221B) transverse bands and various Vandyke Brown (221) scales; iris Sky blue (66); dewlap Pink (7) with dirty white scales and longitudinal series of Olive-Brown (28) flecks that fade away posteriorly.

The coloration in life of another female (MHCH 2234, Figs. 4.20G, Q) was recorded as follows: D ground color Lime Green (159), grading into Chartreuse (158) laterally; D surfaces of body and limbs with partly broken Burnt Sienna (132) transverse bands, Spectrum Yellow (55) transverse stripes and Burnt Sienna (132), Sepia (119) as well as Shamrock Green (162B) mottling; D surface of head Tawny Olive (223D) with a Sepia (219) V-shaped marking and some scale margins shaded in the same color; a Burnt Sienna (132) postocular stripe and blotch anterior to shoulder bordered by Sepia (119); a Spectrum Yellow (55) supralabial stripe extending above ear to above shoulder; supralabial Region Spectrum Yellow (55) with a suggestion of Yellow-Green (58), grading into Opaline Green (162D) towards V surface of head; V surfaces of body, limbs and base of tail Straw Yellow (56) with sparse Cinnamon (123A) mottling; tail grading into Olive-Yellow (52) with broad Sepia (219) transverse bands grading into Army Brown (219B) ventrally; iris Sky Blue (66); dewlap Pink (7) with a suggestion of Salmon Color (6), with Opaline Green (162D) scales aggregating to form longitudinal rows, and a suggestion of Yellowish Olive-Green (50) mottling.

Coloration in preservative. After 22–76 months of preservation in 70% ethanol, colors are largely reduced to white, cream, brown, and black. Some individuals have retained bluish-gray tonalities in certain places, often between eye and shoulder (Figs. 4.19 F–M; 4.29R–S).

Natural history notes. The holotype was encountered at 00:19 sleeping 6 m above ground on a branch in gallery forest. Most other specimens were encountered at night while they were sleeping on leaves, branches, or lianas 0.5–6 m above ground. An individual spotted fleeing on the ground at night had probably been driven from its sleeping site in the vegetation by our disturbance. One adult male was spotted around noon as it moved, trying to secure a flying moth, about 4 m above ground.

Our automatized temperature recordings at collection localities of *Dactyloa ginaelisae* (1430–1830 m asl) range between 12.6–22.2°C. According to my combined dataset of 36 georeferenced occurrences, the species inhabits PMWF and LMWF, with temperatures between 8.6–24.7°C, mean annual temperatures of 14.8–18.7°C and a total annual precipitation of 2208–2524 mm.

Dactyloa ginaelisae is a typical anole species of premontane and lower montane forests, particularly of cloud forests (*sensu* Myers 1969; Figs. 2.3B; 2.4H;2.5A, E–H; 2.6D). Especially in the so-called elfin forest on ridgetops and summits, with its low canopy and exuberant epiphytic vegetation (Fig. 2.5H), *D. ginaelisae* can locally be found in high numbers at certain times. At RFLF and on the western slopes of Cerro Santiago (Map 4.2: localities 10 and 14), we found this species to occur syntopically with *D. casildae,* and in one case even to share a sleeping branch with an individual of that species.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Dactyloa microtus,* which at the time comprised the populations described herein as *D. ginaelisae,* and assigned that species to the IUCN category LC. I calculated the new species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of just 530 km^2 and the continuing deforestation we observed in the region qualify *D. ginaelisae* for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. All previous records of *Dactyloa microtus* from Panama are from the area around Boquete and thus must have been based on individuals of *D. ginaelisae,* considering the distribution of the two species as documented herein. The species' occurrence in Bocas del Toro is rendered plausible by its altitudinal distribution together with the proximity of all records from the Boquete area to the border of that province, especially that of my examined specimens SMF 85070 (< 2.5 km) and SMF 86381 (slightly more than 1 km).

All previous authors have reported the absence of a distinct IP and parietal eye as a diagnostic character for *Dactyloa microtus,* and most individuals of *D. ginaelisae* share this characteristic. However, exceptions exist: three of my 26 specimens have a well-discernable IP with parietal eye (also see remarks concerning this matter for *D. insignis* and *D. microtus*). Apart from the diagnostic differences used here to distinguish *D. ginaelisae* from *D. microtus,* I observed other differences among my material. Without having examined more specimens of the latter species, preferably from both Costa Rica and Panama, I refrain from including these discrepancies in the formal diagnosis, but provide a brief summary in the following.

Regarding general morphology, individuals of *Dactyloa microtus* seem to be able to raise a much higher nuchal crest than representatives of *D. ginaelisae.* To a lesser extent, this also seems to apply to the D crest, at least along its anterior portion.

Regarding scalation, three additional differences deserve mention: First, most individuals of *Dactyloa ginaelisae* have at least two greatly enlarged (at least as high as the adjacent INL) anterior sublabials following the mental plate on each side of the head (Figs. 4.19I, J; 4.20J–N, P). The three individuals of *D. microtus* in my collection have only the first sublabial greatly enlarged, which is followed posteriorly by a much narrower, rather elongate sublabial. This second sublabial (and usually the similarly shaped third one following it) is bordered medially by an enlarged scale which may approximate the size of the greatly enlarged first sublabial (Figs. 4.27E–H, J), but is not, or only very narrowly, in contact with the INL. Second, the D and L scales of adult and subadult *D. ginaelisae* are prominently protruding from the skin and very rugose to wrinkled or clearly keeled (Fig. 4.19K), but rather flat, smooth, and not protruding in the holotype of *D. microtus* (Fig. 4.18G). However, my subadult males of *D. microtus* have the D and L body scales less flat than the holotype, as it seems to be the case with the individuals photographed in Costa Rica. Third, the median subcaudal scales of *D. ginaelisae* bear one very prominent keel (Fig. 4.19L), whereas those of the holotype (Fig. 4.18H) and my subadult males of *D. microtus* are bi-, tri-, or multicarinate.

Regarding coloration, I observed two additional discrepancies. First, individuals of *Dactyloa ginaelisae* typically have an iris color ranging from gray over bluish-gray to bright blue in life (Figs. 4.19; 4.20), whereas the representatives of *D. microtus* of which I have color photos in life (Figs. 4.18; 4.27) have the iris dominated by brownish or purplish tonalities. Second, the dewlap is salmon to pinkish already in the young males of *D. ginaelisae* (Fig. 4.20K), whereas the dewlap is yellowish in the two young males of *D. microtus* (Figs. 4.27E, F).

Dactyloa ibanezi **(Poe, Latella, Ryan and Schaad 2009)**

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Ibáñez' (Giant) Anole; Anolis (gigante) de Ibáñez

Figures 4.12; 4.24; 4.28J–L; 4.29H–J; 4.97A; Maps 4.4; 4.40.

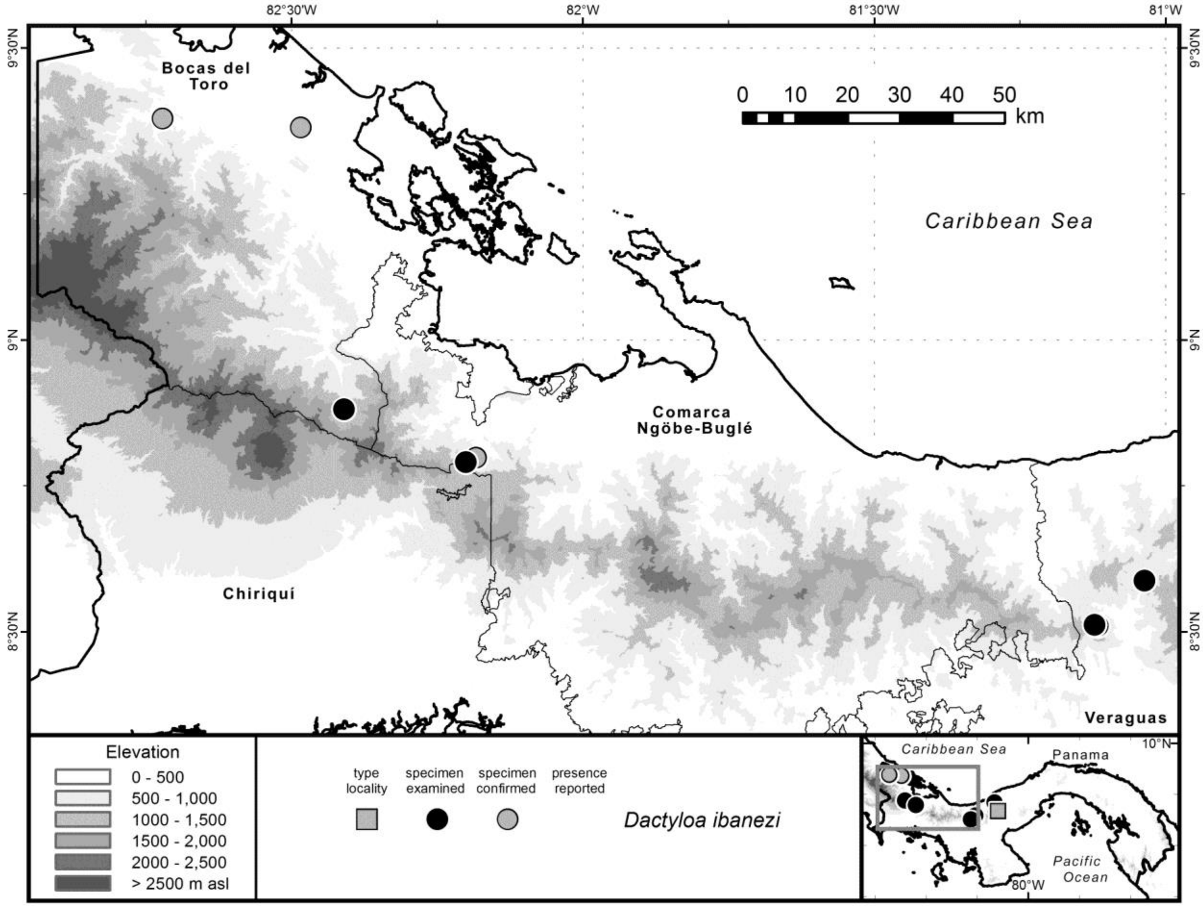
Anolis chocorum: Talbot (1974), Myers (1971: in part.); Auth (1994: in part.); Martínez & Rodríguez (1994); Martínez et al. (1995); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.); Fläschendräger & Wijffels (2009: in part.); Hamad (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010: in part.); Wilson & Johnson (2010); Carrizo (2010: in part.).

Anolis ibanezi: Poe et al. (2009); Castañeda & de Queiroz (2011); Uetz & Hošek (2014).

Dactyloa chocorum: Savage & Guyer (1989: in part.); Savage (2002: in part.); Köhler (2003, 2008: in part.).

Holotype. MSB 72574, male, from the trails of Parque Nacional General de División Omar Torrijos Herrera, 5 km North of El Copé, Coclé province, Panama.

Geographic distribution. Costa Rica to Panama, 160–1070 m asl. In Panama, along the extreme western Caribbean versant and both versants from Veraguas eastwards, including Bocas del Toro, Comarca Ngöbe Buglé, Veraguas, and probably also Chiriquí. In the Cordillera Central, reported from Sendero Culebra, La Fortuna, the Santa Fé area, and PNGDOTH, up to 1070 m asl.



Map 4.40: Distribution of *Dactyloa ibanezi*.

Diagnosis. A large species (maximum SVL 81 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this clade found in western Panama (*D. casildae, D. frenata, D. ginaelisae, D. insignis, D. kunayalae,* and *D. microtus*). *Dactyloa ibanezi* can immediately be distinguished from these six species by its unique coloration consisting of immaculate green dorsal and lateral surfaces with several parallel, narrow, diagonal dark stripes on the flanks and bright yellow surrounding the eye (Fig. 4.24; 4.97A). In addition, *D. ibanezi* differs from *D. ginaelisae, D. insignis, D. kunayalae,* and *D. microtus* in having long legs (tip of 4th toe of adpressed hind limb reaching to eye or beyond *D. ibanezi*), and from *D. casildae, D. frenata,* and *D. insignis* by having fewer subdigital lamellae under the 4th toe (41 or fewer in *D. ibanezi* vs. 42 or more) as well as under the 4th finger (28 or fewer in *D. ibanezi* vs. 29 or more).

Description. TOL to 278 mm*; SVL to 81 mm in males, to 78 mm in females; tail very long, about 2.5 times SVL, compressed, without D crest; legs long, tip of 4th toe of adpressed hind limb reaching to eye or beyond; internasals, canthals, and loreals keeled; scales of frontal and prefrontal area mostly rugose or keeled, almost flat in some specimens; IP distinct, surrounded by smaller, rugose scales; parietal eye distinct; scales of SS conspicuously enlarged, rugose; scales of supraorbital disk less conspicuously enlarged, rugose to slightly keeled; an elongate, keeled anterior superciliary scale, less than half as long as horizontal eye diameter, usually followed by a single similarly keeled, but much shorter scale; anterior sublabials slightly enlarged, but not as high as INL, keeled; scales of temporal arch much larger than those above and below; ear opening moderate, about as high as SPL and INL together, not as high as eye, about the size of IP; low nuchal and D crests present; 0–2 rows of keeled middorsal scales slightly enlarged; other D scales as well as L scales granular, keeled; V larger than largest D, very slightly keeled; scales on anterodorsal surface of thigh unicarinate; scales on D surface of forearm unicarinate, becoming multicarinate towards wrist; 4th toe with well-developed dilated pad, about three times width of distal phalanx; male dewlap large, extending posteriorly to between one-4th and one-third of the distance between axilla and groin in large specimens; female dewlap moderate, extending posteriorly to slightly beyond axilla; interspaces between the conspicuously demarcated gorgetal-sternal scale rows almost free of scales in both sexes.

The completely everted hemipenis of MHCH 2184 (Figs. 4.28J–L) is a medium-sized, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; large asulcate processus and ridge present; lobes finely calyculate, truncus with transverse folds.

Coloration in life. D and L surfaces homogeneously green, grading to yellowish green laterally; three to five parallel, narrow, dark, usually slightly curved lines descending diagonally on flanks; eye surrounded by bright yellow; V surfaces white, light gray, or light greenish yellow; iris brown; male dewlap orange with an uninterrupted white margin in young males, in older males only anterior margin white; female dewlap violet (Fig. 4.24; 4.97A). Our specimens showed little metachrosis, their green color only occasionally changing to greenish brown (compare SMF 89459 in Figs. 4.12 and 4.24E), but never throughout the whole animal. However, the intensity and width of the L stripes can alter considerably (compare Figures 4.24A and B). Color photographs of *Dactyloa ibanezi* have been published by Köhler (2008), Poe et al. (2009), Fläschendräger & Wijffels (2009), and Stadler (2010).

The coloration in life of an adult female (SMF 91475, Figs. 4.24A, B, G–J) was recorded as follows: D ground color of body, base of tail, head, and limbs Parrot Green (260) with a suggestion of Lime Green (159), grading into Lime Green (159) with a suggestion of Chartreuse (158) laterally; flanks with a series of Hooker's Green (162) diagonal stripes; scarce Clay Color (123B) and Hooker's Green (162) mottling scattered on D and L surfaces; tail posterior to base Sepia (219); a Sulfur Yellow (157) ring around eye; V surface of head Lime Green (159), those of body and base of tail Pratt's Payne's Gray (88) mottled with dirty white; iris Cinnamon (123A); dewlap True Violet (172) with a dirty white margin and gorgetal-sternal stripes where scales of the same color are concentrated. The coloration in life of a male paratype (SMF 89459; Figs. 4.12; 4.24E, K, M, N) was recorded as follows (translated from Stadler 2010): D ground color of body, head, limbs, and tail Lime Green (159) with a suggestion of Yellow-Green (58); flanks with four diagonal, parallel dark green stripes; V ground color of body, head, limbs, and tail Chartreuse (158); a dirty white longitudinal stripe running from tip of snout to throat; V surface of thighs speckled with dirty white; eyes encircled by a Sulfur Yellow (157) line; dewlap Spectrum Orange (17) with Chartreuse (158) scales.

Coloration in preservative. After 22 months of preservation in 70% ethanol, all green has turned to blue; male dewlaps are cream white with blue scales, female dewlap dark lilac (Figs. 4.29H–J). In the male paratype SMF 89459, after four years in preservative, the blue has largely turned to lilac (Fig. 4.29H).

Natural history notes. All specimens were encountered at night while they were sleeping on leaves 1–2.5 m above ground. The female SMF 91475 and, one night later, the male SMF 91476 were found at virtually the same place, within less than 5 m distance between their respective sleeping sites. Around our collection sites of this species, we also found *Dactyloa frenata, D. insignis,* and *D. kunayalae.*

Our automatized temperature recordings at localities where we encountered *Dactyloa ibanezi* (480–900 m asl) range between 17.7–27.6°C. According to my combined dataset of 18 georeferenced occurrences, the species inhabits LMF, LWF, PMMF, and PMWF, with temperatures between 15.6–31.8°C, mean annual temperatures of 21.6–26.2°C and a total annual precipitation of 2494–3581 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 8 for *Dactyloa chocorum,* which at the time comprised the populations described by Poe et al. (2009) as *D. ibanezi,* and assigned the species to the IUCN category LC. For *D. ibanezi,* I calculated the EVS as 4 (range) + 3 (persecution) + 4 (ecological distribution) = 11, indicating a medium vulnerability. Its extent of occurrence of 7336 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category VU according to IUCN (2001) criterion B1b(iii).

Remarks. The female dewlap was described and pictured by Poe et al. (2009: Fig. 3B) as "mostly dark orange." Although the female pictured by these authors appears short-snouted and thus rather young, it remains unclear whether the difference in dewlap coloration between their and my female (with a violet dewlap, Fig. 4.24G) is due to individual variation or ontogenetic change. Also, neither of the two possibilities can at this time be ruled out to explain the difference in dewlap coloration among my adult and young males (compare Figs. 4.24E and F).

The new records provided herein document for the first time the occurrence of *Dactyloa ibanezi* in Colón province and the Comarca Ngöbe-Buglé. According to the catalogue of CHP, the specimen CHP 3529 from "Bocas del Toro" was collected at an elevation of 1067 m, which is the highest elevation reported so far for *D. ibanezi.* Köhler (2008, p. 99: Fig. 196) pictured an individual from "Reserva Forestal Fortuna, Panama, 400 m." Since no place within RFLF lies below 900 m asl, and the photo was actually taken on the Caribbean versant (B. Akeret, pers. comm.), the correct locality is BPPS in the Comarca Ngöbe-Buglé, and lies more to the north than the corresponding points mapped by Köhler (2008) and Poe et al. (2009). On their distribution map, the latter authors plotted a point in the Pacific drainage in southwestern Veraguas province, well south of the Cordillera Central. However, no corresponding specimen is mentioned, and I am unaware of any specimen or observation underlying this point. To my knowledge, the species has not yet been reported from the Pacific versant west of the Santa Fé de Veraguas area. However, I regard its presence in Chiriquí, at least at RFLF, as plausible given the proximity of Willie Mazú to the provincial border together with its altitudinal distribution as documented herein.

Dactyloa insignis (Cope 1871)

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Giant Anole; Anolis gigante

Figures 4.12; 4.25; 4.29K–M; 4.97B; Maps 4.4; 4.41.

Anolis microtus: Peters and Donoso-Barros (1970: in part.: referring to the holotype of *Diaphoranolis brooksi*).

Anolis insignes: Myers (1977).

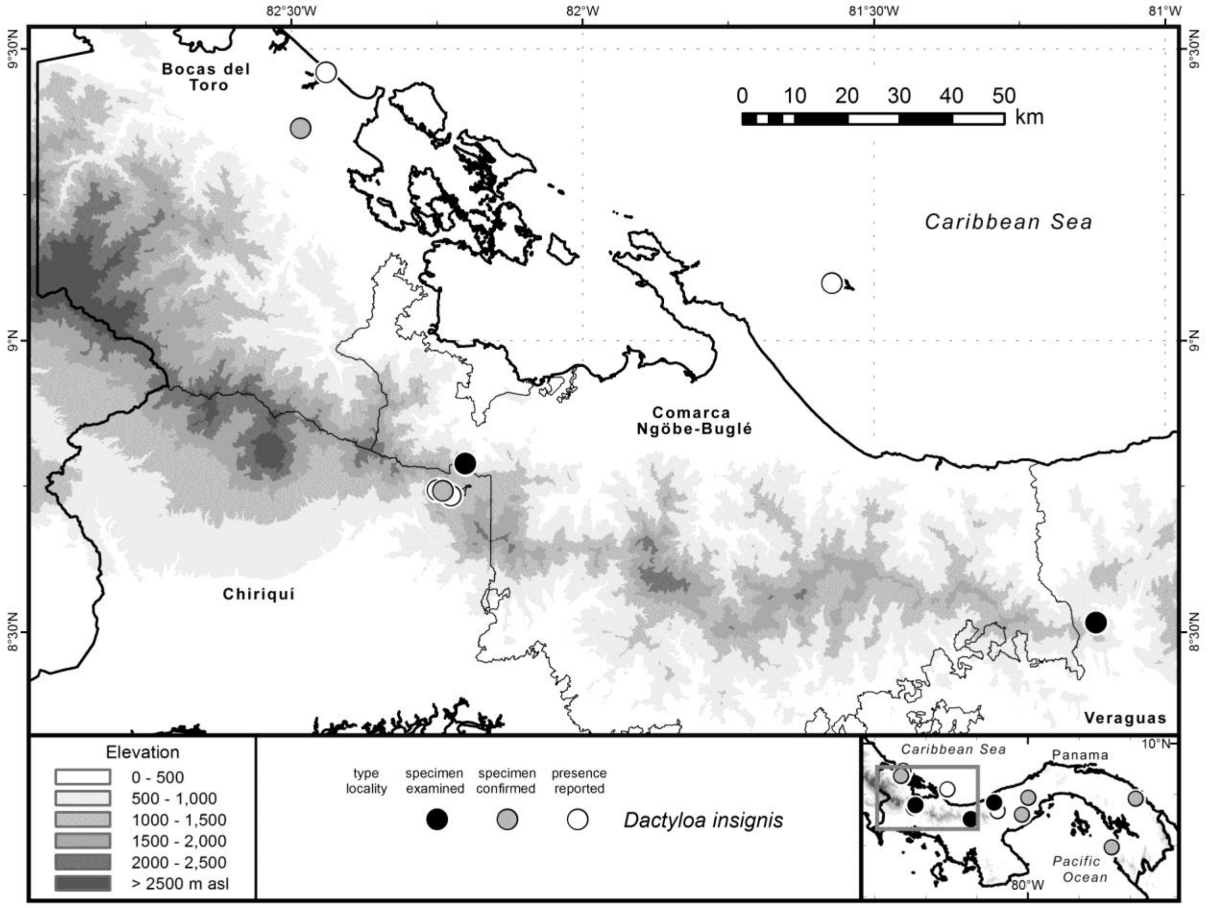
Anolis insignis: Cope (1871, 1876); Boulenger (1885); Dunn (1937a); Taylor (1956); Peters & Donoso-Barros (1970); Savage (1974); Savage & Talbot (1978); Arosemena et al. (1992); Auth (1994); Martínez & Rodríguez (1994); Young et al. (1999); Ibáñez et al. (2001); Poe

(2004); Fundación PA.NA.M.A. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Carrizo (2010); Jaramillo et al. (2010); Lotzkat et al. (2010b); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Castañeda & de Queiroz (2011); Uetz & Hošek (2014).

Diaphoranolis brooksi: Barbour (1923).

Holotype. Lost according to Savage and Talbot (1978); from Costa Rica: Provincia de San José: near Ciudad San José; probably from near La Palma (Savage 1974).

Geographic distribution. Costa Rica and Panama (possibly to Colombia), 0–1820 m asl. In Panama, along both versants throughout most of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Fortuna and Santa Fé areas, PNGDOTH, and Valle de Antón, up to ca. 1050 m asl.



Map 4.41: Distribution of *Dactyloa insignis*.

Diagnosis. A large species (maximum SVL 160 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this clade found in western Panama (*D. casildae, D. frenata, D. ginaelisae, D. ibanezi, D. kunayalae,* and *D. microtus*). *Dactyloa insignis* can readily be distinguished from these six species by its unique coloration of fine reticulate lines forming transverse crossbands on dorsum and flanks, and a preaxillary dark blotch (Fig. 4.25; 4.97B). Moreover, *D. insignis* has all dorsal and lateral body scales smooth (vs. conical, keeled, rugose or wrinkled in the other species), and the highest number of scales around midbody (190 or more vs. 178 or fewer). In addition, *D. insignis* differs from *D. casildae, D. frenata,* and *D. ibanezi* in having short legs (tip of 4th toe of adpressed hind limb reaching at most to a point between shoulder and tympanum in *D. insignis*), and from *D. ginaelisae, D. ibanezi, D. kunayalae,* and *D. microtus* in having more subdigital lamellae under the 4th toe (52 or more in *D. insignis* vs. 50 or fewer) as well as under the 4th finger (40 in *D. insignis* vs. 37 or fewer).

Description. TOL to 464 mm; SVL to 160 mm in males, to 135 mm in females; tail long, about two times SVL, compressed, without D crest; legs short, tip of 4th toe of adpressed hind limb reaching at most to a point between shoulder and tympanum; internasals, canthals, and loreals keeled; scales of frontal and prefrontal area mostly flat, smooth; IP usually distinct, surrounded by not much smaller scales (indistinct from surrounding scales in my juvenile); parietal eye usually distinct (barely visible in my juvenile); scales of SS barely enlarged, smooth; scales of supraorbital disk not conspicuously enlarged, smooth; two or three only slightly elongate, keeled anterior superciliary scales, none reaching a length of one-4th of horizontal eye diameter; anterior sublabials distinctly enlarged, about as high as INL, keeled; scales of temporal arch conspicuously larger than those above and below; ear opening moderate to large, higher than SPL and INL together, slightly lower to higher than eye, much larger than IP; nuchal and D crests present; 0–2 rows of smooth middorsal scales slightly enlarged; other D scales as well as L scales flat, smooth; V much larger than largest D, smooth; scales on anterodorsal surface of thigh mostly smooth, only on anterior edge unicarinate with a few bi- or tricarinate; scales on D surface of forearm smooth, becoming unicarinate towards wrist and anterior edge; 4th toe with well-developed dilated pad, about three times width of distal phalanx; female dewlap moderate, extending posteriorly to slightly beyond axilla, with broad, diffuse gorgetal-sternal rows leaving very narrow interspaces with less densely packed scales.

The hemipenis of *Dactyloa insignis* remains undescribed to my knowledge.

Coloration in life. D and L surfaces white to brown; dorsum, flanks, limbs, and tail with fine reticulate lines conglomerating to form light-centered crossbands that become solid only on posterior portion of tail; lips with dark vertical bars; a pronounced, light-centered blotch between tympanum and axilla, and a dark postorbital stripe extending to above tympanum; V surfaces largely white, except for dark crossbands forming complete rings under tail and dark flank markings and lip bars extending onto V surfaces; iris brown; female dewlap brown, with dark and light blotches and lines (Figs. 4.12; 4.25; 4.97B). *Dactyloa insignis* exhibits considerable metachrosis with ground color ranging from white to dark brown, and the dark markings being green, brown, or almost black. Most notably, in certain situations numerous beige to orange blotches appear on body and head, and even the color of the iris can range from almost white to dark reddish brown (compare Figures 4.25 B, C, and F). Color photographs of *D. insignis* have been published by Savage (2002), Köhler (2003, 2008), Fläschendräger & Wijffels (2009), Stadler (2010), and Uetz & Hošek (2014).

The coloration in life of the adult female (SMF 89482, Figs. 4.12; 4.25B–D, F, G) was recorded as follows: Ground color Sulphur Yellow (57) with Sepia (219) broken crossbands on dorsum which contain Pale Pinkish Buff (121D) blotches; vertical series of Salmon Color (106) blotches between crossbands; several Spectrum Orange (17) blotches on neck; a Raw Umber (23) postorbital stripe; a Burnt Umber (22) blotch with Raw Umber (23) center anterior to shoulder; tail with Sepia (119) crossbands, anterior ones suffused with Natal Brown (219A); V surfaces of body and tail dirty white; D surfaces of limbs with Dark Brownish Olive (129) and Lime Green (59) transverse lines as well as transverse series of Pale Pinkish Buff (121D) flecks; iris Cinnamon-Rufous (40); dewlap Sayal Brown (223C) with Indigo (73) horizontal lines and horizontal series of dirty white flecks.

The coloration in life of the juvenile female (SMF 91477, Figs. 4.12; 4.25A, E, H–L; 4.97B) was recorded as follows: D ground color Opaline Green (162D), grading into dirty white with a suggestion of Pale Horn Color (92) ventrolaterally; head and body with a reticulum of fine Sepia (119) lines that are suffused with, and partly turn into, Emerald Green (163), reach onto venter and accumulate along middorsum to give the impression of four blotches; limbs, toes, and fingers with pairs of transverse Sepia (119) lines; tail with six Sepia (119) transverse bands, the anterior three composed of dense reticula of lines similar to the middorsal blotches; head, body, and limbs with irregularly distributed Orange-Rufous (132C) and Cream Color (54) blotches; V ground color dirty white with a suggestion of Pale Horn Color (92); iris Pale Pinkish Buff (121D); tongue Olive-Gray (42); dewlap dirty white with a suggestion of Pale Horn Color (92) at base, grading into Ground Cinnamon (239) mottled with Buff (24) towards apex, with Sepia (119) longitudinal lines, longitudinal series of dirty white spots, and a Pale Horn Color (92) margin.

Coloration in preservative. After 23–48 months of preservation in 70% ethanol, the ground color has lightened to dirty white, and all markings have assumed grayish or brownish tonalities. Only slight suggestions of blue where green was present in life in my juvenile are still discernable after 23 months (Figs. 4.29K–M).

Natural history notes. Both specimens were encountered at night while they were sleeping on branches 5–6 m above ground. Around our collection sites, *Dactyloa insignis* co-occurs with *D. frenata, D. ibanezi,* and *D. kunayalae.*

Our automatized temperature recordings around our collection sites of *Dactyloa insignis* (640 and 880 m asl) range between 18.2–26.2°C. According to my combined dataset of 36 georeferenced occurrences, the species inhabits LMF, LWF, PMMF, and PMWF, with temperatures between 12.4–33.7°C, mean annual temperatures of 18.0–26.4°C and a total annual precipitation of 1696–4373 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Dactyloa insignis,* and assigned the species to the IUCN category LC. I calculated the species' EVS as 4 (range) + 3 (persecution) + 4 (ecological distribution) = 11, indicating a medium vulnerability. Its extent of occurrence of more than 63000 km^2 does not qualify *D. insignis* for any of the "Threatened" IUCN categories. Considering the continuing deforestation we observed in the region, we place the species in the category NT according to IUCN (2001) criterion B1b(iii).

Remarks. Our record from Willie Mazú (Map 4.2: loc. 9) constitutes the first record for the Comarca Ngöbe-Buglé. In the maps of Köhler (2003, 2008), the distribution area of *Dactyloa insignis* extends into Colombia. Although it is very likely that the species ranges at least into the Colombian Darién, no specimens from this country are known to date. The occurrence of *D. insignis* in the Comarca Kuna Yala as stated by Young et al. (1999) seems plausible considering that the specimen FMNH 170087 was collected at Paradise Camp, which lies less than 4 km west of Camp Summit (Map 4.2: loc. 20) that is situated on the border between Darién province and the Comarca Kuna Yala.

Unfortunately, my sample is composed of just two females. Savage (2002) pictured male individuals from Monteverde in Costa Rica (plates 256, 257), and described the male dewlap as dark red (key on p. 451) or as "primarily orange-red, with or without several horizontal green or white bars and dark spotting" (p. 455) with a white to greenish free margin.

Both Savage (2002) and Köhler (2008) stated that *Dactyloa insignis* has 51 or more lamellae under the 4th toe, and used this as a key characteristic to distinguish this species from *D. microtus,* which has at most 49 according to these authors. Nevertheless, Savage and Talbot (1978) counted just 50 lamellae on the 4th toe of MCZ 16297, a value that is also reached by one of my specimens of *D. ginaelisae* (which formerly was included in *D. microtus*). All previous authors have reported the presence of a distinct IP and parietal eye as a diagnostic character to distinguish *D. insignis* from *D. microtus.* However, the IP is indistinct and the parietal eye barely visible in one of my two specimens (Fig. 4.25H), suggesting that strict adherence to this key characteristic might not always be recommendable (see remarks concerning this matter for *D. ginaelisae* and *D. microtus*).

Savage and Talbot (1978) pointed out differences in anterior head scale surface and coloration between individuals from Costa Rica and Pacific west-central Panama on the one hand and examples from northwestern, central, and eastern Panama on the other hand, concluding that additional material was required to finally evaluate whether or not two species are involved. My examined specimens have smooth anterior D head scales and, just as the individuals photographed by Michael Castillo in Donoso district in Colón province, agree in exhibiting dark lip bars, a dark postorbital marking (in form of a short stripe rather than a spot or blotch), a dark preaxillary blotch, and in having their transverse bands formed by reticula. Thus, these specimens would fall somewhere between Savage and Talbot's (1978) specimens from Costa Rica and their specimen from Valle de Antón (Coclé province). Since I have no male from my study area available, I cannot contribute further to the issue of geographical variation in male dewlap coloration.

A preliminary analysis of its COI barcode (GenBank accession number JN112756.1) revealed the specimen MVUP 2021 from Chiriquí, Reserva Forestal Fortuna" to be more closely related to my barcoded representatives of *Dactyloa microtus,* with uncorrected p-distances of 8.2% to both COI sequences from Río Changena, than to my only COI barcoded specimen of *D. insignis* from nearby Willie Mazú, to which it exhibits a p-distance of 9.8%. Since in view of the distribution of Panamanian highland *Dactyloa* as documented herein I do not expect a specimen from RFLF to really represent *D. microtus* (though if this was true it would be most interesting biogeographically), I see two possible explanations for this phenomenon: First, there might have been a mixup between the tissue samples or sequences of MVUP 2021 and a Costa Rican specimen of *D. microtus* (GenBank accession number AF055947.2; unfortunately, the merely 19 positions of COI contained in the available sequence preclude its inclusion in my analyses of COI barcodes) variously cited as MVZ 204040 (Castañeda & de Queiroz 2011) or MVZ FC14156 (Jackman et al. 1999). Second, MVUP 2021 might represent a divergent genealogical lineage within the nominal taxon *D. insignis.* In the latter case, this specimen could contribute considerably to the issue of possible cryptic species hiding under this name as discussed above. However, without having seen the actual specimen I will not develop this idea any further here.

Dactyloa kunayalae **(Hulebak, Poe, Ibáñez and Williams 2007)**

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

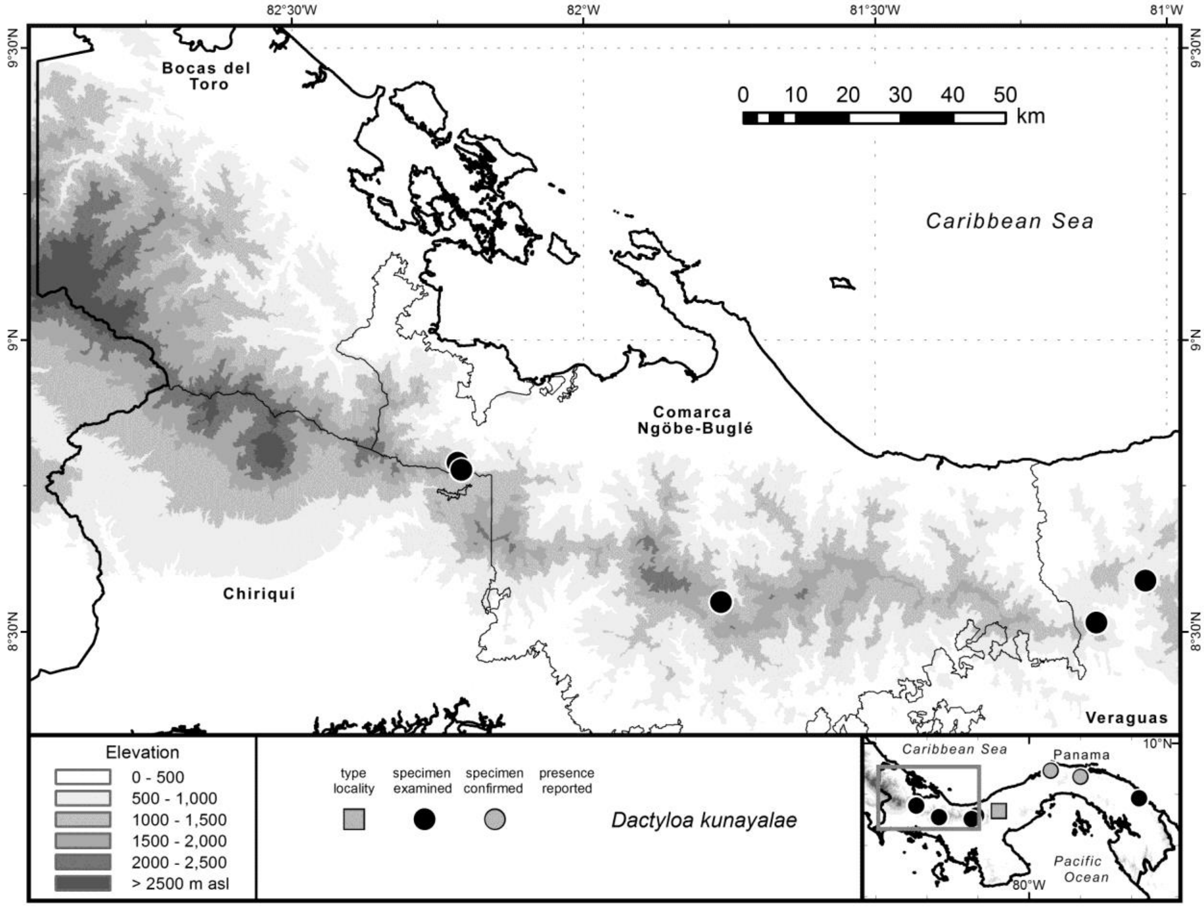
Kuna Yala (Giant) Anole; Anolis gigante de Kuna Yala

Figures 4.12; 4.26; 4.28M–O; 4.29N–Q; 4.97C; Maps 4.5; 4.42.

Anolis kunayalae: Hulebak et al. (2007); Poe et al. (2009); Jaramillo et al. (2010); Wilson & Johnson (2010); Castañeda & de Queiroz (2011); Uetz & Hošek (2014).

Anolis new species 1: Nicholson et al. (2005).

Holotype. MSB 72605, male, from along the trails of Parque National General de División Omar Torrijos Herrera, 5 km North of El Cope, Coclé Province, Panama (8°40.315'N, 80°35.518'W).



Map 4.42: Distribution of *Dactyloa kunayalae*.

Geographic distribution. Endemic to Panama, 320–1050 m asl. Recorded mostly along the Caribbean versant from eastern to western Panama, including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas (possibly also present in Bocas del Toro). In the Cordillera Central, reported from the Fortuna and Santa Fé areas, Río Hacha, and PNGDOTH, 480–1050 m asl.

Diagnosis. A large species (maximum SVL 109 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this clade found in western Panama (*D. casildae, D. frenata, D. ginaelisae, D. ibanezi, D. insignis,* and *D. microtus*). It can readily be distinguished from these six species by its coloration (described below, shown in Figs. 4.12, 4.26, and 4.97C), and by the morphology of its toes: In contrast to the other species, *D. kunayalae* has narrow lamellar pads that are barely dilated under all toes and fingers, a distal phalanx (including claw) of the 4th toe that is longer than phalanges ii and iii combined. Moreover, it has the lowest number of subdigital lamellae under the 4th toe (35 or fewer in *D. kunayalae* vs. 38 or more) and fewer lamellae under the 4th finger than the other species except *D. ibanezi* (25 or fewer in *D. kunayalae* vs. 29 or more). In addition, *D. kunayalae* differs from *D. casildae, D. frenata,* and *D. ibanezi* in having short legs (tip of 4th toe of adpressed hind limb reaching to tympanum in *D. kunayalae*).

Description. TOL to 354 mm (in my material); SVL to 109 mm in males, to 81 mm in females; tail long, about 2–2.5 times SVL, compressed, without D crest; legs short, tip of 4th toe of adpressed hind limb reaching to tympanum; internasals, canthals, and loreals keeled; scales of frontal and prefrontal area mostly rugose to keeled; IP distinct, surrounded by smaller, rugose scales; parietal eye distinct; scales of SS slightly but distinctly enlarged, rugose to keeled; scales of supraorbital disk less conspicuously enlarged, rugose or usually keeled; an elongate, keeled anterior superciliary scale (or two or three accordingly shorter ones, then together) at least half as long as horizontal eye diameter, usually followed by 1–3 similarly keeled, but much shorter scales; anterior sublabials slightly enlarged, but less high than INL; scales of temporal arch much larger than those above and below; ear opening moderate to large, higher than SPL and INL together, slightly lower to higher than eye, much larger than IP; nuchal and D crests present; females without, males with two rows of keeled middorsal scales slightly enlarged; other D scales as well as L scales granular, conical to keeled; V larger than largest D, smooth to slightly keeled; scales on anterodorsal surface of thigh unicarinate; scales on D surface of forearm unicarinate, becoming multicarinate towards wrist; all fingers and toes with very weakly developed dilated pad, not even twice the width of distal phalanx; distal phalanx including claw of 4th toe longer than phalanges ii and iii combined; male dewlap large, extending posteriorly to one-third of the distance between axilla and groin; female dewlap moderate to large, extending posteriorly to up to one-4th of the distance between axilla and groin in large specimens; interspaces between well-demarcated gorgetal-sternal scale rows almost free of scales in both sexes.

The completely everted hemipenis of SMF 91484 (Figs. 4.28M–O) is a small, slightly bilobate organ; sulcus spermaticus bordered by well-developed sulcal lips, opening at base of apex into two broad concave areas, one on each lobe; no asulcate processus or ridge present; lobes finely calyculate, truncus with transverse folds.

Coloration in life. *Dactyloa kunayalae* presents a pronounced sexual dichromatism and apparently also ontogenetic changes in coloration. D and L surfaces in males largely green, turquoise, and blue, with darker green or blue as well as brown and yellow blotches that tend to form transverse and reticulate bands and lines (Figs. 4.26A, F; 4.97C); females chiefly green with dark green to brown blotches usually suggesting transverse bands, and interspersed light markings (Figs. 4.26B–D, G–L); juvenile females with conspicuous dark vertical lip bars that extend onto V surfaces of head; larger females and the adult male with rather immaculate, yellowish green lips; similarly, L pattern extending further onto venter in juveniles, whereas adults have a largely unicolor venter. Both sexes with crossbanded limbs and tail, a diffuse postorbital blotch or stripe, and a reddish brown iris; male dewlap white with an orange-yellow margin; female dewlap white with a narrower margin of lighter yellow (Figs. 4.26; 4.97C). In the course of metachrosis, the ground color may assume a reddish brown similar to the iris, approximate the tonality of the dark markings, or the dark markings may lighten up to become diffuse or barely visible. Color photographs of *D. kunayalae* have been published by Hulebak et al. (2007) and Köhler (2008).

The coloration in life of the adult male (SMF 91484, Figs. 4.26A, F, M; 4.97C) was recorded as follows: D ground color Bunting Green (150) with a suggestion of Lime Green (159), suffused with Cyan (164) on the flanks and bearing a few scattered Natal Brown (219A) areas; body with mottling partly fusing to form a reticulum of Cream Color (54), grading into Raw Sienna (136) anteriorly and on the head; D surfaces of body and legs mottled with Sepia (119); tail Light Drab (119C), grading into Drab-Gray (119D) ventrally, with Sepia (119) crossbands; lips and V surface of head Chartreuse (158); V surfaces of limbs, body and base of tail Sulphur Yellow (57); iris Mahogany Red (132B); dewlap Sulphur Yellow (57) on basal portions, grading into dirty white towards the center, and a broad Spectrum Orange (17) with a suggestion of Orange Yellow (18) margin; dewlap scales dirty white and Chartreuse (158).

The coloration in life of a young female (SMF 91485, Figs. 4.12; 4.26B, H–L, N, O) was recorded as follows: D and L ground color of body, limbs, base of tail, and head Lime Green (159), grading into Pistachio (161) laterally, with Sepia (119) mottling except on snout that partly fuses to form broken crossbands on body, limbs, and base of tail; head, body, and limbs with scattered, diffuse blotches of Mahogany Red (132B); tail Ground Cinnamon (239) with Warm Sepia (221A) crossbands that grade into Sepia (119) dorsally, their Sepia (119) portions ventrally bordered by dirty white mottling; V surfaces of body, head, and limbs Tawny Olive (223D), mottled with Warm Sepia (221A) and dirty white, giving the impression of transverse stripes especially laterally and under head; iris Mahogany Red (132B); dewlap Yellowish Olive-Green (50) with a Buff Yellow (53) margin and broad, partly broken gorgetal-sternal rows of small Buff-Yellow (53) scales.

Coloration in preservative. After 22–74 months of preservation in 70% ethanol all yellow, green, and blue colors have given way to brown, cream, and white. Only a very faint suggestion of yellow is retained on the male dewlap margin after 23 months (Figs. 4.29N–Q).

Natural history notes. Our specimens were encountered at night while they were sleeping on branches and lianas 2–8 m above ground. We found this species to occur in syntopy with *Dactyloa frenata, D. ibanezi,* and *D. insignis* at two sites (Map 4.2: locs. 9 and 16), and with *D. casildae* at one locality (Map 4.2: loc. 13).

Our automatized temperature recordings at localities where we encountered *Dactyloa kunayalae* (480–1050 m asl) range between 17.6–27.6°C. According to my combined dataset of 26 georeferenced occurrences, the species inhabits LMF, PMMF, and PMWF, with temperatures between 14.7–30.1°C, mean annual temperatures of 20.6–25.4°C and a total annual precipitation of 1735–3452 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 12 for *Dactyloa kunayalae,* and assigned the species to the IUCN category LC. I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of 19441 km^2 and the continuing deforestation we observed in the region qualify *D. kunayalae* for the IUCN category VU according to IUCN (2001) criterion B1b(iii).

Remarks. Our findings of *Dactyloa kunayalae* raise the altitudinal maximum by 250 m, originate from up to 180 km west of the documented range, and constitute the first records for Chiriquí, Veraguas, and the Comarca Ngöbe-Buglé (Hulebak et al. 2007). Moreover, GK had the privilege to examine the specimen FMNH 170034 (collected in August 1967 by Michael Duever at "border of Darien, Summit site, 8°55'N 77°51'W, 320m") and identified it as an adult male *D. kunayalae,* probably the first specimen of this species ever collected. This specimen further extends the documented range some 135 km east-southeast from the nearest record in Nusagandí (Hulebak et al. 2007), may be regarded as the first record for Darién province, and sets the new lower vertical limit for the species. I regard the species' presence in Bocas del Toro possible in view of the suitable forest habitat covering the Caribbean slopes of the eastern Talamanca throughout the ca. 16 airline km between the collection site of SMF 91484 and the provincial border.

Hulebak et al. (2007) described *Dactyloa kunayalae* to be long-legged, with the 4th toe reaching "to eye when hindleg pressed against body." This trait was implied as diagnostic in the key of Köhler (2008). Strictly adhering to that key characteristic, all my specimens would have been identified as *D. insignis* or *D. microtus,* since their hind legs are short with the 4th toe merely reaching to tympanum. Although I do not know if there is really so much geographical variation in relative hind limb length in *D. kunayalae,* I consider it rather unlikely and prefer to attribute this discrepancy to different ways of extending or adpressing hind limbs, or bending the specimens' bodies while doing so.

Dactyloa microtus **(Cope 1871)**

[Modified from Lotzkat et al. (2013); see Appendix 8 for original publication]

Small-ear (Giant) Anole; Anolis (gigante) de oreja pequeña

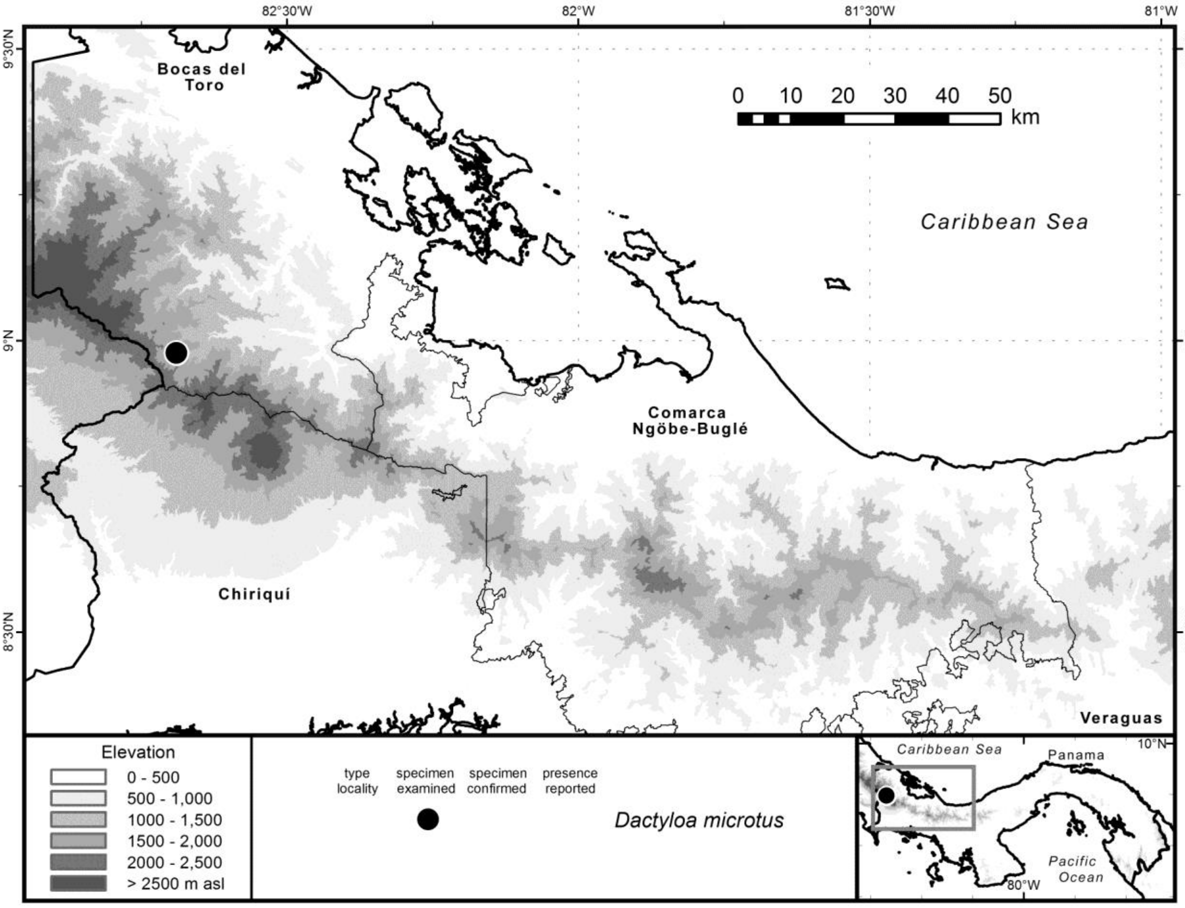
Figures 4.12; 4.18; 4.27; 4.29T–U; 4.97D; Maps 4.5; 4.43.

Anolis microtus: Cope (1871, 1876); Boulenger (1885); Dunn (1937a: in part.); Taylor (1956: in part.); Peters & Donoso-Barros (1970: in part.); Savage (1974); Savage & Talbot (1978: in part.); Arosemena et al. (1992: in part.); Auth (1994: in part.); Poe (2004); Nicholson et al. (2005); Fläschendräger & Wijffels (2009: in part.); Hamad (2009: in part.); Sasa et al. (2010); Wilson & Johnson (2010: in part.); Castañeda & de Queiroz (2011: in part.); Lotzkat et al. (2011); Uetz & Hošek (2014).

Holotype. USNM 31282, female (Fig. 4.18), from Costa Rica: Provincia de San José: near San José; probably from near La Palma (Savage 1974).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and extreme western Panama, 1100 to probably above 2000 m asl (see remarks). In Panama, only recorded from Río Changena in Bocas del Toro province, at 1640 m asl.

Diagnosis. A large species (maximum SVL 111 mm) of the genus *Dactyloa* (*sensu* Nicholson et al. 2012) that is most similar in external morphology to the other members of this genus found in western Panama (*D. casildae, D. frenata, D. ginaelisae, D. ibanezi, D. insignis,* and *D. kunayalae*). *Dactyloa microtus* can readily be distinguished from these six species by its color pattern described below and shown in Figs. 4.12, 4.18, 4.27, 4.29T–U, and 4.97D. It further differs from all mentioned species except *D. ginaelisae* by its low numbers of horizontal loreal rows (4 or fewer in *D. microtus* vs. 5 or more) and total loreal scales (26 or fewer in *D. microtus* vs. 39 or more), and by its low number of scales around midbody (106 or fewer in *D. microtus* vs. 110 or more). Moreover, *D. microtus* differs from *D. casildae, D. frenata,* and *D. ibanezi* in having short legs (tip of 4th toe of adpressed hind limb reaching at most to tympanum in *D. microtus* vs. beyond eye; shank length/SVL = 0.183 or less in *D. microtus* vs. 0.25 or more). Among the short-legged species of *Dactyloa* in western Panama, *D. microtus* further differs from *D. insignis* in having fewer subdigital lamellae under the 4th toe (47 or fewer in *D. microtus* vs. 52 or more) as well as under the 4th finger (37 or fewer in *D. microtus* vs. 40), and from *D. kunayalae* in having more subdigital lamellae under the 4th toe (44 or more in *D. microtus* vs. 35 or fewer) as well as under the 4th finger (32 or more in *D. ginaelisae* vs. 25 or fewer). *Dactyloa microtus* is very similar to *D. ginaelisae,* from which it differs in having shorter legs (tip of 4th toe of adpressed hind limb reaching to a point between shoulder and tympanum in *D. microtus* vs. to a point between tympanum and eye in *D. ginaelisae;* shank length/SVL = 0.183 or less in *D. microtus* vs. 0.19 or more) and by its less conspicuous and clear-cut coloration pattern between eye and shoulder (light postsupralabial and dark postorbital stripe oriented rather ventrally and losing their conspicuousness around ear in *D. microtus* vs. a prominent light stripe extending from supralabials posteriorly above or across the ear before bending down towards shoulder, delineating a dark preaxillary blotch above and posteriorly, and paralleled above by a dark postorbital stripe with darker borders that extends at least to a level above the preaxillary blotch in *D. ginaelisae*). For more characters that might help to distinguish these two very similar species, see remarks section in the species account of *D. ginaelisae.*



Map 4.43: Distribution of *Dactyloa microtus*.

Description. TOL to 331 mm; SVL to 111 mm in males, to 104 mm in females; tail long, about 1.4–1.7 times SVL, compressed, with a low D crest on the anterior portion; legs short, tip of 4th toe of adpressed hind limb reaching to a point between shoulder and tympanum; D and L head scales generally large; internasals, canthals, and loreals rugose to wrinkled; scales of frontal and prefrontal area mostly rugose to wrinkled; IP either distinct or indistinct, if discernable, then usually surrounded by scales of both smaller and equal size; parietal area generally with flat, rugose scales; parietal eye either distinct or indistinct; scales of SS distinctly enlarged, rugose; scales of supraorbital disk conspicuously enlarged, rugose; usually only one slightly elongate, keeled anterior superciliary scale, one-4th to half as long as horizontal eye diameter, usually followed by several similarly keeled, but much shorter scales; one or two sublabials greatly enlarged, higher than INL; scales of temporal arch usually larger than those above and below; ear opening small, by far not as high as eye, less high than SPL and INL together, usually about as high as SPL; prominent nuchal and lower D crest present; no rows of middorsal scales slightly enlarged; other D scales as well as L scales smooth to slightly rugose or wrinkled in two young males, smooth in a very small juvenile, with very small granules scattered in the interspaces between them; V not or only slightly larger than largest D, smooth; scales on anterodorsal surface of thigh multicarinate; scales on D surface of forearm multicarinate; 4th toe with well-developed dilated pad, about three times width of distal phalanx; dewlap of young males large, extending posteriorly to about one-fourth of the distance between axilla and groin, with gorgetal-sternal scale rows of densely arranged scales and widely spaced scales in the broad interspaces between the rows; dewlap of a small juvenile female moderate, extending posteriorly to slightly beyond axilla.

The hemipenis of *Dactyloa microtus* remains undescribed.

Coloration in life. *Dactyloa microtus* exhibits a rather variable coloration. Among the more reliable features usually present are dark crossbands around the tail and, mostly with light centers, on D surfaces of limbs and digits; a light postsupralabial and a dark postorbital stripe extending to near the ear opening; a dark preaxillary blotch. Otherwise, D and L surfaces with spots, blotches, and reticula that are lighter and/or darker than ground color and partly arranged in transverse bars; dorsolateral pattern elements may reach well onto the otherwise comparably unicolor white or yellow V surfaces; ground and marking colors of D and L surfaces ranging from white over different shades of yellow, green, blue, and brown to black; iris purplish blue to brown, or gray with suffusions of these colors; dewlap of young males yellowish; dewlap of a hatchling female pinkish to salmon color (Figs. 4.12; 4.18; 4.27; 4.97D; see remarks section for adult dewlap coloration reported from Costa Rica). This species is capable of considerable metachrosis (compare Figs. 4.27A and B, C and D, F and H). The green phase, usually shown while the animal is sleeping, can culminate in restricting most colors to white, green, and blue, blurring some or all of the otherwise contrasting markings. Similarly, the dark or brown phase, often assumed when the animal is handled, can cause all pattern elements to assume different shades of brown. In between, most pattern elements of a given individual can apparently assume most colors from the palette of this species. A female hatchling was mostly gray when found at daytime. Color photographs of *D. microtus* have been published by Savage (2002). No standardized description of the coloration in life was recorded.

Coloration in preservative. After about two years of preservation in 70% ethanol, colors are largely reduced to white, cream, different shades of brown, and black (Figs. 4.29T–U).

Natural history notes. Two young males were encountered at night while they were sleeping on a leaf and a branch, 1.5 and 3 m above ground, respectively. A hatchling female virtually dropped into camp on 18 July 2010 while we detached tent strings from a tree.

Our automatized temperature recordings at Río Changena (1640 m asl) range between 13.7–19.2°C. According to my combined dataset of 12 georeferenced occurrences (after the exclusion of two localities below 1000 m, see remarks), the species inhabits PMMF, PMWF, LMWF, and LMRF, with temperatures between 7.2–26.4°C, mean annual temperatures of 12.2–20.4°C and a total annual precipitation of 1660–4556 mm.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Dactyloa microtus,* which at the time also comprised the populations described herein as *D. ginaelisae,* and assigned the species to the IUCN category LC. I calculated the EVS for *D. microtus* as 4 (range) + 3 (persecution) + 5 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of just 3346 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. All previous records of *Dactyloa microtus* from Panama must have been based on individuals of *D. ginaelisae,* considering the distribution of the two species as documented herein. Thus, our record from Río Changena is not only the first record of this species from Bocas del Toro province, but also the first and only true record from Panama. Savage (2002) and consequently Köhler (2008) gave the species' lower distributional limit as 425 m asl. Re-examination of the underlying specimens showed them to be misidentified *D. insignis,* raising the lower elevational limit to about 1100 m in Costa Rica and thus for the species as a whole (J. M. Savage, pers. comm.). The high elevation of Cerro Dantas, provenance of the individual photographed by Daniel Cascante (Figs. 4.18K–L), suggests that the species occurs well above the upper elevational limit of 1500 m given by Savage (2002) and Köhler (2008).

All previous authors have reported the absence of a distinct IP and parietal eye as a diagnostic character for *Dactyloa microtus.* However, two of my three specimens do have a well-discernable IP with parietal eye (Fig. 4.27I; also see remarks concerning this matter for *D. ginaelisae* and *D. insignis*). Savage (2002) described the dewlap of adult males as "pink with white scales" or "pale salmon with several vertical rows of white scales," and that of females as "pinkish." Inasmuch as they are visible, the dewlaps of the adult Costa Rican specimens (Figs. 4.18J and L) comply with these descriptions.

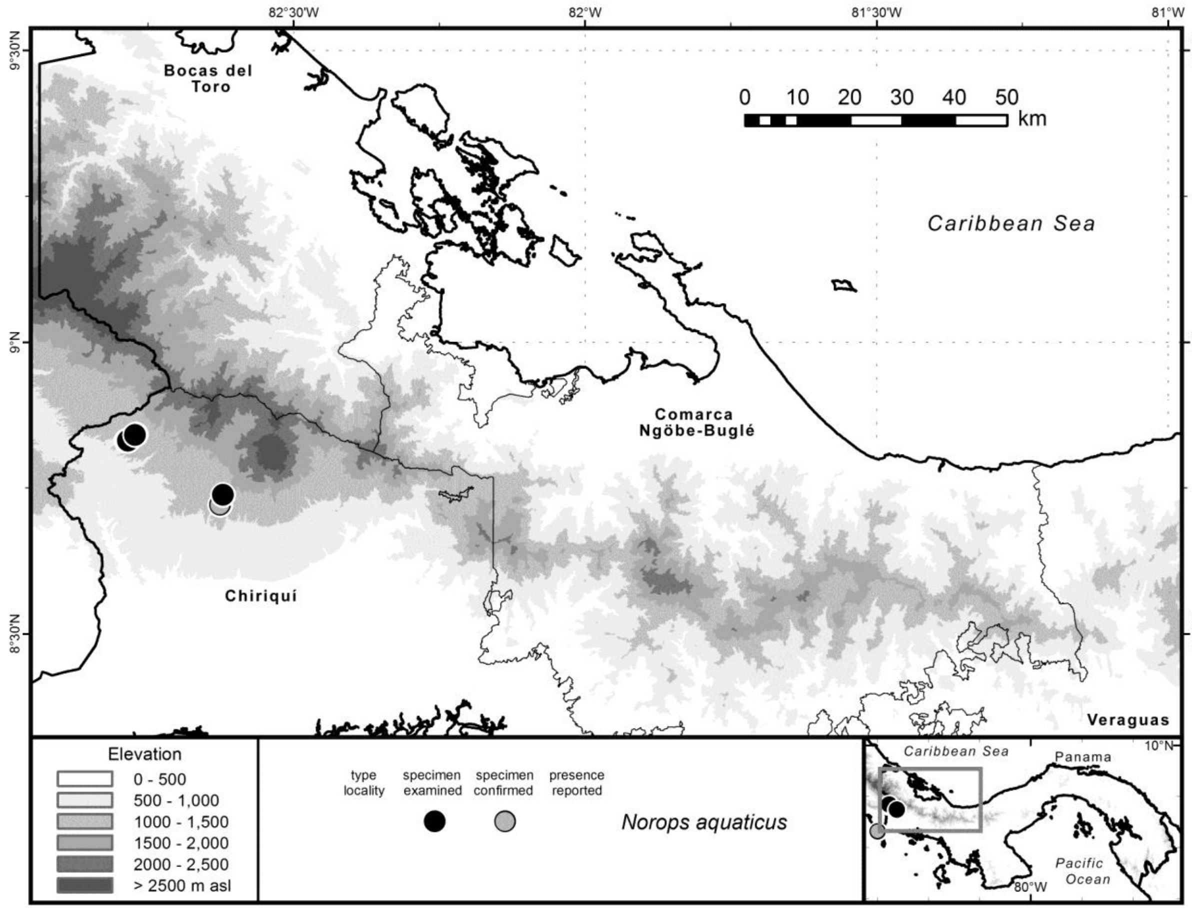
I strongly oppose against the common name "Tiny anole" assigned to this species by Frank and Ramus (1995). Since *Dactyloa microtus* is one of the largest mainland anoles, this common name apparently is derived from a mistranslation of the specific epithet *microtus,* a compound noun in apposition translating to "small ear." If one really needs to use common instead of scientific names for whatever reason, then the correct translation "Small-ear anole", as proposed in the head of this species account, will be much more appropriate.

Norops aquaticus **(Taylor 1956)**

Water Anole; Anolis del agua

Figure 4.97E; Map 4.44.

Anolis aquaticus: Taylor (1956); Peters & Donoso-Barros (1970); Savage (1974); Fitch et al. (1976); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Poe (2004); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Lotzkat et al. (2012a); Uetz & Hošek (2014).



Map 4.44: Distribution of *Norops aquaticus*.

Holotype. KU 34276, male, from Palmar, Puntarenas, Costa Rica (Taylor 1956).

Geographic distribution. Southern Pacific Costa Rica to western Panama, 30–1200 m asl. In Panama, restricted to western Chiriquí. In the Cordillera Central, reported from Santa Clara and the vicinities of Volcán up to 1200 m asl.

Diagnosis. A medium-sized *Norops* (maximum SVL 71 mm) with long legs (4th toe reaching to eye) that is readily distinguished from all other anoles of western Chiriquí by its dark crossbands on body, limbs, and tail, its light supralabial stripe curving upwards near the ear, and its light sublabial stripe extending posteriorly onto or all along the body.

Description. TOL to 188 mm; SVL to 71 mm; tail moderately long, TL/SVL 1.55–1.8*; legs long (tip of 4th toe of adpressed hind limb reaching to eye); D, V, and caudals keeled; Drows 2–4, forming a slightly serrate crest in males that becomes most conspicuous on the tail; SAM 144–168*; males without enlarged PC, but can raise a low nuchal crest; lamellar pads rather narrow; 4toe 29–34; 4finger 23–27*; IO 1–4; IP/SS 5–10*; SBO/SPL 2–3; loreals keeled, 67–84* in 7–8* rows; nuchal crest in males; male dewlap large, female dewlap very small.

The hemipenis of *Norops aquaticus* is a relatively small, slightly bilobed organ with very short calyculate lobes and a large asulcate processus.

Coloration in life. The adult male SMF 89667 was recorded as follows: D and L ground color Raw Umber (223), with a Sepia (119) reticulum forming transverse bands laterally; middorsum and flanks with series of Pale Neutral Gray (86) blotches grading into Cream Color (54) with a suggestion of dirty white ventrolaterally, and turning to crossbands on tail and limbs; a Pratt's Payne's Gray (88) supralabial stripe extending to behind ear; a sublabial stripe of the same color extending to midbody before disintegrating into a series of blotches; V surface of body Cream Color (54) with a suggestion of dirty white, those of limbs, hip, and anterior portion of tail Pale Neutral Gray (86); V surface of head Medium Neutral Gray (84) with shadings of dirty white; iris Olive Brown (28); dewlap Pratt's Rufous (140) with diffuse Sulphur Yellow (57) longitudinal bands, dewlap scales either Sepia (119), dirty white, or both. The rudimentary dewlap of females and juveniles is dirty white with dark longitudinal bands. I observed metachrosis in this species, with the dark ground color lightening or assuming a greenish cast, and the light blotches and stripes assuming greenish or bluish tonalities.

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration is similar to that in life, apart from that all red and yellow tonalities have faded; male dewlaps colorless.

Natural history notes. Diurnal and semiaquatic. Usually found along streams, into which it escapes. Most individuals were encountered at night, sleeping on vegetation less than 1 m above small streams. One juvenile was observed active on a pile of decomposing plant material in the afternoon, about 100 m uphill from the next creek.

Remarks. The juvenile mentioned above, observed at Santa Clara at 1200 m asl, slightly raises the upper elevational limit reported as 1170 m (Savage 2002; Köhler 2008; Sasa et al. 2010). I consider the elevational range of 1200–2200 m reported for Panama by Jaramillo et al. (2010) as clearly erroneous, though I assume that this species will be found at higher elevations than currently documented.

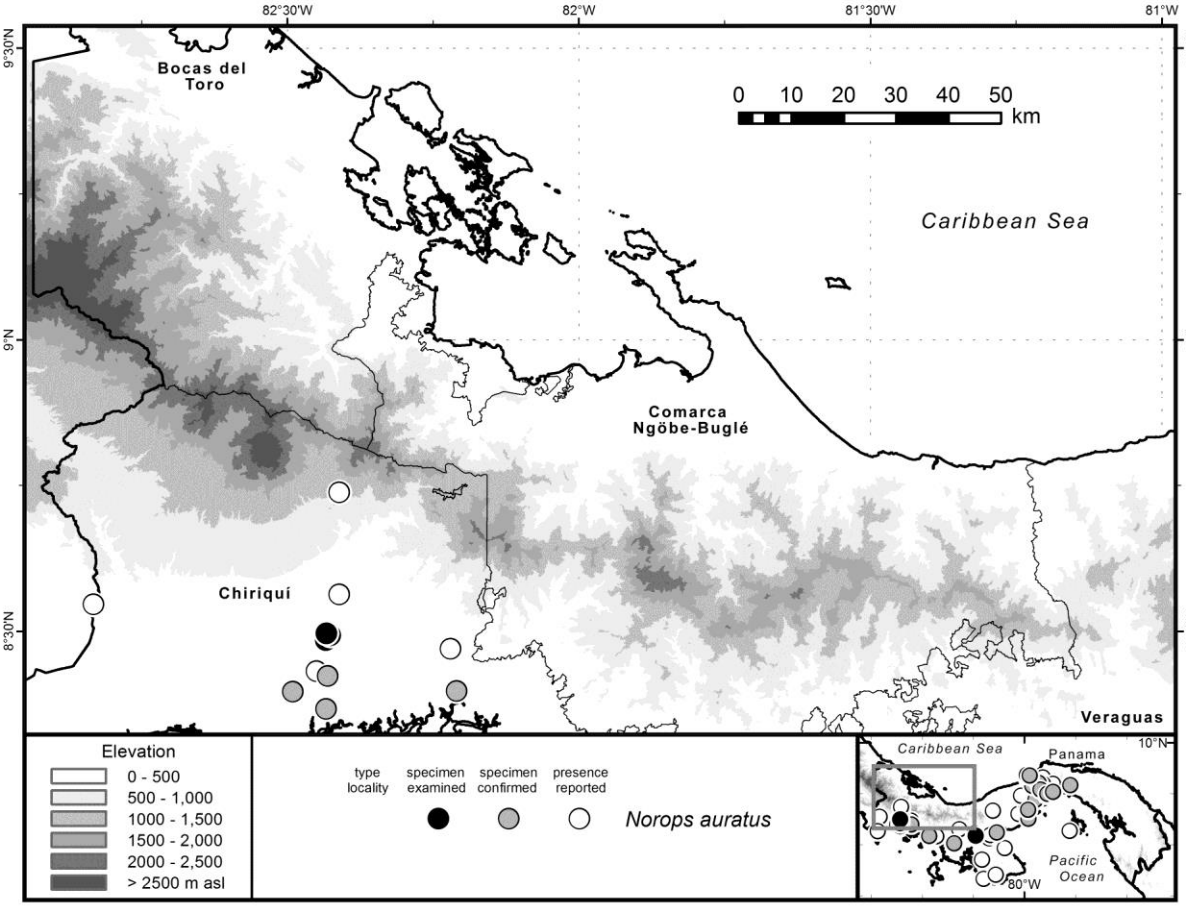
***Norops auratus* (Daudin 1802)**

Grass Anole; Anolis

Figure 4.97F; Map 4.45.

Anolis auratus: Myers & Rand (1969); Peters & Donoso-Barros (1970); Telford (1971); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995; 1996; 1997; 2001); Young et al. (1999); ANAM (2004); Poe (2004); Rodriguez et al. (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Köhler et al. (2007, 2008); Hamad (2009); Fläschendräger & Wijffels (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Batista & Ponce (2011); Lotzkat & Hertz (2011); Uetz & Hošek (2014).

Holotype. Unknown, from Tropical America, restricted to Surinam.



Map 4.45: Distribution of *Norops auratus*.

Geographic distribution. Costa Rica to Ecuador, Colombia, northern Brazil, and the Guayanas, 0–2000 m asl. In Panama, along both versants of central and eastern, and the Pacific versant of western Panama, including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central reported from PNAC, El Valle de Antón, PNGDOTH, and Boquete, up to 1220 m asl.

Diagnosis. A medium-sized *Norops* (maximum SVL 52 mm) with long legs (4th toe reaching to eye) that is readily distinguished from all other Panamanian congeners by its 10 or more rows of enlarged, imbricate, strongly keeled dorsals, its large, imbricate, strongly keeled ventrals, its light labial stripe extending posteriorly to groin, and the blue dewlap bearing large, strongly keeled scales in both sexes.

Description. SVL to 52 mm; legs long (tip of 4th toe of adpressed hind limb reaching to eye); D, V, and caudals large, imbricate, strongly keeled; L granular; Drows 10–12*; males with slightly enlarged PC, without nuchal crest; lamellar pads very narrow; IO 0–1; IP/SS 2–3*; SBO/SPL 1*; all D and L head scales strongly keeled; male dewlap moderate to large, female dewlap very small to small.

The hemipenis of *Norops auratus* is a bilobed organ with stout, calyculate lobes and a long, slender asulcate processus.

Coloration in life. Essentially brown with a conspicuous L stripe, and whitish below; dewlap blue. In the course of metachrosis, the D and L coloration may range from tan over bronze to dark brown, and the light L stripe may range from white to dark brown. The adult male SMF 89444 was described as follows: D surfaces of head, body, tail and limbs Drab (27), except for those of front limbs with transverse flecks or lines of Dusky Brown (19), generally followed posteriorly by a band of Clay Color (26), eventually including shades of Fawn Color (25); flanks Tawny Olive (223D), with a Sulfur Yellow (157) longitudinal stripe bordered by Fuscous (21) shadings; V surfaces of head, body and tail Cream Color (54) with nuances of Buff-Yellow (53), grading into Light Drab (119C) along posterior half of tail; ventrolateral surfaces of body iridescent with Opaline Green (162D), those of the gular region with Sulfur Yellow (157); dewlap Indigo (73), with Sulfur Yellow (157) gorgetals and Cream Color (54) marginals.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is very similar to that in life, including dewlap color. The same holds for specimens at SMF that were collected more than 5 decades ago.

Natural history notes. Diurnal, chiefly found in open habitats. Most individuals of this species were encountered in open secondary vegetation, either active on the ground or sleeping less than 1 m above ground in vegetation.

Remarks. Since no other author has reported this species from Caribbean western Panama or adjacent Costa Rica, I regard the records of *Norops auratus* from HIISSPS (ANAM 2004) as clearly erroneous, probably based on a misidentification. When Köhler et al. (2008) claimed to provide the first record from western Panama they had overlooked the series CAS 79375–81 reported by Slevin (1942) from the Boquete area "at an elevation of approximately 4000 feet" (= 1219 m) that still represent the highest record for Panama (Jaramillo et al. 2010).

Norops benedikti (Lotzkat, Bienentreu, Hertz & Köhler 2011)

[Modified from Lotzkat et al. (2011); see Appendix 8 for original publication]

Benedikt's Anole; Anolis de Benedikt

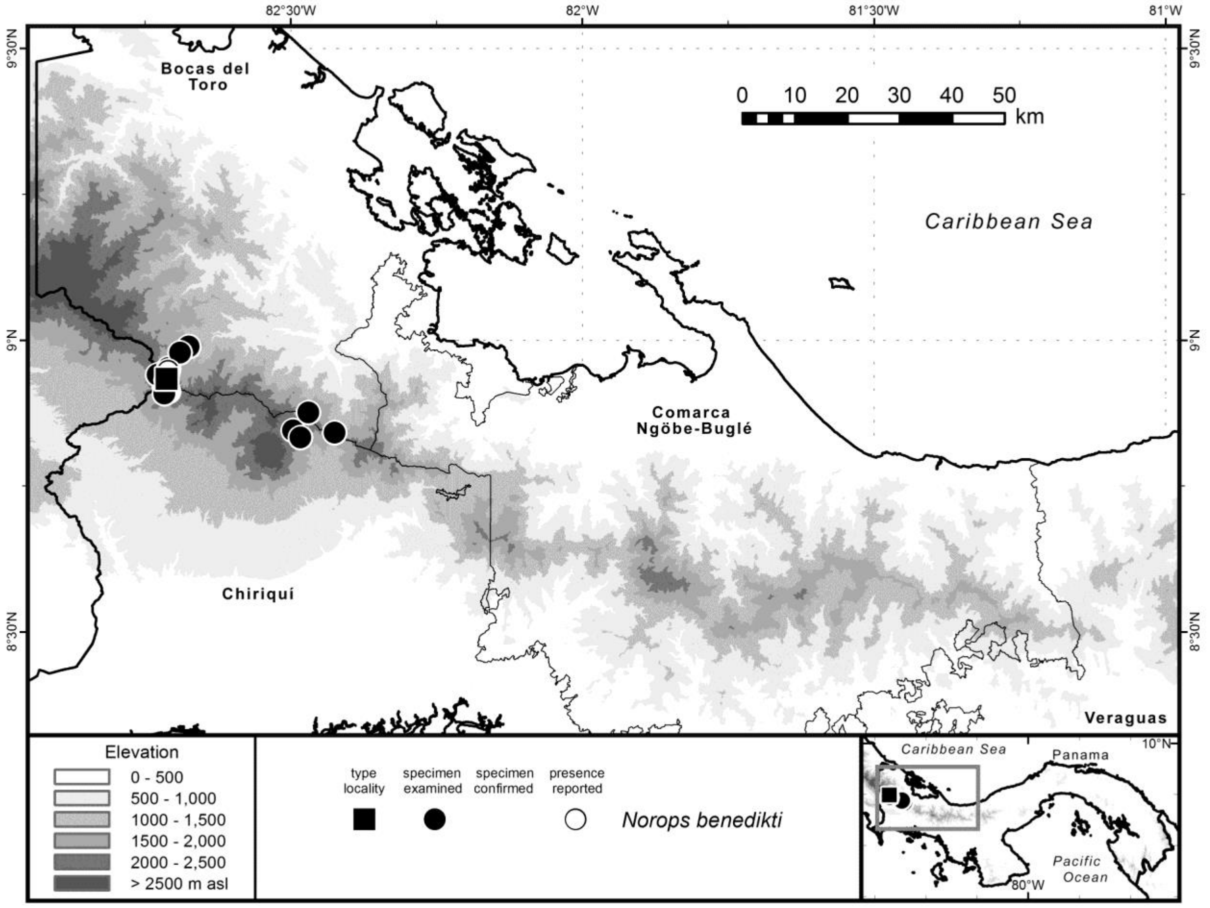
Figures 4.30F–H; 4.33–36; 4.97G; Maps 4.7; 4.8; 4.46.

Anolis benedikti: Lotzkat et al. (2011); Uetz & Hošek (2014).

Anolis pachypus: Taylor (1956); Peters & Donoso-Barros (1970); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Fundación PA.NA.M.A. (2007); Poe & Ibáñez (2007); Köhler et al. (2007); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); all in part.

Anolis sp.: Bienentreu (2011).

Norops pachypus: Savage (2002); Köhler (2008); Savage & Bolaños (2009); all in part.



Map 4.46: Distribution of *Norops benedikti.*

Holotype. SMF 90149 (Figs. 4.30H; 4.34; 4.35A and F), adult male, from the north slope of Cerro Pando, 8.9333°N, 82.7131°W, 2310 m asl, PILA, Bocas del Toro, Panama.

Geographic distribution. Endemic to the Talamancan highlands of eastern Costa Rica and western Panama, recorded between 82.73°W and 82.42°W, 1580–2390 m asl. In Panama, restricted to the Cordillera de Talamanca of Bocas del Toro and Chiriquí, where it has been recorded from around Cerro Pando and north of Boquete, 1580–2390 m asl.

Diagnosis. A medium-sized *Norops* (maximum SVL 50 mm) with long to very long legs (tip of 4th toe reaching to anterior border of eye, usually to nostril or beyond) that is very similar to *N. magnaphallus, N. pachypus,* and *N. pseudopachypus* in having narrow toepads and two slightly enlarged middorsal scale rows, as well as in lacking enlarged postcloacal scales in males. *Norops benedikti* differs from these three species in having the male dewlap red with a yellow anterior margin (vs. solid red in *N. magnaphallus,* red with a central yellow blotch in *N. pachypus,* and solid yellow, sometimes with a suggestion of orange posteriorly, in *N. pseudopachypus*). It further differs from *N. magnaphallus* and *N. pachypus* in having 5 or more, rarely 4, IO and IP/SS, respectively (vs. 4 or fewer, rarely 5), and in having a dark gray tongue in life (vs. light gray). *Norops benedikti* differs from the superficially similar *N. humilis* and *N. lemurinus* in the color of the male dewlap (solid red with yellow margin in *N. humilis* and solid red in *N. lemurinus*) and in having higher numbers of IO and IP/SS (0–3, very rarely 4, IO and 2–4 IP/SS in *N. humilis;* 0–1 IO and 2–3 IP/SS in *N. lemurinus*).

Description. TOL to 130 mm*; SVL to 50 mm*; legs long (tip of 4th toe of adpressed hind limb reaching beyond eye); D, V, and caudals keeled; Drows 2*, slightly enlarged; SAM 128–178*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 28–33*; 4finger 19–26*; IO 4–8*; IP/SS 4–10*; SBO/SPL 2*; loreals keeled, 44–91* in 7–12* rows; male dewlap moderate, female dewlap small.

The hemipenis of *Norops benedikti* is a stout bilobate organ with short lobes and a large asulcate processus; lobes strongly calyculate, truncus with transverse folds.

Coloration in life. Similar to the other four members of the *Norops pachypus* complex, the coloration of *N. benedikti* is rather variable among individuals, mostly concerning the extent and shape of color patterns, i.e., stripes, blotches, and bands on D and L surfaces (compare Figs. 4.35F–O). Common patterns include a broad middorsal band which is often interspersed with blotches or chevrons, flanked by L markings, or disintegrates into diamond-shaped markings posteriorly (Figs. 4.35F–J); a narrow light middorsal stripe, often bordered by narrow dark stripes (Figs. 4.35K–L); and series of triangular markings pointing laterally from middorsum (with or without narrow medial light stripe) which are either offset to form a zig-zag pattern or arranged symmetrically to form a series of diamonds (Figs. 4.35M–O). Most specimens exhibit contrasting markings on D and L surfaces of the head, with postocular stripes and an interorbital bar being the most common. Furthermore, these anoles are capable of metachrosis and, therefore, the coloration of a given individual is subject to physiological change according to time or situation. Most individuals encountered at night exhibited light tonalities, but could turn very dark during the day or when handled (Figs. 4.35K–L). Individuals spotted during the day all appeared dark. In the course of metachrosis, the conspicuousness of individual color patterns may vary considerably (as in the postocular stripes between the two females in Figs. 4.35C–D).

The coloration of the male paratype SMF 89506 (Figs. 4.30G, 4.35B and G) was recorded as follows: D and L ground color Antique Brown (37) suffused with Light Drab (119C) and Tawny (38), laterally grading into Olive-Gray (42) mottled with Burnt Umber (22); a Mars Brown (223A) postorbital stripe mottled with Sepia (219) continues to form a dorsolateral band, which disintegrates into a series of blotches around midbody; a few Sepia (119) middorsal blotches present; D and L surfaces of head Light Drab (119C); occipital region Mars Brown (223A) mottled with Sepia (219); a Mars Brown (223A) interorbital bar and a preorbital stripe bordered by Sepia (219); a dirty white with a suggestion of Yellow-Green (58) L postorbital stripe extending to shoulder; D and L surfaces of limbs and tail Antique Brown (37), with irregular Sepia (219), Tawny (38), and Olive-Gray (42) transverse stripes; V surface of body and head Pearl Gray (81) suffused with Cinnamon-Rufous (40); V surface of tail with a Cinnamon-Rufous (40) midventral stripe; iris Brick Red (132A); tongue Plumbeous (78) with a suggestion of Indigo (73); gular region Flame Scarlet (15); dewlap Flame Scarlet (15) with a small Pearl Gray (81) region at posterior insertion and an Orange Yellow (18) anterior margin; dewlap scales dirty white bordered by Sepia (119) or Sepia (219). The dewlap coloration of the juvenile male SMF 90148 from the vicinity of the type locality was recorded as follows: Flame Scarlet (15), with a suggestion of Chrome Orange (16), grading into Orange Yellow (18) on anterior margin; dewlap scales Sepia (119).

As illustrated in Figs. 4.30F–H, the extent of the yellow coloration on the anterior portion of the male dewlap of *Norops benedikti* varies from covering just the basal part of the anterior margin (Fig. 4.30F) to covering the anterior fourth or third of the dewlap (Fig. 4.30H). The female dewlap (Figs. 4.35C–E) is much smaller than in males, and usually of a whitish color (Fig. 4.35C). Nevertheless, some female individuals bear reddish coloration around their gular area. These females tend to exhibit a reddish dewlap (Figs. 4.35D–E), sometimes even resembling that of males, like the female paratype SMF 89746 (Fig. 4.35E), that was recorded as follows: Dewlap Flame Scarlet (15) posteriorly, grading into Orange Yellow (18) on anterior half and into dirty white with a suggestion of Chamois (123D) on posterior base; dewlap scales mostly Sepia (119), some dirty white.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that all reddish shades have faded, bronze metallic hues are visible in all specimens, and bluish gray ones in some; male dewlaps translucent white.

Natural history notes. Most specimens were encountered at night sleeping on the upper surface of leaves or on twigs, usually 0.5–2 m above ground. During daytime, specimens were spotted when fleeing on the ground, mostly seeking shelter between tree buttresses or bushes. The vegetation at the type locality (Figs. 2.2B) is a lush ridgetop cloud forest rich in palms and with abundant growth of epiphytes that cover virtually every surface. Descending either slope of Cerro Pando, the trees become higher and the canopy cover denser. A detailed description of the forest environments around Cerro Pando was given by Myers (1969). Presently, especially below 2000 m asl on either slope, major clearings for cattle farming disrupt the forest (Figs. 2.1E, F). In these pastures, *Norops benedikti* can be found associated with bushes, single trees, or remnants of cut trees. Annual total precipitation at the type locality is approximately 2600 mm and mean annual temperature approximately 13.6°C, indicating the Lower Montane Wet Forest life zone. Our datalogger recordings (N = 205) at the type locality yielded a temperature range of 11.1–16.7°C, with a mean of 12.7°C ± 1.1°C. Without exception, our collecting localities of *N. benedikti* lie above 1580 m on the Caribbean slope and above 1900 m on the Pacific slope and receive more than 2000 mm of annual precipitation, i.e., are assignable to the Lower Montane Wet Forest life zone. In the immediate surroundings of the type locality, *N. benedikti* was the only reptile species we could find.

Conservation. So far, *Norops benedikti* is almost exclusively documented in protected areas, i.e., the Protective Zone Las Tablas in Costa Rica, PILA in both Panama and Costa Rica, and BPPS as well as PNVB in Panama (the only exception is SMF 85268, collected 550 m east of the PNVB boundary). Theoretically, this renders the new taxon well protected. Nevertheless, nominal designation of an area as “protected” does not necessarily entail adequate protective measures, especially in the rugged mountains of the Cordillera Central. Drawing the minimum convex polygon around the locality records, Lotzkat et al. (2011) calculated the species' extent of occurrence as 225 km^2. Taking into account the collection locality of MHCH 434 (see remarks), I correct this value to 227 km^2. This rather small documented (and presumably rather small total) geographical range and the observation that fragmentation as well as overall reduction of its habitat, the Lower Montane Wet Forest, mostly due to cattle and subsistence farming, is currently ongoing and unlikely to halt in the near future, qualify the species for the IUCN category EN according to IUCN (2001) criterion B1b(iii). I calculated the EVS for *N. benedikti* as 4 (range) + 3 (persecution) + 4 (ecological distribution) = 11, indicating a medium vulnerability.

Remarks. Just as *Norops magnaphallus* and *N. pseudopachypus, N. benedikti* has long been concealed under the name *N. pachypus.* It is included under this name in the key of Köhler (2008), and also comes to mind when Savage (2002) stated that males of *N. pachypus* in the Costa Rican Cordillera de Talamanca "usually" bear a central yellow blotch. Moreover, we regard all *"N. pachypus"* collected on "N slope Cerro Pando" during the expedition carried out in 1966 by Linda Trueb, William Duellman, and Charles Myers (MCZ 100970–9, KU 113257-331) to represent individuals of *N. benedikti,* taking into account that we collected two-thirds of the type series while roughly following their footsteps down Cerro Pando's N slope. Additionaly, this view is supported by the ranges of *N. benedikti* and its allies documented by us, that is, we did not find a single *N. pachypus* on the Caribbean versant.

Norops benedikti seems to dwell predominantly on the Caribbean versant of the Serranía de Talamanca, where we found it from the continental divide at up to 2390 m asl (Cerro Pando) downwards. Descending the Caribbean slope, it has been collected down to 1640 m at Río Changena, 1740 m along the Culebra trail, and 1580 m along the Pianista trail (the specimen MHCH 434, herein additionally referred to *Norops benedikti,* was collected by AB and MP at the latter elevation, which is 60 m below the lower elevational limit given by Lotzkat et al. 2011).

However, in at least three regions, this species is also found on the Pacific versant, where it occurs next to its close relatives: At Las Tablas, in the Costa Rican Province of Puntarenas next to the Panamanian border, SMF 92134 was found at 1960 m, less than a kilometer from the nearest collected *N. pachypus* at 1880 m. Just a few kilometers east, in Jurutungo (Figs. 2.1E–H), we found *N. benedikti* as low as 2020 m at certain places, less than 50 m away from the nearest collection site of *N. pachypus*. Further east, on the slopes of Volcán Barú north of Boquete, about 1 km W of the ranger station of Alto Chiquero close to the upper Río Caldera, we collected four males of *N. benedikti* at 1920 m, as well as a single female farther south. These two sites are close to different collection sites (at both lower and higher elevations) as well as to the type locality of *N. magnaphallus.* At any rate, the biogeography of *Norops benedikti* requires further study, especially to identify possible contact zones with *N. pseudopachypus* and to determine the extent of its distribution in the Talamancan range of Costa Rica, i.e., to clarify if the *"N. pachypus"* without a central yellow blotch mentioned by Savage (2002) belong to this taxon, as we expect.

Norops biporcatus (Wiegmann 1834)

Neotropical Green Anole, Green Tree Anole; Anolis, Camaleón, Escorpión verde, Iguanita arbórea verde

Figures 4.58; 4.97H; Maps 4.11; 4.47.

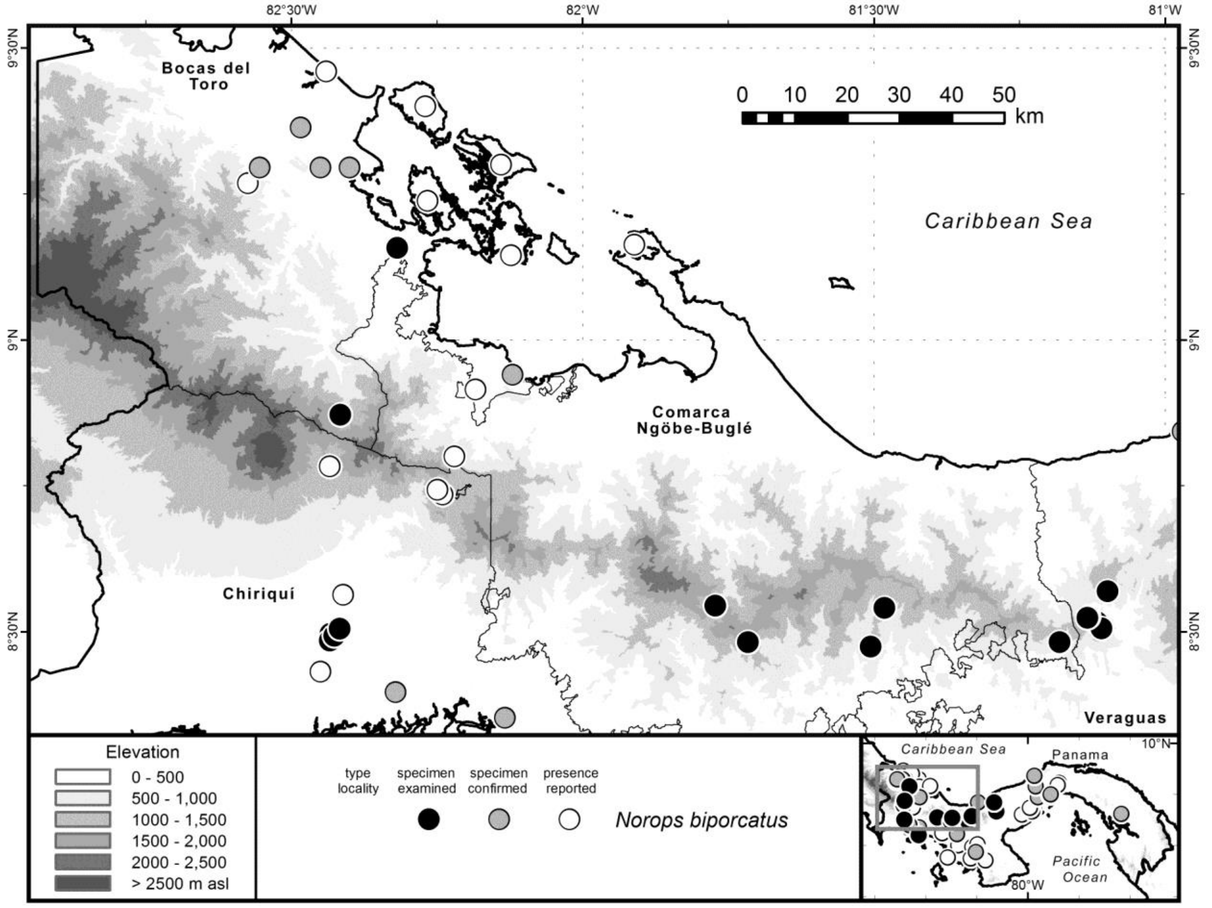
Anolis biporcatus: Taylor (1956); Myers & Rand (1969); Peters & Donoso-Barros (1970); Telford (1971); Rand & Myers (1990); Auth (1994); Martínez & Rodriguez (1994, 2005); Martínez et al. (1995); Ibáñez et al. (1995; 1996; 2001); Young et al. (1999); ANAM (2004, 2009b); Poe (2004); Rodriguez et al. (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Batista & Ponce (2011); Lotzkat & Hertz (2011); Uetz & Hošek (2014).

Anolis copei: Wettstein (1934); Slevin (1942).

Anolis copii: Dunn (1933).

Anolis obtusirostris: Peters (1874).

Holotype. Neotype MNHN 2426, from Santa Rosa de Pansos, Alta Verapaz, Guatemala (Köhler & Vesely 2003).



Map 4.47: Distribution of *Norops biporcatus*.

Geographic distribution. Mexico to western Ecuador, Colombia, and Venezuela, 0–2000 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, documented from numerous localities up to 1240 m asl.

Diagnosis. A large *Norops* (maximum SVL 102 mm) with short legs (tip of 4th usually reaching to ear) that is most similar to species of *Dactyloa,* from which it differs by its strongly keeled ventrals and at most moderate male dewlap (vs. ventrals smooth or very faintly keeled and dewlap large to very large in males). It can readily be distinguished from all other Panamanian *Norops* by its size and coloration.

Description. TOL to 330 mm; SVL to 102 mm; tail long, TL/SVL 1.91–2.33*; legs short (tip of 4th toe of adpressed hind limb reaching to between shoulder and eye, usually to ear); D granular, keeled; V and caudals imbricate, strongly keeled; Drows 2, slightly enlarged; SAM 102–118*; males without enlarged PC, but can raise a low nuchal crest; lamellar pads very broad; 4toe 35–47; 4finger 29–34*; IO 1–3; IP/SS 2–5*; SBO/SPL 0–1; loreals keeled, 38–67* in 5–7* rows; male dewlap small to moderate, female dewlap small.

The hemipenis of *Norops biporcatus* is a large, stout, bilobed organ with short lobes; asulcate processus present; truncus with transverse folds; lobes stout, calyculate (Köhler & Vesely 2003).

Coloration in life. D and L ground color green, usually with darker mottling, reticula, or transverse bars; a yellow ring around each eye; V surfaces white to light gray, often mottled with brown. In the course of metachrosis, all green may give way to brown and the whole animal become much darker. Male dewlap usually with a white base, blue center, and orange to red margin; female dewlap white with dark mottling.

The adult male SMF 89445 was recorded by LS in two stages of metachrosis (Stadler 2010: Figs. A63; A64) as follows (translated from Stadler 2010): D and L surfaces Yellow-Green (58) with faint dirty white spots and Parrot Green (60) blotches forming transverse bands; V surfaces of body, head, tail, and limbs dirty white, those of hands and feet Light Drab (119C); eyes encircled by Sulfur Yellow (157); iris Carmine (8); dewlap Flaxflower Blue (170C) at basally and centrally, grading into Orange Yellow (18) towards posterior and Flame Scarlet (15) towards anterior portion of the margin, and dirty white scales. During the color description, the individual changed to a darker appearence which differs in the following: D surfaces Raw Umber (123) with conspicuous Sepia (219) mottling and some Raw Umber (23) and Yellow-Green (58) blotches; V surfaces dirty white with strong Raw Umber (23) shadings.

Coloration in preservative. After 4–6 years in 70% ethanol, the patterns of blotches, bands, etc. are well-preserved in my examined specimens, but the greenish tonalities have given way to brown and/or bluish gray; some male dewlaps retain suggestions of rusty red along margin.

Natural history notes. Diurnal and arboreal. Animals were encountered in forests and along forest edges, but also in rather open secondary vegetation along cattle pasture and in rural settlements. Most individuals were spotted while sleeping on vegetation 0.5–5 m above ground. The individuals SMF 91448 (male) and MHCH 2113 (female), found sleeping in the same bush at about 0.5 m from each other and placed in the same bag for transport, had severly bitten and wounded each other by the next morning. The juvenile male SMF 91449 squealed when caught.

Remarks. The specimen SMF 89669 from Buabidí at 1241 m asl now constitutes the highest record for Panama (Jaramillo et al. 2010). As detailed in chapter 4.1.7.1, my material of *Norops biporcatus* comprises two deeply divergent mitochondrial lineages, UGL 1 from the Serranía de Tabasará and UGL 2 of unknown geographic origin (presumably Los Algarrobos in lowland Chiriquí), which are separated by uncorrected p-distances of 12.4% in the COI barcode. For reasons visible in Figs. 4.58G–J, the statement "female dewlap absent" of Köhler & Vesely (2003) is clearly erroneous.

Some indigenous Ngöbe people in Santa Clara state that burns, bruises, and abrasions can be relieved or cured by rubbing them with a living *Norops biporcatus*.

Norops capito (Peters 1863)

Bighead Anole, Pug-nosed Anole; Anolis cabezón

Figures 4.59; 4.98A; Maps 4.11; 4.48.

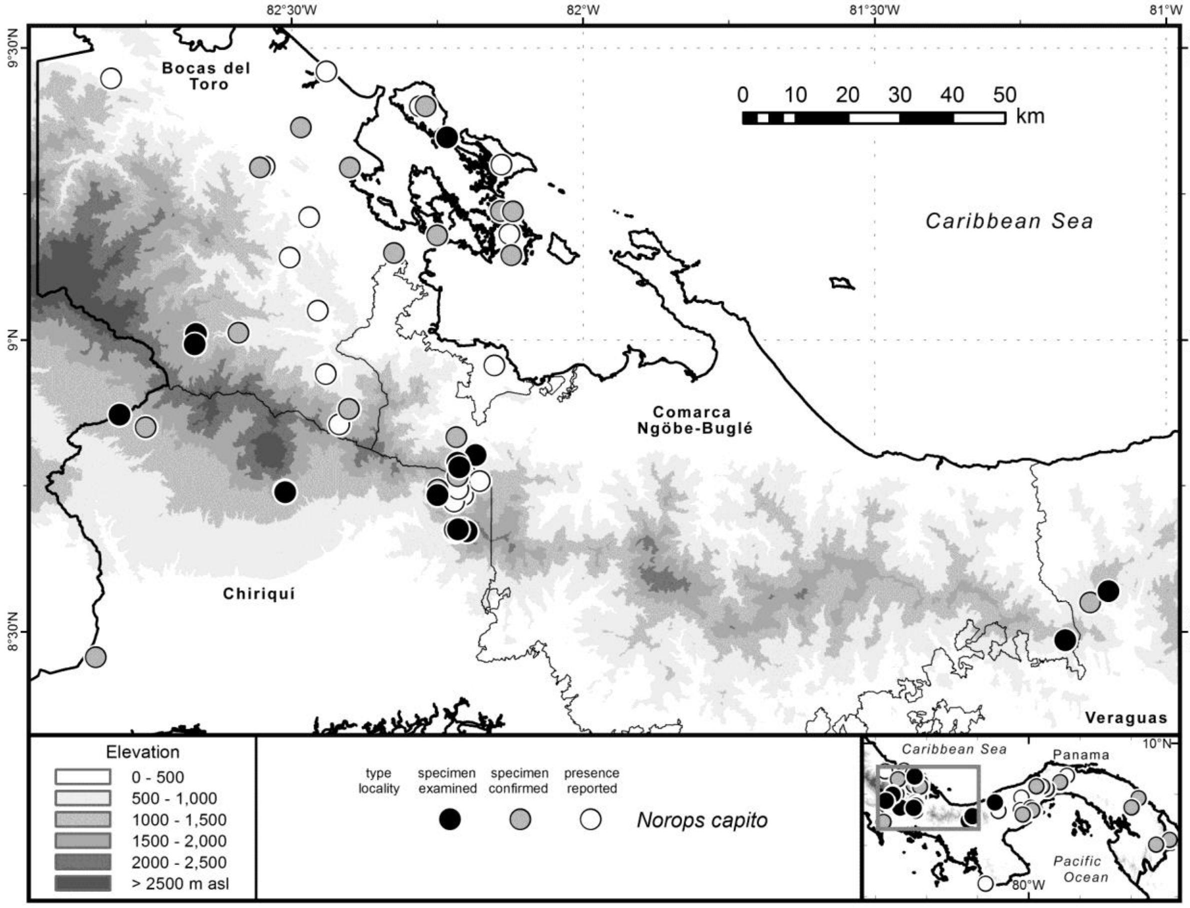
Anolis capito: Peters (1863a); Breder (1946); Taylor (1956); Myers & Rand (1969); Peters & Donoso-Barros (1970); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995; 1996; 2001); Young et al. (1999); Carrizo (2000, 2010); ANAM (2004, 2005a); Poe (2004); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Sunyer (2009); Jaramillo et al. (2010); Lotzkat et al. (2010c); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Anolis longipes: Cope (1893).

Holotype. ZMB 4086, from "Costa Rica" (Peters 1863a; restricted to Palmar according to Taylor 1956).

Geographic distribution. Mexico to Panama and probably adjacent Colombia, 0–1640 m asl. In Panama, throughout the country at low and premontane elevations, including Bocas del

Toro, Chiriquí, Comarca Ngöbe, and Veraguas. In the Cordillera Central, numerous records from both versants up to 1640 m asl.



Map 4.48: Distribution of *Norops capito*.

Diagnosis. A large *Norops* (maximum SVL 96 mm) with very long legs (4th toe reaching to snout or beyond) that is readily identified by its very short and stout head, its large, flat, smooth dorsal scales, and its small yellow dewlap in both sexes.

Description. TOL to 272 mm; SVL to 96 mm; tail short to moderately long, TL/SVL 1.3–1.98*; legs very long (tip of 4th toe of adpressed hind limb reaching at least to nostril, usually beyond snout); D flat, smooth; V and caudals imbricate, strongly keeled; Drows 0; SAM 83–116*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 30–41; 4finger 23–32*; IO 1–3; IP/SS 2–4*; SBO/SPL 0–1; loreals smooth to keeled, 27–61* in 3–6* rows; male and female dewlap small.

The hemipenis of *Norops capito* is a large, stout, bilobed organ with long lobes; asulcate processus present; truncus with few transverse folds; lobes calyculate (Köhler et al. 2005).

Coloration in life. D and L surfaces light to dark brown, with diverse markings (spots, blotches, bars, chevrons, ...) in varying shades of brown, green, yellow, or blue; V surfaces tan, mottled with darker brown. Most specimens with a dark interorbital bar continuing laterally through the eye to corner of mouth; light chin coloration bordered posteriorly by a dark transverse bar followed by a light transverse bar; male and female dewlap yellow to yellowish brown. In the course of metachrosis, all markings can disappear and cause the whole animal to appear solid blackish brown.

A female specimen from the surroundings of the Lost & Found Ecohostel at RFLF was recorded by NH as follows (translated from Hamad 2009): D and L ground color Buff (124); dorsum, snout, and base of tail with broad transverse Dark Brownish Olive (129) bands bordered by fine black lines; a Dark Brownish Olive (129) interorbital bar with a suggestion of black; chin dirty white, just as the thin ring running around the head behind the orbit; V ground color with black mottling; posterior portion of tail Dark Brownish Olive (129); dewlap Dark Brownish Olive (129).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that yellow, blue, and green tonalities have usually faded completely; dewlaps gray.

Natural history notes. Diurnal and arboreal. Individuals were encountered sleeping on vegetation up to 3.5 m above ground, or active on the ground as well as on trunks about 2 m above ground.

Remarks. The female SMF 91452 from between Río Clarito and Río Changena (WP 279, 1641 m asl) raises the upper elevational limit for this species previously given as 1400 or 1405 m (Sunyer 2009; Sasa et al. 2010; Wilson & Johnson 2010). As detailed in chapter 4.1.7.1, my material of *Norops capito* comprises two deeply divergent mitochondrial lineages, UGL 1 from the Carribean versant of the Serranía de Talamanca and the Pacific versant of the Serranía de Tabasará and UGL 2 from Potrerillos on the slopes of Volcán Barú, which are separated by individual uncorrected p-distances of 11.7–13.3% in the COI barcode.

***Norops carpenteri* (Echelle, Echelle & Fitch 1971)**

Carpenter's Anole; Anolis de Carpenter

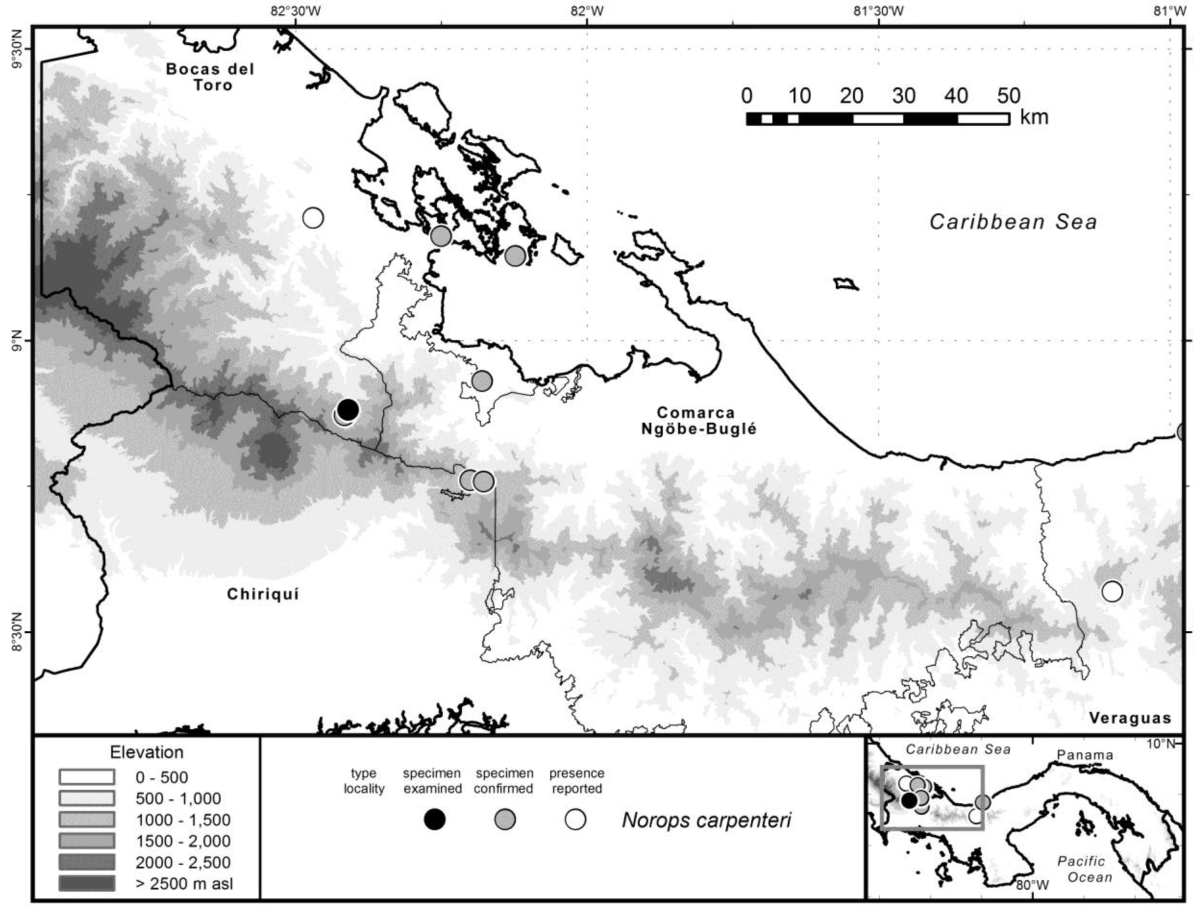
Figure 4.98B; Map 4.49.

Anolis carpenteri: Fitch et al. (1976); Arosemena & de Sousa (1989); Rand & Myers (1990); Auth (1994); Young et al. (1999); Carrizo (2000, 2010); Ibáñez et al. (2001); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Ponce & Köhler (2008); Fläschendräger & Wijffels (2009); Poe et al. (2009); Sunyer (2009); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Anolis procellaris: Myers (1971a); Auth (1994); Carrizo (2000; 2010).

Holotype. KU 132506, male, from "east bank of Río Reventazon, 500+ m elev., 7 km ESE Turrialba, where highway crosses the river, Cartago, Costa Rica" (Echelle et al. 1971).

Geographic distribution. Honduras to Panama, 0–1570 m asl. In Panama, known only from the western provinces, i.e., Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from Sendero Culebra as well as from the Fortuna and Santa Fé areas, up to 1050 m asl.



Map 4.49: Distribution of *Norops carpenteri.*

Diagnosis. A small *Norops* (maximum SVL 45 mm) with short legs (4th toe reaching to ear or slightly beyond) that is readily identified by its slender habitus, greenish overall coloration, and large orange dewlap in males. It can further be distinguished from the superficially similar *N. gruuo* by its smooth dorsal granules (vs. keeled), the lack of distinctly enlarged postcloacals in males (vs. conspicuously enlarged PC present), and its extremely fine, dark dorsal punctations and reticulations that are retained preservative (vs. no such markings).

Description. TOL to 118 mm; SVL to 45 mm; tail moderately long, TL/SVL 1.79–1.86*; legs short (tip of 4th toe of adpressed hind limb reaching to ear or at most slightly beyond); D granular, smooth; V imbricate, smooth; caudals keeled; Drows 0 or 2 very slightly enlarged; SAM 128–148*; males without enlarged PC or nuchal crest; lamellar pads broad; 4toe 29–34;

4finger 20–22*; IO 2–3; IP/SS 3–4*; SBO/SPL 0; loreals keeled, 44–64* in 5–6* rows; male dewlap moderate to large, female dewlap very small.

The hemipenis of *Norops carpenteri* is a small, bilobed organ.

Coloration in life. D and L surfaces green with yellow or brown hues, with minute darker spotting or and/or reticulations whose aggregation can give the appearance of mottling and middorsal blotches; V surfaces white to light gray, often with somewhat darker reticulations entering from the flanks; male dewlap orange, female dewlap orange or white.

Coloration in preservative. This species can be perfectly diagnosed by its coloration in preservative (GK, pers. comm.; verified on Panamanian material): all D and L surfaces turn yellow, leaving the fine dark spots and reticulations very conspicuous; male dewlaps whitish.

Natural history notes. Diurnal, usually occurring at low densities.

Remarks. Most recent authors (e.g., Savage 2002; Köhler 2008) have followed Fitch et al. (1976) in considering *Norops procellaris* (Myers 1971a; type locality in Veraguas, Map 1.13: loc. 21) a junior synonym of *Norops carpenteri,* a concept which I adopt herein. When stating their specimens from RFLF to constitute the first country record for *N. carpenteri,* Arosemena & de Sousa (1989) apparently were unaware of this synonymization. The presence of this species in Honduras has recently been revealed by McCranie & Köhler (2012). The upper elevational limit in Panama of 150 m asl as given by Jaramillo et al. (2010) is clearly erroneous, since already the allegedly first country record was from the Fortuna dam site at approximately 1030–1040 m (Arosemena & de Sousa 1989).

Norops charlesmyersi (Köhler 2010)

Lichen Anole, Charles Myers' Anole; Anolis de Charles Myers

Figures 4.52; 4.56; 4.98C; Maps 4.10; 4.50.

Anolis charlesmyersi: Köhler (2010), Lotzkat & Hertz (2011); Batista & Ponce (2011); Bienentreu et al. (2013).

Anolis pentaprion: Wettstein (1934); Taylor (1956: in part.); Peters & Donoso-Barros (1970: in part.); Myers (1971b: in part.); Auth (1994: in part.); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.); Fläschendräger & Wijffels (2009: in part.); Jaramillo et al. (2010: in part.); Sasa et al. (2010: in part.); Wilson & Johnson (2010: in part.); Uetz & Hošek (2014: photos).

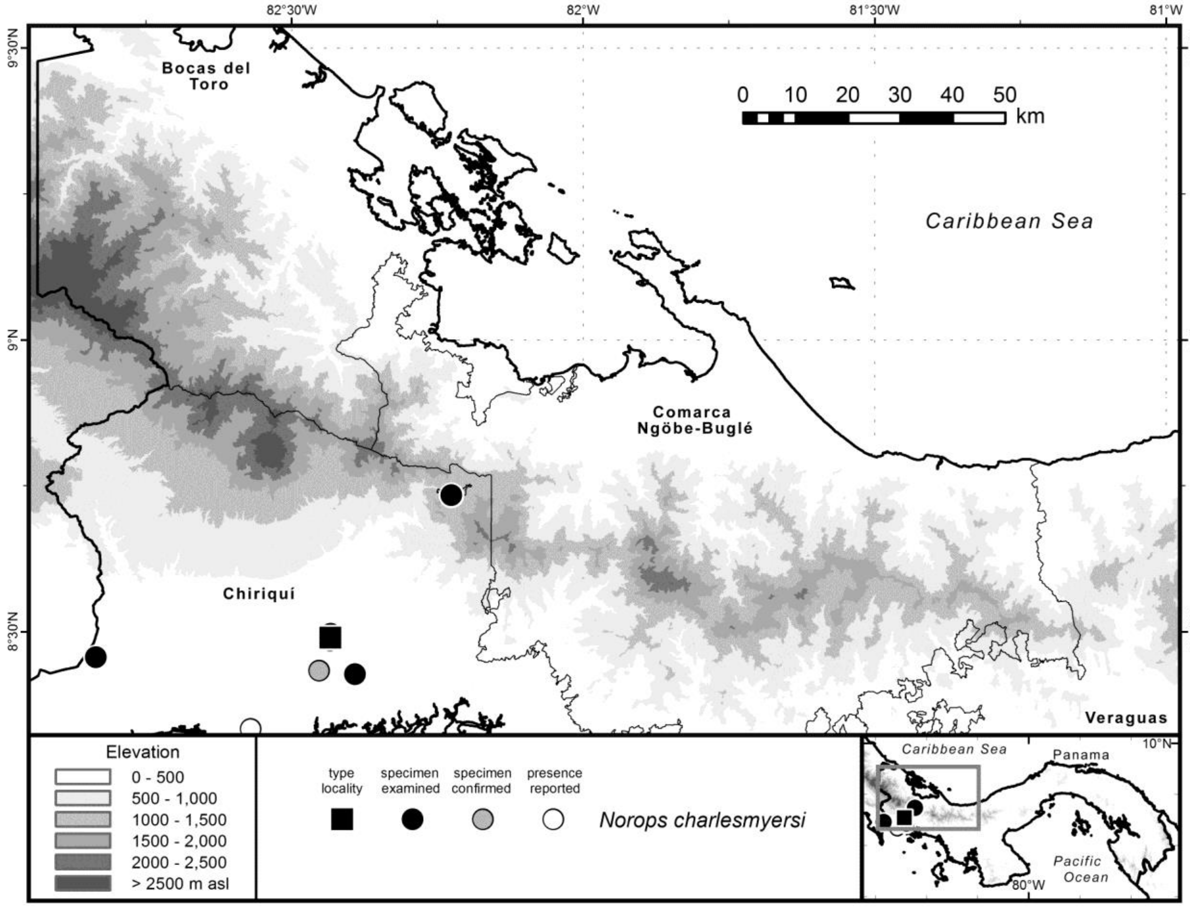
Norops pentaprion: Savage (2002: in part.); McDiarmid & Savage (2005); Köhler (2008: in part.); Savage & Bolaños (2009: in part.).

Anolis vociferans: Arosemena et al. (1992).

Norops vociferans: de Sousa (1999).

Holotype. SMF 89688, male, from "trail to Río Majagua, Los Algarrobos, 8.48927°N, 82.43333°W, ca. 130 m a.s.l., Province Chiriquí, Panama" (Köhler 2010).

Geographic distribution. Pacific versant of Costa Rica and western Panama, 0–1050 m asl. In Panama, reported from Chiriquí and most probably present in the Comarca Ngöbe-Buglé. In the Cordillera Central, one record from RFLF around 1050 m asl (see remarks).



Map 4.50: Distribution of *Norops charlesmyersi*.

Diagnosis. A medium-sized to large *Norops* (maximum SVL 78 mm) with very short legs (4th toe reaching at most to ear) that is most similar in external morphology to *N. pentaprion, N. fungosus,* and *N. salvini.* It can readily be distinguished from these species as well as from the superficially similar *N. datzorum* by its dewlap, which bears few rows of widely spaced, large scales in both sexes (vs. small scales densely arranged in many rows, see Figs. 4.52–4.57). It further differs from the latter three species in lacking enlarged postcloacal scales in males (vs. present) and in having a conspicuous serrated dorsal tail crest (vs. at most strongly keeled middorsal caudal scales).

Description. TOL to 158 mm*; SVL to 78 mm; tail very short, TL/SVL < 1.44; legs very short (tip of 4th toe of adpressed hind limb reaching at most to ear); D and V smooth; caudals keeled, conspicuous serrated D tail crest present; Drows 2 slightly enlarged; SAM 136–200;

males without enlarged PC, but can raise a low nuchal crest; lamellar pads broad; 4toe 33–41*; 4finger 26–30*; IO 0–2; IP/SS 0–3; SBO/SPL 0; loreals slightly keeled, 18–50 in 3–6 rows; male dewlap large to very large, female dewlap moderate (own data combined with that of Köhler 2010).

The hemipenis of *Norops charlesmyersi* is a large bilobed organ; small asulcate processus present; apex finely calyculate; truncus with transverse folds (Köhler 2010).

Coloration in life. Ground color almost white to dark brown, with lighter blotches; dark crossbands on tail and limbs; a short, dark pre- and postocular stripe; gular region and corners of mouth light blue, lining of throat black; dewlap red with darker red blotches and white scales in both sexes.

The male holotype SMF 89688 was recorded in the dark phase (Fig. 4.56B) as follows: D and L surfaces Dark Drab (119B), with diffuse spots and blotches of Vandyke Brown (221) and rather circular dirty white with a suggestion of Pearl Gray (81) blotches; a dirty white with a suggestion of Pearl Gray (81) middorsal stripe interrupted by Sepia (119) blotches; a diffuse dirty white with a suggestion of Pearl Gray (81) L stripe extending from shoulder to groin; tail except for its base Beige (219D) with broad Brussels Brown (121B) transverse bands and fine Sepia (119) mottling; a diffuse Vandyke Brown (221) pre- and postorbital stripe extending about 0.5 cm each anteriorly and posteriorly of orbit; V surfaces of body, limbs, and base of tail dirty white with a suggestion of Pearl Gray (81), with reticulate Dark Drab (119B) mottling; chin and gular region Flaxflower Blue (170C) with a suggestion of Light Sky Blue (168D), with reticulate Hair Brown (119A) mottling; iris Cinnamon (123A); throat Blackish Neutral Gray (82); tongue Cream Color (54); dewlap Poppy Red (108A) with circular Crimson (108) blotches between gorgetal rows; dewlap scales dirty white with a suggestion of, some surrounded by areas of, Lavender Blue (170D). The male paratype SMF 89508 was recorded as follows: D and L surfaces of body, limbs and anterior half of tail Smoke Gray (45) suffused with Cinnamon-Drab (219C), sparse Sepia (219) mottling and scattered flecks of dirty white with a suggestion of Pearl Gray (81); posterior half of tail Drab-Gray (119D) with broad transverse rings of Raw Sienna (136); V surfaces of body, limbs, and anterior half of tail dirty white with a suggestion of Opaline Green (162D); D and L surfaces of head Drab-Gray (119D) with Sepia (219) mottling on supraorbital semicircles, snout, and parietal region; V surface of head Light Sky Blue (168D) with Hair Brown (119A) spots on anteror half; dewlap Spectrum Red (11) with Carmine (8) blotches and dirty white scales.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that the bluish hues have faded and the red dewlap coloration has become less intense. However, the dewlap still retains some red after 6 years.

Natural history notes. Diurnal and arboreal, uses its prehensile tail for climbing. All individuals were spotted sleeping on vegetation at night, usually under horizontal branches or head down on more inclined perches. Around the type locality near Los Algarrobos, Chiriquí, I found the observability of this species to vary greatly: While several individuals were spotted during certain periods (e.g., 3 males in the night of 07.06.2008), at other times weeks could pass without a single individual being seen.

Remarks. The presence of *Norops charlesmyersi* in my study area is based on the specimen MVUP 799 from "Loma del silencio, prov. Chiriquí", catalogued as *Anolis vociferus* (sic), which I have examined and found to actually represent *N. charlesmyersi*. Although the MVUP does not explicitly state the locality to be situated in the La Fortuna area, in view of the associated data for collection date and collector I regard as evident that this is the specimen underlying the listing of *A. vociferans* for the locality "Loma del Silencio" in the herpetofaunistic inventory of RFLF by de Sousa (1999). Unfortunately, neither de Sousa (1999) nor the MVUP catalogue give any further specification for this locality, which I could not trace on maps. Since it has possibly been flooded by the expansion of the Fortuna reservoir, I used generalized coordinates for RFLF near the center of the lake as a georeference, for which the SRTM elevation is 1051 m asl. This record constitutes the highest elevation known for this species, as well as the easternmost georeferenced locality.

In the lowlands of Chiriquí, the easternmost records with good locality data are the specimens MVUP 306A and 306B from Las Lomas, slightly east of Davíd. The specimens with POE field numbers 1449–51, examined by Köhler (2010), doubtlessly were collected further east than Las Lomas, but the associated locality information "Chiriquí or Veraguas: E of David (along PanAm[erican highway]; 20–100 km E of David)" precludes a point georeference appearing on my map. Yet, it can be said that these specimens were most probably not collected in Veraguas province, which is not reached after travelling 100 km along the Carretera Interamericana from Davíd. However, in combination with the specimen from RFLF, they render the occurrence of *N. charlesmyersi* in the Comarca Ngöbe-Buglé plausible. If *N. charlesmyersi* really is present in Veraguas (which I herein regard as possible), it is most likely restricted to that province's westernmost portion, considering the westernmost records of its sister species, *N. pentaprion.*

Norops cryptolimifrons **(Köhler & Sunyer 2008)**

Slender Anole; Anolis, Moracho delgado

Figures 4.71; 4.72; 4.98D; Maps 4.15; 4.51.

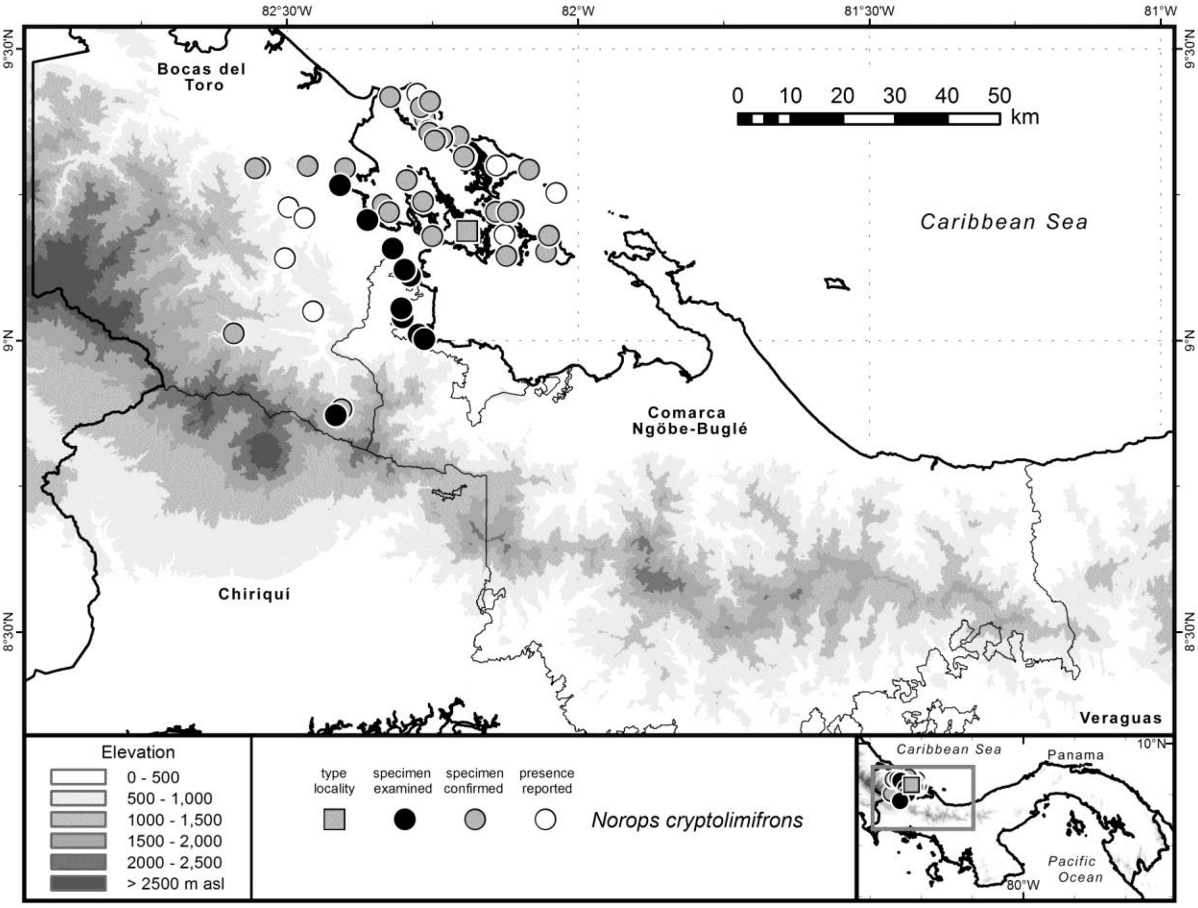
Anolis cryptolimifrons: Köhler & Sunyer (2008); Fläschendräger & Wijffels (2009); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Anolis limifrons: Auth (1994: in part.); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.).

Norops limifrons: Savage (2002: in part.).

Holotype. SMF 85230, male, from Cerro Brujo (9°11'16.4"N, 82°11'25.4"W), 10 m, Bocas del Toro, Panama.

Geographic distribution. Caribbean versant of western Panama and extreme eastern Costa Rica, 0–1005 m asl. In Panama, throughout the Archipiélago de Bocas del Toro and on the southwesterly adjacent mainland in Bocas del Toro and Comarca Ngöbe-Buglé. In the Cordillera Central, reported from the upper Río Changuinola drainage up to 1005 m asl.



Map 4.51: Distribution of *Norops cryptolimifrons*.

Diagnosis. A small *Norops* (maximum SVL 45 mm) with long legs (4th toe reaching to eye or beyond) that is most similar to *N. limifrons* and *N. apletophallus.* It differs from *N. apletophallus* by its white male dewlap with a yellow blotch at the central base (vs. orange-yellow), and from *N. limifrons* in having a large, bilobed hemipenis that bulges the base of tail in adult males (vs. small, unilobed, leaving base of tail slender).

Description. TOL to 122 mm* (probably to above 150 mm); SVL to 45 mm; tail long, TL/SVL 2.1–2.3*; legs long (tip of 4th toe of adpressed hind limb reaching to eye or usually beyond); D granular, keeled; V smooth; caudals keeled; Drows 0–2 slightly enlarged; SAM 122–152*; males with enlarged PC, without nuchal crest; lamellar pads moderately broad; 4toe 29–33*; 4finger 19–22*; IO 1–4; IP/SS 2–5; SBO/SPL 0; loreals slightly keeled, 36–69 in 6–8 rows; male dewlap moderate to large, female dewlap very small to small (data of examined specimens from Sendero Pianista combined with that of Köhler & Sunyer 2008).

The hemipenis of *Norops cryptolimifrons* is a medium-sized, bilobed organ; lobes short and stout; apex and asulcate side of truncus calyculate (Köhler & Sunyer 2008).

Coloration in life. D and L surfaces very light to dark brown, almost unicolor or speckled with lighter and/or darker pigment, in some individuals with a L stripe; females often with a dark middorsal series of blotches or continuous stripe, or a broad, light middorsal band bordered by narrow dark stripes; supralabials white to light gray; V surfaces dirty white or yellowish to light gray or brown; tail usually with dark crossbands; male dewlap white with a yellow blotch at the central base, female dewlap white, a yellow blotch usually present in gular area next to the rudimentary dewlap.

Coloration in preservative. After 5 years in 70% ethanol, the coloration is similar to that in life, apart from that the yellow elements have faded.

Natural history notes. Just as the other members of the *Norops limifrons* complex, this species can be extremely abundant at certain sites. Along the road to Almirante, we found countless individuals in open and semiopen secondary roadside vegetation, either active during daytime or sleeping on branches and leaves at night.

Conservation. Jaramillo et al. (2010) calculated an EVS of 12 for *Norops cryptolimifrons,* and assigned that species to the IUCN category DD. Since the species is neither a Talamancan small-scale nor a Panamanian endemic, I refrained from an own assessment of its conservation status, though current knowledge of its range would easily permit the calculation of its extent of occurrence and placement in an IUCN category other than DD. However, although the known range of *N. cryptolimifrons* (which probably corresponds quite well to the real range) is comparably small, this species does not appear to be too threatened by human interventions given its high abundance in secondary vegetation and disturbed environments.

Remarks. Casa de Ancón at Sendero Pianista, around the headwaters of Río Changuinola, is the southernmost and highest locality reported for this species so far. The specimens collected there by AB and MP extend the known distribution of *Norops cryptolimifrons* about 40 km S from the nearest lowland locality reported by Köhler & Sunyer (2008), and increase the upper elevational limit from 250 m asl reported for Panama by Jaramillo et al. (2010) to 1005 m in

Panama and for the species as a whole. The specimens FMNH 130975–76 from Río Changena at about 730 m, examined by GK, represent a second premontane locality in the Río Changuinola drainage for this species in Panama. In view of these localities, I assigned all "*N. limifrons*" from the upper Río Changuinola drainage housed at CHP to *N. cryptolimifrons*. The single known specimen from Costa Rica, UCR 8477 from SE side Cerro Nimaso (Köhler & Sunyer 2008), is from an unknown but presumably likewise premontane elevation several drainages further west.

As shown in chapter 4.1.7.4, hybridization between *Norops cryptolimifrons* and the respective UGLs of *N. limifrons* occurs both at the eastern and western distributional boundaries of the former species, where males with bilobed hemipenes have mitochondrial haplotypes of the respective neighboring *N. limifrons* lineage.

***Norops datzorum* (Köhler, Ponce, Sunyer & Batista 2007)**

Erika and Walter Datz' Anole; Anolis de Erika y Walter Datz

Figures 4.52; 4.53; 4.98E; Maps 4.10; 4.52.

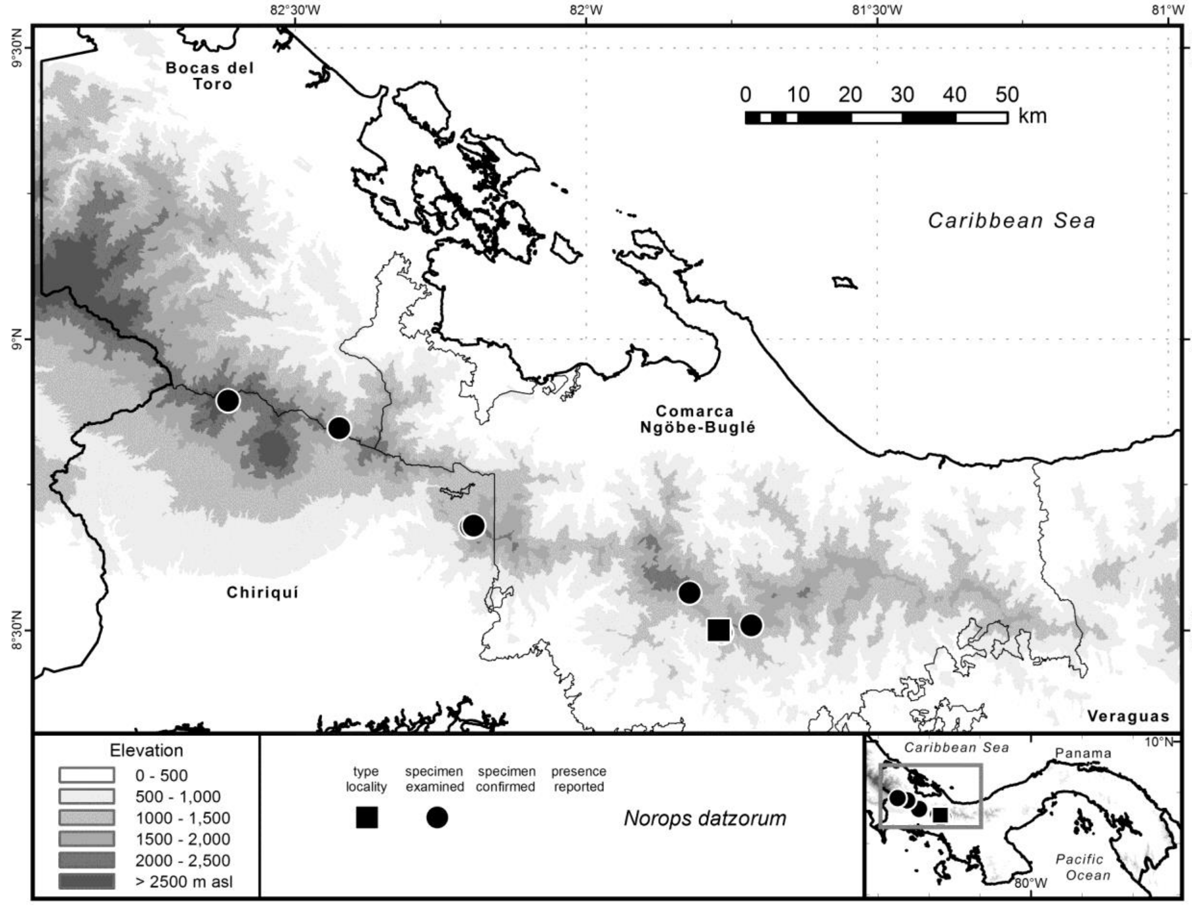
Anolis datzorum: Köhler et al. (2007), Jaramillo et al. (2010); Köhler & Vargas (2010); Lotzkat et al. (2010a); Wilson & Johnson (2010); Stadler (2010).

Holotype. SMF 85093, female, from La Nevera, 8°29'45"N, 81°46'35"W, 1600 m elevation, Serrania de Tabasara, Comarca Ngöbe Bugle, Distrito de Nole Düima, Corregimiento de Jadeberi, Panama (coordinates corrected to 8°30'N, 81°46'20"W by Lotzkat et al. 2010a).

Geographic distribution. Endemic to the Talamancan Highlands of Panama and Costa Rica, 1590–2400 m asl. In Panama, recorded along the Cordillera Central of Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé, east to Cerro Santiago, 1590–2400 m asl.

Diagnosis. A medium-sized *Norops* (maximum SVL 52 mm) with very short legs (4th toe reaching to ear or at most slightly beyond) that might at first glance be confused with the superficially similar *N. salvini, N. fungosus, N. charlesmyersi,* and *N. pentaprion.* It can readily be distinguished from these species by its dewlap, which is yellow in males and white, yellow, or orange in females (vs. red in both sexes, except for blue or purple in female *N. salvini* and yellow in female *N. fungosus*) and by its dorsal head scales, which are all markedly multicarinate (vs. smooth, rugose, or at most unicarinate). It further differs from the latter two species in having enlarged postcloacal scales in males (vs. absent) and from all except *N. salvini* in lacking a conspicuous serrated tail crest (vs. present).

Description. TOL to 133 mm; SVL to 52 mm; tail short to moderately long, TL/SVL 1.53–1.83; legs short (tip of 4th toe of adpressed hind limb usually reaching to between shoulder and ear; sometimes to a point between ear and eye); D granular, keeled; V keeled; caudals keeled; Drows 0–6 slightly enlarged; SAM 106–160; males with slightly to conspicuously enlarged PC; males can raise a low nuchal crest; lamellar pads moderately broad; 4toe 33–38*; 4finger 23–27*; IO 0–2; IP/SS 1–3; SBO/SPL 0; loreals keeled, 28–53 in 4–7 rows; male dewlap large, female dewlap small to moderate (data from all known Panamanian specimens, including that of Köhler et al. 2007).



Map 4.52: Distribution of *Norops datzorum*.

The bilobed hemipenis of *Norops datzorum* was described by JJK as follows (from Lotzkat et al. 2010a): "The hemipenes are about 5 mm long and relatively stout. The lobes are short and hemispherical. The sulcus spermaticus emerges from the cloaca caudally between the two organs and circles around the base of the truncus to the sulcal side, where it changes direction and runs towards the apex. It is bordered by well developed fleshy lips. On the base of the apical region the sulcus spermaticus opens into an unornamented sulcal field that stretches over the sulcal sides of both lobes. The asulcal surface of the lobes is covered with fine calyces that become coarser towards the center and the base of the lobes and gradually turn into folds. At the base of the apical region on the asulcal side between the lobes, a prominent asulcal processus is developed. The asulcal side of the truncus is covered with an ornamentation of transversal folds."

Coloration in life. The coloration of *Norops datzorum* is very variable and can be subject to drastic metachrosis. D and L surfaces light gray, greenish, or light to reddish or dark brown, usually densely mottled or blotched, or marked with chevrons or a middorsal stripe; V surfaces whitish, cream or yellowish, usually mottled with darker pigment; lining of throat not black, but bluish tissue in corners of mouth; male dewlap orange yellow, female dewlap white, yellow, or orange.

The subadult male SMF 89460 was recorded as follows (Lotzkat et al. 2010a): D ground color Sepia (219), grading into Drab-Gray (119D) laterally; D and L surfaces mottled with Sepia (119) and Raw Umber (123), showing shadings of Verona Brown (223B) and Bunting Green (150); body with a series of Verona Brown (223B) dorsolateral blotches bordered by Sepia (119) and connected by middorsal chevrons; center of snout Bunting Green (150) with Sepia (119) longitudinal lines; a Verona Brown (223B) interorbital stripe and two postorbital stripes of the same color bordered by Sepia (119); L surface of head dirty white with a suggestion of Yellow-Green (58); V ground color Cream Color (54) with a suggestion of Pistachio (161) at midventer and fine Cinnamon (123A) mottling; iris Cinnamon (123A); dewlap Orange Yellow (18); sternals and posterior marginals dirty white with a suggestion of Pistachio (161), grading into Cream Color (54) towards the gorgetals and anterior marginals; some gorgetals and sternals with Light Neutral Gray (85) centers.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that some specimens exhibit bluish gray and/or bronze metallic hues; dewlaps whitish.

Natural history notes. Diurnal and arboreal. Köhler & Vargas (2010) found remnants of Hymenoptera, Diptera, and Pseudoscorpiones in a fecal pellet of SMF 90325. Usually, only singular individuals of *Norops datzorum* are found, rather sporadically, probably not in the least owing to the effective camouflage provided by its color pattern. However, I encountered 5 of the 12 individuals which I have seen in life (including SMF 90100–1) on 11.11.2009 within less than 90 min while they were sleeping 1.5–5 m above ground in ridgetop cloud forest near the type locality.

Remarks. Lotzkat et al. (2010a; original publication in Appendix 8) provided a thorough morphological description of the first two male specimens collected at the type locality, complemented with notes on natural history and relationships, as well as the correct coordinates of the type locality. Köhler & Vargas (2010) extended the species' distribution to extreme E Costa Rica based on SMF 90325 from Las Tablas, next to the Panamanian border.

As detailed in chapter 4.1.6, my material of *Norops datzorum* comprises two divergent mitochondrial lineages, DCL 1 from the Cerro Pata de Macho massif at RFLF and DCL 2 from around Cerro Santiago, which are separated by individual uncorrected p-distances of 4.6–4.8% in the COI barcode. I expect the populations from further west along the Serranía de Talamanca to represent similarly divergent DCLs.

Norops fortunensis **(Arosemena & Ibáñez 1993)**

La Fortuna Anole; Anolis de La Fortuna

Figures 4.44A; 4.45; 4.46; Maps 4.9; 4.53.

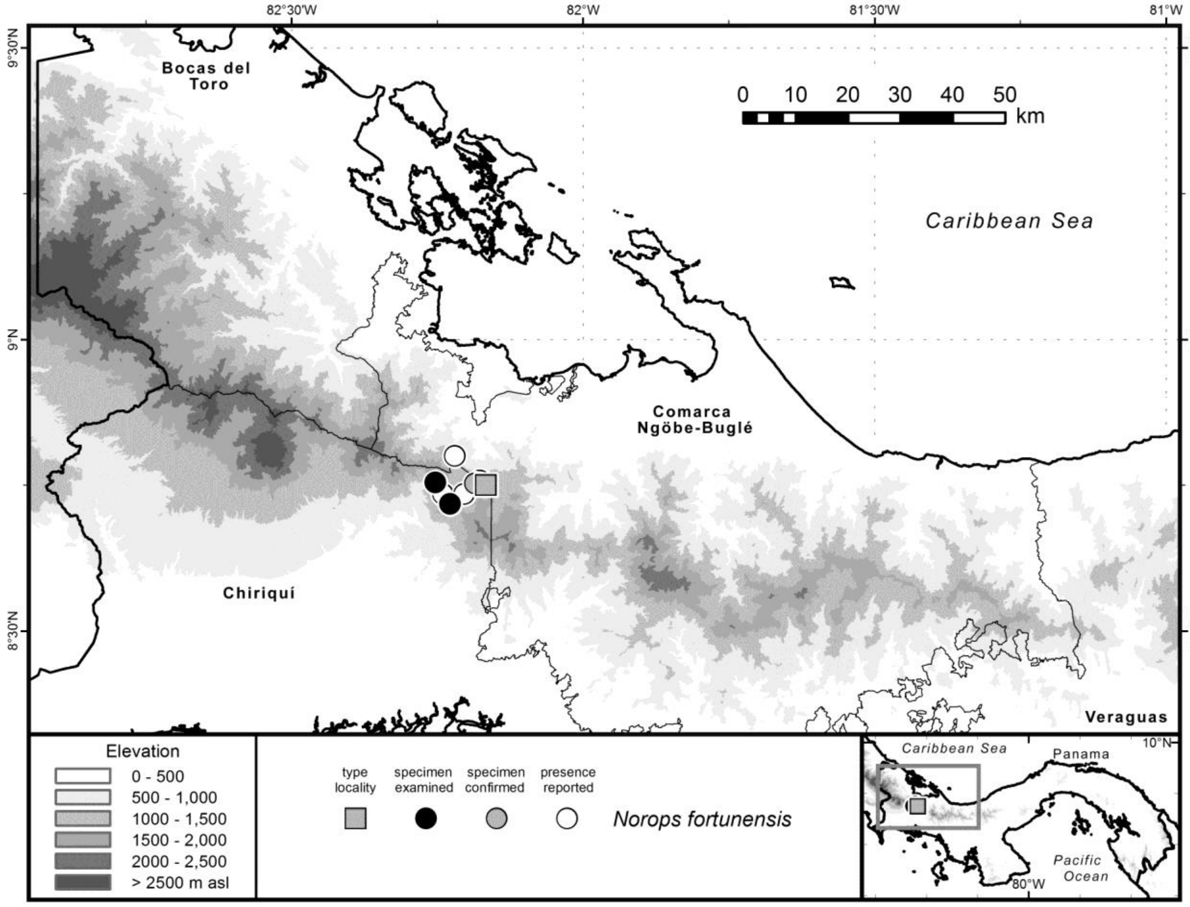
Anolis exsul: Arosemena & Ibáñez (1994); Young et al. (1999); Hofer & Bersier (2001); Ibáñez et al. (2001); Fundación PA.NA.M.A. (2007); Köhler et al. (2007).

Anolis exul: Köhler et al. (2007).

Anolis fortunensis: Arosemena & Ibáñez (1993); Young et al. (1999); Ibáñez et al. (2001); Köhler et al. (2007); Ponce & Köhler (2008); Fläschendräger & Wijffels (2009); Köhler (2009; 2011); Jaramillo et al. (2010); Stadler (2010); Wilson & Johnson (2010); Gutpelet (2012); Lotzkat et al. (2012c: in part.); Uetz & Hošek (2014).

Norops exsul: Fundación PA.NA.M.A. (2007).

Norops sp.: de Sousa (1999: in part.).



Map 4.53: Distribution of *Norops fortunensis*.

Holotype. MVUP 756, male, from "las márgenes del Río Chiriquí (8°45'N, 82°10'W), frente a la estacion hidrometeorologica del Instituto de Recursos Hidráulicos y Electrificación (IRHE) en Bijau, entre 1050-1075 m sobre el nivel del mar, dentro de la Reserva Forestal de Fortuna, en la Cordillera Central, Provincia de Chiriquí" (Arosemena & Ibáñez 1993).

Geographic distribution. Endemic to Panama, 1050–1200 m asl. Only known from the surroundings of the La Fortuna reservoir at RFLF, Chiriquí, and adjacent Caribbean slopes in BPPS, Comarca Ngöbe-Buglé.

Diagnosis. A medium-sized *Norops* (maximum known SVL 50 mm) with short legs (4th toe reaching to ear, rarely beyond) that is most similar in external morphology to *N. carpenteri, N. gruuo, N. pseudokemptoni,* and *N. kemptoni.* It can readily be distinguished from these species by the large male dewlap, which is red with a greenish-yellow posterior portion (vs. orange or yellow in the former two species, and unicolor red or red with a posterior portion of magenta, vinaceous, or similar, but never greenish, shadings in the latter two). It further differs from the former three species in having a small, unilobate hemipenis (vs. bilobate).

Description. TOL to 138 mm; SVL to 50 mm; tail moderately long, TL/SVL 1.66–1.83; legs short (tip of 4th toe of adpressed hind limb reaching at most to ear); D keeled; V smooth; caudals keeled; Drows 0–2 slightly enlarged; SAM 108–150; males with slightly to distinctly enlarged PC, without nuchal crest; lamellar pads broad; 4toe 33–37; 4finger 21–26; IO 1–2; IP/SS 2–3; SBO/SPL 0; loreals smooth, 47–58 in 5–7 rows; male dewlap large to very large, female dewlap moderate (data from five Panamanian specimens, including that of Ponce & Köhler 2008 and Gutpelet 2012; see chapter 4.1.5 for detailed morphological data).

The hemipenis of *Norops fortunensis* (Fig. 4.44A) is a small, unilobed organ with an asulcate processus; apex calyculate; sulcus spermaticus opening into two concave areas.

Coloration in life. D and L surfaces brown, with darker mottling suggesting transverse bands; tail and usually also limbs with dark crossbands; lips white or almost white especially below eye; V surfaces white to light gray with diffuse darker mottling or reticulations; male dewlap red, with a greenish or greenish-yellow hue on the posterior portion; female dewlap dirty white, in SMF 86406 with brown mottling whose presence in the other females at SMF I could not ascertain due to their preserved state.

Coloration in preservative. After 5 years in 70% ethanol, the coloration of SMF 90103 is similar to that in life, apart from the dewlap which is whitish.

Natural history notes. Diurnal and arboreal (Arosemena & Ibáñez 1993, 1994). The juvenile male SMF 90103 was encountered by FH and JFB around 22:00 while it was sleeping on a leaf 1.2 m above ground.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Norops fortunensis,* and assigned that species to the IUCN category DD, in which it is also listed by the official IUCN Red List (IUCN 2014). I calculated the species EVS as 6 (range) + 3 (persecution) + 5 (ecological distribution) = 14, indicating a high vulnerability. Its extent of occurrence of only 44 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category CR according to IUCN (2001) criterion B1b(iii).

Remarks. Although *Norops fortunensis* occurs in the one of the most thoroughly studied regions of my study area, it remains known from only a few specimens (holotype MVUP 756; MVUP 900–2 on which the original description of *N. exsul* was based; and the five specimens examined by myself), leaving much of its actual variation and geographic distribution to be revealed. Apart from the male dewlap coloration in life, to my knowledge there is no character of external morphology that distinguishes *N. fortunensis* from its cryptic sibling species *N. kemptoni* (see chapter 4.1.5 for a discussion of characters regarded as diagnostic by Arosemena & Ibáñez 1993, 1994, or Ponce & Köhler 2008). Populations from the southeastern portion of RFLF around Lost & Found Ecohostel and Cerro Pata de Macho were only through DNA barcoding revealed to be assignable to *N. kemptoni* (Gutpelet 2012; chapter 4.1.5 of this work). The specimens collected in this area had in the past been misidentified based on morphological characters alone, and accordingly were treated under the name *Anolis fortunensis* by Hamad (2009), Köhler et al. (2010a), Stadler (2010), and Lotzkat et al. (2010a, c, 2012c). As a consequence, the altitudinal range extension proclaimed by Lotzkat et al. (2010c) on the basis of specimens from Cerro Pata de Macho does not apply to *N. fortunensis.*

In view of their collection locality (northernmost point in Map 4.53), I tentatively assign the specimens reported as *A. exsul* by Hofer & Bersier (2001) to *N. fortunensis.* These specimens constitute the only record for BPPS, the Comarca Ngöbe-Buglé, and the Caribbean slopes, though the species' presence in these areas is rendered plausible by their proximity to the collection sites of the holotype and the examined specimen SMF 90103.

Norops fungosus (Myers 1971)

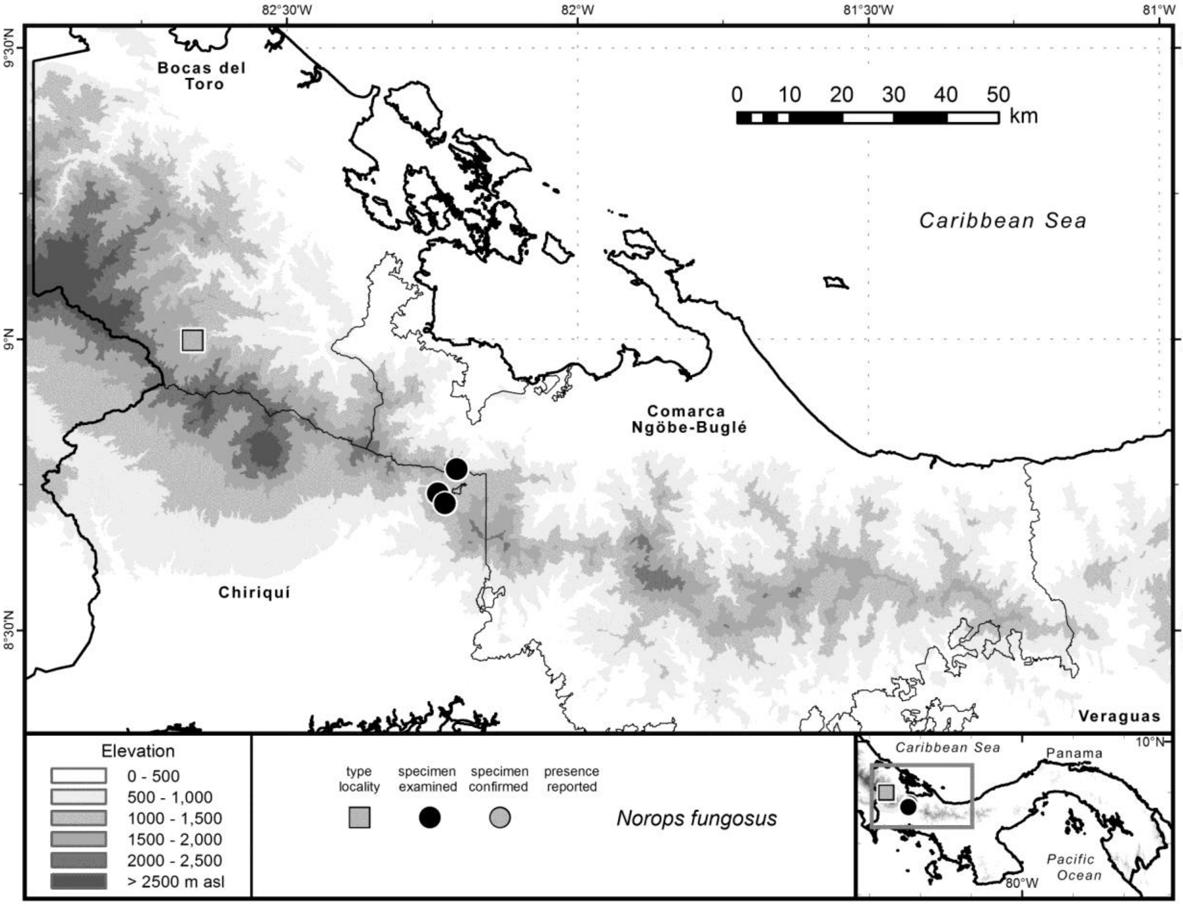
Lichen Anole, Myers' Anole; Anolis de Myers

Figures 4.52; 4.55; 4.98F; Maps 4.10; 4.54.

Anolis fungosus: Myers (1971b); Auth (1994); Ibáñez et al. (2001); Young et al. (1999); ANAM (2004); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Köhler (2010); Fläschendräger & Wijffels (2009); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Holotype. KU 113451, male, from "Campo Mojica, a clearing on a trail at 1450 meters elevation, on the north slopes of Cerro Pando, upper watershed of Río Changena, in the Cordillera de Talamanca, Bocas del Toro Province, Republic of Panama" (Myers 1971b).

Geographic distribution. Endemic to the Talamancan Highlands of Panama and Costa Rica, 1030–1600 m asl. In Panama, restricted to Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé, at premontane elevations of 1030–1450 m asl along the Serranía de Talamanca east to the Fortuna depression.



Map 4.54: Distribution of *Norops fungosus*.

Diagnosis. A medium-sized *Norops* (maximum SVL 49 mm) with very short legs (4th toe reaching to shoulder) that is most similar in external morphology to *N. pentaprion, N. charlesmyersi,* and *N. salvini.* It can readily be distinguished from these species as well as from the superficially similar *N. datzorum* by the presence of two bony parietal protuberances (vs. absent) and by its tail, which lacks a serrated middorsal crest but bears two rows of enlarged paramedian subcaudals forming a conspicuous serrated subcaudal double crest (vs. no such double subcaudal crest). *Norops fungosus* further differs from the former two species in lacking two rows of slightly enlarged middorsal scales (vs. present) and in having enlarged postcloacal scales at least in some males (vs. always absent), and from the latter two species in having smooth loreal, dorsal, and ventral scales (vs. at least slightly keeled).

Description. TOL to 104 mm; SVL to 49 mm; tail very short, TL/SVL < 1.2; legs very short (tip of 4th toe of adpressed hind limb reaching at most to shoulder); D and V smooth; most caudals keeled; Drows 0; SAM 116*; males with or without enlarged PC, without nuchal crest; lamellar pads broad; 4toe 30–34; 4finger 25*; IO 2; IP/SS 1–2; SBO/SPL 0; loreals smooth, 16–19 in 3 rows; male dewlap moderate to large, female dewlap small (own data combined with that of Myers 1971b and Savage 2002).

The hemipenis of *Norops fungosus* is a medium-sized bilobed organ with an asulcate processus; lobes calyculate, truncus with transverse folds (Myers 1971b; Fig. 4.55M).

Coloration in life. Ground color dirty white to dark gray or brown; D, L, and ventrolateral surfaces with dense lighter and/or darker mottling, blotches, and/or reticulations giving an overall lichenous appearance; V surfaces at most sparsely mottled; lining of throat black, corners of mouth blue; male dewlap red, female dewlap yellow. As exemplified by the photos taken at different times of MVUP 2095 (Figs. 4.55C–G, I) individuals of *Norops fungusus* undergo considerable metachrosis involving all scales including those on the dewlap.

Coloration in preservative. After 8 years in 70% ethanol, SMF 86385 is largely dirty white, with light to medium brown markings; no blue coloration remains visible around the corners of the mouth; the dewlap has faded to medium brown; the parietal protuberances and portions of the supraorbital semicircles appear dark gray due to rubbed off scale surfaces.

Natural history notes. Diurnal and arboreal (Myers 1971b), probably uses its prehensile tail for climbing as the other Panamanian members of the *Norops pentaprion* group do.

Remarks. This species remains known from very few examples. In addition to the Panamanian holotype and the four Costa Rican specimens recounted by Savage (2002), three specimens from RFLF have been collected recently (Fig. 4.55): the females MVUP 2095 and MHCH 509, and the male SMF 86385, thus totaling 8 specimens including four Panamanian ones. The two former specimens are the first adult females of this species to be collected. As a consequence, the female dewlap is described for the first time herein.

The collection locality for SMF 86385, based on which Köhler et al. (2008) extended the species' distribution to the Fortuna area, was given as "Quebrada Arena" by Köhler (2010) and as "near Río Hornito" by Köhler et al. (2008). In the corresponding field notes, the locality is specified as "Cable Car", with coordinates matching those of entries from "near Río Hornito" and verified by myself to correspond to a point along the course of Río Hornito, about 800 airline meters upstream from the Fortuna reservoir. I am certain that this locality is the true provenance of SMF 86385. In fact, Quebrada Arena, almost 7 km further N, is specified in the corresponding field notes as the collection locality of the female MHCH 509 collected by AB and MP on the same day as SMF 86385. This site's ubication less than 300 m from the Comarca's border, together with the occurrence at premontane elevations in Bocas del Toro, renders the species' occurrence in the Comarca Ngöbe-Buglé plausible. Moreover, MHCH 509 was collected at 1030 m asl, extending the lower elevational limit previously reported as 1075 m (Köhler et al. 2008). The listing of *Norops fungosus* for the Humedal de Importancia Internacional San San Pond Sak (ANAM 2004) is clearly erroneous since this species is not to be expected anywhere near sea level.

Myers (1971b) and Savage (2002) stated males of *Norops fungosus* to lack enlarged postcloacal scales. However, SMF 86385 does possess a set of slightly but clearly enlarged postcloacal scales (see Fig. 4.55M). Since I have not examined the holotype or any Costa Rican material, at this point I cannot tell whether the males examined by Myers and Savage really have no suggestion of enlarged postcloacals, or actually exhibit a set of only slightly enlarged postcloacals similar to those of SMF 86385.

Norops gaigei **(Ruthven 1916)**

[In part modified from Köhler et al. (2012b); see Appendix 8 for original publication]

Gaige's Anole; Anolis de Gaige

Figures 4.62B; 4.63B; 4.64; 4.65; 4.98H; Maps 4.12; 4.13; 4.55.

Anolis gaigei: Barbour (1923); Köhler et al. (2012b); Uetz & Hošek (2014).

Anolis limifrons: Martínez & Rodriguez (2005: in part.: Fig. 22B).

Anolis polylepis: Martínez & Rodriguez (2005); Rodriguez et al. (2005); Ibáñez (2006: in part.).

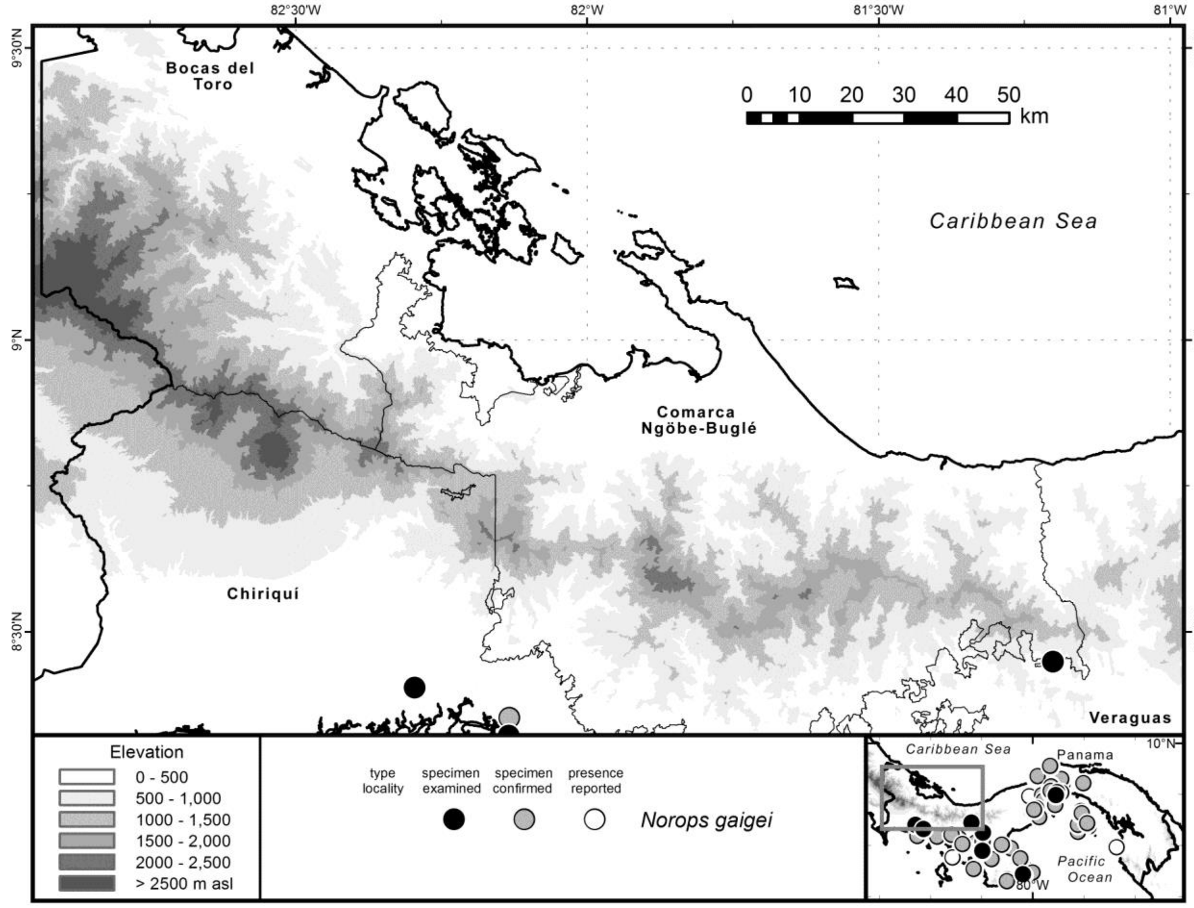
Anolis sallaei: Barbour (1906).

Anolis tropidogaster: Swanson (1945); Cochran (1946); Evans (1947); Myers & Rand (1969); Peters & Donoso-Barros (1970: in part.); Telford (1971); Rand & Myers (1990); Auth (1994: in part.); Ibáñez et al. (1996; 1997; 2001: in part.); Young et al. (1999: in part.); Poe (2004: in part.); Fundación PA.NA.M.A. (2007: in part.); Fläschendräger & Wijffels (2009: in part.); Jaramillo et al. (2010: in part.); Wilson & Johnson (2010: in part.).

Norops tropidogaster: Nicholson et al. (2005); Neal (2007); Köhler (2008: in part.).

Holotype. UMMZ 48304, from San Lorenzo, Santa Marta Mountains, Colombia, elevation of 2,700 ft. (Köhler et al. 2012b).

Geographic distribution. Panama and northern Colombia (probably also NW Venezuela), 0–900 m asl. In Panama, along both versants of the central (and probably also the eastern) portion of the country, and the Pacific versant of western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from the Pacific foothills in Veraguas and PNAC up to 640 m asl.



Map 4.55: Distribution of *Norops gaigei*.

Diagnosis. A medium-sized *Norops* (maximum SVL 53 mm) with long legs (4th toe reaching to eye or beyond) that is most similar in external morphology to *N. polylepis* and *N. limifrons,* and bears superficial similarities to *N. carpenteri* and *N. gruuo.* It can readily be distinguished from these four species by its male dewlap which is yellow with a central orange portion, and by its strongly keeled ventral scales (vs. smooth, at most faintly keeled in some specimens). It further differs from the latter two species in having long legs (vs. short, 4th toe not reaching eye), and from *N. polylepis* in having a very small, unilobed hemipenis (vs. bilobed and relatively large, bulging the base of tail) and one pair of greatly enlarged postcloacal scales in males (vs. several slightly enlarged PC).

Description. TOL to 168 mm; SVL to 53 mm; tail long, TL/SVL 1.9–2.34; legs long (tip of 4th toe of adpressed hind limb reaching at least to center of eye, usually to between eye and nostril); D keeled; V imbricate, strongly keeled; caudals keeled; Drows 2–4; SAM 94–138; males with one pair of greatly enlarged PC, can raise a low nuchal crest; lamellar pads rather narrow; 4toe 31*; 4finger 21*; IO 1–4; IP/SS 2–4; SBO/SPL 0–2; loreals keeled, 32–51 in 5–

8 rows; male dewlap large, female dewlap very small (data from Panamanian specimens including that of Köhler et al. 2012b; see chapter 4.1.7.2 for detailed morphological data).

The hemipenis of *Norops gaigei* (Fig. 4.63B) is a very small and delicate, unilobed organ without calyces or transverse folds; sulcus spermaticus opening into a single concave area.

Coloration in life. D and L surfaces light to medium brown, with a conspicuous dark postorbital stripe extending onto base of tail; V surfaces rather unicolor cream or light brown; male dewlap yellow with a darker orange central portion.

The male SMF 91529 (Fig. 4.65A, F, K, L) was recorded as follows: D and L surfaces of body and forelimbs Tawny Olive (223D); two broad Natal Brown (219A) longitudinal stripes extending from eye paravertebrally to base of tail, suffused with Walnut Brown (221B); a series of Sepia (119) blotches between occipital region and base of tail; D surface of head Raw Umber (123), laterally grading into Tawny Olive (223D); V ground color Pale Horn Color (92), suffused with Orange-Rufous (132C) beneath tail; D and L surfaces of tail and hind limbs Sayal Brown (223C) with the suggestion of diffuse Orange-Rufous (132C) crossbars; iris Robin Rufous (340); dewlap Warm Buff (118) at anterior base and outer margin, Pale Horn Color (92) at posterior base; center Burnt Orange (116), especially anterior portions suffused with Grayish Olive (43); dewlap scales dirty white.

Coloration in preservative. After 4 years in 70% ethanol, the coloration of SMF 91529 is similar to that in life, apart from that all red and yellow tonalities have faded; dewlap whitish with a slightly darker central area.

Natural history notes. Just as Köhler et al. (2012b) at all of their collection sites in western Panama, I found *Norops gaigei* to be very abundant in semi-open environments at Finca La Providencia, where sleeping individuals were perched on vegetation, while active ones were moving on the ground as well as up to 2 m above ground on trees and bushes.

Remarks. As detailed by Köhler et al. (2012b) and in chapter 4.1.7.2, *Norops gaigei* has long been confused with *N. tropidogaster* in central Panama, and repeatedly been misidentified as *N. polylepis* in western Panama. It appears in a bulk of publications under either name (see Köhler 2012b for a more comprehensive synonymy especially regarding literature on central Panamanian populations) and was to my knowledge solely recognized under its correct name by Barbour (1923). While *N. tropidogaster* does occur in eastern Panama, any *tropidogaster*-like anole from central and western Panama, west to near the eastern city limit of Davíd, Chiriquí, in fact represents the nominal taxon *N. gaigei.* The same applies to all populations reported as *N. polylepis* from Veraguas or the eastern portions of Chiriquí and the Comarca Ngöbe-Buglé, respectively. The presence of *N. gaigei* in the Comarca Ngöbe-Buglé is rendered plausible by its altitudinal distribution (up to 900 m asl fide Köhler et al. 2012b, recorded up to 760 m in Panama according to my dataset) and the collection locality of SMF 91530 at Los Valles, less than 500 m straight line distance from the Comarca's border.

Köhler et al. (2012b) gave the TL/SVL ratio as 1.37–2.34. The lower limit is based on the specimen SMF 85302 whose TL recording of 59 mm is simply unlogical (most probably owing to transposed digits) given its SVL of 43 mm. Exclusion of this TL and the resulting TL/SVL values results in the ratio as reported herein.

Norops gruuo (Köhler, Ponce, Sunyer & Batista 2007)

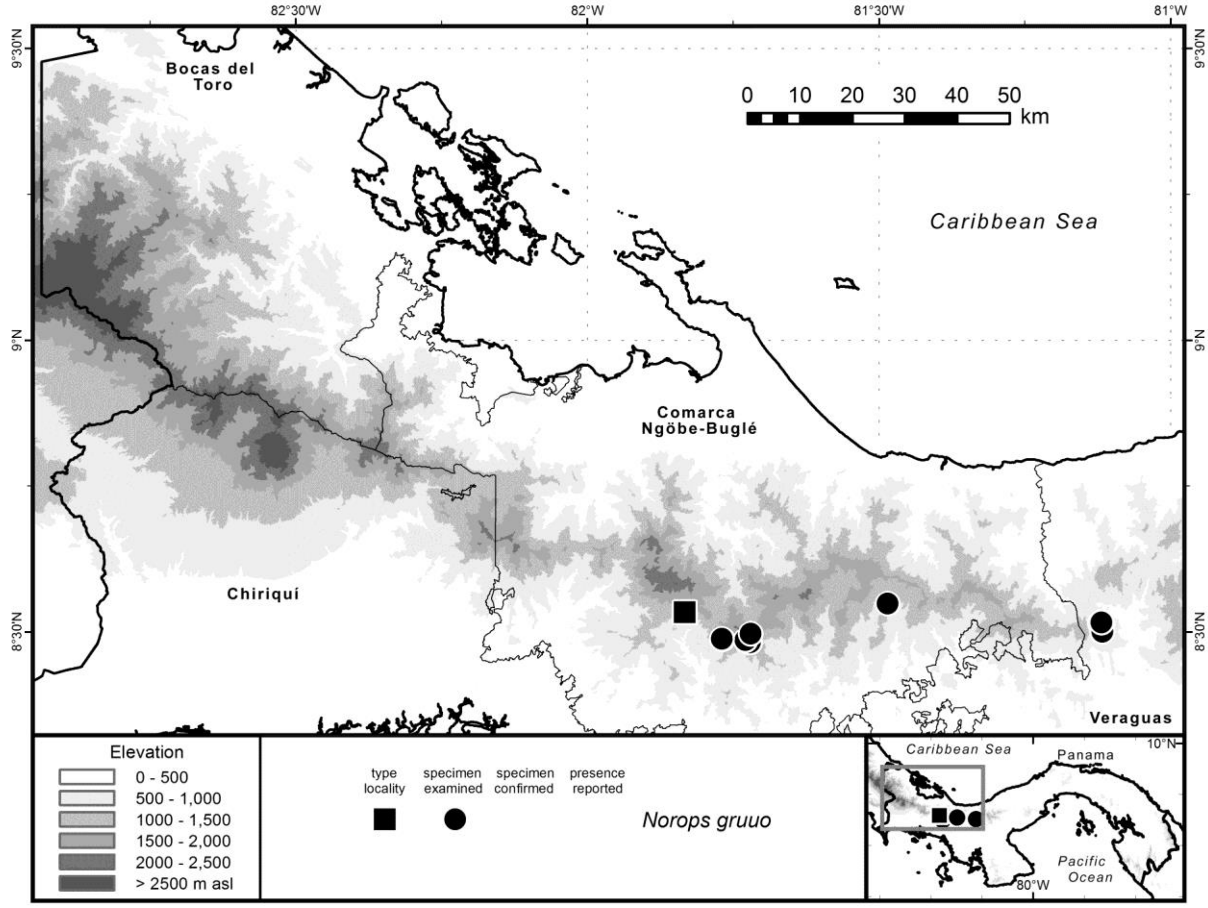
[In part modified from Lotzkat et al. (2012c); see Appendix 8 for original publication]

Tabasará Anole; Anolis de Tabasará

Figures 4.44C; 4.45; 4.47; 4.99A; Maps 4.9; 4.56.

Anolis gruuo: Köhler et al. (2007); Ponce & Köhler (2008); Hamad (2009); Köhler (2009; 2011); Jaramillo et al. (2010); Stadler (2010); Wilson & Johnson (2010); Gutpelet (2012); Lotzkat et al. (2012c, d, 2014); Uetz & Hošek (2014).

Holotype. SMF 85416, male, from "near the headwaters of Río San Félix, ca. 2 km N Escopeta Camp, ca. 8°32'N, 81°50'W, Serranía de Tabasará, 900 m elevation, Comarca Ngöbe Bugle, Distrito de Nole Düima, Corregimiento de Jadeberi, Panama" (Köhler et al. 2007).



Map 4.56: Distribution of *Norops gruuo*.

Geographic distribution. Endemic to the Serranía de Tabasará in the Comarca Ngöbe-Buglé and Veraguas province of western Panama. Recorded exclusively from the Pacific versant between the type locality on the S slopes of Cerro Saguí over approximately 80 km to the NE slopes of Cerro Mariposa, at premontane elevations of 860–1530 m asl.

Diagnosis. A medium-sized *Norops* (maximum known SVL 52 mm) with short legs (4th toe reaching to ear, rarely beyond) that is most similar in external morphology to *N. carpenteri, N. pseudokemptoni, N. fortunensis,* and *N. kemptoni.* It can readily be distinguished from the latter three species by the male dewlap, which is orange (vs. unicolor red or red with a posterior portion of magenta, vinaceous, or greenish shadings). It further differs from latter two species in having a large, bilobate hemipenis (vs. small, unilobate), from *N. pseudokemptoni* in having hemipenial lobes that are longer than wide (vs. wider than long) and from *N. carpenteri* by its keeled dorsal granules (vs. smooth), the presence of conspicuously enlarged postcloacals in males (vs. no distinctly enlarged PC), and the lack of fine, dark dorsal punctations and reticulations that are retained preservative (vs. present).

Description. TOL to 137 mm; SVL to 52 mm; tail moderately short, TL/SVL 1.46–1.79; legs short (tip of 4th toe of adpressed hind limb usually reaching at most to ear, in very few specimens to posterior border of eye); D keeled; V smooth or weakly keeled; caudals keeled; Drows 0–6, usually only slightly enlarged; SAM 110–144; males with distinctly enlarged PC, can raise a low nuchal crest; lamellar pads moderately broad; 4toe 27–37; 4finger 20–24; IO 0–4; IP/SS 1–5; SBO/SPL 0; loreals keeled, 28–73 in 4–7 rows; male dewlap large to very large, female dewlap small (data from all known specimens except MHCH 1315–1318; see chapter 4.1.5 for detailed morphological data).

The hemipenis of *Norops gruuo* (Fig. 4.44C) is a medium-sized to large, bilobed organ with an asulcate processus (at least in large examples, contrary to what was stated by Köhler et al. 2007) and long lobes; lobes and distal portion of truncus calyculate, base of truncus with transverse folds.

Coloration in life. D and L surfaces very light to dark brown, usually with mottling and blotches that are evenly distributed or form transverse bands; some females with a middorsal stripe; tail usually light-colored with dark transverse crossbands; V surfaces unicolor light or spotted with darker pigment; male dewlap orange, female dewlap white, reddish orange in young females.

Leonhard Stadler recorded the coloration of three specimens from Veraguas as follows (translated from Stadler 2010): Adult male SMF 89469 (Figs. 4.47E, J) from Cerro Mariposa: D ground color Grayish Olive (43), with Blackish Neutral Gray (82) mottling on dorsum and limbs and a broad middorsal stripe of the same color stretching from posterior part of upper head to anterior tail region; thereafter tail Grayish Olive (43) with contrasting transverse Blackish Neutral Gray (82) bands; chin dirty white with a darker white longitudinal stripe and Natal Brown (219A) flecks; venter dirty white with Natal Brown (219A) mottling; iris Tawny (38); dewlap Orange Yellow (18), gorgetals Dark Grayish Brown (20).

Adult female SMF 89470 from Cerro Mariposa: D ground color Olive-Brown (28) with Olive-Yellow (52) mottling on limbs and anterior tail region; thereafter tail Olive-Brown (28) with contrasting transverse Olive-Yellow (52) bands; D surface of head Olive-Brown (28) posteriorly, grading into a lighter Olive-Yellow (52) anteriorly and then into Olive-Brown (28) again on the snout; a Grayish Horn Color (91) interorbital bar; chin and venter dirty white, mottled with a mixture of Straw Yellow (56) and Citrine (51); V surface of tail Olive-Yellow (52); iris Kingfisher Rufous (240).

Adult female SMF 89471 (Figure 4.47F) from Alto de Piedra: D ground color Fuscous (21) suffused with Smoke Gray (45); a Fawn Color (25) middorsal stripe stretches from posterior part of head to base of tail; thereafter tail Smoke Gray (45) with slight Fuscous (21) mottling; D surface of head Smoke Gray (45) with Fuscous (21) mottling and a Citrine (51) interorbital bar; chin and snout region fade into Straw Yellow (56); venter dirty white, slightly speckled with Fawn Color (25) laterally; iris Kingfisher Rufous (240).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all red and yellow tonalities have faded; dewlaps whitish.

Natural history notes. Diurnal and arboreal. Almost all individuals were encountered at night, sleeping on vegetation between 0.4 and 4 m above ground. The only exception is SMF 89468, which was collected while it was active during heavy rainfall after dusk, about 0.3 m above ground on an ornamental plant in the restaurant at Alto de Piedra. The specimens come from habitats (compare photographs in Figs. 2.6A–D, H; 2.7B–D) ranging from roadsides, gardens, plantations, and secondary forest to apparently pristine cloud forest. However, apart from this variety of documented habitats, *Norops gruuo* seems to be dependent on the presence of at least some tree cover, and thus is probably absent from the almost treeless savannas that cover a considerable portion of the Pacific slopes of the Serranía de Tabasará.

Conservation. Jaramillo et al. (2010) calculated an EVS of 14 for *Norops gruuo,* and assigned that species to the IUCN category VU. Based on the now available data, I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. While only the easternmost populations of *N. gruuo* live inside a protected area, its extent of occurrence of just 386 km^2 and the continuing deforestation (resulting in a decline of the preferred shaded habitats) we observed in the region qualify this species for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. As to be expected, the examination of 23 additional specimens resulted in a more comprehensive notion of the variability within this species which was described on the basis of 4 specimens (Köhler et al. 2007). Especially noteworthy is that the conspicuously contrasting dark and pale banding of the tail, stated as a diagnostic character for *N. gruuo* (Köhler et al. 2007; Köhler 2008; Ponce & Köhler 2008), is not always evident in all specimens (e.g., due to metachrosis according to the time of day or the nature of the situation), and in some even completely absent. Moreover, *N. gruuo* is now revealed to exhibit a considerable overlap in loreal scale number with *N. pseudokemptoni,* rendering another character formally considered as diagnostic to be not. See chapter 4.1.5 for a discussion of characters regarded as diagnostic for the species of the *N. kemptoni* complex.

The localities reported by Stadler (2010) and Lotzkat et al. (2012c) extend the known geographic and elevational range of *Norops gruuo,* which was formerly known from a single locality. Cerro Mariposa at Alto de Piedra, approximately 80 km east of the type locality, now constitutes the easternmost locality reported for the species and extends its distribution into Veraguas Province. The juvenile female SMF 89713 was collected near Quebrada Ardilla at 1530 m, which is the highest elevation reported so far for this species, followed by the adult male SMF 91464, collected near Guayabito at 1500 m. The females SMF 89468 and 89471, collected around Alto de Piedra in Veraguas at 860 m, now constitute the lower elevational limit for *N. gruuo.*

Thus, the known range of *N. gruuo* stretches over 80 airline km from 81°07'W to 81°50'W at premontane elevations between 860 and 1530 m asl along the Pacific drainage of the Serranía de Tabasará. Future field work most probably will expand these range limits, but I do not expect this expansion to be too extensive. About 40 km west of the type locality begins the La Fortuna area within RFLF, while the area around El Copé within PNGDOTH lies some 50 km east of Alto de Piedra. Both areas have been extensively surveyed and it is rather unlikely that *N. gruuo* should have gone unnoticed. East of Alto de Piedra, the Cordillera Central drops well below 1000 m repeatedly, possibly constituting a physiographic barrier. Toward La Fortuna, *N. gruuo* might be replaced by *N. fortunensis,* which is known to occur there between 1050–1200 m (see remarks for that species). The presence of *N. gruuo* on the Caribbean slopes might be suspected at least in the eastern portion of the Serranía de Tabasará, where several passes fall below the species' upper elevational limit. However, in the area between the type locality and Buabidí, we found *N. pseudokemptoni* instead of *N. gruuo* along the continental divide and on the Caribbean slopes.

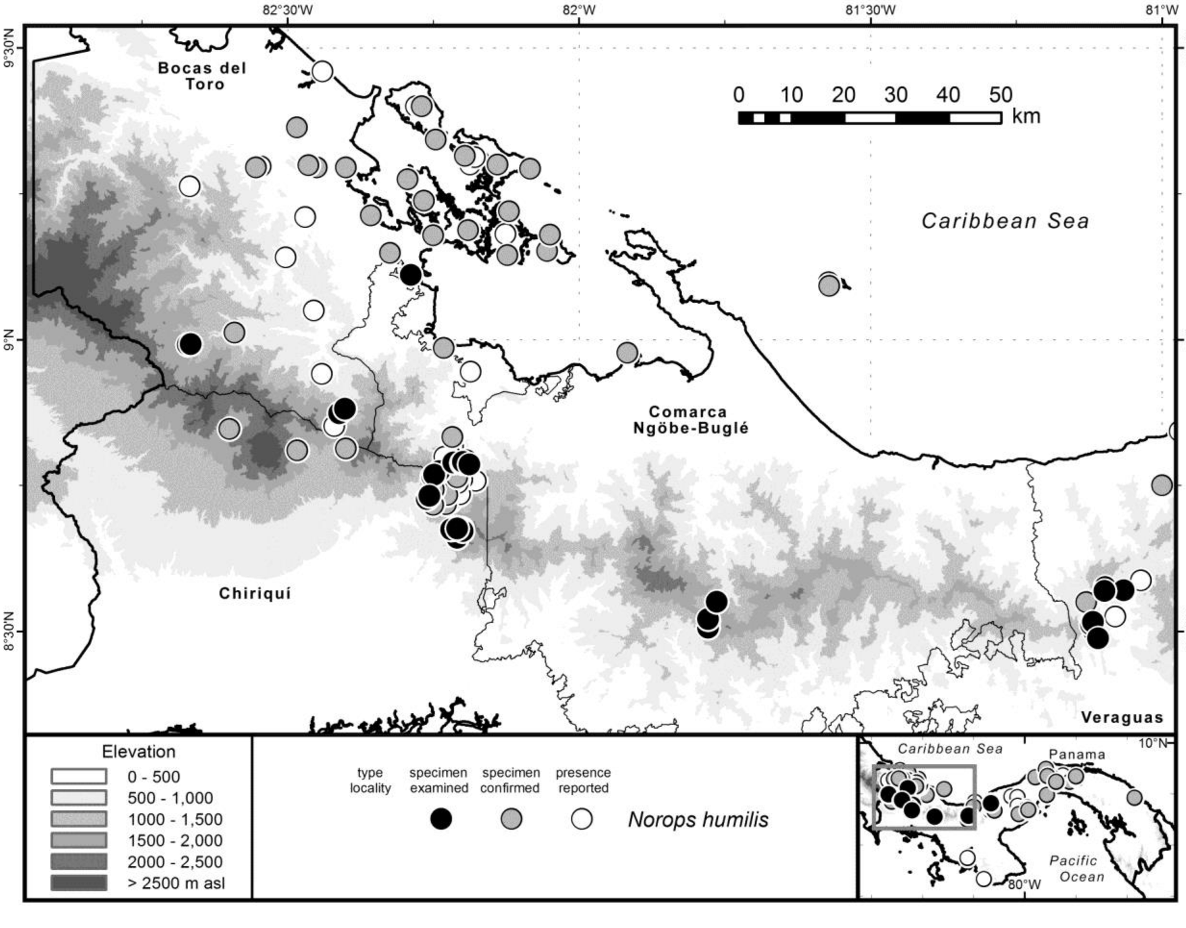
Norops humilis **(Peters 1863)**

Humble Anole, Ground Anole; Anolis, Morachito de suelo

Figures 4.67; 4.99B; Maps 4.14; 4.57.

Anolis humilis: Peters (1863a); Dunn (1933); Wettstein (1934); Taylor (1956); Peters & Donoso-Barros (1970); Myers (1971a, 1977); Auth (1994); Martínez & Rodriguez (1994, 2005); Martínez et al. (1995); Ibáñez et al. (1995, 1996, 1997, 2001); de Sousa (1999); Young et al. (1999); Carrizo (2000, 2010); Hofer & Bersier (2001); ANAM (2004, 2009b); Poe (2004); Rodriguez et al. (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Köhler et al. (2007; 2010a); Poe & Ibáñez (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Lotzkat et al. (2010b, c, 2011, 2013); Uetz & Hošek (2014).

Syntypes. ZMB 500 and 55223, from "Veragua" (Peters 1863a).



Map 4.57: Distribution of *Norops humilis*.

Geographic distribution. Costa Rica and Panama, 0–2000 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from numerous sites up to 1750 m asl on both versants.

Diagnosis. A small *Norops* (maximum SVL 45 mm) with long legs (4th toe reaching at least to eye, in most specimens well beyond) that is readily distinguished from all Panamanian congeners by its 8–12 rows of greatly enlarged, strongly keeled middorsal scales as well as its strongly keeled dorsal head scales. The only Panamanian anoles with which it might be confused at first glance are juveniles of *N. lemurinus* and members of the *N. pachypus* complex, all of which have only 2 middorsal rows slightly enlarged.

Description. TOL to 112 mm*; SVL to 42 mm*; tail short to long, regenerated portions often barely discernible, TL/SVL usually 1.22–1.89*, but in some specimens up to 2.28*; legs long (tip of 4th toe of adpressed hind limb usually reaching well beyond eye, in very few specimens to anterior border or center of eye); D strongly keeled; V keeled; caudals keeled; Drows 8–12, greatly enlarged and strongly keeled; SAM 88–116*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 23–33*; 4finger 16–24*; IO 1–4*; IP/SS 2–4*; SBO/SPL 0–1*; loreals keeled, 24–57 in 4–6 rows; male dewlap moderate, female dewlap small (based on 66 Panamanian specimens examined by myself, see remarks).

The hemipenis of *Norops humilis* is a relatively large (compared to the size of the lizard), bilobed organ; lobes elongate, as long as or longer than truncus; lobes and truncus finely calyculate.

Coloration in life. The coloration and pattern of *Norops humilis* are extremely variable and seem to include every shape and arrangement of markings known for the genus, including blotches, chevrons, diamonds, longitudinal stripes, etc; a dark interorbital bar is usually present. Every pattern element can be subject to extensive metachrosis ranging from whitish gray over greenish and reddish shades and any imaginable brown to almost black. Male dewlap red with a narrow yellow margin, female dewlap white or red, sometimes with a yellow margin.

The male male SMF 89714 was recorded as follows: D and L ground color of body, head and limbs Burnt Umber (22), grading into Chestnut (32) on tail; dorsum with Light Drab (119C) blotches proliferating in lines onto flanks, separated by Burnt Umber (22) angles pointing posteriorly; a u-shaped Light Drab (119C) marking on back of head, with the tips reaching posterior border of orbits; V surfaces Dark Drab (119B) spotted with Pearl Gray (81); D surfaces of tail and hind limbs with Mars Brown (223B) crossbands; iris Clay Color (123B); dewlap Scarlet (14) with a Spectrum Yellow (55) margin and Sepia (119) scales, some of which have dirty white centers.

Leonhard Stadler recorded the adult male SMF 89472 as follows (translated from Stadler 2010): D and L surfaces Olive Brown (28) with broad transverse Mars Brown (223A) bars arranged in an irregular zig-zag-pattern from the nuchal area to tip of tail; V surfaces Dark

Drab (119B) with dirty white spots on venter; iris Sulfur Yellow (157); dewlap Burnt Orange (116) with a Spectrum Yellow (55) margin and Sepia (119) and dirty white scales.

Nadim Hamad recorded a specimen from RFLF as follows (translated from Hamad 2009): Dorsum Greenish Olive (49) with suggestion of Citrine (51); a longitudinal Olive-Brown (28) stripe on enlarged middorsal scale rows with transverse Amber (36) lines; an interorbital Amber (36) bordered by a black line; Venter Dark Neutral Gray (83) speckled with dirty white except for the gular region, which is Germanium (12) laterally and otherwise Orange-Yellow (18) with a suggestion of Spectrum Yellow (55).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that the red, yellow, and green shadings usually have completely faded; some specimens with a bronze metallic and/or bluish gray cast; dewlaps whitish, with a suggestion of orange around the center in a few males.

Natural history notes. Diurnal and largely terrestrial. Found in the shaded forest interior, apparently associated with abundant leaf litter and tree buttresses. Specimens were encountered active on the forest floor (then usually escaping into or onto tree buttresses) during daytime, or sleeping in low vegetation 0.2–1 m above floor at night. In Panama's Cordillera Central, *Norops humilis* is being replaced by members of the *N. pachypus* complex that appear to occupy a similar ecological niche at elevations of 1500–1750 m asl, depending on the exact site.

Remarks. Köhler et al. (2003) resurrected *Norops quaggulus* (Cope 1885) from the synonymy of *N. humilis* based on hemipenial morphology, restricting the latter name to populations from Lower Central America with the long, calyculate hemipenis lobes described above. They further concluded that *N. humilis marsupialis* (Taylor 1956) should remain in the synonymy of *N. humilis.* However, recent studies have shed new light on the distinctiveness of the populations described by Taylor (1956) from Pacific Costa Rica, in a way that *N. humilis marsupialis* is likely to be removed from the synonymy of *N. humilis* in the near future (J.J. Köhler, pers. comm. 2013). Since Köhler et al. (2003, 2006) and Savage (2002) included specimens from Pacific Costa Rica assignable to *N. humilis marsupialis* in their descriptions of *N. humilis,* I restrict my morphological description presented above to the Panamanian specimens I have examined myself. I regard as possible that both *N. quaggulus* and *N. (humilis) marsupialis* might range into western Panama, and that the former taxon might even be included in my sample constituting either UGL 1 or UGL 2 identified in chapter 4.1.7.3. Targeted collecting of adult males throughout the Panama-Costa Rica border region is warranted to answer these questions.

Lotzkat et al. (2010c) reported the specimen SMF 89480 from 1660 m asl at RFLF to represent the highest elevation known for this species. However, my georeference for the specimen MCZ 165191 from "Chiriquí: between Cerro Punta + Bambito" yields a higher SRTM elevation value of ca. 1750 m. The occurrence of *Norops humilis* at this elevation is confirmed for the Caribbean slope by the specimen SMF 91474 collected by AH and myself between Río Clarito and Río Changena, Bocas del Toro, at 1752 m. Although I have found the forest floors of the Lower Montane belt to be primarily occupied by members of the *N. pachypus* complex, the species might occur at still higher elevations in Panama, given that Sasa et al. (2010) raised the altitudinal limit for Costa Rica to 2000 m.

Peters (1863a) noted that the types were collected by Warszewicz in "Veragua". Considering the route taken by Warszewicz (Savage 1970), it seems possible that the type locality lies somewhere between Davíd, Chiriquí, and the Laguna de Chiriquí, Bocas del Toro, either in Chiriquí or Bocas del Toro provinces, or in the Comarca Ngöbe-Buglé.

Norops kemptoni **(Dunn 1940)**

Kempton's Anole; Anolis de Kempton

Figures 4.44B; 4.45; 4.48; 4.99C; Maps 4.9; 4.58.

Anolis altae: Montero (2005).

Anolis fortunensis: Hamad (2009); Köhler et al. (2010a); Stadler (2010); Lotzkat et al. (2010a, c, 2012c).

Anolis kemptoni: Dunn (1940); Arosemena & de Sousa (1989); Arosemena & Ibáñez (1993, 1994); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Köhler et al. (2007); Ponce & Köhler (2008); Fläschendräger & Wijffels (2009); Köhler (2009; 2011); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010); Gutpelet (2012); Lotzkat et al. (2012c: in part.); Uetz & Hošek (2014).

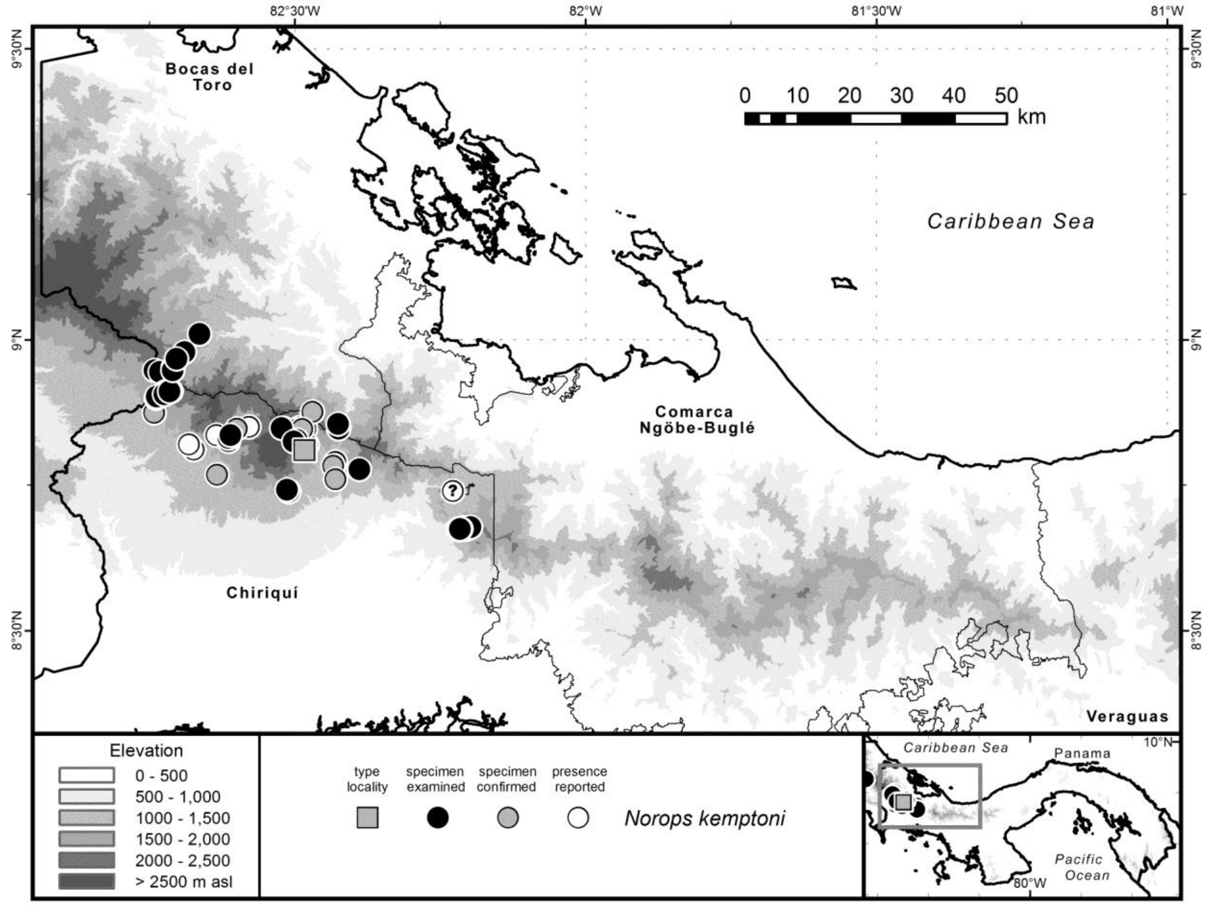
Anolis pandoensis: Hulebak & Poe (2006).

Norops pandoensis: Savage & Guyer (1998); Savage (2002); Hulebak & Poe (2006).

Anolis polylepis: Slevin (1942: in part.: referring to CAS 79595 from 6500 feet [= ca. 1981 m]).

Holotype. ANSP 21708, male, from "Finca Lérida, 5300 feet [= ca. 1615 m], above Boquete, Chiriquí" (Dunn 1940).

Geographic distribution. Endemic to the Talamancan Highlands of eastern Costa Rica and western Panama, 1000–2390 m asl. In Panama, along both versants of the Serranía de Talamanca in Bocas del Toro, Chiriquí, and Comarca Ngöbe-Buglé, east to Cerro Pata de Macho at RFLF, 1090–2390 m asl.



Map 4.58: Distribution of *Norops kemptoni*.

Diagnosis. A medium-sized *Norops* (maximum SVL 57 mm) with short legs (4th toe reaching to between shoulder and ear, rarely beyond) that is most similar in external morphology to *N. carpenteri, N. gruuo, N. pseudokemptoni,* and *N. fortunensis.* It can readily be distinguished from the former three species by its small, unilobate hemipenis (vs. bilobate). It further differs from these species except *N. pseudokemptoni* by the large male dewlap, which is unicolor red or red with a posterior portion of magenta, vinaceous, or similar shadings (vs. orange or yellow in the former two, and red with a greenish-yellow posterior portion in *N. fortunensis*), and from *N. pseudokemptoni* in the coloration of the female dewlap, which is white or cream (vs. usually yellow, rarely white or orange).

Description. TOL to 173 mm; SVL to 57 mm; tail moderately long to long, TL/SVL 1.61–2.25; legs short (tip of 4th toe of adpressed hind limb not reaching further than ear in most specimens); D keeled; V smooth to keeled; caudals keeled; Drows 0–4, rarely 6, usually only slightly enlarged; SAM 102–154; males with enlarged PC, can raise a nuchal crest; lamellar pads moderately broad; 4toe 29–37*; 4finger 19–25*; IO 0–3; IP/SS 1–4; SBO/SPL 0; loreals smooth to keeled, 31–83 in 4–8 rows; male dewlap large to very large, female dewlap small (data from Panamanian specimens, including that of Ponce & Köhler 2008 and Gutpelet 2012; see chapter 4.1.5 for detailed morphological data).

The hemipenis of *Norops kemptoni* (Fig. 4.44B) is a small, unilobed organ with an asulcate processus; apex calyculate; sulcus spermaticus opening into two concave areas.

Coloration in life. D and L surfaces light to dark, greenish, reddish, or grayish brown, unicolor or with darker mottling or transverse bands; females often with a continuous or broken middorsal stripe that is sometimes very broad and bordered laterally by darker stripes; tail and sometimes also limbs with dark crossbands; lips white or almost white especially below eye; V surfaces white to light gray, unicolor or with sparse darker mottling; male dewlap unicolor red or red with a posterior portion of magenta, vinaceous, or similar shadings, sometimes with a small light-colored area on anterior basal portion; female dewlap dirty white to cream color, rarely yellowish. *Norops kemptoni* is capable of considerable metachrosis that may alter the pattern elements, in a way that, e.g., a continuous middorsal stripe can change into a series of middorsal blotches.

The subadult male MHCH 2154 was recorded as follows: D and L surfaces of body, head, limbs, and base of tail Light Drab (119C) with broad Sepia (219) transverse bands of irregular zig-zag shape, those on body with flecks of Light Drab (119C) and disintegrating into mottling laterally; a Warm Sepia (221A) interorbital stripe present, bordered by and grading into Ground Cinnamon (239) on the supraorbital scales; D surface of posterior portion of tail Drab-Gray (119D) with broad Sepia (119) transverse bands grading into Vandyke Brown (221) laterally; V surfaces of body, head, limbs, and base of tail dirty white with a suggestion of Pale Horn Color (92), sparsely mottled with Russet (34); V surface of posterior portion of tail Pale Neutral Gray (86) with a mere suggestion of Vandyke Brown (221) transverse bands; iris Mikado Brown (121C); dewlap Ruby (10) with a suggestion of Magenta (19) and dirty white scales which, except for the marginals, are faintly bordered by Dark Neutral Gray (83).

The male SMF 89485 (Fig. 4.48G) was recorded as follows: D and L ground color Light Drab (119C), with shadings of Hair Brown (119A) suggesting transverse bands; L surface of body, limbs, and anterior portion of tail with irregular lines of Robin Rufous (340) mottling and very sparse Dark Brownish Olive (129) mottling; D surface of head Mars Brown (223A) with shadings of, and laterally grading into, Light Drab (119C); tail grading into Pearl Gray (81) posteriorly, with transverse bands of Sepia (219); a Cream Color (54) supralabial stripe present; labial region as well as V surfaces of body, limbs and base of tail Pale Horn Color (92) with sparsely distributed Grayish Horn Color (91) mottling; V surface of head dirty white with more densely distributed Grayish Horn Color (91) mottling; iris Raw Sienna (136); dewlap Sulphur Yellow (57) at central base, with the free margin Spectrum Red (11) anteriorly, grading into Spinel Red (108B) posteriorly, and dirty white scales.

The dewlap of the male SMF 89716 (Fig. 4.48I) was recorded as follows: posterior two-thirds Deep Vinaceous (4) with a suggestion of Magenta (2), anterior third Chrome Orange (16) with a suggestion of Flame Scarlet (15).

Nadim Hamad recorded a specimen from RFLF as follows (translated from Hamad 2009): D surfaces from nuchal area to tip of tail Citrine (51) with transverse Grayish Horn Color (91) stripes, some of which have a fine black border; flanks mottled with Citrine (51) and Sulphur-Yellow (57); venter dirty white mottled with Cream Color (54); V surface of tail Straw Yellow (56); dewlap Geranium Pink (13) with a suggestion of Scarlet (14) and dirty white scales.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all red, yellow, and green shadings have faded; dewlaps whitish, in a few males with a faint orangish hue.

Natural history notes. Diurnal and arboreal. Active individuals were found on the ground or up to 2 m above ground on trunks, walls, or in bushes, sleeping individuals were perched up to 5 m above ground.

Remarks. Apart from the male dewlap coloration in life, to my knowledge there is no character of external morphology that distinguishes *Norops kemptoni* from its cryptic sibling species *N. fortunensis,* with which it occurs in close para- if not sympatry at RFLF (see chapter 4.1.5 for a discussion of characters regarded as diagnostic for the species of the *N. kemptoni* complex). Populations from the SE part of RFLF around Lost & Found Ecohostel and Cerro Pata de Macho were only through DNA barcoding revealed to be assignable to *N. kemptoni* (Gutpelet 2012; chapter 4.1.5 of this work). The specimens collected in this area had previously been misidentified based on morphological characters alone, and accordingly treated under the name *Anolis fortunensis* by Hamad (2009), Köhler et al. (2010a), and Lotzkat et al. (2010a, c, 2012c).

I could not find any record of *Norops kemptoni* to substantiate the lower elevational limit of 1000 m asl as given by Köhler (2008), though it appears somewhat possible in view of the elevational range of its close relative *N. fortunensis*. My lowest collection site is the Lost & Found Ecohostel at 1250 m, Jaramillo et al. (2010) gave the lower limit in Panama as 1100 m, and the overall lowest elevation I could detect is approximately 1090 m, inferred from SRTM elevation data for my georeference of Quebrada Los Chorros, RFLF. However, this record of de Sousa (1999) is not substantiated by any traceable voucher specimen (contrary to other records from this publication, see remarks for *N. charlesmyersi*) and lies somewhat within the range documented herein for *N. fortunensis.* Since I found geographically complex range borders and contact zones to occur between several pairs of closely related *Norops* species along the Cordillera Central, I refrain from dismissing the record of de Sousa (1999). Yet, it requires verification (and is therefore marked with a question mark in Map 4.58), just as the areal borders and contact zones of *N. kemptoni* and *N. fortunensis* at RFLF do. Less doubts exist about the upper elevational limit of *Norops kemptoni,* which was previously given as 1950 m asl for Costa Rica (Savage 2002; Sasa et al. 2010) and 2000 m for Panama (Jaramillo et al. 2010). Near Sendero Quetzales, AH and myself collected the male SMF 89721 downhill from Mirador Las Rocas at 2268 m (WP 159). According to the CHP catalogue, the specimen CHP 5703 was collected at Mirador Las Rocas itself, where I took my WP 158 at an elevation of 2390 m. The respective distances of less than 5 km between the Comarca's border and the collection sites of my examined specimens from Cerro Pata de Macho and Cerro Altrillería render the species' presence in the Comarca Ngöbe-Buglé plausible.

***Norops lemurinus* (Cope 1861)**

Ghost Anole, Lemur Anole; Anolis, Moracho saltador

Figures 4.74; 4.99D; Maps 4.16; 4.59.

Anolis palpebrosus: Peters (1874).

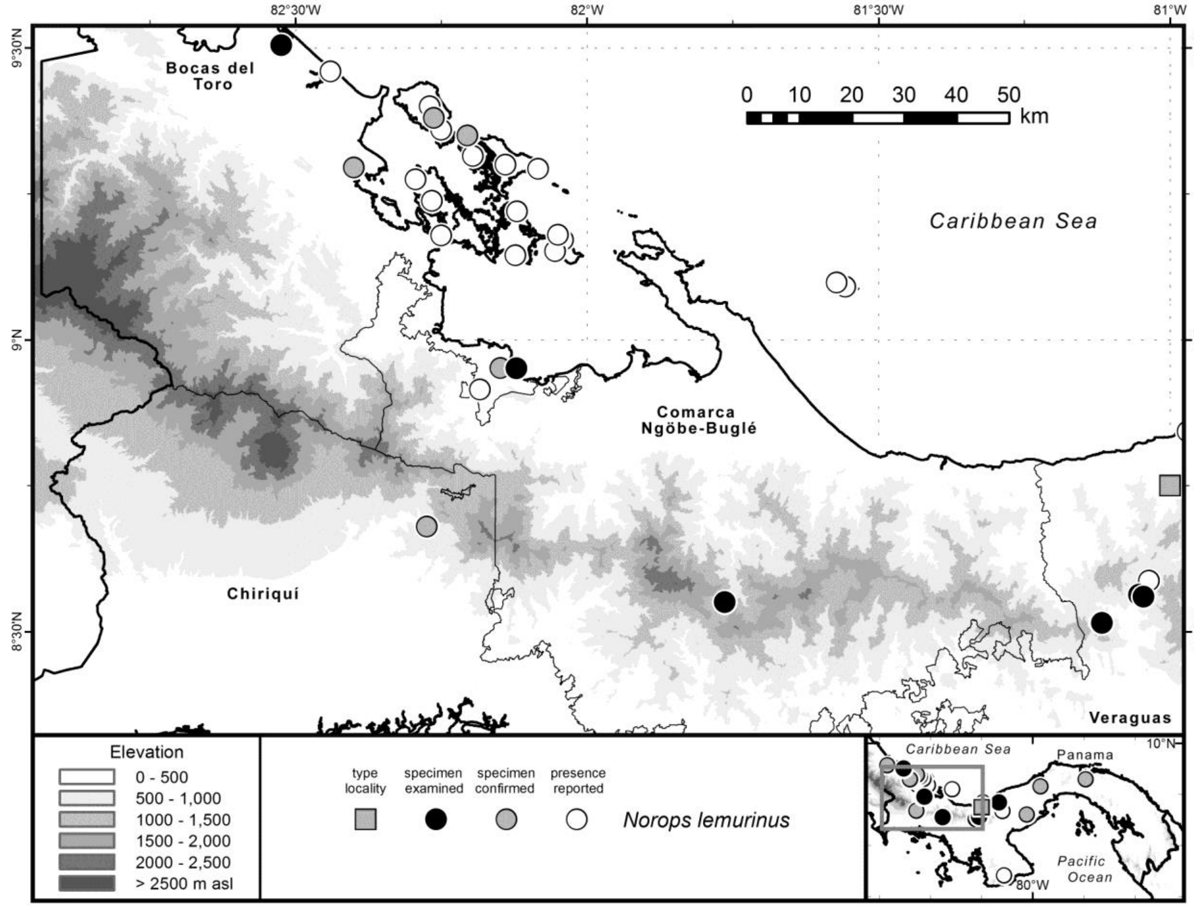
Anolis lemurinus: Cope (1861c); Taylor (1956); Peters & Donoso-Barros (1970); Myers (1971a); Auth (1994); Martínez & Rodriguez (1994); Martínez et al. (1995); Young et al. (1999); Ibáñez et al. (2001); ANAM (2004, 2009b); Poe (2004); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Poe & Ibáñez (2007); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Anolis vittigerus: Myers & Rand (1969: in part.); Rand & Myers (1990: in part.).

Syntypes. Three males and a female at ANSP, from "Veragua, New Grenada" (Cope 1861c), herein regarded to be Cocuyos de Veraguas.

Geographic distribution. Mexico to Panama, 0–2000 m asl. In Panama, throughout the western and central portions of the country to slightly east of the canal (see remarks), including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from both versants up to almost 990 m asl.

Diagnosis. A large *Norops* (maximum SVL 79 mm) with long legs (4th toe reaching to eye or beyond) that is most similar in external morphology to *N. vittigerus,* from which it differs in having only two slightly enlarged middorsal scale rows (vs. 10–20 very slightly and gradually enlarged ones) and in lacking a contrasting central blotch on the dewlap (vs. present in both sexes). *Norops lemurinus* is often confused with *N. capito,* from which it can readily be distinguished by its small, granular dorsals (vs. large and flat) and its red (males) or white (females) dewlap (vs. yellow in both sexes). Juveniles of *N. lemurinus* might be confused with *N. humilis,* from which they differ in lacking 8–12 rows of greatly enlarged, strongly keeled middorsal scales (vs. present), and with members of the *N. pachypus* complex, from which they differ in having strongly keeled ventral scales (usually smooth or weakly keeled) and 0–1 scales between the supraorbital semicircles (vs. 2 or usually more SS).



Map 4.59: Distribution of *Norops lemurinus*.

Description. TOL to 228 mm; SVL to 79 mm; legs long (tip of 4th toe of adpressed hind limb reaching to eye or beyond); tail long, TL/SVL 2.0–2.43*; D granular, keeled; V imbricate, mucronate and strongly keeled; caudals keeled, middorsal rows forming a low crest; Drows 2, slightly enlarged; SAM 136–178*; males without enlarged PC, but able to raise a nuchal crest; lamellar pads rather narrow; 4toe 31–41; 4finger 25–27*; IO 0–1; IP/SS 2–3*; SBO/SPL 0–1; loreals keeled, 37–46* in 5–6* rows; male dewlap small to moderate, female dewlap small.

The hemipenis of *Norops lemurinus* is a bilobed organ with a long truncus and moderately slender, calyculate lobes and a calyculate asulcate processus.

Coloration in life. Ground color ranging from whitish gray to dark brown in the course of metachrosis; usually with a middorsal series of blotches, chevrons, or diamonds that extends posteriorly to suggest dark crossbands on tail; D surface of head usually with a dark interorbital bar and a lyriform marking on back of head; body, limbs, and tail variably mottled; male dewlap red, female dewlap whitish.

The male MHCH 2197 was recorded as follows: Ground color Drab-Gray (119D) with a suggestion of Light Drab (119C), with dense Dark Brownish Olive (129) mottling on D and L surfaces of head and body and Vandyke Brown (221) crossbands on tail and limbs; iris True Cinnamon (139); dewlap Burnt Orange (116) with dirty white and Sepia (119) scales.

Leonhard Stadler recorded the adult male SMF 89486 (Stadler 2010: Figs. A77; A78) as follows (translated from Stadler 2010): Dorsum with a broad middorsal Clay Color (26) band extending from nuchal area to base of tail, interrupted by large, regularly spaced Sepia (119) blotches that are bordered laterally by a Pale Horn Color (92) stripe; V surfaces Sulphur Yellow (57) with heterogeneous Sepia (119) mottling; D tip of snout Buff (24), bordered by Raw Umber (23) scales, followed posteriorly by a broad transverse Pale Horn Color (92) bar, a Raw Umber (23) interorbital bar bordered by Raw Umber (123), a butterfly-shaped Pale Horn Color (92) marking, and a Tawny Olive (223D)blotch; D surface of limbs with a geterogeneous pattern of Clay Color (26), Sepia (119), and Sulphur Yellow (57); D surface of tail Clay Color (26) with broad Sepia (119) crossbars and scattered Pale Horn Color (92) scales; V surfaces Sulphur Yellow (57) with irregular Sepia (119) blotches on venter and chin; iris Raw Sienna (136); dewlap Burnt Orange (116) with black and white scales.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that almost all red shadings have faded and bronze metallic hues are present especially dorsally; dewlaps whitish, in some males with suggestions of orangish hues.

Natural history notes. Diurnal and arboreal. I found individuals of this species in singular trees on otherwise open pasture, plantations, and in closed forest, while they were sleeping 1.5–5 m above ground. Stadler (2010) found two individuals active in direct sunlight on a meadow in Alto de Piedra.

Remarks. The specimen SMF 91486 from Río Hacha at 986 m asl raises the upper elevational limit which was previously reported as 910 m for Panama (Jaramillo et al. 2010). The range-wide elevational limit of 2000 m provided by Wilson & Johnson (2010) is much higher than reported elsewhere (Savage 2002; Köhler 2008; Sasa et al. 2010). Some MCZ specimens from Panama province (including Barro Colorado Island and localities east of the canal) catalogued as *Norops vittigerus* or *N. palpebrosus* were identified as representing *N. lemurinus* by GK, which is why I include the listings of these names by Myers & Rand (1969) and Rand & Myers (1990) in partim in my synonymy for this species. I have examined the specimen MVUP 292 from "Minas de Cocuyo, Calovebora, Veragua", catalogued as *Anolis tropidogaster,* and found it to actually represent *N. lemurinus.*

As detailed in chapter 4.1.7.5, my material of *Norops lemurinus* comprises two deeply divergent mitochondrial lineages, UGL 1 from the Serranía de Tabasará and UGL 2 from San San Pond Sak, which are separated by uncorrected p-distances of 8.6% in the COI barcode. My morphological data differs in several aspects from the description provided by Savage (2002), for example regarding relative hind limb length which I classify as long while Savage (2002) states the 4th toe to reach "beyond shoulder, usually to tympanum", whereas the legs among my examined material are much longer. I further obtained larger ranges for several counts, like SBO/SPL and 4toe.

***Norops limifrons* (Cope 1862)**

Slender Anole, Border Anole; Anolis, Moracho delgado

Figures 4.71; 4.73; 4.99E; Maps 4.15; 4.60.

Anolis biscutiger: Taylor (1956); Fitch et al. (1976).

Anolis godmani: Taylor (1956).

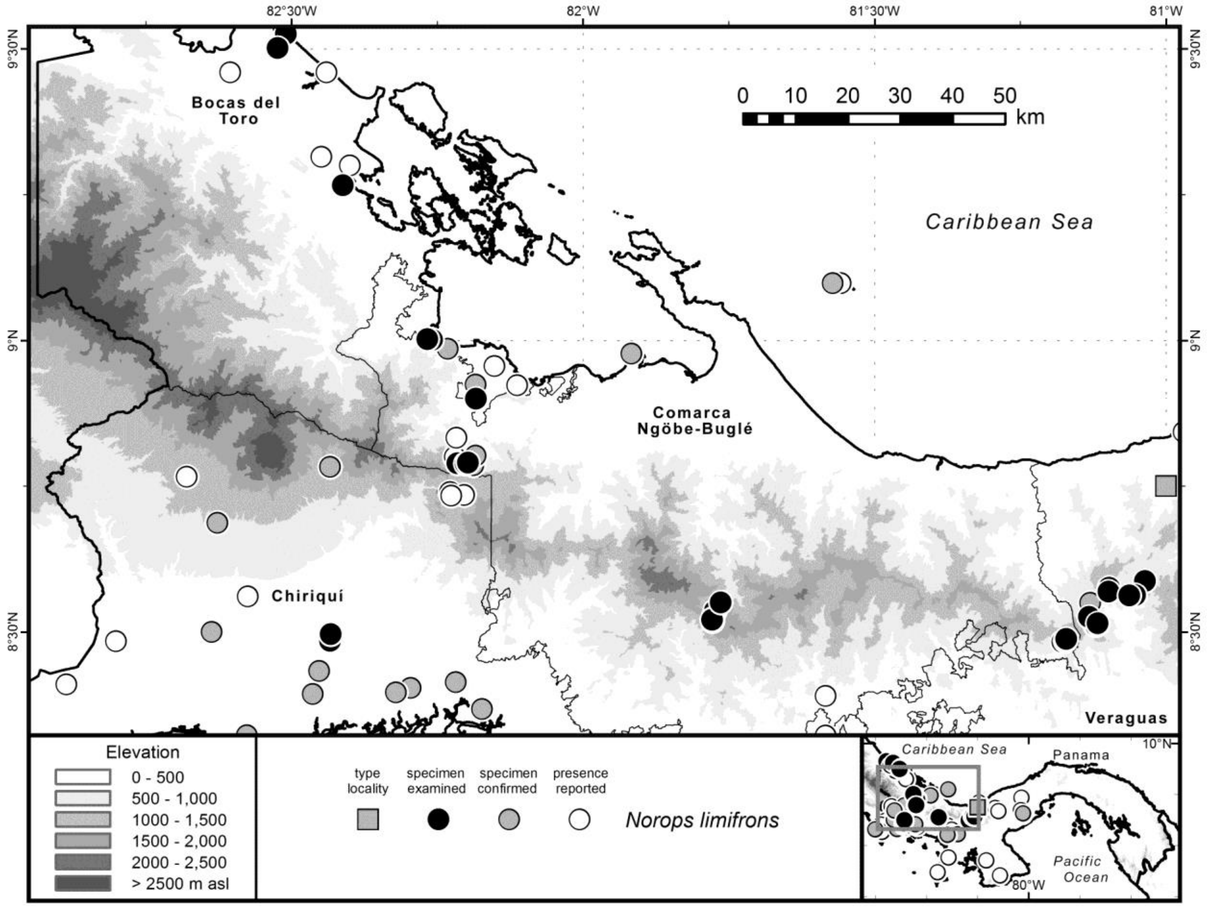
Anolis limifrons: Cope (1862d); Dunn (1933); Wettstein (1934); Taylor (1956); Peters & Donoso-Barros (1970: in part.); Myers (1971a, 1977); Auth (1994: in part.); Martínez & Rodriguez (2005); de la Riva (1997); de Sousa (1999); Young et al. (1999: in part.); Carrizo (2000, 2010); Hofer & Bersier (2001); Ibáñez et al. (2001: in part.); ANAM (2004, 2009b); Poe (2004); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007: in part.); Köhler et al. (2007); Köhler & Sunyer (2008); Hamad (2009); Fläschendräger & Wijffels (2009); Poe et al. (2009); Sunyer (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Lotzkat & Hertz (2011); Batista & Ponce (2011); Lotzkat et al. (2012d); Uetz & Hošek (2014).

Anolis pulchripes: Peters (1874).

Norops sp.: Rodriguez et al. (2005).

Syntypes. ANSP 7900 and 7901, from "Veragua" (Cope 1862d), herein regarded to be Cocuyos de Veraguas, a notion shared by Fitch et al. (1976), Savage (2002), and Köhler & Sunyer (2008), among others.

Geographic distribution. Eastern Honduras to west-central Panama, 0–1360 m asl. In Panama, throughout the western part of the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, recorded from numerous sites along both versants, east to El Valle de Antón and up to 1360 m asl.



Map 4.60: Distribution of *Norops limifrons*.

Diagnosis. A small, delicate *Norops* (maximum SVL 45 mm) with long legs (4th toe reaching to eye or beyond) that is most similar to *N. apletophallus* and *N. cryptolimifrons.* It differs from these two species in having a small, unilobed, hemipenis leaving base of tail slender in adult males (vs. large, bilobed, bulging the base of tail). It might at first glance be confused with *N. gaigei* and *N. polylepis,* but differs from these in the coloration of the male dewlap which is white and possibly bears yellow areas (vs. yellow and orange throughout). It further differs from *N. gaigei* in having smooth ventrals (vs. strongly keeled) and from *N. polylepis* by its small, unilobed hemipenis (vs. large, bilobed). It can readily be distinguished from the superficially similar members of the *N. kemptoni* complex as well as from *N. carpenteri* by its long legs (vs. 4th toe not reaching eye) and the white male dewlap bearing at most a restricted yellow area (vs. orange-yellow or red with at most a small white portion).

Description. TOL to 156 mm; SVL to 45 mm; tail moderately long to long, TL/SVL 1.53–2.52; legs long (tip of 4th toe of adpressed hind limb reaching at least to eye, usually beyond, sometimes even beyond snout); D granular, keeled; V smooth; caudals keeled; Drows 0–2 slightly enlarged*; SAM 114–156*; males with moderately to greatly enlarged PC, without nuchal crest; lamellar pads rather narrow; 4toe 27–33*; 4finger 18–23*; IO 0–5; IP/SS 1–6; SBO/SPL 0; loreals slightly keeled, 24–68 in 5–8 rows; male dewlap moderate to large, female dewlap very small to small (own data combined with that of Savage 2002 and Köhler & Sunyer 2008).

The hemipenis of *Norops limifrons* is a small, unilobed organ without conspicuous ornamentation or asulcate processus (Köhler & Sunyer 2008).

Coloration in life. D and L surfaces very light gray to dark brown, almost unicolor or speckled with lighter and/or darker pigment, in some individuals with a L stripe; females often with a dark middorsal series of blotches or continuous middorsal stripe, or a broad, light middorsal band bordered by narrow dark stripes; supralabials white to light gray; V surfaces dirty white or yellowish to light gray or brown; tail usually with dark crossbands; male dewlap white, with a yellow blotch at the central base or diffuse yellow areas around basal portion, female dewlap white to yellow.

Leonhard Stadler recorded the adult female SMF 89487 as follows (translated from Stadler 2010): D surfaces Olive Green (51); dorsum mottled with Greenish Olive (49) and a broad middorsal Glacous (79) stripe from back of head to base of tail; D surface of tail Chrome Orange (16) on on anterior, Olive Green (51) on posterior half; V surfaces dirty white with Brownish Olive (29) blotches on L portions of venter; D and V coloration separated by a Burnt Umber (22) L stripe extending from eye to groin and fading gradually posterior to shoulder; iris Spectrum Orange (17).

Coloration in preservative. After 4–7 years in 70% ethanol, the coloration is similar to that in life, apart from that the yellow elements have faded.

Natural history notes. I encountered specimens of *Norops limifrons* active on the ground or in low vegetation during daytime, or at night sleeping up to 2.5 m above ground. Similar to the observations provided by Savage (2002), I found this species to reach extremely high population densities in open and semi-open environments, whereas individuals appeared much more sparsely distributed in closed forests.

Remarks. The female MVUP 1367, collected at Lagunas del Volcán at 1360 m asl, raises the upper elevational limit documented for this species, previously reported as 1200 m for Panama (Jaramillo et al. 2010) and 1350 m for the species as a whole (Köhler 2008).

As detailed in chapter 4.1.7.4, Köhler & Sunyer (2008) described populations with bilobate hemipenes formerly referred to as *Norops limifrons* from Bocas del Toro and central Panama as two separate species. All pre-2008 records from the Panama Canal Zone and eastern Panama, as well as those from as far west as PNAC, are referable to *N. apletophallus,* including a large bulk of ecological, ethological, and physiological studies primarily carried out on Barro Colorado Island. In western Panama, all records from the Archipiélago de Bocas del Toro are referable to *N. cryptolimifrons.* On the adjacent mainland, the situation is more complex. See chapter 4.1.7.4 and the species account of *N. cryptolimifrons* for geographical boundaries and hybridization between this species and *N. limifrons.* As revealed in chapter 4.1.7.4, my material of *Norops limifrons* comprises four deeply divergent mitochondrial lineages: UGL 1 from the extreme eastern Serranía de Tabasará, UGL 2 from the central Tabasará, BPPS near La Fortuna, and the Caribbean lowlands N of La Fortuna, UGL 3 from west of Almirante, and UGL 4 from lowland Chiriquí. The average uncorrected p-distance of 6.2% in the 16S barcode between UGLs 2 and 3 is higher than that of any of these UGLs to the geographically interjacent *N. cryptolimifrons* (4.2 and 4.4%, respectively). Similarly, means of uncorrected COI p-distances between UGLs 1–4 range from 9.9–13.8%, i.e., are similar to those calculated between any of these UGLs and *N. apletophallus* (10.6–13.2%) or *N. cryptolimifrons* (10.7–12.8%), respectively. Thorough morphological and molecular studies involving material from western Panama and Costa Rica are needed to clarify and characterize the distinctness of the four UGLs documented herein. If such studies show the necessity of taxonomic conclusions, names long sunk into the synonymy of *N. limifrons* like *N. biscutiger* (Taylor 1956), *N. godmani* (Boulenger 1885), and *N. pulchripes* (Peters 1874) might be revalidated.

Norops lionotus **(Cope 1861)**

Lion Anole; Anolis

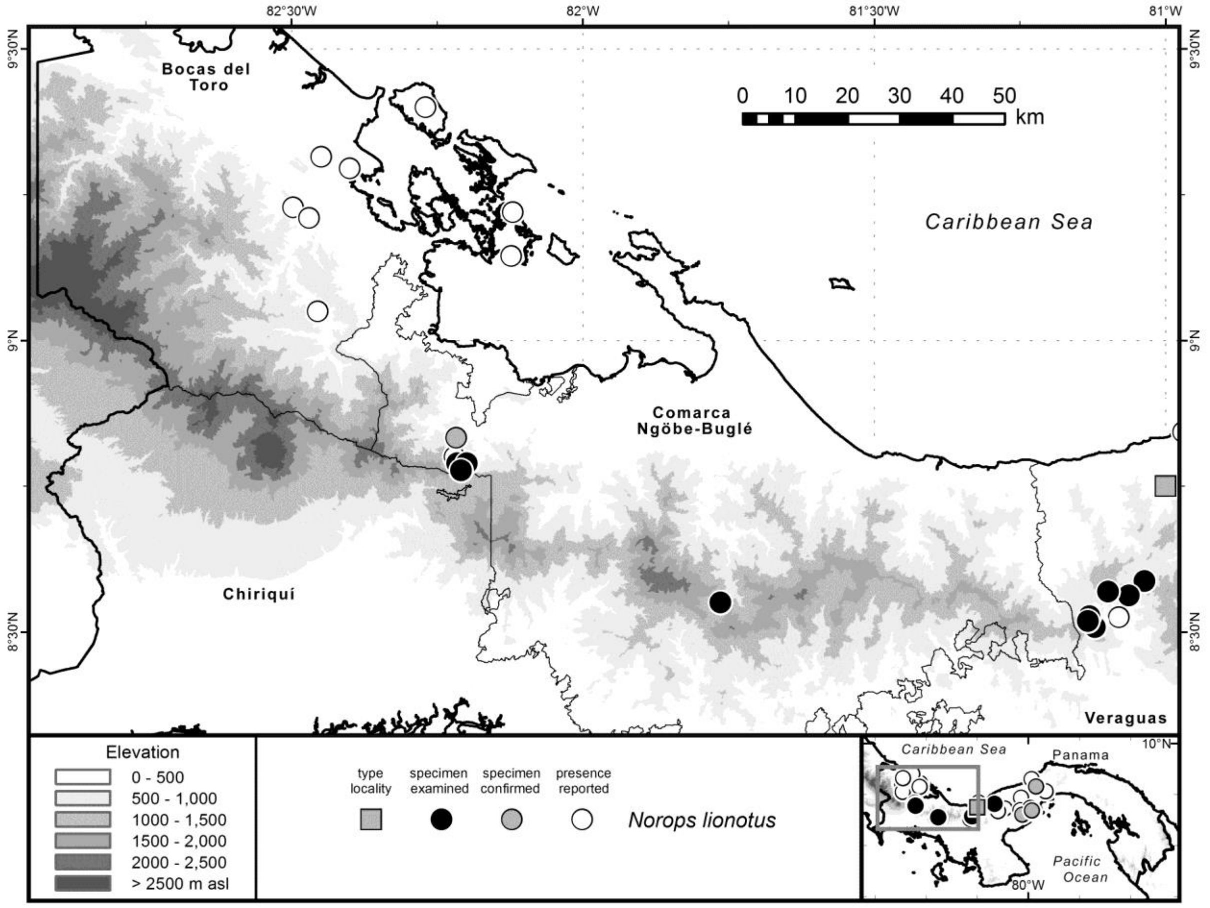
Figures 4.75; 4.99F; Maps 4.16; 4.61.

Anolis aquaticus: Hofer & Bersier (2001).

Anolis lionotus: Cope (1861c); Dunn (1933); Evans (1947); Myers & Rand (1969); Peters & Donoso-Barros (1970: in part.); Myers (1971a); Williams (1984); Rand & Myers (1990); Auth (1994: in part.); Martínez & Rodriguez (1994); Martínez et al. (1995); Ibáñez et al. (1996, 1997, 2001: in part.); Obermeier (1998: in part.); Young et al. (1999: in part.); Fundación PA.NA.M.A. (2007: in part.); Köhler et al. (2007); Hamad (2009); Fläschendräger & Wijffels (2009: in part.); Poe et al. (2009); Carrizo (2010); Jaramillo et al. (2010: in part.); Stadler (2010); Wilson & Johnson (2010); Lotzkat et al. (2012d); Uetz & Hošek (2014).

Holotype. ANSP 7909, from "Cocuyas de Veraguas, New Grenada" (Cope 1861c; = Cocuyos de Veraguas, Panama).

Geographic distribution. Endemic to western and central Panama east to the canal, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, 0–1200 m asl. In the Cordillera Central, recorded from the Caribbean versants of the Serranías de Talamanca and Tabasará at up to 1200 m asl, and from the Pacific versant at La Fortuna and around Santa Fé.



Map 4.61: Distribution of *Norops lionotus*.

Diagnosis. A large *Norops* (maximum SVL 78 mm) with long legs (4th toe reaching to eye or beyond) that is most similar in external morphology to *N. aquaticus* and *N. oxylophus.* It can readily be distinguished from these two species by its usually 10–14 rows of enlarged, flat middorsal scales that are larger than the ventrals (vs. middorsal scales keeled and about the size of the ventrals or smaller in both species, more than 14 enlarged rows in *N. oxylophus,* and only 2 in *N. aquaticus*).

Description. TOL to 223 mm*; SVL to 78 mm* legs long (tip of 4th toe of adpressed hind limb reaching to eye or beyond); tail moderately long to long, TL/SVL 1.59–2.29*; D of enlarged rows flat, smooth to rugose or slightly keeled, juxtaposed, larger than V; L granular, keeled; V imbricate, keeled; caudals keeled, Drows 10–14, rarely 16*; SAM 108–132*; males with enlarged PC, able to raise a nuchal crest*; lamellar pads narrow; 4toe 32–39*; 4finger 22–29*; IO 0–3*; IP/SS 0–4*; SBO/SPL 0–1; loreals keeled, 39–94* in 5–8* rows; male dewlap large to very large, female dewlap small (based exclusively on my sample of 24 specimens from western Panama).

The hemipenis of *Norops lionotus* is a bilobed organ with rather long, stout, calyculate lobes that bear transverse flounces proximally on the asulcate side.

Coloration in life. Generally similar to *Norops pachypus,* but usually with a more clear-cut and contrasting pattern. D and L surfaces light to dark brown, with a series of broad, dark transverse bars reaching onto flanks; usually a light labial stripe extending posteriorly onto body, to groin in some specimens; L surfaces often with light spots between the dark crossbands; V surfaces white to gray or brown; chin area often reticulated with dark brown; limbs and tail with dark crossbands; animals may appear solid blackish brown with whitish spots in the dark phase of metachrosis; male dewlap yellow, often with orange shadings in the posterior portion; female dewlap yellow to orange.

The male SMF 89495 was recorded as follows: D ground color Olive-Green (Auxiliary) (48), with irregular transverse stripes of Sepia (219) which diverge to encircle Natal Brown (219A) blotches on dorsolateral surfaces of the body; L surfaces of body Cinnamon-Drab (219C) grading into Spectrum Orange (17) ventrally, and reticulated with Sepia (219) except for L longitudinal stripe that extends from shoulder to midbody; V surfaces of body, tail, and limbs Olive-Yellow (52) speckled with Spectrum Orange (17) ventrolaterally; L surface of tail Raw Umber (23) mottled with Sepia (219); L surface of head Beige (219D) with Hair Brown (119A) irregular vertical stripes; V surface of head dirty white with a suggestion of Pearl Gray (81); iris Ferruginous (41); dewlap Spectrum Orange (17) with a suggestion of Orange Yellow (18) and dirty white scales.

Leonhard Stadler recorded the subadult male SMF 89492 as follows (translated from Stadler 2010): D ground color Brownish Olive (29) grading into Citrine (51) laterally, with regularly spaced transverse bars extending over middorsum from flank to flank bordered by Dark Grayish Brown (20); D surfaces of body and head with scattered Sulfur Yellow (157) spots; V surfaces of body and limbs Sulfur Yellow (157) gefärbt; chin dirty white mottled with Glaucous (79); tail Brownish Olive (29) with dark crossbands; iris Raw Umber (123); dewlap Spectrum Orange (17) with a suggestion of Orange Yellow (18) and white scales.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all yellow and orange shades have faded; dewlaps whitish except for slight suggestions of orange in a few males.

Natural history notes. Diurnal and semiaquatic. Without exception, individuals were encountered in the immediate proximity of water courses, usually while they were sleeping on rocks or vegetation 0.3–5 m above the water surface. In some cases, specimens excaped by diving into the water. One then hid under a rock at the creek's bottom, another emerged on the opposite bank of the river.

Conservation. Jaramillo et al. (2010) calculated an EVS of 12 for *Norops lionotus,* and assigned that species to the IUCN category LC, in which it is also listed by the official IUCN

Red List (IUCN 2014). I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of 13399 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category VU according to IUCN (2001) criterion B1b(iii).

Remarks. The specimen SMF 91495 from the headwaters of Río Chiriquí Malí collected at 1045 m asl, and the specimens reported by Hofer & Bersier (2001) as *Anolis aquaticus* (which can be confidently ruled out given the distribution of that species) from their transect of BPPS, for which my georefence corresponds to a SRTM altitude of 1200 m, confirm the upper elevational limit of 1200 m given by Köhler (2008; though this value might include *Norops oxylophus*) and raise the documented elevational maximum for Panama (previously reported as 850 m by Jaramillo et al. 2010).

As detailed in chapter 4.1.7.5, my material of *Norops lionotus* comprises two deeply divergent mitochondrial lineages. UGL 1 from the eastern Serranía de Tabasará around Santa Fé and UGL 2 from the central Tabasará and eastern Talamanca N of La Fortuna are separated by uncorrected p-distances in the COI barcode averaging 16.1%. This value is larger than the mean uncorrected p-distances of any of these UGLs to *N. oxylophus,* whose presence in Panama is herein documented based on SMF 90120 from San San Pond Sak. Ongoing studies on the taxonomy and phylogeography of the *N. lionotus* group will tell if the two UGLs should be regarded as separate species (as I assume), and whether the specimens reported as *N. lionotus* from lowland Bocas del Toro are really referable to this species or if some or all of the corresponding white circles in Map 4.61 actually represent individuals of *N. oxylophus.* I am convinced that the latter taxon certainly ranges into my study area, but according to the criteria specified in chapter 3.5.1 must classify its presence as merely "possible" (see distribution map in Appendix 7), since the occurrence at San San Pond Sak does not necessarily entail the presence in premontane portions of the corresponding drainage systems, as exemplified by the peculiar distribution that is suggested by the records of *N. limifrons* UGL 3 and *N. cryptolimifrons* in western Bocas del Toro, the latter of which must be assumed to range much farther west along premontane elevations than in the lowlands considering the Costa Rican record (Köhler & Sunyer 2008). Another issue surrounding *N. lionotus* that requires clarification is the eastward extent of its distribution, including the exact ubication of the areal borders between this species and the similar *N. poecilopus* in central Panama.

***Norops magnaphallus* (Poe & Ibáñez 2007)**

Large Phallus Anole; Anolis vergote, Anolis muy macho

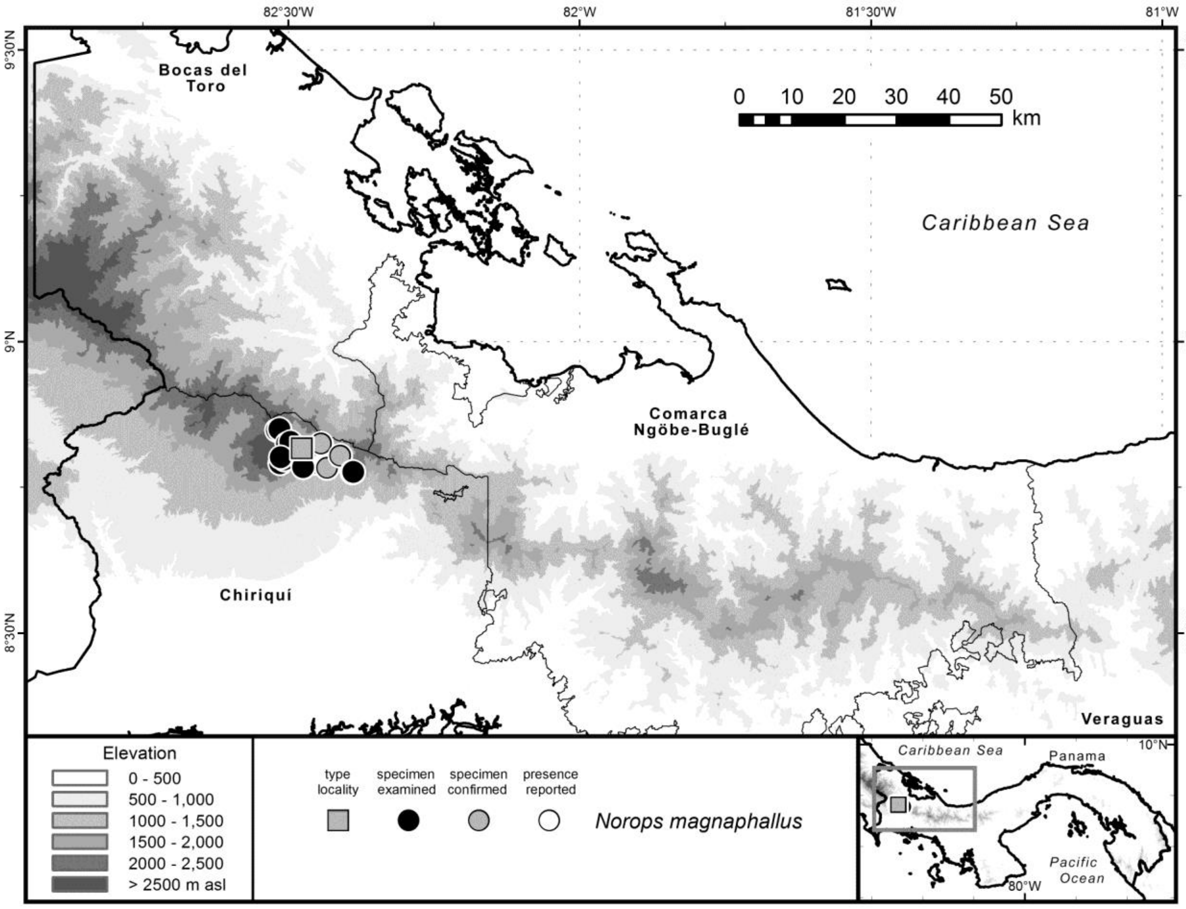
Figures 4.30A; 4.36; 4.39; 4.99G; Maps 4.7; 4.8; 4.62.

Anolis magnaphallus: Poe & Ibáñez (2007), Jaramillo et al. (2010); Wilson & Johnson (2010); Bienentreu (2011); Lotzkat et al. (2011); Uetz & Hošek (2014).

Anolis pachypus: Slevin (1942); Walters (1953); Peters & Donoso-Barros (1970: in part.); Auth (1994: in part.); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.); Köhler et al. (2007: in part.).

Norops pachypus: Savage (2002: in part.).

Holotype. MSB 72579, male, from "eastern entrance to Sendero Quetzales, 8 km N of Boquete, approximately 08°49.0'N, 82°28.6'W, Chiriquí Province, Panama" (Poe & Ibáñez 2007).



Map 4.62: Distribution of *Norops magnaphallus*.

Geographic distribution. Endemic to the Serranía de Talamanca of western Panama, 1033–2580 m asl. Only recorded from the Pacific versant in Chiriquí, between the N and E slopes of Volcán Barú at 82.52°W and Cerro Altrillería near Alto Jaramillo at 82.38°W.

Diagnosis. A medium-sized *Norops* (maximum SVL 59 mm) with long to very long legs (4th toe reaching at least to eye, usually well beyond) that is very similar to *N. benedikti, N. pachypus,* and *N. pseudopachypus.* It differs from these three species in having the male dewlap solid red without yellow areas (vs. red with a yellow anterior margin in *N. benedikti,* red with a central yellow blotch in *N. pachypus,* and solid yellow, sometimes with a suggestion of orange posteriorly, in *N. pseudopachypus*). It further differs from *N. benedikti* and *N. pseudopachypus* in having 4 or fewer, rarely 5, IO and IP/SS, respectively (vs. 5 or more, rarely 4), and in having a light gray tongue in life (vs. dark gray). *Norops magnaphallus* differs from the superficially similar *N. humilis* in the color of the male dewlap (solid red with yellow margin in *N. humilis*) and by the presence of only 2 slightly enlarged middorsal rows (vs. 8–12 rows of greatly enlarged, strongly keeled middorsal rows). It can be distinguished from the superficially similar *N. lemurinus* by the presenceof 2–4 scales between the supraorbital semicircles (vs. 0–1 in *N. lemurinus*) as well as by its usually smooth to weakly keeled ventrals (vs. strongly keeled).

Description. TOL to 148 mm*; SVL to 59 mm*; legs long (tip of 4th toe of adpressed hind limb usually reaching beyond eye); D keeled; V smooth to keeled; caudals keeled; Drows 2*, slightly enlarged; SAM 126–158*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 27–32*; 4finger 22–25*; IO 2–4*; IP/SS 2–4*; SBO/SPL 2*; loreals keeled, 47–97* in 7–12* rows; male dewlap moderate, female dewlap small.

The hemipenis of *Norops magnaphallus* is a stout bilobate organ with short, stout lobes and an asulcate processus; lobes calyculate, truncus with transverse folds.

Coloration in life. Generally similar to *Norops pachypus,* but usually with a more clear-cut and contrasting pattern. D and L surfaces light grayish brown to dark brown, variably marked with chevrons, bars, and/or blotches; often with a broad middorsal band, females often with a narrow middorsal stripe; often with a dark pre- and postocular stripe extending posteriorly onto flanks and a light labial stripe extending posteriorly to shoulder; a dark interorbital bar and vaguely lyriform occipital marking usually present; V surfaces white to light gray, sometimes sparsely mottled with darker pigment, especially on ventrolateral portions and chin area; considerable portions of reddish tonalities present in some specimens; tongue light gray; male dewlap red, female dewlap white to red.

The male SMF 89734 was recorded as follows: D and L ground color Drab-Gray (119D); D and L surfaces of body, tail, and limbs with Brussels Brown (121B) transverse markings and spots, two Brussels Brown (121B) postorbital stripes bordered by Raw Umber (223) present, the lower one reaching to shoulder, the upper one extending dorsolaterally until midbody; head with a preorbital stripe, an interorbital bar and an occipital bar of the same colors; snout and parietal region Cinnamon (123A); L surfaces of head and neck dirty white with a suggestion of Sulfur Yellow (157), and Pratt's Rufous (140) mottling around lips; V ground color dirty white with a suggestion of Cream Color (54) with sparsely distributed Pale Neutral Gray (86) mottling and the suggestion of a Pale Neutral Gray (86) midventral line on body; iris Ferruginous (41); dewlap Burnt Orange (116) with a suggestion of Spectrum Red (11) and dirty white scales. The dewlap of the male SMF 89728 was recorded as Carmine (8). Joe-Felix Bienentreu recorded the male MHCH 2224 as follows: D and L ground colour Straw Yellow (56); a Sepia (119) L stripe extending from eye to midbody, disintegrating into blotches; a dirty white supralabial stripe extending from nostril to shoulder; V surface of head dirty white, mottled with Burnt Orange (116) and Sepia (119); dewlap Mahogany Red (132B), with dirty white scales.

The female SMF 89735 was recorded as follows: D and L ground color Sayal Brown (223C), grading into Drab-Gray (119D) laterally; a Chamois (123D) middorsal stripe bordered by Mars Brown (223A) extending from occipital region posteriorly and dissolving into elongated blotches on tail; a Raw Umber (123) interorbital bar bordered by Prout's Brown (121A); V surfaces dirty white with a suggestion of Pale Horn Color (91); iris Cinnamon-Rufous (40); dewlap dirty white with dirty white scales. Joe-Felix Bienentreu recorded the female SMF 90127 as follows: Chin and throat area Burnt Orange (116), mottled with Vandyke Brown (121); dewlap Orange-Rufuos (132C), grading into Salmon Color (106) anterior to center, with Vandyke Brown (121), and Orange Rufuos (132C) scales.

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration is similar to that in life, apart from that most or all reddish shades have faded, bronze metallic hues are visible in most specimens, and bluish gray ones in some; the formerly red male dewlaps are assuming a translucent white, but some still retain orangish shadings to a certain extent.

Natural history notes. Active individuals were found at daytime on the ground, sleeping individuals were perched on low vegetation 0.5–1.6 m above ground.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Norops magnaphallus,* and assigned that species to the IUCN category LC. I calculated the species' EVS as 6 (range) + 3 (persecution) + 3 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of just 64 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category CR according to IUCN (2001) criterion B1b(iii).

Remarks. The morphological data obtained from my examined material, as presented by Bienentreu (2011) and Lotzkat et al. (2011), greatly extends the documented morphological variation within *Norops magnaphallus,* e.g., by raising the maximum SVL to 59 mm. Most notably, my dataset fails to confirm most of the pholidotic characters, especially the differences in loreals, D, and SS, that were proposed to distinguish *N. magnaphallus* from *N. pachypus* by Poe & Ibañez (2007). In some characters, such as numbers of loreal scales and loreal rows, the observed incongruities might well be due to different counting methods, and in the case of Drows and SBO/SPL they definitely are. On the other hand, five of the nine "*N.*

pachypus" examined by Poe & Ibañez (2007) actually represent *N. benedikti* (MCZ 100970–2, 100976–7; see remarks for that species), which renders their comparisons especially for SS unreproducible.

The specimens SMF 90130–1 from the vicinities of the camping area Mamecillos along the road to the summit of Volcán Barú extend the highest elevation known for this species to about 2580 m asl, making it the anole species with the highest documented elevation in Panama. Previously, the upper elevational limit was given as 1600 m by Jaramillo et al. (2010), who must have overlooked the records of "*Anolis pachypus*" from the eastern slope of Volcán Barú by Walters (1953) and with explicit mention of a solid red dewlap by Slevin (1942), both from 7000 feet (= ca. 2130 m), as well as the altitudes of 1650–1700 m specified in the CHP catalogue for their paratypes CHP 1046, 1050, 1052, and 1055. The lowest documented elevation was given as 1033 m for the specimen CHP 1042 (Poe & Ibañez 2007). I herein retain this value even though it seems somewhat disputable, since the CHP catalogue states this individual to have been collected at 1650–1700 m.

Several specimens of *N. magnaphallus* were collected less than 5, some even less than 2 km from the border between Chiriquí and Bocas del Toro, and the specimens collected by JFB at Cerro Altrillería were secured less than 5 airline km from the border between Chiriquí and the Comarca Ngöbe-Buglé. These specimens render the occurrence of *N. magnaphallus* in Bocas del Toro and the Comarca Ngöbe-Buglé plausible according to the criteria applied herein. Yet, in view of the peculiar areal borders between this species and *N. benedikti* in the area N of Boquete, the northward extent of the distribution of *N. magnaphallus* remains to be investigated and its occurrence on the Caribbean slopes to be confirmed. The same applies to the exact ubication of the contact zones between this and the other three members of the *N. pachypus* complex.

Norops pachypus **(Cope 1876)**

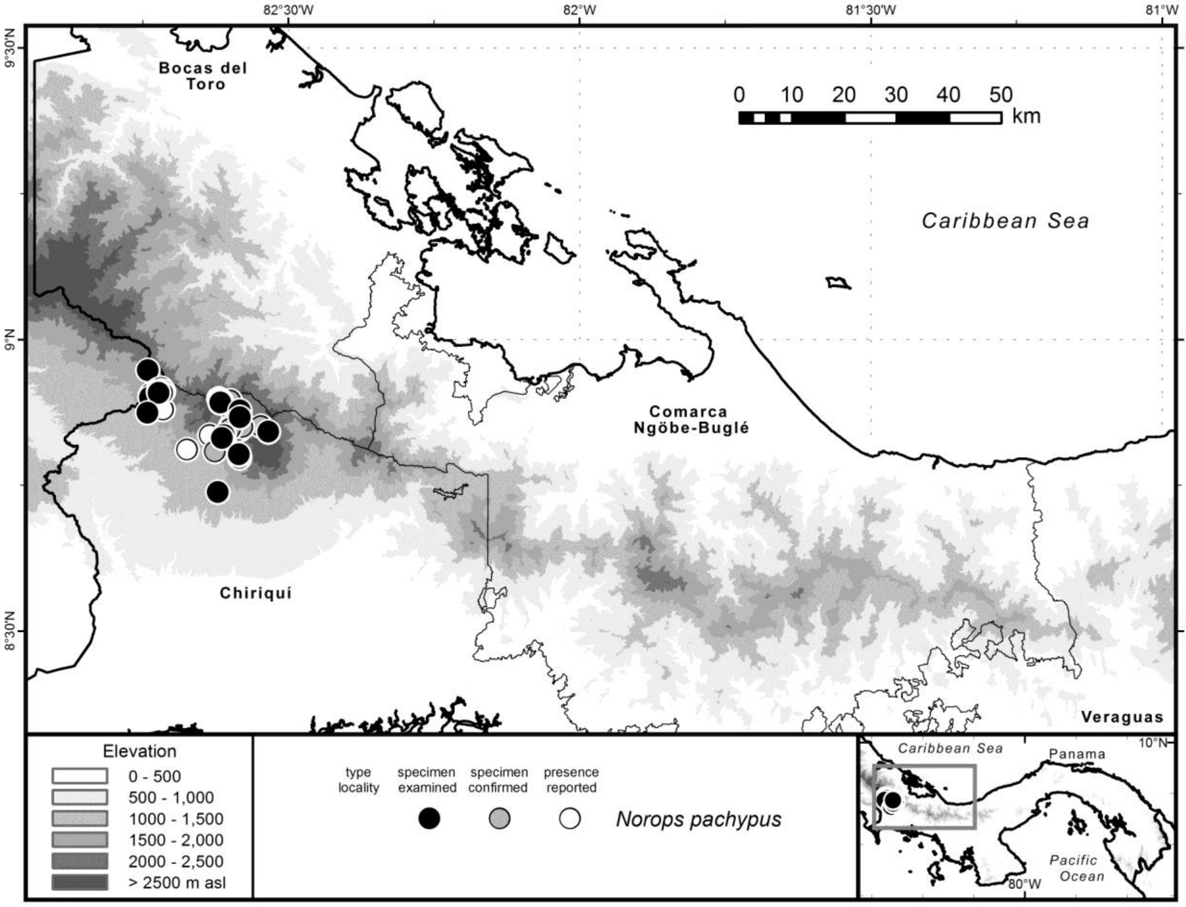
Thick-foot Anole; Anolis

Figures 4.30C–E; 4.36; 4.40; 4.99H; Maps 4.7; 4.8; 4.63.

Anolis pachypus: Cope (1876); Taylor (1956); Peters & Donoso-Barros (1970: in part.); Auth (1994: in part.); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.); Köhler et al. (2007: in part.); Poe & Ibáñez (2007: in part.), Jaramillo et al. (2010: in part.); Sasa et al. (2010: in part.); Wilson & Johnson (2010: in part.); Bienentreu (2011); Lotzkat et al. (2011); Uetz & Hošek (2014).

Holotype. USNM 30683, male, from the slope of the Pico Blanco (= Cerro Utyum, Cantón de Talamanca, Provincia de Limón fide Savage 1970, 1974, 2002), Costa Rica.

Geographic distribution. Endemic to the Talamancan Highlands of Costa Rica and western Panama, 1160–2555 m asl. In Panama, recorded from the Pacific slopes of the Serranía de Talamanca in Chiriquí, east to Paso Respingo and the W and NW slopes of Volcán Barú at about 82.52°W, between 1160–2555 m asl.



Map 4.63: Distribution of *Norops pachypus*.

Diagnosis. A medium-sized *Norops* (maximum SVL 57 mm) with long to very long legs (4th toe reaching at least to eye, usually well beyond) that is very similar to *N. benedikti, N. magnaphallus,* and *N. pseudopachypus.* It differs from these three species in having the male dewlap red with a central yellow blotch, and in Panama usually also with a narrow yellow margin (vs. red with a yellow anterior margin in *N. benedikti,* solid red without yellow areas in *N. magnaphallus,* and solid yellow, sometimes with a suggestion of orange posteriorly, in *N. pseudopachypus*). It further differs from *N. benedikti* and *N. pseudopachypus* in having 4 or fewer, rarely 5, IO and IP/SS, respectively (vs. 5 or more, rarely 4), and in having a light gray tongue in life (vs. dark gray). *Norops pachypus* differs from the superficially similar *N. humilis* in the color of the male dewlap (solid red with yellow margin but no yellow blotch in *N. humilis*) and by the presence of only 2 slightly enlarged middorsal rows (vs. 8–12 rows of greatly enlarged, strongly keeled middorsal rows). It can be distinguished from the superficially similar *N. lemurinus* by the presence of 2–5 scales between the supraorbital semicircles (vs. 0–1 in *N. lemurinus*) as well as by its usually smooth to weakly keeled ventrals (vs. strongly keeled).

Description. TOL to 151 mm*; SVL to 57 mm*; legs long (tip of 4th toe of adpressed hind limb reaching at least to eye, usually well beyond); D keeled; V smooth to keeled; caudals keeled; Drows 2*, slightly enlarged; SAM 126–158*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 26–34*; 4finger 20–24*; IO 2–5*; IP/SS 2–5*; SBO/SPL 2–3*; loreals keeled, 41–75* in 7–11* rows; male dewlap moderate, female dewlap small.

The hemipenis of *Norops pachypus* is a stout bilobate organ with short, stout lobes and an asulcate processus; lobes calyculate, truncus with transverse folds.

Coloration in life. Generally similar to *Norops magnaphallus,* but usually with less contrasting and clear-cut pattern. D and L surfaces light grayish brown to dark brown, variably marked with chevrons, bars, and/or blotches; some specimens with an irregular, broad middorsal band, females often with a narrow middorsal stripe; often with a dark pre- and postocular stripe and/or a light labial stripe extending posteriorly to level shoulder; a dark interorbital bar and vaguely lyriform occipital marking usually present; V surfaces white to light gray, sometimes sparsely mottled with darker pigment, especially on ventrolateral portions and chin area; considerable portions of reddish tonalities present in some specimens; tongue light gray; male dewlap red with a central yellow blotch and (in Panama) usually a narrow yellow margin, female dewlap usually white, with red portions in some individuals.

The male SMF 89504 was recorded as follows: D ground color Raw Sienna (136), grading into Drab-Gray (119D) mottled with Hair Brown (119A) laterally; middorsum with a diffuse Light Drab (119C) longitudinal line bearing a series of small Sepia (119) blotches; L surface of body with a few Pale Pinkish Buff (121D) transverse lines or blotches irregularly bordered by Vinaceous Pink (221C); interorbital stripe, preorbital stripe, and transverse markings on occipital region Cinnamon-Drab (219C) bordered by Warm Sepia (221A); a broad postorbital stripe of the same color diffuses behind ear opening, and is bordered by two Cream Color (54) postorbital stripes, the lower of which extends to insertion of forelimbs; subocular region Cream Color (54); D and L surfaces of tail Fawn Color (54) with Burnt Umber (22) transverse bars bordered by Pale Horn Color (92) and diffusing laterally; V surfaces of body and head Smoke Gray (44) with a suggestion of dirty white, mottled with Hair Brown (119A) on chin region; V surfaces of limbs and base of tail Smoke Gray (44) diffusely mottled with Hair Brown (119A); V surface of posterior portion of tail Smoke Gray (45) with Ferruginous (41) shadings anteriorly; iris Cinnamon-Rufous (40); tongue Pale Horn Color (92), grading into Grayish Horn Color (91) at the tip; dewlap Scarlet (14) with a large Spectrum Yellow (55) central blotch and a very narrow Spectrum Yellow (55) anterior margin; dewlap scales dirty white, some bordered by Glaucous (79), or completely Glaucous (79).

During a trip to Jurutungo, a field party comprising AB, GK, MP, and JS recorded the dewlap of the male SMF 85269 as Flame Scarlet (15) with a Sulphur Yellow (57) blotch.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that most or all reddish shades have faded, bronze metallic hues are visible in all specimens, and bluish gray ones in some; most of the formerly red and yellow dewlaps are translucent white, but some retain orangish hues.

Natural history notes. Active individuals were found at daytime on the ground, sleeping individuals perched on low vegetation 0.5–2 m above ground.

Remarks. The morphological data obtained from my examined material, as presented by Bienentreu (2011) and Lotzkat et al. (2011), greatly extends the documented morphological variation within *Norops pachypus,* e.g., by raising the maximum SVL to 57 mm. For characters stated to distinguish *N. pachypus* from *N. magnaphallus* by Poe & Ibáñez (2007), see remarks for the latter species.

The specimens SMF 90143–47 and MHCH 2241, collected by JFB and FH at Alto Respingo up to 2555 m asl, are the easternmost specimens of *Norops pachypus* known to me and raise the highest documented elevation for this species which was previously reported as 2140 m for Panama (Jaramillo et al. 2010) and 2500 m for the species as a whole (Wilson & Johnson 2010). The same authors gave the lower elevational extreme as 1370 m, which is lowered to 1160 m by the female SMF 89363 from the village Cordillera. At Jurutungo, Las Nubes, and Paso Respingo, several specimens of *N. pachypus* were collected less than 2, some even less than 1 km from the border between Chiriquí and Bocas del Toro, rendering the occurrence of *N. pachypus* in Bocas del Toro plausible according to the criteria applied herein. Yet, in view of the peculiar areal borders between this species and *N. benedikti* at Jurutungo, the northward extent of the distribution of *N. pachypus* remains to be investigated and its occurrence on the Caribbean slopes to be confirmed.

Apparently, many specimens of *Norops pachypus* remain catalogued under synonymous names in several collections. This applies to all Panamanian specimens catalogued as *Anolis curtus* at KU and as *A. tropidolepis* at FMNH and MCZ. The other way round, I regard all "*A. pachypus*" collected on "N slope Cerro Pando" during the expedition carried out in 1966 by Linda Trueb, William Duellman, and Charles Myers (MCZ 100970–79, KU 113257-331) to actually represent individuals of *N. benedikti.* The listing of *N. pachypus* for the Humedal de Importancia Internacional San San Pond Sak (ANAM 2004) is clearly erroneous since this species is not to be expected anywhere near sea level. See Bienentreu (2011) and Lotzkat et al. (2011) for more confusions involving *N. pachypus.*

The common name "Thick Anole" (Frank & Ramus 1995) is yet another example of an incompletely translated specific epithet. I suggest "Thick-foot Anole" as an English common name instead.

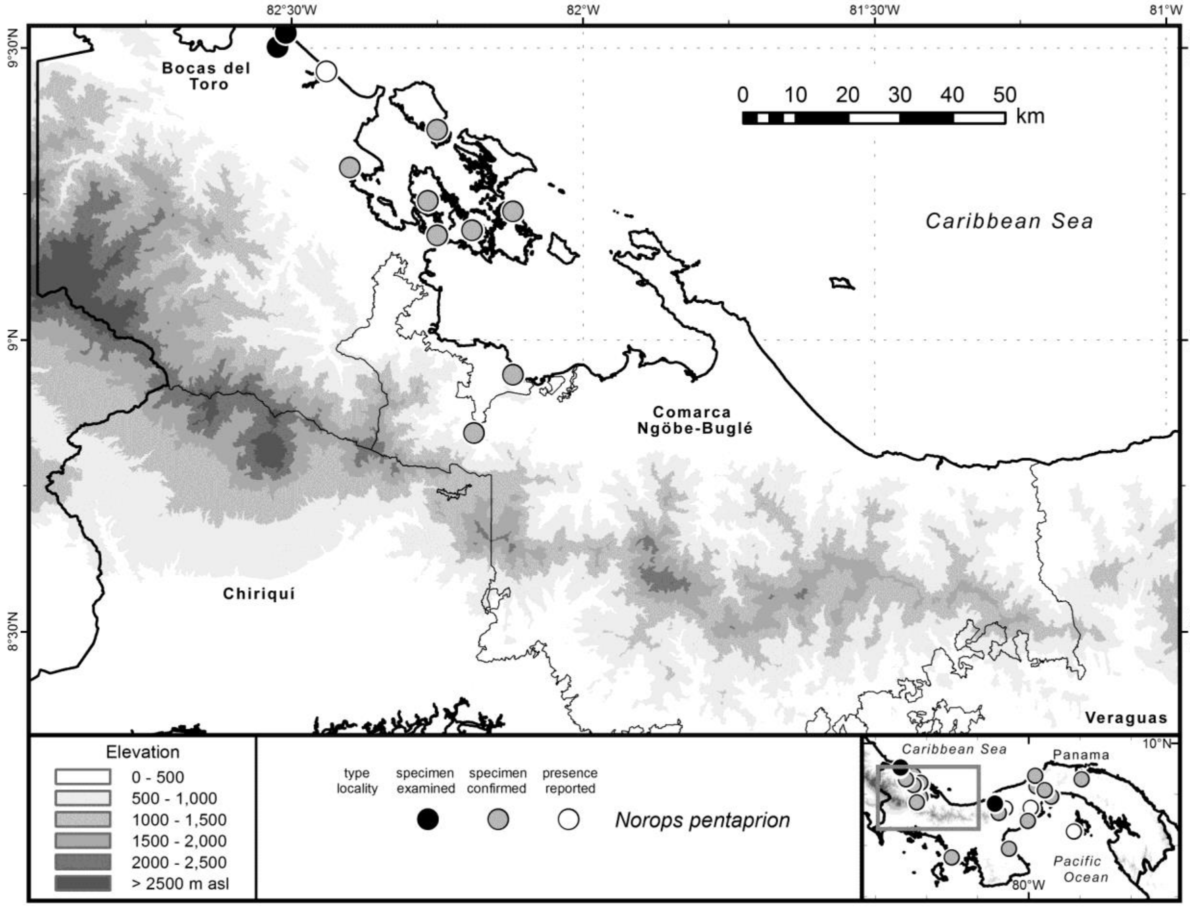
Norops pentaprion (Cope 1862)

Lichen Anole; Anolis

Figures 4.52; 4.57; 4.100A; Maps 4.10; 4.64.

Anolis panamensis: Boulenger (1890).

Anolis pentaprion: Cope (1862b); Swanson (1945); Cochran (1946); Taylor (1956: in part.); Myers & Rand (1969); Peters & Donoso-Barros (1970: in part.); Myers (1971b: in part.); Rand & Myers (1990); Auth (1994: in part.); Ibáñez et al. (1996, 1997, 2001: in part.); Young et al. (1999: in part.); ANAM (2004); Poe (2004); Fundación PA.NA.M.A. (2007: in part.); Köhler (2008: in part.); Fläschendräger & Wijffels (2009: in part.); Hamad (2009); Poe et al. (2009); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010: in part.); Köhler (2010); Sasa et al. (2010: in part.); Stadler (2010); Wilson & Johnson (2010: in part.); Uetz & Hošek (2014).



Map 4.64: Distribution of *Norops pentaprion.*

Neotype. SMF 83608, male, from "San Rafael, ca. 15 km S Los Chiles, 10.73719°N, 84.49378°W, 60 m elevation, Alajuela Province, Costa Rica" (Köhler 2010; holotype at USNM apparently lost, from New Grenada, near the river Truando).

Geographic distribution. Southern Nicaragua to northwestern Colombia, 0–900 m asl. In Panama, along the Caribbean versant throughout the country, including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, as well as on the Pacific versant from Veraguas eastwards apparently absent from Chiriquí). In the Cordillera Central, recorded from the Caribbean slopes N La Fortuna, near PNGDOTH, and from PNAC, up to 620 m asl.

Diagnosis. A medium-sized to large *Norops* (maximum SVL 77 mm) with very short legs (4th toe reaching at most to ear) that is most similar in external morphology to *N. charlesmyersi, N. fungosus,* and *N. salvini.* It can readily be distinguished from the very similar *N. charlesmyersi* by its purple dewlap which bears many rows of densely arranged small scales in both sexes (vs. red with few rows of widely spaced large scales, see Figs. 4.52; 4.56–4.57). It differs from the latter two species, as well as from the superficially similar *N. datzorum,* in lacking enlarged postcloacal scales in males (vs. present) and in having a conspicuous serrated dorsal tail crest (vs. at most strongly keeled middorsal caudal scales).

Description. TOL to 148 mm; SVL to 77 mm; tail very short, TL/SVL < 1.42; legs very short (tip of 4th toe of adpressed hind limb reaching at most to ear); D and V smooth; caudals keeled, conspicuous serrated D tail crest present; Drows 2 slightly enlarged; SAM 134–190; males without enlarged PC, but can raise a low nuchal crest; lamellar pads broad; 4toe 36–39*; 4finger 24–31*; IO 0–1; IP/SS 1–4; SBO/SPL 0; loreals slightly keeled, 13–29 in 3–6 rows; male dewlap large to very large, female dewlap moderate (own data combined with that of Köhler 2010; see chapter 4.1.6 for morphological data based exclusively on Panamanian specimens).

The hemipenis of *Norops pentaprion* is a large bilobed organ; small asulcate processus present; apex finely calyculate; truncus with transverse folds (Köhler 2010).

Coloration in life. Ground color almost white to dark brown, with lighter blotches; dark crossbands on tail and limbs; gular region and corners of mouth with a bluish hue, lining of throat black; V surfaces speckled or reticulated with darker pigment especially laterally and under chin; dewlap pink to magenta with purple blotches between the gorgetal-sternal scale rows in both sexes.

The male SMF 90150 (Fig. 4.57B; 4.100A) was described as follows: Ground color dirty white with a suggestion of Pearl Gray (81), with shadings of Walnut Brown (221B) and dense Sepia (219) and Mars Brown (223A) blotches and mottling suggesting a reticulum in many parts; tail with a series of Sepia (219) with a suggestion of Mars Brown (223A) crossbands; V surfaces of head and chest Light Sky Blue (168D) with Mars Brown (223A) mottling; iris Cinnamon (123A); dewlap Rose (9), with dirty white with a suggestion of Light Sky Blue (168D) scales arranged in neat rows and partly fusing Purple (1) blotches between the gorgetal-sternal rows.

Coloration in preservative. After 4.5 years in 70% ethanol, the coloration is similar to that in life, apart from that the bluish hues have faded and the red dewlap coloration has become less intense, but the dewlaps still retain some red after 4.5 years.

Natural history notes. Diurnal and arboreal, uses its prehensile tail for climbing. The three individuals which I encountered at San San Pond Sak (my only collected specimens in Panama) were sleeping on vegetation at night: MHCH 2254 was found 2.5 m above ground on a leaf in a strip of mangrove bordering the Río San San, whereas SMF 90150–1 were clinging to extremely long "beards" of *Tillandsia usneoides* hanging from the rather singular large trees in an otherwise open, swampy pasture, 3 m above ground. Several additional individuals were spotted in equivalent perches up to approximately 6 m above ground.

Remarks. The presence of *Norops pentaprion* in my study area is based on the specimen POE 1855 from "13.8 km S of turnoff to Almirante (14.5 km N of province boundary), Fortuna road, 235 m" (Köhler 2010). Although stated to come from Bocas del Toro province (a common misconception concerning several specimens collected by different workers on the Caribbean descent of the road leading from La Fortuna to Chiriquí Grande), this specimen simultaneously documents the presence of *N. pentaprion* in the Comarca Ngöbe-Buglé.

Köhler (2010) restricted the distribution of *Norops pentaprion* to Nicaragua and south of it, and described populations formerly referred to as *N. pentaprion* from Pacific Costa Rica and adjacent western Panama as a separate species, *N. charlesmyersi.* As far as I know, all past records of *N. pentaprion* from Chiriquí are assignable to *N. charlesmyersi.* I could not trace any record that would substantiate the upper elevational limit of 1830 m asl for Panama (Jaramillo et al. 2010) which I must assume to result from a misidentification of a *N. fungosus* or *N. salvini.* Indeed, this altitude coincides with the record of Walters (1953) from near Cerro Punta, based on the specimen AMNH 69621 which later became the holotype of *N. vociferans* (Myers 1971b, now a synonym of *N. salvini*). Thus, I refrain from adopting this value, just as the maximum elevation of 1780 m in Mexico (Köhler 2008; Wilson & Johnson 2010) that must be based on a representative of *N. beckeri* or *N. cristifer* (Köhler 2010), and stick to the 900 m limit "traditionally" provided for Costa Rica (Savage 2002; Sasa et al. 2010). The highest Panamanian record known to me is from PNAC ("Cerro Trinidad y Cerro Vallolí"; Ibáñez et al. 1996), my georeference of which yields a SRTM elevation of approximately 620

m. Taking into account that *N. charlesmyersi* has been collected slightly above 1000 m at la Fortuna, I am convinced that *N. pentaprion* occurs at comparable elevations in Panama.

***Norops polylepis* (Peters 1874)**

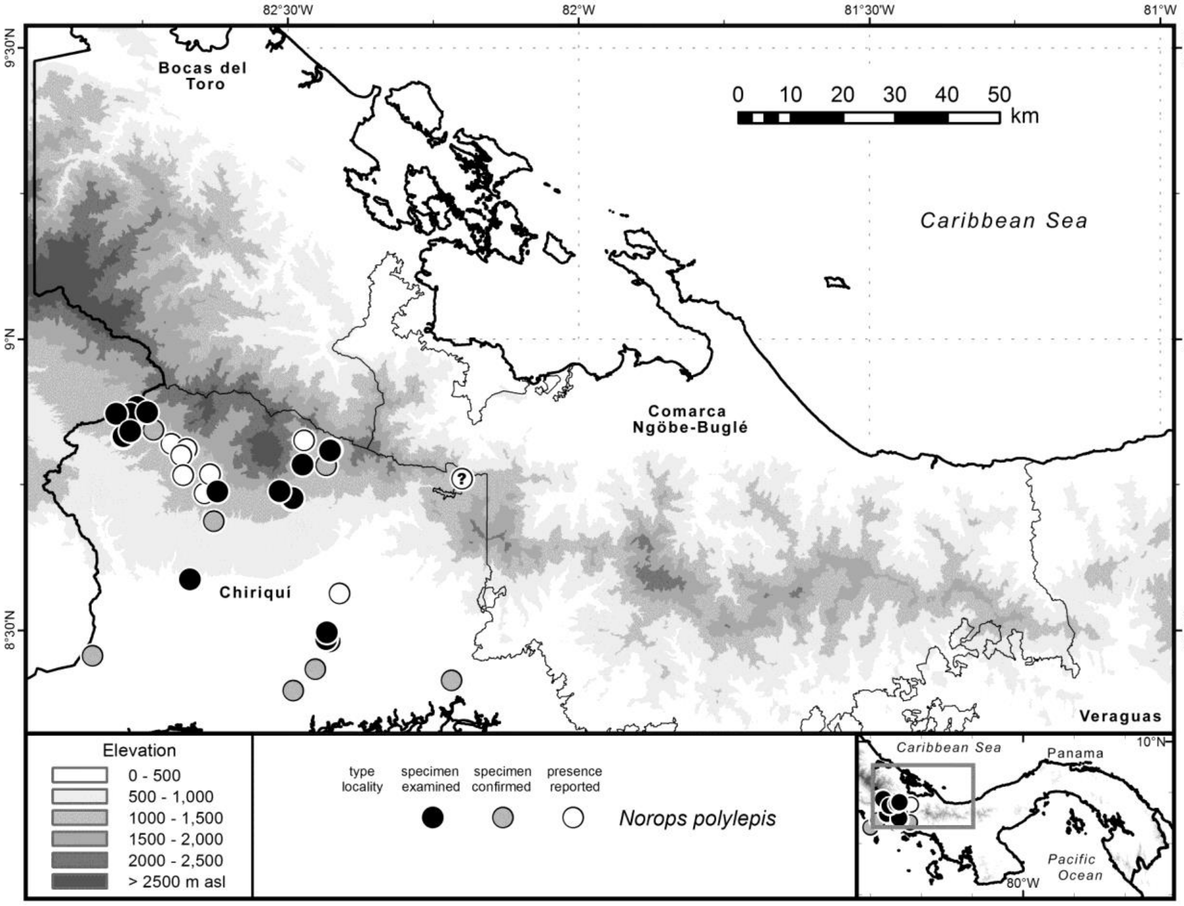
Many-scaled Anole; Anolis

Figures 4.62C; 4.63C; 4.64; 4.66; 4.100B; Maps 4.12; 4.13; 4.65.

Anolis polylepis: Peters (1874); Slevin (1942: in part.); Taylor (1956); Peters & Donoso-Barros (1970); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Ibáñez (2006: in part.); Fundación PA.NA.M.A. (2007); Köhler et al. (2007, 2008; 2010b, 2012a, b); Fläschendräger & Wijffels (2009); Hamad (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Lotzkat & Hertz (2011); Batista & Ponce (2011); Lotzkat et al. (2012a); Uetz & Hošek (2014).

Syntypes. ZMB 7825–26, 7830, 58002–09, and MCZ 21962-63 from "Chiriquí" (Köhler et al. 2010b).

Geographic distribution. Pacific versant of Costa Rica and adjacent western Panama, 0–1615 m asl. In Panama, only recorded from Chiriquí. In the Cordillera Central, along the Pacific slopes of the Serranía de Talamanca east to the Fortuna area, up to 1615 m asl.



Map 4.65: Distribution of *Norops polylepis*.

Diagnosis. A medium-sized *Norops* (maximum SVL 59 mm) with long legs (4th toe reaching to eye or beyond) that is most similar in external morphology to *N. gaigei* and *N. limifrons*. It can readily be distinguished from these species by its male dewlap which is yellow with a basal orange portion and bears somewhat unevenly distributed rows of more than 25 small scales (vs. similarly colored but with equally distributed rows each comprising 15 or fewer scales in *N. gaigei,* and white with yellow portions in *N. limifrons*), and by its relatively large, bilobed hemipenis (vs. small, unilobed). It further differs from *N. gaigei* in having smooth, at most faintly keeled ventral scales (vs. strongly keeled) and several usually slightly enlarged postcloacal scales in males (vs. one pair of greatly enlarged PC). *Norops polylepis* is superficially similar to *N. carpenteri* and members of the *N. kemptoni* complex, from which it differs in having long legs (vs. short, 4th toe not reaching eye).

Description. TOL to 169 mm*; SVL to 53 mm; tail long, TL/SVL 1.69–2.19; legs long (tip of 4th toe of adpressed hind limb reaching at least to eye, usually well beyond); D keeled; V juxtaposed, smooth to faintly keeled; caudals keeled; Drows 0–4, often only slightly enlarged; SAM 124–180*; males with two or more pairs of slightly enlarged PC, can raise a low nuchal crest; lamellar pads relatively broad; 4toe 27–36*; 4finger 16–31*; IO 1–5; IP/SS 2–7; SBO/SPL 0–1; loreals keeled, 32–92 in 4–10 rows; male dewlap large, female dewlap very small (own data combined with that of Köhler et al. 2010b; see chapter 4.1.7.2 for detailed morphological data based exclusively on Panamanian specimens).

The hemipenis of *Norops polylepis* (Fig. 4.63C) is a relatively large, bilobed organ with short, stout lobes. Asulcate processus present, lobes finely calyculate, truncus with transverse folds.

Coloration in life. D and L surfaces light grayish to very dark brown, unicolor, mottled, or variably marked with blotches; females often with a narrow to broad middorsal stripe often bordered by darker stripes; many individuals with a light L stripe extending from shoulder posteriorly, sometimes to groin; V surfaces unicolor cream or finely mottled; male dewlap yellow with an orange basal portion around the basally concentrated gorgetal-sternal rows, female dewlape white, mottled with dark, or yellowish.

The male SMF 89509 (Fig. 4.66H) was described as follows: D ground color Citrine (51) suffused with Dark Brownish Olive (129); a narrow Dark Brownish Olive (129) interorbital bar present; L stripe Cream Color (54); venter Cream Color (54), with a suggestion of Lime Green (59); V surfaces of limbs Dark Drab (119B); iris Raw Sienna (136); dewlap Spectrum Orange (17) with the apical portion more yellowish; gorgetals Raw Umber (23).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that all yellow and reddish shades have faded; male dewlaps whitish, usually translucent.

Natural history notes. During daytime, individuals were encountered active on the floor or low vegetation, at night they were found sleeping up to 3 m above ground. An uncollected individual sleeping on a leaf of *Cyclanthus bipartitus* on the banks of Río Cochea had been approached very closely and almost seized by an adult *Imantodes cenchoa* (SMF 89772) when I found it around 20:20. At Río Pedro, *Norops polylepis* occurs in very close para- if not sympatry with *N. kemptoni* around 1320–1360 m asl, just as at the headwaters of Río Chevo around 1615 m asl.

Remarks. As detailed by Köhler et al. (2012b) and in chapter 4.1.7.2, *Norops gaigei* has repeatedly been misidentified as *N. polylepis* in western Panama. See remarks for the former species and chapter 4.1.7.2 for details.

The occurrence of *Norops polylepis* in the Comarca Ngöbe-Buglé is rendered possible by its easternmost lowland records, and should be rendered plausible by reports from Quebradas Arena and Bijau at RFLF (de Sousa 1999; MVUP 752, 803). However, since I have not examined the underlying voucher specimens and a misidentification of members of the *N. kemptoni* complex cannot be ruled out, this record requires verification (and is therefore marked with a question mark in Map 4.65).

Köhler et al. (2008) elevated the documented upper elevational limit to 1615 m asl based on SMF 85442 from Río Chevo. Having examined this specimen, I can confirm their record. On the contrary, I regard the elevational maximum of 1980 m provided for Panama by Jaramillo et al. (2010) as erroneous, assuming it to be based on Slevin's (1942) record of CAS 79595 from "south slope of the Volcan Chiriquí at an approximate elevation of 6500 feet" (= ca. 1981 m). Notwithstanding the fact that *Norops polylepis* co-occurs along its upper elevational limit with *N. kemptoni* (along the lower elevational limit of the latter, see above), the latter species is known to occur at elevations around 1800–1900 m (own specimens from Bajo Mono) along the Pacific slope, and found down to around 1615 m (type locality at Finca Lérida) in the Boquete area E and at Río Chevo W of Volcán Barú, as well as around 1320–1360 m at Río Pedro on the S slopes of Volcán Barú. This renders the presence of *N. polylepis* at almost 2000 m very unlikely in my opinion. The listing of *Norops polylepis* for the Humedal de Importancia Internacional San San Pond Sak (ANAM 2004) is clearly erroneous since this species is not to be expected anywhere near the Caribbean coast. The same applies to the specimens MVUP 1524, 1527–29, 1532–34, and 1536 from different premontane sites on the Caribbean slopes within PILA, Bocas del Toro.

Norops pseudokemptoni (Köhler, Ponce, Sunyer & Batista 2007)

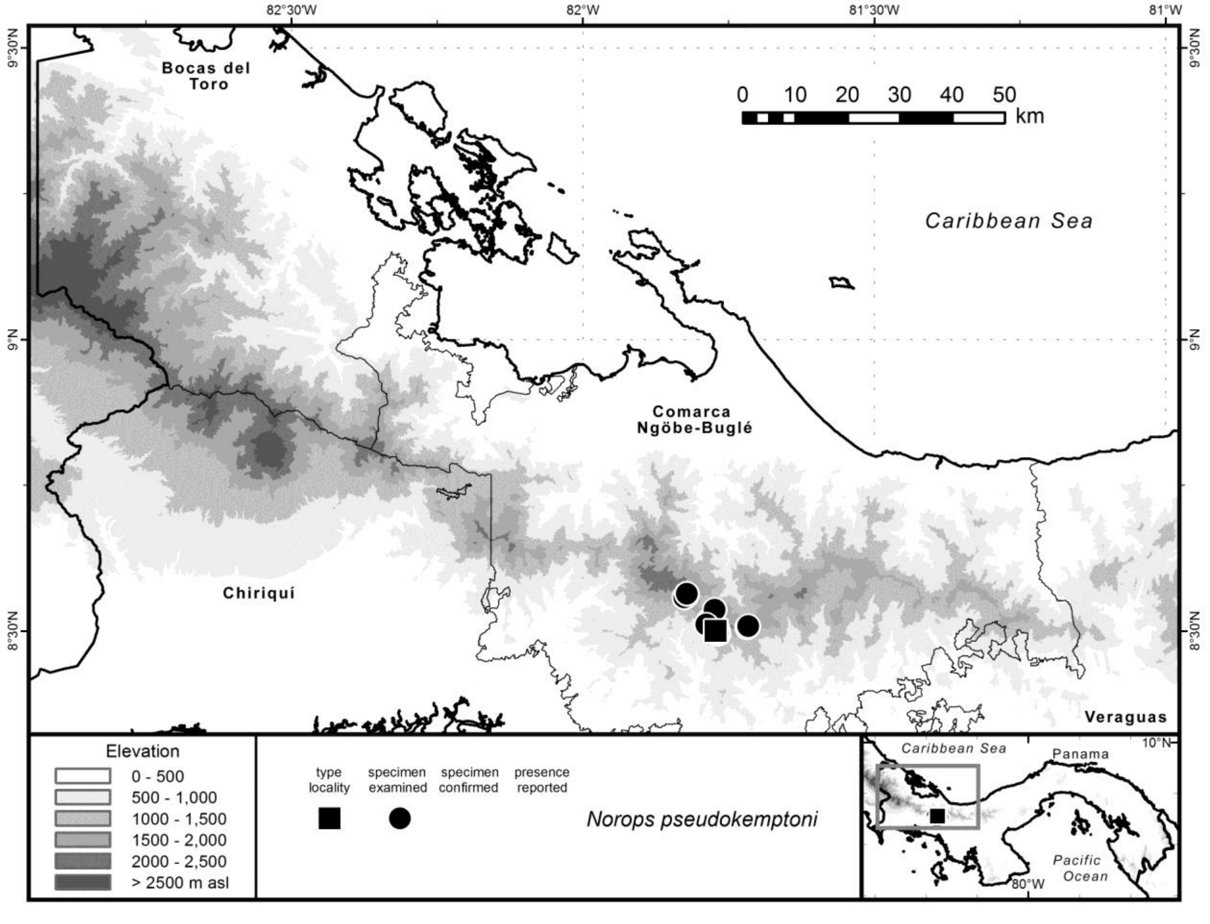
[In part modified from Lotzkat et al. (2014); see Appendix 8 for original publication]

Cerro Colorado Anole; Anolis de Cerro Colorado

Figures 4.44D; 4.45; 4.49; 4.100C; Maps 4.9; 4.66.

Anolis pseudokemptoni: Köhler et al. (2007); Ponce & Köhler (2008); Köhler (2009, 2011); Jaramillo et al. (2010); Wilson & Johnson (2010); Lotzkat et al. (2010a, 2012c, d, 2014); Gutpelet (2012); Uetz & Hošek (2014).

Holotype. SMF 85420, male, from La Nevera, 8°29'45"N, 81°46'35"W, 1600 m elevation, Serrania de Tabasara, Comarca Ngöbe Bugle, Distrito de Nole Düima, Corregimiento de Jadeberi, Panama (coordinates corrected to 8°30'N, 81°46'20"W by Lotzkat et al. 2010a).



Map 4.66: Distribution of *Norops pseudokemptoni*.

Geographic distribution. Endemic to the Cordillera Central of western Panama, 1130–2010 m asl. Recorded from the central Serranía de Tabasará in the Comarca Ngöbe-Buglé, chiefly along the Caribbean versant, between the E slopes of Cerro Saguí around 81°49'30"W and the E slopes of Cerro Santiago around 81°43'W.

Diagnosis. A medium-sized *Norops* (maximum known SVL 55 mm) with short legs (4th toe reaching to between eye and ear, rarely to eye) that is most similar in external morphology to

N. carpenteri, N. gruuo, N. fortunensis, and *N. kemptoni.* It can readily be distinguished from the former three species by the large male dewlap, which is red or red with a posterior portion of magenta, vinaceous, or similar shadings (vs. orange or yellow in the former two, and red with a greenish-yellow posterior portion in *N. fortunensis*). It further differs from *N. fortunensis* and *N. kemptoni* in having a large, bilobed hemipenis bulging the base of tail in adlt males (vs. small, unilobate, not bulging the base of tail).

Description. TOL to 153 mm*; SVL to 55 mm*; tail moderately long, TL/SVL 1.64–1.98*; legs short (tip of 4th toe of adpressed hind limb reaching to ear or slightly beyond, very rarely to eye); D slightly keeled; V smooth; caudals keeled; Drows 0–4 slightly enlarged; SAM 114–148*; males with slightly to distinctly enlarged PC, without nuchal crest; lamellar pads broad; 4toe 31–39; 4finger 20–27*; IO 1–2*; IP/SS 1–4*; SBO/SPL 0*; loreals smooth to slightly keeled, 56–100* in 6–8* rows; male dewlap large to very large, female dewlap small to moderate (data from all known specimens except MHCH 1335; see chapter 4.1.5 for detailed morphological data).

The hemipenis of *Norops pseudokemptoni* (Fig. 4.44D) is a relatively large, bilobed organ with short, stout lobes and an asulcate processus; lobes finely calyculate, truncus with transverse folds.

Coloration in life. D and L surfaces light to dark, greenish, reddish, or grayish brown, unicolor or with darker mottling or transverse bands; females often with a continuous or broken middorsal stripe that is sometimes very broad and bordered laterally by darker stripes; tail and sometimes also limbs with dark crossbands; lips white or almost white especially below eye; V surfaces white to light gray, unicolor or with sparse darker mottling; male dewlap unicolor red or red with a posterior portion of magenta, vinaceous, or similar shadings, usually with a small light-colored area on anteriormost basal portion next to chin; female dewlap usually yellow, in some individuals cream, white, or orange. *Norops pseudokemptoni* is capable of considerable metachrosis that may alter the pattern, in a way that, e.g., a unicolor light gray animal can assume reddish brown crossbands (Figs. 4.49E, F).

The young male SMF 89515 (Fig. 4.49A, G) was recorded as follows: D and L ground color Drab-Gray (119D), with Vandyke Brown (121) mottling forming transverse bands on body, limbs and base of tail; middorsum with a faint suggestion of Dark Drab (119B); D surface of head Sepia (219); lips and V surface of head dirty white with a suggestion of Pale Horn Color (92); V surfaces of body and hind limbs dirty white with a suggestion of Pearl Gray (81) with fine Fawn Color (25) mottling; V surface of front limbs as well as soles of hands and feet Light Drab (119C); V surfaces of body and tail as well as cloacal region Tawny Olive (223C); posterior portion of tail Pearl Gray (81) with a suggestion of Pale Horn Color

(92), with Dark Brownish Olive (129) transverse bars grading into Grayish Horn Color (91) ventrally; iris True Cinnamon (139); dewlap Spinel Red (108B) with a suggestion of Poppy Red (108A) posteriorly, Spectrum Red (11) anteriorly, with a Burnt Orange (116) anterior border and dirty white scales, bordered by Dark Neutral Gray (83) except for the marginals.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that red, yellow, and green shadings have faded; male dewlaps mostly whitish, but retaining certain amounts of orangish brown pigment especially along gorgetal-sternal rows; female dewlaps white.

Natural history notes. All individuals were encountered at night, sleeping on vegetation between 1 and 4 m above ground. The collection sites encompass different habitats (Figs. 2.5A, C–H; 2.6E) ranging from roadsides, riverbanks, pastures, plantations, and secondary forest to apparently pristine premontane and lower montane moist or wet forest, including cloud forest. While we found the species as low as 1130 m on the Caribbean slopes, and down to 1390 m atop the continental divide, the only two records from the Pacific slopes are much higher at 1560 and 1660 m, respectively, while still very close to the continental divide. At lower elevations on the Pacific slope, we found *Norops gruuo* instead of *N. pseudokemptoni* (Lotzkat et al. 2012c). The parapatric distribution of our collection sites of these two species suggests that they do not occur in syntopy with each other. Rather, *N. gruuo* seems to be a species of the Pacific drainage, living at premontane elevations up to around 1530 m, whereas *N. pseudokemptoni* appears to occupy the continental divide and adjacent Caribbean slopes, only descending onto the Pacific slopes down to somewhere near the upper elevational limit of *N. gruuo.*

Conservation. Jaramillo et al. (2010) calculated an EVS of 14 for *Norops pseudokemptoni,* and assigned that species to the IUCN category VU. I calculated the species' EVS as 6 (range) + 3 (persecution) + 4 (ecological distribution) = 13, indicating a high vulnerability. The currently known range of *Norops pseudokemptoni* stretches over only 13 airline km, or 16 km along the course of the continental divide. I suspect *N. pseudokemptoni* to be a true microendemic species restricted to the central Serranía de Tabasará around the region known as Cerro Colorado. Its extent of occurrence of only 32.35 km^2 (which is the smallest value calculated for any of the Talamancan small-scale endemics in this work) and the continuing deforestation (resulting in a decline of the obviously preferred forest habitats) that is obvious in the region qualify *N. pseudokemptoni* for the IUCN category CR according to IUCN (2001) criterion B1b(iii).

Remarks. The localities reported by Lotzkat et al. (2014) extend the known geographic and elevational range of *Norops pseudokemptoni.* The records from Cerro Saguí, approximately 9 km NW of the type locality, now constitute the westernmost records for the species, and raise the upper elevational limit to 2010 m. The individuals from Hacha at 1130 m set the lower elevational limit for *N. pseudokemptoni.* The trail ascending the southeastern slopes of Cerro Santiago above Río Rey, approximately 6 km E of the type locality, now constitutes the easternmost locality reported for the species, and the only locality situated below the continental divide on the Pacific slopes of the Serranía de Tabasará. Future fieldwork most probably will expand these range limits, but I am convinced that this expansion will be minor and mostly extend the current limits vertically as well as further to the east within the Comarca Ngöbe-Buglé, following my reasoning for *N. gruuo* in this regard and considering the fact that we did not find *N. pseudokemptoni* during our extensive surveys around Santa Fé.

Accordingly, while *Norops gruuo* ranges east into Veraguas province (Lotzkat et al. 2012c), *N. pseudopachypus* is distributed westerly to the Fortuna area in Chiriquí province (Lotzkat et al. 2010c), and *N. datzorum* has been reported from Costa Rica (Köhler & Vargas 2010), *N. pseudokemptoni* is the only of the four species described from the central Tabasará range by Köhler et al. (2007) that, 7 years after its description, remains known only from near its type locality in the Comarca Ngöbe-Buglé.

The examination of 20 additional specimens allows for a more comprehensive assessment of the variation in external morphology. Most notably, the minimum number of loreal scales is lowered to 56 arranged in 6 loreal rows, revealing an overlap in these characters with *Norops fortunensis*, *N. kemptoni,* and *N. gruuo* (see chapter 4.1.5). Consequently, the high number of loreal scales and rows considered unique among these four closely related species by Ponce and Köhler (2008) loses its value as a non-overlapping diagnostic character. However, animals with 70 or more loreal scales are still highly likely to be representatives of *N. pseudokemptoni.* See chapter 4.1.5 for a discussion of other characters regarded as diagnostic for the species of the *N. kemptoni* complex.

Norops pseudopachypus **(Köhler, Ponce, Sunyer & Batista 2007)**

La Nevera Anole; Anolis de La Nevera

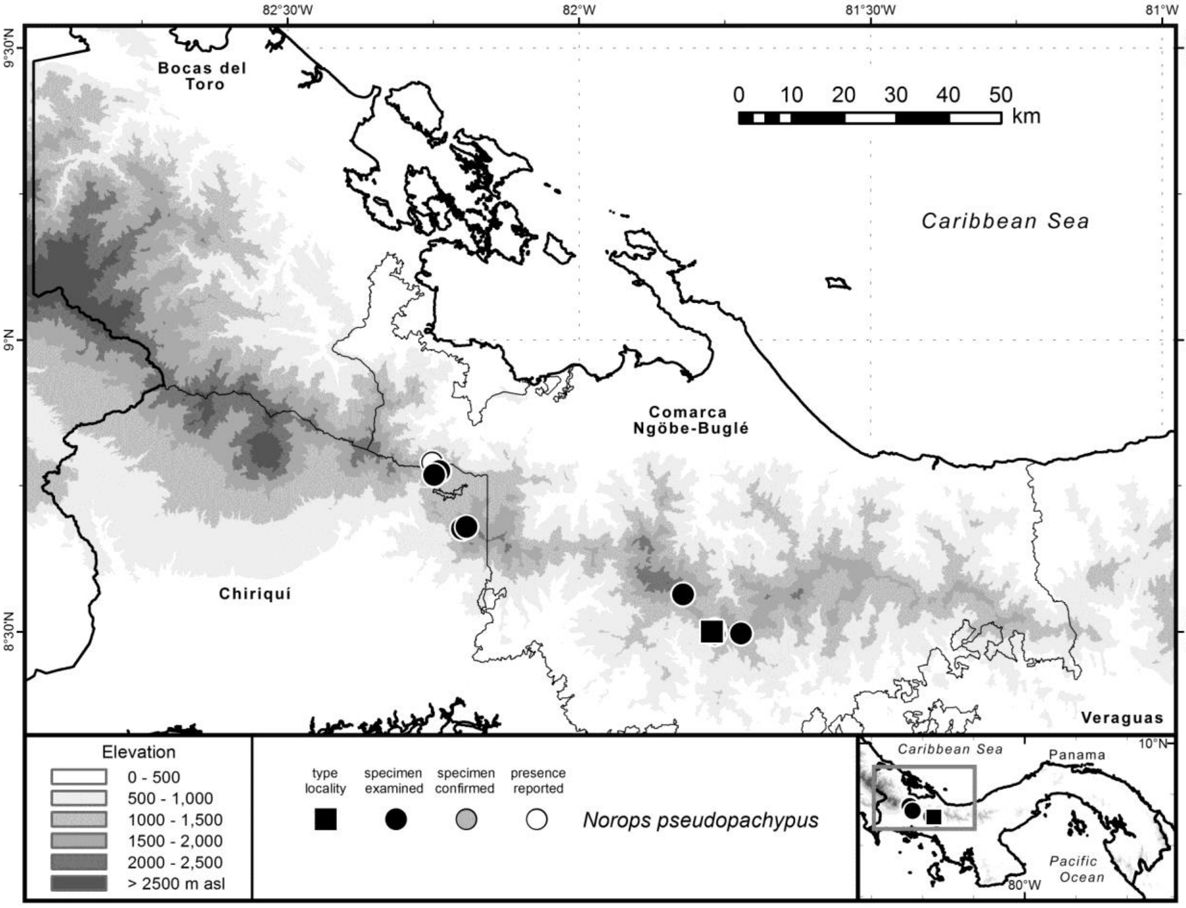
Figures 4.30I–J; 4.36; 4.41; 4.100D; Maps 4.7; 4.8; 4.67.

Anolis pachypus: Auth (1994: in part.); Young et al. (1999: in part.); Hofer & Bersier (2001); Ibáñez et al. (2001: in part.); Fundación PA.NA.M.A. (2007: in part.).

Anolis pseudopachypus: Köhler et al. (2007); Ponce & Köhler (2008); Hamad (2009); Jaramillo et al. (2010); Wilson & Johnson (2010); Lotzkat et al. (2010a, c, 2011; 2012c, d, 2014); Stadler (2010); Bienentreu (2011); Köhler (2011); Uetz & Hošek (2014).

Holotype. SMF 85153, male, from La Nevera, 8°29'45"N, 81°46'35"W, 1600 m elevation, Serrania de Tabasara, Comarca Ngöbe Bugle, Distrito de Nole Düima, Corregimiento de Jadeberi, Panama (coordinates corrected to 8°30'N, 81°46'20"W by Lotzkat et al. 2010a).

Geographic distribution. Endemic to the Cordillera Central of western Panama, 1530–2030 m asl. Recorded from Chiriquí and the Comarca Ngöbe-Buglé, along both versants between the eastern extreme of the Serranía de Talamanca at Cerro Guayabo and the eastern Slopes of Cerro Santiago.



Map 4.67: Distribution of *Norops pseudopachypus*.

Diagnosis. A medium-sized *Norops* (maximum SVL 51 mm) with long to very long legs (tip of 4th toe reaching at least to eye, usually well beyond) that is very similar to *N. benedikti, N. magnaphallus,* and *N. pachypus* in having narrow toepads and two slightly enlarged middorsal scale rows, as well as in lacking enlarged postcloacal scales in males. *Norops pseudopachypus* differs from these three species in having the male dewlap solid yellow, sometimes with a suggestion of orange posteriorly (vs. red with a yellow anterior margin in *N. benedikti,* solid red in *N. magnaphallus,* and red with a central yellow blotch in *N. pachypus*). It further differs from *N. magnaphallus* and *N. pachypus* in having 5 or more, very rarely less, IO and IP/SS, respectively (vs. 4 or fewer, rarely 5), and in having a dark gray tongue in life (vs. light gray). *Norops pseudopachypus* differs from the superficially similar *N. humilis* and *N. lemurinus* in the color of the male dewlap (solid red with yellow margin in *N. humilis* and solid red in *N. lemurinus*) and in having higher numbers of IO and IP/SS (vs. 0–3, very rarely 4, IO and 2–4 IP/SS in *N. humilis;* 0–1 IO and 2–3 IP/SS in *N. lemurinus*), among others.

Description. TOL to 139 mm*; SVL to 51 mm*; legs long (tip of 4th toe of adpressed hind limb reaching at least to eye, usually well beyond eye); D keeled; V smooth to faintly keeled; caudals keeled; Drows 2*, slightly enlarged; SAM 126–156*; males without enlarged PC or nuchal crest; lamellar pads narrow; 4toe 28–35*; 4finger 20–26*; IO 3–8*; IP/SS 4–11*; SBO/SPL 1–2*; loreals keeled, 43–110* in 8–12* rows; male dewlap moderate, female dewlap small (own data combined with that of Bienentreu 2011; see chapter 4.1.4 for detailed morphological data).

The hemipenis of *Norops pseudopachypus* is a bilobate organ with short lobes and an asulcate processus; lobes strongly calyculate, truncus with transverse folds.

Coloration in life. Generally similar to the other members of the *Norops pachypus* complex. D and L surfaces light grayish brown to dark brown, in most individuals variably marked with chevrons, bars, and/or blotches; some specimens with an irregular, broad middorsal band, females often with a narrow middorsal stripe that may be bordered by zig-zag lines; often with a dark pre- and postocular stripe and/or a light labial stripe extending posteriorly to level shoulder; a dark interorbital bar and vaguely lyriform occipital marking usually present; V surfaces white to light gray, sometimes sparsely mottled with darker pigment, especially on ventrolateral portions and chin area; considerable portions of reddish tonalities present in some specimens; tongue dark gray; male dewlap solid yellow or yellow grading into orange-yellow on the posterior portion, female dewlap usually white, but with orange or yellow hues or red portions in some individuals, and orange-red in young females.

The male SMF 89524 (Fig. 4.41I) was recorded as follows: D ground color Brussels Brown (121B) with a series of Sepia (119) flecks, grading into Smoke Gray (45) laterally; irregular Mars Brown (223A) transverse stripes partly bordered by Sepia (219) extending from flanks barely onto middorsum, but forming transverse bands on tail and head, as well as a pre- and a postorbital stripe; a dirty white postorbital stripe extending to shoulder, interrupted by a Sepia (119) line just below ear opening; lower lips dirty white suffused with Sepia (119); chin region and V surface of neck Sepia (119); V surface of body dirty white suffused with Sepia (219); V surface of limbs and anterior portion of tail Light Drab (119C) sparsely mottled with Dark Drab (119B); dewlap Orange Yellow (18), grading into Spectrum Orange (17) posteriorly; dewlap scales Sepia (119), a few gorgetals with dirty white centers.

The female SMF 89526 (Figs. 4.41E, O) was recorded as follows: D and L ground color Army Brown (219B) suffused with Sepia (119) especially on supraorbital region, snout, and flanks; a Sepia (119) middorsal stripe bordered by Mars Brown (223A) reaching from occipital region onto first third of tail; posterior portion of tail and distal portions of limbs dorsally grading into Raw Umber (223), with a series of Drab-Gray (119C) blotches including Verona Brown (223B) shadings and bordered by Sepia (219) on tail; V surfaces of head and body dirty white suffused with Ferruginous (41) laterally; chin region mottled with Sepia (119); lips dirty white; V surface of tail grading from Cinnamon-Drab (219C) into Verona Brown (223B) posteriorly; V surfaces of limbs Drab-Gray (119D) slightly mottled with Cinnamon-Drab (219C); iris Brick Red (132A); dewlap Pearl Gray (81) with mostly dirty white, but also a few Sepia (119) and even fewer Ferruginous (41) scales in the center.

Joe-Felix Bienentreu recorded the male SMF 90164 as follows: D and L ground color Sepia (219); a single Yellow Ocker (123C) D stripe extending from neck to groin; a Sepia (119) L stripe extending from eye to midbody, disintegrating into blotches; two Flesh Ocker (132D) D stripes extending to tip of tail; midbody with L Olive-Yellow (52) patches; ventrolateral surface of body with Sepia (119) and Burnt Orange (116) blotches; V surface of head Sepia (119) with dirty-white mottling; V surface of body Pale Horn Color (92), mottled with Sepia (119); iris Salmon Color (106).

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration is similar to that in life, apart from that all reddish and yellow shades have faded, bronze metallic hues are visible in all specimens, and bluish gray ones in some; the dewlaps are translucent white.

Natural history notes. Diurnal and largely terrestrial, reaching high population densities in certain places. Individuals were either encountered active at daytime, then usually fleeing towards tree buttresses or onto vegetation, or sleeping at night on low vegetation 0.3–2 m above ground. Analogously to what I observed around the lowest Caribbean collection sites of *Norops benedikti* along the Changena trail, *N. pseudopachypus* seems to occupy a niche similar to that of *N. humilis,* and to replace that species from a certain elevation upwards. For example, the lowest elevation where we found *N. pseudopachypus* on the W slope of Cerro Pata de Macho at RFLF is 1652 m asl near WP 53 and coincides with the highest collection site of *N. humilis* on this slope. On the S slope of Cerro Guayabo, JFB found *N. pseudopachypus* down to 1559 m, and *N. humilis* up to 1701 m.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Norops pseudopachypus,* and assigned that species to the IUCN category VU. I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of just 372 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. The morphological data obtained from the material examined by JFB and myself, as presented by Bienentreu (2011) and partially also by Lotzkat et al. (2011), greatly extend the documented morphological variation within *Norops pseudopachypus,* e.g., by documenting a certain variability in dewlap and overall coloration, and by raising the maximum SVL to 51 mm. The comparisons of the D head scalation as a diagnostic character between *N. pseudopachypus,* and *N. pachypus* by Köhler et al. (2007) remain valid inasmuch *N. pseudopachypus* does have smaller and more numerous D head scales and ill-defined SS, but the respective numeric values have changed in the light of larger samples of this species, and especially as a consequence of the descriptions of *N. benedikti* and *N. magnaphallus* (see chapter 4.1.4 and species accounts for the other members of the *N. pachypus* complex).

Likewise, the documented distribution of *Norops pseudopachypus* has been greatly extended horizontally and vertically (Hamad 2009; Lotzkat et al. 2010c, 2011; Bienentreu 2011). The westernmost provenance of specimens I have examined is Cerro Guayabo NW of the Fortuna reservoir, a further 11 km NNW of the localities at Cerro Pata de Macho reported by Hamad (2009) and Lotzkat et al. (2010c). Based on this record and the distribution of the members of the *N. pachypus* complex as documented in this work, I am convinced that the specimens reported as *Anolis pachypus* by Hofer & Bersier (2001) from the Caribbean slopes of Cerro Guayabo in BPPS (white circle in Map 4.67) actually represent *N. pseudopachypus.* However, the westward extension of this species' range remains to be documented, and with it the question whether or not it ranges west into Bocas del Toro province or is replaced by *N. benedikti* east of the corresponding boundary. Currently, there are sampling gaps of 16 km to the easternmost collection sites of *N. magnaphallus* and 21 km to those of *N. benedikti.* To the east, the distribution extension documented by my collection is minor, with a mere 6 km from the type locality to the E slopes of Cerro Santiago at Quebrada Ardilla. Vertically speaking, we collected the species up to 2033 m asl at Cerro Saguí, as well as down to 1533 m on the Caribbean and 1559 m on the Pacific slopes in certain places.

Norops salvini (Boulenger 1885)

[In part modified from Bienentreu et al. (2013); see Appendix 8 for original publication]

Salvin's Anole, Squealing Anole; Anolis de Salvin, Anolis chillador

Figures 4.52; 4.54; 4.100E; Maps 4.10; 4.68.

Anolis intermedius: Slevin (1942).

Anolis pentaprion: Walters (1953).

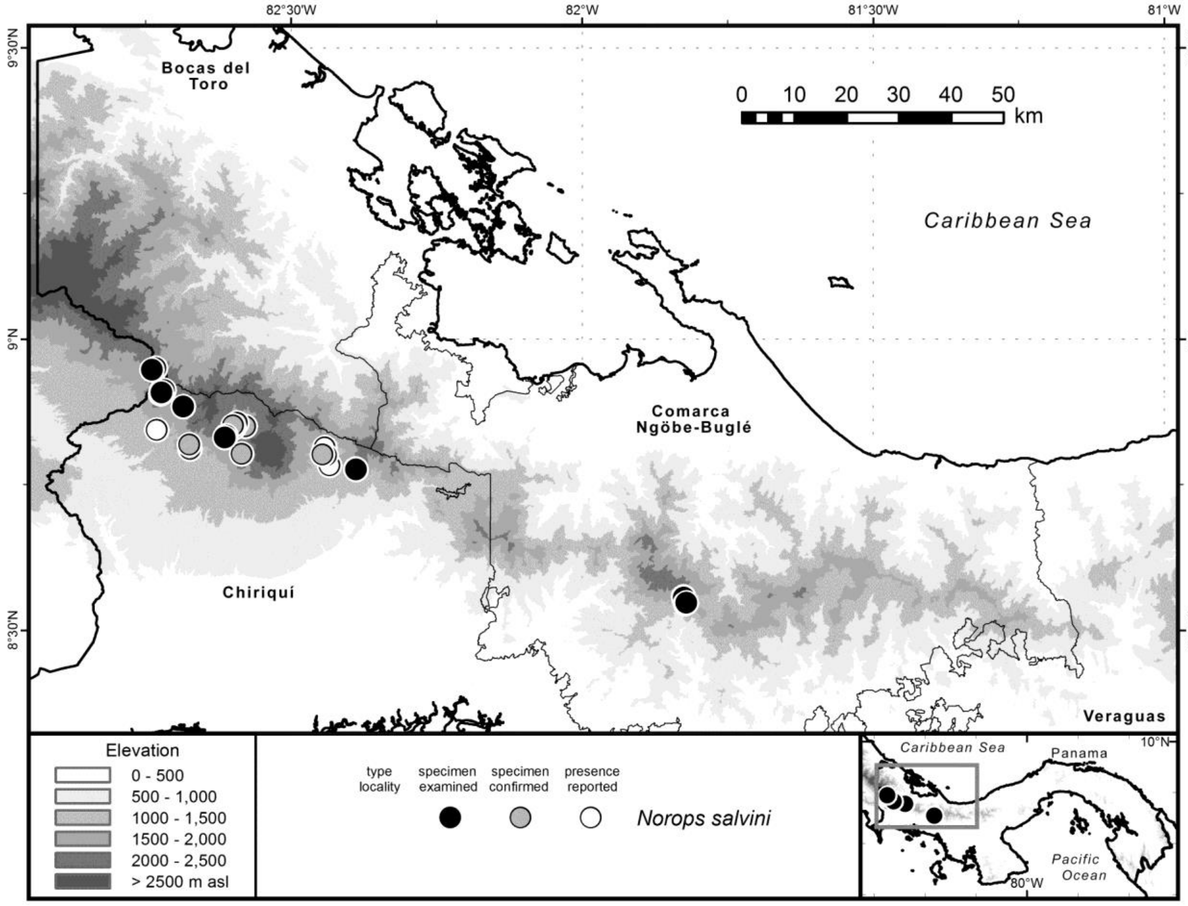
Anolis salvini: Boulenger (1885); Köhler (2007, 2010, 2011); Lotzkat et al. (2010c); Bienentreu et al. (2013); Uetz & Hošek (2014).

Anolis vociferans: Myers (1971b), Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Köhler et al. (2007); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010).

Norops vociferans: Savage (2002), Köhler (2003); Savage & Bolaños (2009).

Holotype. BMNH 1946.9.8.19, from Guatemala (locality in error fide Köhler 2007).

Geographic distribution. Endemic to the Talamancan Highlands of Costa Rica and Panama, 1310–2050 m asl. In Panama, recorded from numerous localities along the Pacific versant of the Serranía de Talamanca in Chiriquí, and from both versants of Cerro Saguí in the central Serranía de Tabasará, Comarca Ngöbe-Buglé, 1310–2050 m asl.



Map 4.68: Distribution of *Norops salvini*.

Diagnosis. A medium-sized *Norops* (maximum SVL 66 mm) with very short legs (4th toe reaching to between shoulder and ear) that is most similar in external morphology to *N. pentaprion, N. charlesmyersi,* and *N. fungosus.* It can readily be distinguished from these species by the lack of conspicuous serrated caudal crests (vs. a single dorsal caudal crest in *N. pentaprion* and *N. charlesmyersi,* and a double subcaudal crest in *N. fungosus*), and from the former two by the presence of enlarged postcloacal scales in males (vs. absence). *Norops* *salvini* differs from the superficially similar *N. datzorum* in dewlap coloration which is red in males and red, blue, or purple in females (vs. yellow in males and white, yellow, or orange in females) and by lacking multiple keels on the dorsal head scales (vs. all dorsal head scales markedly multicarinate).

Description. TOL to 143 mm*; SVL to 66 mm*; tail very short, TL/SVL < 1.45*; legs very short (tip of 4th toe of adpressed hind limb reaching to between shoulder and ear); D keeled; V at least slightly keeled; caudals keeled, D and V rows strongly keeled giving a serrate appearance, but not forming a conspicuous crest; Drows 0; SAM 106–142*; males with enlarged PC and a very low nuchal crest; lamellar pads broad; 4toe 32–32; 4finger 23–28*; IO 0–1; IP/SS 1–3; SBO/SPL 0; loreals smooth to (usually only slightly) keeled, 12–39 in 2–4* rows; male dewlap moderate to large, female dewlap small to moderate (own data including that of Bienentreu et al. 2013 combined with that of Myers 1971b and Savage 2002).

The hemipenis of *Norops salvini* is a medium-sized bilobed organ with an asulcate processus; lobes calyculate, truncus with transverse folds.

Coloration in life. Ground color dirty white to dark gray or brown; D, L, and ventrolateral surfaces with dense lighter and/or darker mottling, blotches, and/or reticulations giving an overall lichenous appearance; yellow and green shadings may be present to a variable extent; V surfaces usually sparsely mottled with dark; lining of throat black, corners of mouth blue or blue-silver; a dark interorbital bar as well as usually a series of dark middorsal markings and a dark butterfly-shaped marking on base of tail; male dewlap orange-red to red, female dewlap red, purple, or blue. As exemplified by the photos taken at different times of SMF 89756 (Figs. 4.54C–D; F) individuals of *Norops salvini* undergo considerable metachrosis that may cause most or all coloration elements to disappear and involves the dewlap scales.

The female SMF 89527 was recorded as follows: D ground color Smoke Gray (44), grading into Drab-Gray (119D) laterally; D and L surfaces with dense Brownish Olive (29) mottling and some diffuse Opaline Green (162D) and Chamois (123D) flecks; interorbital stripe and snout Sepia (219) suffused with Army Brown (219B); V surfaces dirty white with a suggestion of Pearl Gray (81) with Light Drab (119C) spots; D and L surfaces of tail with a series of diffuse Sepia (119) suffused with Light Neutral Gray (85) and Pearl Gray (81) transverse bands; iris Raw Umber (123); dewlap dirty white at posterior and anterior base, with a Purple (1) free margin suffused with Mauve (172C) anteriorly, grading into Royal Purple (172A) towards apex; dewlap scales dirty white.

The dewlap of the male SMF 89758 (Fig. 4.54E) was recorded as Spectrum Red (11) with dirty white and Blackish Neutral Gray (82) scales; that of the juvenile male SMF 89756 (Fig. 4.54F) was recorded as Crimson (108) with most marginals, sternals and gorgetals dirty white, and some sternals and gorgetals Sepia (119). The dewlap of the juvenile female SMF 89757 (Fig. 4.54 K) was recorded as Royal Purple (172A) with dirty white scales.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all yellow, green, and bluish hues have faded and the red or lilac dewlap coloration has become less intense, but dewlaps sill retain some reddish or lavender color after 6 years.

Natural history notes. Diurnal and arboreal, uses its prehensile tail for climbing. All individuals were encountered sleeping on vegetation at night, usually head down, 0.5–5 m above ground. Most specimens were found in semi-open habitats such as forest edges or rows of trees along paths or property boundaries. At Jurutungo, I found the observability of this species to vary greatly: While only one female was found during two weeks AH and I spent around Jurutungo in 2008, our short stays in April and November 2009 yielded 8 and 6 specimens, respectively, that were spotted in the *Thuja* conifers in the close vicinity of WP 59.

Both sexes of *Norops salvini* have the ability to emit a distress sound when molested. This squealing vocalization could most easily be initiated when catching sleeping individuals from their resting position at night. At day time annoyance had to be heavier to provoke vocalization. Bienentreu et al. (2013) presented an analysis of the distress call of SMF 90176.

Remarks. The records published by Bienentreu et al. (2013) extend the known geographic range of *Norops salvini* eastwards as well as uphill. The adult female SMF 90169, collected on Cerro Altrillería at 2050 m asl, extends the known elevational distribution of the species 70 m upward (Lotzkat et al. 2010c), followed by the specimens collected in Jurutungo at 2000 m. The localities in the surroundings of Cerro Saguí, approximately 70 km east of the previously easternmost reported localities near Boquete (ZMFK; CAS; CHP), now constitute the easternmost records reported for the species, extending its distribution into the Serranía de Tabasará and the Comarca Ngöbe-Buglé. Here, the findings at Quebrada Juglí also are the first records from the Caribbean versant of the Talamancan Highlands.

While other workers state values around 1400 m asl (Savage 2002; Köhler 2008), Jaramillo et al. (2010) and consequently also Bienentreu et al. (2013) gave the lower elevational limit of *Norops salvini* as 1100 m. Since I was unable to trace any record from this elevation, I assume that the former authors referred to the record of de Sousa (1999) from RFLF and the corresponding specimen MVUP 799, which I found to represent *N. charlesmyersi* upon examining it. The lowest record in my dataset (including that of Bienentreu et al. 2013) is the specimen MVUP 964 from Cotito. My georeference placed centrally in that village yields a SRTM elevation of 1310 m, which I adopt as the lowest documented elevation herein. The listing of *N. salvini* for the Humedal de Importancia Internacional San San Pond Sak (ANAM 2004) is clearly erroneous since this species is not to be expected anywhere near sea level.

The common name Roaring Anole (Frank & Ramus 1995) is highly inadequate considering the sound emitted by *Norops salvini.* I thus suggest Squealing Anole as a more appropriate alternative.

***Norops vittigerus* (Cope 1862)**

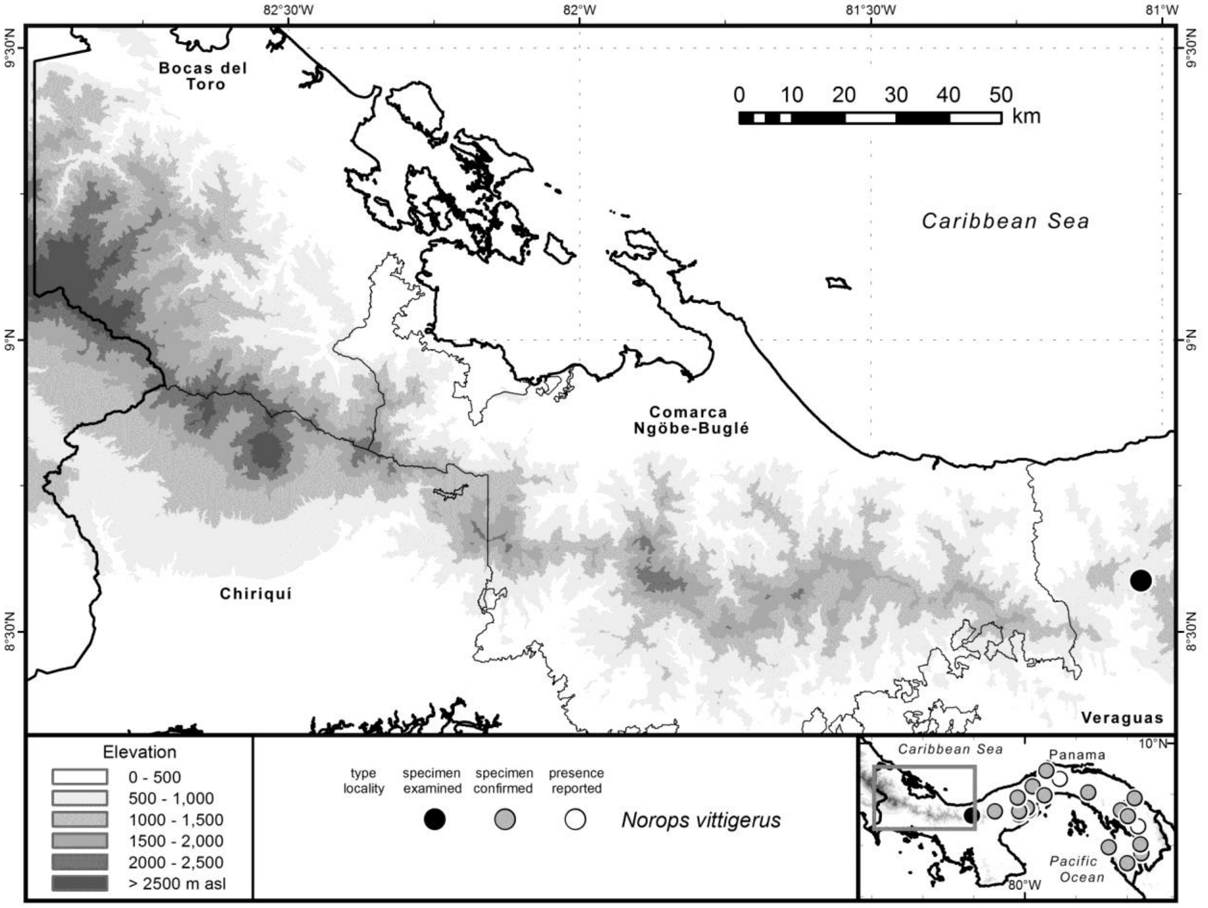
Garland Anole; Anolis

Figure 4.100F; Map 4.69.

Anolis binotatus: Barbour (1923).

Anolis vittigerus: Cope (1862b); Myers & Rand (1969: in part.); Rand & Myers (1990: in part.); Ibáñez et al. (1995, 1996, 1997, 2001); Young et al. (1999); Fundación PA.NA.M.A. (2007); Köhler et al. (2007); Poe & Ibáñez (2007); Fläschendräger & Wijffels (2009); Hamad (2009); Carrizo (2010); Jaramillo et al. (2010); Lotzkat et al. (2010c); Stadler (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Holotype. Supposedly at USNM, from "Truando region, New Granada" (= Colombia) (Cope 1862b).



Map 4.69: Distribution of *Norops vittigerus*.

Geographic distribution. Colombia and Panama, 0–900 m asl. In Panama, throughout the central and eastern portions of the country west to Veraguas, 20–850 m asl. In the Cordillera Central, recorded from PNAC, Valle de Antón, PNGDOTH, and Río Chilagres, up to ca. 890 m asl (Lotzkat et al. 2010c).

Diagnosis. A large *Norops* (maximum SVL 72 mm) with long legs (4th toe reaching to eye or beyond) that is most likely to be confused with *N. lemurinus* and members of the *N. pachypus* complex, from which it differs in having 10–20 very slightly and gradually enlarged middorsal scale rows (vs. only two slightly enlarged ones) and in exhibiting a contrasting red or dark central blotch on the dewlap in both sexes (vs. so such blotch, except a yellow one in *A. pachypus*). Juveniles of *N. vittigerus* might be confused with *N. humilis,* from which they differ in lacking 8–12 rows of greatly enlarged, strongly keeled middorsal scales (vs. present).

Description. TOL 196 mm*; SVL to 72 mm; legs long (tip of 4th toe of adpressed hind limb reaching to eye or beyond); tail long, TL/SVL 2.16*; D keeled; V imbricate, mucronate and strongly keeled; caudals keeled, Drows 2*, barely enlarged; SAM 52*; males without enlarged PC, but able to raise a nuchal crest; lamellar pads rather narrow; 4toe 35*; 4finger 26*; IO 0–2; IP/SS 2–4; SBO/SPL 0–1; loreals keeled, 45* in 6* rows; male dewlap moderate, female dewlap small. (data of examined specimen SMF 89528 combined with that of Köhler 1999, 2008 and Poe & Ibáñez 2007).

The hemipenis of *Norops vittigerus* is a bilobed organ (Köhler 1999).

Coloration in life. Generally similar to *Norops lemurinus;* with a distinct postorbital stripe bordered above and below by light stripes and extending posteriorly onto body, a dark interorbital bar, and usually a lyriform marking in occipital region; male dewlap red with a dark blotch, female dewlap lilac with a red blotch.

The female SMF 89528 was recorded as follows: D ground color Mars Brown (223A), grading into Brussels Brown (121B) laterally, with a series of five Vandyke Brown (221) middorsal blotches on body; a Cream Color (54) dorsolateral stripe extending from eye to just behind shoulders, where it dissolves into a series of blotches; irregular Vandyke Brown (221) and Cream Color (54) mottling present on D and L surfaces of head, body, tail and limbs; V surfaces of body, limbs, and base of tail Cream Color (54) with a suggestion of Straw Yellow (56) and sparse, irregular Brussels Brown (121B) mottling; a short Sepia (119) line on the neck bifurcates in the occipital region, but is interrupted before by an irregular, in the same direction bifurcated mottling of Vandyke Brown (221) and Cream Color (54); a few Sepia (119) spots also present on dorsum; V surface of head dirty white with a suggestion of Cream Color (54) and dense Plumbeous (78) mottling on the chin and along lower lips; lips mottled with Cream Color (54); tail Antique Brown (37) with sparse Mars Brown (223A), Vandyke

Brown (221) and Cream Color (54) mottling; iris Brussels Brown (121B); dewlap Indigo (73) with a purple spot in the center; apicosternals Cream Color (54), distomarginals and distal gorgetals dirty white with a suggestion of Indigo (73); remaining dewlap scales dirty white.

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 89528 is less vivid but very similar to that in life, including the dewlap.

Natural history notes. Diurnal and arboreal. The only specimen known from my study area was encountered around 14:10 while it was active under the thatched roof of a small shelter, 2.5 m above ground.

Remarks. The female SMF 89528 reported by Lotzkat et al. (2010c) constitutes the westernmost record for this species, extending its documented distribution into Veraguas and my study area. The occurrence of *Norops vittigerus* in the Comarca Ngöbe-Buglé appears possible given the distance of less than 15 km from Río Chilagres to the Comarca's border. My georeference for the specimen CHP 5037 from "Río Indio Arriba" (Poe & Ibañez 2007) yields a SRTM elevation of 890 m asl which is slightly above the upper elevational limit of 850 m reported for Panama (Jaramillo et al. 2010). Some MCZ specimens from Panama province (including Barro Colorado Island and localities east of the canal) catalogued as *Norops vittigerus* were identified as representing *N. lemurinus* by GK, which is why I include the listings of these names by Myers & Rand (1969) and Rand & Myers (1990) in partim in my synonymy for the latter species. According to Köhler (2008), the record of *Anolis binotatus* from E Panama by Barbour (1923) are based on misidentified *N. vittigerus*.

Norops woodi (Dunn 1940)

Wood's Anole; Anolis de Wood

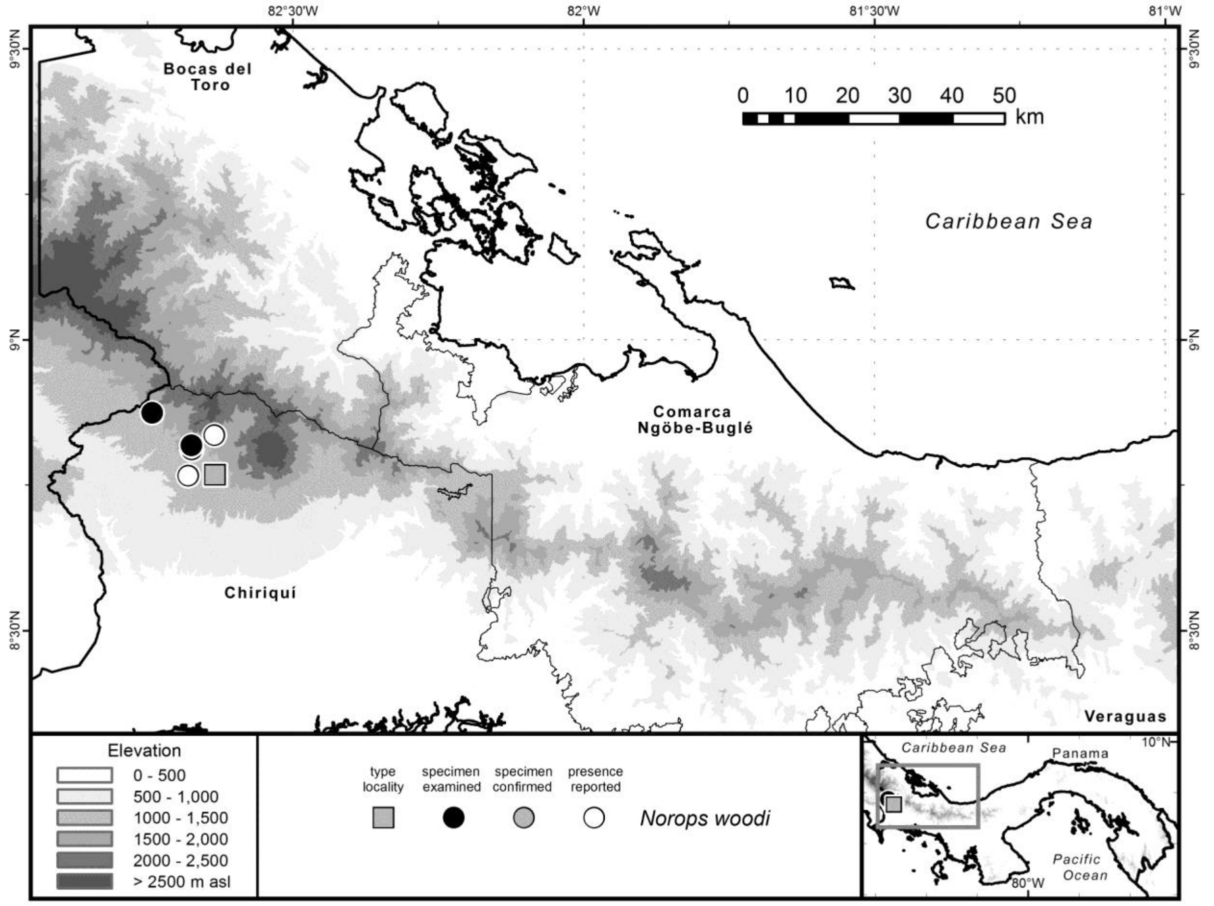
Figure 4.100G; Map 4.70.

Anolis attenuatus: Fitch et al. (1976).

Anolis woodi: Dunn (1940); Taylor (1956); Peters & Donoso-Barros (1970); Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Ibáñez (2006: in part.); Fundación PA.NA.M.A. (2007); Köhler et al. (2007, 2013); Fläschendräger & Wijffels (2009); Hamad (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Köhler (2011); Uetz & Hošek (2014).

Holotype. AMNH 62647, female, from "El Volcán, Chiriquí, Panama" (Dunn 1940; AMNH collection database at http://sci-web-001.amnh.org/db/emuwebamnh/index.php).

Geographic distribution. Endemic to the Talamancan Highlands of Costa Rica and Panama, 1150–2500 m asl. In Panama, recorded from the Pacific versant of the Serranía de Talamanca in Chiriquí east to Volcán Barú, 1230–2060 m asl.



Map 4.70: Distribution of *Norops woodi*.

Diagnosis. A large *Norops* (maximum SVL 100 mm) with long legs (4th toe reaching beyond eye) that is most similar to *N. aquaticus, N. biporcatus,* and *N. capito.* It can readily be distinguished from these species by its blue eyes in life. It further differs from *N. aquaticus* in having 34 or more lamellae under the 4th toe (vs. 34 or less), from *N. biporcatus* in having long legs as well as a very large dewlap and enlarged postcloacal scales in males (vs. short legs, moderate dewlap and no enlarged PC in males), and from *N. capito* in having granular, keeled dorsals (vs. smooth, flat). *Norops woodi* differs from Panamanian species of *Dactyloa* in having strongly keeled, mucronate ventrals (vs. at most faintly keeled, but always smooth to the naked eye).

Description. TOL to 345 mm; SVL to 100 mm; tail long, TL/SVL 2.0*; legs long (tip of 4th toe of adpressed hind limb reaching beyond eye); D, V, and caudals keeled; Drows 4–12, slightly enlarged; SAM 124–140*; males with enlarged PC, can raise a nuchal crest; lamellar pads broad; 4toe 34–43; 4finger 24–26*; IO 2–3; IP/SS 3–6*; SBO/SPL 0–1; loreals keeled, 40–53* in 5* rows; male dewlap very large, female dewlap small to moderate.

The hemipenis of *Norops woodi* is a bilobed organ as judged from the incompletely everted hemipenes among my examined specimens.

Coloration in life. D and L surfaces light olive to blackish brown, often with reddish shades, with a broad irregular middorsal band connecting to dark transverse bars, and/or lighter or darker mottling; iris blue; capable of considerable metachrosis including the skin of the dewlap; male dewlap yellow, orange, red, green, purple, or black; female dewlap cream to flesh-colored.

Coloration in preservative. After 8–11 years in 70% ethanol, the coloration of my examined material is similar to that in life, except that all red and yellow shades have faded; male dewlap light gray after 8 years in SMF 85435, white with a bluish hue after 11 years in SMF 85398.

Natural history notes. Diurnal and arboreal.

Remarks. I regard the record of *Norops woodi* from the Santa Fé area in Veraguas (Martínez et al. 1995) as erroneous based on the current knowledge on the range of this species. The specimens MCZ 171132–34 from Palo Santo, 1230 m asl (examined by GK), as well as KU 76012–14 from "S slope Cerro Santa Catalina, ca 8 km NW El Volcan" (my georeference for which yields a SRTM elevation of 2057 m) greatly extend the vertical distribution documented for Panama (Jaramillo et al. 2010). Köhler et al. (2013) recently extended the species' distribution northward to Costa Rica's Cordillera de Guanacaste.

Family Hoplocercidae Frost & Etheridge 1989

Enyalioides heterolepis (Bocourt 1874)

Bocourt's Dwarf Iguana; Iguana enana

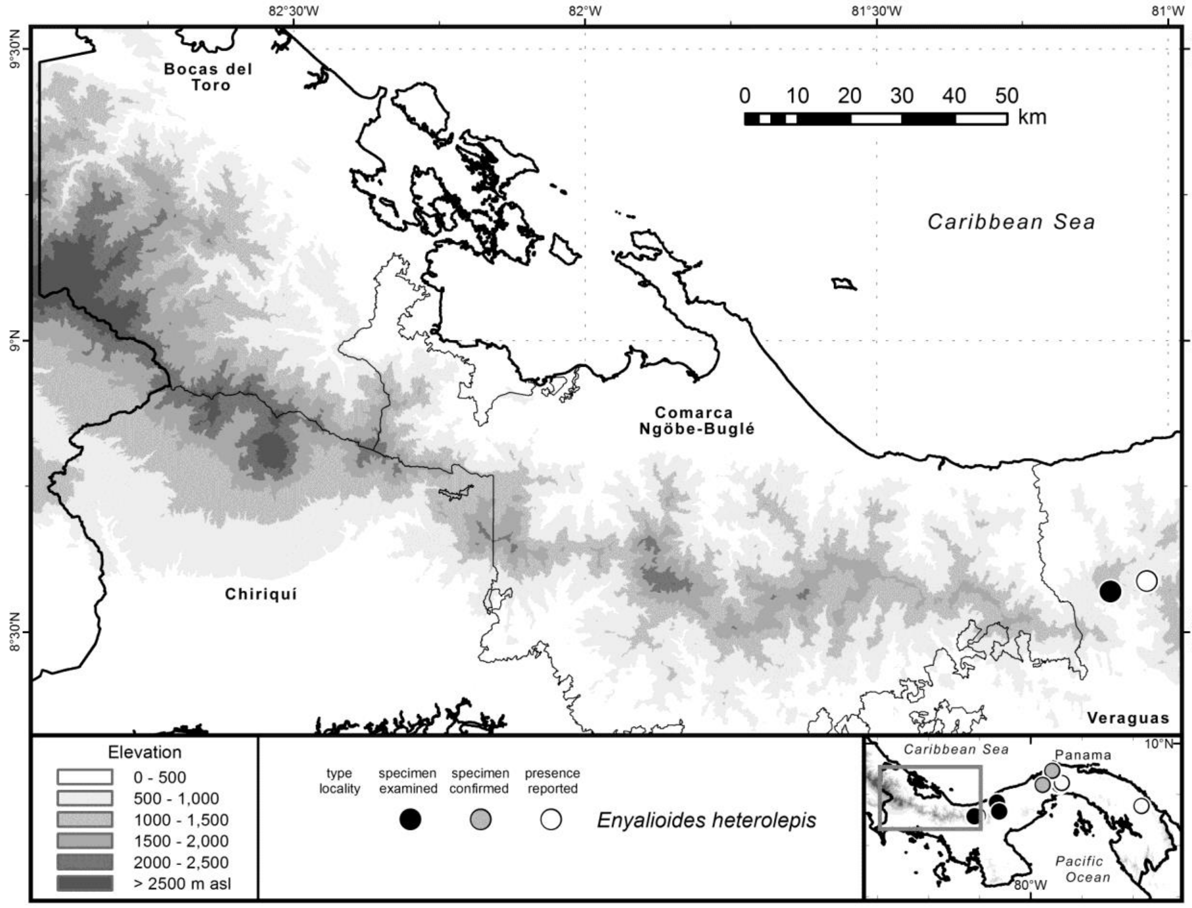
Figure 4.100H; Map 4.71.

Sceloporus squamosus: Martínez et al. (1995).

Holotype. MHNP 4067, from Veragua, Panama.

Geographic distribution. Panama to Colombia and Ecuador west of the Andes, 0–900 m asl. In Panama, reported from scattered localities in the eastern and central portions of the country, and west to Veraguas, on both versants. In the Cordillera Central, recorded from PNGDOTH and the Santa Fé area, up to ca. 860 m asl.

Diagnosis. This medium-sized iguana (maximum SVL 138 mm) can hardly be confused with any other Panamanian lizard given its overall appearance, its rather low serrated middorsal crest which is continuous with a slightly higher nuchal one, and its enlarged, tuberculate scales scattered throughout dorsum, flanks, and dorsal portions of hind limbs.



Map 4.71: Distribution of *Enyalioides heterolepis*.

Description. TOL to 255 mm*; SVL to 138 mm; tail short, TL/SVL 1.34–1.38*; D granular, keeled, with interspersed enlarged, tuberculate scales; V imbricate, keeled, mucronate; greatly enlarged, spine-like middorsal scales forming a nuchal crest that is continuous with a lower D and caudal crest; tail with whorls of slightly but visibly enlarged scales; IP small if present; SAM 111–115*; 4toe 24–26*; 4finger 16–20*.

The hemipenis of *Enyalioides heterolepis* is a relatively small, bilobed organ with calyculate lobes.

Coloration in life. D ground color light to dark brown, often with a reddish hue, with lighter and/or darker mottling or reticulations; dorsum usually with diffuse dark crossbands reaching onto flanks and a dorsolateral series of light blotches, the anteriormost two of which exhibit extensions towards tympanum and shoulder, respectively; tail and limbs with light and dark mottling or reticulations and usually dark crossbands; lips usually lighter than remaining L surfaces of head; V surfaces cream to brown, unicolor or mottled with darker pigment.

Coloration in preservative. After 6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, except that most reddish shades have faded; a rusty brown is partially retained, and a bluish gray hue has appeared on some light markings.

Natural history notes. A diurnal, arboreal sit-and-wait predator. During a preserving session on 30.07.2008 at noon, I found the juvenile SMF 89550 under my fieldbook which had been lying for a while on a fallen log in the middle of our camp.

Remarks. The records of Lotzkat et al. (2010c) extended the species' distribution into Veraguas and my study area, and clarified that no source for the records of *Enyalioides heterolepis* from Bocas del Toro province (Köhler 2008) can be traced. Moreover, Lotzkat et al. (2010c) revealed that a now lost individual from Cerro Narices listed as *Sceloporus squamosus* by Martínez et al. (1995) actually represented an *E. heterolepis* (A. Rodriguez, pers. comm.). Considering the airline distance of less than 8 km between the collection localities of my examined specimens from Cerro Negro and the Comarca's border, I regard the presence of *E. heterolepis* in the Comarca Ngöbe-Buglé as possible. None of the three specimens which I have examined in the laboratory has a discernable IP.

Family Iguanidae Gray 1827

Iguana iguana (Linnaeus 1758)

Iguana, Green Iguana; Iguana, Iguana verde

Figure 4.101A; Map 4.72.

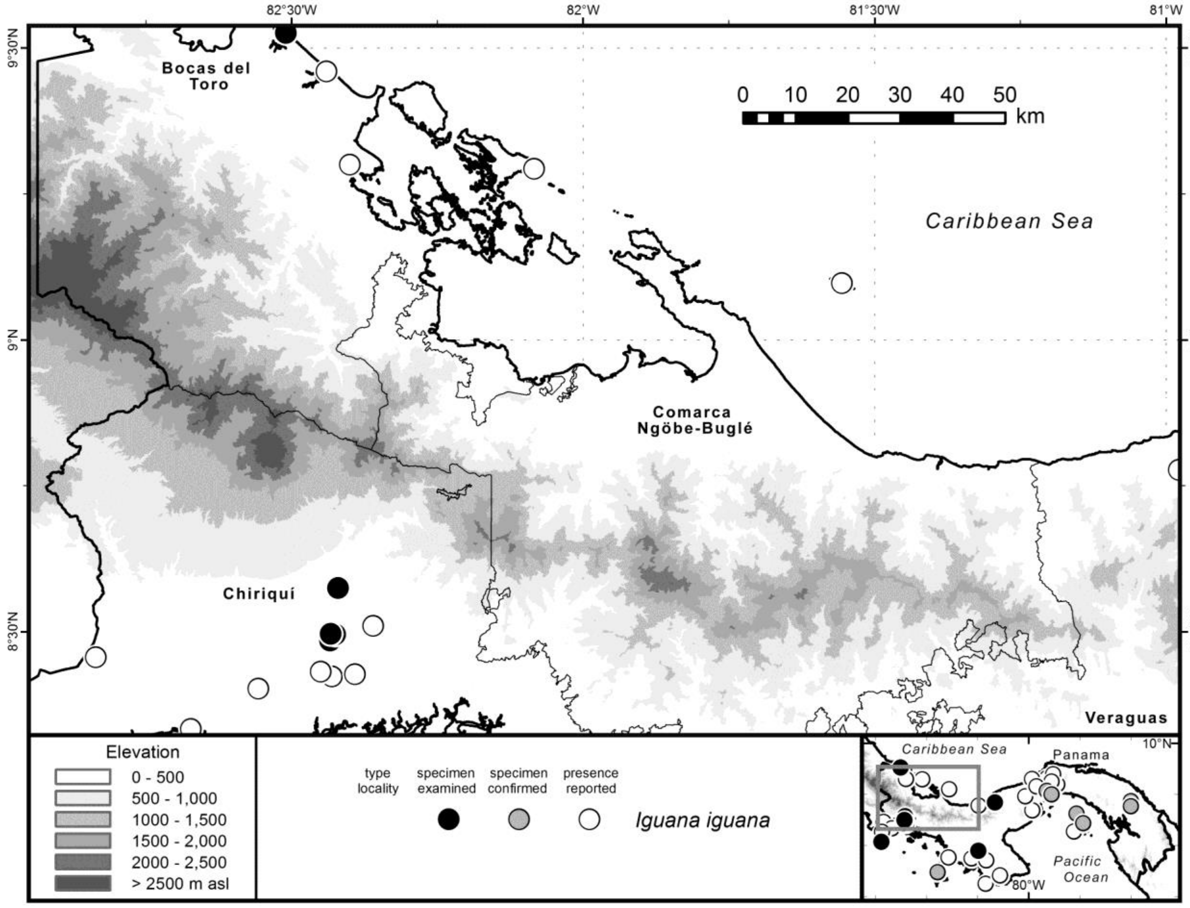
Iguana tuberculata: Barbour (1906).

Syntypes. One specimen at NRM (NHRM), another in the Gyllenborg collection in Uppsala, from Indiis.

Geographic distribution. Mexico through Central America to Ecuador, Bolivia, Paraguay, and Brazil, several islands of the Lesser Antilles and Puerto Rico (introduced in Florida), 0–1000 m asl. In Panama, throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, 0–850 m asl. In the Cordillera Central only reported from PNAC but probably occurring at premontane elevations along both versants.

Diagnosis. This large iguana (maximum SVL 580 mm) is very unlikely to be confused with any other Panamanian lizard given its size, the middorsal crest of enlarged, spine-like scales extending from nuchal area onto tail, and the greatly enlarged smooth scale below the ear.

Description. TOL to 2010 mm; SVL to 580 mm; tail moderate to long; D imbricate, keeled, with interspersed, greatly enlarged, tuberculate scales between head and level of shoulder; V imbricate, keeled; greatly enlarged, spine-like middorsal scales forming a nuchal crest that is continuous with D and caudal crest; tail without whorls of enlarged scales; a pendulous, dewlap-like gular appendage present, with triangular apical scales in males; 18–46 total femoral pores present in both sexes.



Map 4.72: Distribution of *Iguana iguana*.

Coloration in life. D and L surfaces usually green to brown, but may assume hues or mottling of gold, orange, or blackish brown; flanks often with light-bordered dark crossbands; tail with dark crossbands; V surfaces whitish, yellow, or light green.

Coloration in preservative. The green may turn gray, brown, or bluish, but some green is retained in SMF specimens collected in the 1940s.

Natural history notes. Diurnal and arboreal. Individuals were encountered in semi-open and open secondary vegetation ranging from pastures to urbanized areas. Sleeping specimens were spotted in vegetation up to 3 m above ground at night. During daytime, I have seen individuals as high as 12 m above ground in trees, but in several cases also basking or moving about on the ground. At Boca San San, a group of about half a dozen subadult iguanas spent most of the day on the ground next to the buildings at Centro AAMVECONA in May 2010. At Río Bartola in Nicaragua, a subadult specimen tried to escape by diving into the river and swimming underwater.

Conservation. This very widespread and common species was classified as LC by Jaramillo et al. (2010), who calculated the species' EVS as 10, indicating a medium vulnerability. Despite being found virtually everywhere where there are trees, it is subject to high anthropogenic pressure in many parts of its range.

Remarks. The record from PNAC and the general distribution of this species render its presence in my study area plausible. In and around Los Algarrobos (as well as in most, if not all, rural areas of Panama), *Iguana iguana* is eagerly pursued for food by local people. At least every weekend, hunting parties of several men browse the lines of trees along fences and watercourses in search of these lizards, which they drive down from the trees by climbing up and approaching them, in order to have the dropping lizard secured by the men remaining on the ground. The lizards are constrained by sewing their hands and feet behind their back using their own claws and attached tendons as needles and threads. The day's catch, which I have whitnessed to consist of up to 17 lizards, is usually broiled the same afternoon.

Family Phrynosomatidae Fitzinger 1843

Sceloporus malachiticus Cope 1864

Green Spiny Lizard; Lagartija espinosa

Figures 4.101B, C; Map 4.73.

Sceloporus formosus malachiticus: Wettstein (1934); Slevin (1942).

Syntypes. USNM 101062 (5 specimens), formerly 12186, earlier 6492, from "Costa Rica, near Arriba" (Cope 1864; according to Savage 1974, "this name apparently was applied loosely to the Meseta Central by Charles N. Riotte, who sent these specimens to Cope").

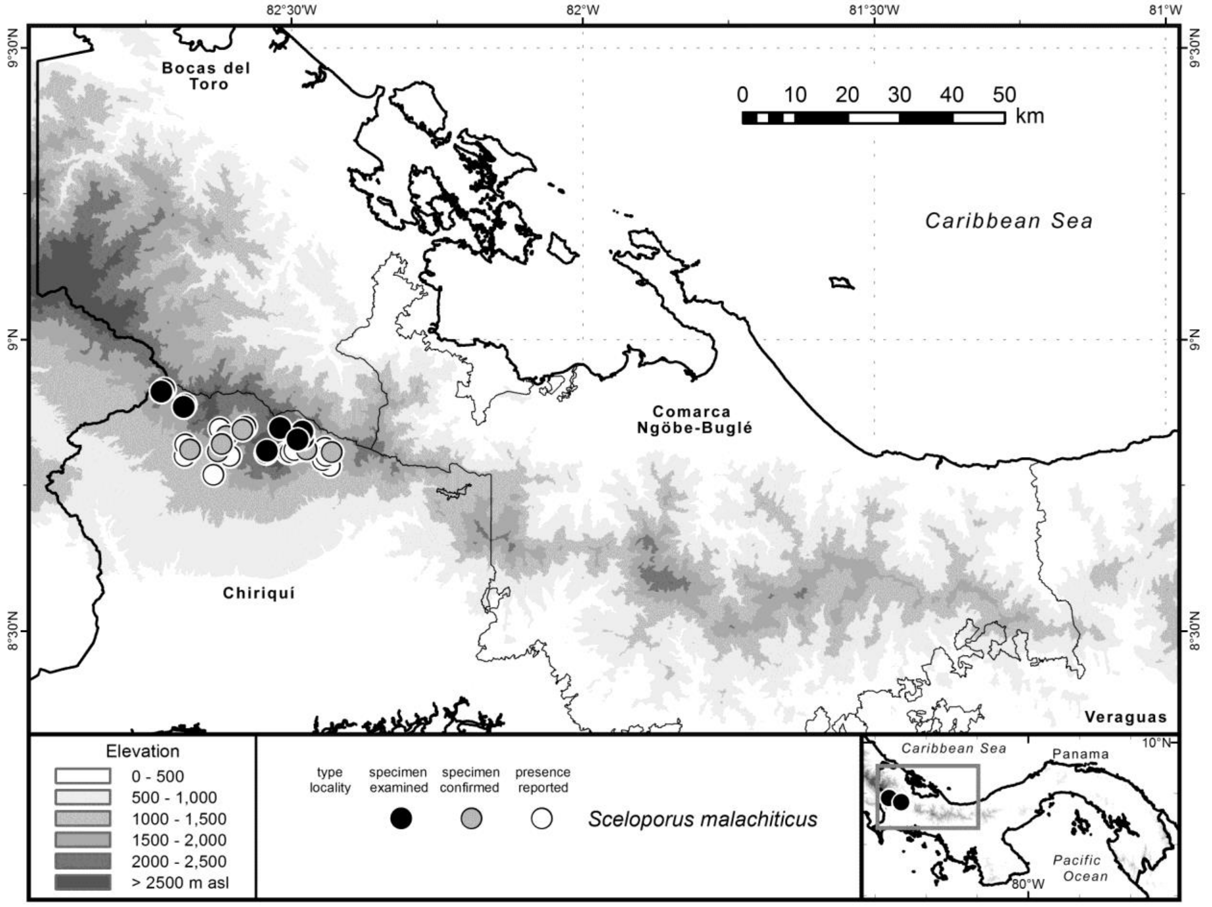
Geographic distribution. El Salvador and Honduras (see remarks) to Costa Rica and Panama, 540–3800 m asl. In Panama, recorded from the Pacific versant of the Serranía de Talamanca in Chiriquí (probably also present in Bocas del Toro), 1120–3420 m asl.

Diagnosis. This medium-sized lizard (maximum SVL 98 mm) is readily distinguished from all other Panamanian lizards by its spiny appearance owing to its imbricate, mucronate, strongly keeled scales.

Description. TOL to 190 mm; SVL to 98 mm; tail short, not longer than SVL; D and L scales of body, tail, and limbs imbricate, mucronate, and keeled; V imbricate, smooth; 22–34 total femoral pores present in both sexes; males with enlarged PC; SAM 28–45; 4toe 20–21*; 4finger 16–17*.

Coloration in life. D and L surfaces gray, brown, and/or bright to bluish green; juveniles and females more or less densely mottled with greenish to blackish brown; adults with blue areas on gular region and ventrolateral portions of body, bordered by black in males; other V surfaces and those of juveniles cream to light gray or brown, with a hue of flesh color.

Coloration in preservative. After 4.5–6 years in 70% ethanol, the coloration of my examined juveniles and female involves much more green and blue than in life.



Map 4.73: Distribution of *Sceloporus malachiticus*.

Natural history notes. Diurnal and largely terrestrial, common in open and semi-open habitats, along roads, and in forest clearings at lower montane and montane elevations in Chiriquí. Individuals were commonly seen in the morning or early afternoon while they were basking or moving about on the ground, rocks, or fallen logs, as well as on anthropogenic structures such as pipelines and wooden huts up to 2 m above ground.

Conservation. If future studies reveal that the name *Sceloporus malachiticus* should be restricted to the "unquestioned" populations in LCA (Savage 2002), the classification as "Least Concern" (Jaramillo et al. 2010; IUCN 2014) might warrant reconsideration.

Remarks. Together with *Mesaspis monticola,* this species is one of the highest-ranging reptiles in Panama, where it has been recorded from elevations up to 3420 m asl (Walters

1953; Jaramillo et al. 2010; own observations up to 3400 m near the summit of Volcán Barú). Contrary to the coloration description by Savage (2002), there is no definite black collar in most Panamanian specimens I have seen, nor does the adult female SMF 89785 have blue areas on throat or venter. As more and more "widespread" highland species among Central American reptiles are splitted as a result of integrative taxonomic studies, I share the doubts of Savage (2002) regarding the affiliation of populations from north of the Nicaraguan depression to the nominal species *Sceloporus malachiticus.*

My georeference for the specimen USNM 51975 from "Boquete" yields a SRTM elevation of 1121 m asl, which is well below the lowest elevation of 1500 m given for Panama by Jaramillo et al. (2010). The lowest verbatim elevation from Panama I am aware of is 1250 m (USNM 129921–3). The occurrence on the Caribbean slopes of the Talamancan Highlands in Costa Rica (Savage 2002) and the short distances from specimens observed and/or collected at Jurutungo (< 1.2 km) and Sendero Quetzales (< 2.5 km) to the border of Bocas del Toro render the presence of *Sceloporus malachiticus* in this province plausible. The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible.

Family Polychrotidae Fitzinger 1843

Polychrus gutturosus (Berthold 1845)

Neotropical Chameleon, Berthold's Bush Anole; Camaleón

Figure 4.101D; Map 4.74.

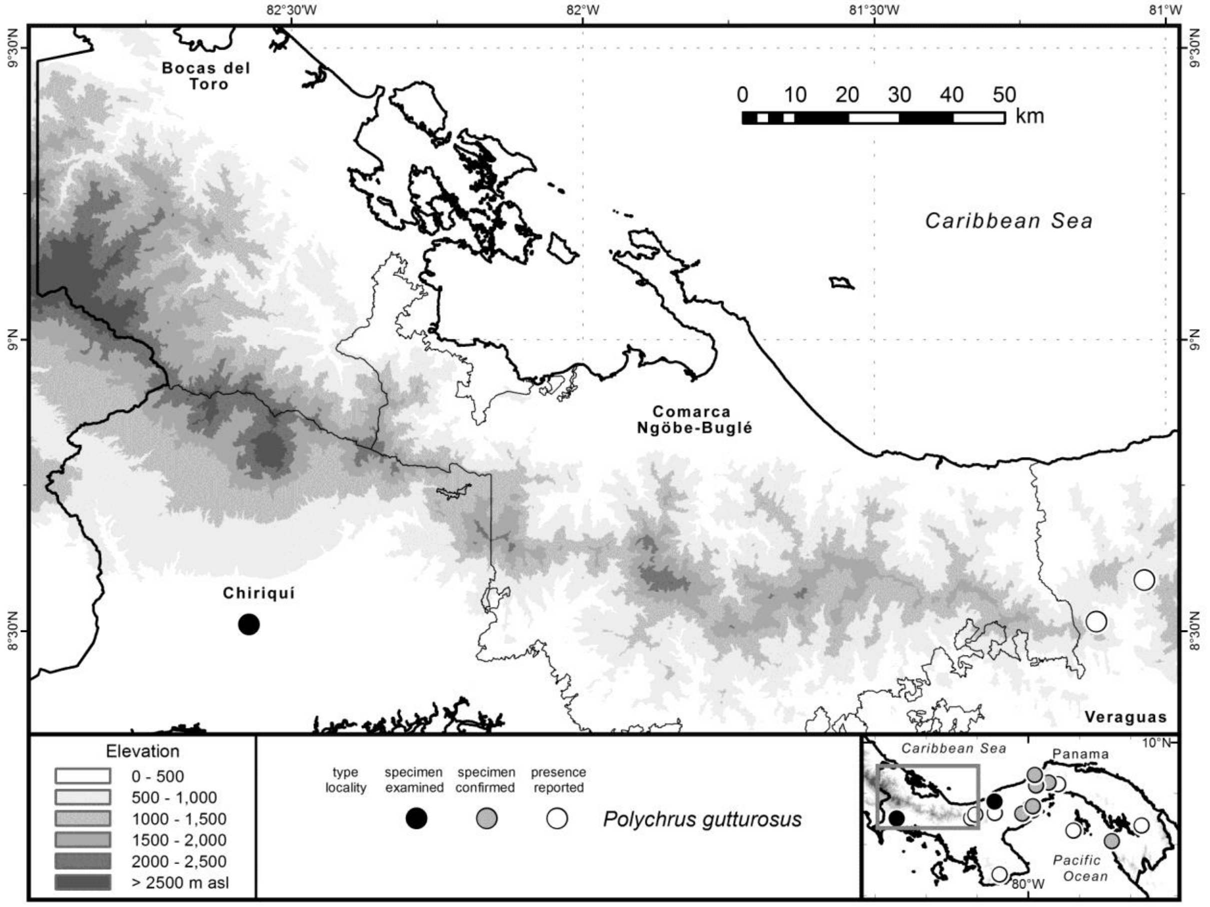
Polichrus gutturosus: Martínez & Rodriguez (1994).

Polychrus marmoratus: Breder (1946).

Holotype. ZFMK 21341, from Popayán, western Colombia

Geographic distribution. N Honduras through Central America to Colombia and NW Ecuador, 0–1300 m asl (Koch et al. 2011). In Panama, presumably present throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, 0–880 m asl. In the Cordillera Central, reported from PNAC, El Valle de Antón, near PNGDOTH, and the Santa Fé area.

Diagnosis. This medium-sized (maximum SVL 170 mm) false chameleon is unlikely to be confused with any other Panamanian lizard given its general habitus and very long tail. Among the somewhat similar iguanian lizards of Panama, *Polychrus gutturosus* differs from species of *Dactyloa* and *Norops* by its keeled, unexpanded subdigital lamellae (vs. smooth, expanded) and from species of *Basiliscus, Enyalioides,* and *Iguana* in lacking any nuchal, dorsal, or caudal crests, scaly fringes on the outer toes, whorls of enlarged caudals, and a greatly enlarged scale below ear (vs. crests and one of the latter features present).



Map 4.74: Distribution of *Polychrus gutturosus*.

Description. TOL to 700 mm; SVL to 170 mm; tail very long, TL/SVL > 3; D keeled, V about same size as D, keeled (uni- to multicarinate); dewlap-like gular appendage present in both sexes; 9–21 femoral pores per side present in both sexes; IP small if present; SAM 63–82; 4toe 35–45; 4finger 25–36 (data of Savage 2002 and Koch et al. 2011).

Coloration in life. D and L ground color green, with a light middorsal stripe, variable lighter and darker mottling, and often darker green transverse bands; usually with a narrow, dark postorbital stripe extending to about level of ear and a narrow, dark suborbital stripe extending to corner of mouth, and a large, light-colored blotch between these stripes; V surfaces of a lighter green. In the course of metachrosis, color and pattern may vary considerably, including brown, orange, and yellow shades.

Coloration in preservative. Chiefly different shades of brown, often with blue portions.

Natural history notes. Diurnal and highly arboreal.

Remarks. Recently, Koch et al. (2011) provided a redescription of *Polychrus gutturosus* and concluded that *P. spurelli* Boulenger should remain in the synonymy of this species.

My georeference for the record of Martínez and Rodriguez (1994) from Cerro Mariposa yields a SRTM elevation of 883 m asl, which is slightly above the upper elevational limit of 850 m reported for Panama by Jaramillo et al. (2010). The proximity of this locality to the Comarca's border, together with the records from the Caribbean versant east of Veraguas and in Costa Rica (Savage 2002) render the species' presence in Bocas del Toro and the Comarca Ngöbe-Buglé plausible.

Infraorder Scinciformata Vidal & Hedges 2005

Family Mabuyidae Mittleman 1952

Marisora unimarginata (Cope 1862)

Central American Mabuya, Bronze-backed Climbing Skink; Esquinco, Lisa, Limpiacasa de raya blanca

Figure 4.101E; Map 4.75.

Mabuia cepedei: Cope (1876).

Mabuia agilis: Barbour (1906).

Mabuya brachypoda: Busack (1966).

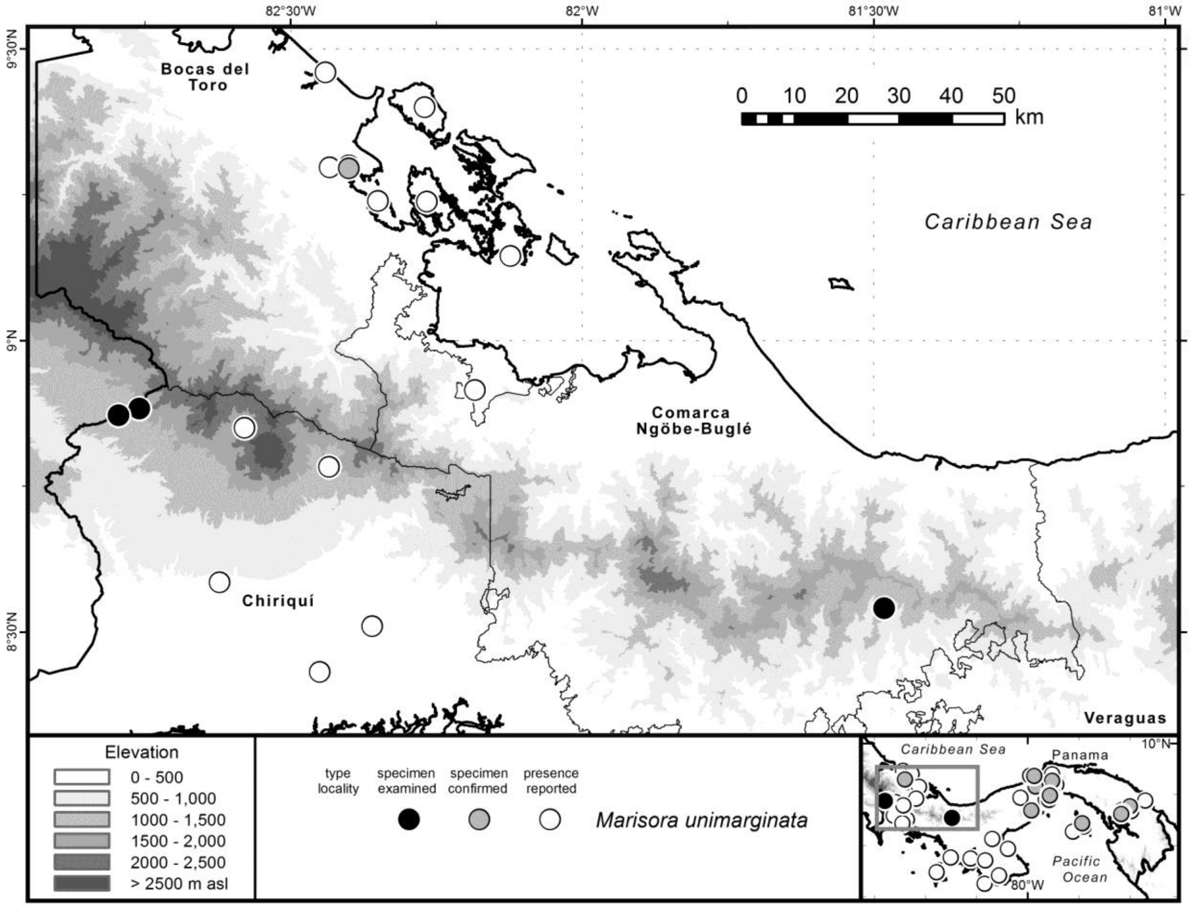
Mabuya mabuya: Slevin (1942).

Mabuya mabouya: Swanson (1945); Breder (1946); Cochran (1946); Myers & Rand (1969).

Mabuya unimarginata: Cope (1862b); Taylor (1956); Peters & Donoso-Barros (1970: in part.); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1996, 1997, 2001); de la Riva (1997); Martínez et al. (1999); Young et al. (1999); Savage (2002: in part.); ANAM (2004, 2005a, 2009b); McDiarmid & Savage (2005); Montero (2005); Rodriguez et al. (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Neal (2007); Köhler (2008: in part.); Santos-Barrera et al. (2008); Hamad (2009); Savage & Bolaños (2009: in part.); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010: in part.); Stadler (2010); Wilson & Johnson (2010: in part.); Batista & Ponce (2011).

Holotype. Unlocated and probably lost, from "Panama" (Cope 1862b; Hedges & Conn 2012).

Geographic distribution. Costa Rica and Panama, 0–1960 m asl. In Panama, throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported primarily along the Pacific versant up to 1960 m asl.



Map 4.75: Distribution of *Marisora unimarginata*.

Diagnosis. A medium-sized (maximum SVL 91 mm) skink that is immediately distinguished from the skink-like anguids (*Celestus, Diploglossus*) and gymnophthalmids (*Gymnophthalmus, Bachia*) as well as from the skinks of the genus *Scincella* by the presence of one pair of small internasals that are in contact, thus separating the large frontonasal from the rostral (vs. 2 pairs of IN preventing contact of FN with rostral in anguids, and no IN in *Gymnophthalmus, Bachia,* and *Scincella*). *Marisora unimarginata* further differs from Panamanian *Scincella* in having two small frontoparietals separating the frontal from the parietal and interparietal plates (vs. a single, large FP).

Description. TOL to 246 mm; SVL to 91 mm; PF 2–3*; FN 1*; IN 2*; FP 2*; SPL 7–9*, 5th or 6th contacting eye*; SAM 29–30*; 4toe 16–19*; 4finger 13–16*; D, L, V, and caudals cycloid, smooth.

Coloration in life. Dorsum and tail brown mottled with black; a broad, dark brown band extending from eye to groin, bordered below by a whitish L stripe which disintegrates into brown mottling ventrolaterally; V surfaces dirty white to yellow.

The male SMF 89582 was recorded as follows: Dorsum of head Mars Brown (223A), grading into Verona Brown (223B) on body and tail with Sepia (119) flecks on dorsum and tail; a broad Sepia (119) L stripe from nostrils to insertion of hind limbs, bordered below by a

Pale Pinkish Buff (121D) longitudinal stripe that is bordered below by a Mikado Brown (121C) stripe that contains Sepia (119) and Pale Pinkish Buff (121D) flecks; V surface of head dirty white, grading into Straw Yellow (56) on V surface of body, tail and limbs, which contain faint Sepia (119) longitudinal lines; iris Sepia (119); V surfaces of hands and feet Sepia (119)

Coloration in preservative. After 4–6 years in 70% ethanol, similar to that in life.

Natural history notes. Diurnal and chiefly terrestrial, but also good climbers. Supposedly common especially in semi-open and open habitats, but very shy. At Hacienda Café de Eleta, two individuals were found at night under logs lying in a *Citrus* plantation. Of several individuals openly basking on different substrates at Guayabito, SMF 91565 was the only one that could be secured.

Conservation. If thorough taxonomic studies confirm that the name *Marisora unimarginata* should be restricted to populations in Lower Central America as suggested by Hedges & Conn (2012), the classification as "Least Concern" (Jaramillo et al. 2010; IUCN 2014) might warrant reconsideration.

Remarks. *Marisora unimarginata* is the type species of the genus *Marisora* Hedges & Conn 2012. While most recent authors regarded *M. unimarginata* to range throughout Central America, Hedges & Conn (2012) concluded that *M. alliacea* (Cope 1876) and *M. brachypoda* (Taylor 1956) should be recognized as valid species, thus restricting the range of *M. unimarginata* to Costa Rica and Panama. Nevertheless, their study did not include genetic data from *M. unimarginata,* and they did not provide explicit diagnoses for *M. alliacea* and *M. brachypoda.* Thus, the taxonomy and biogeography of Central American mainland *Marisora* remains to be satisfactorily resolved.

Both Savage (2002) and Köhler (2008) pictured D head views of *Marisora unimarginata* showing the internasals separated from each other by a narrow contact between the large frontonasal and the rostral. In the four specimens which I have examined, the IN are in contact and thus separate the FN from the rostral. In SMF 89582, there is a small scale (counted as a third PF) between the tips of the two "normal" PF that excludes the frontal from contact with the FN. Since the morphological variation reported by Savage (2002) probably includes individuals that would be referable to *M. alliacea* and *M. brachypoda,* I restrict the scale counts to my examined specimens.

My examined specimens SMF 89582 and MHCH 2349 were collected at Hacienda Café de Eleta at 1464 m asl, well below the highest elevation documented for Panama (1200 m according to Jaramillo et al. 2010). My georeference for the specimens UMNH 5200–2 from "Cerro Punta" yields a SRTM elevation of 1959 m, which is almost 160 m higher than the maximum documented elevation for Central American *Marisora* (*M. unimarginata* "sensu lato", i.e., including the other species recognized by Hedges & Conn 2012) given as 1800 m (Wilson & Johnson 2010).

Family Sphenomorphidae Welch 1982

Scincella cherriei **(Cope 1893)**

Brown Forest Skink, Litter Skink; Esquinco, Lisa

Figure 4.101F; Map 4.76.

Leiolopisma cherriei: Taylor (1956); Peters & Donoso-Barros (1970).

Lygosoma (Mocoa) cherriei: Wettstein (1934).

Mocoa assata: Cope (1876).

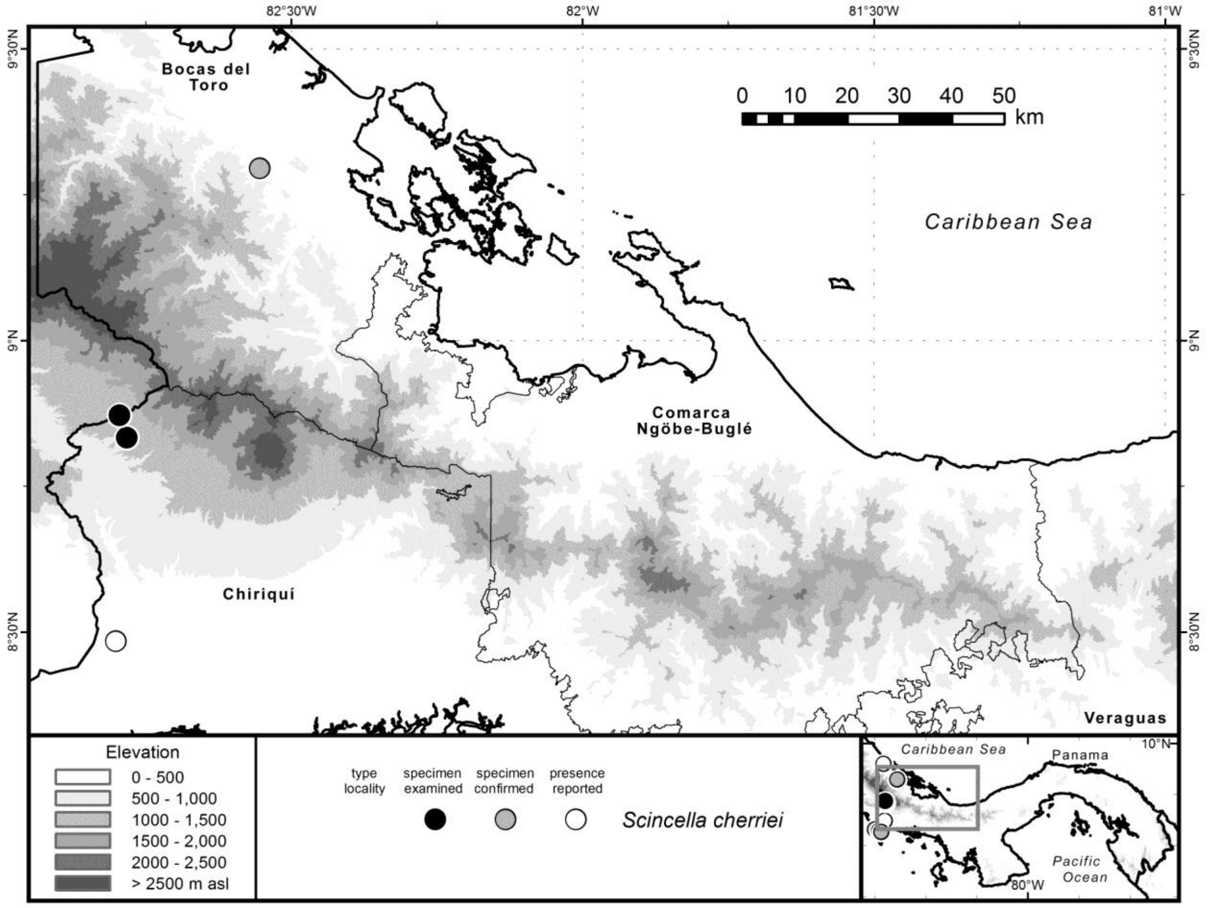
Mocoa cherriei: Cope (1893).

Sphenomorphus cherriei: Taylor (1956); Myers & Donnelly (1991); Auth (1994); Fuenmayor (1997); Ibáñez et al. (2001); Young et al. (1999); Savage (2002); ANAM (2004, 2005a, 2009b); McDiarmid & Savage (2005); Montero (2005); Ibáñez (2006); Fundación PA.NA.M.A. (2007); Köhler (2008); Santos-Barrera et al. (2008); Hamad (2009); Savage & Bolaños (2009: in part.); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Köhler et al. (2013).

Holotype. AMNH 9551, juvenile, from Palmar Norte, Puntarenas province, Costa Rica (Myers & Donnelly 1991).

Geographic distribution. Mexico to Panama, 0–1860 m asl. In Panama, known from the Caribbean foothills in Bocas del Toro and low and premontane elevations up to 1210 m asl in western Chiriquí.

Diagnosis. A medium-sized (maximum SVL 68 mm) skink that is immediately distinguished from the skink-like anguids (genera *Celestus* and *Diploglossus*) and the skink *Marisora unimarginata* by the lack of internasals resulting in a broad contact between the frontonasal and the rostral (vs. two pairs of IN in the anguids and one in *M. unimarginata*). It further differs from *M. unimarginata* in having a single, very large frontoparietal between the frontal and the IP and parietals (vs. 2 FP). This single FP also distinguishes *Scincella cherriei* from the skink-like gymnophthalmids (vs 2 FP in the genera *Gymnophthalmus* and *Bachia*), from which it is further distinguished by the presence of 4 large supraoculars (vs. less and/or small SO) and 5 fingers (vs. 4). The species differs from its only Panamanian congener, *S. rara,* in having two PF which narrow the contact between frontal and FN (vs. no PF, broad contact).



Map 4.76: Distribution of *Scincella cherriei*.

Description. TOL to 178 mm; SVL to 68 mm; PF 2; FN 1; IN 0; FP 1, larger than frontal; SPL 7*, 5th contacting eye*; SAM 29–34 4toe 13–19; 4finger 9–11*; D, L, V, and caudals cycloid, smooth.

Coloration in life. D surfaces of head and body brown with light and/or dark mottling; a dark pre-and postorbital stripe extending onto body but disintegrating into mottling around midbody; ventrolateral and V surfaces of head and body light gray mottled with dark; tail assuming darker and more grayish tonalities posteriorly.

The specimen SMF 90210 was recorded as follows: D surfaces of head and body Natal Brown (219A) with Sepia (119) mottling becoming denser posteriorly; a broad Sepia (119) dorsolateral longitudinal band on head and body dissolving into mottling lateroventrally; flanks Olive-Gray (42) mottled with Sepia (119); D surfaces of limbs and tail Sepia (119) sparsely mottled with Natal Brown (219A); V surfaces of head and body dirty white with a suggestion of Pearl Gray (81) and Pale Horn Color (92); V surfaces of tail and limbs Pale Neutral Gray (86) grading into Lavender Blue (170 D) towards tip of tail; iris Sepia (119).

Coloration in preservative. After 5 years in 70% ethanol, similar to that in life.

Natural history notes. Diurnal and terrestrial. At Santa Clara, two specimens were found on a small clearing next to a shade coffee plantation. One was active in the afternoon, the other fled from me around 21:00.

Remarks. Linkem et al. (2011) transferred *Sphenomorphus cherriei* to the genus *Scincella,* and Hedges & Conn (2012) included this genus in the family Sphenomorphidae. My examined specimens were collected at 1200 (SMF 90210 and MHCH 2368 from Santa Clara) and 1210 m asl (SMF 85436 from Finca C.A.S.A.), well above the highest elevation of 200 m documented for Panama (Jaramillo et al. 2010). Recently, Köhler et al. (2013) raised the upper elevational limit for Costa Rica to 1420 m.

Scincella rara (Myers & Donnelly 1991)

Litter Skink; Esquinco, Lisa

Map 4.77.

Sphenomorphus rarus: Myers & Donnelly (1991); Auth (1994); Ibáñez et al. (2001); Young et al. (1999); Fundación PA.NA.M.A. (2007); Köhler (2008); Jaramillo et al. (2010); Wilson & Johnson (2010); Uetz & Hošek (2014).

Scincella rarus: Linkem et al. (2011).

Holotype. AMNH 129836, male, from "lower montane rain forest on the southwestern headwaters of the Río Guabo, 780 m elev. (8°47'N, 8211 'W), Province of Bocas del Toro, western Panama" (Myers & Donnelly 1991).

Geographic distribution. Endemic to western Panama, 450–780 m asl. Only known from the type locality on the Caribbean slopes adjacent to the Fortuna depression and Alto Yorxin near the border to Costa Rica.

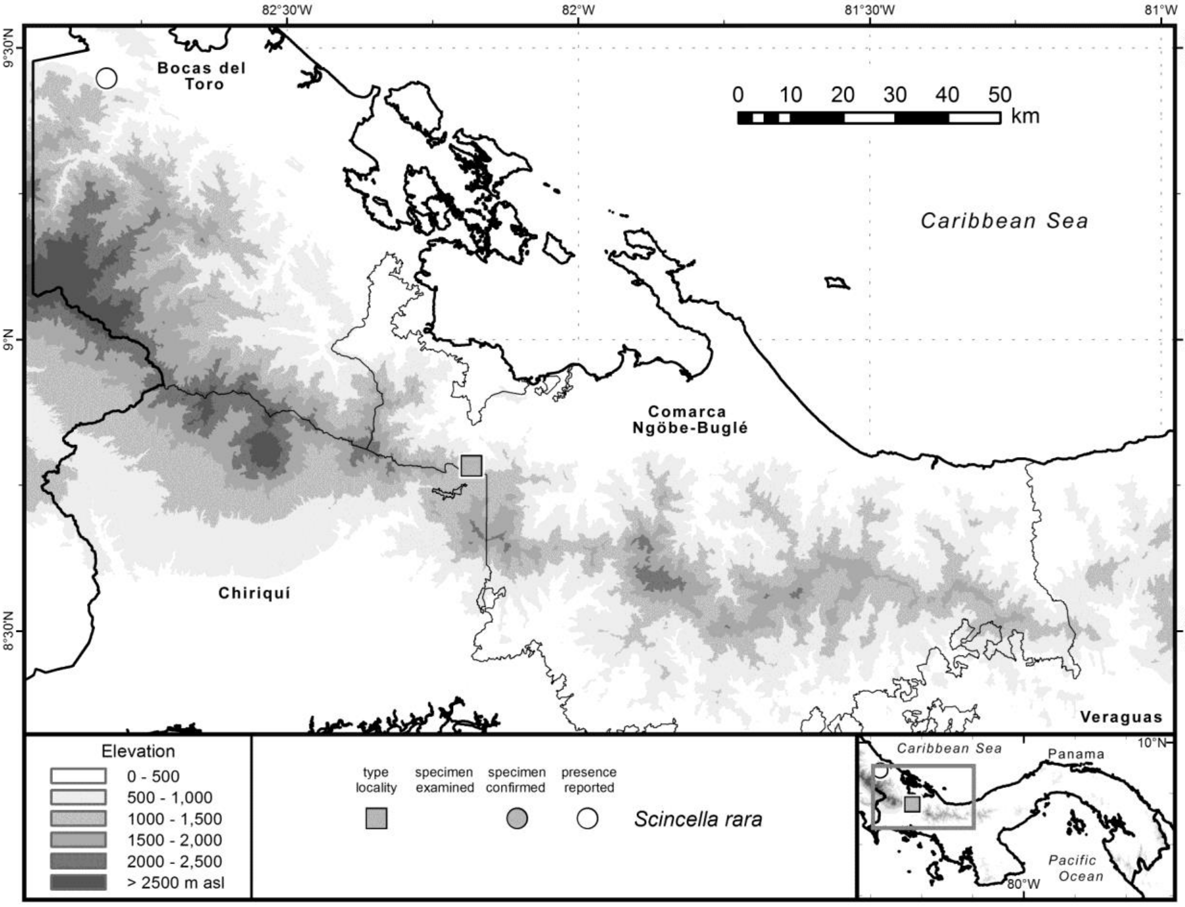
Diagnosis. A medium-sized (SVL of holotype 52 mm) skink that is distinguished from the skink-like anguids (genera *Celestus* and *Diploglossus*) and gymnophthalmids (genera *Gymnophthalmus* and *Bachia*), as well as the skink *Marisora unimarginata* by the same characters as *Scincella cherriei.* The species differs from its only Panamanian congener in lacking prefrontals, thus exhibing a broad contact between the frontal and frontonasal plates, the latter of which has a markedly concave posterior border (vs. PF 2, narrow contact between frontal and FN along a rather straight portion of the otherwise convex posterior border of the latter), and in having only 11 subdigital lamellae under the 4th toe and 7 under the 4th finger (vs. 4toe 13 or more, 4finger 9 or more), among others.

Description. TOL 101+x mm (tail partly regenerated); SVL 52 mm; PF 0; FN 1; IN 0; FP 1, larger than frontal; SPL 6; SAM 26; 4toe 11; 4finger 7; D, L, V, and caudals cycloid, smooth (data of the holotype as reported by Myers & Donnelly 1991).

The hemipenis of *Scincella rara* is a bilobed organ with slender lobes. No spines or other conspicuous microornamentation (Myers & Donnelly 1991).

Coloration in life. Apparently similar to *Scincella cherriei,* but with stronger reddish shadings on ventrolateral portions of head and body, and a golden yellow venter (Myers & Donnelly 1991; Köhler 2008: Fig. 454).

Coloration in preservative. All in all lighter, with patterns of longitudinal stripes on dorsum and spotting on limbs more evident than in life (Myers & Donnelly 1991).



Map 4.77: Distribution of *Scincella rara*.

Natural history notes. Probably diurnal and terrestrial; the holotype was found active in the afternoon (Myers & Donnelly 1991).

Conservation. Jaramillo et al. (2010) calculated an EVS of 14 for *Scincella rara,* and assigned that species to the IUCN category VU , whereas the official IUCN Red List (IUCN 2014) lists it as DD. I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. The merely two localities from which *S. rara* has been reported do not allow for calculating a meaningful extent of occurrence. However, based on current knowledge I have to assume a very restricted distributional range for this species. If one, for example, includes the entire terrestrial surface from the Caribbean coastline to the maximum elevation reported for the species between the longitudes of the two collection sites, the resulting area would still amount to less than 5000 km^2. This small inferred extent of occurrence, together with only two known localities and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criteria B1ab(iii).

Remarks. The second locality plotted on Map 4.77 is based on MVUP 1537 that was collected by Fernando Arosemena on 13.07.1003 at "Alto Yorxin, 09°26'51.4"N, 82°48'33.7"W, Parque Internacional La Amistad, Rep. Panama [...] ± 450 m asl." Unfortunately, I have not examined this specimen.

Being known from only one published and one additional specimen, the taxon described as *Sphenomorphus rarus* has been involved in an exemplary case of taxonomic confusion recently. Based on the position of the New World taxa that were until then known as *Sphenomorphus cherriei* and *S. assatus* in their molecular phylogeny, Linkem et al. (2011) transferred these species to the genus *Scincella,* creating the new combinations *Scincella cherriei* and *Scincella assata.* Logically, they concluded that the remaining two species of Mesoamerican "*Sphenomorphus*" should be assignable to *Scincella,* too, but upon creating the new combinations *Scincella incertus* and *Scincella rarus* they unfortunately did not feminize the endings of either of the specific epithets (both are latin adjectives). Yet, another issue resulting from this generic transfer was graver: the name *Scincella rara* did already exist somehow. Darevsky & Orlov (1997) had described *Paralipinia rara* gen. et sp. nov. from Vietnam, which Greer & Shea (2003) placed in *Scincella* although they found the evidence "not compelling one way or the other". I follow the reasoning of Nguyen et al. (2010) and consider *Paralipinia* as a distinct genus, thus avoiding secondary homonymy of two *Scincella rara,* a name which in any case would be applicable to the Panamanian taxon which was described first.

Family Xantusiidae Baird 1859

Lepidophyma flavimaculatum Duméril 1851

Yellow-spotted Night Lizard, Tropical Night Lizard; Lagartija nocturna

Figure 4.101G; Map 4.78.

Lepidophyma anomalum: Taylor (1955)

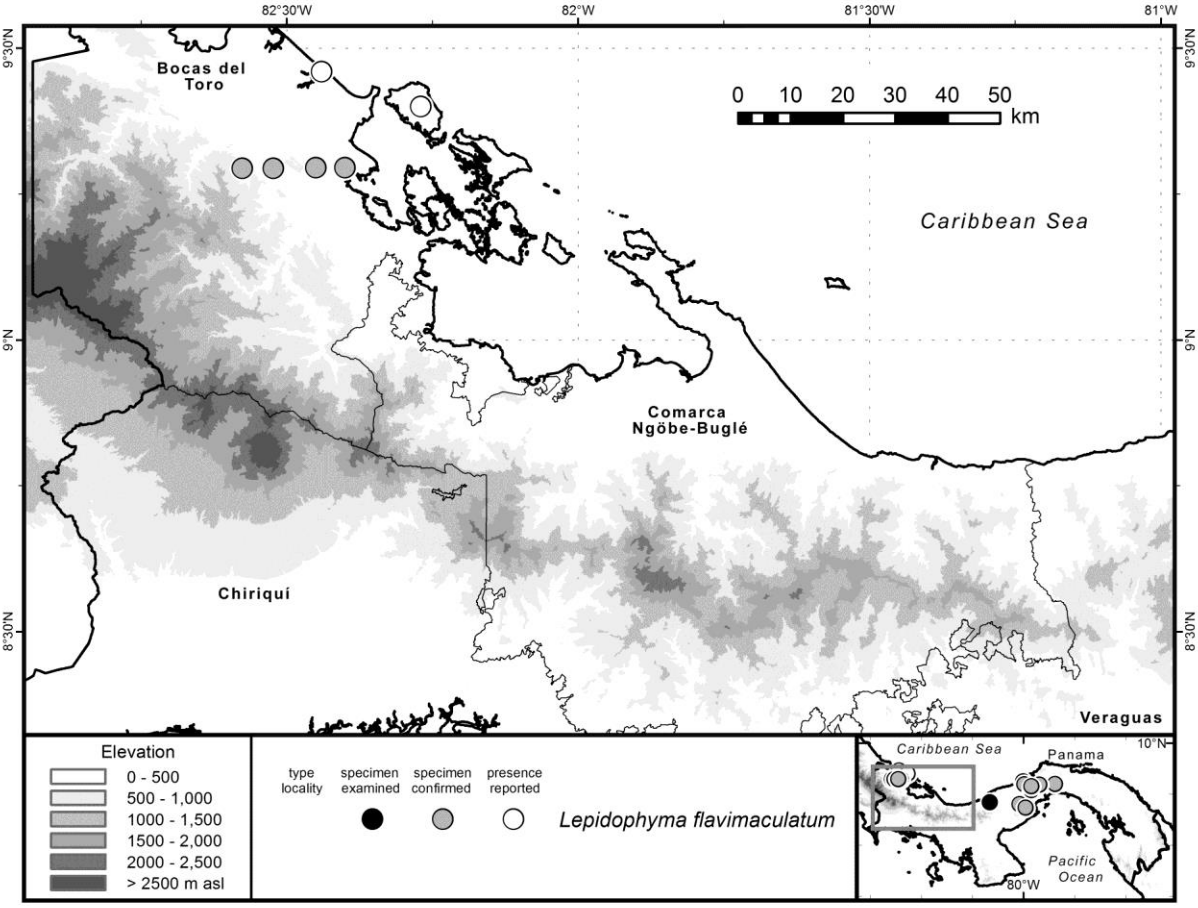
Lepidophyma flavomaculatum obscurum: Barbour (1924); Myers & Rand (1969).

Lepidophyma obscurum: Taylor (1955, 1956).

Lepidophyma ophiophthalmum: Taylor (1955, 1956).

Holotype. MNHN 782, from Province du Petén (America centrale); restricted to Río de la Pasión, Guatemala (Bezy & Camarillo 2002).

Geographic distribution. Mexico to Panama, chiefly on the Caribbean versant, 0–1400 m asl. In Panama, along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, and on both versants in Central Panama, 0–820 m asl. In the Cordillera Central, reported from PNAC and the Caribbean foothills in Bocas del Toro.



Map 4.78: Distribution of *Lepidophyma flavimaculatum*.

Diagnosis. This medium-sized lizard (maximum SVL 102 mm) is immediately recognized as a member of the genus *Lepidophyma* by its granular dorsals with interspersed enlarged tubercles contrasting sharply with the large dorsal head plates, whorls of enlarged caudal scales, and the infralabials that are fused with the chin shields. It is further distinguished from the superficially similar *Echinosaura panamensis* and *Potamites apodemus* by its large, symmetrical dorsal head plates (vs. fragmented, somewhat irregular) and the lack of moveable eyelids (vs. present). It differs from its only Panamanian congener, *L. reticulatum,* in having the second pair of chin shields in broad contact (vs. separated by granular scales) and in lacking dark reticulations on the throat region (vs. usually present).

Description. TOL to 245 mm; SVL to 127 mm; tail short, only slightly longer than SVL; D and L body scales granular, with interspersed enlarged tubercles on flanks and in 2 paravertebral rows; V rectangular, smooth; caudals keeled, whorls of enlarged caudals separated by 3–4 whorls of smaller scales (enlarged whorls inconspicuous or absent on regenerated tail portions); 26–33 total femoral pores present in both sexes; 4toe 25–31; 2nd pair of fused INL/chin shields in broad contact.

Coloration in life. D and L surfaces dark brown to black; body with yellowish circular blotches; head lighter brown, with yellow crossbars on lips; venter and gular area cream to yellowish and mottled with brown.

Coloration in preservative. Similar to that in life, apart from that the yellow shades fade.

Natural history notes. Crepuscular and nocturnal. Viviparous; the populations in Panama and most of Costa Rica apparently contain no males (Bezy & Camarillo 2002). In Nicaragua, I saw a specimen of this species about 2 m above ground on the trunk of a large tree at night.

Remarks. Bezy & Camarillo (2002) referred to *Lepidophyma flavimaculatum* as a complex of populations possibly containing more than one species. In view of the wide distribution of this nominal taxon, I do not incorporate the morphological data presented by these authors (e.g., maximum SVL 127 mm), but restrict the morphological description above to the data provided by Taylor (1956) and Savage (2002) for Costa Rican populations.

Together with the highest documented elevation in Costa Rica (1100 m asl according to Sasa et al. 2010), the records from PNAC (Ibáñez et al. 1996) and the Caribbean foothills in Bocas del Toro (Bezy & Camarillo 2002) render the species' presence in my study area as well as in the Comarca Ngöbe-Buglé plausible.

Lepidophyma reticulatum Taylor 1955

Tropical Night Lizard; Lagartija nocturna, Lagartija pintada

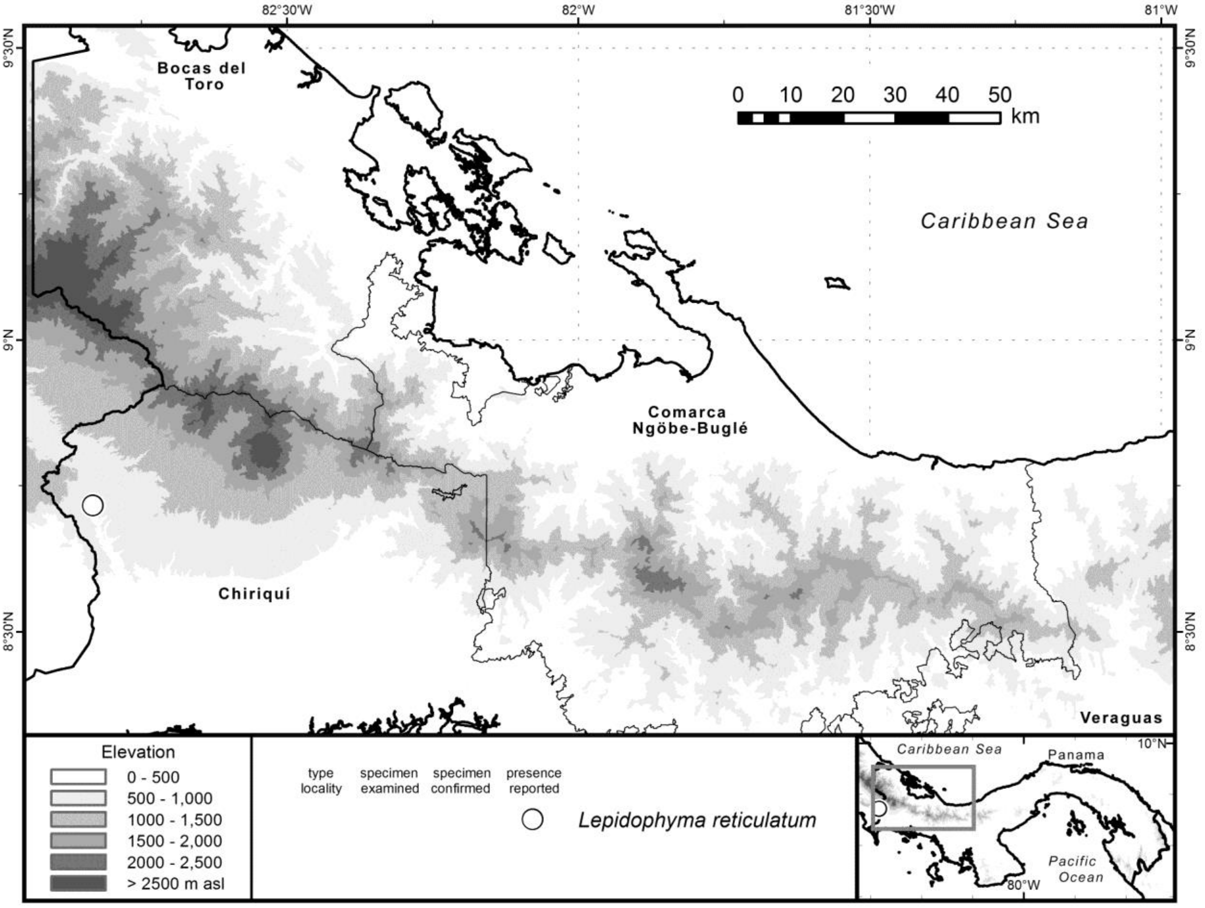
Figure 4.101H; Map 4.79.

Lepidophyma flavimaculatum: Young et al. (1999: in part.).

Holotype. KU 36245, from Agua Buena, Puntarenas province, Costa Rica.

Geographic distribution. Pacific versant of Costa Rica and western Panama, 10–1250 m asl. In Panama, only reported from extreme western Chiriquí at Río Chiriquí Viejo, 515 m asl (Batista et al. in prep. b).

Diagnosis. This medium-sized lizard (maximum SVL 103 mm) is immediately recognized as a member of the genus *Lepidophyma* by its granular dorsals with interspersed enlarged tubercles contrasting sharply with the large dorsal head plates, whorls of enlarged caudal scales, and the infralabials that are fused with the chin shields. It is further distinguished from the superficially similar *Echinosaura panamensis* and *Potamites apodemus* by its large, symmetrical dorsal head plates (vs. fragmented, somewhat irregular) and the lack of moveable eyelids (vs. present). It differs from its only Panamanian congener, *L. flavimaculatum,* in having the second pair of chin shields separated by small, granular scales (vs. in broad contact) and by the dark reticulations usually present on the throat region (vs. absent).



Map 4.79: Distribution of *Lepidophyma reticulatum*.

Description. TOL to 220 mm; SVL to 103 mm; tail short, only slightly longer than SVL; D and L body scales granular, with interspersed enlarged tubercles on flanks and in 2 paravertebral rows; V rectangular, smooth; caudals keeled, whorls of enlarged caudals separated by 3–4 whorls of smaller scales (enlarged whorls inconspicuous or absent on regenerated tail portions); 25–43 total femoral pores present in both sexes; 4toe 26–31; 2nd pair of fused INL/chin shields separated by small, granular scales (data of Taylor 1956 combined with that of Bezy & Camarillo 2002 and Savage 2002).

Coloration in life. D and L surfaces dark brown to black; body with yellowish circular blotches; head lighter brown, with yellow crossbars on lips; venter and gular area cream to yellow, gular area usually with contrasting dark reticulations partially or completely enclosing rounded light areas.

Coloration in preservative. Similar to that in life, apart from that the yellow shades fade.

Natural history notes. Probably similar to *Lepidophyma flavimaculatum,* i.e., nocturnal and/or crepuscular as well as viviparous. All known specimens are females.

Remarks. The six specimens collected by MP at Río Chiriquí Viejo (Batista et al. in prep. b) represent the long expected first record for Panama and extend the distribution of this species into my study area. Previous records of *Lepidophyma flavimaculatum* from Chiriquí without further locality information (Young et al. 1999) might be based on *L. reticulatum.*

Infraorder Teiformata Vidal & Hedges 2005

Family Gymnophthalmidae Merrem 1820

Anadia ocellata Gray 1845

Ocellated Anadia; lagartija

Figure 4.102A; Map 4.80.

Anadia metallica arborea: Taylor (1955, 1956).

Anadia metallica attenuata: Taylor (1955, 1956).

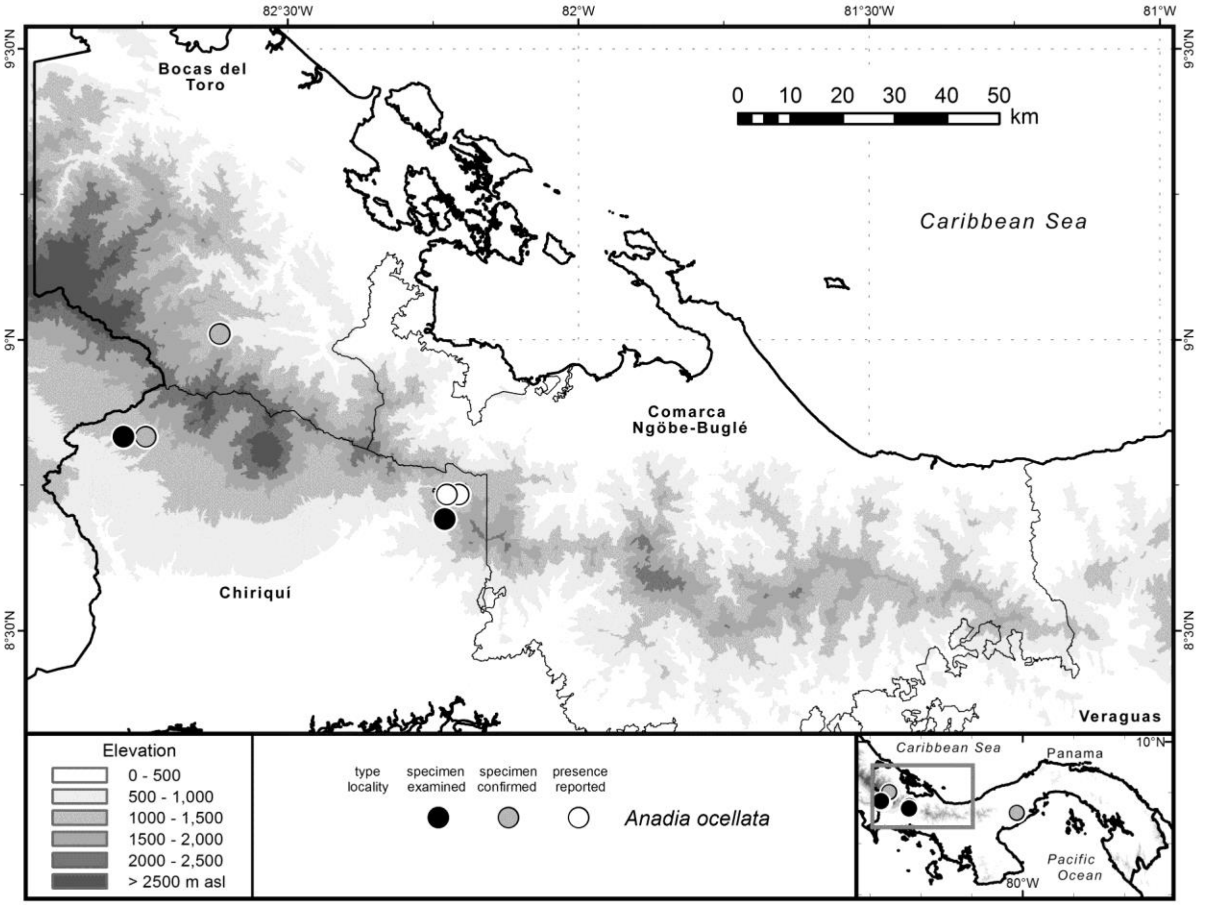
Anadia metallica metallica: Taylor (1955, 1956).

Chalcidolepis metallicus: Cope (1876).

Holotype. BMNH 1946.8.2.2, from Tropical America (corrected to "Costa Rica or Panama"; Oftedal 1974).

Geographic distribution. Endemic to the Talamancan Highlands of Costa Rica and Panama, 500–1530 m asl. In Panama, along both slopes of the Cordillera Central including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veragaus. In the Cordillera Central, reported from PNAC, La Fortuna, and Santa Clara, 600–1310 m asl.

Diagnosis. This medium-sized microteiid (maximum SVL 75 mm) is immediately distinguished from all other lizards of western Panama by its slender body and long, prehensile tail both covered by rectangular scales arranged in transverse annuli, and its pointed head. It differs from its eastern Panamanian congener *Anadia vittata* in having 8–11 femoral pores per side in males (vs. 11–14), 23–32 scales around midbody (vs. 30–37), and the possibly present light dorsolateral stripes less than 3 scales wide (vs. 3 or more). It differs from the superficially similar *Bachia blairi* in having well-developed limbs with 5 fingers and 5 toes (vs. 4 and 3) and a large ear opening (vs. none).



Map 4.80: Distribution of *Anadia ocellata*.

Description. TOL to 231 mm; SVL to 75 mm; tail long, TL/SVL = 1.86–2.33; FN 1; FP 2; gulars 8–9*; D, V, and caudals rectangular, smooth, arranged in complete whorls; males with 8–11, females with 2–6 femoral pores per side; SAM 23–32; 4toe 13–14*; 4finger 11*.

The hemipenis of *Anadia ocellata* is a bilobate organ with rows of spinules.

Coloration in life. Generally with a metallic appearance; D and L surfaces of body and tail either uniformly brown or bronze, with two irregular, light-colored dorsolateral lines extending from eyes posteriorly and assuming a zig-zag appearance on tail, separating the D from the L coloration which may be uniform or blotched or mottled with brown, olive, or bronze. A light-centered, dark-outlined ocellus above shoulder may be followed posteriorly by up to 7 light spots along the flanks, the anterior of which may have a similarly ocellate appearance. V surfaces whitish to yellow, occasionally with light or dark mottling. Leenders (2005) assumed this species to exhibit sexual dichromatism, with males being less contrastingly or uniformly colored.

The male SMF 90095 (Fig. 4.102A) was recorded as follows: D ground color Walnut Brown (221B), grading into Dark Drab (119B) laterally and into Hair Brown (119A) on head, with Sepia (219) mottling dorsally on body and tail; a Jet Black (89) ocellus (slightly broken up on right side) with a single dirty white scale in its center just above shoulder; V ground color Pearl Gray (81) with a suggestion of dirty white, grading into dirty white with a suggestion of Sulphur Yellow (57) towards the head and into Beige (219D) with a suggestion of dirty white towards tip of tail; venter with numerous small Dark Drab (119B) dots which are also present, together with two ventrolateral series of Sepia (219) mottling, on anterior two-thirds of tail; iris Clay Color (26); tympanum Blackish Neutral Gray (82); anterior portion of tongue Dark Neutral Gray (83) with Blackish Neutral Gray (82) tips.

Coloration in preservative. After 4.5 years in 70% ethanol, the coloration of SMF 90095 is very similar to that in life, though with less reddish hues in the D brown.

Natural history notes. Arboreal, uses its prehensile tail for climbing. Leenders (2005) provided a detailed account on observations made at a Costa Rican locality, including habitat use, locomotion, foraging, and courtship. The specimen SMF 89443 was found by Ralph Mangelsdorff dead on the road at La Fortuna. The adult male SMF 90095 was spotted during a tree-climbing operation in the early afternoon about 1 m above ground as it walked up a tree from which it might have been driven down during the installation of the climbing rope.

Remarks. Contrary to what was reported by Savage (2002) and Leenders (2005), the male SMF 90095 lacks precloacal pores, i.e., pores on shields of the precloacal plate, having only 10 femoral pores per side instead of a single continuous series of pores as one could understand these authors. I assume the precloacal pores mentioned by these authors to constitute the proximal femoral pore(s) on scales adjacent to the precloacal plate. Taylor (1956) noted that the "innermost" pore "might be regarded a preanal pore but is practically continuous with the femoral series", while Oftedal (1974) stated the femoral pores of males to include "1–2 on interfemoral scales". Cope's (1876) value of 23 SAM was reproduced during a re-examination of USNM 30568 by Doris Cochran (Taylor 1956), but has not been adopted by subsequent authors, probably because it was left uncommented by Oftedal (1974) who gave the lowest SAM value as 27. The quite uniform coloration of the male SMF 90095 supports the notion of sexual differences in coloration as proposed by Leenders (2005).

I was unable to find any discrete record that substantiates the lower elevational limit given as 240 m asl for Panama and the species as a whole by Jaramillo et al. (2010), while other authors give higher values around 500 m (Savage 2002; Leenders 2005; Sasa et al. 2010; Wilson & Johnson et al. 2010), and the lowest Panamanian record (MCZ 165192 from El Valle de Antón) comes from an approximate elevation of 600 m. However, if the specimen MCZ 86792 from Curundú in Panama province, catalogued as *Anadia metallica metallica,* was eventually confirmed to represent *A. ocellata,* it would provide an even lower as well as the easternmost record for this species. Likewise, I could not trace any specimen or report that would support the occurrence of *A. ocellata* in the highlands of E Panama or of *A. vittata* in the Cordillera Central as stated by Jaramillo et al. (2010), and regard the former taxon to not range into eastern, and the latter not to range into western Panama. Records of *A. ocellata* from eastern Panama, Colombia, and Ecuador most probably derive from confusions with other species of the genus (Oftedal 1974). Since the specimen MCZ 165192 from El Valle de Antón, catalogued as *Anadia lionotus,* was confirmed by GK to represent *A. ocellata,* the specimens MCZ 165193–34 from the same locality catalogued under the same name most probably also represent *A. ocellata.* Together with the distribution documented for Costa Rica, the records from Río Changena and PNAC as well as the distance of less than 5 km between Quebrada Mellizas (provenance of the specimen MVUP 1159) and the Comarca's border render the species' occurrence in the Comarca Ngöbe-Buglé and Veraguas plausible.

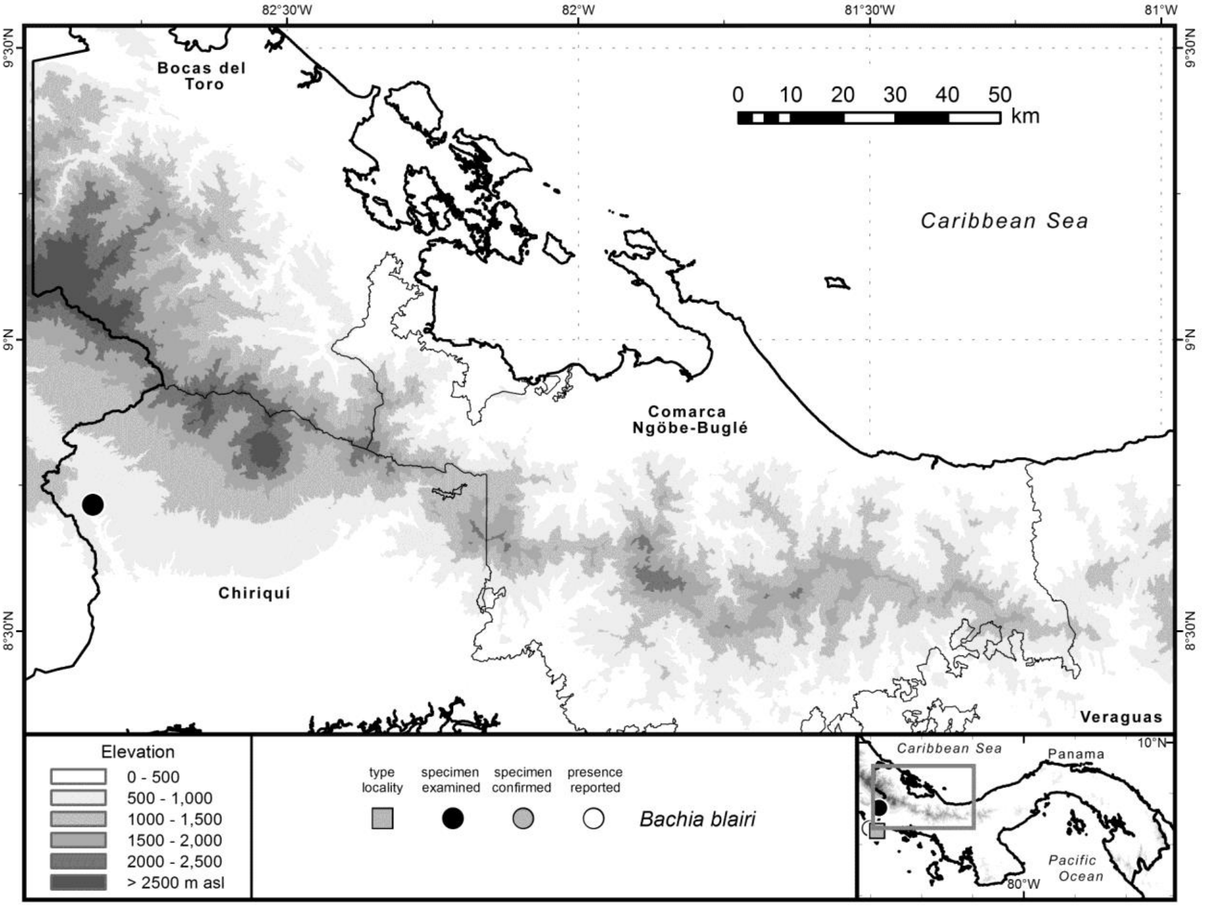
Bachia blairi **(Dunn 1940)**

Blair's Bachia; Lagartija cabeza lisa

Figure 4.102B; Map 4.81.

Bachia pallidiceps: Uetz & Hošek (2014).

Scolecosaurus blairi: Dunn (1940).



Map 4.81: Distribution of *Bachia blairi*.

Holotype. ANSP 21773, from Puerto Armuelles, Chiriquí, Panama.

Geographic distribution. Endemic to the Pacific versant of eastern Costa Rica and western Panama, 0–515 m asl. In Panama, only known from extreme western Chiriquí. In the Cordillera Central, reported from Río Chiriquí Viejo, 515 m asl (Batista et al. in prep. b).

Diagnosis. This medium-sized microteiid (maximum SVL 63 mm) is immediately distinguished from all other lizards occurring in western Panama by its slender body covered just as the tail by rectangular to hexagonal scales arranged in transverse annuli and by its very short limbs bearing only 4 fingers and 3 toes, all of which are rudimentary. It further differs from the superficially similar *Anadia ocellata* in having a rather blunt head (vs. conspicuously acuminate), and from this species as well as *Gymnophthalmus speciosus* in having no external ear opening (vs. present), and the large frontal in contact with the very large parietals (vs. separated by 2 FP).

Description. TOL to 160 mm; SVL to 63 mm; tail moderately short, TL/SVL = 1.5–1.7; FN 1; FP 0; D and caudals hexagonal, smooth; V, and C rectangular, smooth; scales of body and tail arranged in complete transverse whorls; males with 2, females without precloacal pores; SAM 24–25.

Coloration in life. Almost unicolor brown to black, lighter on anterior V surfaces.

Coloration in preservative. Probably similar to that in life.

Natural history notes. Semifossorial, known from very few examples. The specimens from Río Chiriquí Viejo were found during the flooding of a hydroelectric reservoir.

Remarks. I follow Savage (2002) and the references cited therein in considering *Bachia blairi* a distinct species. The specimens MHCH 1689–90, collected by MP at Río Chiriquí Viejo (Batista et al. in prep. b) document the occurrence of this species in my study area and greatly extend the known vertical distribution more than 470 m upwards from the formerly documented 40 m asl (Wilson & Johnson 2010, among others).

Echinosaura panamensis Barbour 1926

Panama Teiid, Rough Teiid; Lagartija quillada

Figure 4.102C; Map 4.82.

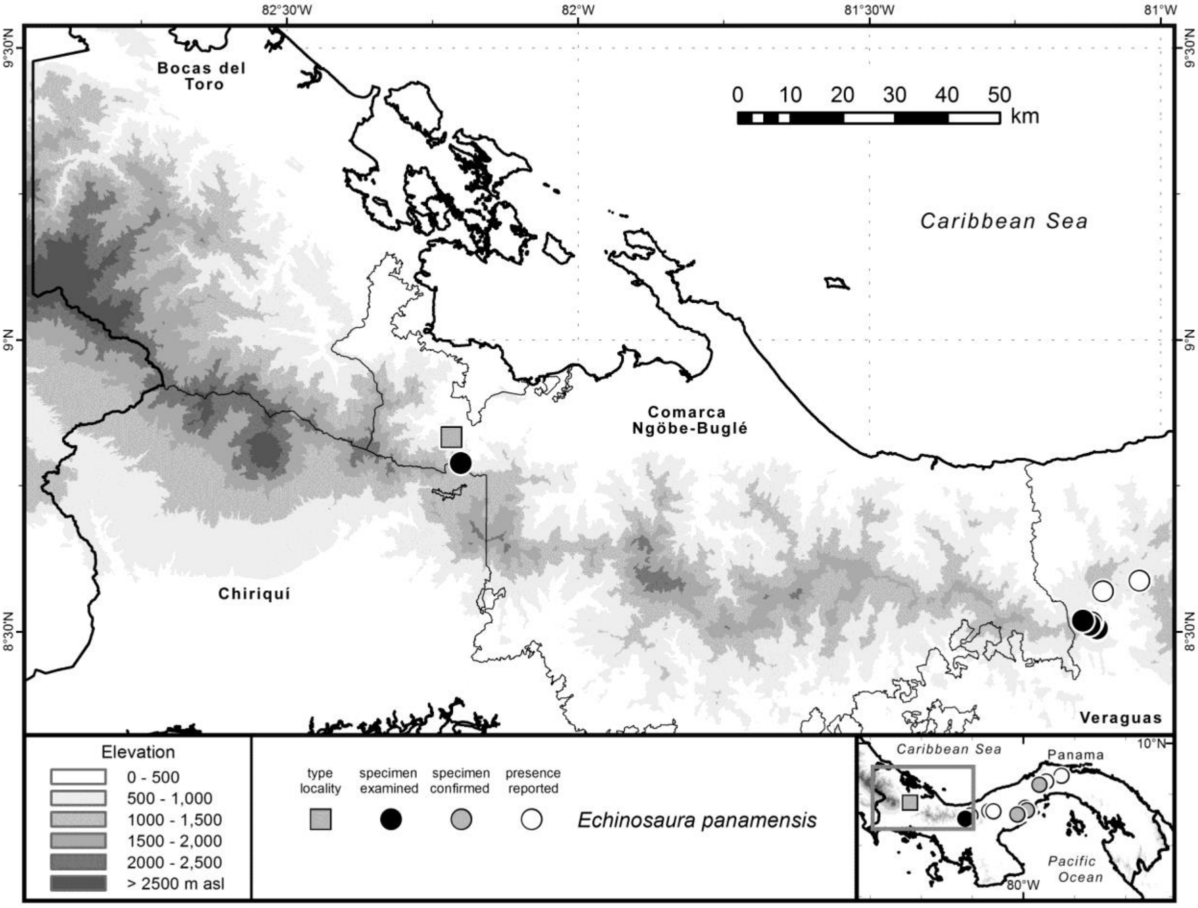
Echinosaura horrida: Auth (1994); Martínez & Rodriguez (1994); Martínez et al. (1995); Ibáñez et al. (1995, 1996, 1997); Young et al. (1999); Carrizo (2000); Fundación PA.NA.M.A. (2007).

Echinosaura horrida panamensis: Uzzell (1965, 1966).

Echinosaura panamansis: Dunn (1933).

Holotype. MCZ 17746, male, from "La Loma in the mountains of Bocas del Toro Province, western Panama" (Barbour 1924; today this place pertains to the Comarca Ngöbe-Buglé).

Geographic distribution. Endemic to Panama, 60–900 m asl. In Panama, restricted to the western and central portions of the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Caribbean versant N of La Fortuna and in PNGDOTH, as well as from the Pacific versant around Santa Fé, PNGDOTH, El Valle de Antón, and PNAC.



Map 4.82: Distribution of *Echinosaura panamensis*.

Diagnosis. This medium-sized lizard (maximum SVL 71 mm) is immediately distinguished from most lizards in western Panama by its "rough" appearance owing to the granular dorsals with interspersed enlarged tubercles, and from members of the genus *Lepidophyma* sharing this characteristic by its rugose to multicarinate, small, mostly irregularly fragmented dorsal head scales (vs. smooth to rugose, large dorsal head plates contrasting sharply with the dorsal granules), the presence of moveable eyelids (vs. absent), and its infralabials that are not fused with the chin shields (vs. fused). It differs from the rather similar *Potamites apodemus* in having a transversely divided frontal and two large prefrontal plates clearly discernible and multicarinate (vs. irregularly fragmented, rugose to unicarinate scales in the frontal and prefrontal area), and two undulating paravertebral rows of enlarged, conical tubercles (vs. two straight paravertebral rows of large, distinctly unicarinate scales).

Description. TOL to 153 mm*; SVL to 71 mm; tail short, TL/SVL = 1.25–1.43*; PF 2*; FP 3–4*; collar indistinct; D and L body scales granular, conical to keeled, with interspersed enlarged tubercles on flanks and in 2 undulated paravertebral rows; V rectangular, keeled; D and L caudals irregularly rounded, rugose to keeled, with whorls of separated enlarged tubercles; median SC rounded to rectangular, keeled; females without, males with 13–15 total femoral pores (almost indiscernible in my sample); SAM 53–73*; 4toe 19–25; 4finger 13–16 (own data combined with that of Uzzell 1965).

The hemipenis of *Echinosaura panamensis* is a slightly bilobed organ with enlarged basal spines and spinulate flounces (Uzzell 1995).

Coloration in life. D and L surfaces predominantly gray to brown, generally lighter and more grayish in dry animals and assuming a darker and more vivid brown when the animal is wet; often with diffuse lighter and/or darker areas especially around neck, shoulders, and base of tail; several larger plates especially on V surfaces darker brown; V surfaces usually with white, cream, and/or orange blotches or mottling.

The specimen SMF 89557 (Fig. 4.102C) from Cerro Mariposa was described as follows: Ground color Olive Brown (28); scales bordering mouth, and chin shields, Dusky Brown (19); V shields of body and tail including precloacal shields Dusky Brown (19), partially mottled with Orange Yellow (18) with a suggestion of Spectrum Orange (17).

The female SMF 91542 from Willie Mazú, near the type locality, was described as follows: D and L ground color Dark Grayish Brown (20), suffused with diffuse Cinnamon (123A) blotches; a pair of Clay Color (26) blotches dorsally on base of tail; V ground color Sepia (119), suffused with Cinnamon (123A) under neck; V surface of head mottled with dirty white; V surfaces of body and tail with Straw Yellow (56) blotches; cloacal plates mottled with Ferruginous (41); iris Burnt Umber (23).

Leonhard Stadler recorded the juvenile MHCH 2312 as follows (translated from Stadler 2010): D surfaces a mixture of Olive Brown (28) and Ground Cinnamon (239) with Clay Color (26) blotches posterior to head and on base of tail; V scales Dark Brownish Olive (129) with Clay Color (26) borders forming a reticulum on venter; subcaudals Dark Brownish Olive (129) with Buff (124) borders forming a reticulum; V surface of head unicolor Dark Brownish Olive (129).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all orange tonalities have faded.

Natural history notes. Terrestrial, apparently mostly crepuscular and nocturnal. All seven specimens I found together with AH were found at ground level, with one exception at night. Four of these (including the only diurnal encounter) were discovered under logs, two spotted while fleeing from our disturbance, and one while it was actively moving through the leaf litter. Uzzell (1965) cited several observations of individuals becoming absolutely stiff when handled. I recall these animals to at least not oppose to my handling too vigorously.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Echinosaura panamensis,* and assigned that species to the IUCN category LC, in which it is also listed by the official IUCN Red List (IUCN 2014). I calculated the species' EVS as 5 (range) + 3 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of 11854 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category VU according to IUCN (2001) criterion B1b(iii).

Remarks. I adopt the notion of most recent authors (Fritts et al. 2002; Köhler 2008; Jaramillo et al. 2010) in regarding *Echinosaura palmeri* and *E. panamensis* as valid species rather than subspecies of *E. horrida.* Consequently, *E. horrida* does not occur in Panama. The femoral pores are almost indiscernible in the specimens I have examined. In the two specimens from Willie Mazú near the type locality, the chin shields are more symmetrically arranged and the V less pronouncedly keeled than in the examined specimens from Cerro Mariposa.

The occurrence of *Echinosaura panamensis* in Bocas del Toro and Chiriquí provinces is rendered plausible by the respective proximity of the georeference provided for La Loma by Savage & Watling (2008) to the border of the former and that of my own collection site Willie Mazú to the border of the latter province.

I could not find any locality record to substantiate the upper elevational limit of 1500 m asl (Köhler 2008; Wilson & Johnson 2010). This value probably derives from the altitude of 5000 ft (= 1524 m) given for the type locality in the original description (Barbour 1924). However, all other elevations provided for the "La Loma" collections of E.R. Dunn and C.B. Duryea are much lower, usually ranging between 300–600 m (Dunn 1924b; Savage & Watling 2008). In fact, Uzzell (1965) states the type series of *Echinosaura panamensis* to come from "La Loma (600 m)", and the coordinates provided for La Loma by Savage & Watling (2008) yield a SRTM elevation of 412 m. I thus consent with Jaramillo et al. (2010) in regarding the second highest published elevation ("Cerro Campana (900 m)" fide Uzzell 1965) as the documented elevational maximum for this species, which is confirmed by the specimens SMF 91541 and MHCH 2314 from Cerro Mariposa. The elevation of 8400 m stated by Uzzell (1965: p. 86) is clearly erroneous.

Gymnophthalmus speciosus (Hallowell 1861)

Golden Spectacled Tegu; Lisa, Limpia casa

Figure 4.102D; Map 4.83.

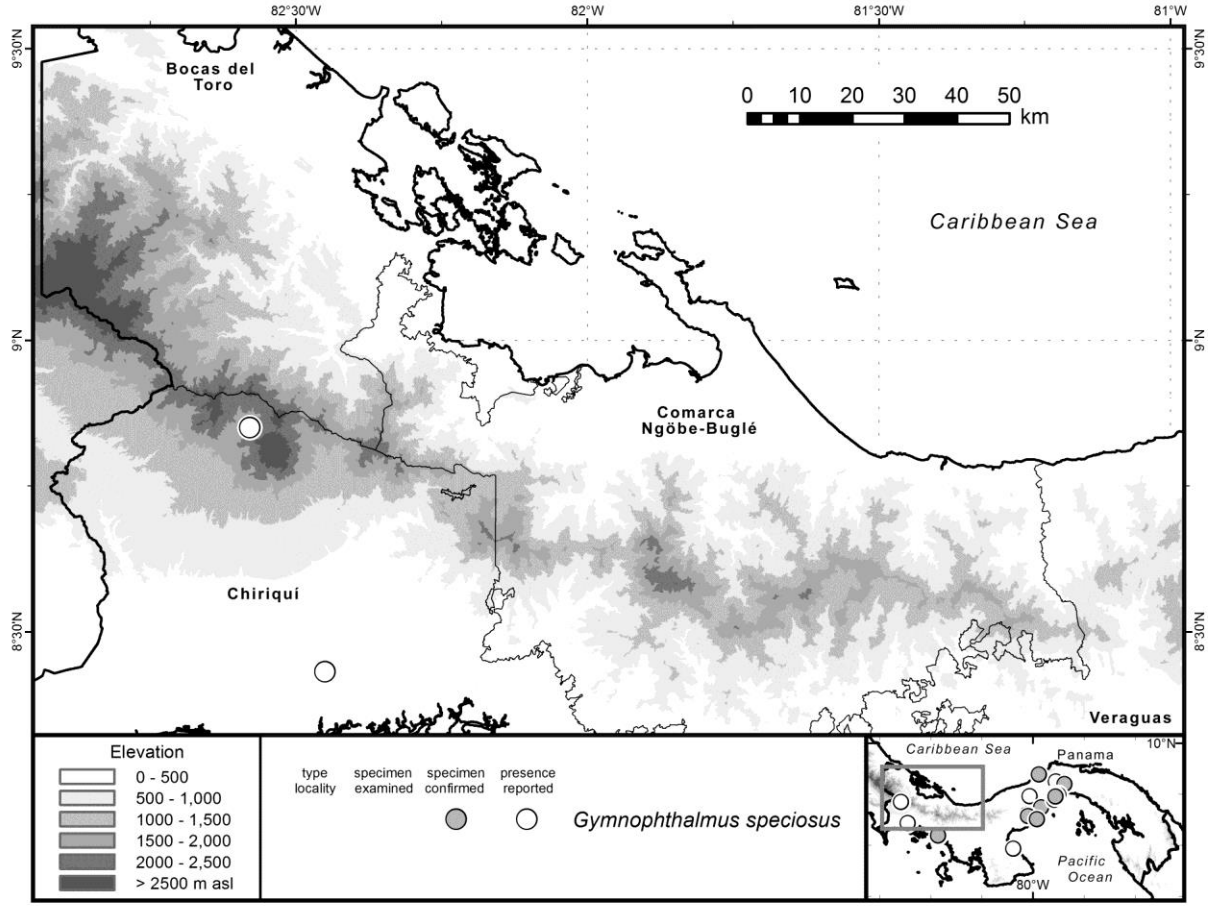
Epaphelus sumichrastii: Cope (1867).

Gymnophthalmus laevicaudus: Cope (1893).

Gymnophthalmus sumichrasti: Wettstein (1934).

Holotype. Unknown, from Nicaragua.

Geographic distribution. Mexico to Colombia, Venezuela, and Guyana, 0–1520 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Pacific versant at PNAC, Valle de Antón, and Cerro Punta, up to 1520 m asl.



Map 4.83: Distribution of *Gymnophthalmus speciosus*.

Diagnosis. This small (maximum SVL 44 mm) skink-like lizard differs from all other skink-like lizards in Panama in having only 4 fingers (vs. 5), and in lacking moveable eyelids (vs. present). It further differs from the skink-like anguids of the genera *Celestus* and *Diploglossus* as well as from *Marisora unimarginata* in having a single large frontonasal between the rostral and the prefrontals (vs. two pairs of internasals separating the rostral from the first unpaired dorsal head plate in the anguids and one pair of IN in *Marisora*), and from the skinks of the genus *Scincella* in having two frontoparietals between the frontal and the IP and parietals (vs. a single, very large FP). *Gymnophthalmus speciosus* can further be distinguished from the slender gymnophthalmids of the genera *Anadia* and *Bachia* by its smooth cycloid scales around body and tail (vs. rectangular or hexagonal).

Description. TOL to 122 mm; SVL to 44 mm; tail moderately long, TL/SVL = 1.7–2.1; FN 1; FP 2; collar indistinct; D, V, and caudals cycloid, smooth; males with 4–13 total femoral and precloacal pores; SAM 13–15.

The hemipenis of *Gymnophthalmus speciosus* is a bilobed organ.

Coloration in life. D surfaces of head and body bronze; L surfaces below an often present narrow light dorsolateral line dark to blackish brown; venter cream in juveniles, darkening with age; tail red unless regenerated.

Coloration in preservative. Similar to that in life, except that red tails fade to cream.

Natural history notes. Diurnal and terrestrial to fossorial, usually found in open, sunny habitats. Telford (1971) provided data on the life history of a population in Panama City.

Remarks. The specimen UMNH 5275, collected by J.M. Legler at Cerro Punta, 5000 ft (= ca. 1524 m), raises the upper elevational limit for this species from the previously reported 1320 m (Wilson & Johnson 2010). Yet, most of the area pertaining to the settlement of Cerro Punta lies well above 1600 m asl. Notwithstanding the lack of records from the Caribbean versant of western Panama, the records from central Panama together with the distribution documented for Costa Rica render the occurrence of this species in Bocas del Toro and Veraguas provinces as well as in the Comarca Ngöbe-Buglé plausible. Whether the South American populations referred to this species are conspecific with the Central American form remains questionable (see Savage 2002 and references therein).

Leposoma southi Ruthven & Gaige 1924

South's Leposoma; Lagartija quillada

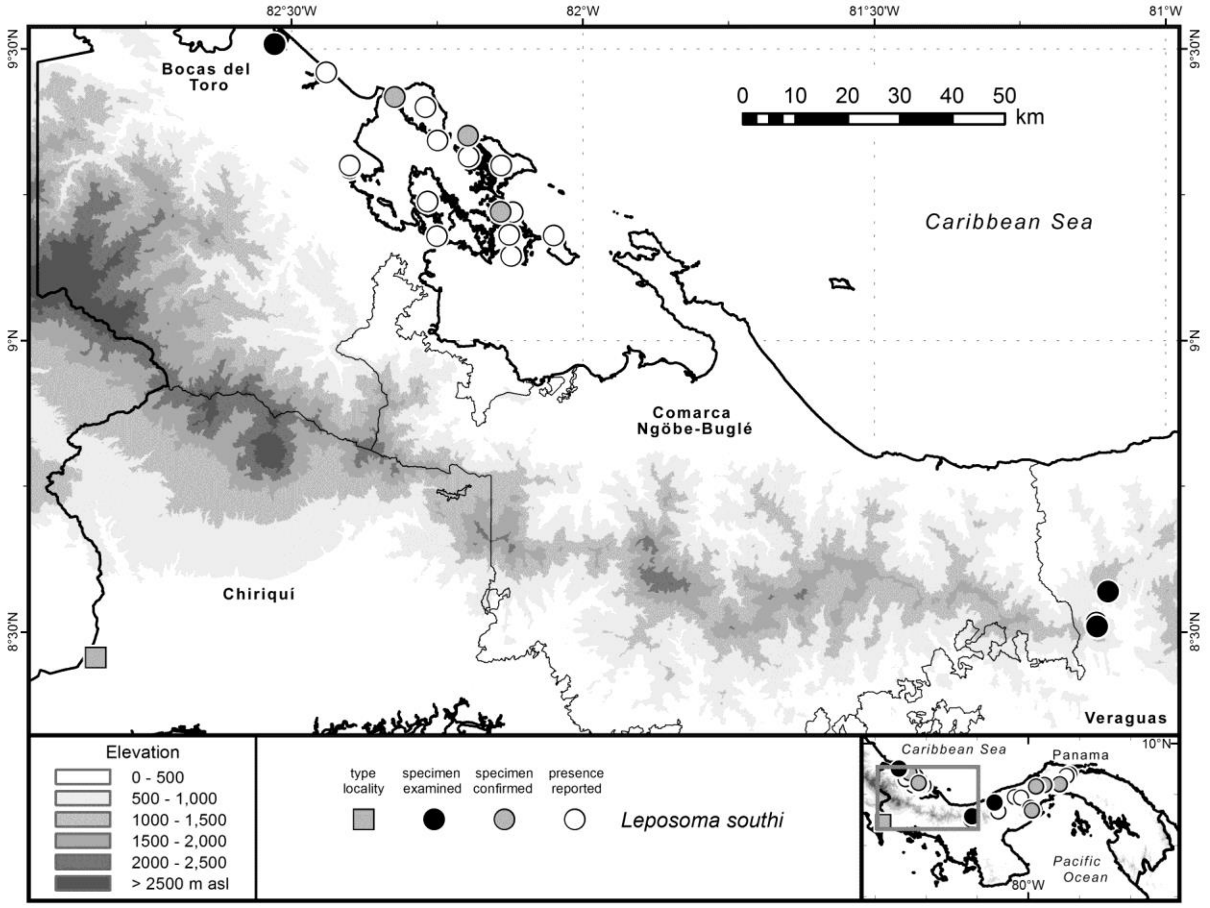
Figure 4.102E; Map 4.84.

Leposoma bisecta: Taylor (1949).

Leposoma southi orientalis: Taylor (1955).

Holotype. UMMZ 48065, from "Progreso (90 ft. elev.), Chiriquí Province, Panama (Ruthven & Gaige 1924).

Geographic distribution. Costa Rica to Colombia, 0–900 m asl. In Panama, throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC, PNGDOTH, and the Santa Fé area, up to 900 m asl.



Map 4.84: Distribution of *Leposoma southi*.

Diagnosis. This medium-sized lizard (maximum SVL 55 mm) is immediately recognized as a member of the genus *Leposoma* by its strongly keeled, imbricate, and mucronate dorsal, lateral, and ventral body scales in combination with strongly keeled dorsal head scales. It differs from *L. rugiceps,* its only congener in Panama, in having the frontonasal divided longitudinally (= 2 FN; vs. single) and the lateral neck scales between ear opening and shoulder conical and non-imbricate (vs. imbricate and keeled, resembling the dorsals).

Description. TOL to 103 mm; SVL to 55 mm; tail moderately long, TL/SVL = 1.7–2.0; FN 2; FP 2; gulars 8*; D, V, and caudals roughly rectangular, strongly keeled, mucronate, imbricate; males with 8–14 total femoral and 4 precloacal pores, females with 2 precloacal pores; SAM 20–26; 4toe 13–16*; 4finger 9–12*.

The hemipenis of *Leposoma southi* is a unilobed organ with transverse flounces which bear 4 longitudinal rows of spine-like, pointed extensions.

Coloration in life. D and L surfaces brown, usually with two lighter brown dorsolateral stripes; venter cream, orange in males.

Leonhard Stadler recorded the adult male SMF 89577 (Stadler 2010: Fig. A61) as follows (translated from Stadler 2010): D ground color Sepia (119), with two L Russet (34) longitudinal stripes extending from posterior portion of head to tail; V ground color Orange

Rufous (123C), becoming lighter on chin region; lips Sepia (119) with vertical Orange Rufous (132C) bars; iris Orange Rufous (132C).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all orange shadings have faded.

Natural history notes. Terrestrial. While *Leposoma southi* has been reported to be strictly diurnal (Savage 2002) and the male SMF 89964 from Cerro Negro has been caught at 11:00, all specimens which I observed at San San Pond Sak were active at night, just as the specimen SMF 89577 at Cerro Mariposa (Stadler 2010). In the flooded forests of San San Pond Sak, this species appeared very abundant. *Leposoma southi* has been reported to occur in sympatry (Ibañez et al. 1995, 1996) and even syntopy (Gutierrez & Arredondo 2007) with *L. rugiceps* at certain sites. At San San Pond Sak, Lotzkat et al. (2012b) found the two species less than 3 km from each other in different habitats. Accordingly, they assumed an ecological separation of these two similar species at this lowland site.

Remarks. The specimen SMF 89577 from Cerro Mariposa raised the highest documented elevation for this species to 900 m asl (Lotzkat et al. 2010c) and, together with other records from the Santa Fé area, documents the species' occurrence in my study area. The distance of less than 4 km between the collection site at Cerro Mariposa and the Comarca's border, together with the records from W of the Comarca on both versants, render the occurrence of *Leposoma southi* in the Comarca Ngöbe-Buglé plausible.

Although merely judged "possible" according to the criteria applied herein (see chapter 3.5.1), the presence of *Leposoma rugiceps* (Cope 1869) in my study area is highly likely given that it occurs at premontane elevations above 600 m asl, has been collected at PNAC and El Valle de Antón, and recently been reported from San San Pond Sak, 275 W of the formerly documented range (Dunn 1933; Ibáñez et al. 1996; Lotzkat et al. 2012b; see distribution map in Appendix 7). Yet, these records render the occurrence of *L. rugiceps* in the Comarca Ngöbe-Buglé plausible. In view of their identical appearance at first glance and the documented cases of sympatry and syntopy, any *Leposoma* specimen from western Panama should be checked thoroughly to ascertain its specific identity.

***Potamites apodemus* (Uzzell 1966)**

[In part modified from Lotzkat et al. (2012a); see Appendix 8 for original publication]

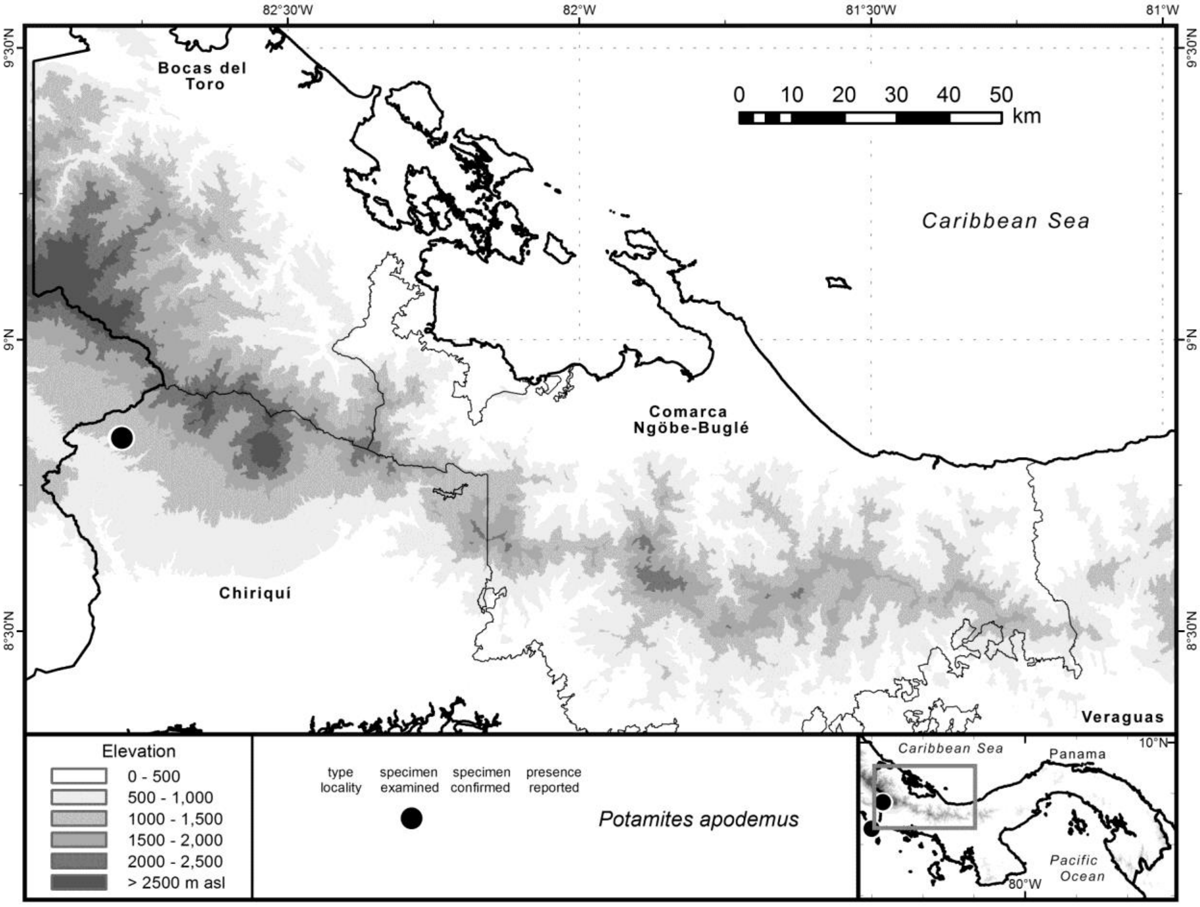
Uzzell's Neusticurus, Water Tegu; Lagartija aquática

Figure 4.102F; Map 4.85.

Neusticurus apodemus: Uzzell (1966); Peters & Donoso-Barros (1970); Savage (2002); McDiarmid & Savage (2005); Montero (2005); Köhler (2008); Santos-Barrera et al. (2008); Sasa et al. (2010); Stadler (2010); Lotzkat et al. (2012a); Uetz & Hošek (2014).

Holotype. KU 67375, male, from "15 kilometers southwest of San Isidro del General, San José, Costa Rica; 865 meters above sea level" (Uzzell 1966).

Geographic distribution. Southern Pacific Costa Rica to western Panama, 30–1200 m asl. In Panama, only recorded from extreme western Chiriquí. In the Cordillera Central, reported from Santa Clara between 1120 and 1150 m asl (Lotzkat et al. 2012a).



Map 4.85: Distribution of *Potamites apodemus*.

Diagnosis. This medium-sized lizard (maximum SVL 65 mm) is immediately distinguished from most lizards in western Panama by its "rough" appearance owing to the small, flat dorsals with interspersed enlarged, keeled scales, and from members of the genus *Lepidophyma* sharing a heterogeneous body scalation by its rugose to multicarinate, small, mostly irregularly fragmented dorsal head scales (vs. smooth to rugose, large head plates contrasting sharply with the dorsal granules), the presence of moveable eyelids (vs. absent), its infralabials that are not fused with the chin shields (vs. fused), and the dorsal scales, even the keeled ones of which are at most slightly conical (vs. distinctly conical, spine-like). The latter characteristic also distinguishes *Potamites apodemus* from the rarather similar *Echinosaura panamensis,* from which it further differs in having irregularly fragmented, rugose to unicarinate scales in the frontal and prefrontal area (vs. a transversely divided frontal and two large prefrontal plates clearly discernible and multicarinate) and two straight paravertebral rows of large, distinctly unicarinate scales (vs. two undulating paravertebral rows of enlarged, conical tubercles).

Description. TOL to 157 mm; SVL to 65 mm; tail moderate, TL/SVL = 1.46–1.86; PF and FN irregularly fragmented; gulars 4*; D and L body scales small, irregular, flat to rugose or slightly conical or keeled, with enlarged, unicarinate scales on in 2 diffuse dorsolateral and well-defined, straight paravertebral rows; V rectangular, smooth; D and L caudals rectangular, keeled, with whorls of enlarged scales separated by 2 whorls of smaller ones; median SC rectangular, smooth; females with 4 precloacal pores, males with a continuous series of 26–32 precloacal and total femoral pores; SAM 53–73*; 4toe 19–25; 4finger 13–16 (own data combined with that of Uzzell 1965).

The hemipenis of *Potamites apodemus* is a bilobed organ with a long truncus lacking ornamentation and transverse flounces on the lobes (Uzzell 1966).

Coloration in life. D and L surfaces predominantly gray to brown, generally more unicolor and more grayish in dry animals and assuming a more conspicuous pattern of more vivid colors when the animal is wet; often with diffuse lighter and/or darker blotches on body and tail that may suggest two dorsolateral light stripes; conspicuous light areas on upper arms; conspicuous light blotches along lips; a large white blotch or ocellus posteroventral to ear, as well as a series light ventrolateral dots or ocelli along body; throat and venter usually mottled with light and dark; chin area of adult males bright orange.

The male SMF 89779 from Santa Clara (Fig. 4.102F) was recorded as follows: D and L ground color Light Drab (119C), with diffuse Sepia (219) mottling; flanks with a series of five diffuse Sepia (219) ocelli with Drab-Gray (119C) centers; L surfaces of head and neck with dirty white mottling; two dirty white stripes descending from below orbit onto INL; a large dirty white blotch posterior to tympanum; V surfaces of head and body Pearl Gray (81) with heavy Sepia (119) mottling, those of head and neck also with dirty white blotches; V surface of tail Sepia (119), the anterior median portion dirty white with a suggestion of Pale Horn Color (92); mental, PM, first chin shields, and parts of adjacent scales Burnt Orange (116); D surfaces of arms with Buff (124) blotches; iris Raw Umber (223). The male SMF 92117 from Chorogo was recorded as follows: D and L ground color Vandyke Brown (121), except Warm Sepia (221A) D head; dirty white line radiating out from eye; Chamois (123D) blotches behind tympanum; chin Salmon Color (106); venter Sepia (119) with Pearl Gray (81) blotches on each scale and a suffusion of Orange-Rufous (132C) medially; iris Prout's Brown (121A).

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration is similar to that in life, apart from that the orange chin coloration of the males has faded to white.

Natural history notes. All individuals reported by Lotzkat et al. (2012a) were encountered between leaf litter and stones very close to small streams (Fig. 2.1B), generally within the streambed less than one meter from the water, and in one case (SMF 89779) even submerged. With the exception of two juveniles from Chorogo, that were found between 10:00 and 12:00, and two specimens from Río Coco, Costa Rica, encountered around 17:00, these authors encountered all specimens at nighttime. These observations support the view of Savage (2002) that *Potamites apodemus* is a riparian species of predominantly crepuscular and nocturnal activity. Nevertheless, it can also be found at daytime, and at some distance from streams (Uzzell 1966; McDiarmid & Savage 2005; Santos-Barrera et al. 2008).

Conservation. In the official IUCN Red List (IUCN 2010), this species is listed as LC. However, the minimum convex polygon drawn around the localities summarized by Lotzkat et al. (2012a) for *Potamites apodemus* yields an extent of occurrence of merely 6411 km^2. This value, together with the ongoing decrease of forested areas in the Golfo Dulce region of Costa Rica and western Panama qualify this species for the category VU according to IUCN (2001) criterion B1b(iii). I further calculated the EVS for *P. apodemus* as 4 (range) + 3 (persecution) + 4 (ecological distribution) = 11, indicating a medium vulnerability.

Remarks. Doan & Castoe (2005) erected the genus *Potamites* for Uzzell's (1966) *Neusticurus strangulatus* group, introducing the new combination *Potamites apodemus.* Summarizing the hitherto 10 Costa Rican localities and reporting on another Costa Rican and the first two Panamanian collection sites, Lotzkat et al. (2012a) extended the distribution of *P. apodemus* into the latter country and my study area, and provided the following observations.

As suspected by Uzzell (1966), *Potamites apodemus* obviously exhibits sexual dimorphism not only in the number of femoral-precloacal pores (both sexes have four precloacal pores that are hardly discernible in our juveniles, whereas femoral pores are present only in males, and visible already in juvenile males), but also in the arrangement of the scales of the precloacal plate: In all of our specimens that have femoral pores (i.e., that are males), the precloacal plate is composed of two large marginal (i.e., bordering the cloacal opening, called posterior preanals by Uzzell 1966) scales, that are preceded anteriorly by two large central and two very small L scales (called anterior preanals by Uzzell 1966). In the specimens that lack femoral pores (i.e., females), the precloacal plate has four marginal scales that are preceded by a similar arrangement of four scales anteriorly. The juveniles MHCH 1618, with 29 mm SVL, and SMF 933701, with 26 mm SVL, are the smallest juveniles reported for the species.

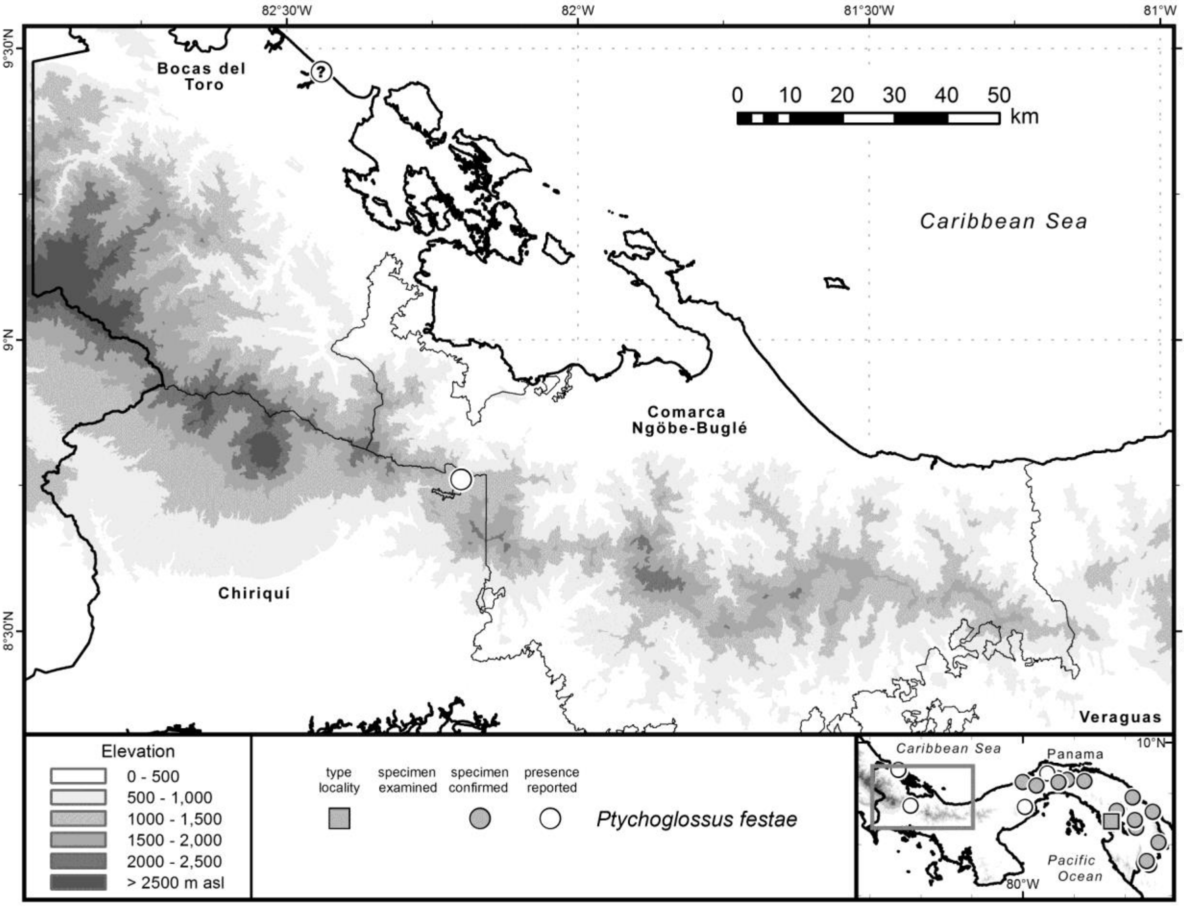
Ptychoglossus festae **(Peracca 1896)**

Peracca's Largescale Lizard; Lagartija de hojarasca quillada

Figure 4.102G; Map 4.86.

Holotype. MSNTO R228, male, from the forest of the Río Cianati [= Río Chanati (mouth at 8°27'N, 78°16'W, along the north shore of Golfo de San Miguel)], Darién Province, Panama (Harris 1994).

Geographic distribution. Panama to northern Colombia, 0–1050 m asl. In Panama, along both versants in eastern and central portions of the country to the western Caribbean lowlands, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC and RFLF up to 1050 m asl (see remarks).



Map 4.86: Distribution of *Ptychoglossus festae*.

Diagnosis. This medium-sized lizard (maximum SVL 57 mm) is immediately recognized as a member of the genus *Ptychoglossus* by its smooth head scales, the posterior borders of interparietal and parietal plates forming a straight transverse line, its rectangular to hexagonal, keeled dorsals, and its rectangular, smooth ventrals. It differs from its Panamanian congeners *P. myersi* and *P. plicatus* in having a conspicuous longitudinal fold of small, granular scales separating the keeled dorsal and lateral scales from the smooth ventral scales (vs. no such fold) and extremely widened scales in the first to postparietal rows (vs. scales of these rows about as wide as those of posteriorly adjacent ones; data from Harris 1994).

Description. SVL to 57 mm; FN 1; PF 2, usually in contact; FP 2; gulars 6; D and L rectangular to hexagonal, keeled, mucronate; one row of granules in the fold separating L from V; V rectangular, smooth, imbricate; caudals keeled dorsally, smooth ventrally; males with 2–3 total precloacal pores and 10–14 femoral pores per side, females without precloacal but with 0–5 femoral pores per side; SAM 30–38; 4toe 15–20, paired (all from Harris 1994).

The hemipenis of *Ptychoglossus festae* is a unilobed organ with 22–24 transverse flounces and three pairs of fleshy protuberances at the tip (Harris 1994).

Coloration in life. D and L surfaces of body, neck, and base of tail as well as L surface of neck dark bown with light mottling suggesting dorsolateral stripes; D surface of head medium brown; V surfaces orange in males and grayish white, green, or yellow in females (Fig. 4.102G; Harris 1994).

Coloration in preservative. Similar to that in life, except that orange and yellow hues fade.

Natural history notes. Terrestrial, probably a leaf-litter inhabitant like *Ptychoglossus plicatus,* but thought to occur at generally lower elevations than that species (Harris 1994).

Remarks. Harris (1994) and Köhler (2008) restricted the Panamanian distribution of *Ptychoglossus festae* to the central and eastern portions of the country. However, Ibáñez et al. (1996) reported its occurrence in the Cordillera Central listing it for PNAC. Later, the species was reported for Bocas del Toro province (Young et al. 1999) and the Humedal de Importancia Internacional San San Pond Sak (ANAM 2004; though this listing probably was based solely on the preceding reference and is therefore marked with a questionmark in Map 4.86). The species' presence in my study area is reportedly documented by the specimen CHP 5826 from Quebrada Arena, RFLF, Chiriquí. While the correct identification of this specimen may be assumed given that the species is well distinguishable from its congener *P. plicatus* (which is represented in the same collection with the specimen CHP 3416 from the nearby Quebrada Bonito), and considerable distribution extensions into extreme western Panama for species long considered to range only to Coclé and/or Colón are all but impossible (as exemplified by Lotzkat et al. 2012b for *Leposoma rugiceps*), not having examined CHP 5826 myself I retain certain doubts concerning the occurrence of this species in my study area. However, strictly adhering to the criteria specified in chapter 3.5.1, I have to list it as "documented". My georeference for this specimen yields a SRTM elevation of 1051 which is

150 m above the highest elevation published for this species (Wilson & Johnson 2010). Together with the records form PNAC (Ibáñez et al. 1996), this record renders the species' occurrence in Veraguas and the Comarca Ngöbe-Buglé plausible.

Ptychoglossus plicatus (Taylor 1949)

Taylor's Largescale Lizard; Lagartija de hojarasca quillada

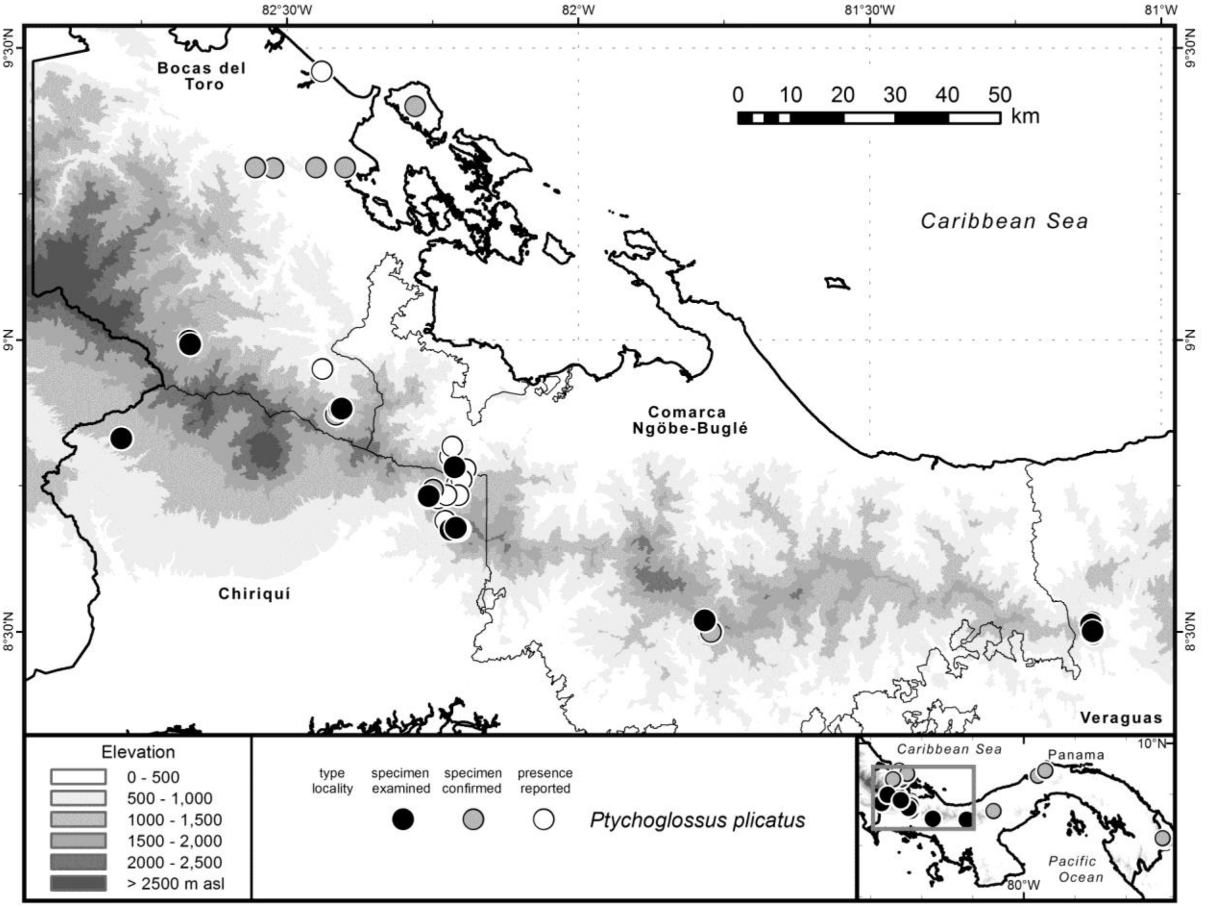
Figure 4.102H; Map 4.87.

Alopoglossus plicatus: Taylor (1949).

Ptycoglossus plicatus: Santos-Barrera et al. (2008).

Holotype. KU 23800, male, from "the Morehead Finca, 5 miles southwest of Turrialba, [Cartago province], Costa Rica" (Taylor 1949).

Geographic distribution. Costa Rica to northern Colombia, 0–1890 m asl. In Panama, apparently throughout most of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities along both versants, up to 1700 m asl atop the Continental divide.



Map 4.87: Distribution of *Ptychoglossus plicatus*.

Diagnosis. This medium-sized lizard (maximum SVL 67 mm) is immediately recognized as a member of the genus *Ptychoglossus* by its mostly smooth head scales, the posterior borders of interparietal and parietal plates forming a straight transverse line, its hexagonal, keeled dorsals, and its rectangular, smooth ventrals. It differs from *P. festae,* its only congener in western Panama, in lacking a conspicuous longitudinal fold of small scales separating the keeled dorsal and lateral scales from the smooth ventral scales (vs. present) and in having the scales of the first two postparietal rows about as wide as those of the posteriorly adjacent rows (vs. some postparietal scales extremely widened). It differs from *P. myersi* of eastern Panama in having 23 or more transverse hemipenial flounces (vs. 12 or fewer) (including data from Harris 1994).

Description. TOL to 195 mm; SVL to 67 mm; tail moderately long, TL/SVL = 1.64–2.0; FN 1; PF 2, usually in contact; FP 2; some D head plates with low keels; gulars 5–8; D and L hexagonal, keeled, imbricate, and mucronate; V rectangular, smooth, imbricate; caudals keeled, except for smooth median SC; males with 1–3 total precloacal pores and 9–13 femoral pores per side, females with 0–3 precloacal pores, some also with 1–3 femoral pores per side; SAM 31–39; 4toe 15–21, mostly paired; 4finger 11–15 (including data from Harris 1994).

The hemipenis of *Ptychoglossus plicatus* is a unilobed organ with 23–28 transverse flounces (Harris 1994).

Coloration in life. D and L surfaces predominantly brown, usually with an often diffuse light dorsolateral stripe extending from neck to midbody or base of tail, bordered with dark brown mottling especially below; dorsum and especially L surfaces of head and body with dark to blackish brown brown mottling of variable density and intensity; V surfaces usually almost unicolor cream to salmon except for dark mottling on chin region in females, usually heavily mottled with blackish brown in males

The female SMF 89784 was recorded as follows: D ground color Warm Sepia (221A), with Sepia (119) mottling especially dorsolaterally, and grading into Sepia (119) towards tip of tail; L and dorsolateral surfaces of body and head with Pale Horn Color (92) spots suggesting a dorsolateral stripe and loosely continuing onto flanks; V surfaces Pale Horn Color (92), with Sepia (119) mottling on chin, neck, tail, and ventrolateral portions of body and head; soles of hands and feet Sepia (219); iris Pratt's Rufous (140).

Leonhard Stadler recorded the subadult female MHCH 2357 as follows (translated from Stadler 2010): D ground color Raw Umber (223); dorsum with a broad longitudinal Mars Brown (223A) band bearing a Sepia (119) middorsal stripe and bordered laterally by a Cinnamon (39) as well as a slightly broader Sepia (119) dorsolateral stripe; flanks True Cinnamon (139) mottled with Sepia (119); V ground color of body, hind limbs, and base of tail Salmon Color (106), of forelimbs, head, and throat Pale Horn Color (92); ventrolateral portions of head mottled with Sepia (119) outer borders of chin shields Sulfur Yellow (157); iris Antique Brown (37).

Nadim Hamad recorded a specimen from RFLF as follows (translated from Hamad 2009): Dorsum with a broad middorsal Mars Brown (223A) band partially mottled with Vandyke Brown (221) and bordered laterally by a narrow Yellow Ocher (123C) stripe; flanks chiefly Sepia (119), with an alternate pattern of Sepia (119) and Sulfur Yellow (159) stripes extending to snout; D surface of head unicolor Raw Umber (223); D surface of limbs Vandyke Brown (221); venter dirty white with a suggestion of Sulfur Yellow (157).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration is similar to that in life, apart from that all salmon or otherwise reddish tonalities have faded.

Natural history notes. Terrestrial and supposedly diurnal. Of the 10 specimens I personally encountered, two were found in pitfall traps and four on the forest floor at daytime, including one under a rock and one while it intended to flee from my disturbance. Of the remaining four specimens which were found at night, two were spotted while they were fleeing and two while they were actively moving about, one around 05:00 between the rocks in the streambed of Río Marabí at 1230 m asl, the other on a bed of *Sphagnum* moss in open vegetation just below the N summit of Cerro Mariposa at almost 1440 m. Stadler (2010) caught 3 specimens in pitfall traps and another in a funnel trap placed along the associated drift fence. Of the 25 specimens whose morphological data I recorded, 10 have regenerated tails.

Remarks. In 10 of the 25 specimens whose morphological data I recorded, the PF are separated from each other allowing contact between the frontal and the FN. The specimens SMF 91576 from 1690 m on the N slope of Cerro Pando and MHCH 606 from ca. 1700 m at La Nevera raise the upper vertical limit in Panama from 1460 m (Jaramillo et al. 2010).

Family Teiidae Gray 1827

Ameiva praesignis (Baird & Girard 1852)

Giant Ameiva; Borriguero, Borriguero común, Borriguera común

Figure 4.103A; Map 4.88.

Ameiva ameiva or *A. ameiva praesignis:* Dunn (1940); Swanson (1945); Breder (1946); Cochran (1946); Busack (1966); Peters & Donoso-Barros (1970: in part.); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1996, 1997, 2001); Martínez et al. (1995, 1999); Young et al. (1999); Savage (2002); ANAM (2005a); McDiarmid & Savage (2005); Martínez

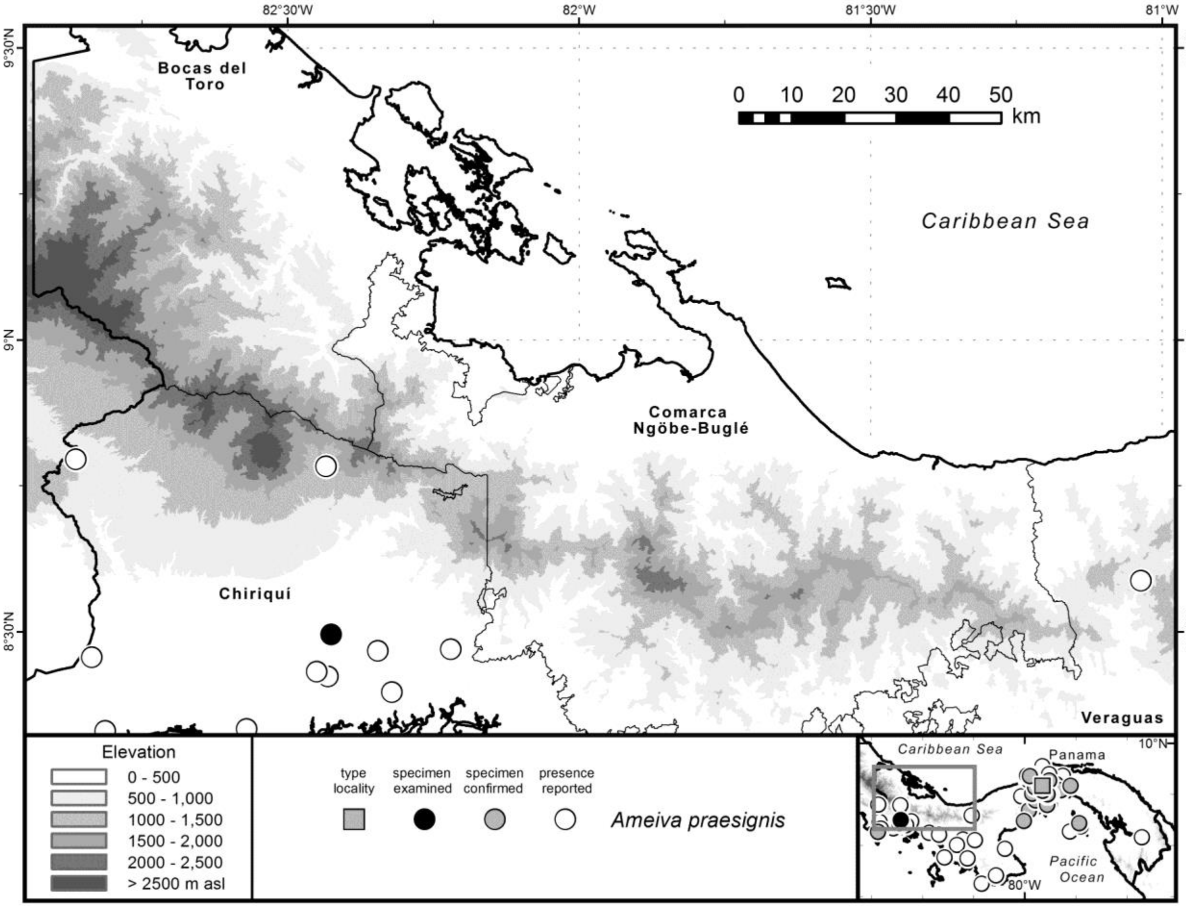
& Rodriguez (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Neal (2007); Köhler (2008); Hamad (2009); Savage & Bolaños (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Batista & Ponce (2011); Lotzkat & Hertz (2011).

Ameiva surinamensis: Barbour (1906).

Cnemidophorus praesignis: Baird & Girard (1852).

Syntypes. USNM 5519 and UMMZ 3823, from Chagres, Panama (Ugueto & Harvey 2011).

Geographic distribution. Southern Pacific Costa Rica to Colombia and northern Venezuela, 0–1120 m asl, and introduced in Florida (Ugueto & Harvey 2011). In Panama, along both versants in central and eastern, and the Pacific versant of western Panama including Chiriquí, Veraguas, and the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from PNAC, the Santa Fé area, Boquete, and Altamira, up to about 1120 m asl.



Map 4.88: Distribution of *Ameiva praesignis*.

Diagnosis. This large lizard (maximum SVL 243 mm) is immediately recognized as a member of the family Teiidae, and thus distinguished from the members of all other lizard families occurring in Panama, by its large, smooth, symmetrical dorsal head plates in combination with homogeneously small, granular dorsals and large, smooth, rectangular ventrals. It differs from *Cnemidophorus duellmani* in having a single row of greatly enlarged scales on the upper surface of the upper arm (vs. 3 or more rows of moderately enlarged scales) and 10 longitudinal rows of ventrals at midbody (vs. 8). The latter characteristic also distinguishes it from the more or less similar Panamanian species of *Holcosus,* from which it further differs in usually having 5 large shields (IP + 2 parietals per side) in the parietal area (vs. 3) (including data from Ugueto & Harvey 2011).

Description. TOL to 737 mm; SVL to 243 mm; tail long, TL/SVL = 2.0–2.56; IN 2, usually excluding FN from contact with rostral; FN 1; PF 2; FP 2, in contact with IP and median parietals; parietals 4; 3 or more rows of anterior gulars moderately enlarged; posterior gulars small or slightly enlarged; 2–3 rows of mesoptychial scales moderately enlarged; D and L small, granular; V large, smooth, rectangular, in 10 longitudinal rows at midbody; caudals rectangular, imbricate, keeled; 14–21 femoral pores per side; SAM 121–167; 4toe 29–40; 4finger 13–18 (largely based on data from, and following the terminology of, Ugueto & Harvey 2011).

The hemipenis of *Ameiva praesignis* is a medium-sized, bilobed organ with very short, stout lobes; truncus and lobes with transverse folds (Harvey et al. 2012).

Coloration in life. Body green to brown; head usually brown; tail brown to blue; venter white to light blue; D and L body surfaces of juveniles with numerous light spots and two dorsolateral light stripes extending diffusely onto tail; females with the light stripes, light spots on flanks, and irregular dark transverse middorsal bars; adult males usually without stripes, but numerous green to orange spots.

Coloration in preservative. Chiefly gray to brown, but greenish and/or bluish shadings may be retained a long time.

Natural history notes. Diurnal and terrestrial. This heliophilic species is a typical inhabitant of open areas, where it can be quite common.

Remarks. In an in-depth revision of the *Ameiva ameiva* species complex, Ugueto & Harvey (2011) removed *A. praesignis,* along with other taxa formerly considered subspecies of a wide-ranging *A. ameiva,* from the synonymy of *A. ameiva* and provided a thorough description of this and other former subspecies. As a consequence, the variation in several characters stated by these authors and consequently herein differs to a certain extent from that reported for *A. ameiva* by previous authors (e.g., Savage 2002; Köhler 2008), whose morphological descriptions were apparently not restricted to the Central American populations of the former *A. ameiva* that are now referred to *A. praesignis.*

The specimens MVUP 22 from Altamira near the Costa Rican border (934 m SRTM elevation for my georeference) and MVUP 434 from Boquete (1121 SRTM elevation for my georeference) were apparently collected well above upper elevational limit of 850 m asl reported for this species in Panama (Jaramillo et al. 2010). However, the possibility that these specimens represent misidentified species of *Holcosus* cannot be ruled out. Such misidentification must have been underlying the listing of *Ameiva ameiva* for San San Pond Sak (ANAM 2004), which I regard as clearly erroneous since no other author has reported this species from Caribbean western Panama or adjacent Costa Rica.

***Holcosus festivus* (Lichtenstein & von Martens 1856)**

Middle American Ameiva, Central American Whiptail; Borriguero, Borriguero centroamericano

Figure 4.103B; Map 4.89.

Ameiva eutropia: Cope (1862a).

Ameiva festiva: Barbour (1923); Dunn (1933, 1940); Wettstein (1934); Breder (1946); Taylor (1956); Myers & Rand (1969); Peters & Donoso-Barros (1970); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1996, 1997, 2001); Martínez & Rodriguez (1994, 2005); Martínez et al. (1995); Young et al. (1999); Savage (2002); ANAM (2004, 2009b); McDiarmid & Savage (2005); Montero (2005); Fundación PA.NA.M.A. (2007); Köhler (2008); Santos-Barrera et al. (2008); Hamad (2009); Savage & Bolaños (2009); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010).

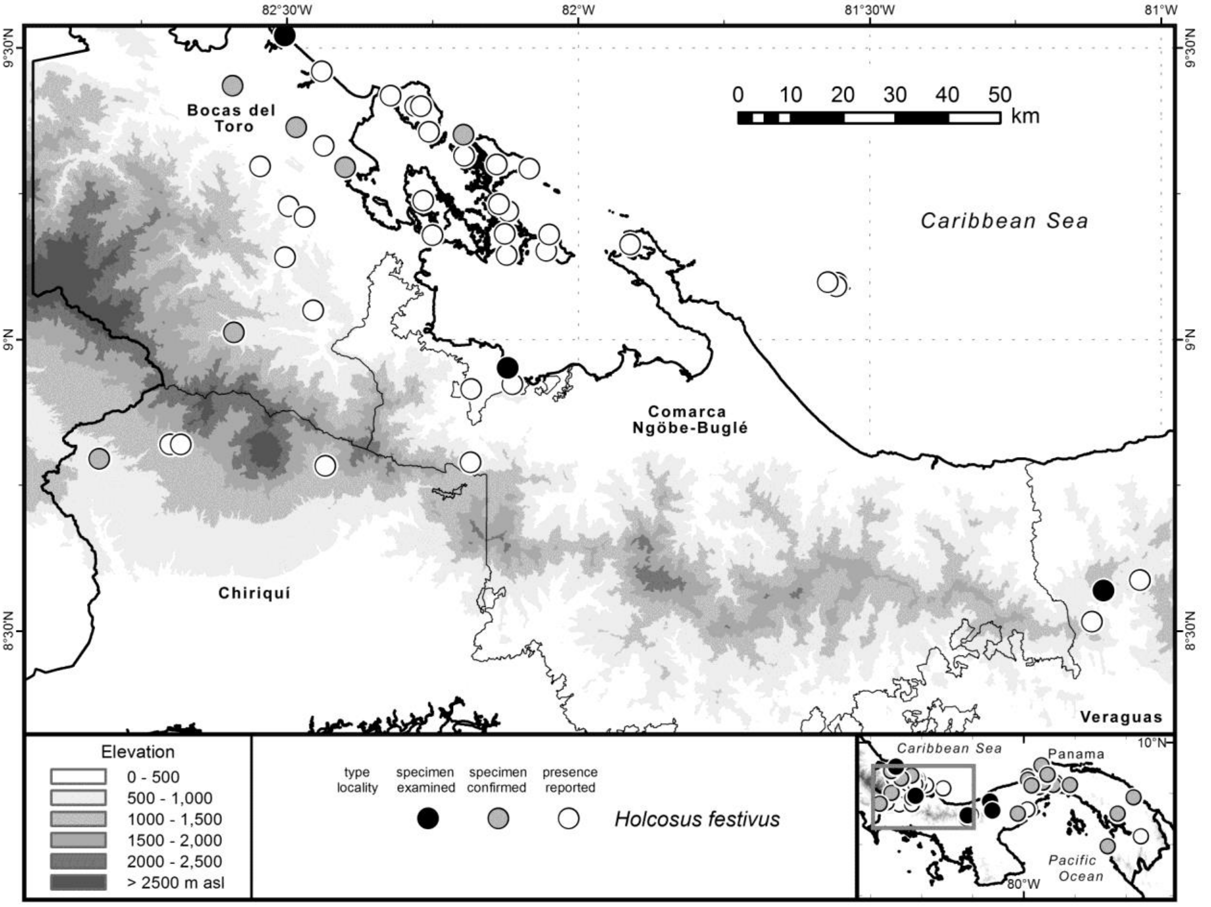
Amiva festiva: Cope (1876, 1893).

Cnemidophorus festivus: Lichtenstein & von Martens (1856).

Syntypes. ZMB 881, from "Veragoa" (Lichtenstein & von Martens 1856).

Geographic distribution. Mexico to Colombia, 0–1470 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites along both versants up to 1470 m asl.

Diagnosis. This large lizard (maximum SVL 129 mm) is immediately recognized as a member of the family Teiidae, and thus distinguished from the members of all other lizard families occurring in Panama, by its large, smooth, symmetrical dorsal head plates in combination with homogeneously small, granular dorsals and large, smooth, rectangular ventrals. It is readily distinguished from *Cnemidophorus duellmani* by its single row of greatly enlarged scales on the upper surface of the upper arm (vs. 3 or more rows of moderately enlarged scales). It differs from *Ameiva praesignis* in having 8 longitudinal rows of ventrals at midbody (vs. 10) and in having 3 large shields (IP + 1 parietal per side) in the parietal area (vs. usually 5). *Holcosus festivus* differs from its Panamanian congeners in having a conspicuous patch of greatly enlarged anterior gulars surrounded by much smaller scales (vs. at most moderately enlarged, gradually increasing in size towards midgular area), and in exhibiting a light middorsal stripe in all except very old individuals (vs. no such stripe).



Map 4.89: Distribution of *Holcosus festivus*.

Description. TOL to 345 mm; SVL to 129 mm; tail long, TL/SVL = 1.85–2.40; IN 2, excluding FN from contact with rostral; FN 1; PF 2; FP 2, in contact with IP and parietals or separated from them by small scales; parietals 2; 3 or more anterior gulars greatly and abruptly enlarged, usually larger than mesoptychial scales; posterior gulars small; one row of mesoptychial scales moderately to greatly enlarged; D and L small, granular; V large, smooth, rectangular, in 8 longitudinal rows at midbody; caudals rectangular, imbricate, keeled; 32–55 total femoral pores; SAM 160*; 4toe 23–34; 4finger 12–17 (including data from Harvey et al. 2012).

The hemipenis of *Holcosus festivus* is a medium-sized, bilobed organ with very short, stout lobes; truncus and lobes with transverse folds (Harvey et al. 2012).

Coloration in life. D and L surfaces of body and head brown, with a light middorsal stripe extending from snout well onto tail that gradually fades from posterior to anterior and assumes undulated borders as individuals grow older; two dorsolateral light stripes that may be broken up into dashes or spots, often enclosing a dark dorsolateral band that may bear irregular transverse extensions towards middorsum; tail blue in young specimens, brown in adults; V surfaces of head and body pale blue.

Coloration in preservative. After 4–6 years in 70% ethanol the coloration of my examined specimens is similar to that in life; all reddish and yellow hues have faded, and the fully developed middorsal stripes are bluish gray throughout body and tail.

Natural history notes. Diurnal and terrestrial. *Holcosus festivus* inhabits shaded forest habitats. The specimens SMF 89894 at Cerro Negro and SMF 90093 at San San Pond Sak were spotted at night while fleeing from members of our field party and taking cover under a rock and dead wood, respectively.

Remarks. In their revision of teiid morphology, Harvey et al. (2012) transferred this species from the genus *Ameiva* Meyer to the resurrected genus *Holcosus* Cope, placing it in their *H. undulatus* group. My georeference for the specimens USNM 129931–2 from "Cerro Pardo" (according to nearby USNM numbers, I assumed this to actually mean "Cerro Pando" and referenced it at the village "Silla de Pando") yields a SRTM elevation of 1470 m asl, which is somewhat higher than the documented elevational maximum of 1370 m for Panama (Jaramillo et al. 2010) and 1435 m for the species as a whole (Sasa et al. 2010).

Holcosus leptophrys (Cope 1893)

Delicate Ameiva; Borriguero

Figure 4.103C; Map 4.90.

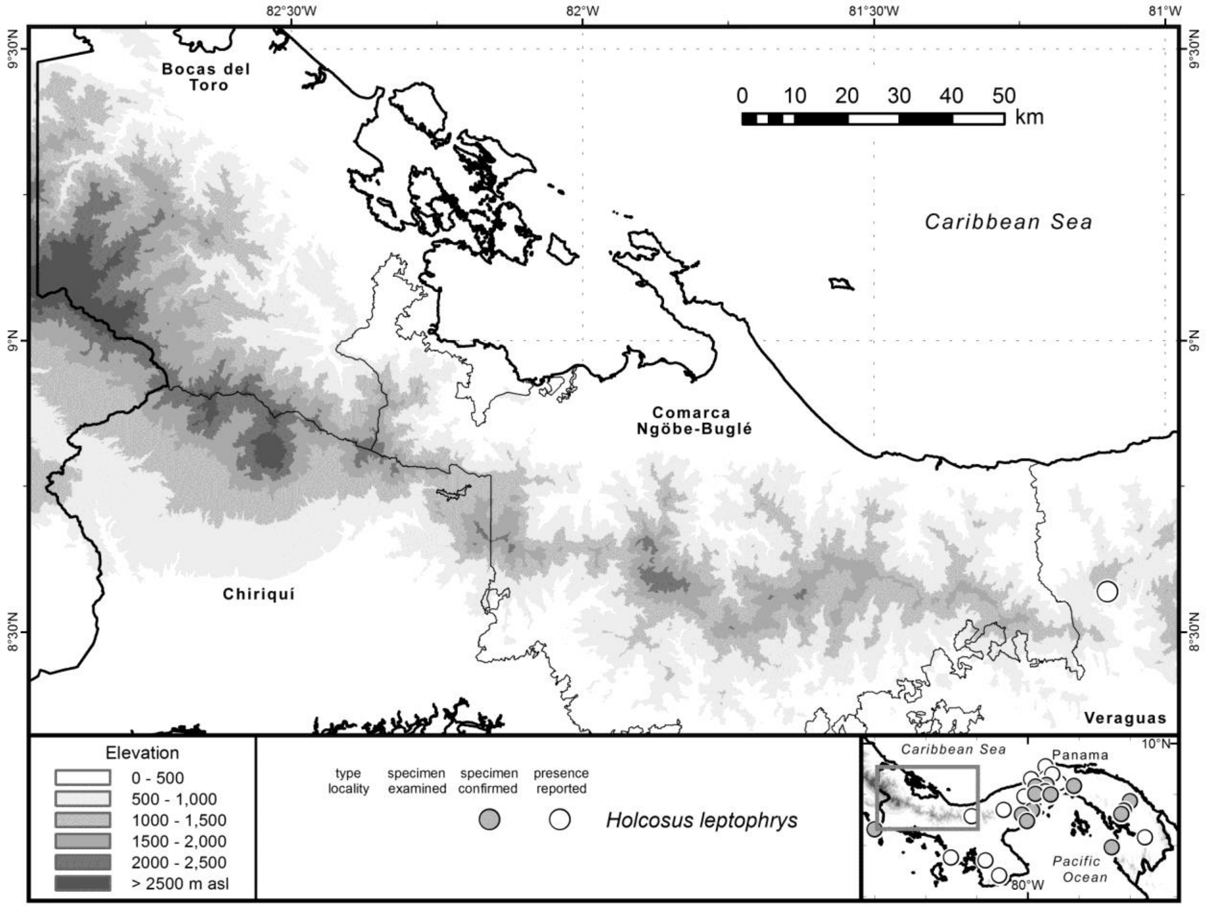
Ameiva leptophris: Elizondo et al. (2007).

Ameiva leptophrys: Dunn (1940); Breder (1946); Evans (1947); Taylor (1956); Myers & Rand (1969); Peters & Donoso-Barros (1970); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1996, 1997, 2001); Young et al. (1999); Carrizo (2000, 2010); Savage (2002); Rodriguez et al. (2005); McDiarmid & Savage (2005); Fundación PA.NA.M.A. (2007); Köhler (2008); Hamad (2009); Savage & Bolaños (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010).

Amiva leptophrys: Cope (1893).

Holotype. AMNH 9506, from "Buenos Ayres, Costa Rica" (Cope 1893; Dunn 1940).

Geographic distribution. Costa Rica and Panama, 0–900 m asl. In Panama, along both versants of central and eastern, and the Pacific versant of western Panama including Chiriquí, Veraguas, and probably also the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from PNAC, el Valle de Antón, PNGDOTH, and Cerro Negro, up to 850 m asl.



Map 4.90: Distribution of *Holcosus leptophrys*.

Diagnosis. This large lizard (maximum SVL 133 mm) is immediately recognized as a member of the family Teiidae, and thus distinguished from the members of all other lizard families occurring in Panama, by its large, smooth, symmetrical dorsal head plates in combination with homogeneously small, granular dorsals and large, smooth, rectangular ventrals. It is readily distinguished from all other Panamanian teiids by the small scales which separate the interparietal from the frontoparietals (vs. IP in contact with both FP), and by a small plate (often called parietal) separating each parietal from the respective frontoparietal (vs. a large parietal in contact with the respective FP). It further differs from *Cnemidophorus duellmani* in having single row of greatly enlarged scales on the upper surface of the upper arm (vs. 3 or more rows of moderately enlarged scales), and from *Ameiva praesignis* in having 8 longitudinal rows of ventrals at midbody (vs. 10).

Description. TOL to 439 mm; SVL to 133 mm; tail long, TL/SVL = 1.85–2.33; IN 2, excluding FN from contact with rostral; FN 1; PF 2; FP 2, separated from IP by small scales and from parietals by small plates; parietals 2; anterior gulars becoming gradually enlarged posteriorly and medially towards mid-throat, at most as large as mesoptychial scales, abruptly giving way to small posterior gulars; one row of mesoptychial scales moderately to greatly enlarged; D and L small, granular; V large, smooth, rectangular, in 8 longitudinal rows at midbody; caudals rectangular, imbricate, keeled; 34–61 total femoral pores; 4toe 24–35; 4finger 15–17 (including data from Harvey et al. 2012).

The hemipenis of *Holcosus festivus* is a medium-sized, bilobed organ with very short, stout lobes; truncus and lobes with transverse folds (Harvey et al. 2012).

Coloration in life. D and L surfaces brown; body with two usually undulating and broken light dorsolateral stripes continuing onto tail, enclosing a dark brown dorsolateral band that usually bears irregular transverse extensions towards middorsum and often also onto flanks; V surfaces white, cream, or coppery; dark transverse bars most pronounced in males; males with yellow to red chin and throat areas and the light dorsolateral stripes reduced to absent.

Coloration in preservative. Similar to that in life, except that yellow and red shades fade.

Natural history notes. Diurnal and terrestrial, inhabiting shaded forest habitats.

Remarks. In their revision of teiid morphology, Harvey et al. (2012) transferred this species from the genus *Ameiva* Meyer to the resurrected genus *Holcosus* Cope, placing it in their *H. undulatus* group.

The presence of *Holcosus leptophrys* in extreme western Chiriquí has recently been confirmed by the specimen GK 3397 from Chorogo. East of this locality, no records exist over a distance of 175 km to Bahía Honda (SDNHM 7308, 10168) and 212 km to Cerro Negro (Carrizo 2000). This hiatus bears a question mark in the map of Köhler (2008: p. 168) and can only be explained by numerous, repeated misidentifications (e.g., as *Ameiva praesignis,* for which many records exist in this area) or by the actual absence of the species in most of Chiriquí as stated by Savage (2002). I regard the listing of *Holcosus leptophrys* for San San Pond Sak (ANAM 2004) as clearly erroneous, given the distribution of this species as documented by recent comprehensive works (Savage 2002; Köhler 2008) and that no other author has reported this species from Caribbean western Panama or adjacent Costa Rica. The record from Cerro Negro (Carrizo 2000), less than 8 km from the Comarca's border, renders the occurrence of *H. leptophrys* in the Comarca Ngöbe-Buglé possible. Moreover, its presence at premontane elevations in Chiriquí may be assumed given the maximum elevation of 700 m asl in Costa Rica (Savage 2002; Sasa et al. 2010).

Holcosus quadrilineatus (Hallowell 1861)

Four-lined Ameiva, Four-lined Whiptail; Borriguero, Borriguero de cuatro rayas

Figure 4.103D; Map 4.91.

Ameiva quadrilineata: Cope (1862a); Dunn (1940); Slevin (1942); Taylor (1956); Peters & Donoso-Barros (1970); Auth (1994); de la Riva (1997); Martínez et al. (1999); Young et al. (1999); Ibáñez et al. (2001); Savage (2002); ANAM (2004, 2009b); McDiarmid & Savage

(2005); Montero (2005); Rodriguez et al. (2005); Elizondo et al. (2007); Fundación PA.NA.M.A. (2007); Köhler (2008); Santos-Barrera et al. (2008); Hamad (2009); Savage & Bolaños (2009); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010).

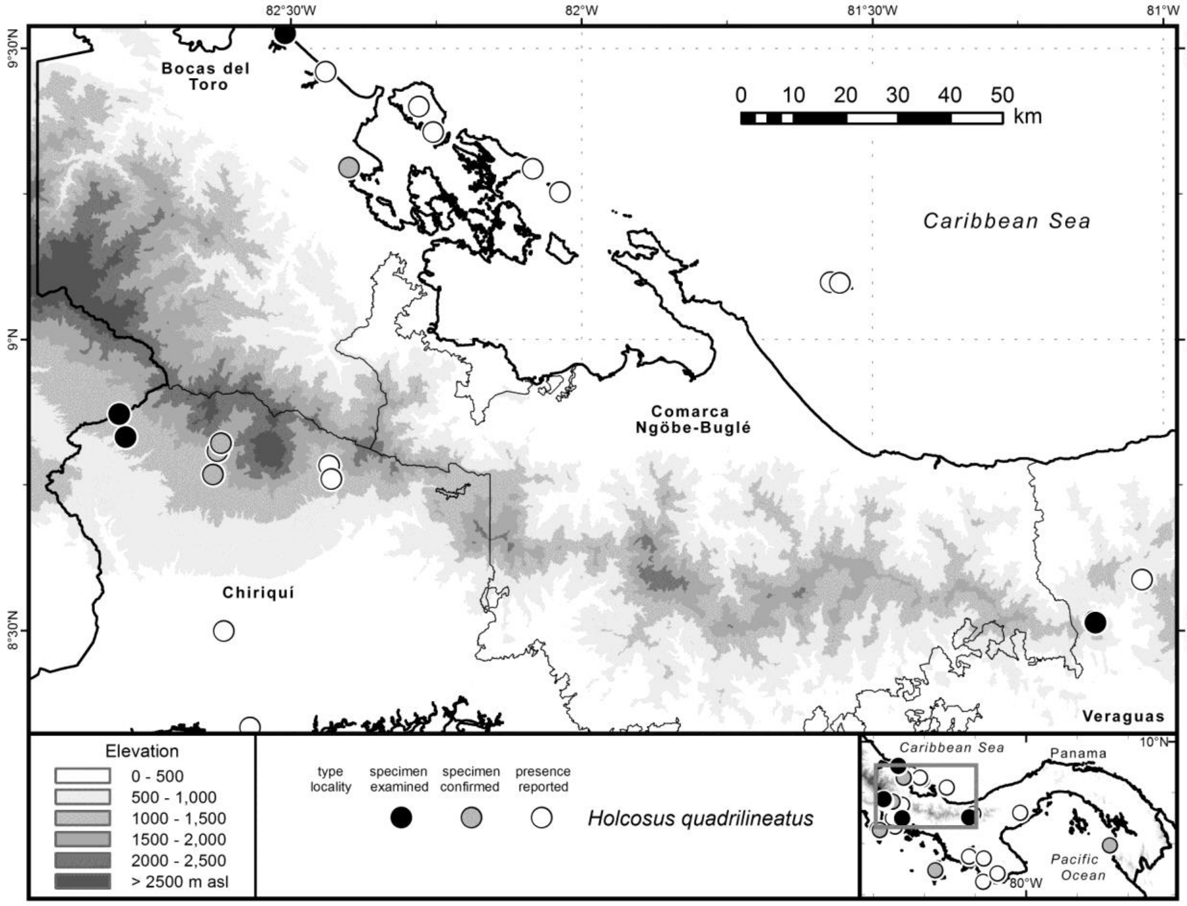
Amiva gabbiana: Cope (1876).

Amiva quadrilineata: Cope (1893).

Ameiva undulata or *A. undulata quadrilineata:* Barbour (1923); Dunn (1933); Martínez & Rodriguez (1994); Martínez et al. (1995); ANAM (2005a).

Syntypes. USNM 6053, from Nicaragua; restricted to Greytown (Dunn 1940).

Geographic distribution. Southeastern Nicaragua to Panama, 0–1680 m asl. In Panama, along both versants of western Panama including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and reported from one locality in Pacific eastern Panama. In the Cordillera Central, reported from various localities along the Pacific slopes east to El Valle de Antón, up to ca. 1680 m asl (see remarks).



Map 4.91: Distribution of *Holcosus quadrilineatus*.

Diagnosis. This medium-sized lizard (maximum SVL 88 mm) is immediately recognized as a member of the family Teiidae, and thus distinguished from the members of all other lizard families occurring in Panama, by its large, smooth, symmetrical dorsal head plates in combination with homogeneously small, granular dorsals and large, smooth, rectangular ventrals. It is readily distinguished from *Cnemidophorus duellmani* by its single row of greatly enlarged scales on the upper surface of the upper arm (vs. 3 or more rows of moderately enlarged scales). It differs from *Ameiva praesignis* in having 8 longitudinal rows of ventrals at midbody (vs. 10) and in having 3 large shields (IP + 1 parietal per side) in the parietal area (vs. usually 5). *Holcosus quadrilineatus* differs from *H. festivus* in lacking a conspicuous patch of greatly enlarged anterior gulars surrounded by much smaller scales on all sides (vs. present) as well as a light middorsal stripe (vs. present), and from *H. leptophrys* in having the interparietal in contact with the frontoparietals (vs. IP separated from FPs by small scales) as well as its respective single large parietal on each side in contact with the respective frontoparietal (vs. each parietal separated from respective FP by a small plate).

Description. TOL to 283 mm; SVL to 88 mm; tail long, TL/SVL = 1.92–2.33; IN 2, usually excluding FN from contact with rostral; FN 1; PF 2; FP 2, in contact with IP and parietals; parietals 2; anterior gulars becoming gradually enlarged posteriorly and medially towards mid-throat, at most as large as mesoptychial scales, abruptly giving way to small posterior gulars; one row of mesoptychial scales moderately to greatly enlarged; D and L small, granular; V large, smooth, rectangular, in 8 longitudinal rows at midbody; caudals rectangular, imbricate, keeled; 18–42 total femoral pores; SAM 140–150*; 4toe 25–34; 4finger 15–19 (including data from Harvey et al. 2012).

The hemipenis of *Holcosus festivus* is a medium-sized, bilobed organ with very short, stout lobes; truncus and lobes with transverse folds (Harvey et al. 2012).

Coloration in life. D and L surfaces brown, with two light dorsolateral stripes per side extending from head onto tail and enclosing a dark brown to black dorsolateral band; broad middorsal band between the respective upper light stripes of each side with straight borders; dorsum and flanks often with light and/or dark mottling or reticulations; V surfaces of head and body white, cream, or coppery; tail blue in young specimens, brown in adults; adult males with yellow to orange throat.

Leonhard Stadler recorded the adult male SMF 89442 (Stadler 2010: Fig. A84) as follows (translated from Stadler 2010): Dorsum from nuchal area to base of tail with a broad middorsal Raw Umber (123) band spotted with Sepia (119) and bordered laterally by several parallel longitudinal stripes extending onto flanks in the following order: a narrow Sepia (119) stripe, a narrow Sulfur Yellow (157) stripe, a broad Sepia (119) stripe mottled with Raw Sienna (136), a narrow Sulfur Yellow (157) stripe, a broad Antique Brown (37) and a broad Pearl Gray (81) stripe both mottled with Sepia (119); D surface of head Smoke Gray (45); D surfaces of limbs Raw Umber (23), forelimbs speckled with Sepia (119), hind limbs speckled with Sepia (119), Sulfur Yellow (157), and Robin's Egg Blue (93); V surfaces of body, tail, and hind limbs Robin´s Egg Blue (93); V surfaces of head and forelimbs dirty white; D surfaces of tail Sayal Brown (223C), with Sepia (119) longitudinal stripes on anterior portion; iris Cinnamon-Brown (33).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration of SMF 89442 and 91444 is similar to that in life; all reddish and yellow hues have faded, light stripes are light bluish gray; ventrolateral surfaces of body blue, in the larger SMF 89442 also the limbs.

Natural history notes. Diurnal and terrestrial, a heliophilic species typically inhabiting open areas. The male SMF 89442 was handed over to LS after having been found by a local worker along a roadside at 06:30. At San San Pond Sak, the juvenile specimen SMF 90094 was recovered from the stomach of the juvenile *Mastigodryas melanolomus* SMF 90197 which had already digested the anterior portions of the lizard. At Santa Clara, the small juvenile SMF 91444 was dug out of loose soil in an open area at night.

Remarks. In their revision of teiid morphology, Harvey et al. (2012) transferred this species from the genus *Ameiva* Meyer to the resurrected genus *Holcosus* Cope, placing it in their *H. undulatus* group. The specimen SMF 85447 has a divided IP. In SMF 89442, the FN is in contact with the rostral, separating the INs.

Recent authors (Savage 2002; Köhler 2008) have located the eastern distributional limit of *Holcosus quadrilineatus* around the Peninsula de Azuero in W Panama. However, the specimens MCZ 17195–17201 from "E. Panama, Río Jesvisito Sapo Mts" (= Río Jesusito; certainly the specimens reported by Barbour 1923 as *Ameiva undulata quadrilineata*) were recently examined by GK and confirmed to represent *H. quadrilineatus.* The specimens FMNH 68168–70 from "Llano above Paso Ancho, 4800 ft" (= ca. 1463 m) and especially FMNH 68175–7 from "Llano del Volcan above Paso Ancho, 5500 ft (= ca. 1676 m), all examined by GK, raise the highest documented elevation for this species from 1400 m asl (Jaramillo et al. 2010). The multitude of records from E and W of the Comarca Ngöbe-Buglé render the occurrence of *H. quadrilineatus* in this political subdivision plausible.

Suborder Serpentes Linnaeus 1758

Infraorder Caenophidia Hoffstetter 1939

Family Colubridae Oppel 1811

Chironius exoletus **(Linnaeus 1758)**

Green Whipsnake, Linnaeus' Sipo; Culebra, Cazadora, Serpiente de látigo verde

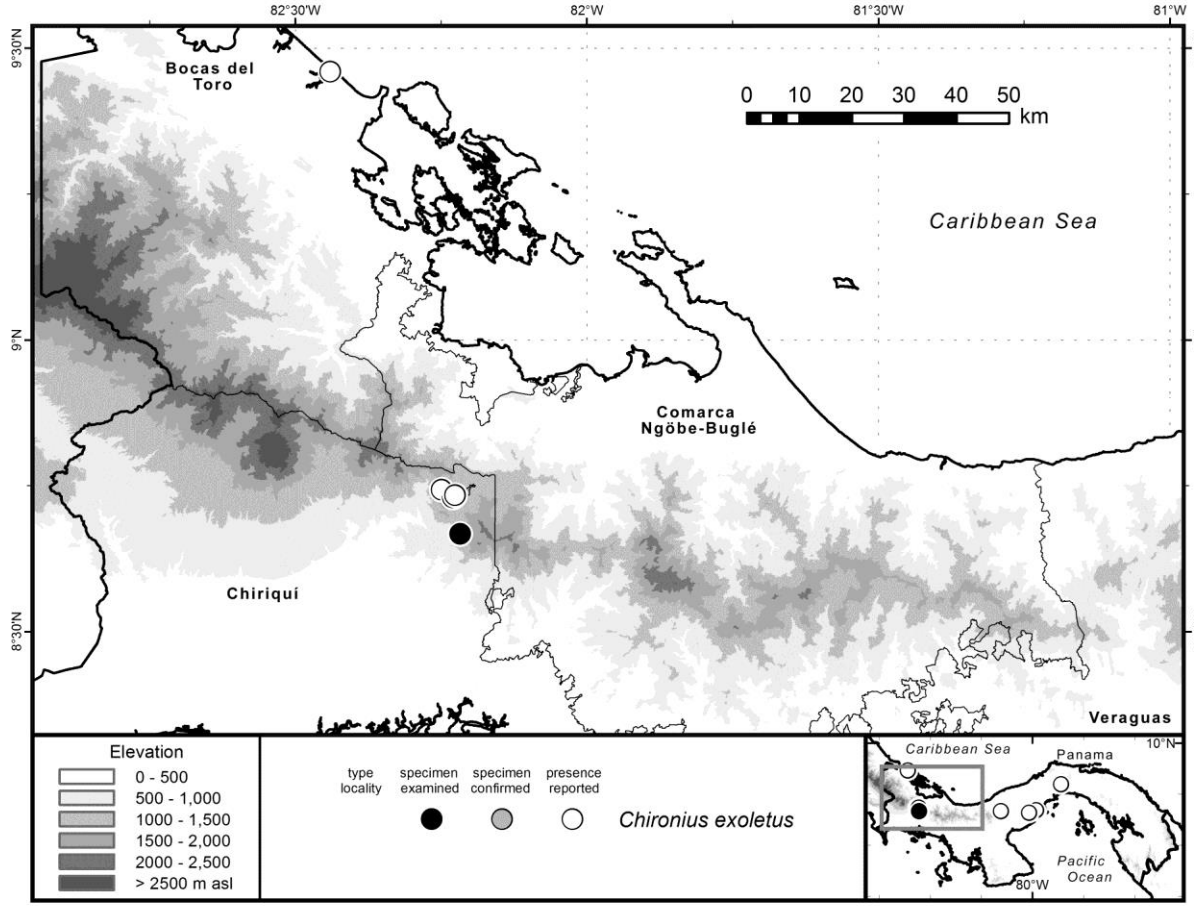
Figure 4.103E; Map 4.92.

Chironius carinatus: Taylor (1951: in part.).

Chironius (especie nueva): Myers (1977).

Holotype. ZMUU 135, from Indiis.

Geographic distribution. Costa Rica to Ecuador, Bolivia, Argentina, and Brazil, 10–2170 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC, Valle de Antón, PNGDOTH, and the Fortuna area, up to ca. 1130 m asl.



Map 4.92: Distribution of *Chironius exoletus.*

Diagnosis. This large snake (maximum TOL 1545 mm) with round pupils is readily recognized as a member of the genus *Chironius* by its large dorsals arranged in oblique rows of even number at midbody. It differs from *C. grandisquamis* in having 12 dorsal rows at midbody (vs. 10), and from *C. flavopictus* in having a rather unicolor green dorsum and light green venter (vs. dorsum olive, gray, bluish, or brown with pale vertebral stripe and venter white or yellow) in adults.

Description. (including data from Dixon et al. 1993) TOL to 1545 mm; SVL to 1000 mm; tail moderate to long, TL/TOL = 0.28–0.44; D keeled on paravertebral rows, otherwise smooth, in (12–16)—12—(8–10) oblique rows; V 123–162; SC 111–160; SPL 7–10; INL 9–13; loreal 1*; Preoc 1*; Postoc 2–3; Tant 1, Tpost 1–2; cloacal scute usually divided; AP 1 on anterior middorsals*; eyes large, pupil round.

The hemipenis of *Chironius exoletus* is a unilobed organ with or without spinules on the pedicel; truncus with enlarged spines, apex calyculate.

Coloration in life. D and L surfaces dark green; V surfaces pale green, grading into yellowish white towards head; labials yellow.

Coloration in preservative. After almost 4 years in 70% ethanol, SMF 91535 is blue, partially with a greenish hue, dorsally; V surfaces of body and tail white with a suggestion of blue, grading into white towards the head.

Natural history notes. Diurnal, terrestrial and arboreal, feeding primarily on frogs. The adult SMF 91535 was found dead on the Fortuna road at the upper limit of Valle de la Mina.

Remarks. Individuals of *Chironius exoletus* from Lower Central America have long been referred to *C. flavopictus* (usually as *C. carinatus,* see Savage 2002 for details). The mention of "*Chironius* (especie nueva) (especie montana verde ampliamente distribuída)" in the first herpetofaunistic list for the Fortuna area (Myers 1977) seems clearly attributable to *C. exoletus.* As pointed out by Savage (2002), the wide-ranging and variable nominal taxon *C. exoletus* might contain several taxa warranting specific status.

The distributional records of this species as shown in Map 4.92 render its presence in the Comarca Ngöbe-Buglé and Veraguas province plausible. The listing of "*Chironius* sp." for Cerro Tute (Martínez & Rodriguez 1994) could refer to this taxon.

Chironius flavopictus **(Werner 1909)**

Keeled Whipsnake, Sipo; Culebra, Cazadora, Serpiente de látigo quillada

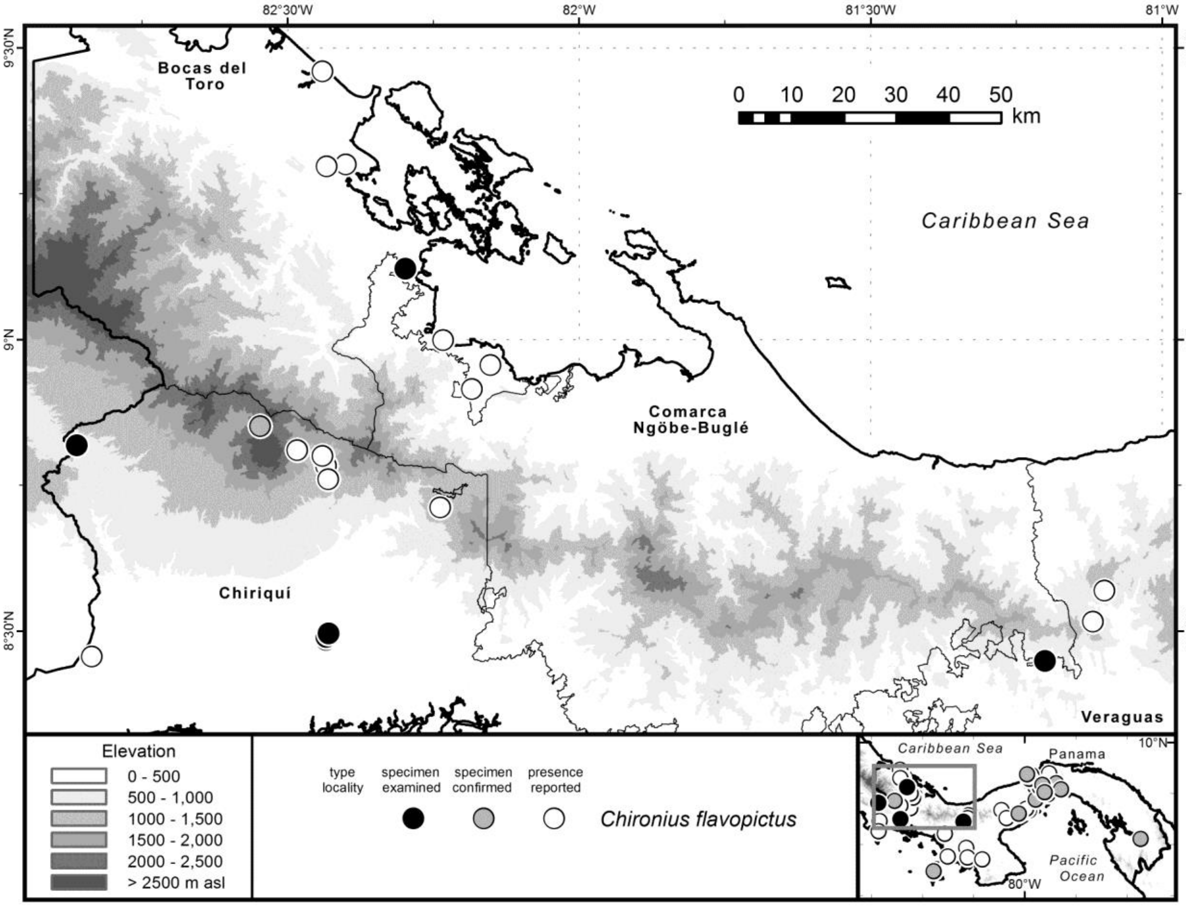
Figures 4.103F, G; Map 4.93.

Chironius carinatus or *C. carinatus flavopictus:* Dunn & Bailey (1939); Slevin (1942); Dunn (1947); Breder (1946); Taylor (1951: in part., 1954); Smith (1958); Myers & Rand (1969); Peters & Orejas-Miranda (1970: in part.); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1996, 1997, 2001); Perez-Santos & Martínez (1997); Martínez et al. (1999); Perez-Santos (1999); Young et al. (1999); Carrizo (2000, 2010); Savage (2002); ANAM (2004, 2009b); Solórzano (2004); McDiarmid & Savage (2005); Montero (2005); Rodriguez et al. (2005); Fundación PA.NA.M.A. (2007); Köhler (2008); Hamad (2009); Savage & Bolaños (2009); Stadler (2010); Lotzkat & Hertz (2011); McConnell (2014); Uetz & Hošek (2014).

Herpetodryas carinatus: Cope (1899).

Lectotype. ZMH 651, from Guayaquil, Ecuador (Dixon et al. 1993).

Geographic distribution. Costa Rica to Colombia and Ecuador, 0–1980 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities along both versants up to 1980 m asl.



Map 4.93: Distribution of *Chironius flavopictus.*

Diagnosis. This large snake (maximum TOL 2055 mm) with round pupils is readily recognized as a member of the genus *Chironius* by its large dorsals arranged in oblique rows of even number at midbody. It differs from *C. grandisquamis* in having 12 dorsal rows at midbody (vs. 10), and from *C. exoletus* in having the dorsum olive, gray, bluish, or brown, usually with a pale vertebral stripe, and the venter white or yellow (vs. rather unicolor green dorsum and light green venter).

Description. (including data from Dixon et al. 1993) TOL to 2055 mm; SVL to 1388 mm; tail long, TL/TOL = 0.30–0.40; D keeled on paravertebral rows, otherwise smooth, in (12–16)—12—(8–10) oblique rows; V 143–169; SC 108–139; SPL 8–10; INL 8–12; loreal 1; Preoc 1;

Postoc 2–3; Tant 1, Tpost 1–3; cloacal scute divided; AP 1 on anterior middorsals; eyes large, pupil round.

The hemipenis of *Chironius flavopictus* is a unilobed organ lacking spinules on the pedicel; truncus with enlarged spines, apex calyculate.

Coloration in life. D and L surfaces in adults olive, gray, bluish, or brown, usually with a light middorsal stripe and light spots or blotches on the 1st D row; D and L surfaces in juveniles predominantly brown, sometimes with obscure crossbands, light stippling on edges of D, and/or ventrolateral dark stripes between V and 1st D row; V surfaces and labials white to yellow.

The female SMF 89540 was recordes as follows: D scales Olive-Gray (42) with a suggestion of Grayish Olive (43), towards the V increasingly suffused with Pratt's Payne's Gray (88), mostly bordered by fine Army Brown (219B) and Cinnamon-Drab (219C) stripes, and with irregular Sepia (119) markings at apex and base; an Olive-Yellow (52) longitudinal middorsal stripe extending from neck onto tail is most contrasting at midbody, where it is bordered by Dark Brownish Olive (129) shadings which almost replace it on tail; V and subcaudals dirty white; L tips of subcaudals Dark Brownish Olive (129) forming a ventrolateral stripe that extends from cloaca onto tail; rostral and 1st supralabial Light Russet Vinaceous (221D); D surface of head uniformly Dark Brownish Olive (129).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration is similar to that in life, apart from that all yellow and pinkish shades have faded to cream. D and L surfaces of adults bluish gray, especially where the scale oberhäutchen have been lost, those of juveniles brownish, or light gray where oberhäutchen have been lost; V surfaces of adults largely cream suffused with greenish or bluish hues.

Natural history notes. Diurnal, terrestrial and arboreal, apparently feeding exclusively on frogs. With the exception of a specimen that had been killed with a machete, all specimens were encountered while sleeping on vegetation at night. Juveniles were found 1–1.5, adults 3.5–6 m above ground. Irritated individuals flatten their neck laterally and vibrate their tails, may hiss and strike.

Remarks. In a morphological revision of the genus *Chironius,* Hollis (2006) elevated the former subspecies *C. carinatus flavopictus* to species level. This notion was accepted by some (Jaramillo et al. 2010; Sasa et al. 2010; Wilson & Johnson 2010), but not all subsequent authors. Suspecting that molecular analyses will corroborate the morphological results of Hollis (2006) and Dixon et al. (1993), I adopt the concept of the former author.

In all juveniles which I have seen and photographed in Panama, the continuous dark ventrolateral stripes are restricted to the tail. With 412 mm TOL, the juvenile male SMF

89768 is smaller than the smallest specimen reported by Dixon et al. (1993). All 3 adult specimens which I have examined have incomplete tails with 43–104 remaining SC.

The specimen FMNH 154534, examined by GK, from "Cerro Punta, on trail to Boquete, 6500 ft" (= ca. 1981 m asl) raises the highest documented elevation for this species from 1600 m (Jaramillo et al. 2010, probably based on Dunn's record from Finca Lérida). The listing of "*Chironius* sp." for Cerro Tute (Martínez & Rodriguez 1994) could refer to this taxon. The distribution of this species as documented herein, and especially the specimens SMF 89768 and 91534, both collected less than 1 km from the Comarca's border, render the presence of *C. flavopictus* in the Comarca Ngöbe-Buglé plausible.

***Chironius grandisquamis* (Peters 1868)**

Ebony Keelback, Ecuador Keelback, Shiny Whipsnake; Culebra, Cazadora, Zopilota, Serpiente de látigo negra

Figure 4.103H; Map 4.94.

Chironius fuscus or *C. fuscus grandisquamis:* Wettstein (1934); Dunn & Bailey (1939); Cochran (1946); Dunn (1947); Smith (1958).

Chironius melas: Taylor (1951, 1954).

Herpetodryas carinatus: Cope (1876).

Herpetodryas fuscus: Barbour (1906).

Herpetodryas fuscus grandisquamis: Wettstein (1934).

Herpetodryas grandisquamis: Cope (1876).

Herpetodryas melas: Cope (1886).

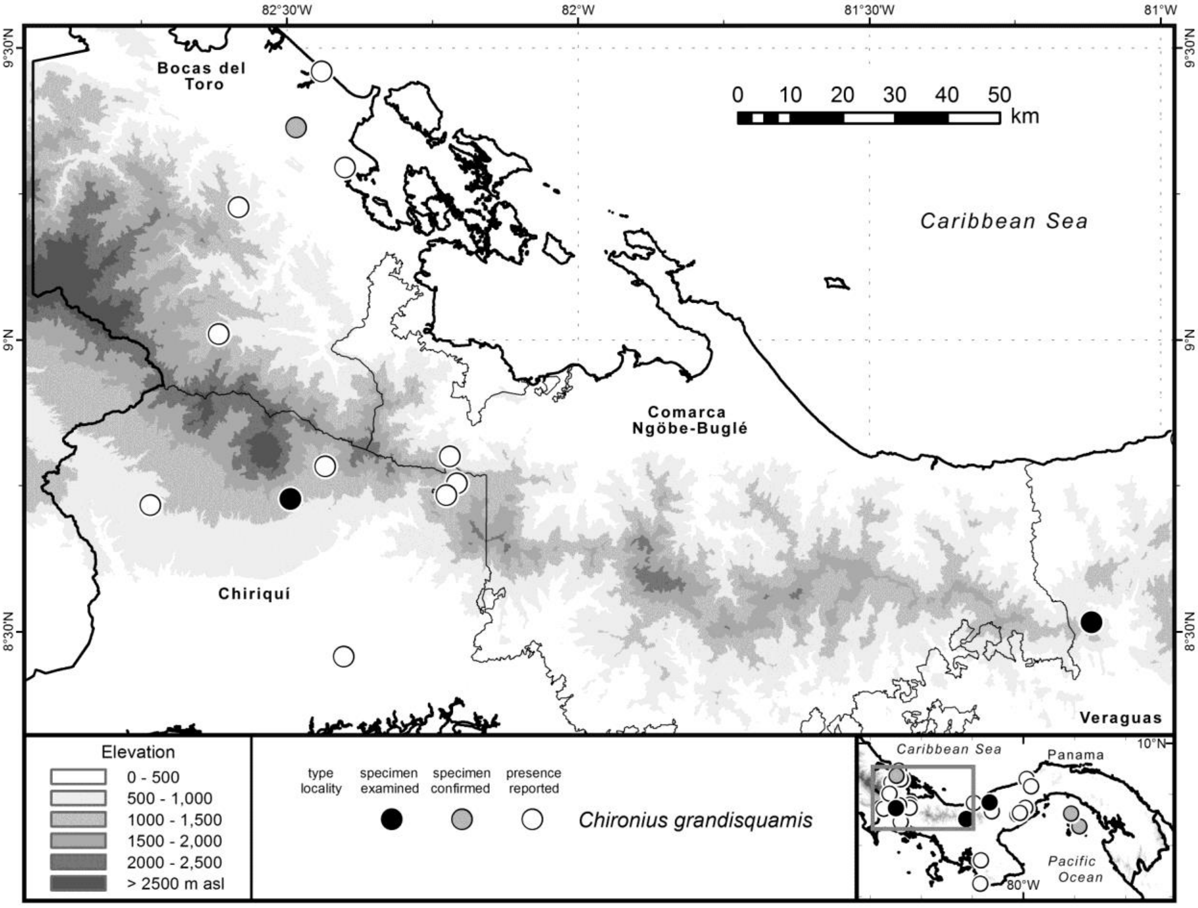
Holotype. ZMB 3940, from Costa Rica.

Geographic distribution. Honduras to Colombia and Ecuador, 0–1600 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities along both versants up to 1220 m asl.

Diagnosis. This large snake (maximum TOL 2718 mm) with round pupils is readily recognized as a member of the genus *Chironius* by its large dorsals arranged in oblique rows of even number at midbody. It differs from *C. exoletus* and *C. flavopictus* in having 10 (rarely 8) dorsal rows at midbody (vs. 12), and in normally having black upper surfaces as an adult (vs. dorsum olive, gray, bluish, green, or brown).

Description. (including data from Dixon et al. 1993) TOL to 2718 mm; SVL to 1610 mm; tail long, TL/TOL = 0.33–0.43; D keeled on paravertebral (in adult males also in 4–6 adjacent) rows, otherwise smooth, in (9–12)—(8–10)—(8–10) oblique rows; V 151–170; SC 125–155;

SPL 8–10; INL 9–12; loreal 1; Preoc 1; Postoc 2–3; Tant 1–2, Tpost 1–2; cloacal scute divided; AP 1 anteriorly; eyes large, pupil round.



Map 4.94: Distribution of *Chironius grandisquamis.*

The hemipenis of *Chironius grandisquamis* is a unilobed organ with a spinulate pedicel; truncus with enlarged spines, apex calyculate.

Diagnosis. This large snake (maximum TOL 2718 mm) with round pupils is readily recognized as a member of the genus *Chironius* by its large dorsals arranged in oblique rows of even number at midbody. It differs from *C. exoletus* and *C. flavopictus* in having 10 (rarely 8) dorsal rows at midbody (vs. 12), and in normally having black upper surfaces as an adult (vs. dorsum olive, gray, bluish, green, or brown).

Description. (including data from Dixon et al. 1993) TOL to 2718 mm; SVL to 1610 mm; tail long, TL/TOL = 0.33–0.43; D keeled on paravertebral (in adult males also in 4–6 adjacent) rows, otherwise smooth, in (9–12)—(8–10)—(8–10) oblique rows; V 151–170; SC 125–155; SPL 8–10; INL 9–12; loreal 1; Preoc 1; Postoc 2–3; Tant 1–2, Tpost 1–2; cloacal scute divided; AP 1 anteriorly; eyes large, pupil round.

The hemipenis of *Chironius grandisquamis* is a unilobed organ with a spinulate pedicel; truncus with enlarged spines, apex calyculate.

Coloration in life. Adults with black D and L surfaces that are rarely mottled with white, black V surfaces grading into white or yellow anteriorly, and yellow labials; juveniles with a pattern of more or less contrasting light and dark crossbands dorsally and white venter.

Coloration in preservative. After 5 years in 70% ethanol the coloration of SMF 89766 is similar to that in life, apart from that all yellow tonalities have faded to light brown and the pitch black has assumed a bluish hue; D scales with lost oberhäutchen dark bluish gray.

Natural history notes. Diurnal and largely terrestrial, foraging mostly on the ground to feed on frogs and other small vertebrates. The adult male SMF 89766 was found at night sleeping 4 m above the Río Cochea in a tree, as typical for the species, and showed the typical neck inflation with L flattening when handled the next day.

Remarks. See Savage (2002) for the taxonomic history of this species. Adult individuals in some Honduran populations retain the banded pattern of juveniles (McCranie 2011).

Dendrophidion apharocybe Cadle 2012

Keeled, Barred, or Lowland Forest Racer; Culebra, Corredora, Corredora quillada

Figure 4.104A; Map 4.95.

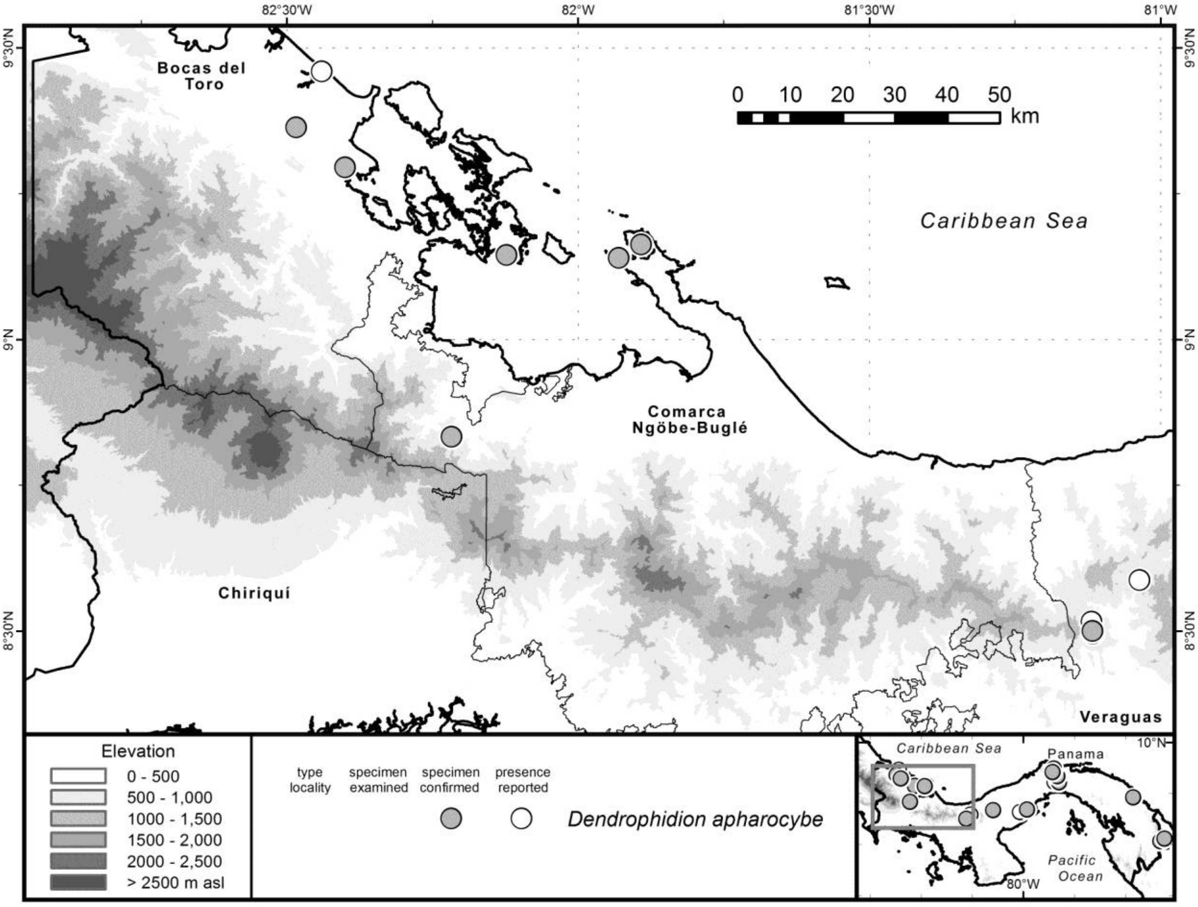
Dendrophidion dendrophis: Dunn & Bailey (1939); Taylor (1951: in part.).

Dendrophidion vinitor: Taylor (1954: in part.); Smith (1958); Peters & Orejas-Miranda (1970: in part.); Lieb (1988: in part.); Auth (1994: in part.); Ibáñez et al. (1995, 1996, 2001); Martínez & Rodriguez (1994); Martínez et al. (1995); Perez-Santos (1999); Young et al. (1999: in part.); Köhler (2001, 2008: in part.); Savage (2002: in part.); ANAM (2004, 2009b); Solórzano (2004: in part.); McDiarmid & Savage (2005: in part.); Fundación PA.NA.M.A. (2007); Hamad (2009: in part.); Ray (2009); Savage & Bolaños (2009: in part.); Sunyer (2009); Carrizo (2010: in part.); Jaramillo et al. (2010: in part.); Sasa et al. (2010: in part.); Stadler (2010: in part.); Wilson & Johnson (2010: in part.); McCranie (2011: in part.); McConnell (2014: in part.).

Holotype. LACM 148593, male, from Finca La Selva, 40 m elevation, Heredia Province, Costa Rica (Cadle 2012a).

Geographic distribution. Eastern Honduras to E Panama and probably into Colombia, 0–1430 m asl. In Panama, from the Caribbean versant of extreme W Panama including Bocas del Toro and Comarca Ngöbe-Buglé along both versants from Veraguas eastwards. In the Cordillera Central, reported from La Loma, the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to 1433 m asl (Cadle 2012a).

Diagnosis. This medium-sized snake (maximum TOL 1045 mm) with round pupils is readily identified as a member of the genus *Dendrophidion* by its overall habitus and coloration. It differs from all Panamanian *Dendrophidion* except *D. clarkii* and *D. crybelum,* as well as from the somewhat similar species of *Drymobius,* in having the caudal scale row reduction from 8 to 6 posterior to subcaudal 25 (vs. anterior to 25th SC). It differs from *D. clarkii* in having fewer than 130 subcaudals (vs. 139 or more) and from *D. crybelum* in having immaculate ventrals and subcaudals (vs. dark spots on SC and posterior V) as well as in having fewer than 45 moderately enlarged spines on the hemipenis (vs. > 70 greatly enlarged) which is rather short and has a large, bulbous apex comprising over a third of its length (vs. longer with short, non-bulbous apex comprising < 25%) (including data from Cadle 2012a).



Map 4.95: Distribution of *Dendrophidion apharocybe.*

Description. TOL to 1045 mm; SVL to 672 mm; tail long, TL/TOL = 0.29–0.38; D keeled on most rows, in 17—17—15 rows; V 149–168; SC 111–129; D caudal reduction at SC 26–63; SPL 8–10; INL 7–10; loreal 1; Preoc 1; Postoc 2–3; Tant 1–2, Tpost 1–2; cloacal scute entire; AP 2; eyes large, pupil round (Cadle 2012a).

The hemipenis of *Dendrophidion apharocybe* is a unilobed organ with a large, bulbous apex bearing several membranous flounces, moderately enlarged spines around the truncus, and a short, naked pedicel (Cadle 2012a).

Coloration in life. D and L surfaces of body and tail gray to brown often including bluish and/ or orangish tonalities; body with 46–69 dark-edged light crossbands usually becoming broken up into transverse series of ocelli posteriorly; often with a pale vertebral and/or a narrow dark ventrolateral stripe posteriorly; V surfaces immaculate white, often with greenish or orangish hues (Cadle 2012a).

Coloration in preservative. Similar to that in life, with colors largely reduced to brown and gray (Cadle 2012a).

Natural history notes. Diurnal, terrestrial and arboreal, feeding mainly on frogs.

Remarks. Cadle (2012a) removed Atlantic versant populations from E Honduras to E Panama from the Synonymy of *Dendrophidion vinitor* Smith 1941, which he redescribed and whose distribution he restricted to Mexico, Guatemala, and Belize. His exemplary revision contains a thorough description of *D. apharocybe,* comparisons to all Central American congeners, and a discussion of the distribution of this species including doubtful or erroneous reports of "*D. vinitor*". Except the listing for Chiriquí province (Young et al. 1999), virtually all previous records of *D. vinitor* from Panama, including several paratypes of that nominal taxon, are based on individuals of *D. apharocybe.* Together with the altitudinal distribution, the proximity of the record from La Loma to the border of Chiriquí around the Fortuna pass (slightly more than 5 km) renders the occurrence of this species on the Pacific slopes from the Fortuna depression eastwards possible.

***Dendrophidion clarkii* Dunn 1933**

Red-headed Forest Racer; Culebra, Corredora, Corredora cabezaroja

Figure 4.104B; Map 4.96.

Dendrophidion clarki: Smith (1958); Köhler (2008).

Dendrophidion dendrophis: Dunn & Bailey (1939); Taylor (1951: in part.); Martínez & Rodriguez (1994); Martínez et al. (1995); Perez-Santos (1999).

Dendrophidion nucale: Ray (2009).

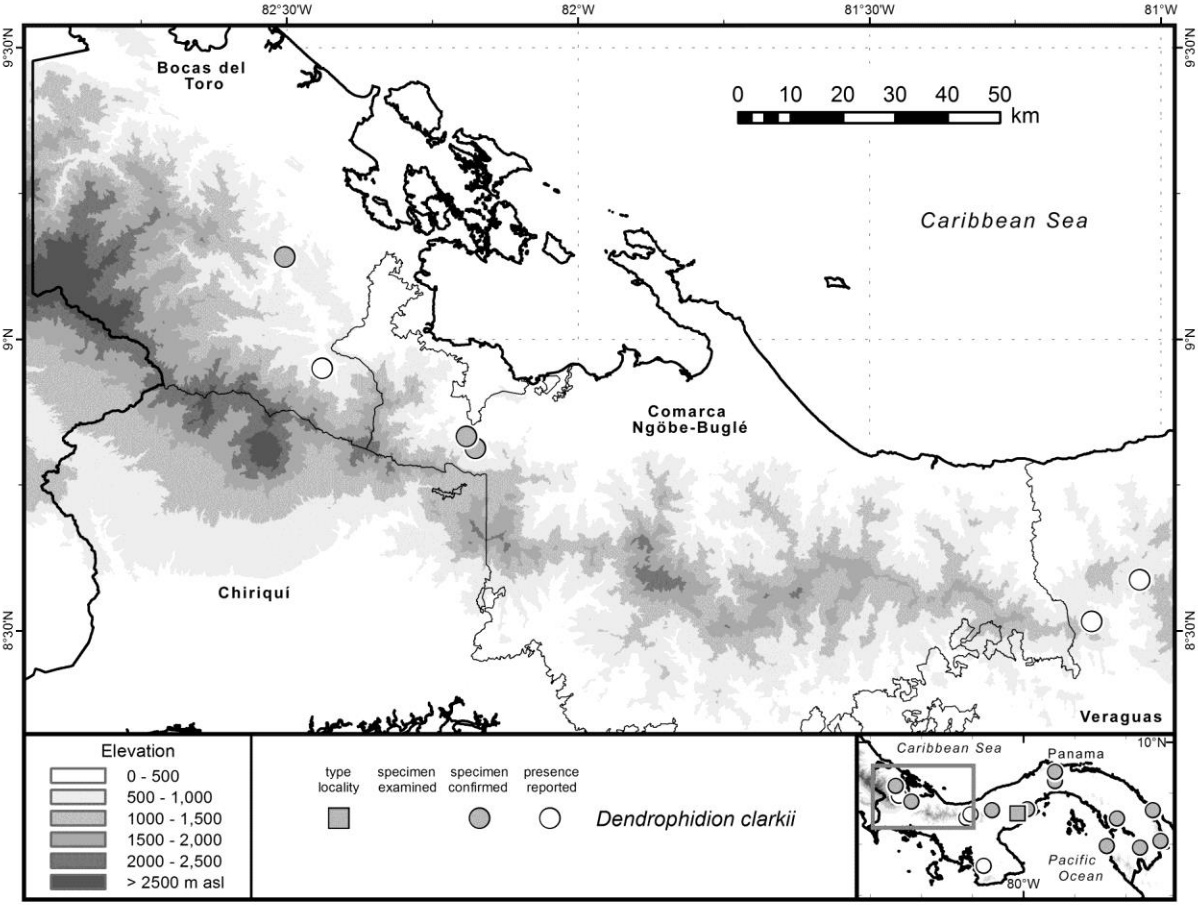
Dendrophidion nuchale: Auth (1994: in part.); Ibáñez et al. (2001); Perez-Santos (1999); Young et al. (1999); Savage (2002: in part.); Solórzano (2004: in part.); Montero (2005); Köhler (2008: in part.); Hamad (2009: in part.); Savage & Bolaños (2009: in part.); Carrizo (2010: in part.); Jaramillo et al. (2010); Sasa et al. (2010: in part.); Stadler (2010: in part.); Wilson & Johnson (2010: in part.); Cadle (2012a: in part.); McConnell (2014).

Dendrophidion nuchalis: Lieb (1988: in part.); Ibáñez et al. (1996); Fundación PA.NA.M.A. (2007).

Drymobius dendrophis: Boulenger (1894: in part.).

Holotype. MCZ 34878, male, from El Valle de Antón, Panama (Dunn 1933).

Geographic distribution. Costa Rica to W Ecuador, 0–1800 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from several localities along the Caribbean slopes of the Talamancan range and from the Pacific slopes in the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to about 910 m asl (Cadle & Savage 2012).



Map 4.96: Distribution of *Dendrophidion clarkii.*

Diagnosis. This medium-sized snake (maximum TOL 1550+x mm) with round pupils is readily identified as a member of the genus *Dendrophidion* by its overall habitus and coloration. Adults can readily be distinguished from all other Panamanian snakes by having green heads and necks followed by brown coloration posteriorly, and a dark nuchal collar. It further differs from all Panamanian *Dendrophidion* except *D. apharocybe* and *D. crybelum,* as well as from the somewhat similar species of *Drymobius,* in having the caudal scale row reduction from 8 to 6 posterior to subcaudal 25 (vs. anterior to 25th SC). It further differs from *D. apharocybe* and *D. crybelum* in having 139 or more subcaudals (vs. < 130) (including data from Cadle & Savage 2012).

Description. TOL to 1550+x mm; SVL to 942 mm; tail long, TL/TOL = 0.34–0.41 D keeled on most or all rows, in (17–19)—17—15 rows; V 158–175; SC 139–161; D caudal reduction at SC 27–65; SPL 8–10; INL 8–12; loreal 1; Preoc 1; Postoc 2–3; Tant 1–2, Tpost 1–2; cloacal scute entire or divided; AP 2; eyes large, pupil round (Cadle & Savage 2012).

The hemipenis of *Dendrophidion crybelum* is a unilobed organ with a non-bulbous apex bearing calyces and membranous flounces; enlarged spines around the truncus including two greatly enlarged sulcal and two less prominently enlarged asulcate ones proximally, and a complete annulus of spines distally; pedicel short with minute spines (Cadle & Savage 2012).

Coloration in life. Adults with a distinct dark brown to black nuchal collar and green or brown D head surface anterior to it; D and L surfaces of body bright green anteriorly, grading into brown with dark-edged light crossbars or ocelli posteriorly and on tail; V surfaces white, yellow, reddish, brown, or gray, usually with narrow dark transverse lines and/or posteriorly increasing dark suffusions; lips white to yellow. Juveniles may lack a collar and have the crossbars/ocelli extending more anteriorly (Cadle & Savage 2012).

Coloration in preservative. Similar to that in life, with colors largely reduced to brown and gray; formerly green anterior parts may assume bluish hues (Cadle & Savage 2012).

Natural history notes. Diurnal, terrestrial and arboreal, apparently relatively uncommon

Remarks. In recent literature, this species has variously been referred to as *Dendrophidion clarkii* or *D. nuchale.* In an exemplary revision of the *Dendrophidion nuchale* complex, Cadle & Savage (2012) revalidated *D. clarkii* Dunn 1933 (including all Panamanian populations) and described populations from Central Costa Rica northwards as a new species, *D. rufiterminorum,* thus restricting the name *D. nuchale* to populations of N Venezuela and providing thorough descriptions and comparisons for all three species. The distribution as documented by these authors and especially the distance of less than 5 km between the collection site of USNM 347917 and the border of Chiriquí province render the presence of *D. clarkii* in Chiriquí plausible.

Dendrophidion crybelum Cadle 2012

Keeled Forest Racer, Barred Forest Racer; Culebra, Corredora, Corredora quillada

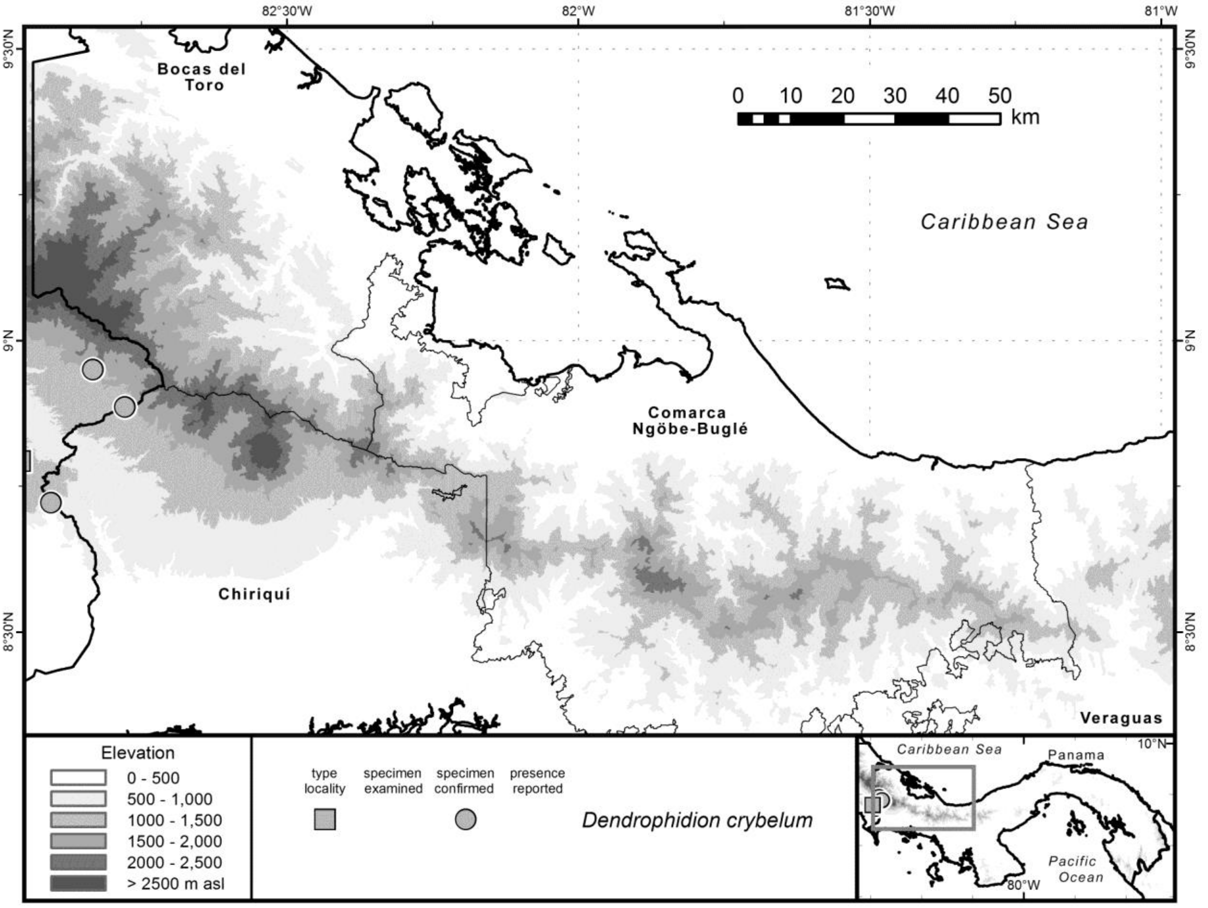
Map 4.97.

Dendrophidion vinitor: Peters & Orejas-Miranda (1970: in part.); Lieb (1988: in part.); Auth (1994: in part.); Young et al. (1999: in part.); Savage (2002: in part.); Solórzano (2004: in part.); Montero (2005); Köhler (2008: in part.); Hamad (2009: in part.); Savage & Bolaños (2009: in part.); Carrizo (2010: in part.); Sasa et al. (2010: in part.); Stadler (2010: in part.); Wilson & Johnson (2010: in part.); McCranie (2011: in part.); McConnell (2014: in part.).

Drymobius dendrophis: Boulenger (1894: in part.).

Holotype. LACM 148599, male, from Finca Las Cruces, near San Vito de Java, 4 km S San Vito, 1,200 m elevation, Puntarenas Province, Costa Rica (Cadle 2012a).

Geographic distribution. Endemic to the Pacific slopes of the Talamancan Highlands in eastern Costa Rica and extreme western Panama, 1100–1330 m asl. In Panama, expected to occur in western Chiriquí (Cadle 2012a; see remarks).



Map 4.97: Distribution of *Dendrophidion crybelum* in Costa Rica.

Diagnosis. This medium-sized snake (maximum TOL 985 mm) with round pupils is readily identified as a member of the genus *Dendrophidion* by its overall habitus and coloration. It differs from all Panamanian *Dendrophidion* except *D. apharocybe* and *D. clarkii,* as well as from the somewhat similar species of *Drymobius,* in having the caudal scale row reduction from 8 to 6 posterior to subcaudal 25 (vs. anterior to 25th SC). It differs from *D. clarkii* in having fewer than 120 subcaudals (vs. 139 or more) and from *D. apharocybe* in having dark spots on subcaudals and posterior ventrals (vs. immaculate SC and V) as well as in having more than 70 greatly enlarged spines on the hemipenis (vs. < 45 moderately enlarged) which is rather long and has a short, non-bulbous apex comprising less than a quarter of its length (vs. shorter with large, bulbous apex comprising > 33%) (including data from Cadle 2012a).

Description. TOL to 985 mm; SVL to 631 mm; tail long, TL/TOL = 0.34–0.36; D keeled on most rows, in 17—17—15 rows; V 150–162; SC 112–119; D caudal reduction at SC 42–58; SPL 8–9; INL 9; loreal 1; Preoc 1; Postoc 2; Tant 2, Tpost 2; cloacal scute entire; AP 2; eyes large, pupil round (Cadle 2012a).

The hemipenis of *Dendrophidion crybelum* is a long, unilobed organ with a short, non-bulbous apex bearing calyces and membranous flounces, greatly enlarged spines around the truncus, and a short, naked pedicel (Cadle 2012a).

Coloration in life. D and L surfaces of body and tail gray to brown; body with 36–62 dark-edged light crossbands usually becoming broken up into transverse series of ocelli posteriorly, and becoming more diffuse with age at least posterior to neck; often with a pale vertebral and/or a narrow dark ventrolateral stripe posteriorly; V surfaces immaculate white, often with greenish or orangish hues (Cadle 2012a).

Coloration in preservative. Similar to that in life, with colors largely reduced to brown and gray (Cadle 2012a).

Natural history notes. Diurnal, terrestrial and arboreal, feeding mainly on frogs.

Conservation. Jaramillo et al. (2010) calculated an EVS of 9 for *Dendrophidion vinitor,* which at that time included populations now assigned to *D. crybelum,* and assigned that species to the IUCN category LC. Taking into account all four localities provided for the species in its original description (Cadle 2012a), I calculated the EVS for *D. crybelum* as 4 (range) + 4 (persecution) + 5 (ecological distribution) = 13, indicating a high vulnerability. Its extent of occurrence of just 210 km^2, the fact that it is known from only 4 localities, and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1ab(iii).

Remarks. Cadle (2012a) removed the populations from the San Vito/Las Cruces area of extreme eastern Pacific Costa Rica from the Synonymy of *Dendrophidion vinitor* Smith 1941, which he rediscribed and whose distribution he restricted to Mexico, Guatemala, and Belize. His exemplary revision contains a thorough description of *D. crybelum,* comparisons to all Central American congeners, and a discussion of the distribution of this species including doubtful or erroneous reports of "*D. vinitor*" from near the documented areal of *D. crybelum.* Since Cadle (2012a) repeatedly states the cloacal scute to be entire ("anal plate single") in his diagnosis of *D. crybelum,* I assume the contrary statement ("anal plate divided") in the subsequent species description to be erroneous.

Except the listing for Chiriquí province (Young et al. 1999) and mentions of a specimen (Boulenger 1894; not examined by Cadle 2012a) there are no historic records of "*D. vinitor*" from western Chiriquí, leaving the occurrence of *D. crybelum* in Panama and my study area unsubstantiated. However, the distances of less than 1 km between the respective collection sites of some paratypes (LACM 148590, 148620; UF 16425) and the Panamanian border render the occurrence of this species at least in extreme western Chiriquí plausible.

Dendrophidion paucicarinatum **(Cope 1894)**

White-lipped Forest Racer, Cope's Forest Racer; Culebra, Corredora de labios blancos

Figure 4.104C; Map 4.98.

Dendrophidion paucicarinatus: Slevin (1942); Dunn (1947); Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970).

Dendrophidium paucicarinatus: Myers (1977).

Drymobius chloroticus: Taylor (1951, 1954).

Drymobius paucicarinatus: Cope (1894).

Holotype. AMNH 17268, female, from La Candelaria (= Monte Redondo, Cantón de Aserrí, Provincia de San José according to Savage 1974), Costa Rica (Lieb 1991).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 1000–2000 m asl. In Panama, reported from numerous localities along both versants of the Cordillera Central east to Cerro Santiago, 1020–1980 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1400 mm) with round pupils is readily identified as a member of the genus *Dendrophidion* by its overall habitus and coloration. It differs from all Panamanian *Dendrophidion* as well as from the somewhat similar species of *Drymobius* in having each of its yellow ventrals with a complete dark posterior margin (vs. at most dark-edged laterally, or dark anterior margins and dark mottling). It further differs from *Dendrophidion apharocybe, D. clarkii,* and *D. crybelum* in having the caudal scale row reduction from 8 to 6 anterior to subcaudal 25 (vs. posterior to 25th SC), and from *D. percarinatum* in having 179 or more ventrals (vs. 170 or fewer) (including data from Cadle 2012b).

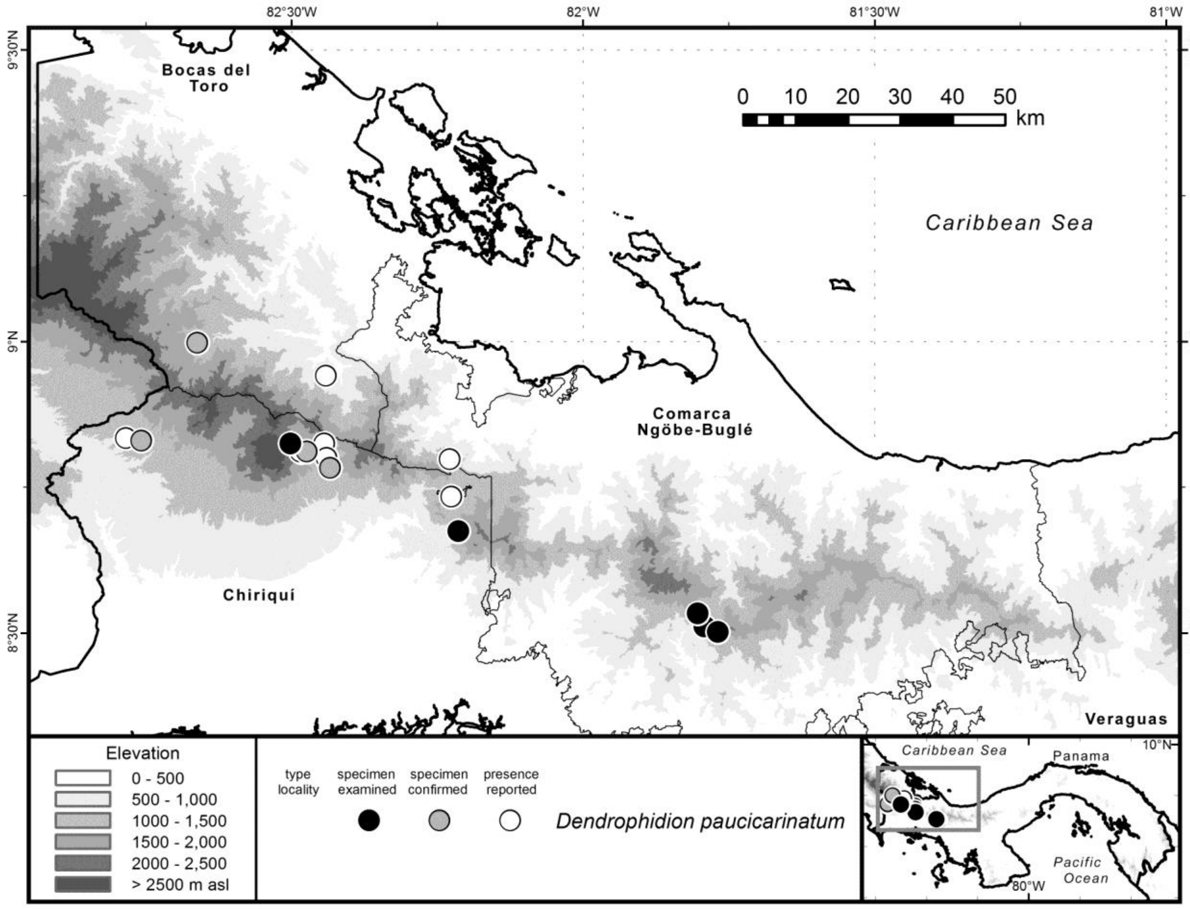
Description. (including data of Lieb 1991) TOL to 1400 mm; SVL to 661 mm*; tail long, TL/TOL = 0.32–0.35; D keeled on 5–13 upper rows (keeling increasing posteriorly*), in 17—17—15 rows; V 179–195; SC 119–146; D caudal reduction at SC 7–24; SPL 8–10; INL 9–12; loreal 1; Preoc 1; Postoc 2–3; Tant 2, Tpost 2; cloacal scute entire or divided; AP 2; eyes large, pupil round.

The hemipenis of *Dendrophidion paucicarinatum* is a unilobed organ with a short, non-bulbous apex bearing calyces and membranous flounces, greatly enlarged spines around the truncus, and a short, naked pedicel.

Coloration in life. D and L surfaces of body and tail essentially brown, variously stippled with light and dark; V surfaces yellow, with continuous dark posterior borders of V and SC; lips below a narrow dark supralabial stripe yellow.

The juvenile male SMF 89544 was recorded as follows: D scales of body and tail Burnt Umber (22), grading into Brownish Olive (29) on the neck; all D irregularly bordered by Dusky Brown (19) and sometimes dirty white; V surfaces of body and tail Sulphur Yellow (57), grading into Straw Yellow (56) towards the neck, with dark posterior scale borders; D and L scales on head Burnt Umber (22), delimited by Dusky Brown (19) and seperated from supralabials by a Dusky Brown (19) longitudinal stripe; supralabials, infralabials and V surface of head dirty white with a slight suggestion of Sulfur Yellow (157).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration of my examined specimens is similar to that in life, apart from that all yellow shades have faded to cream and the D colors are largely reduced to gray and brown, or bluish gray where the oberhäutchen have been lost.



Map 4.98: Distribution of *Dendrophidion paucicarinatum.*

Natural history notes. Diurnal, terrestrial and arboreal, probably feeding on frogs and lizards like its better-known congeners. Active individuals were found at day- or nighttime on the ground, the only sleeping individual was found under a rock at night. Two of the five specimens in my collection have incomplete tails.

Remarks. The juvenile SMF 89544 has 146 subcaudals, the highest count reported for this species so far. Wilson (1970) revealed that several examples of this species had been misidentified as *Drymobius chloroticus* by Taylor (1951, 1954). Likewise, I found the specimen MVUP 1120, collected in June 1980 by R.J. Izor at Cerro Colorado and catalogued as *Drymobius margaritiferus,* to represent *Dendrophidion paucicarinatum.* This renders the specific identities of other specimens from that area which are catalogued as *Drymobius margaritiferus* (USNM 297711–16), partially collected the same year and maybe even by the same collector, somewhat questionable. I agree with Savage (2002) that records from elevations below 1000 m asl for this species are suspect and questionable, and thus refrain from adopting the lower elevational limit of 750 m given by Perez-Santos (1999).

Dendrophidion percarinatum (Cope 1893)

Barred Forest Racer, Brown Forest Racer; Culebra, Corredora, Corredora de barras

Figure 4.104D; Map 4.99.

Dendrophidion dendrophis: Taylor (1951: in part.).

Dendrophidion percarinatus: Taylor (1954); Smith (1958); Myers & Rand (1969); Rand & Myers (1990).

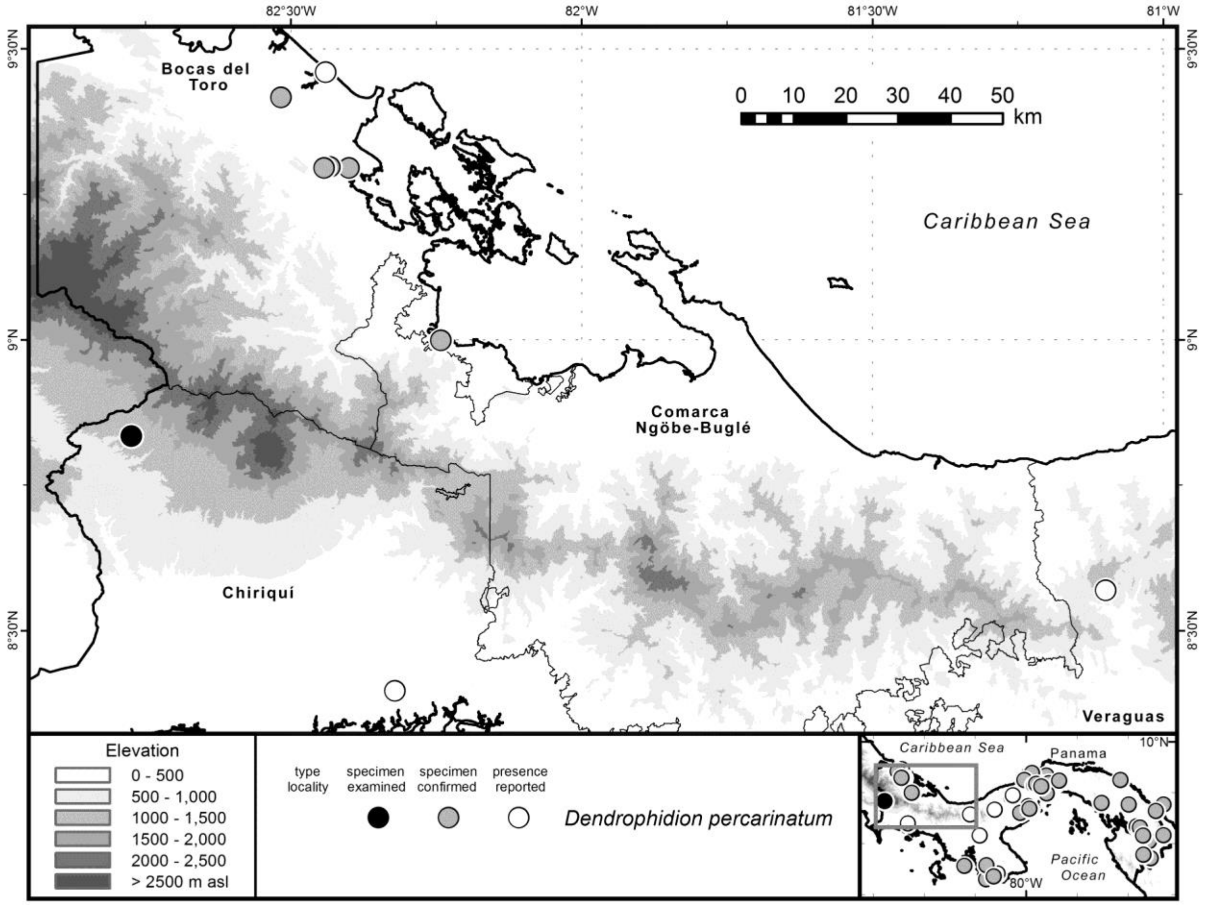
Drymobius dendrophis: Boulenger (1894).

Drymobius percarinatus: Cope (1893, 1894).

Lectotype. AMNH 17366, male, from Boruca, Puntarenas, Costa Rica (Cadle 2012b).

Geographic distribution. Northern Honduras to Colombia and NW Venezuela, 0–1200 m asl (Cadle 2012b). In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Caribbean foothills of the Talamancan range and from the Pacific slopes at Santa Clara, the Santa Fé area, PNGDOTH, and PNAC, up to 1160 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1358+x mm) with round pupils is readily identified as a member of the genus *Dendrophidion* by its overall habitus and coloration. It further differs from all Panamanian *Dendrophidion* except *D. paucicarinatum* in having the caudal scale row reduction from 8 to 6 usually anterior to subcaudal 25 (vs. posterior to 25th SC), from *D. apharocybe* and *D. crybelum* in having 133 or more subcaudals (vs. 129 or less) and from *D. clarkii* and *D. paucicarinatum* in having an immaculate venter (vs. ventrals with dark mottling or complete dark margins) (including data from Cadle 2012b).



Map 4.99: Distribution of *Dendrophidion percarinatum.*

Description. TOL to 1358+x mm; SVL to 852 mm; tail long, TL/TOL = 0.35–0.45; D keeled on most rows, in 17—17—15 rows; V 147–170; SC 133–163; D caudal reduction at SC 5–26; SPL 8–10; INL 8–12; loreal 1; Preoc 1–2; Postoc 1–3; Tant 1–2, Tpost 1–3; cloacal scute divided; AP 2; eyes large, pupil round (including data of Lieb 1991).

The hemipenis of *Dendrophidion percarinatum* is a unilobed organ with a bulbous apex bearing two membranous flounces, 26–40 enlarged spines around the truncus, and a narrow, naked pedicel (Cadle 2012b).

Coloration in life. D and L surfaces of body and tail gray to brown, usually with more or less conspicuous narrow dark-edged pale crossbands anteriorly that often grade into dark crossbands or ocelli posteriorly; sometimes with pale and/or dark longitudinal stripes especially posteriorly; V surfaces immaculate, white or with yellow or salmon hues; lips below a narrow dark supralabial stripe white to yellow (including data from Cadle 2012b).

Coloration in preservative. Similar to that in life, largely reduced to brown and gray.

Natural history notes. Diurnal, terrestrial and arboreal, feeding on frogs and lizards. SMF 89545 was found dead on the road to Río Sereno at Santa Clara.

Remarks. In an exemplary revision of the *Dendrophidion percarinatum* complex, Cadle (2012b) described two new species from South America and redescribed *D. percarinatum*.

The distribution as documented by his records and herein, especially the distance of less than 3 km between the collection site of KU 107647 and the Comarca's border, render the presence of *D. percarinatum* in the Comarca Ngöbe-Buglé plausible. The specimen SMF 89545 was collected at Santa Clara around 1157 m asl, about 160 m higher than the upper elevational limit reported for Panama (Jaramillo et al. 2010). Since no record seems to be known to recent authors to substantiate this elevation, I refrain from adopting the maximum elevation of 1500 m given by Perez-Santos (1999).

Drymarchon melanurus **(Duméril, Bibron & Duméril 1854)**

Indigo Snake, Black-tailed Cribo, Central American Cribo; Zopilota, Sabanera real

Figure 4.104E; Map 4.100.

Drymarchon corais or *D. corais melanurus:* Dunn & Bailey (1939); Slevin (1942); Swanson (1945); Cochran (1946); Dunn (1947); Taylor (1951, 1954); Smith (1958); Myers (1969a); Myers & Rand (1969); Peters & Orejas-Miranda (1970: in part.); Rand & Myers (1990); Auth (1994); Martínez & Rodriguez (1994); Martínez et al. (1995); Ibáñez et al. (1997, 2001); Perez-Santos (1999); Young et al. (1999); Köhler (2001, 2008); Savage (2002); ANAM (2004); Fundación PA.NA.M.A. (2007); Carrizo (2010); Hamad (2009); Stadler (2010); McConnell (2014).

Spilotes corais or *S. corais melanurus:* Cope (1876).

Lectotype. MNHN 3185, from Mexico.

Geographic distribution. Southern USA and Mexico through Central America to Peru, Ecuador, Colombia and N Venezuela, 0–2500 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from various localities up to 1615 m asl along the Pacific slope including Volcán, Boquete, La Fortuna, the Santa Fé area, and PNAC.

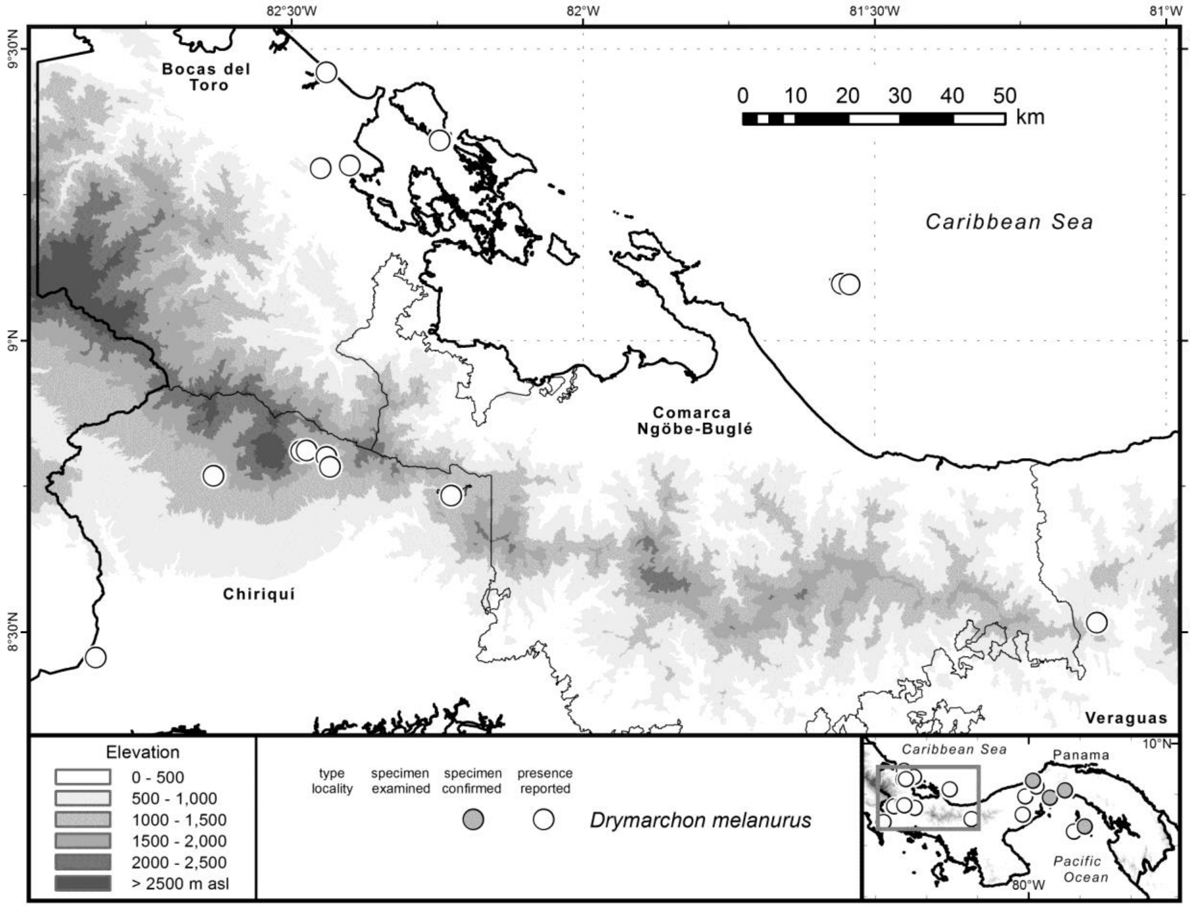
Diagnosis. This very large snake (maximum TOL 2950 mm) is immediately recognized by its three dark subocular stripes radiating from the eye between the supralabial sutures, a fourth transverse dark stripe between the posterior two SPL, the lack of dark supralabial markings anterior to eye, and a diagonal dark marking on each side of the neck.

Description. TOL to 2950 mm; SVL to 2450 mm; tail short, TL/TOL = 0.16–0.24; D smooth except for supracloacal region in males, in (17–21)—17—(13–15) rows; V 182–215; SC 55–93; SPL 7–9; INL 7–10; loreal 1; Preoc 1; Postoc 2; Tant 2, Tpost 1–3; cloacal scute entire; AP 2; eyes large, pupil round (including data of Duellman 1960 and Wüster et al. 2001).

The hemipenis of *Drymarchon melanurus* is a slightly bilobed organ with a naked pedicel, small spines on truncus, and fringed calices on the apex.

Coloration in life. Adults usually gray to brown, often with light and/or dark scale margins, grading into dark brown or black towards tail; V surfaces light brown anteriorly, grading into darker tonalities along with D and L surfaces; V scales usually with irregularly arranged, narrow dark L and/or posterior borders that may extend as dark stripes onto flanks; juveniles with obscure dark crossbands anteriorly.

Coloration in preservative. Similar to that in life.



Map 4.100: Distribution of *Drymarchon melanurus.*

Natural history notes. Mostly diurnal and terrstrial, feeding on a variety of vertebrates.

Remarks. In the course of describing *Drymarchon caudomaculatus* from NW Venezuela, Wüster et al. (2001) revealed constant morphological differences between the *D. corais corais* and *D. corais melanurus,* and in consequence elevated both subspecies to species level. All Panamanian populations are referable to *D. melanurus.*

Drymobius margaritiferus (Schlegel 1837)

Speckled Racer; Culebra, Corredora, Ranera, Ranera común, Margarita

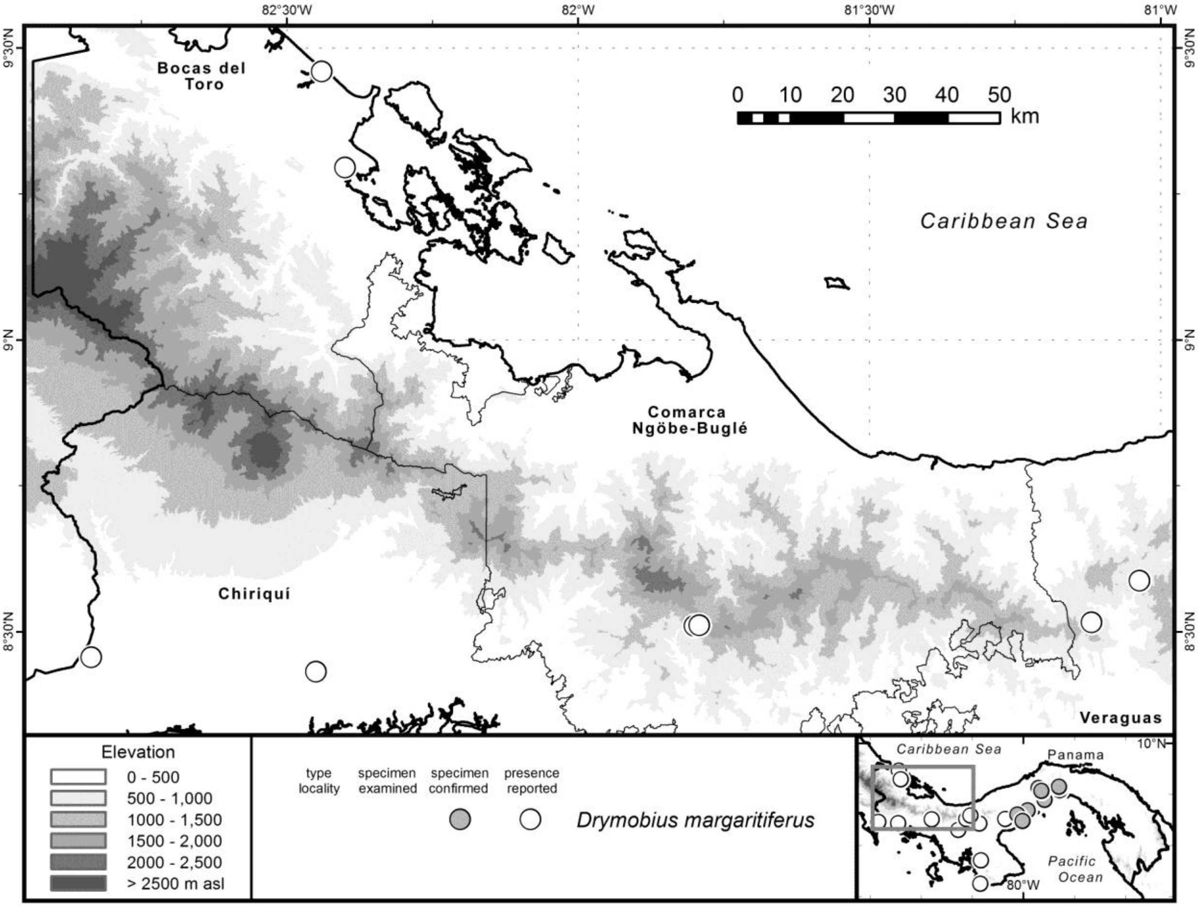
Figure 4.104F; Map 4.101.

Drymobius chloroticus: Martínez et al. (1995: probably).

Masticophis margaritiferus: Cope (1871).

Holotype. MNHN 7309, from New Orleans (in error); restricted to Córdoba, Veracruz, Mexico.

Geographic distribution. Southern USA and Mexico to Colombia, 0–2000 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Cerro Colorado and Santa Fé areas, Valle de Antón, and PNAC, up to ca. 1500 m asl.



Map 4.101: Distribution of *Drymobius margaritiferus.*

Diagnosis. This medium-sized snake (maximum TOL 1339 mm) with round pupils is readily distinguished from all other Panamanian snakes by its dark-edged dorsal scales bearing lighter centers that are green, yellow, orange, or red. Adults exhibit this coloration throughout the body and tail, while juveniles have dark crossbands anteriorly.

Description. TOL to 1339 mm; SVL of Honduran specimens to 649 mm; tail long, TL/TOL = 0.26–0.37; D keeled except on 1st and sometimes also 2nd row, in 17—17—15 rows; V 135–158; SC 98–138; SPL 8–10; INL 9–12; loreal 1; Preoc 1; Postoc 2; Tant 2, Tpost 1–3; cloacal scute divided; AP 2; eyes large, pupil round.

The hemipenis of *Drymobius margaritiferus* is a medium-sized, slightly bilobed organ with spines around the truncus and papillate calyces on the apex.

Coloration in life. Scales on D and L surfaces of body and tail black-edged with light centers of yellow, yellowish brown, green, orange, or red, producing an overall reticulate pattern; juveniles with dark crossbands on anterior portion of body and light nuchal spots; dark supralabial sutures; V surfaces cream to yellow, V scales with dark margins at least laterally.

Coloration in preservative. Similar to that in life, apart from that the formerly colorful D scale centers assume cream, gray, or brown shades.

Natural history notes. Chiefly diurnal and terrestrial, feeding primarily on anurans.

Remarks. Despite its unique and diagnostic coloration, this species has been confused with *Dendrophidion paucicarinatum* in my study area (see remarks for that species). In their inventory of Cerros Narices and La Anselma, Martínez et al. (1995) list *Drymobius chloroticus* (Cope 1886) which ranges from Mexico to Nicaragua. Among the species of documented or plausible occurrence in Veraguas, *D. margaritiferus* is the most likely candidate for the real identity of the snake in question.

An even more likely candidate would be *D. melanotropis* (Cope 1876), a species that has been documented to occur south to Caribbean Costa Rica close to the Panamanian border, and whose presence in Panama, Bocas del Toro, and my study area I regard as possible (see distribution map in Appendix 7). The verbatim elevations given in the USNM catalogue for the *D. margaritiferus* specimens USNM 297712–16 range between 1250 and 1500 m asl, which is well above the upper elevational limit of 1000 m given for Panama (Jaramillo et al. 2010). However, there is a chance that these specimens might actually represent *Dendrophidion paucicarinatum* (see remarks for that species).

Drymobius rhombifer **(Günther 1860)**

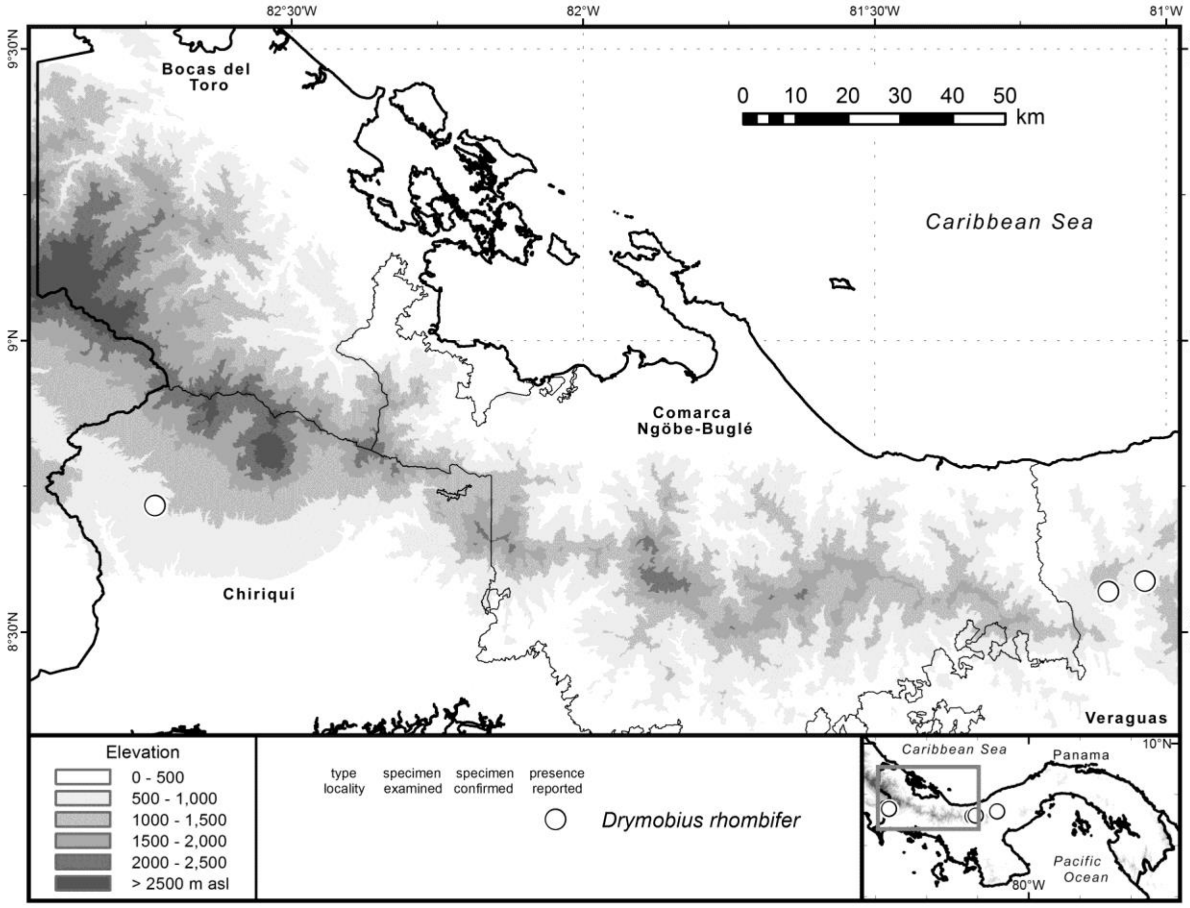
Blotched, Diamondback, or Esmeralda Racer; Culebra, Corredora, Ranera manchada

Figure 4.104G; Map 4.102.

Drymobius rhombifera: Breder (1946).

Holotype. ZMB 9525, from Esmeraldas, Ecuador.

Geographic distribution. Nicaragua to Brazil, Bolivia, and Peru, 0–1200 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from western Chiriquí, the Santa Fé area, and PNGDOTH, up to ca. 850 m asl.



Map 4.102: Distribution of *Drymobius rhombifer.*

Diagnosis. This medium-sized snake (maximum TOL 1270 mm) with round pupils is readily distinguished from most Panamanian snakes by large, dark-outlined, rhomboid dorsal markings. It differs from the superficially similar *Xenodon rabdocephalus* in having the keeled dorsals arranged in 17 straight rows at midbody (vs. smooth, in 19 oblique rows at MB), and from the superficially similar species of *Atropoides* and *Bothrops* in lacking a loral pit (vs. present) and having a round pupil (vs. vertically elliptical).

Description. TOL to 1270 mm; tail long, TL/TOL = 0.30–0.34; D keeled, in 17—17—15 rows; V 145–163; SC 84–108; SPL 9; INL 8–10; loreal 1; Preoc 1; Postoc 2; Tant 2, Tpost 2; cloacal scute divided; AP 2; eyes large, pupil round.

The hemipenis of *Drymobius rhombifer* is a medium-sized, slightly bilobed organ with spines around the truncus and papillate calyces on the apex.

Coloration in life. D and L surfaces gray to brown, with a single median series of rhomboid markings with dark edges and light centers, and a ventrolateral series of much smaller dark markings; V surfaces cream to yellow, with dark mottling in juveniles that is restricted to posterior portions of body and tail in adults.

Coloration in preservative. Similar to that in life.

Natural history notes. Diurnal and terrestrial.

Remarks. Although I could not trace any records from Bocas del Toro or Comarca Ngöbe-Buglé, the distribution of *Drymobius rhombifer* throughout both versants of western Panama as stated by Ray & Knight (2013) appears plausible in view of the distribution in Costa Rica and South America as documented by Savage (2002). Since I could not find any discrete record to substantiate it, I refrain from adopting the upper elevational limit of 1250 m asl given by Perez-Santos (1999).

Lampropeltis triangulum (Lacépède 1789)

Milk Snake, Tropical Milksnake, Tropical Kingsnake; Culebra de leche tropical, Falsa coral, Coral falsa, Serpiente de leche

Figure 4.104H; Map 103.

Lampropeltis doliata spp.: Cope (1860c); Taylor (1951, 1954).

Lampropeltis micropholis: Cope (1860c); Ray & Knight (2013).

Lampropeltis triangula: Cope (1860c).

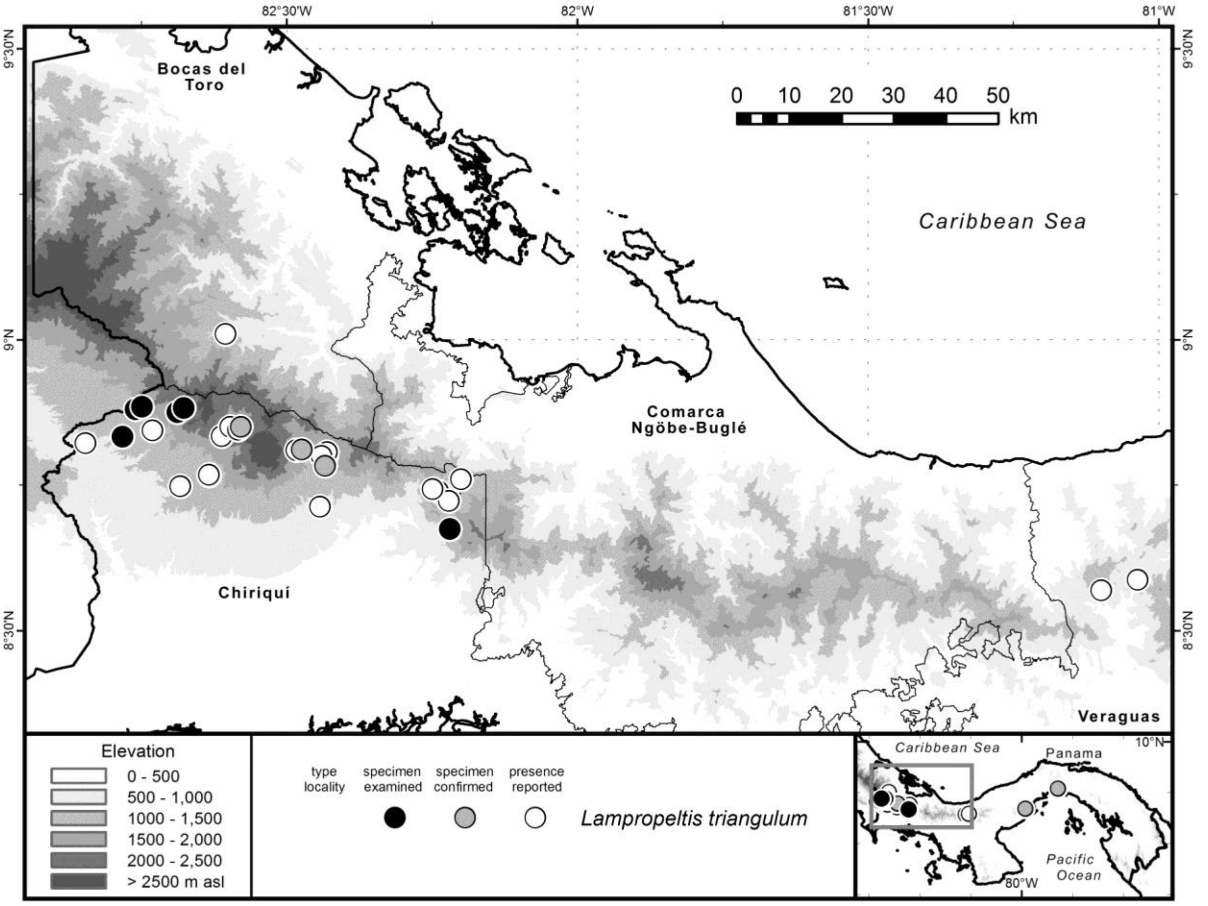
Holotype. Unknown, from Amerique.

Geographic distribution. SE Canada and USA through Central America to Colombia, Ecuador, and N Venezuela, 0–2500 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC, the Santa Fé area, Bocas del Toro, and numerous sites in Chiriquí, up to 2000 m asl.

Diagnosis. This large snake (maximum TOL 1990 mm) with round pupils either exhibits a coralsnake-like pattern of alternating rings (black-white or yellow-black-red) or is completely black when seen from above. Ringed individuals differ from the similarly ringed *Erythrolamprus bizona* in having the cloacal scute entire (vs. divided) and 19 or more dorsal rows at midbody (vs. 15). The melanistic adults found in the Cordillera Central differ from the similarly black species of *Clelia* in having their venters entirely black or with black mottling and remnants of red, black, and light rings (vs. unicolor white, cream, or light gray), and from melanistic adults of *Oxyrhopus petolarius* in having 63 or fewer subcaudals (vs. 77 or more) as well as from both in having round pupils (vs. vertically elliptical).

Description. TOL to 1990 mm; SVL to 1310 mm*; tail short, TL/TOL = 0.11–0.19; D smooth, in (19–23)—(19–23)—(15–19) rows; V 205–244; SC 39–63; SPL 6–9; INL 8–11; loreal 0–1; Preoc 1–2; Postoc 1–3; Tant 1–3, Tpost 2–3; cloacal scute entire; AP 2; eyes moderate, pupil round (including data from Dunn 1937b).

The hemipenis of *Lampropeltis triangulum* is a moderate, bilobed organ with a naked pedicel, spinulate truncus, and calyculate apex.



Map 4.103: Distribution of *Lampropeltis triangulum.*

Coloration in life. Either a tricolor coralsnake-like pattern with the black rings arranged in dyads (black-white or yellow-black-red) or assuming a more or less completely black coloration with age. All of these melanistic individuals which I have seen from the highlands of western Panama have retained some traces of the ringed juvenile pattern and/or reddish coloration elements thereof at least on anterior V surfaces.

The specimen SMF 89575 was recorded as follows: D ground color Blackish Neutral Gray (82), on posterior half of body grading into shadings of Plumbeous (78); L surfaces of head and neck mottled with Peach Red (94); V ground color Blackish Neutral Gray (82); V surface of head with a mottling of Salmon Color (6) and Pale Horn Color (92); forming a broad transverse band; V surface of neck mottled with Peach Red (94); venter with sparse mottling of Salmon Color (6) and Pale Horn Color (92) suggesting transverse bars about 3–4 V wide; V surface of tail with 4 less sparsely mottled transverse bars about two subcaudals wide.

The male SMF 90188 (Fig. 4.104H) was recorded as follows: Body, tail and head Jet Black (89) with a suggestion of Blackish Neutral Gray (82); supralabials, infralabials, rostral, mental and chin area mottled with Yellow Ocher (123 C), Flesh Ocher (132D), and Pearl Gray (81); iris Burnt Sienna (132).

Coloration in preservative. After 4.5–6 years in 70% ethanol the coloration of my examined specimens is similar to that in life, apart from that the reddish and yellowish shades have faded.

Natural history notes. Terrestrial, feeding on different vertebrates. Though usually noted to be nocturnal or crepuscular, at least the melanistic populations of the Talamancan highlands are often found active at daytime. The adult male SMF 90188 was found moving along a tree buttress in a shade coffee plantation at 14:20. The specimen SMF 89575 was handed to us around 10:00, shortly after having been killed by a rural worker. Dunn (1937b) noted *Lampropeltis triangulum* to be "extremely rare in lowland Panama." This contrasts with the situation in highland Chiriquí, where it seems to be a common and abundant species.

Remarks. Dunn (1937b) described *Lampropeltis triangulum gaigeae* subsp. nov. from the Talamancan highlands of Panama and Costa Rica (holotype UMMZ 57967, male, from Boquete), diagnosing it as "a *L. triangulum* which is black when adult", a characteristic apparently applying to all highland populations of LCA (Savage 2002; own observation). The three specimens for which I recorded morphological data have (19–21)—19—15 D. The posterior reduction to 15 has been noted by Dunn (1937b), but was not included in recent comprehensive works (Savage 2002; Köhler 2008). My largest examined specimen (SMF 90188) has 1310 mm SVL + 300 mm TL = 1610 mm TOL. The proximity of several records from RFLF to the Comarca's border (especially that of Castillo et al. 1990 from Quebrada Arenas, less than 2 km) as well as the records east and west of the Comarca Ngöbe-Buglé render this species' occurrence in the Comarca plausible.

For now, contrary to Ray & Knight (2013) I refrain from adopting the split of *Lampropeltis triangulum* into several species as proposed by Ruane (2013), since this proposal is made within an unpublished PhD dissertation and in my opinion does not justify the synonymization of *L. t. gaigeae* with *L. t. micropholis* on the basis of the examined material. Nevertheless, I am convinced that a sound taxonomic study elevating hitherto subspecific taxa of *L. triangulum* to full species is to be expected soon.

Leptophis ahaetulla (Linnaeus 1758)

Giant or Green Parrotsnake, Northern Green Frog-eater or Frogger, Parrot Snake; Bejuquilla, Bejuquilla verde gigante, Lora falsa, Lora falsa gigante

Figure 4.105A; Map 4.104.

Leptophis occidentalis: Cope (1894, 1899); Barbour (1906); Wettstein (1934); Dunn & Bailey (1939); Slevin (1942); Swanson (1945); Cochran (1946); Taylor (1954).

Leptophis praestans: Cope (1876, 1894).

Leptophis ultramarinus: Cope (1894).

Thalerophis occidentalis: Dunn (1947); Evans (1947).

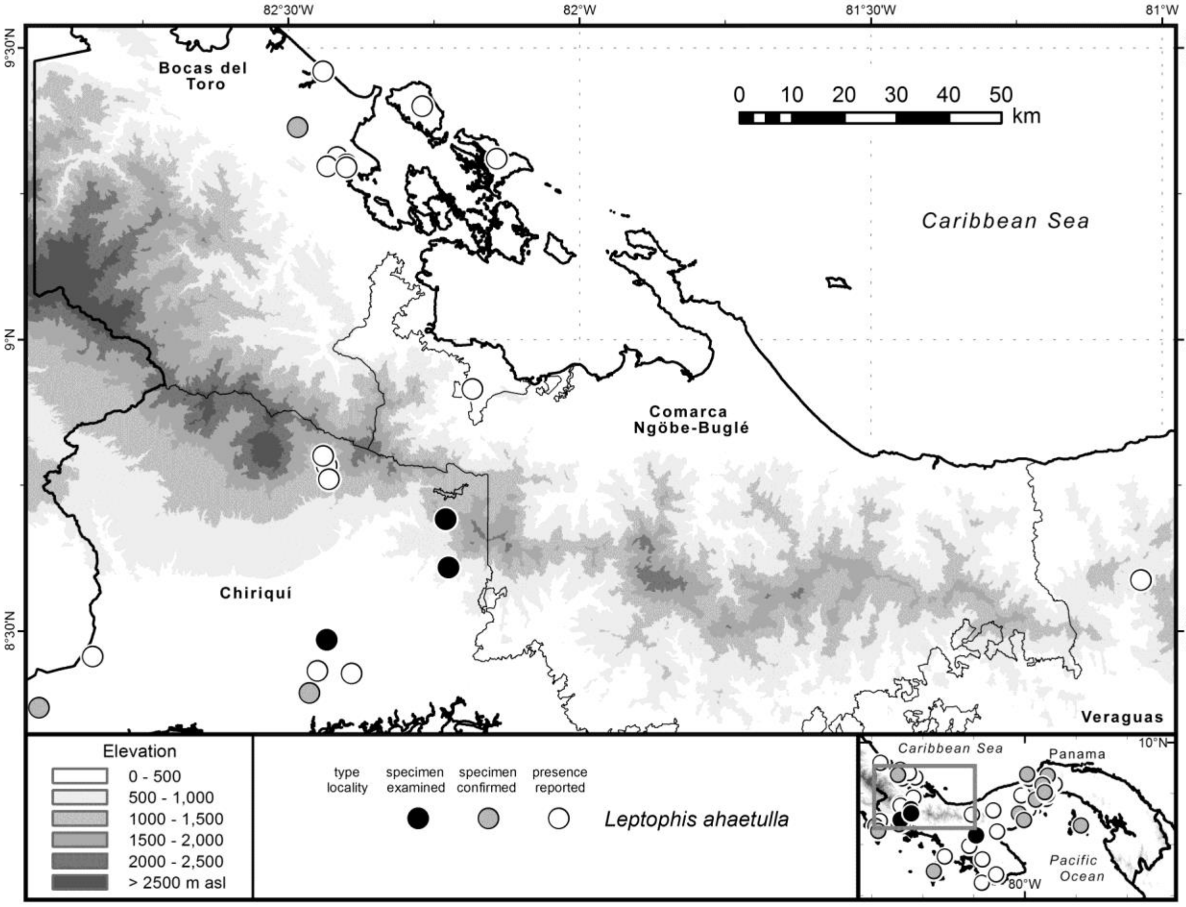
Thalerophis richardi occidentalis: Taylor (1951).

Thrasops ahaetulla: Cope (1861b).

Thrasops occidentalis: Cope (1861b).

Thrasops praestans: Cope (1869).

Lectotype. Exact specimen assignment unclear, type locality by lectotype designation: "America" (see McCranie 2011).



Map 4.104: Distribution of *Leptophis ahaetulla.*

Geographic distribution. Mexico to Ecuador and Argentina, 0–1680 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Boquete, Fortuna, and Santa Fé areas, PNGDOTH, Valle de Antón, and PNAC, up to ca. 1320 m asl.

Diagnosis. This large snake (maximum TOL > 2250 mm) with round pupils is immediately recognized as a member of the genus *Leptophis* by its keeled dorsals arranged in 15—15—11 oblique rows, divided cloacal scute, and immaculate venter. *Leptophis ahaetulla* differs from *L. depressirostris* in lacking a loreal and thus having the prefrontals in contact with the supralabials (vs. loreal present, separating PF from SPL), from *L. riveti* in being predominantly green above (vs. bronze) and in lacking keels on the 1st dorsal row (vs. keels on all D rows), and from *L. nebulosus* in being predominantly green above (vs. bronze with a greenish blue lateral stripe).

Description. TOL to > 2250 mm; SVL of Honduran specimens to 1444 mm; tail long, TL/TOL = 0.33–0.41; D keeled at least on upper rows, in 15—15—11 oblique rows; V 147–183; SC 137–189; SPL 7–10; INL 7–12; loreal 0; Preoc 1; Postoc 1–4; Tant 1, Tpost 1–2; cloacal scute divided; AP 1, 2 on some scales; eyes large, pupil round.

The hemipenis of *Leptophis ahaetulla* is a slightly bilobed organ; pedicel almost naked, truncus with large spines proximally and smaller ones distally, apex with papillate calyces.

Coloration in life. D and L surfaces unicolor green or with short, narrow black dashes along singular scale margins or dorsalmost keels; V surfaces yellow to light green; a narrow dark postocular stripe; iris yellow; juveniles with dark green to blue crossbands.

The juvenile male SMF 89580 was recorded as follows: D surfaces of body and tail Parrot Green (260), grading into Lime Green (159) on the neck and into Paris Green (63) laterally; V surfaces of body and tail dirty white with a suggestion of Opaline Green (162D); D surface of head Lime Green (159), grading into dirty white laterally; a black postorbital stripe present; iris Trogon Yellow (153); V surface of neck dirty white.

Coloration in preservative. After 6 years in 70% ethanol the coloration of SMF 89580 chiefly metallic blue with some bronze areas and darker blue blotches dorsally, and very light blue ventrally.

Natural history notes. Diurnal and largely arboreal, feeding mainly on frogs. Notorious for its defensive behaviour of facing potential aggressors with the mouth wide open (indeed it is rather rare to find a photo of this species with closed mouth), and not at all reluctant to bite when handled. An adult individual from Los Algarrobos that later freed itself was found sleeping on vegetation 3 m above ground next to the Río Majagua. The juvenile male SMF 89580 was spotted at 10:00 while it was moving along branches in burnt pasture shrubland. A bite delivered by this juvenile to me caused no effects whatsoever, while another bite delivered to AH caused local pain.

Remarks. My georeference for the records from "vicinity N of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is somewhat above the elevational maximum given as 1200 m for Panama (Jaramillo et al. 2010) and seems plausible in view of the 1400 m given by most recent authors for Costa Rica (e.g., Solórzano 2004; Sasa et al. 2010) or both countries combined (Ray & Knight 2013). The numerous records east and west of the Comarca Ngöbe-Buglé render this species' occurrence therein plausible.

Leptophis depressirostris **(Cope 1861)**

Cope's Parrotsnake, Golden-eyed Parrot Snake, Satiny Parrotsnake, Parrot Snake; Bejuquilla, Bejuquilla verde, Lora falsa, Lora falsa de ojos dorados

Figure 4.105B; Map 4.105.

Leptophis aeruginosus: Cope (1876); Boulenger (1894); Taylor (1954).

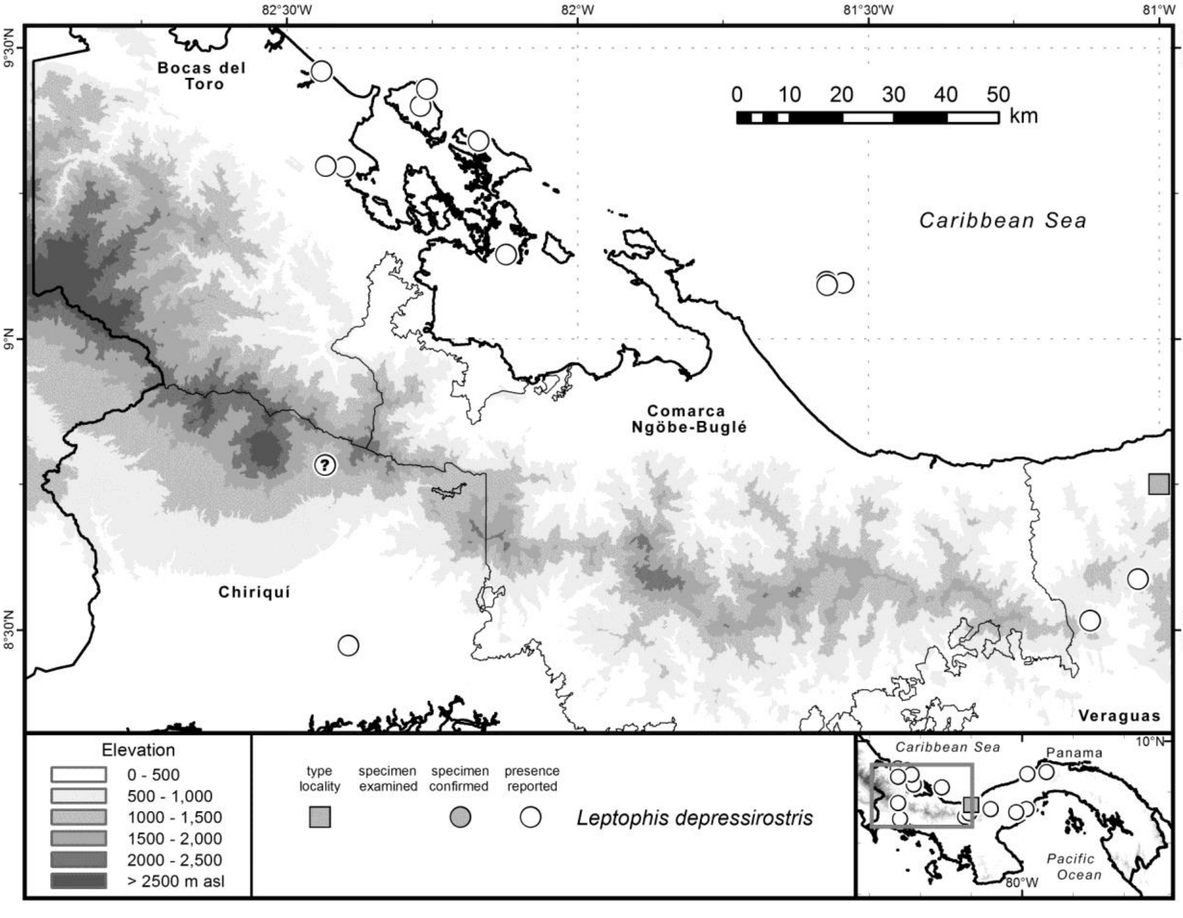
Leptophis bilineatus: Boulenger (1894); Wettstein (1934).

Leptophis saturatus: Cope (1876); Boulenger (1894).

Philothamnus depressirostris: Cope (1861b).

Thalerophis depressirostris: Taylor (1951).

Holotype. ANSP 5207, from "Cocuyas de Veraguas, New Granada" (Cope 1861b).



Map 4.105: Distribution of *Leptophis depressirostris.*

Geographic distribution. Honduras to Colombia and Ecuador, 0–1300 m asl. In Panama, throughout the Pacific versant and along the Caribbean versant of the western and central portions of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Santa Fé area, PNGDOTH, El Valle, and PNAC up to at least 1000 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1500 mm) with round pupils is immediately recognized as a member of the genus *Leptophis* by its keeled dorsals arranged in 15—15—11 oblique rows, divided cloacal scute, and immaculate venter. *Leptophis depressirostris* differs from all other Panamanian *Leptophis* in having a loreal that separates the prefrontals from the supralabials (vs. loreal absent, PF in contact with SPL).

Description. TOL to 1500 mm; SVL of Honduran specimens to 604 mm; tail long, TL/TOL = 0.36–0.40, but tail often incomplete; D keeled only on paravertebral rows, in 15—15—11 oblique rows; V 144–158; SC 158–170; SPL 7–10; INL 9–11; loreal 1; Preoc 1; Postoc 1–2; Tant 1, Tpost 1–3; cloacal scute divided; AP 1 on most scales; eyes large, pupil round.

The hemipenis of *Leptophis depressirostris* is a slightly bilobed organ; pedicel almost naked, truncus with large spines, apex with papillate calyces.

Coloration in life. D and L sufaces unicolor green or with narrow dark paravertebral stripes; V surfaces light green; a broad dark postocular stripe; iris yellow.

Coloration in preservative. D surfaces bluish green, V surfaces cream, grading into green posteriorly and greenish blue under tail; juveniles brownish above and cream grading into greenish brown posteriorly below.

Natural history notes. Diurnal and arboreal, showing the gaping threat display and willingness to bite if touched that are typical for *Leptophis.*

Remarks. The occurrence of *Leptophis depressirostris* in the Serranía de Talamanca is documented by the specimens MVUP 693 and 694 from "Volcán Barú, prov. Chiriquí". Since the MVUP catalogue does not further specify the specimen's collection locality, I arbitrarily placed (and therefore marked with a question mark in Map 4.105) my georeference at Boquete, where most herpetological collecting in the surroundings of Volcán Barú has taken place. My generalized coordinates for this settlement yield a SRTM elevation of 1121 m asl, which would constitute the highest record from Panama so far, almost 300 m above the maximum elevation of 850 m given by Jaramillo et al. (2010). Notwithstanding the great uncertainty concerning the exact collection site, an elevation above 1000 m can confidently be assumed in view of the verbal locality descriptor. The records east and west of this political subdivision, as well as the distance of less than 5 km between the record from Cerro Mariposa (alias Cerro Tute; Martínez & Rodriguez 1994) to the Comarca's border, render the presence of *L. depressirostris* in the Comarca Ngöbe-Buglé plausible.

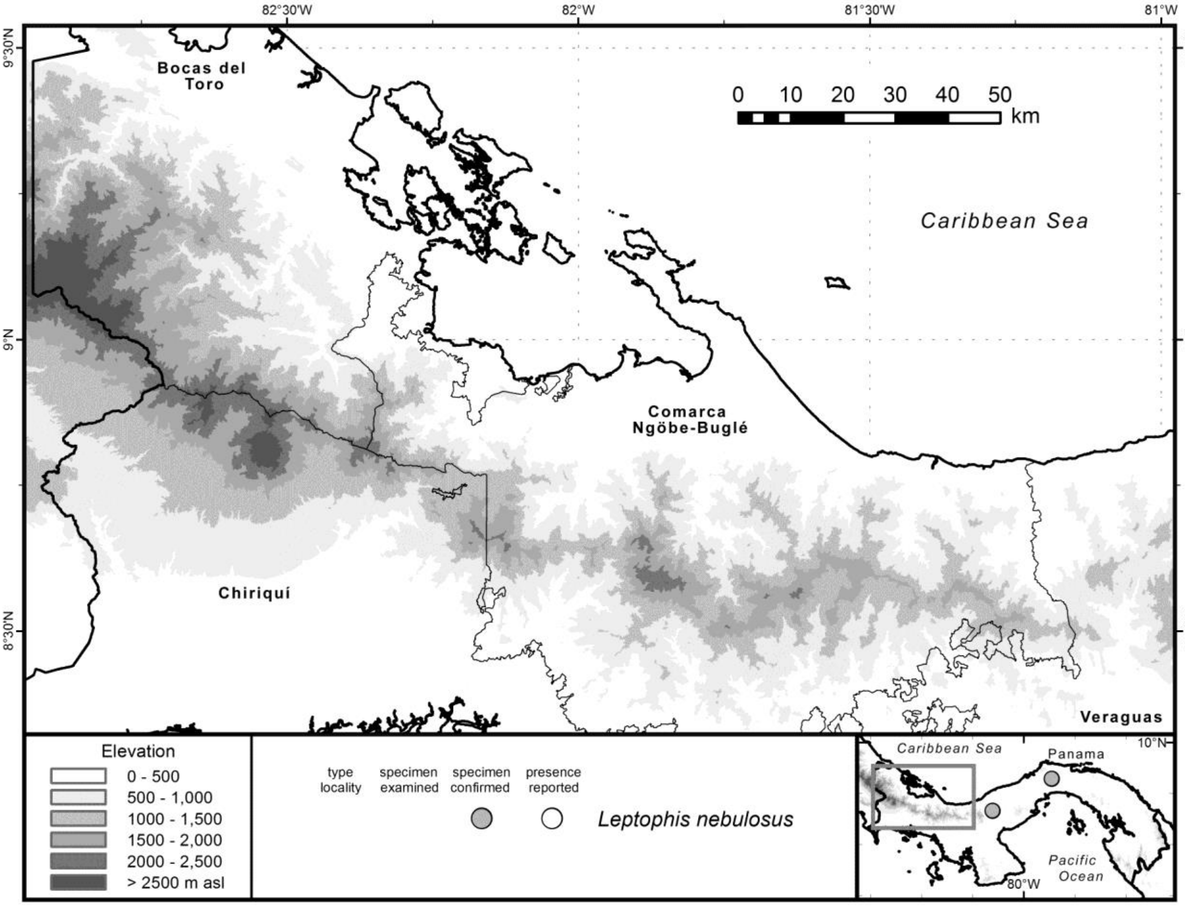
Leptophis nebulosus (Oliver 1942)

Bronze-striped Parrotsnake, Oliver's Parrotsnake, Striped Parrotsnake; Bejuquilla, Lora falsa, Lora falsa enana

Figure 4.105C; Map 4.106.

Holotype. MCZ R-15287, from Cariblanca, Costa Rica.

Geographic distribution. Honduras to Panama, 0–1600 m asl. In Panama, east to the Río Chagres drainage, presumably along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNGDOTH at up to 800 m asl.



Map 4.106: Distribution of *Leptophis nebulosus.*

Diagnosis. This medium-sized snake (maximum TOL 854 mm) with round pupils is immediately recognized as a member of the genus *Leptophis* by its keeled dorsals arranged in 15—15—11 oblique rows, divided cloacal scute, and immaculate venter. *Leptophis nebulosus* differs from *L. depressirostris* in lacking a loreal and thus having the prefrontals in contact with the supralabials (vs. loreal present, separating PF from SPL), from *L. riveti* in lacking keels on the 1st dorsal row (vs. keels on all D rows), and from *L. ahaetulla* in having a bronze middorsum with a broad greenish blue lateral stripe per side (vs. predominantly green above).

Description. TOL to 854 mm; SVL of Honduran specimens to 474 mm; tail long, TL/TOL = 0.37–0.42, but tail often incomplete; D keeled except on 1st row, in 15—15—11 oblique rows;

V 146–160; SC 134–151; SPL 8–9; INL 10–11; loreal 0; Preoc 1; Postoc 1–2; Tant 1, Tpost 2; cloacal scute divided; AP 1 on most scales; eyes large, pupil round.

The hemipenis of *Leptophis nebulosus* is a slightly bilobed organ; pedicel naked, truncus with large spines proximally and smaller ones distally, apex calyculate.

Coloration in life. D surfaces of body and tail bronze to gold, sometimes with green or bluish mottling; a broad (2–3 D rows wide) bluish green L stripe per side that may be bordered ventrolaterally by a narrow yellow stripe and grade into brown posteriorly; D surface of head green; V surfaces white to beige or coppery; a narrow dark pre- and postocular stripe; iris yellow.

Coloration in preservative. Similar to that in life, apart from that the green L stripe fades to brown and the V surfaces lighten up.

Natural history notes. Diurnal and arboreal, feeding on sleeping frogs; showing the gaping threat display and probably also the willingness to bite if touched that are typical for *Leptophis.*

Remarks. While Savage (2002) judged this species to be common in Costa Rica, there are only two locality records from Panama: The first country record from Quebrada Las Pavas (Jaramillo & Ibáñez 2003) slightly east of the Panama Canal, and the record from PNGDOTH that is variably given with 700 (Ray 2011) or 800 m asl. Still, these records together with the distribution in Costa Rica (Savage 2002; Solórzano 2004) render the occurrence of this species in my study area and its four political subdivisions plausible. An individual of *Leptophis* photographed by AB at RFLF (McConnell 2014: Figs. 241 and 242, labelled as *L.* aff. *riveti*) shows the coloration described as typical for *L. nebulosus* by recent authors (Savage 2002; Solórzano 2004; McCranie 2011). I thus regard it to represent the latter species rather than *L. riveti,* but refrain from including this record on Map 4.106 pending examination of the specimen.

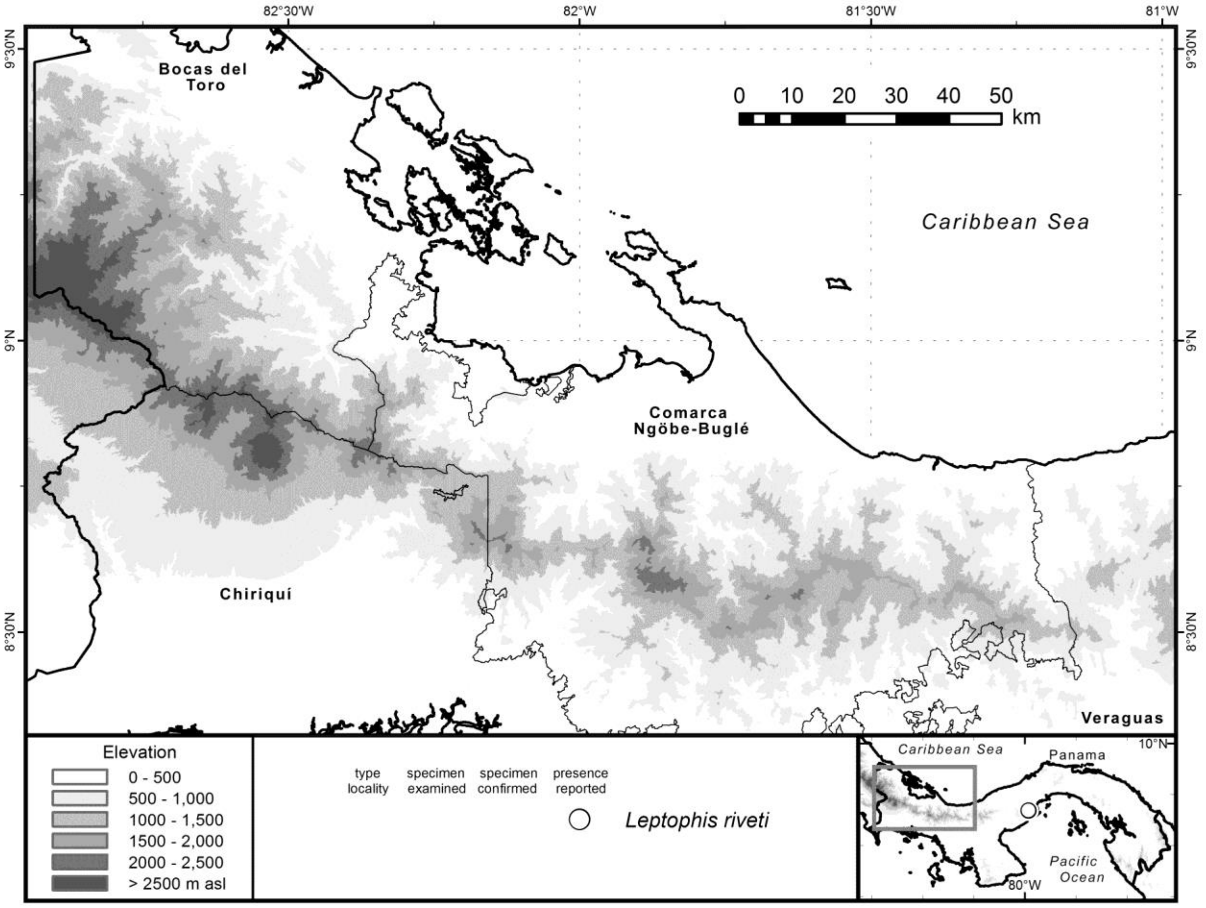
Leptophis riveti Despax 1910

Turquoise Parrotsnake, Despax's Parrotsnake; Lora falsa azulada

Figure 4.105D; Map 4.107.

Holotype. MNHN 06.259, from Gualaquiza, Ecuador, 730 m elevation.

Geographic distribution. Costa Rica to Colombia, Ecuador, and Peru, as well as on Trinidad, 0–1800 m asl. In Panama, presumably throughout the country at least on the Pacific versant including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNAC at about 850 m asl.



Map 4.107: Distribution of *Leptophis riveti.*

Diagnosis. This medium-sized snake (maximum TOL 1000 mm) with round pupils is immediately recognized as a member of the genus *Leptophis* by its keeled dorsals arranged in 15—15—11 oblique rows, divided cloacal scute, and immaculate venter. *Leptophis riveti* differs from all other Panamanian *Leptophis* in having all dorsal scale rows keeled (vs keels lacking at least on the 1st dorsal row) and in having a predominantly bronze dorsum with short green transverse bands (vs. unicolor or with longitudinal stripes).

Description. TOL to 1000 mm; tail long, TL/TOL = 0.30–0.41, but tail often incomplete; D keeled on all rows, in 15—15—11 oblique rows; V 133–155; SC 135–145; SPL 8; INL 9–11; loreal 0; Preoc 1; Postoc 1–2; Tant 1, Tpost 1–2; cloacal scute divided; AP 1 irregularly distributed; eyes large, pupil round.

The hemipenis of *Leptophis riveti* is a slightly bilobed organ without enlarged spines proximally on truncus.

Coloration in life. D and L surfaces of body and tail chiefly bronze, with narrow and short bright green transverse bands; D surface of head green; V surfaces bronze posteriorly, grading into white anteriorly; a narrow dark post- and sometimes also preocular stripe; iris yellow.

Coloration in preservative. Not described to my knowledge, but presumably similar to that in life, apart from that the greenish colors can be expected to fade to blue or brown with time.

Natural history notes. Little is known about this species, which is assumed to be a diurnal and arboreal frog-eater like its Panamanian congeners.

Remarks. I was unable to reveal the sources of the points plotted by Köhler (2008: p. 245) in western Chiriquí and near the Panama Canal, or the records underlying the listing of this species for Chiriquí and Coclé provinces (Young et al. 1999) and the Pacific lowlands of Panama (Jaramillo et al. 2010). The only Panamanian record for this species which I was able to trace is from PNAC (Ibáñez et al. 1996, locality 3) without reference to a specimen. My georeference for this locality yields a SRTM elevation of 847 m asl that corresponds well with the highest elevation for Panama given as 850 m (Jaramillo et al. 2010). Nevertheless, this record from PNAC, together with the distribution as given by recent authors (Savage 2002; Solórzano 2004; Köhler 2008) render the occurrence of this species in my study area and three of the associated political subdivisions (Chiriquí, Comarca Ngöbe-Buglé, and Veraguas) as well as in the Caribbean and Pacific lowlands of Panama plausible. Concerning the *Leptophis* photographed by AB at RFLF (McConnell 2014: Figs. 241 and 242, labelled as *L.* aff. *riveti*), see remarks for *L. nebulosus.*

Mastigodryas melanolomus (Cope 1868)

Neotropical Racer, Dark Tropical Racer, Salmon-bellied Racer, Orange-bellied Racer; Culebra, Corredora común, Zumbadora, Borriguera, Borriguera común

Figure 4.105E; Map 4.108.

Dryadophis boddaertii or *D. boddaertii alternatus:* Dunn & Bailey (1939); Slevin (1942); Dunn (1947).

Dryadophis melanomus: Myers (1977).

Dryadophis melanolomus or *D. melanolomus alternatus:* Swanson (1945); Cochran (1946); Taylor (1951); Smith (1958); Myers & Rand (1969); Auth (1994); Ibáñez et al. (1995, 1996, 1997); de Sousa (1999); Köhler (2001); ANAM (2004); Fundación PA.NA.M.A. (2007); Batista & Ponce (2011).

Dryadophis sanguiventris: Taylor (1954).

Drymobius boddaertii: Cope (1876, 1899); Wettstein (1934).

Masticophis melanolomus: Cope (1868).

Mastigodryas alternatus: McCranie (2011).

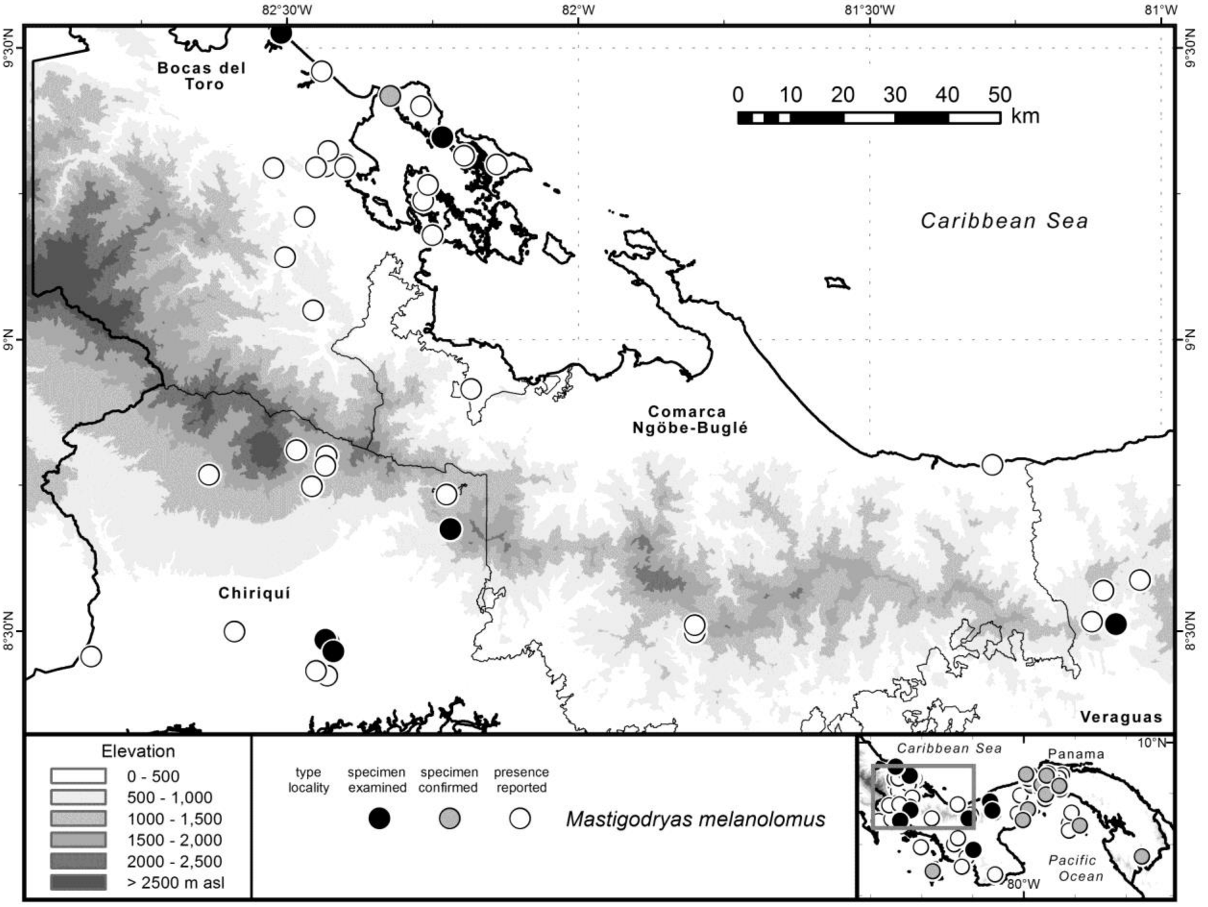
Mastigodryas bifosatus: Martínez & Rodriguez (1994); Martínez et al. (1995).

Mastigodryas boddaerti: Perez-Santos & Martínez (1997); Perez-Santos (1999).

Mastigodryas sanguiventris: Peters & Orejas-Miranda (1970); Martínez & Rodriguez (1994); Martínez et al. (1995).

Holotype. USNM 24985, from Yucatan.

Geographic distribution. Mexico to Panama and probably Colombia, 0–1760 m asl. In Panama, along both versants throughout the western and central portions of the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and one record from Darién. In the Cordillera Central, recorded from numerous sites along both versants up to 1615 m asl.



Map 4.108: Distribution of *Mastigodryas melanolomus.*

Diagnosis. This medium-sized snake (maximum TOL ca. 1500 mm) with round pupils is immediately recognized as a member of the genus *Mastigodryas* by its smooth dorsals with 2 apical pits arranged in 17—17—15 rows, divided cloacal scute, immaculate venter, as well as a dorsal pattern of alternating crossbands or blotches in combination with dark labial markings in juveniles and unicolor brown or with light dorsolateral stripes in adults. It differs from *M. pleei,* its only Panamanian congener, in lacking 3 dark middorsal stripes that merge posteriorly in adults (vs. dark middorsal stripes present).

Description. TOL to 1500 mm; SVL to 1069 mm*; tail long, TL/TOL = 0.24–0.35; D smooth, in 17—17—15 rows; V 160–195; SC 85–136; SPL 8–10; INL 9–11; loreal 1–2;

Preoc 1; Postoc 2–3; Tant 1–2, Tpost 2–3; cloacal scute divided; AP 2; eyes large, pupil round.

The hemipenis of *Mastigodryas melanolomus* is a very weakly bilobed organ with a short naked pedicel, many large spines around the truncus, and a long apex with spinulate calyces.

Coloration in life. Adults: D and L surfaces unicolor brown or with a narrow light dorsolateral stripe and sometimes a similar ventrolateral stripe; usually at least with the suggestion of a dark pre- and postocular stripe; V surfaces and labials unicolor cream, gray, or yellow to orange, sometimes with dark mottling on chin. Juveniles with a contrasting pattern of alternating broad dark middorsal blotches or short crossbars with more narrow light interspaces, alternating with similar L crossbars on flanks; and a pronounced dark pre- and postocular stripe as well as usually heavy dark mottling on labials, chin, and throat. The contrasting juvenile pattern gradually fades from posterior to anterior.

Coloration in preservative. After 5–6 years in 70% ethanol the coloration of my examined specimens is similar to that in life, apart from that all yellowish shades have faded to cream; D scales without oberhäutchen are light bluish gray.

Natural history notes. Diurnal and terrestrial, feeding on lizards and other vertebrates. The juvenile SMF 90197 from San San Pond Sak contained a half-digested juvenile (SMF 90094) of *Holcosus quadrilineatus.* A very common species especially in pastures and other largely deforested landscapes. I found three specimens sleeping up to 3 m above ground in vegetation, three others active on the ground between noon and sundown, and one dead on road. This racer is rather irritable and not reluctant to bite when handled. Only 2 of the 6 specimens whose morphological data I recorded possessed complete tails.

Remarks. McCranie (2011) suggested to remove the populations from E Honduras to central Panama from the synonymy of *Mastigodryas melanolomus,* creating the new combination *M. alternatus.* However, for now I refrain from following this decision pending further studies, and include the variation for *M. melanolomus* as delimited by most recent authors (e.g., Savage 2002, Köhler 2008) in the morphological description. As revealed in the synonymy above, some authors have identified Panamanian populations of *Mastigodryas* as *M. bifossatus* or *M. boddaerti,* both species restricted to South America according to current knowledge (Uetz & Hošek 2014). In view of the superficial similarities between these species, I regard all previous records of these species from Panama, including the unsubstantiated mention of supposed holo- and paratypes of *M. boddaerti* from Boquete (Perez-Santos 1999), to actually represent *M. melanolomus.*

I could not trace any record to substantiate the upper elevational limit of 1750 m asl given for Panama by Perez-Santos (1999), though this value does not appear too high in view of the

1760 m reported for Costa Rica (Savage 2002, Sasa et al. 2010). The highest Panamanian record is from Finca Lérida with a verbatim elevation of 5300 ft (= ca. 1615 m), slightly above the 1600 m reported by Jaramillo et al. (2010). Most recent authors (e.g., Savage 2002; Köhler 2008; McCranie 2011) have located the southern distributional limit of *Mastigodryas melanolomus* in central Panama. However, the specimen MCZ 42751 from Minas de Cana, Darién province, catalogued as *Eudryas boddaertii,* was examined by GK and confirmed to represent this species thus substantiating its presence in eastern Panama and rendering its occurrence in Colombia as stated by Uetz & Hošek (2014; also see remarks in Savage 2002: p. 675) very likely.

The only Panamanian congener of this species, *Mastigodryas pleei* (Duméril, Bibron & Duméril 1854) has recently been found at Río Corito very close to my study area (Batista et al. in prep. b) and at PNGDOTH (Ray 2009). The former record documents its presence in Veraguas and renders its occurence in my study area and the Comarca Ngöbe-Buglé possible (see distribution map in Appendix 7).

Oxybelis aeneus (Wagler 1824)

Brown Vinesnake, Narrow-headed Vine Snake, Mexican Vinesnake; Bejuquilla, Bejuquilla común, Bejuquilla chocolate, Bejuquilla café

Figure 4.105F; Map 4.109.

Dryiophis acuminatus: Cope (1876).

Dryophis acuminatus: Cope (1861b).

Oxybelis acuminata: Cope (1893).

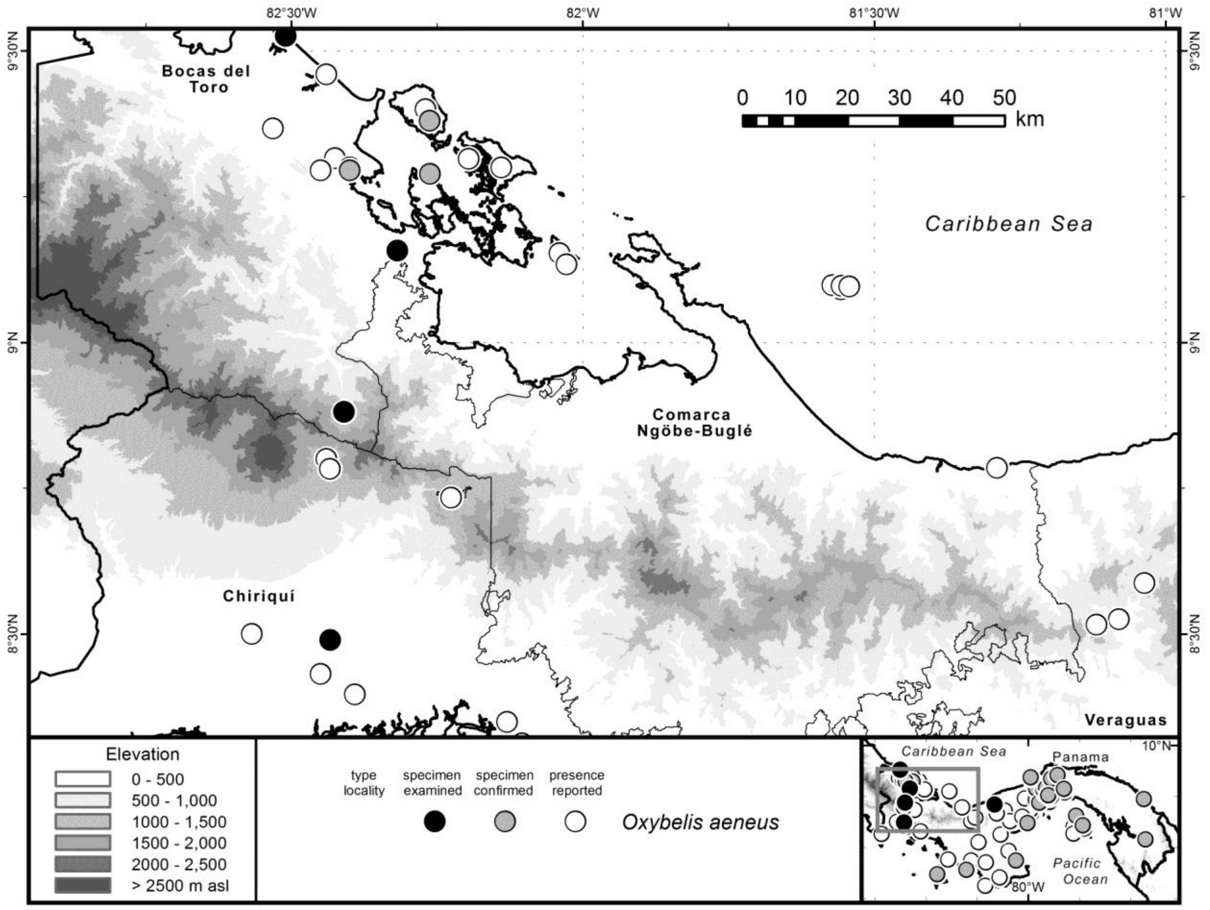
Oxybelis acuminatus: Cope (1868, 1899); Barbour (1906); Slevin (1942); Cochran (1946).

Oxybelis aenus: Ray (2009).

Lectotype. ZMH 2645/0, from forest adjacent to the Solimoes River, near Ega [= Tefé], Brasil.

Geographic distribution. Southern USA and Mexico through Central America to Peru, Bolivia, and Brazil, 0–2500 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites along both versants up to ca. 1320 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1700 mm) with round pupils cannot be confused with any other Panamanian snake due to its extremely slender body and tail and narrow, pointed head coupled with an overall gray or brown dorsal coloration, black mouth lining, smooth or slightly keeled dorsals usually arranged in 17—17—13 rows, and the lack of a loreal.



Map 4.109: Distribution of *Oxybelis aeneus.*

Description. TOL to 1700 mm; SVL in Honduran specimens to 878 mm; tail long, TL/TOL = 0.35–0.45; D smooth to slightly keeled on upper rows in larger specimens, in 17—(15–17)—(12–15) rows; V 173–205; SC 137–203; SPL 6–10; INL 6–11; loreal 0, PF in contact with SPL; Preoc 1; Postoc 2; Tant usually 1, Tpost usually 2; cloacal scute usually divided; AP 0; eyes large, pupil round.

The hemipenis of *Oxybelis aeneus* is a uni- or weakly bilobed organ with a naked pedicel, small spines around truncus, and calyculate apex.

Coloration in life. D and L surfaces gray to brown, unicolor, iridescent, or with light and/or dark dashes, spots, or mottling, D surface of head usually unicolor darker brown; V surfaces white to cream anteriorly (including labials), grading into tonalities similar to the D surfaces posteriorly; often with a narrow dark pre- and postocular stripe along upper sutures of SPL that may continue onto neck; lining of mouth black.

The female MHCH 2354 was recorded as follows: D and L surfaces of body Drab-Gray (119D) with a suggestion of Light Drab (119C), with Sepia (119) mottling and dirty white scale margins; tail Drab-Gray (119D) with a suggestion of Light Drab (119C), mottled with Sepia (119); venter dirty white with Light Drab (119C) speckles on posterior two-thirds that increase in density on posterior half so as to cover almost all the V surface; D ground color grading into Brussels Brown (121B) on neck; D and dorsolateral surfaces of head Brussels Brown (121B); a narrow Sepia (119) longitudinal stripe extending along upper edges of supralabials; supralabials dirty white with a suggestion of Cream Color (54); V surfaces of head and neck dirty white with a suggestion of Light Sky Blue (168C); iris dirty white with a suggestion of Chamois (123D) D and ventral, but Sepia (119) anterior and posterior to pupil; throat Blackish Neutral Gray (82).

Coloration in preservative. After 4.5–5 years in 70% ethanol the coloration of my examined specimens is very similar to that in life, apart from that the D colors have lightened up and assumed a more metallic aspect.

Natural history notes. Chiefly diurnal and arboreal, feeding on anoles and other small vertebrates. I encountered all five individuals at night, three of them while they were actively moving about in vegetation 0.8–2 m above ground several hours after sunset. All five were found in open or semi-open secondary vegetation. *Oxybelis aeneus* shows a gaping threat display similar to that of *Leptophis* showing its black mouth and throat lining, and is likely to bite when handled.

Remarks. My georeference for the records from "vicinity N of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is somewhat above the elevational maximum given as 1200 m for Panama (Jaramillo et al. 2010) and appears plausible in view of the 1340 or 1400 m given by recent authors for Costa Rica (e.g., Solórzano 2004; Sasa et al. 2010) or both countries combined (Ray & Knight 2013).

***Oxybelis brevirostris* (Cope 1861)**

Cope's Vine Snake, Short-nosed Vinesnake; Bejuquilla, Bejuquilla de hócico corto

Figure 4.105G; Map 4.110.

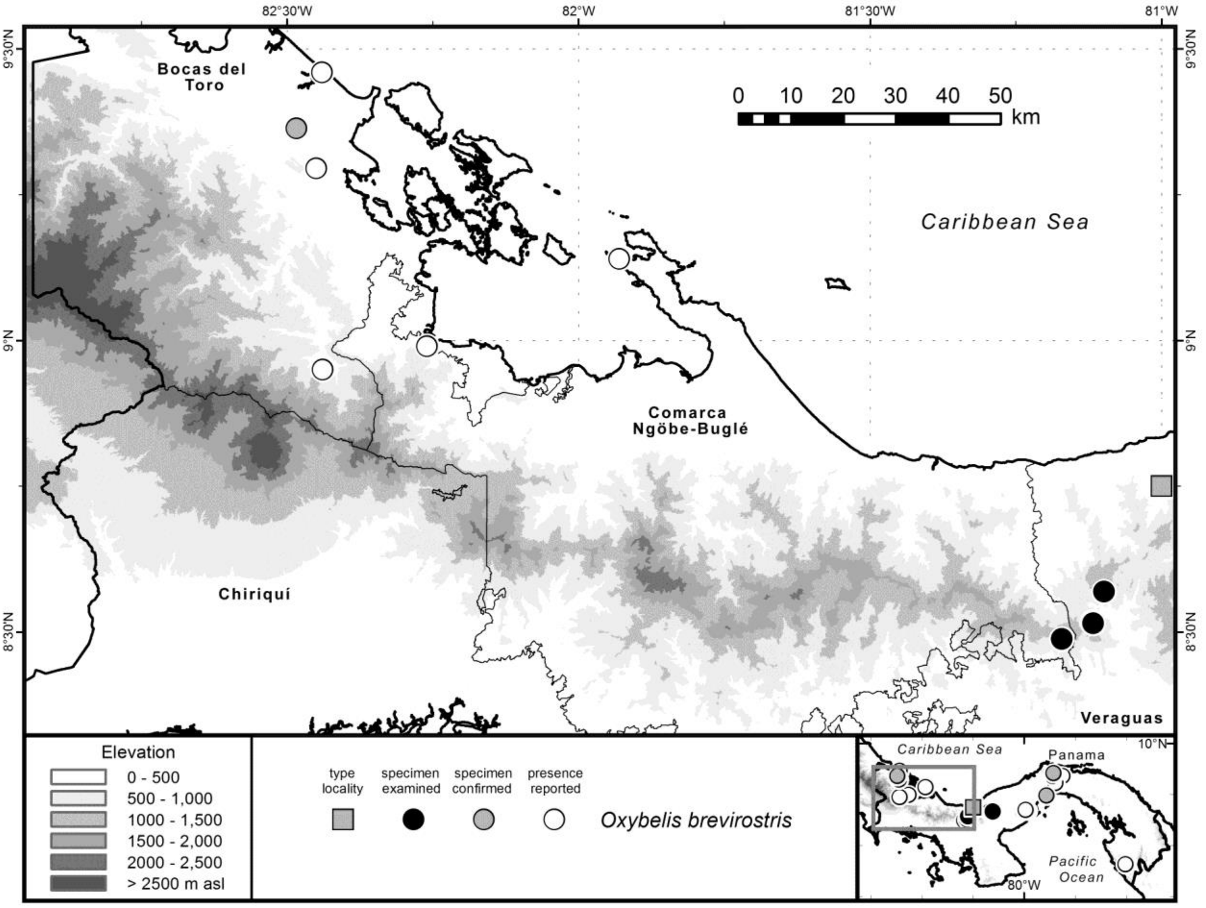
Dryiophis brevirostris: Cope (1876).

Dryophis brevirostris: Cope (1861b).

Leptophis depressirostris: Sunyer (2009: in part.: Fig. 196).

Holotype. USNM 31349, from "Veraguas, New Grenada" (Cope 1861b; = most probably Cocuyos de Veraguas, Panama).

Geographic distribution. Honduras to Colombia and Ecuador, 0–910 m asl. In Panama, along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, and both versants from Veraguas eastwards. In the Cordillera Central, recorded from BPPS in Bocas del Toro, El Paredón and the Santa Fé area, as well as PNGDOTH and PNAC, up to 910 m asl.



Map 4.110: Distribution of *Oxybelis brevirostris.*

Diagnosis. This medium-sized snake (maximum TOL 1200 mm) with round pupils is unlikely to be confused with any other Panamanian snake due to its extremely slender body and tail and narrow, elongate head coupled with an overall green dorsal coloration, smooth to usually slightly keeled dorsals arranged in 15—15—13 rows, a usually undivided cloacal scute, and the lack of a loreal.

Description. TOL to 1200 mm; SVL to 684 mm*; tail long, TL/TOL = 0.36–0.42; D smooth to slightly keeled (keeled in all examined specimens), in 15—15—13 rows; V 164–186; SC 151–179; SPL 5–7; INL 6–8; loreal 0, PF in contact with SPL; Preoc 1; Postoc 1–2; Tant usually 1, Tpost 1–2; cloacal scute usually entire; AP 0, 1 weakly developed on some anterior D in some specimens; eyes large, pupil round.

The hemipenis of *Oxybelis brevirostris* is a slightly bilobed organ with a naked pedicel, spines on truncus large proximally and decreasing in size distally, and a calyculate apex.

Coloration in life. D and L surfaces unicolor green or grading into greenish brown towards middorsum, often with light and/or dark dashes especially anteriorly; V surfaces yellowish light green, usually losing the yellowish hues posteriorly; a narrow dark pre- and postocular stripe along upper border of SPL; iris yellow; tongue yellow with brown tips.

The juvenile SMF 89781 was recorded as follows: D surfaces of head, body, and tail Olive-Green (Basic) (46), grading into Apple Green (61) laterally; anterior two-thirds of body with irregularly distributed Natal Brown (219A) scale margins; V surfaces of body and tail Opaline Green (162D); head with the suggestion of a fine Sepia (119) longitudinal line extending from nostril posteriorly; L surface of head below this line Pistachio (161), grading into Chartreuse (158) on chin shields; iris Spectrum Yellow (55) with a horizontal Sepia (119) stripe.

Leonhard Stadler recorded the adult male MHCH 2355 (Stadler 2010: Fig. A91) as follows (translated from Stadler 2010): D ground color Olive-Green (Basic) (46); V surface of head Chartreuse (158) with Sulfur Yellow (157) scale borders; V surfaces of body and tail Chatreuse (158) anteriorly, grading into Lime Green (159) towards base of tail; head with a L Sepia (119) stripe running through the eye; iris Trogon-Yellow (153).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration of my examined specimens is similar to that in life, apart from that the green tonalities have turned blue.

Natural history notes. Diurnal and arboreal, feeding chiefly on frogs and lizards. All five individuals I have personally encountered were found at night while they were sleeping in vegetation 1–3 m above ground. With the exception of SMF 91570, coiled up in tall grass in a forest clearing, all were in closed forest.

Remarks. Several counts obtained from my examined specimens are lower than reported so far for this species (Savage 2002; McCranie 2011): The specimen SMF 91570 has 5 SPL on the left side of the head; SMF 89781 has 164 ventrals; 4 out of 7 specimens have only 6 INL either on one or both sides of the head. All 7 specimens have keeled D and the vertebral and paravertebral rows slightly enlarged.

Solórzano (2004) and consequently also Ray & Knight (2013) gave the highest documented elevation for *Oxybelis brevirostris* as 1200 m asl, Perez-Santos (1999) even as 1250 m. I suspect the former value to be based on ANSP 5245 from San José. That record has been judged as questionable by Savage (2002), which may have been the reason for several subsequent authors (Köhler 2008; Sasa et al. 2010; Wilson & Johnson 2010; McCranie 2011) to not adopt this elevational record. The highest records which I could trace are MHCH 2356, collected by AH and myself on Cerro Mariposa at 883 m, and MVUP 1080 from Culebra, Bocas del Toro, for which my georeference placed centrally in that settlement yields a SRTM elevation of 905 m.

Oxybelis fulgidus (Daudin 1803)

Green Vinesnake; Bejuquilla, Bejuquilla verde, Lora

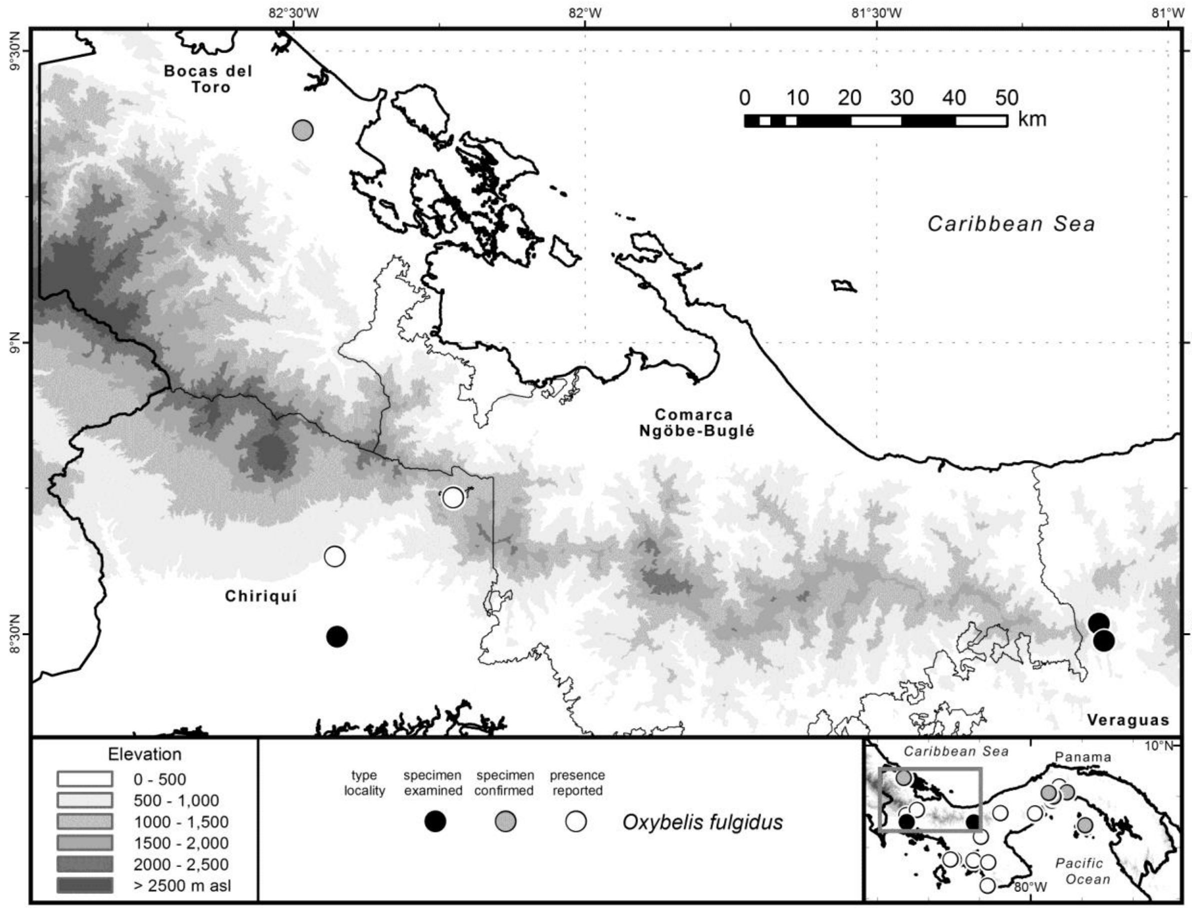
Figure 4.105H; Map 4.111.

Dryophis fulgidus: Cope (1861b).

Oxybelys fulgidus: de Sousa (1999).

Holotype. At MNHN, from the neighborhood of Port-au-Prince, Santo Domingo (in error). Type locality restricted to Surinam.

Geographic distribution. Mexico to Peru, Bolivia, and Argentina, 0–1600 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Fortuna and Santa Fé areas, PNGDOTH, and PNAC, up to ca. 1050 m asl.



Map 4.111: Distribution of *Oxybelis fulgidus.*

Diagnosis. This large snake (maximum TOL > 2000 mm) with round pupils cannot be confused with any other Panamanian snake due to its extremely slender body and tail and narrow, pointed head, its uniformly green coloration with a light ventrolateral stripe, keeled dorsals arranged in 17—17—13 rows, and the lack of a loreal.

Description. TOL to > 2000 mm; SVL to 1303 mm*; tail long, TL/TOL = 0.28–0.42; D keeled, in 17—17—13 rows; V 194–217; SC 133–186; SPL 9–12; INL 9–12; loreal 0, PF in contact with SPL; Preoc 1; Postoc 1–3; Tant 1–2, Tpost 1–3; cloacal scute usually divided; AP usually 0, 1 on anterior D in some specimens; eyes large, pupil round.

The hemipenis of *Oxybelis fulgidus* is a slightly bilobed organ with a naked pedicel, spines on truncus large proximally and decreasing in size distally, and a calyculate apex.

Coloration in life. D and L surfaces unicolor green, separated by a narrow white, cream, or yellowish ventrolateral stripe from the lighter green to yellowish green V surfaces; iris yellow; tongue green.

Coloration in preservative. After 4.5–6 years in 70% ethanol, all green has turned to blue.

Natural history notes. Diurnal and arboreal, feeding on various vertebrates. Both SMF 89584 and 90205 were found dead on roads through semi-open secondary vegetation.

Remarks. SMF 89584 has 194 V and 3 postoculars on each side, which constitute the lowest V and highest Postoc counts reported for this species so far.

I was unable to trace any record that would substantiate the upper elevational limit of 1250 m asl in Panama (Perez-Santos 1999), though this elevation is well surpassed in neighboring Costa Rica, where the species has been documented to occur up to 1600 m (Savage 2002 and subsequent workers). The highest Panamanian record which I could find is from Fortuna (Myers 1977), my georeference of which yields a SRTM elevation of 1051 m, followed by a record without associated specimen from "Fortuna - 1000 m" (Perez-Santos 1999).

Phrynonax poecilonotus (Günther 1858)

Bird Snake, Bird-eating Snake, Mahogany Rat Snake, Northern Birdsnake, Puffing Snake; Culebra, Pajarera, Sabanera, Voladora

Figure 4.106A; Map 4.112.

Pseustes shropshirei: Taylor (1951, 1954); Peters & Orejas-Miranda (1970); Auth (1994); Perez-Santos (1999); Jadin et al. (2013); Uetz & Hošek (2014).

Pseustes poecilinotus: Jadin et al. (2013: Figs. 2 and 3).

Pseustes poecilonotus: Dunn & Bailey (1939); Evans (1947); Taylor (1951, 1954); Smith (1958); Myers & Rand (1969); Peters & Orejas-Miranda (1970: in part.); Rand & Myers (1990); Ibáñez et al. (1995; 1996, 1997, 2001); Perez-Santos & Martínez (1997); Perez-Santos (1999); Young et al. (1999); Carrizo (2000, 2010); Köhler (2001, 2008); Savage (2002); ANAM (2004, 2009b); Solórzano (2004); McDiarmid & Savage (2005); Montero (2005); Rodriguez et al. (2005); Fundación PA.NA.M.A. (2007); Santos-Barrera et al. (2008); Hamad (2009); Ray (2009); Savage & Bolaños (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010: in part.); Jadin et al. (2013); Köhler et al. (2013); McConnell (2014); Uetz & Hošek (2014: in part.).

Pseustes shropshiirei: Martínez & Rodriguez (1994); Martínez et al. (1995).

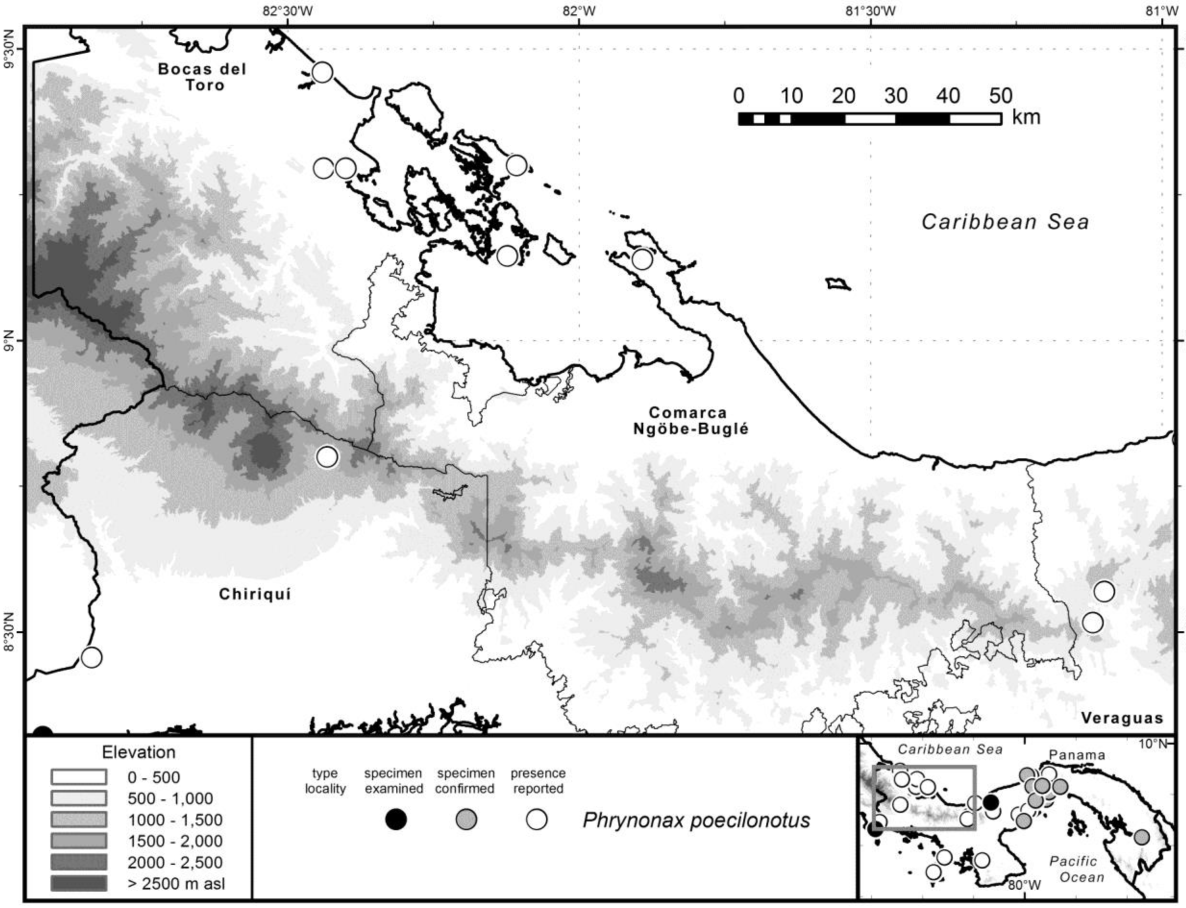
Phyrnonax pecilonotus shropshirei: Dunn (1933).

Spilotes chrysobronchus: Cope (1876).

Synchalinus corallioides: Cope (1893).

Lectotype. BMNH 1946.1.7.41, reportedly from Honduras but probably from Belize (= British Honduras; see remarks in McCranie 2011).

Geographic distribution. Honduras or Belize (or further northwest) to Panama, and probably to Colombia (or further into South America), 0–1610 m asl (see remarks). In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Boquete and Santa Fé areas, PNGDOTH, Valle de Antón, and PNAC, up to ca. 1230 m asl.



Map 4.112: Distribution of *Phrynonax poecilonotus.*

Diagnosis. This large snake (maximum TOL 2400 mm) with round pupils is very variable in coloration, but readily distinguished from all other Panamanian snakes by its 19–25 oblique rows of dorsals at midbody, of which only the upper ones are keeled and which are reduced to 13–15 one head length anterior to cloaca, in combination with its undivided cloacal scute.

Description. TOL to 2400 mm; SVL in Honduran specimens to 1306 mm; tail moderate, TL/TOL = 0.26–0.32; D keeled on upper rows (3–13 at midbody), in (19–21)—(19–25)—(13–15) oblique rows; V 181–220; SC 95–149; SPL 6–10; INL 11–14; loreal 1; Preoc 1; Postoc 1–3; Tant 1–2, Tpost 2–3; cloacal scute entire; AP 2; eyes large, pupil round.

The hemipenis of *Phrynonax poecilonotus* is a unilobed organ; pedicel and proximal half of truncus naked, distal half of truncus with numerous moderate and some enlarged spines, apex comprising about half of the organ's length, calyculate.

Coloration in life. Extremely variable; D and L surfaces yellow, orange, green, brown, or gray, uniform or with more or less contrasting spots, blotches, or crossbands; labials usually light-colored; V surfaces yellow to brown with dark markings or black; Juveniles yellow to orange with dark-edged brown bands and yellow to brown venters.

Coloration in preservative. Similar to that in life, apart from that all yellow, green, and orange tonalities fade to different shades of gray and/or brown over time.

Natural history notes. Diurnal, terrestrial and arboreal, feeding mainly on birds and mammals. Threat display similar to that of *Chironius* and *Spilotes,* with L neck flattening, hissing, and mouth gaping, easily culminating in strikes which are not feigned. Meike Piepenbring provided me with a series of photos showing how an adult individual on a fence at San Bartolo, western Chiriqí, finishes swallowing a bat in plain daylight.

Remarks. Jadin et al. (2013) showed the paraphyly of *Pseustes* and accordingly transferred *P. sulphureus* to *Spilotes* and all other species of *Pseustes* to the resurrected *Phrynonax.* Based on the position which samples from Ecuador, Brazil, and Suriname assumed in their phylogenetic tree, these authors considered *P. poecilonotus polylepis* to be a valid species, to which I fully agree. They moreover showed populations of what they called *Pseustes* sp./*Phrynonax* sp. from Honduras and Guatemala to be deeply divergent from their samples of *Phrynonax poecilonotus* from Honduras, Nicaragua, and Panama. However, since they did not include a single sample of *Phrynonax shropshirei,* which they also awarded full species status, I prefer to follow Savage (2002) in considering *P. shropshirei* (Barbour & Amaral 1924) a synonym of *P. poecilonotus* until solid evidence is published.

While Jadin et al. (2013) left no doubt about the distinctness of *Phrynonax poecilonotus* from both the northern *Phrynonax* sp. and the SA *P. polylepis,* they left the complete extent of the distributional range of the actual *P. poecilonotus* unclear, merely stating that it might be "broadly sympatric" with *Phrynonax* sp. and that it is geographically separated from *P. polylepis* "somewhere between western Panama and northern SA". Thus, I herein tentatively retain a SA distribution outside Colombia for *P. poecilonotus.* Based on SMF 92538 from

Costa Rica, Köhler et al. (2013) recently raised the highest documented elevation for this species to 1610 m asl.

Rhinobothryum bovallii **Andersson 1916**

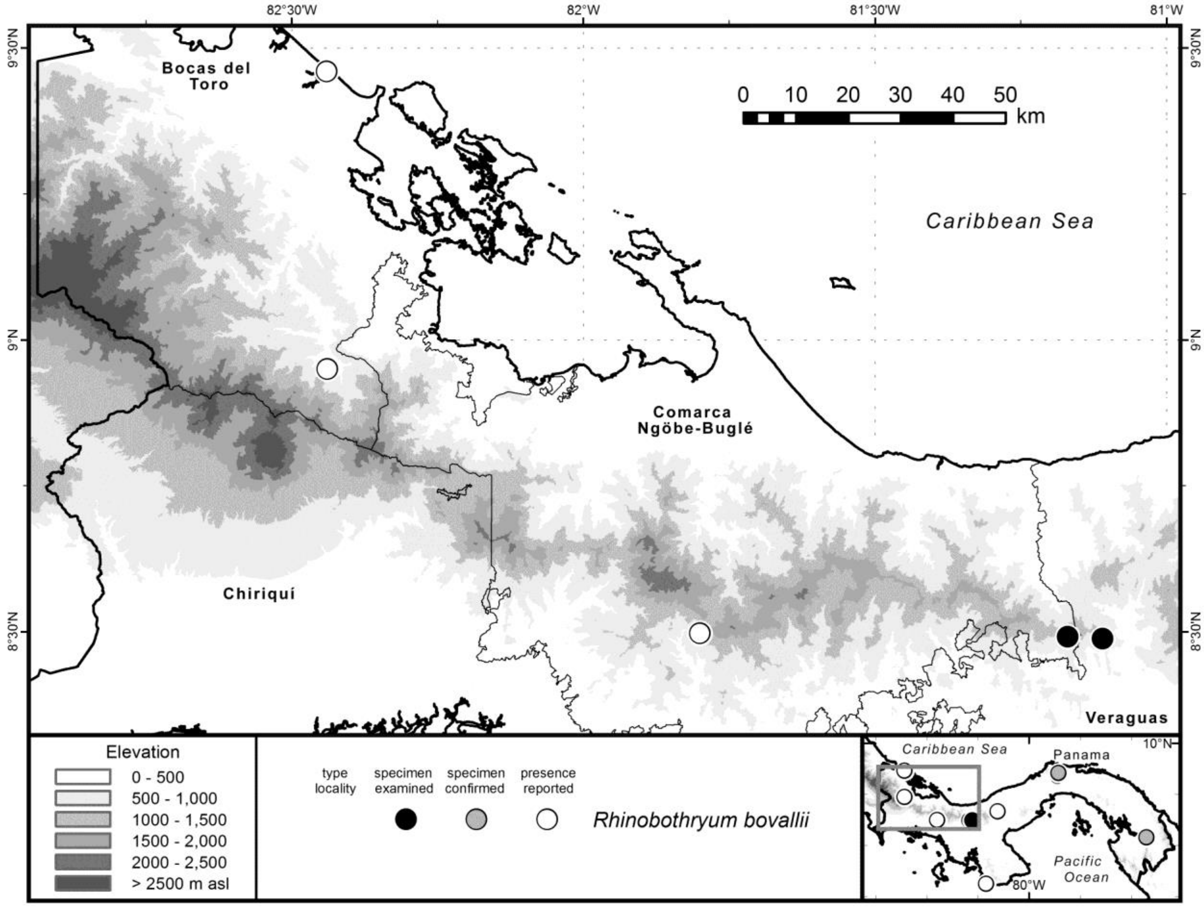
Northern Ringed Snake, False Tree Coral; Falsa coral, Cabeza de tortuga

Figure 4.106B; Map 4.113.

Rhinobothryum bovalli: Smith (1958).

Holotype. NHMG 1221, from Siquirres, Costa Rica.

Geographic distribution. Honduras to Ecuador, Colombia, and Venezuela, 0–1120 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from Culebra, the Cerro Colorado and Santa Fé areas, and PNGDOTH, up to ca. 1120 m asl.



Map 4.113: Distribution of *Rhinobothryum bovallii.*

Diagnosis. This large snake (maximum TOL 1762 mm) with vertically elliptical pupils is unique among Panamanian tricolor (red-white-black) ringed snakes in having all dorsal head plates black with light margins.

Description. TOL to 1762 mm; SVL to 898 mm*; tail moderate, TL/TOL = 0.22–0.27; D keeled on upper 5–9 rows (except on neck; keeling increasing posteriorly*), in (21–23)—(19–21)—(15–17) rows; V 239–246; SC 115–129; SPL 8; INL 10; loreal 1; Preoc 1; Postoc 2–3; Tant 2–3, Tpost 2–3; cloacal scute divided; AP 1–2; eyes large, pupil vertically elliptical.

The hemipenis of *Rhinobothryum bovallii* remains undescribed to my knowledge.

Coloration in life. Tricolor ringed pattern of mostly complete red-white-black-white rings with black and red rings broader than white ones and black mottling on the red D; D head plates black with narrow white, orange, or red margins.

The female SMF 91577 (Fig. 4.106B) was recorded as follows: Body with 13 complete, broad Crimson (108) rings, where most D scales bear a Jet Black (89) blotch on their posterior portion, and with 13 broad Jet Black (89) rings; the broad rings alternate with narrow (2-3 dorsals long) Cream Color (54) rings; on posterior portion of body two Jet Black (89) rings are broken up on one flank each by a L interconnection of the two neighboring Crimson (108) rings, respectively; tail with 7 Crimson (108) rings mottled as on body, and 7 Jet Black (89) rings, separated from each other by narrow Cream Color (54) rings; tip of tail Jet Black (89); V portions of all rings with the same color as respective ring but suffused with a milky white and thus appearing somewhat lighter; a Cream Color (54) neck band present; D surface of head Crimson (108), grading into Cream Color (54) mottled with Crimson (108) anteriorly and laterally; V surface of head Cream Color (54); all head plates, most D and L head scales, mental, first infralabials and adjacent chin scales with Jet Black (89) blotches; iris Jet Black (89) speckled with Drab-Gray (119D).

Coloration in preservative. After 4–6 years in 70% ethanol the coloration is similar to that in life, apart from that the all red has faded to light brown, and black portions are gray where the oberhäutchen have been lost.

Natural history notes. Nocturnal and apparently terrestrial as well as arboreal, thought to be a canopy species of primary forests by some authors (e.g., Savage 2002; Köhler 2008) and to be largely terrestrial by others (Solórzano 2004; Ray 2009). Feeding on lizards and other vertebrates. I encountered the specimen SMF 91577 at 22:10 while it was slowly moving over a tree about 5 m above a small creek. Once driven down from the tree, the snake first tried to escape by swimming down the creek, and later bit me when handled.

Remarks. The specimen SMF 90022 was collected by AC on Cerro Tute at 1116 m asl, which is well above the highest elevation of 860 m reported for Panama and the species as a whole (Jaramillo et al. 2010). Moreover, this specimen has 129 subcaudals, which is the highest number of SC reported so far for this species. Although *Rhinobothryum bovallii* is obviously present in Nicaragua, a verified record of the species is still pending. There seems to be a general paucity of records for this "rare" (Savage 2002) and "seldom-seen" (Köhler 2008) species, in a way that the two individuals collected by AC, AH, and myself bring the number of Panamanian specimens known to me to 10 (plus 3 records without voucher). I could not trace any record for Chiriquí but regard the presence of *R. bovallii* in this province, at least from the Fortuna depression eastwards, as plausible in view of the record from Cerro Colorado (USNM 297732) and the altitudinal distribution as documented herein.

Scaphiodontophis venustissimus **(Günther 1893)**

Coral Neckband Snake, Skinkeater, Neck-banded Snake, Shovel-toothed Snake; Falsa coral variable

Figure 4.106C; Map 4.114.

Scaphiodontophis annulatus: Auth (1994); Young et al. (1999); Ibáñez et al. (2001); Köhler (2001); Savage (2002); Solórzano (2004); McDiarmid & Savage (2005); Montero (2005); Fundación PA.NA.M.A. (2007); Santos-Barrera et al. (2008); McConnell (2014).

Scaphiodontophis sp.: Ray (2009).

Scaphiodontophis zeteki: Smith (1958); Perez-Santos (1999).

Sibynophis zeteki: Dunn (1930a).

Sibynophis venustissimus: Wettstein (1934); Dunn (1942).

Lectotype. BMNH 1946.1.1.35-36, from Nicaragua, Matagalpa, Hacienda Rosa de Jerico, 3250 feet (= ca. 991 m).

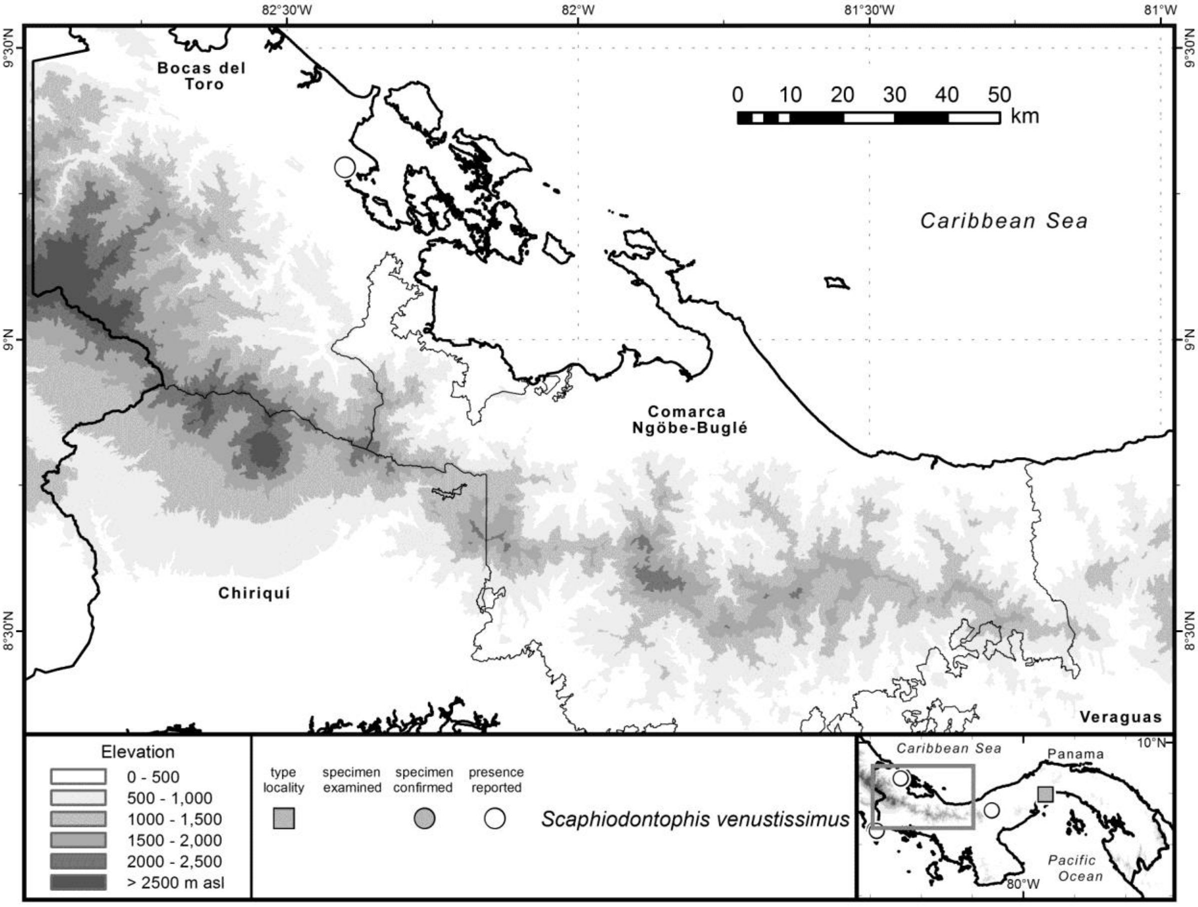
Geographic distribution. Eastern Honduras to Colombia, 0–1300 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNGDOTH at 800 m asl.

Diagnosis. This medium-sized snake (maximum TOL 920 mm) with round pupils is unique among Panamanian snakes in having a tricolor pattern (red-yellow-black-yellow) of usually at least partly irregular and/or offset bands that do not cross the venter sometimes giving way to brownish non-banded coloration posteriorly, and smooth dorsals in 17—17—17 rows.

Description. TOL to 920 mm; SVL in Honduran specimens to 400 mm; tail long, TL/TOL = 0.33–0.49, but fragile and often incomplete; D smooth, in 17—17—17 rows; V 125–156; SC 92–121; SPL 9; INL 10; loreal 1; Preoc 1; Postoc 2; Tant 1–2, Tpost 2–3; cloacal scute divided; AP 0; eyes moderate to large, pupil round.

The hemipenis of *Scaphiodontophis venustissimus* is a unilobed organ; pedicel with small spines, truncus with large basal hooks followed by large spines decreasing in size distally, apex with papillate calyces.

Coloration in life. Very variable; adults usually with a black snout and a tricolored pattern of somewhat irregular, often assymmetrically offset bands (red-yellow-black-yellow) that do not extend across venter and may be interrupted or giving way to a unicolor or mottled brown portion posteriorly; juveniles with white snout; young juveniles with melanistic red bands; V surfaces yellow to brown, unicolor or mottled; SC with dark blotches except in very young specimens; iris brown.



Map 4.114: Distribution of *Scaphiodontophis venustissimus.*

Coloration in preservative. Similar to that in life, apart from that the yellow bands fade to white and the red bands fade to brown.

Natural history notes. Diurnal and terrestrial to semifossorial, preying chiefly on skinks of the genus *Scincella,* which are rapidly swallowed alive with the aid of the shovel-like teeth, and other lizards.

Remarks. Mainly based on differences in color pattern and subcaudal numbers, McCranie (2006b) removed the populations from E Honduras southward from the synonymy of *Scaphiodontophis annulatus.*

Spilotes pullatus **(Linnaeus 1758)**

Oriole Snake, Tiger Ratsnake, Tropical Chicken Snake, Tropical Ratsnake, Tiger Tree Snake; Mica, Ratonera, Javá, Zumbadora, Iguanera, Zopilote

Figure 4.106D; Map 4.115.

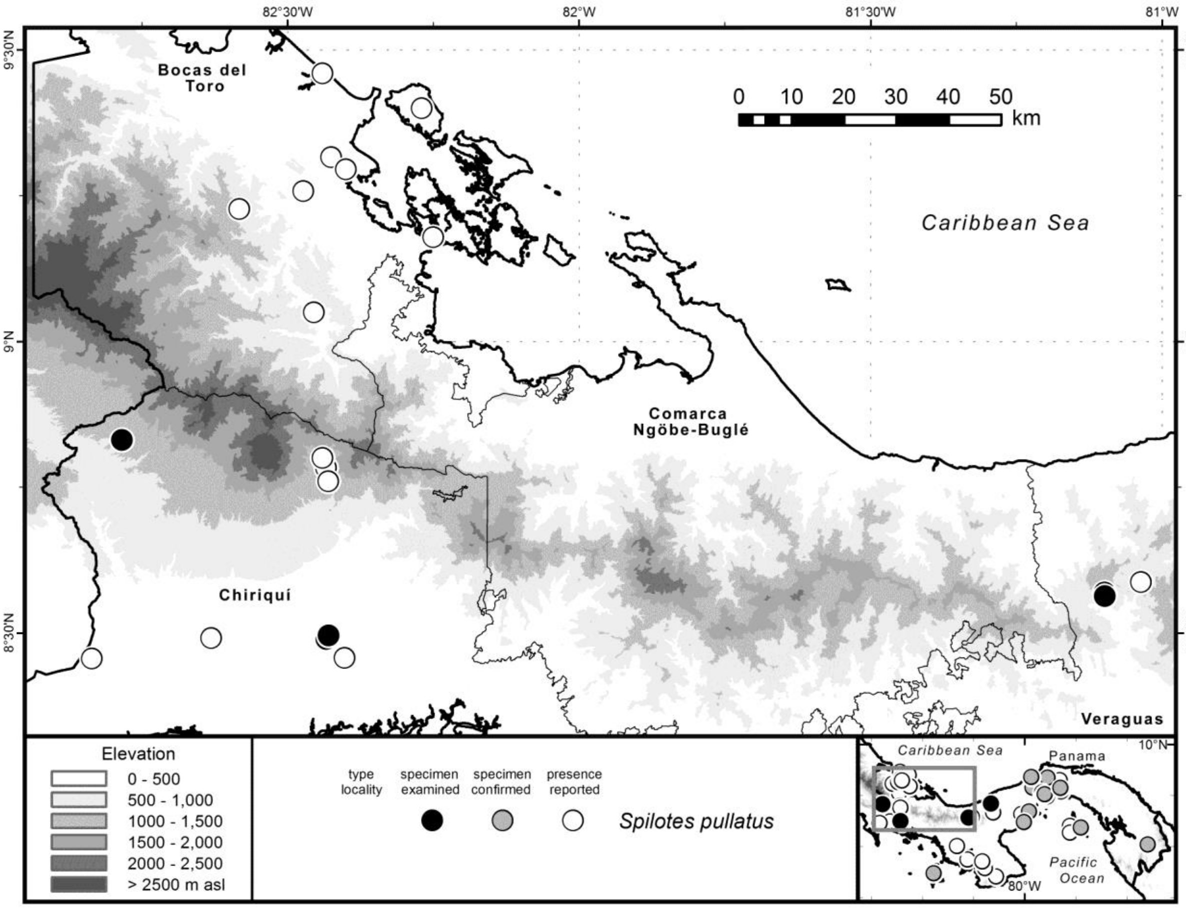
Spilotes megalolepis: Boulenger (1894).

Spilotes salvinii: Barbour (1906).

Spilotes variabilis: Peters (1859).

Holotype. LinnMus 40, from Asia (in error).

Geographic distribution. Mexico to Ecuador and Argentina, 0–1500 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Río Changuinola drainage, Santa Clara, the Boquete and Santa Fé areas, PNGDOTH, and PNAC, up to ca. 1320 m asl.



Map 4.115: Distribution of *Spilotes pullatus.*

Diagnosis. This large snake (maximum TOL 2650 mm) with round pupils is readily distinguished from all other Panamanian snakes by its contrasting black and white or yellow coloration and its keeled dorsals arranged in an even number of nonoblique rows at midbody.

Description. TOL to 2650 mm; SVL to 1830 mm*; tail moderate, TL/TOL = 0.24–0.28; D keeled, in (14–20)—(14–18)—(10–14) rows; V 198–241; SC 100–142; SPL 6–9; INL 6–10; loreal 0–1; Preoc 1–2; Postoc 1–2; Tant 0–1, Tpost 1–2; cloacal scute entire; AP 2; eyes moderate, pupil round.

The hemipenis of *Spilotes pullatus* is a unilobed organ with a short naked pedicel, moderately-sized spines around the truncus, and papillate calyces on the distal half.

Coloration in life. Variably banded, blotched, or striped with black and white and/or cream or yellowish; black bars on some to all labial sutures; in Panamanian examples which I have seen the lighter tonalities are largely restricted to the head and anterior portions of body, while posterior portions of body and the tail are almost or entirely black.

The male SMF 89600 was recorded as follows: D and L surfaces Jet Black (89), on anterior half of body very sparsely mottled with Cream Color (54) showing shadings of Sulphur Yellow (57); D surface of head with irregular, broken, transverse bands of Cream Color (54), grading into dirty white with a suggestion of Sulphur Yellow (57) laterally; V surface of head Jet Black (89) with Sulphur Yellow (57) mottling partly continuing the L bands; V surfaces of body and tail Jet Black (89) with whitish iridescence; V surface of anterior half of body with transverse bands of Sulphur Yellow (57), increasing towards the head in number and intensity of Trogon Yellow (153) shadings, which are present especially in the centers of the respective ventrals.

Coloration in preservative. Similar to that in life, apart from that the yellow fades to cream.

Natural history notes. Diurnal, arboreal and terrestrial, feeding on mammals and other vertebrates. Threat display similar to that of *Chironius* and *Phrynonax,* with L neck flattening, hissing, and mouth gaping, easily culminating in strikes. The large male SMF 89600 (SVL 1830 mm + TL 509+x mm = TOL 2439+x mm) caught the attention of AH around 15:00 when it dropped into a bush during a thus failed attemt to reach a bird's nest on the branch of a "living fence" tree above the bush. The juvenile SMF 89788 from Santa Clara crossed a small creek around noon, as did an uncollected large specimen at Cerro Negro around 13:00. Another uncollected specimen from near Los Algarrobos was encountered at 02:30 sleeping on a tree about 4 m above ground. This very light-colored animal had 26 ticks attached mainly on the anterior portions of its body, SMF 89600 had 8 after an unknown number had let go.

Remarks. Many people in Los Algarrobos and elsewhere in western Panama know "La Mica", which is usually acknowledged to be nonvenomous and even beneficial eating rodents. My georeference for the records from "vicinity N of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is somewhat above the elevational maximum given as

1200 m for Panama (Jaramillo et al. 2010) and appears plausible in view of the 1435 m given by recent authors for Costa Rica (Savage 2002; Sasa et al. 2010).

***Stenorrhina degenhardtii* (Berthold 1845)**

Degenhardt's Scorpion-eating Snake, Degenhardt's Scorpion-eater, Southern Scorpion-eater; Alacranera, Alacranera sureña

Figure 4.106E; Map 4.116.

Stenorhina degenhardtii: Cope (1871, 1876: both in part.; 1899); Wettstein (1934); Dunn & Bailey (1939); Slevin (1942); Dunn (1947); Evans (1947).

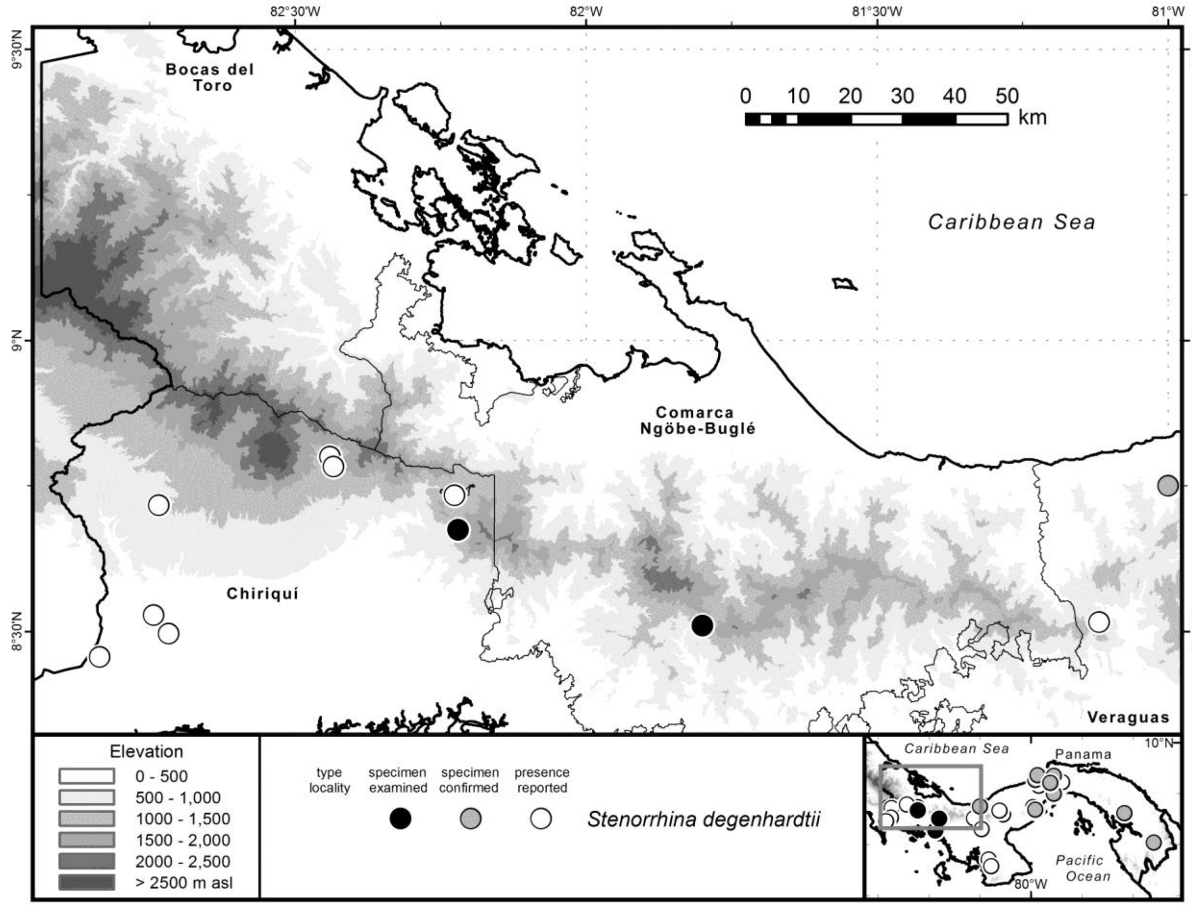
Stenorrhina freminvillei: Uetz & Hošek (2014: in part., referring to Panama).

Stenorrhina freminvillii: Peters & Orejas-Miranda (1970: in part., referring to Panama); Auth (1994); Martínez & Rodriguez (1994); Perez-Santos (1999); Rodriguez et al. (2005)

Stenorrhina degenhardti: Smith (1958); Perez-Santos (1999).

Stenorrhina ventralis: Cope (1871, 1876).

Holotype. ZFMK 36828, no precise locality (Neu-Granada and/or Provinz Popayan implied in original publication).



Map 4.116: Distribution of *Stenorrhina degenhardtii.*

Geographic distribution. Mexico to Peru, Colombia, and Venezuela, 0–1900 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites along the Pacific versant up to ca. 1320 m asl.

Diagnosis. This medium-sized snake (maximum TOL 800 mm) with round pupils is unique among Panamanian snakes in having a flattened snout, no loreal, and each internasal fused to the adjacent anterior nasal.

Description. TOL to 800 mm; SVL in Honduran specimens to 658 mm; tail short to moderate, TL/TOL = 0.12–0.25; D smooth, in 17—17—17 rows; V 136–174; SC 30–50; SPL 6–7; INL 7–9; loreal 0, PF contacting SPL; Preoc 1; Postoc 1–2; Tant 1–2, Tpost 1–3; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Stenorrhina degenhardtii* is a long, unilobed organ; pedicel naked, truncus with enlarged basal hooks and small spines distally, apex calyculate.

Coloration in life. D and L surfaces gray to brown or reddish brown, unicolor or with darker mottling or large, light-edged dark middorsal and smaller L blotches; V surfaces cream to light brown, immaculate or with darker mottling, blotches, or median stripe.

The specimen AH 563 (Fig. 4.106E) was recorded by a member of AH's field party in 2013 as follows (modified from field notes of AH): Base color brown, with large darker brown D blotches 2–3 scales long and 5–6 scales wide bordered with drab; flanks drab with irregular darker brown mottling and blotches; V surfaces cream, posterior to neck with brown flecks increasing in number posteriorly; iris chestnut, tongue raw umber.

Coloration in preservative. Similar to that in life, apart from that reddish hues that may have been present fade.

Natural history notes. Diurnal, terrestrial and semifossorial, feeding primarily on scorpions and spiders. The specimen AH 563 was found active at daytime.

Remarks. The specimen MVUP 304 has 6 SPL on the right side of the head, which is the lowest value reported for this species so far.

The occurrence in Bocas del Toro is rendered plausible by lowland records east and west of this province (e.g., Evans 1947; Savage 2002) and by the distance of less than 5 km between the border to Bocas and the records from "vicinity N of Boquete" (Perez-Santos 1999). My georeference for the latter locality yields a SRTM elevation of 1323 m asl, which is somewhat above the elevational maximum given as 1200 m for Panama (Jaramillo et al. 2010) and appears plausible in view of the 1600 m given by Sasa et al. (2010) for Costa Rica.

All records of *Stenorrhina freminvillii* from Panama (Peters & Orejas-Miranda 1970; Auth 1994; Uetz & Hošek 2014), where it has been reported from Fortuna and localities in central and eastern Panama (Perez-Santos 1999: p. 221, although stating that only *S. degenhardtii* occurs in Panama), from the Santa Fé area (Martínez & Rodriguez 1994), and from Reserva Forestal El Montuoso (Rodriguez et al. 2005) are based on misidentified, probably unicolored specimens of *S. degenhardtii* according to Savage (2002).

Tantilla alticola **(Boulenger 1903)**

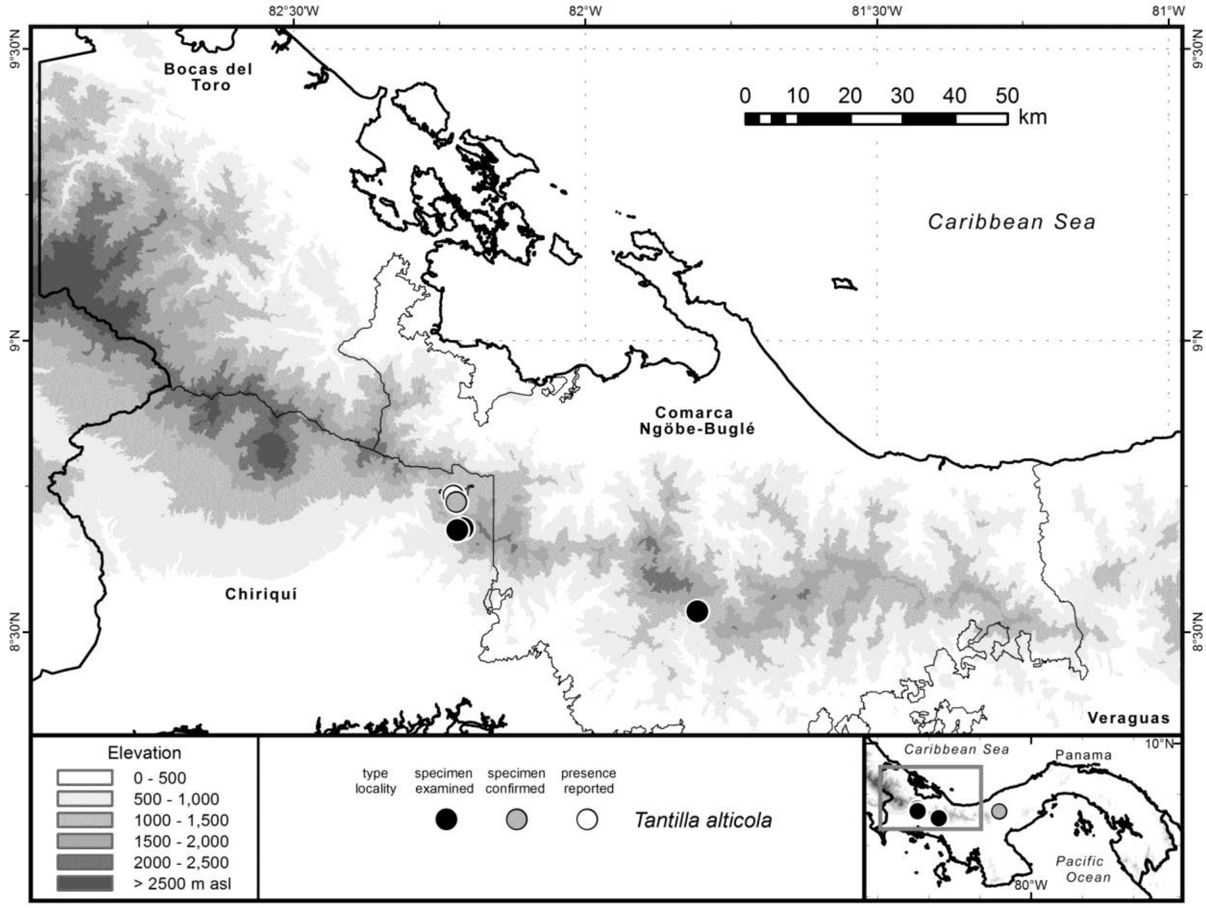
Boulenger's Centipede Snake; Brown Crowned Snake; Culebra, Hojarasquera, Cabeza plana café

Figure 4.106F; Map 4.117.

Tantilla costaricensis: Taylor (1954).

Syntypes. BMNH 1946.1.8.63–65, from from Santa Rita, north of Medellin, Colombia, 9000 ft (ca. = 2743 m asl).

Geographic distribution. Nicaragua to Colombia, 40–2740 m asl. In Panama, exclusively reported from the Cordillera Central at the Fortuna and Cerro Colorado areas as well as PNGDOTH, 740–1600 m asl.



Map 4.117: Distribution of *Tantilla alticola.*

Diagnosis. This small snake (maximum TOL 340 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla alticola* differs from its Panamanian congeners in lacking contrasting longitudinal stripes and in having immaculate yellow to red ventral surfaces (whitish in juveniles) in combination with a light nuchal band separating the dark dorsal head coloration from a diffuse dark neckband, light pre- and postocular blotches, and a light-colored snout.

Description. TOL to 340 mm; SVL in Panamanian specimens to 274 mm; tail moderate, TL/TOL = 0.17–0.27; D smooth, in 15—15—15 rows; V 128–150; SC 32–60; SPL 6–7; INL 6; loreal 0, PF in contact with SPL or excluded by contact between nasal and Preoc; Preoc 1; Postoc 2; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes small, pupil round (including data of Castillo et al. 1990 and Myers et al. 2013).

The hemipenis of *Tantilla alticola* remains undescribed. The partially everted hemipenis of SMF 79899 from Nicaragua is a slender unilobed organ with a spinulate pedicel that bears small spines along the sulcus spermaticus and numerous large hooks on the remaining surfaces of the distalmost everted portion.

Coloration in life. D and L surfaces of body and tail brown, unicolor, becoming darker posteriorly, and/or with a faint light vertebral and/or L stripe; D surface of head dark brown to black, snout area lighter; a similarly dark, more or less diffuse neck band posterior to a light nuchal collar that involves tips of parietals; a large light postocular blotch, and a smaller light preocular blotch, both including SPL; V surfaces immaculate yellow, orange, or red; juveniles with a much more contrasting pattern on head and nuchal area, and white or cream V surfaces.

The female SMF 91582 (Fig. 4.106F) was recorded as follows: D ground color Warm Sepia (221A), grading into Walnut Brown (221B) laterally and into Sepia (219) towards tail; a faint suggestion of a Walnut Brown (221B) vertebral stripe extending from shortly behind head to base of tail; D surface of head Dusky Brown (19) except for Walnut Brown (221B) nuchal collar (tips of parietals and first two D), prefrontals and internasals; a Salmon Color (106) blotch posterior to orbit; V surface of head Light Russet Vinaceous (221D), connecting to nuchal collar and nostril; rostral Dusky Brown (19); V surfaces of body and tail Buff Yellow (53) with a suggestion of Olive-Yellow (52); iris Jet Black (89); tongue Blackish Neutral Gray (82), tips of tongue dirty white with a suggestion of Pearl Gray (81).

The hatchling SMF 91583 was recorded as follows: D and L ground color Mars Brown (223A), grading into Dark Neutral Gray (83) on posterior half of body and tail; a weakly suggested Sayal Brown (223C) vertebral stripe barely discernible from neck to midbody; two L stripes of the same color on second and fourth D row even less discernible; V surfaces Drab

Gray (119D), grading into Pearl Gray (81) on posterior portion of body and tail; D and L surfaces of head Sepia (119); snout, lips, and lower postocular region Cream Color (54); sutures on snout Sepia (119); a Cream Color (54) nuchal collar comprising posterior tips of parietals, second Temporals, and one or two D scales posterior to these, bordered posteriorly by a Sepia (119) neck band that grades into D ground color over the next four D scale rows; a Sepia (119) spot on the median D scale adjacent to parietals; iris Jet Black (89).

Coloration in preservative. After 4 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that yellow elements have faded to white.

Natural history notes. Terrestrial and semifossorial, presumably feeding on invertebrates. Individuals are usually found under rocks, dead wood, or in the leaf litter. The female SMF 91582 was discovered by AH under a log at 11:00. I found the two eggs containing SMF 91583 and MHCH 2369 on 09.07.2010 under a rock lying on the grassy side-strip of the dirt road from Cerro Colorado to Ratón. Both eggs were secured and incubated at ambient temperature in Los Algarrobos at 141 m asl. MHCH 2369 was the first to hatch and discovered at 11:00 on 10.08.2010, but died a few hours later while we were on the way to La Fortuna. After we had arrived at the Lost & Found Ecohostel, SMF 91583 hatched the same day around 15:00 and was preserved the next day. Upon hatching, the smaller SMF 91583 measured 80 + 18 = 98 mm, and the larger MHCH 2369 85 + 19 = 104 mm.

Remarks. The records from E and W of Veraguas render the presence of *Tantilla alticola* in this province plausible. The hatchlings from the road to Ratón were collected at 1600 m asl, which is 400 m above the highest elevation documented for Panama (MVUP 1123–4 according to Castillo et al. 1990 and Solís 1991; Jaramillo et al. 2010).

Castillo et al. (1990) provided the maximum size of 340 mm TOL for this species, which was subsequently overlooked by other authors. SMF 91582 and MHCH 2369 bear the barely discernible suggestion of a single "subapical" pit on the D scales of the anterior third of their bodies. The venters of both adult specimens from Fortuna which I have seen (SMF 91582 and an individual from near Río Hornito photographed by Robert Maurer) were bright yellow in life, while Savage (2002) describes the V surfaces of Costa Rican specimens as "bright red", and Myers et al. (2013) state the venter their specimen from PNGDOTH to have been "orange red that darkened towards the tail".

Tantilla alticola is likely to be, and has repeatedly been, confused with its most similar congener, *T. schistosa* (see Savage 2002: p. 696 and references therein). The difference in SC numbers between these species stated by Savage (2002: 42 or more in *T. alticola* vs. 42 or fewer in *T. schistosa*) do not seem to hold in light of the minimum number of SC given as 32 for *T. alticola* by Köhler (2008), provided that the latter value is correct.

Tantilla armillata **(Cope 1876)**

Centipede Snake, Black-necked Crowned Snake; Culebra, Hojarasquera, Cabeza plana de cuello negro

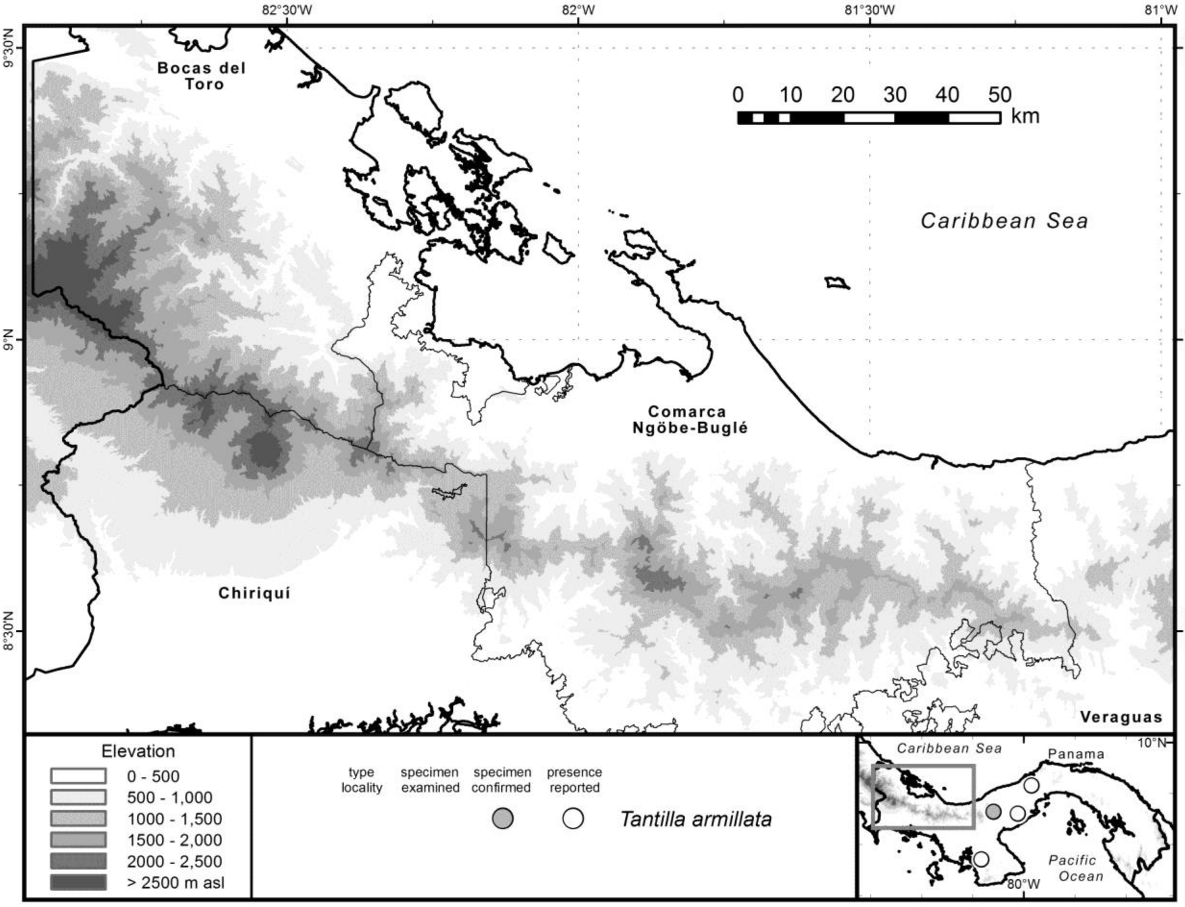
Figure 4.106G; Map 4.118.

Tantilla melanocephala: Cope (1871), Auth (1994: in part.); Ibáñez et al. (1995: possibly, 1996: possibly); Perez-Santos (1999: in part.); Young et al. (1999: in part.); Köhler (2001: in part.); Fundación PA.NA.M.A. (2007: in part.); Ray (2009); Jaramillo et al. (2010: in part.).

Tantilla ruficeps: Ibáñez et al. (2001: in part.)

Holotype. ANSP 3363, from "Middle Costa Rica" (Cope 1876).

Geographic distribution. Guatemala to Panama, 0–1435 m asl. In Panama, along the Pacific versant of western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, east to Coclé or the canal. In the Cordillera Central, reported from PNGDOTH, 380–800 m asl.



Map 4.118: Distribution of *Tantilla armillata.*

Diagnosis. This small snake (maximum TOL 490 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla armillata* differs from its Panamanian congeners by its very dark head cap bearing a pair of light parietal spots and extending well onto neck, is followed by a light nuchal collar that is narrowly interrupted by the dark middorsal stripe. It further differs from the similar *T. ruficeps* in having 155 or more ventrals in males and 158 or more in females (vs. 148 or fewer in males and 156 or fewer in females).

Description. TOL to 490 mm; SVL in Honduran specimens to 234 mm; tail moderate, TL/TOL = 0.15–0.23; D smooth, in 15—15—15 rows; V 155–177; SC 42–65; SPL 5–8; INL 4–7; loreal 0, PF in contact with SPL or excluded by contact between nasal and Preoc; Preoc 1; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Tantilla armillata,* presumably a unilobed organ, lacks basal hooks but has a spinulate truncus and the apical area covered with papillate calyces.

Coloration in life. Dorsum brown, with a dark middorsal stripe connecting to the head cap and usually a dark-edged light L stripe; head cap blackish brown to black, extending 3 or more D scale rows onto neck; posteriorly adjacent light collar interrupted medially by the dark middorsal stripe; a pair of light spots on posterior portion of parietals; light preocular, postocular, and supralabial blotches as well as light area on rostral and/or internasals usually present; V surfaces immaculate white to brownish.

Coloration in preservative. Similar to that in life.

Natural history notes. Terrestrial and semifossorial, probably feeding on invertebrates and usually found under cover. Knight et al. (2012) reported a female carrying two eggs.

Remarks. Together with the occurrence at premontane elevations in Pacific Costa Rica (Savage 2002; Solórzano 2004), the record from PNGDOTH (Knight et al. 2012) renders the occurrence of this species in my study area and all three political subdivisions along its Pacific drainage plausible.

Savage (2002) resurrected *Tantilla armillata* from the synonymy of *T. melanocephala* and gave Costa Rica as the southern limit of its distribution. In consequence, the species was not listed for Panama by subsequent authors (Köhler 2008; Jaramillo et al. 2010). However, the animal from Reserva Forestal El Montuoso pictured by Rodriguez et al. (2005) as *Tantilla* sp. and considered "close to *T. armillata*" by these authors shows all the characteristics mentioned as diagnostic for this species, and almost perfectly resembles the animal pictured, by Savage (2002: p. 693–4 and plate 453). Moreover, Knight et al. (2012) reported on the reproduction of a specimen from just S of PNGDOTH, which they identified as *T. armillata* using the diagnosis of Savage (2002). Based on these two records, I regard this species to range well into Pacific western Panama. Yet, it remains to be clarified which of the numerous records of *T. armillata, T. melanocephala,* and *T. ruficeps* from western and central Panama are actually referable to *T. armillata,* and which to *T. ruficeps.* This uncertainty applies, for example, to the record of *T. armillata* from Barro Colorado Island (Rand & Myers 1990; plotted on Map 4.118), the specimen CHP 3335 (listed as *T. melanocephala* in the CHP catalogue; plotted on Map 4.118), and the records of *T. melanocephala* from PNAC and PN Chagres (Ibáñez et al. 1995, 1996; plotted on Map 4.120) and Progreso (UMMZ 58423 according to Perez-Santos 1999; plotted on Map 4.120). Apart from some MCZ and FMNH specimens examined by GK and identified as *T. ruficeps*, I somewhat arbitrarily assigned the specific names *T. armillata* and *T. ruficeps* to records of *T. melanocephala* from west of the canal, all of which require verification.

Since GK also identified several MCZ and FMNH specimens catalogued as *T. melanocephala* from eastern Panama as *T. ruficeps*, I have doubts concerning the occurrence of *T. melanocephala* in Panama, but retain it in my country list until otherwise demonstrated. By any means, since the taxonomy and distribution of these three species throughout Panama is unsatisfactorily resolved and a thorough study sorely needed, the distributional information presented herein for *T. armillata* and *T. ruficeps* should be regarded as very tentative and will probably be subject to corrections in the future.

***Tantilla reticulata* (Cope 1860)**

Lined Crowned Snake, Reticulate Centipede Snake, Reticulated Crowned Snake; Culebra, Hojarasquera, Cabeza plana rayada

Figure 4.106H; Map 4.119.

Tantilla virgata: Wettstein (1934); Taylor (1951, 1954).

Holotype. ANSP 3361, apparently lost, from "Cocuyas de Veraguas, New Grenada" (Cope 1860c).

Geographic distribution. Nicaragua to Colombia, 0–1430 m asl. In Panama, along the Caribbean versant including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas in the western, and presumably both versants in the central and eastern portions of the country. In the Cordillera Central, reported from Yorkín in western Bocas del Toro at 850 m asl.

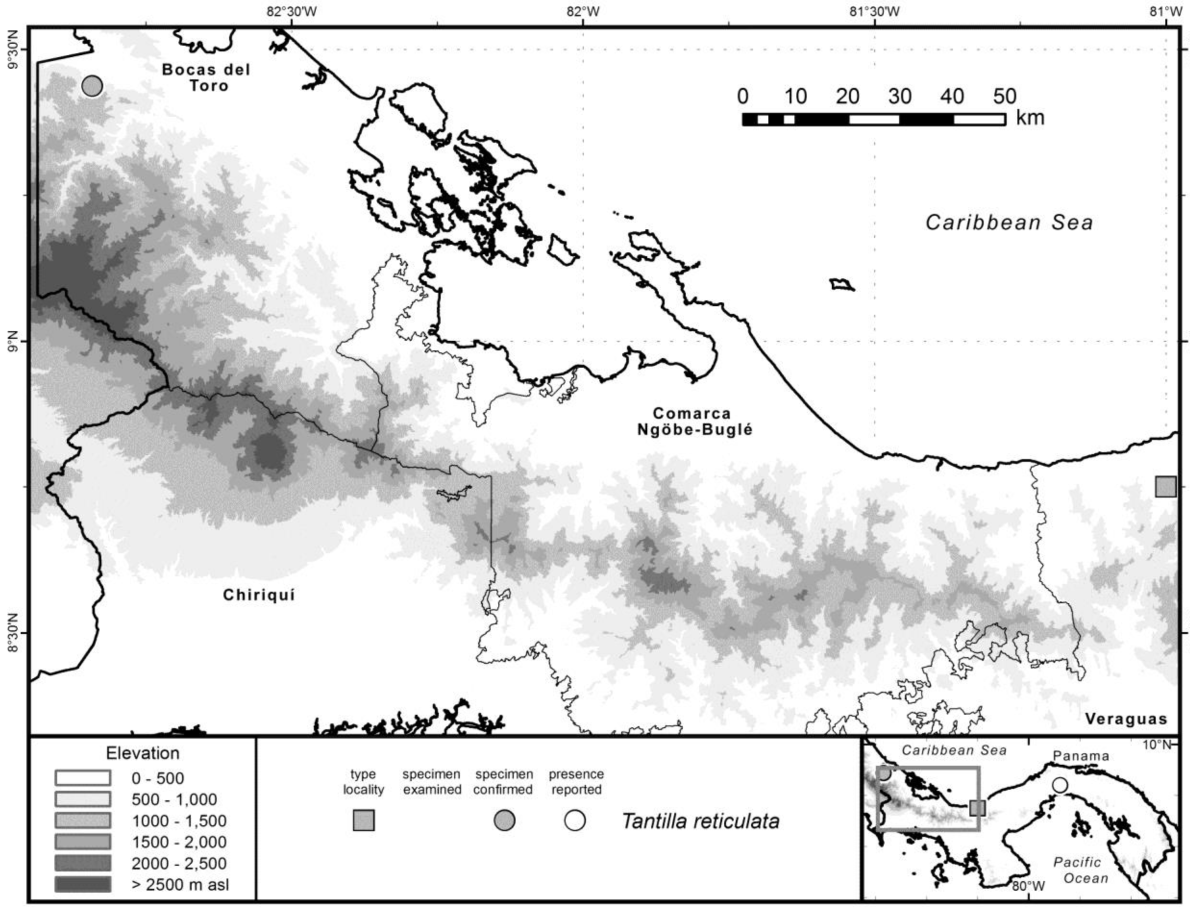
Diagnosis. This small snake (maximum TOL 312 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla reticulata* is readily distinguished from its Panamanian congeners by its contrasting pattern of alternating light and dark stripes including a light middorsal stripe, in combination with its light nuchal collar that is broadly interrupted medially.

Description. TOL to 312 mm; tail moderate, TL/TOL = 0.21–0.24; D smooth, in 15—15—15 rows; V 158–173; SC 58–70; SPL 5–8; INL 4–7; loreal 0, PF in contact with SPL or excluded by contact between nasal and Preoc; Preoc 1; Postoc 2; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Tantilla reticulata* is a short unilobed organ with numerous hooks.

Coloration in life. D and L surfaces of body and tail with a striped pattern including a broad light middorsal stripe and 2–3 narrow dark stripes per side, often with a reticulate pattern owing to dark scale margins in light-colored areas; head cap light brown bordered by dark posteriorly, not extending posterior to parietals, followed by a broad light nuchal collar that is broadly interrupted medially and bordered by dark posteriorly; V surfaces immaculate yellow except for dark pigmentation forming a ventrolateral stripe along outer edges of V.

Coloration in preservative. Similar to that in life.



Map 4.119: Distribution of *Tantilla reticulata.*

Natural history notes. Terrestrial and semifossorial, probably feeding chiefly on invertebrates. Solórzano et al. (2012) published photos of the Panamanian specimen MVUP 1988 swallowing a comparably large centipede of the genus *Scolopocryptops,* which was wider than the snake's body.

Remarks. The presence of *Tantilla reticulata* in my study area is documented by the record from Yorkín (Solórzano et al. 2012). The confirmed records from E and W of the Comarca Ngöbe-Buglé render the species' occurrence therein plausible.

Tantilla ruficeps (Cope 1894)

Orange-bellied Crowned Snake, Striped Crowned Snake; Culebra, Hojarasquera, Cabeza plana lineada

Map 4.120.

Homalocranium fuscum: Barbour (1906).

Pogonaspis ruficeps: Cope (1894).

Tantilla armillata: Taylor (1954: in part., referring to KU 31960),

Tantilla melanocephala: Cope (1871), Auth (1994: in part.); Ibáñez et al. (1995: probably, 1996: probably); Perez-Santos (1999: in part.); Köhler (2001: in part.); Young et al. (1999: in part.); Fundación PA.NA.M.A. (2007: in part.).

Holotype. AMNH 17272, from "Jimenez", Costa Rica (Cope 1894).

Geographic distribution. Nicaragua to Panama, 0–1600 m asl. In Panama, along the Pacific versant of western and eastern portions of the country including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and both versants in central Panama. In the Cordillera Central, reported from Palo Santo and PNAC, up to ca. 1340 m asl.

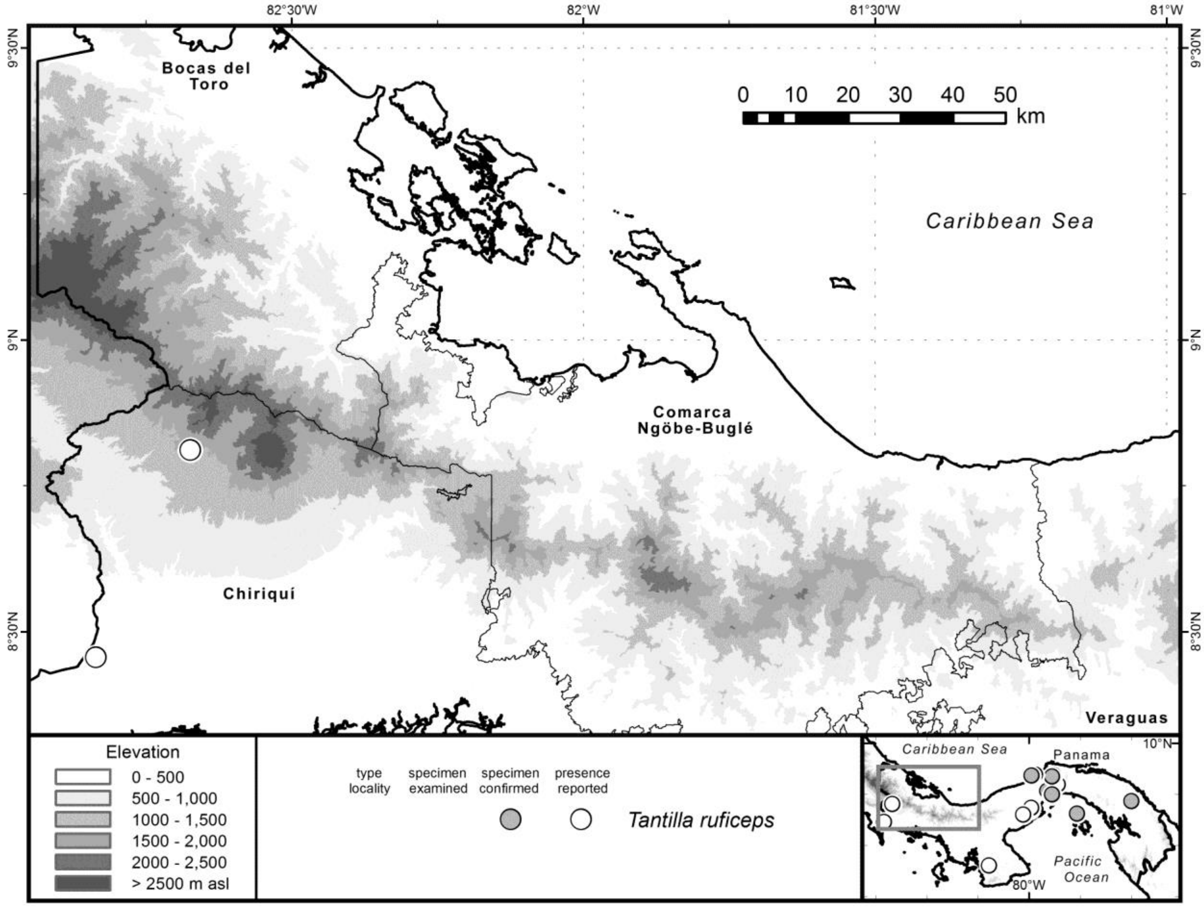
Diagnosis. This small snake (maximum TOL 500 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla ruficeps* differs from its Panamanian congeners by its red venter, its dark middorsal stripe in combination with a light lateral stripe bordered below by a dark stripe, and its reduced or absent light nuchal collar posterior to a head cap that does not extend onto neck. It further differs from the similar *T. armillata* in having 148 or fewer ventrals in males and 156 or fewer in females (vs. 155 or more in males, 158 or more in females).

Description. TOL to 50 mm; tail moderate, TL/TOL = 0.23–0.31; D smooth, in 15—15—15 rows; V 139–156; SC 59–83; SPL 7; INL usually 6; loreal 0, PF usually in contact with SPL, sometimes excluded by contact between nasal and Preoc; Preoc 1; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Tantilla ruficeps* is a moderate-sized, unilobed organ with basal hooks.

Coloration in life. D and L surfaces of body and tail brown, with a narrow dark middorsal stripe and 1–2 variably dark-edged light L stripes (at least 1 bordered by dark below); head cap brown, not extending onto neck, often bordered posteriorly by light L and/or dorsolateral areas that appear like remnants of a light nuchal collar, which is never continuous; often with the indication of a dark nuchal band; most of SPL light-colored or with light pre- and postocular spots; small light nuchal spots, if present, usually posterior to parietals; V surfaces whitish anteriorly, red posteriorly, with dark markings on L portions of V possibly forming longitudinal stripes.

Coloration in preservative. Probably similar to that in life, apart from that the reddish shades can be expected to fade with time.



Map 4.120: Distribution of *Tantilla ruficeps.*

Natural history notes. Diurnal and crepuscular, terrestrial and semifossorial, feeding primarily on invertebrates. Solórzano (2004) published a photo of an individual swallowing a comparably large *Scolopendra.*

Remarks. My georeference for the specimen KU 75758 from "Finca Palo Santo, 6 km WNW El Volcan" yields an SRTM elevation of 1343 m asl which is close to the highest elevation of 1370 m reported for Panama (Jaramillo et al. 2010). The occurrence of this species in the Comarca Ngöbe-Buglé is rendered plausible by the records from both E and W of it.

Concerning the unresolved taxonomy of Panamanian *Tantilla* populations variously referred to as *T. armillata, T. melanocephala,* or *T. ruficeps,* , see remarks for *T. armillata.*

Tantilla schistosa (Bocourt 1883)

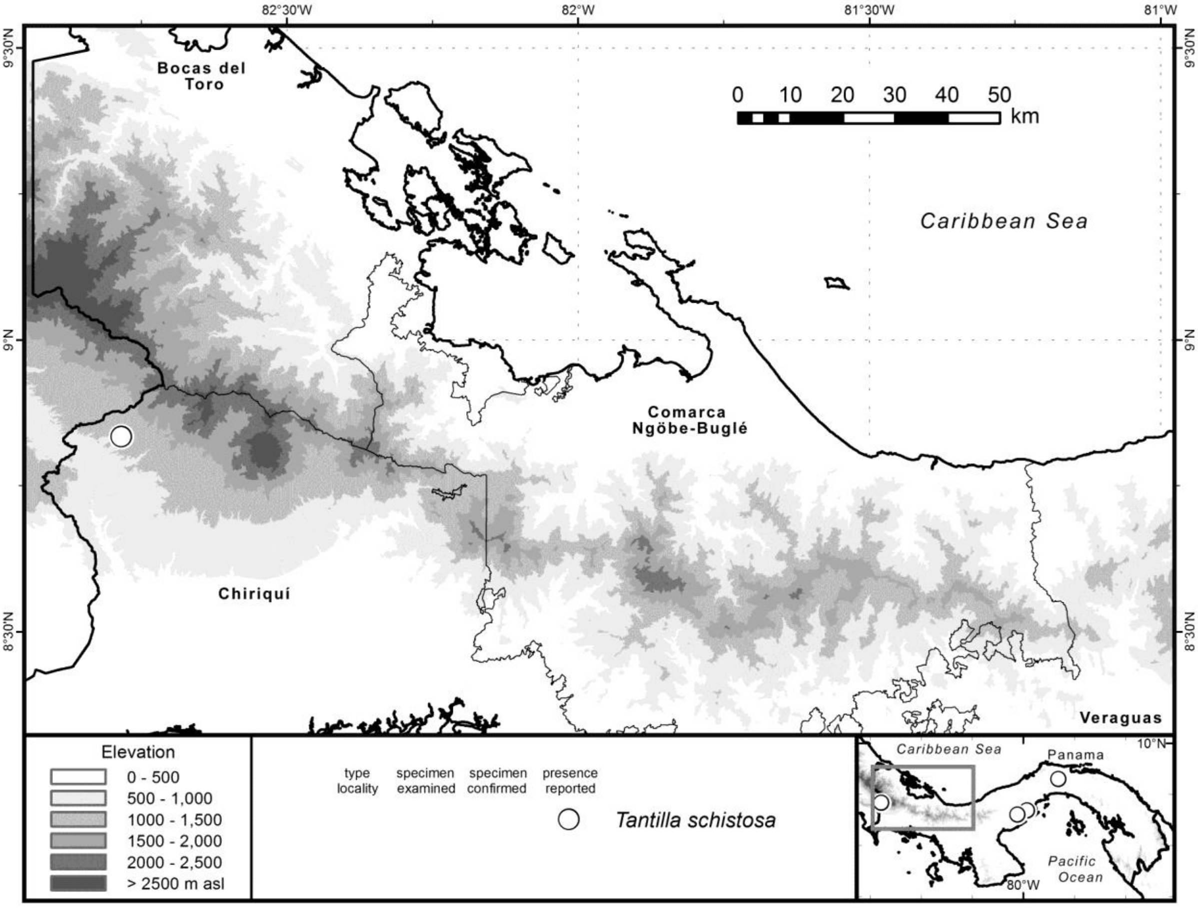
Collared Crowned Snake, Red Earth Centipede Snake; Culebra, Hojarasquera, Cabeza plana de collar

Map 4.121.

Tantilla shistosa: Taylor (1951).

Lectotype. MNHN 6221, from Vera Paz and Mexique (probably from Alta Vera Paz; McCranie 2011).

Geographic distribution. Mexico to Panama, 0–1760 m asl. In Panama, presumably along both versants of western and central Panama, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, east to the Río Chagres drainage. In the Cordillera Central, reported from Santa Clara, Valle de Antón, and PNAC, 590–1370 m asl.



Map 4.121: Distribution of *Tantilla schistosa.*

Diagnosis. This small snake (maximum TOL 350 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla schistosa* differs from its Panamanian congeners in having a unicolor brown dorsum, a complete light nuchal collar, and an immaculate red venter, while lacking light pre- and postocular blotches.

Description. TOL to 350 mm; SVL in Honduran specimens to 310 mm; tail short to moderate, TL/TOL = 0.12–0.20; D smooth, in 15—15—15 rows; V 117–147; SC 24–42; SPL 6–7; INL 5–6; loreal 0, but PF usually excluded from SPL by contact between nasal and Preoc; Preoc 1; Postoc 1–2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Tantilla schistosa* is a unilobed organ with a naked pedicel, numerous small spines distally to the basal hooks on truncus, and a calyculate apex.

Coloration in life. D and L surfaces of head, body, and tail brown to almost black, sometimes with a faint suggestion of a pale middorsal stripe; a more or less conspicuous complete light nuchal collar involving posterior portions of parietals and 1–2 D scale rows; V surfaces immaculate red; usually no contrasting pre- or postocular light spots or blotches.

Coloration in preservative. Similar to that in life, except that the reddish shades fade.

Natural history notes. Terrestrial and semifossorial, feeding primarily on centipedes.

Remarks. *Tantilla schistosa* has often been confused with its most similar congener, *T. alticola* (see Savage 2002: p. 696 and references therein, as well as remarks for *T. alticola* in this work). The presence at low and premontane elevations throughout both versants of western and central Panama, including Bocas del Toro, Veraguas, and the Comarca Ngöbe-Buglé, is rendered plausible by the records from Valle de Antón, PNAC, and PN Chagres together with the distribution as documented by recent authors for Panama (Köhler 2008) and Costa Rica (Savage 2002; Solórzano 2004).

Tantilla supracincta (Peters 1863)

Banded Centipede Snake, Coral Crowned Snake, Tricolored Crowned Snake; Culebra, Hojarasquera, Coral falsa, Cabeza plana anillada

Figure 4.107A; Map 4.122.

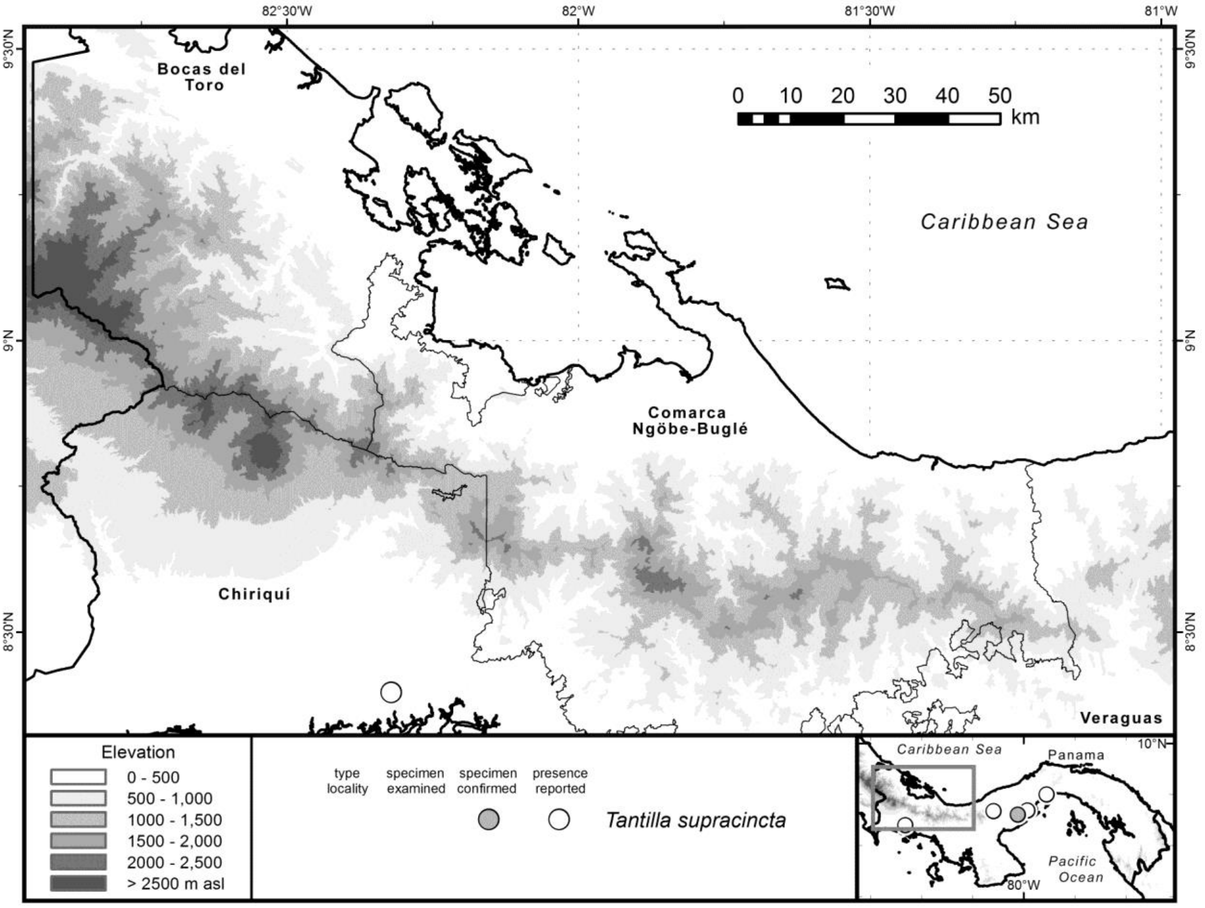
Homalocranion supracinctum: Peters (1863b).

Tantilla annulata: Dunn & Bailey (1939); Dunn (1940); Taylor (1951, 1954); Smith (1958); Perez-Santos (1999).

Holotype. ZMB 4791, from "Umgebung von Guayaquil" (= surroundings of Guayaquil, Ecuador).

Geographic distribution. Nicaragua to Ecuador, 0–970 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and

Veraguas. In the Cordillera Central, reported from PNGDOTH, Valle de Antón, and PNAC, up to ca. 850 m asl.



Map 4.122: Distribution of *Tantilla supracincta.*

Diagnosis. This small snake (maximum TOL 590 mm) with round pupils is immediately recognized as a member of the genus *Tantilla* by its smooth dorsals arranged in 15—15—15 rows in combination with a divided cloacal scute, the presence of a preocular, and absence of a loreal. *Tantilla supracincta* differs from its Panamanian congeners in having a coralsnake-like dorsal pattern of usually offset, black-edged light bands that do not cross the venter on red ground color.

Description. TOL to 590 mm; SVL tail moderate, TL/TOL = 0.19–0.24; D smooth, in 15—15—15 rows; V 138–155; SC 52–65; SPL 7; INL 6; loreal 0, but PF usually excluded from SPL by contact between nasal and Preoc; Preoc 1; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 1; eyes small, pupil round.

The hemipenis of *Tantilla supracincta* is a unilobed organ with hooks.

Coloration in life. D and L surfaces of body and tail red, with black-edged light transverse bands that are typically divided at middorsum or completely offset, and may be restricted to anterior portion of body; black head cap extending to posterior edges of parietals, followed posteriorly by a light nuchal collar that may be divided medially; snout light-colored; a conspicuous light postocular blotch on SPL; V surfaces red; juveniles chiefly black with light crossbars, black ground color giving way to red with age.

Coloration in preservative. Similar to that in life, apart from that the red fades to brown.

Natural history notes. Terrestrial and semifossorial, feeding only or chiefly on centipedes. This alimentary preference was already noted by Peters (1863b), who found a 10 cm long *Scolopendra* in the stomach of the holotype (TOL 530 mm). *Tantilla supracincta* has been observed to be preyed upon by *Clelia clelia,* and *Erythrolamprus bizona* (Savage 2002).

Remarks. The presence at low and premontane elevations throughout both versants of western Panama, including Bocas del Toro, Veraguas, and the Comarca Ngöbe-Buglé, is rendered plausible by the records from Valle de Antón, PNAC, and PNGDOTH together with the distribution as documented by recent authors for Panama (Köhler 2008) and Costa Rica (Savage 2002; Solórzano 2004). Though I could not find any particular record to substantiate the upper elevational limit given as 970 m asl for Panama (Jaramillo et al. 2010) and the species as a whole, I consider this value plausible.

Family Dipsadidae Bonaparte 1838

Amastridium veliferum Cope 1861

Common Rustyhead, Rustyhead Snake, Ridge-nosed Snake; Culebra, Cabeza de herrumbre

Figure 4.107B; Map 4.123.

Amaestridium veliferum: Castillo et al. (1990); de Sousa (1999).

Holotype. ANSP 3738, male, from "Cocuyas de Veraguas, N. Grenada" (Cope 1861b; = Cocuyos de Veraguas, Panama).

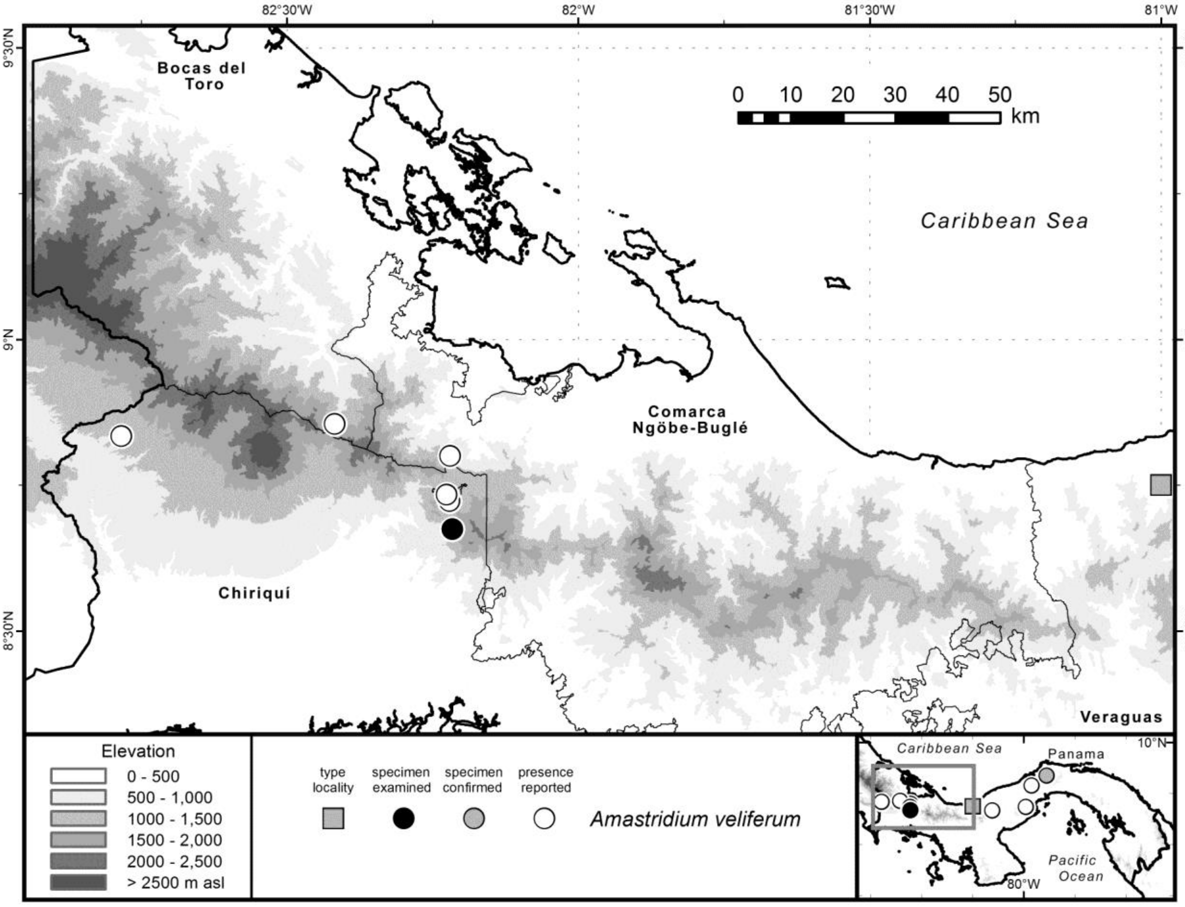
Geographic distribution. Nicaragua to Colombia, 0–1434 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from various sites along both versants east to the Fortuna area as well as from PNGDOTH and PNAC, up to 1434 m asl.

Diagnosis. This medium-sized snake (maximum TOL 725 mm) with round pupils is readily distinguished from all other Panamanian snakes by its overall brown coloration with at most diffuse markings on body and contrasting white spots on supra- and infralabials, smooth dorsals arranged in 17—17—17 rows, the lack of a loreal, and a pronounced canthus rostralis.

Description. TOL to 725 mm; SVL to 231 mm*; tail moderate, TL/TOL = 0.25–0.32; D smooth except posteriorly in adult males, in 17—17—17 rows; V 111–134; SC 69–92; SPL 7;

INL 8–9; loreal 0; Preoc 1–2; Postoc 2; Tant 1, Tpost 2; cloacal scute entire* or divided; AP 2 on anterior portion of body; eyes moderate to large, pupil round.

The hemipenis of *Amastridium veliferum* is a unilobed organ with basal spines, two enlarged basal hooks (3 in SMF 90092), and a calyculate apex.



Map 4.123: Distribution of *Amastridium veliferum.*

Coloration in life. D and L surfaces predominantly dark gray to brown with scattered light spots, otherwise unicolor or with diffuse longitudinal dark stripes and/or wavy lines; V surfaces gray, brown, or black, with light spots anteriorly or throughout; head rust colored or brown, with darker markings; white or cream spots on frontal plate and snout, white blotches or stripes on loreal region, labials, and chin.

Joe-Felix Bienentreu recorded the male SMF 90092 (Fig. 4.107B) as follows: D and L ground colour Brownish Olive (29); a Sepia (119) ventro-lateral longitudinal stripe extending from head to cloaca, between 1st and 2nd D row; a Sepia (119) L longitudinal stripe extending from head to tip of tail; a triangular Sepia (119) marking on the neck continues posteriorly to form 2 Sepia (119) D stripes, which disintegrate to form irregular D patterns that merge to form a single D Sepia (119) stripe on tail; scales of the 5th and 6th D row irregularly spotted with Buff-Yellow (53), partly bordered with Sepia (119); V surfaces of body and tail Dark

Brownish Olive (129), densely spotted with Pale Horn Color (92); D and L surfaces of head Warm Sepia (221A) with Sepia (119) markings and fine Pale Horn Color (92) spots, posterior SPL and V surface of head with dirty white spots and short lines, bordered by Sepia (119) mottling which extends to neck; iris Prout's Brown (121A).

Coloration in preservative. After 4.5 years in 70% ethanol, the coloration of SMF 90092 is similar to that in life, apart from that the D and L head color has lightened up considerably and now constrasts much more with the darker body coloration.

Natural history notes. Diurnal and crepuscular, terrestrial and semifossorial, reported to feed on frogs. SMF 90092 was encountered by JFB and FH as it moved through the leaf-litter atop a mountain ridge at 10:46.

Remarks. The male SMF 90092 has 92 SC, which is the highest number reported for this species so far, while the tail appears incomplete. Moreover, with 132 V it has the highest number of V reported for males of this species, whereas its 8 INL represent the lowest count reported for the species, 2 preoculars, and an undivided cloacal scute. The rusty colored head stated as diagnostic (Savage 2002; Solórzano 2004) is not very evident in this specimen from most perspectives, maybe owing to its comparably light ground color. Contrary to the diagnosis of Savage (2002), SMF 90092 does exhibit diffuse, but rather well-discernible dark stripes and lines throughout the body as also evident in the specimens pictured by Solórzano (2004: Fig. 38) and Köhler (2008: Fig. 543). These incongruities in coloration possibly are the result of an apparent skin shedding shortly before capture, as deducible from the specimen's iridescent and comparably vivid coloration, or otherwise of individual variation.

I could not find any record to substantiate the upper elevational limit of 1500 m asl given for this species by Perez-Santos (1999). Instead, SMF 90092, collected at 1434 m, comes from the highest elevation documented for this species so far (Jaramillo et al. 2010; Sasa et al. 2010; Wilson & Johnson 2010), slightly above the specimen MVUP 1302 that was collected by Fernando Arosemena at Culebra, 1400 m.

Clelia clelia (Daudin 1803)

Common Mussurana, Mussurana; Culebra, Zopilota, Zopilota común, Mussurana, Víbora de sangre (juveniles)

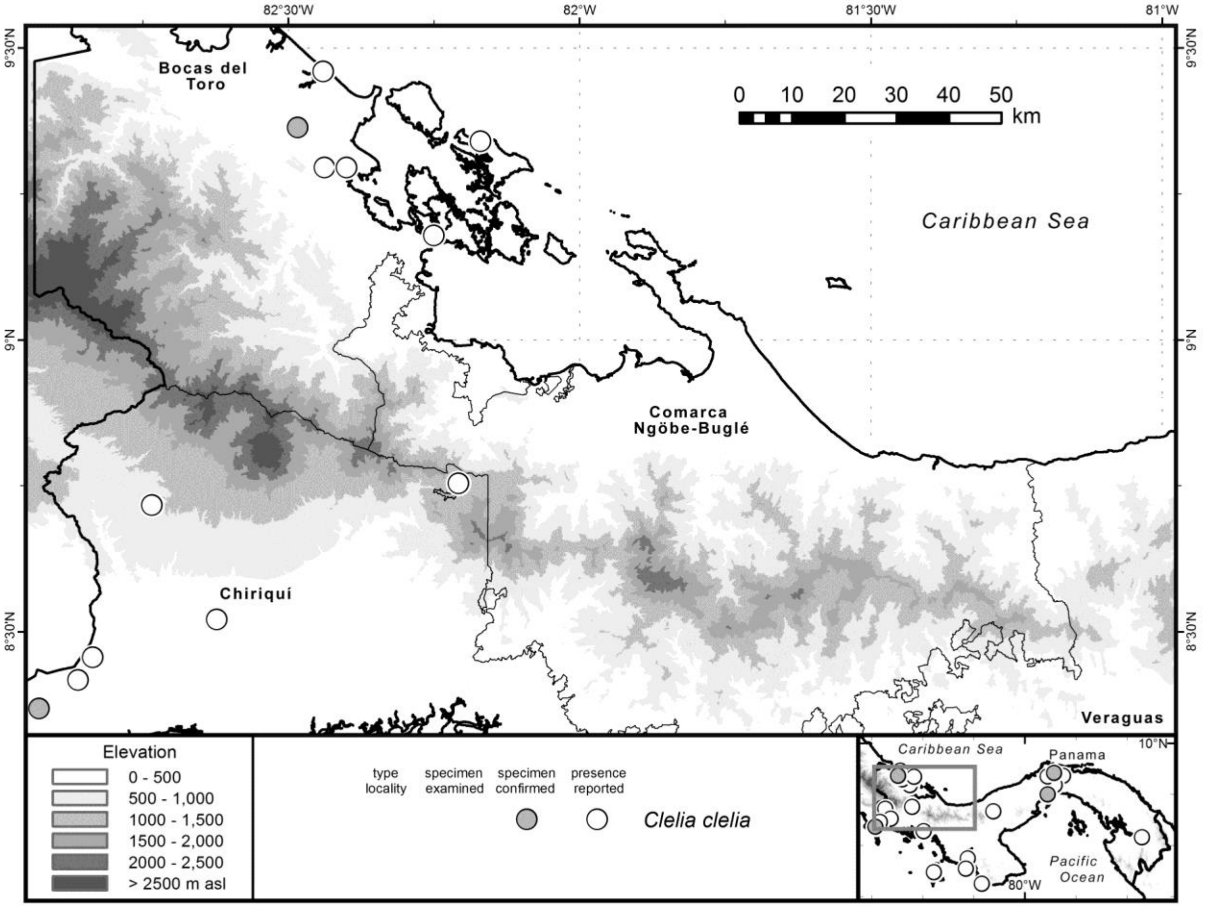
Figure 4.107C; Map 4.124.

Clelia cloelia: Wettstein (1934).

Oxyrhopus cloelia: Cope (1899); Barbour (1906).

Pseudoboa clelia: Dunn & Bailey (1939).

Syntypes. Apparently lost, from Surinam en Amérique.



Map 4.124: Distribution of *Clelia clelia.*

Geographic distribution. Guatemala and Belize to Peru, Bolivia, and Argentina, 0–1200 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Pacific versant of the Serranía de Talamanca, RFLF, and PNGDOTH, up to 1050 m asl.

Diagnosis. This large snake (maximum TOL 2750 mm) with vertically elliptical pupils is readily identified as a member of the genus *Clelia* by its smooth dorsals arranged in 17 rows one head length anterior to cloaca and entire cloacal scute, as well as by its coloration which is black above in adults and red except for a black nuchal band, black anterior head, and white nuchal collar involving the parietals in juveniles, while the ventral surfaces are white to cream at all ages. Juveniles of this genus further differ from the similar *Pseudoboa neuwiedii* in having divided subcaudals (vs. undivided). *Clelia clelia* differs from its Panamanian congeners in having 19—19—17 rows of dorsals (vs. 17—17—17).

Description. TOL to 2750 mm; SVL in Honduran specimens to 1959 mm; tail moderate, TL/TOL = 0.16–0.21; D smooth, in 19—19—17 rows; V 198–247; SC 75–98; SPL 7–8; INL 7–9; loreal 0–1; Preoc 1; Postoc 2; Tant 2, Tpost 2–3; cloacal scute entire; AP 0 or usually 2; eyes small to moderate, pupil vertically elliptical.

The hemipenis of *Clelia clelia* is a bilobed organ with a naked pedicel; truncus with a few large spines, apices calyculate.

Coloration in life. D and L surfaces of adults bluish black; juveniles with D and L surfaces of body and tail red with small dark spots on each scale, a black nuchal band, black anterior head, and white nuchal collar involving at least posterior portion of parietals; V surfaces white to cream at all ages, sometimes with scattered dark markings on SC and posterior V.

Coloration in preservative. Similar to that in life, apart from that the red tonalities of juveniles fades to pink and later to cream.

Natural history notes. Terrestrial, diurnal and nocturnal, feeding primarily on snakes but also taking other vertebrates which it kills by constriction and envenomation. This species appears to be immune to pitviper venom and individuals have been observed to successfully prey on snakes which are only slightly smaller than themselves.

Remarks. In Panama and elsewhere in Central America, *Clelia* species are widely known and appreciated for killing venomous snakes. Ironically, the brightly colored juveniles are called "Víbora de sangre" ("blood viper") in Panama and Costa Rica, and feared for their alledged venomousness, which is said to cause bleeding all over the body and a rapid, painful death.

In the key to the colubrid genera of Köhler (2008: p. 197), the target couplets in couplet 53 are mixed up in a way that SC counts of 93 or fewer direct the reader towards couplet 54 containing *Siphlophis* and *Tripanurgos* (today also in the genus *Siphlophis*), both of which actually have more than 100 SC. Correctly, these lower counts should be leading to couplet 55 containing *Drymarchon* and "*Clelia* (in part)", i.e., specimens of *Clelia* with a reduction of D scale rows posterior to midbody that in all cases represent *C. clelia.*

Clelia equatoriana (Amaral 1924)

Ecuatorial Mussurana; Culebra, Zopilota, Mussurana, Víbora de sangre (juveniles)

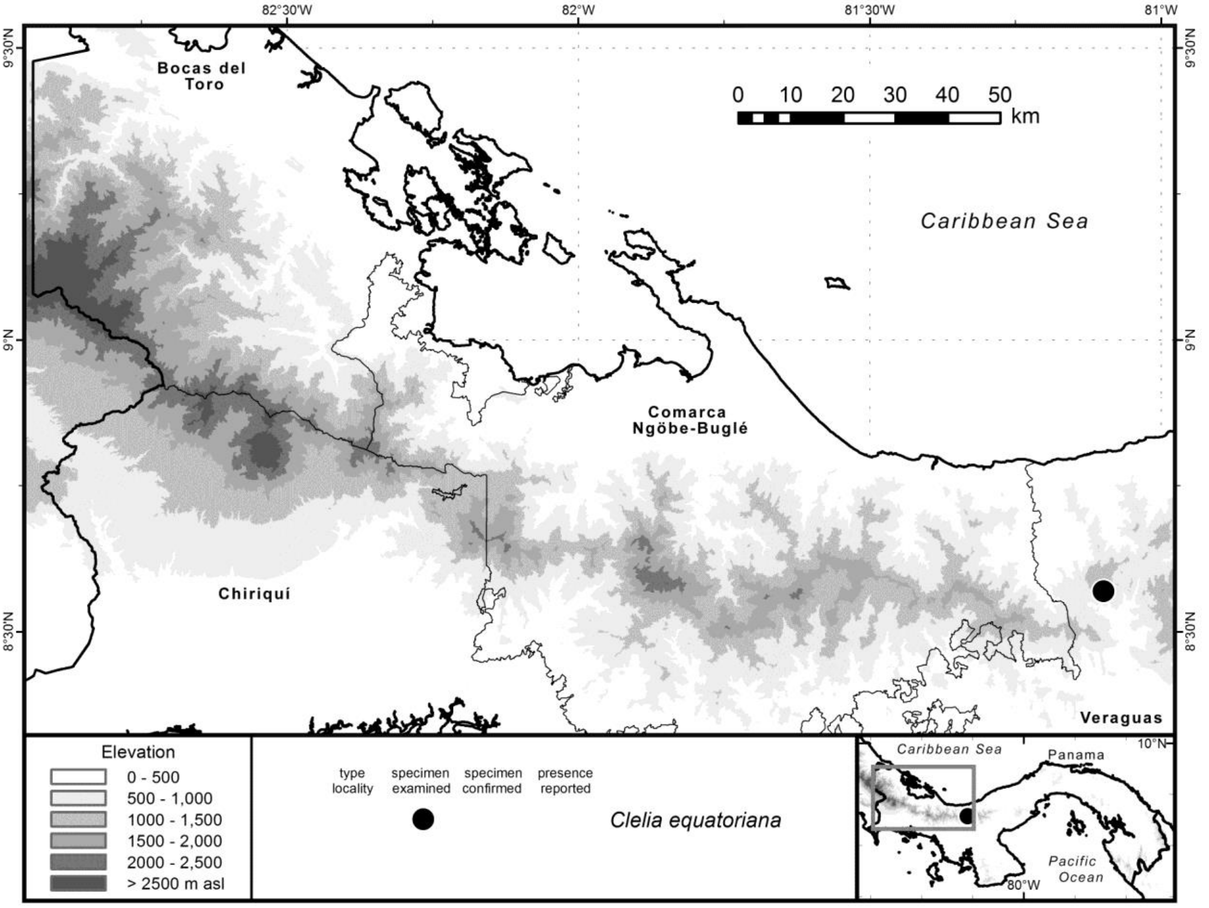
Figure 4.107D; Map 4.125.

Clelia scytalina: Savage (2002); Solórzano (2004), Sasa et al. (2010): all possibly and in part.

Holotype. USNM 62790, from Guayaquil, Ecuador.

Geographic distribution. Costa Rica to Colombia and Ecuador, 0–1900 m asl. In Panama, reported from the eastern highlands at 1530 m asl and from the Cordillera Central at Cerro Negro, Veraguas, at 725 m asl.

Diagnosis. This large snake (maximum TOL 1575 mm) with vertically elliptical pupils is readily identified as a member of the genus *Clelia* by its smooth dorsals arranged in 17 rows one head length anterior to cloaca and entire cloacal scute, as well as by its coloration which is black above in adults and red except for a black nuchal band, black anterior head, and white nuchal collar involving the parietals in juveniles, while the ventral surfaces are white to cream at all ages. Juveniles of this genus further differ from the similar *Pseudoboa neuwiedii* in having divided subcaudals (vs. undivided). *Clelia equatoriana* differs from *C. clelia* in having 17—17—17 rows of dorsals (vs. 19—19—17) and from *C. scytalina* in lacking apical pits (vs. 2 AP present).



Map 4.125: Distribution of *Clelia equatoriana.*

Description. TOL to 1575 mm; SVL to 1071 mm*; incomplete tail* moderate, incomplete TL/TOL = 0.21*; D smooth, in 17—17—17 rows; V 202–217; SC 56–80; SPL 7*; INL 8*; loreal 1*; Preoc 2*; Postoc 2*; Tant 1*, Tpost 3*; cloacal scute entire; AP 0; eyes small to moderate, pupil vertically elliptical.

The hemipenis of *Clelia equatoriana* is a bilobed organ with a naked pedicel; truncus with a few large spines, apices calyculate.

Coloration in life. D and L surfaces of adults black; juveniles with D and L surfaces of body and tail red, a black nuchal band, black anterior head, and white nuchal collar; V surfaces white to cream at all ages.

Coloration in preservative. Similar to that in life, apart from that the red tonalities of juveniles fade with time.

Natural history notes. Life history similar to that of *Clelia clelia.*

Remarks. Together with the occurrence in Costa Rica (Köhler 2008; Savage & Bolaños 2009), the examined specimen from Veraguas renders the occurrence in Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé plausible.

Since the ubication of the seemingly singular locality from the E Panamanian highlands (Jaramillo et al. 2010) remains obscure, the specimen SMF 89923, collected by AC at Cerro Negro, constitutes the only traceable point record for this species from Panama. This specimen was identified as *Clelia equatoriana* based on the key of Köhler (2008) and the diagnostics provided by Savage (2002), chiefly due to the absence of AP on its D scales. The issue of the taxonomic identity and biogeography of the *Clelia* populations with 17—17—17 D rows in Costa Rica and Panama, as discussed briefly by Savage (2002) and in perfect detail by Sasa et al. (2010), is utterly confusing and remains far from being resolved. Having examined a single specimen of this genus, I refrain from drawing any conclusions on my own, or wallowing in this taxonomic mire at all. Thus, for now, I tentatively follow Savage & Bolaños (2009), Jaramillo et al. (2010), and Sasa et al. (2010) in considering 3 species of this genus to be present in LCA. Only a thorough integrative taxonomic study involving material from Mexico to Ecuador will eventually resolve this matter.

Clelia scytalina **(Cope 1867)**

Highland Mussurana, Mexican Snake-eater; Culebra, Zopilota de altura, Mussurana, Víbora de sangre (juveniles)

Map 4.126.

Clelia clelia: Taylor (1951, 1954).

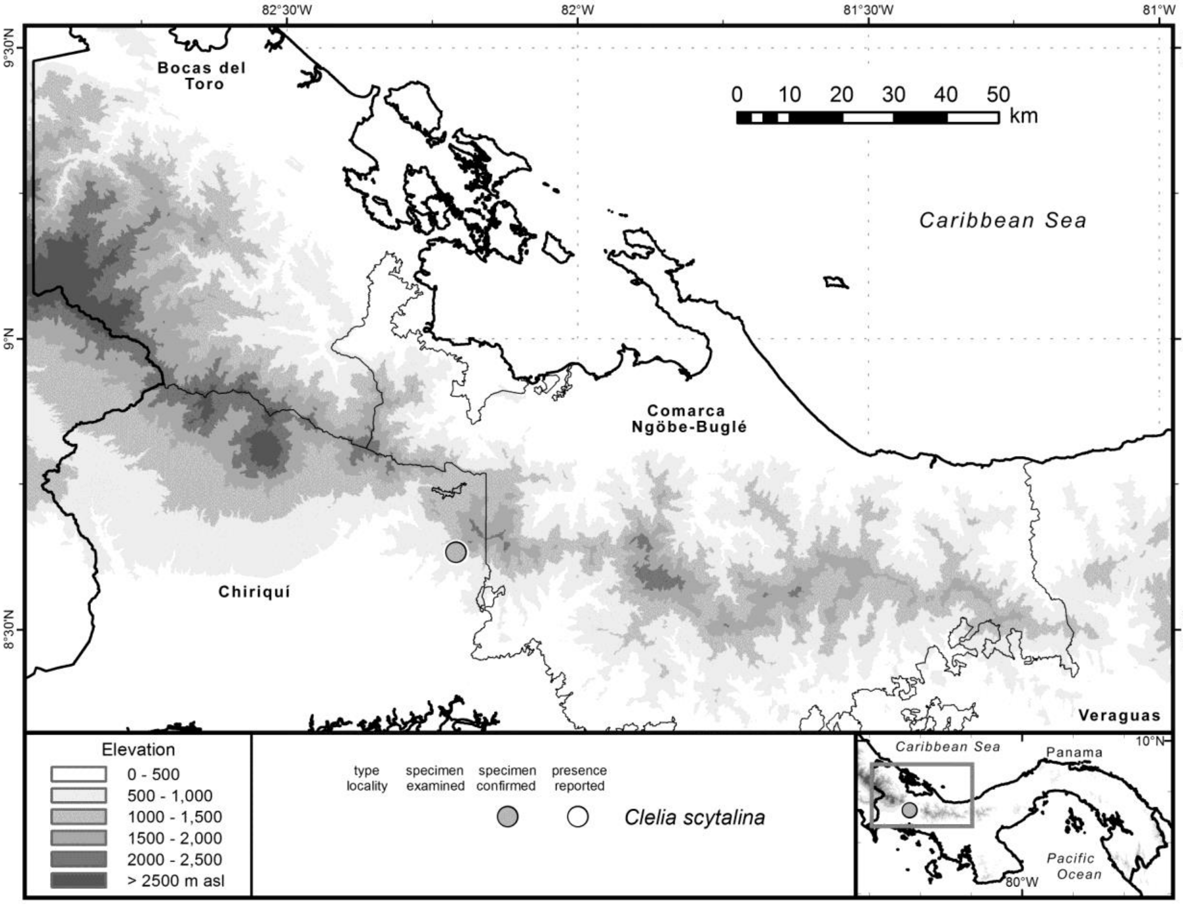
Clelia equatoriana: Köhler (2008: in part.).

Scolecophis scytalinus: Cope (1867).

Holotype. USNM 6581, from near Tabasco, Mexico.

Geographic distribution. Mexico to Panama and possibly Colombia, 0–2000 m asl. In Panama, exclusively reported from the Cordillera Central at La Fortuna, ca. 1050 m asl, and an unspecified locality at 1783 m asl.

Diagnosis. This large snake (maximum TOL 1800 mm) with vertically elliptical pupils is readily identified as a member of the genus *Clelia* by its smooth dorsals arranged 17 rows one head length anterior to cloaca and entire cloacal scute, as well as by its coloration which is black above in adults and red except for a black nuchal band, black anterior head, and white nuchal collar involving the parietals in juveniles, while the ventral surfaces are white to cream at all ages. Juveniles of this genus further differ from the similar *Pseudoboa neuwiedii* in having divided subcaudals (vs. undivided). *Clelia scytalina* differs from *C. clelia* in having 17—17—17 rows of dorsals (vs. 19—19—17) and from *C. equatoriana* in having 2 apical pits (vs. AP absent).



Map 4.126: Distribution of *Clelia scytalina.*

Description. TOL to 1800 mm; tail moderate, TL/TOL = 0.15–0.22; D smooth, in 17—17—17 rows; V 202–228; SC 75–92; SPL 7–8; INL 7–9; loreal 0–1; Preoc 1; Postoc 2; Tant 2, Tpost 2–3; cloacal scute entire; AP 2; eyes small to moderate, pupil vertically elliptical.

The hemipenis of *Clelia scytalina* is a bilobed organ.

Coloration in life. D and L surfaces of adults black or brown; juveniles with D and L surfaces of body and tail red with a black spot on each D scale, a black nuchal band, black anterior head, and white nuchal collar; V surfaces white to cream at all ages.

Coloration in preservative. Similar to that in life, apart from that the red tonalities of juveniles fade with time.

Natural history notes. Life history similar to that of *Clelia clelia.*

Remarks. Together with the occurrence in Costa Rica (Köhler 2008; Savage & Bolaños 2009), the record from RFLF renders the occurrence in Bocas del Toro and the Comarca Ngöbe-Buglé plausible. The specimen MVUP 144, collected by F. Crastz at Cerro Hornito, RFLF (Solís et al. 1991), my georeference for which yields a SRTM elevation of 1045 m asl, constitutes the only traceable point record for this species from Panama. The ubication of the apparently second locality from the Cordillera Central (at 1783 m fide Jaramillo et al. 2010) remains obscure. Regarding the taxonomic issue concerning *Clelia* populations with 17 D-MB in Costa Rica and Panama, see remarks for *C. equatoriana.* Savage & Bolaños (2009: p. 17) stated that "most Costa Rica examples [of *C. scytalina*] appear to be *C. equatoriana.*"

Coniophanes fissidens **(Günther 1858)**

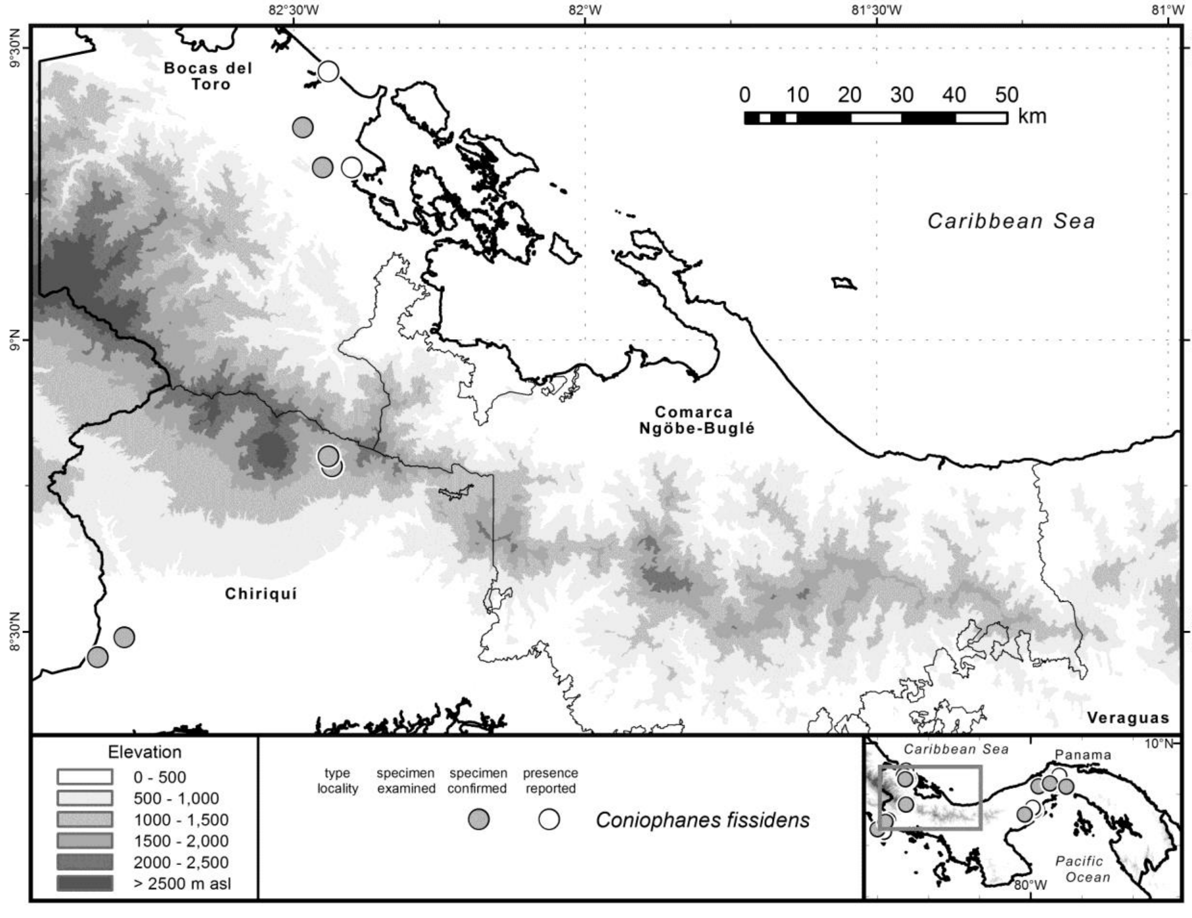
Brown Debris Snake, Brown Spotbelly, White-lipped Spotbelly Snake Yellowbelly Snake; Culebra, Ranera café

Figure 4.107E; Map 4.127.

Coniophanes punctigularis: Cope (1860c).

Lectotype. BMNH 1946.1.8.20, from Mexico and America.

Geographic distribution. Mexico to Colombia and Peru, 0–2200 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Boquete area, Valle de Antón, and PNAC, up to ca. 1320 m asl.



Map 4.127: Distribution of *Coniophanes fissidens.*

Diagnosis. This medium-sized snake (maximum TOL 800 mm) with round pupils is identified as a member of the genus *Coniophanes* by its divided cloacal scute, smooth dorsals without apical pits arranged in (19–23)—(19–21)—17 rows, the presence of a loreal, and a striped pattern. Among the Panamanian congeners, *C. fissidens* differs from *C. joanae* of eastern Panama in usually having 19–21 dorsal rows at midbody (vs. 17) and from *C. bipunctatus* in having the venter irregularly spotted or mottled with dark (vs. two large, round spots laterally on each ventral scale, forming two regular lateroventral series of dark spots).

Description. TOL to 800 mm; SVL in Honduran specimens to 432 mm; tail long, TL/TOL = 0.26–0.42; D smooth except for keeled supracloacals in adult males, in (19–23)—(19–21)—17 rows (very rarely 17 D-MB); V 109–146; SC 53–103; SPL 7–8; INL 9–10; loreal 1; Preoc 1–2; Postoc 1–2; Tant 1, Tpost 2–3; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Coniophanes fissidens* is a unilobed organ with a naked pedicel; truncus with large basal spines; apex calyculate.

Coloration in life. D and L surfaces brown, often with orange hues; a narrow dark L stripe, sometimes interrupted, usually light-edged above and/or grading into dark ventrolateral coloration; often with a dark middorsal band or series of spots; labials often with dark-centered ocelli, usually spotted with dark just as chin region; a white supralabial stripe usually present posterior to orbit; venter white to yellow or orange with dark mottling.

Coloration in preservative. Similar to that in life, apart from that the yellow and orange shadings fade over time.

Natural history notes. Terrestrial, diurnal and crepuscular, feeding on a variety of vertebrates and their eggs, as well as arthropods while juvenile. The bite of this opistoglyphous species can cause severe local symptoms in humans.

Remarks. The numerous records from E and W of these political subdivisions render the presence of *Coniophanes fissidens* in Veraguas and the Comarca Ngöbe-Buglé plausible. My georeference for the specimens CAS 79015–6 from "vicinity north of Boquete" (Myers 1969a; Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is slightly above the highest elevations of 1200 (Jaramillo et al. 2010) or 1250 m (Perez-Santos 1999) documented for Panama. In view of the unusually high variation in segmental counts, McCranie (2011) suggested more than one species is contained in this nominal taxon.

Dipsas articulata (Cope 1868)

Red-striped Thirst Snake, American Snail-eater; Caracolera, Caracolera rosada

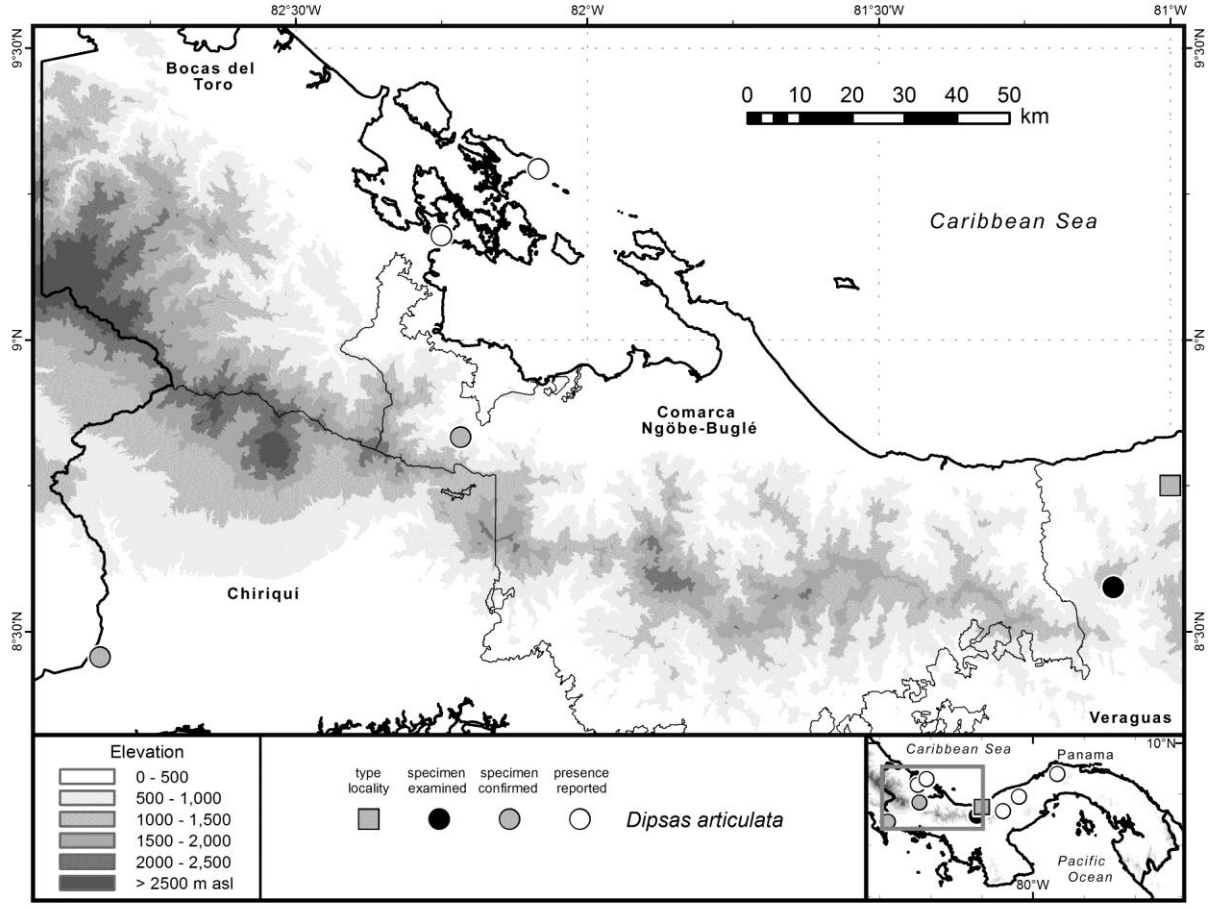
Figures 4.86A–C; 4.107F; Map 4.128.

Dipsas brevis: Cope (1860c).

Leptognathus articulata: Cope (1868).

Holotype. ANSP 10113, male, from "Veraguas, Costa Rica" (Cope 1868; Cocuyos de Veraguas, Panama, can be assumed; see remarks in Peters 1960: p. 35–36).

Geographic distribution. Nicaragua to Panama, 0–1000 m asl. In Panama, along both versants of the western and central portions of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from La Loma, the Santa Fé region, and PNGDOTH, up to 1000 m asl.



Map 4.128: Distribution of *Dipsas articulata.*

Diagnosis. This medium-sized snake (maximum TOL 752 mm) with vertically elliptical pupils is immediately recognized as a member of the genus *Dipsas* by its large eyes, rectangular chin shields, the lack of a mental groove, and its smooth dorsals arranged in 15—15—15 rows. Among its Panamanian congeners, it differs from *D. nicholsi, D. temporalis,* and *D. viguieri* in having complete light and dark rings around body and tail (vs. lateral blotches that are offset at least posteriorly). It further differs from *D. temporalis* in having the 1st pair of infralabials in contact with each other (vs. separated), 9 or more supralabials (vs. 8 or fewer), and 11 or more infralabials (vs. 10 or fewer). It differs from the only Panamanian *Dipsas* with complete light and dark rings, *D. tenuissima,* in having the light rings suffused with reddish tonalities but not mottled with dark pigment (vs. heavily marked with dark posteriorly) and in having 217 or fewer ventrals (vs. 225 or more) and 11 or more infralabials (vs. 10 or fewer) (including data from Harvey 2008).

Description. TOL to 752 mm; SVL to 514* mm; tail long, TL/TOL = 0.30–0.32; D smooth, in 15—15—15 rows, vertebral and paravertebral rows slightly enlarged; V 196–217; SC 108–135; SPL 9–10; INL 11–14; loreal 1; Preoc 0 or a small one allowing for contact between loreal and orbit; Postoc 2–4; Tant 2–3, Tpost 2–3; cloacal scute entire; AP 0; eyes large, pupil vertically elliptical.

The hemipenis of *Dipsas articulata* is a slightly bilobed organ; truncus with large spines basally and small spines distally, apex calyculate.

Coloration in life. Body and tail with alternating complete light (white to cream) and dark (dark brown) rings; the light rings suffused with yellowish to reddish shades especially dorsally; head white to cream suffused with yellow to red, mottled with dark dorsally and on snout; iris reddish brown

Coloration in preservative. After 6 years in 70% ethanol, SMF 89952 is white and brown.

Natural history notes. Nocturnal and arboreal, reported to feed exclusively on gastropods but probably also consuming other soft-bodied prey as suggested for related species by Ray et al. (2012). The only specimen collected in the course of this project was found while it was moving about in low vegetation at 21:00.

Remarks. In view of the photos of this species published by Solórzano (2004: Figs. 61 and 62) and Köhler (2008: Figs. 589 and 591), as well as the specimen SMF 89952 collected by AC, AH, and myself at Cerro Negro, I cannot consent with the statement of Savage (2002: p. 597) that *Dipsas articulata* has a "tricolor monad pattern of alternating red-cream-dark-cream-red rings". An animal more or less suiting this description is pictured by Köhler (2008: Fig. 586) as *D. bicolor,* while the photos of this species published by Savage (2002: plates 365 and 366) look much like the aforementioned *D. articulata* to me. Both species are said to be very similar, and despite the striking difference in chin shields (Savage 2002; Köhler 2008) were synonymized by Solórzano (2004) based on unpublished data on head shield variation. Concerning this issue, I follow McCranie (2011) in not adopting this synonymization of *D. bicolor* with *D. articulata* until solid evidence is published, while recognizing that a certain degree of taxonomic confusion surrounds these two nominal species. The animal pictured by Köhler (2008: Fig. 592) and Stadler (2010: Fig. A85) as *D. articulata* is a paratype of *Sibon noalamina* (Lotzkat et al. 2012d).

Based on the specimen SMF 89952, Lotzkat et al. (2010c) raised the upper elevational limit documented for this species to 1000 m asl and provided the first explicit record for

Veraguas province. This individual has a TOL of 514 + 238 = 752 mm, 217 V, and 137 SC, each being the highest respective value reported for this species so far.

I regard the presence of another species of *Dipsas* with a pattern of light and dark rings, *D. tenuissima* Taylor 1954, in my study area as possible in view of its distribution in Pacific Costa Rica, where it occurs up to 970 m asl, and adjacent lowland Chiriquí (Savage 2002; Köhler 2008; Jaramillo et al. 2010; see distribution map in Appendix 7).

***Dipsas temporalis* (Werner 1910)**

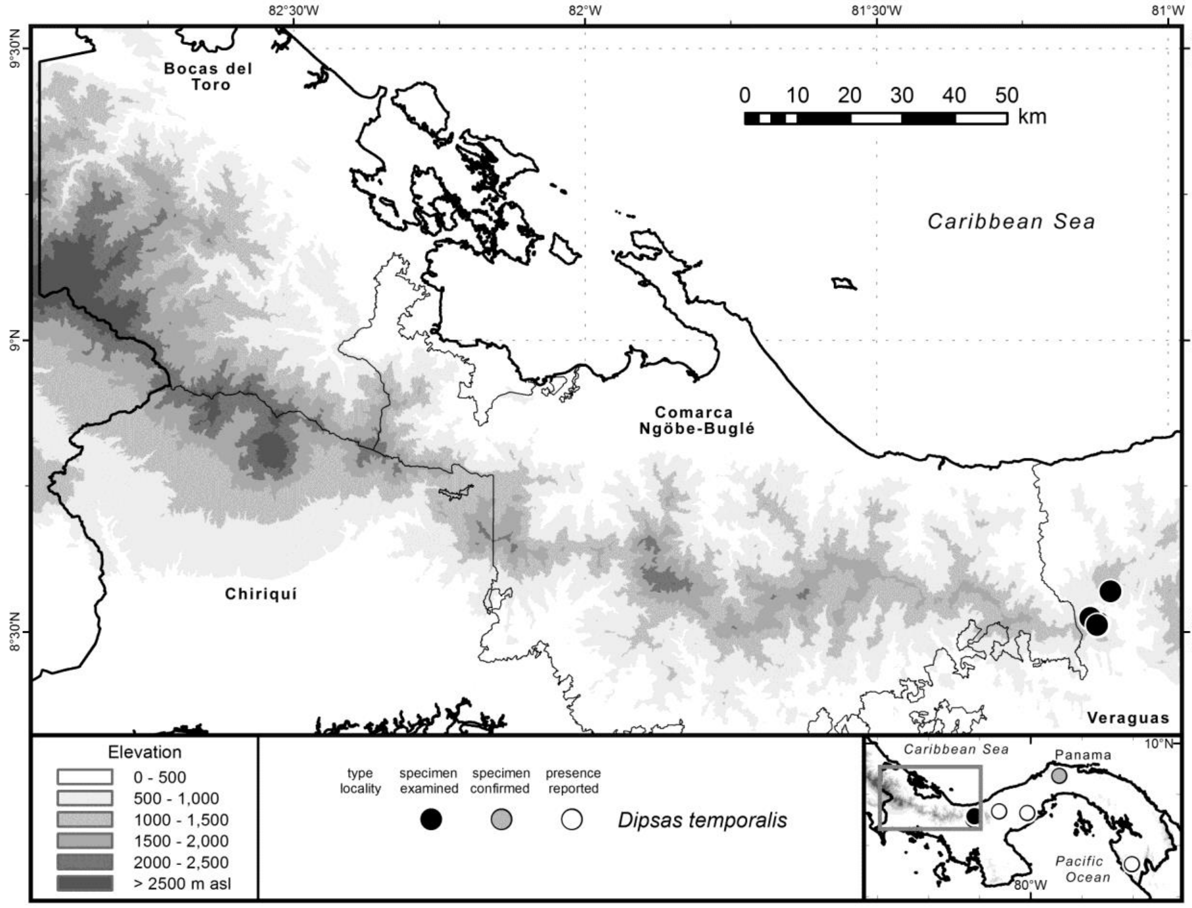
Temporal Snail-eater; Caracolera

Figures 4.86D–H; 4.107G; Map 4.129.

Dipsas sp.: Ray (2009); Ray et al. (2012).

Sibon temporalis: Dunn & Bailey (1939).

Holotype. At ZMH, lost, from Esmeraldas, Ecuador.



Map 4.129: Distribution of *Dipsas temporalis.*

Geographic distribution. Panama to Colombia and Ecuador, 500–1000 m asl. In Panama, presumably along both versants of the eastern, central, and adjacent western portions of the country, including Veraguas and the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from Valle de Antón, PNGDOTH, and the Santa Fé area, up to ca. 990 m asl.

Diagnosis. This medium-sized snake (maximum TOL 688 mm*) with vertically elliptical pupils is immediately recognized as a member of the genus *Dipsas* by its large eyes, rectangular chin shields, the lack of a mental groove, and its smooth dorsals arranged in 15—15—15 rows. *Dipsas temporalis* is differs from all congeners in having the 1st pair of infralabials separated by 1–2 postmentals (vs. 1st pair of infralabials in contact medially).

Description. TOL to 688 mm*; SVL to 455 mm*; tail long, TL/TOL = 0.32–0.35*; D smooth, in 15—15—15 rows, vertebral row enlarged*; V 170–192*; SC 110–133* SPL 7*; INL 8–9*; loreal 1*; Preoc 1*; Postoc 2–4*; Tant 2–3*, Tpost 1–3*; cloacal scute entire; AP 0; eyes large, pupil vertically elliptical.

The hemipenis of *Dipsas temporalis* is a slightly bilobed organ; truncus with large spines and two basal hooks, apex calyculate.

Coloration in life. D and L ground color of body dirty white to light brown, with broad dark brown bands that reach well onto, but not in all cases completely across venter; posteriorly on body, the dark bands disintegrate into light-edged dark L blotches that are at least partially offset in a way that some or all do not meet and merge on middorsum posterior to a certain point; simultaneously, the light interspaces become increasingly suffused with brown pigment caudad until, posterior to a certain point, they are solid brown except for their very borders edging the dark blotches; on tail, the dark blotches and by now brown interspaces show a tendency to assume the same shade of brown; D and L surfaces of head brown, usually with some light and dark mottling around labials; V surface of head whitish with dark mottling; iris brown to gray.

The juvenile SMF 89769 was recorded as follows: D and L ground color dirty white, with Verona Brown (223B) mediodorsal mottling on anterior portion of body that increasingly extends further laterally to cover almost all of dorsum and flanks on posterior portion of body, grading into Raw Umber (223) on tail; anterior portion of body with a series of Raw Umber (223) blotches that posteriorly separate to form two series of partly fused L blotches, always bordered by dirty white, merging into the Raw Umber (223) ground color of posterior portion of tail; V surfaces of head and body dirty white with spots and mottles of Raw Umber (223) and Verona Brown (223B); V surface of tail Raw Umber (223) with a few dirty white flecks; D and L surfaces of head Mars Brown (223A) with a suggestion of Raw Umber (223) with dirty white mottling partly bordered by Sepia (119) laterally; iris Drab-Gray (119D).

Leonhard Stadler recorded the adult female SMF 89551 (Stadler 2010: Fig. A87) as follows (translated from Stadler 2010): D surfaces of body and tail Mars Brown (223A) grading into Tawny Olive (223D) on anterior portion of flanks; D surfaces from head to tip of tail with transverse Dark Grayish Brown (20) bars that are increasingly broken up dorsally on the posterior portion of body; D surface of head Raw Umber (223) grading into Mars Brown (223A) posteriorly; venter Pale Horn Color (92) mottled with Dark Grayish Brown (20); V surface of tail ist Dark Grayish Brown (20); iris Grayish Horn Color (91).

Coloration in preservative. After 4–6 years in 79% ethanol, the coloration of my examined specimens is similar to that in life.

Natural history notes. Nocturnal and arboreal, presumed to feed chiefly on gastropods but reported to consume substantially more oligochaetes by Ray et al. (2012). All individuals collected in the course of this study (including the four specimens reported by Stadler 2010) were encountered at night while they were active in low vegetation 0.3–2 m above ground.

Remarks. While Harvey (2008) in his redescription of *Dipsas temporalis* did not note profound geographical variation between populations from different parts of the species' areal, Sheehy (2012) found individuals from PNGDOTH to be profoundly differentiated genetically from the single Colombian individual in his sample, suggesting that two species are contained in this nominal taxon. Likewise, populations of the taxon herein referred to as *D. temporalis* from PNGDOTH have been called *Dipsas* sp. by Ray (2009) and Ray et al. (2012). The latter authors even stated their *Dipsas* sp. from PNGDOTH to contain "as many as three cryptic species, at least one of which is undescribed". While individuals from the population inhabiting the Santa Fé area already show a rather ample individual variation in coloration (e.g., the D ground color ranging from solid white to solid brown, dark anterior rings from medium to blackish brown; compare Figs. 4.86 D–F), animals from Cerro Cituro in E Panama pictured by Harvey (2008: Figs 2C and 7, regular rings throughout body and tail) and Cadle & Myers (2003: Fig. 16: pattern similar to that found in the Veraguas population) intuitively appear to me like two different species. In view of these manifold cues, I conclude that the taxonomy of what hitherto has been called *D. temporalis* by most authors remains to be fully resolved, and that at least one South American and one Panamanian species are currently included under this name. I thus restrict my morphological description above to the material examined by myself from around Santa Fé de Veraguas. The V counts of three specimens are below the lower limit of 183 reported by Harvey (2008).

I could not find any record to substantiate the upper elevational limit for this species given as 1250 m asl by Perez-Santos (1999) and Wilson & Johnson (2010). The highest record known to me are the specimens KU 110299–309 from "S slope Cerro Cituro, Serranía de Pirre, 1000 m" (Harvey 2009), followed by SMF 89552 that was collected by LS and NH on Cerro Mariposa at 993 m (Lotzkat et al. 2010c). The distance of less than 3 km between the collection site of SMF 98553–4 and the Comarca's border render the presence of *Dipsas temporalis* in the Comarca Ngöbe-Buglé plausible.

I regard the presence of another species of *Dipsas* with a pattern of L blotches, *D. nicholsi* (Dunn 1933), in Veraguas and my study area as possible in view of its distribution extending W to PNGDOTH and up to 855 m asl (Myers et al. 2007; Ray 2009; Jaramillo et al. 2010; Ray et al. 2012; see distribution map in Appendix 7).

Enuliophis sclateri **(Boulenger 1894)**

Colombian Longtail Snake, Sock-headed Snake, White-headed Snake; Culebra, Cabeza blanca

Figure 4.107H; Map 4.130.

Enulius sclateri: Taylor (1951, 1954); Smith (1958); Myers & Rand (1969); Peters & Donoso-Barros (1970); Rand & Myers (1990); Auth (1994); Martínez & Rodriguez (1994); Martínez et al. (1995); Ibáñez et al. (1996, 1997); Perez-Santos (1999); Young et al. (1999); Savage (2002); McDiarmid & Savage (2005); Montero (2005).

Enulius slateri: Dunn (1938a).

Leptocalamus sclateri: Boulenger (1894).

Holotype. BMNH 1946.1.21.72, from S. America.

Geographic distribution. Honduras to Colombia, 0–1400 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the area around Volcán, the Santa Fé area, and PNAC, up to ca. 1390 m asl.

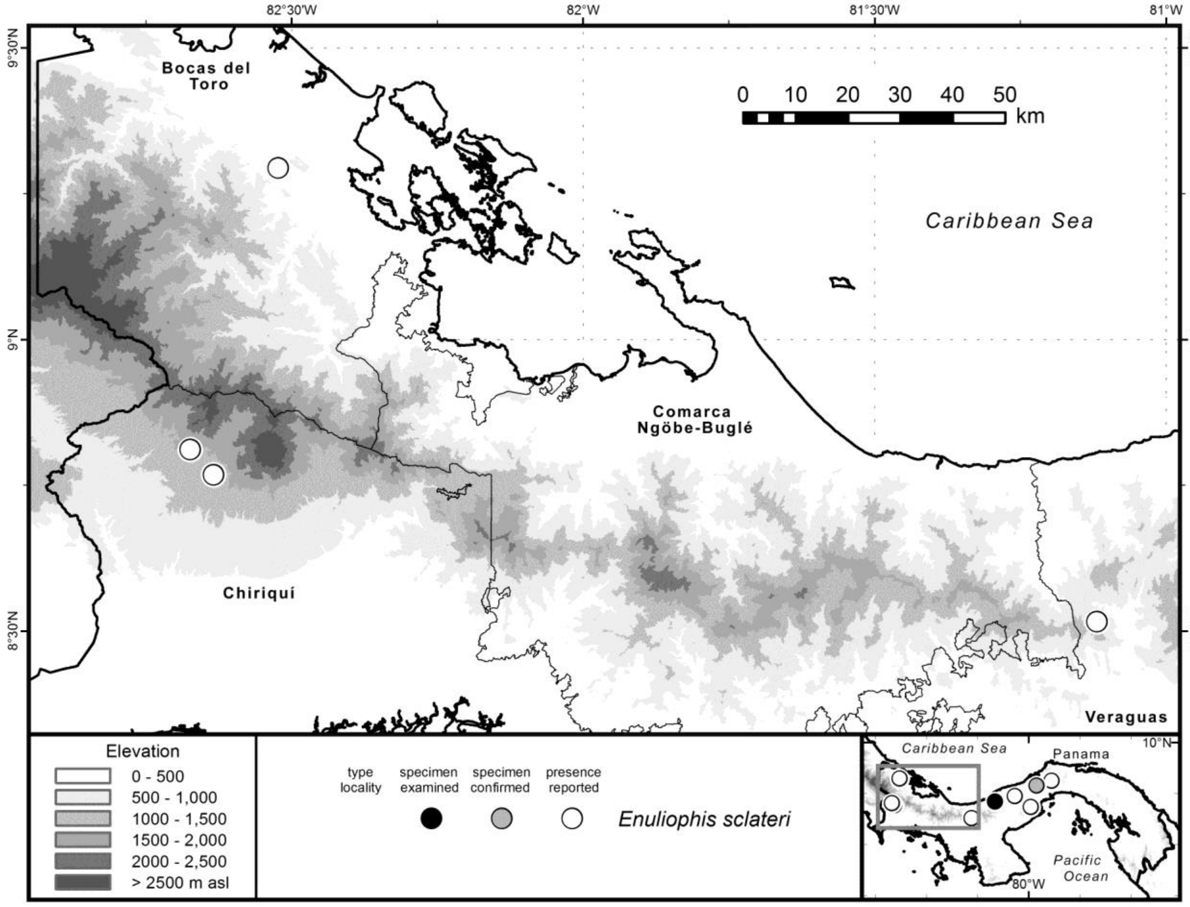
Diagnosis. This small snake (maximum TOL 550 mm) with round pupils is unique among Panamanian snakes in having smooth dorsals with two apical pits arranged in 15—15—15 rows, a loreal but no preocular, a divided cloacal scute, and a unicolor blackish dorsal body and tail coloration combined with white coloration forming a nuchal collar or covering the entire head except for the black snout and orbits. It further differs from *Enulius flavitorques* in having the snout rounded in profile (vs. shovel-shaped).

Description. TOL to 550 mm; SVL in Honduran specimens to 295 mm; tail long, TL/TOL = 0.36–0.42; D smooth, in 15—15—15 rows; V 129–155; SC 88–109; SPL 6–7; INL 6; loreal 1; Preoc 0; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 2; eyes small, pupil round.

The hemipenis of *Enuliophis sclateri* is a slightly bilobed organ; pedicel naked on asulcate, with many small spines on sulcate side; truncus with one very large and 3–4 large spines on either side of sulcus spermaticus; apex naked with a few small spines.

Coloration in life. D and L surfaces of body and tail dark brown to black, except for a white nuchal collar covering the posterior tip of the frontal, the parietals, and the first D scale rows, or a white head cap that covers the entire head except for the tip of the snout and the orbital areas which are dark; V surfaces of head and body white; V surface of tail white to gray, sometimes with dark mottling or median stripe; iris black.

Coloration in preservative. Similar to that in life.



Map 4.130: Distribution of *Enuliophis sclateri.*

Natural history notes. Diurnal and fossorial, feeding on reptile eggs.

Remarks. I could not find any specimen record to substantiate the upper elevational limit of 1500 m asl given by Perez-Santos (1999). The highest Panamanian records are KU 75693 from "El Volcán", for which my georeference placed in the settlement Volcán yield a SRTM elevation of 1388 m, which is close to the highest elevation of 1400 m documented for this species by Solórzano (2004). The occurrence of this species in the Comarca Ngöbe-Buglé is rendered plausible by the records from both E and W of this political subdivision.

Enulius flavitorques (Cope 1869)

Pacific Longtail Snake, Thick-tailed Snake; Culebra, Cabeza puntiaguda

Figure 4.108A; Map 4.131.

Enulius torquatus: Cope (1894).

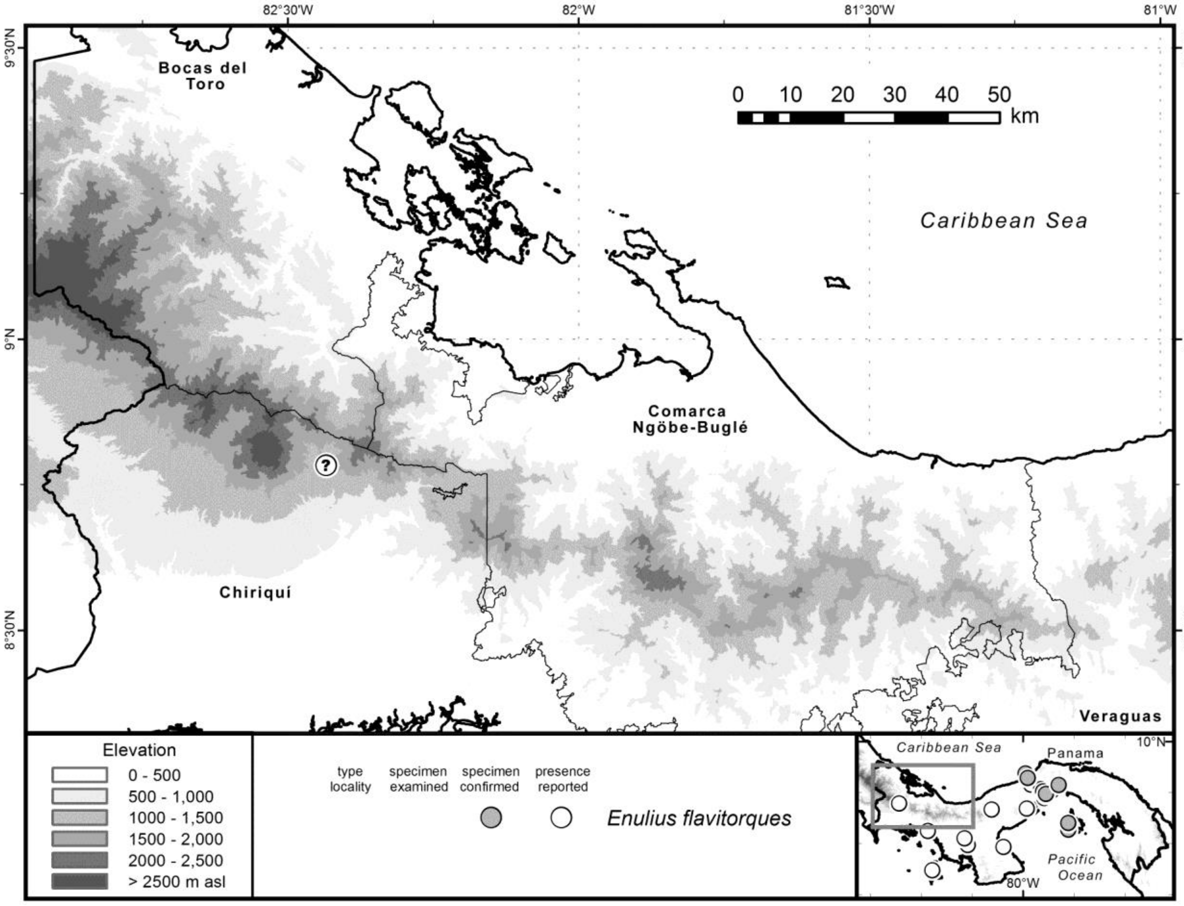
Leptocalamus torquatus: Barbour (1923).

Liophis flavitorques: Cope (1869).

Tantilla albiceps: Perez-Santos & Martínez (1997).

Holotype. ANSP 3695, from "Magdalena River, New Grenada" (= Colombia) (Cope 1869).

Geographic distribution. Mexico to Colombia, 0–3000 m asl. In Panama, along the Pacific versant of western and both versants of central and eastern Panama, including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from Volcán Barú, PNGDOTH, and PNAC, up to at least 1000 m asl.



Map 4.131: Distribution of *Enulius flavitorques.*

Diagnosis. This small snake (maximum TOL 500 mm) with round pupils is unique among Panamanian snakes in having smooth dorsals with one apical pit arranged in (15–17)—(15–17)—(15–17) rows (usually 17 throughout body), a loreal but usually no preocular, a divided cloacal scute, and a unicolor dark brown dorsal body and tail coloration combined with white or yellow nuchal collar and a light ventral coloration extending laterally at least to the 2nd dorsal scale row. It further differs from *Enuliophis sclateri* in having the snout shovel-shaped in profile (vs. rounded).

Description. TOL to 500 mm; SVL in Honduran specimens to 289 mm; tail long, TL/TOL = 0.27–0.41; D smooth, in (15–17)—(15–17)—(15–17) rows; V 165–216; SC 85–121; SPL 6–8; INL 6–8; loreal 1; Preoc 0–1; Postoc 1–2; Tant 1, Tpost 1–2; cloacal scute divided; AP 1; eyes small, pupil round.

The hemipenis of *Enulius flavitorques* is a slightly bilobed organ; pedicel, truncus, and most of apex with uniformly small spines; lobes papillate distally.

Coloration in life. D and L ground color dark brown to black; V ground color cream, reaching onto 2nd or 3rd D row; usually with a white to yellow nuchal collar (covering the posterior tip of the frontal, most of the parietals, and the first D scale rows) that may be interrupted or indented medially, or rarely be absent; iris black.

Coloration in preservative. Similar to that in life, apart from that yellow nuchal collars fade to cream or white

Natural history notes. Diurnal and fossorial, feeding on reptile eggs.

Remarks. The presence of *Enulius flavitorques* in my study area is documented by the specimen MVUP 707 from "Volcán Barú, prov. Chiriquí". Since the MVUP catalogue does not further specify the specimen's collection locality, I arbitrarily placed (and therefore marked with a question mark in Map 4.131) my georeference at Boquete, where most herpetological collecting in the surroundings of Volcán Barú has taken place. My generalized coordinates for this settlement yield a SRTM elevation of 1121 m asl, which would constitute the highest record from Panama so far, almost 300 m above the maximum elevation given by Jaramillo et al. (2010). Notwithstanding the great uncertainty concerning the exact collection site, an elevation above 1000 m can confidently be assumed in view of the verbal locality descriptor. The upper elevational limit of 3000 m (Wilson & Johnson 2010) seems very high compared to the 1000–1300 m provided by other authors (Savage 2002; Solórzano 2004; Köhler 2008; Sasa et al. 2010) for Costa Rica or the species as a whole. The occurrence of this species in the Comarca Ngöbe-Buglé is rendered plausible by the records from both E and W of this political subdivision. The record of *Tantilla albiceps* from Isla Coiba (Perez-Santos & Martínez 1997) was based on an individual of *E. flavitorques* (Myers 2003).

Erythrolamprus bizona **Jan 1863**

Black-ringed False Coral, Central American Coralsnake Mimic, False Coralsnake, Jan's False Coral Snake; Coral falsa, Falsa coral de naríz manchada

Figure 4.108B; Map 4.132.

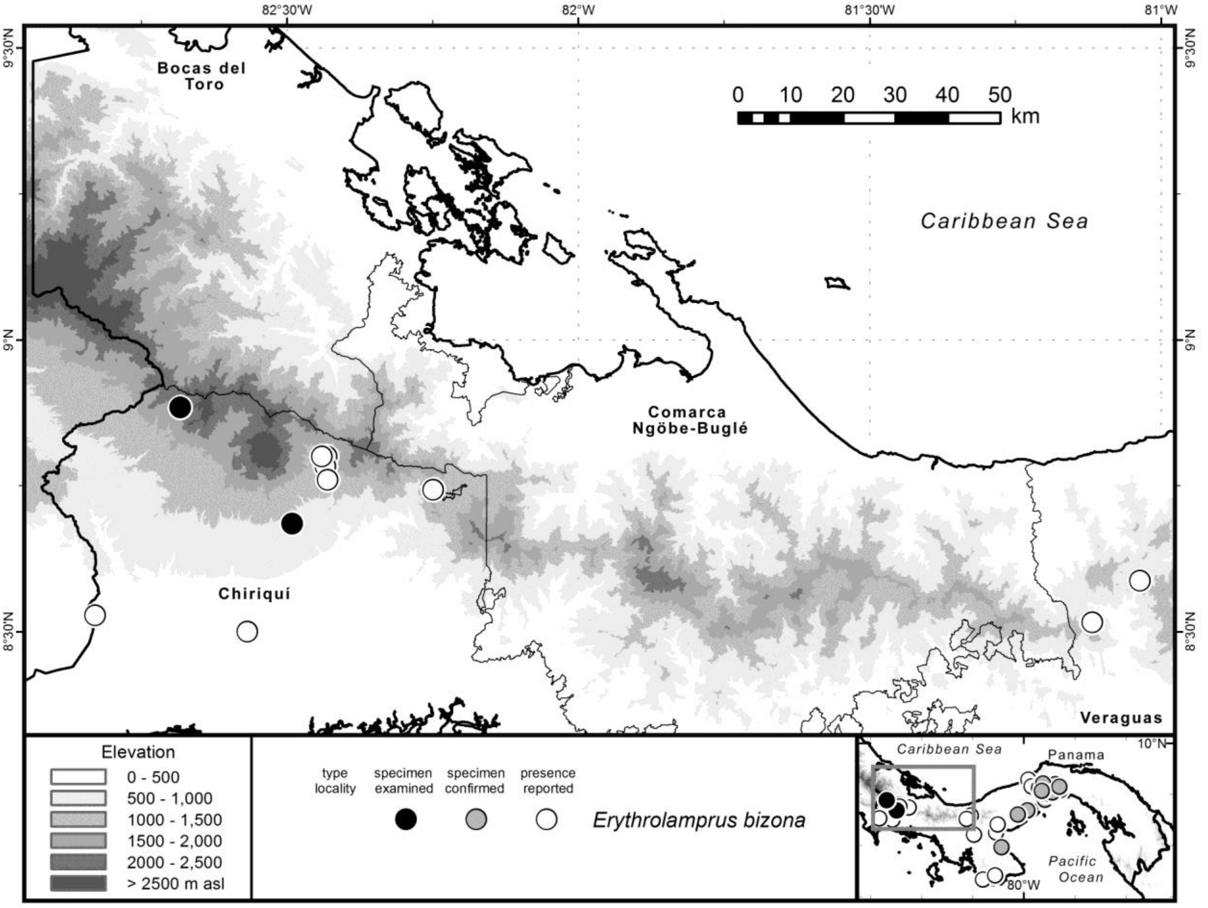
Erythrolamprus bizonus: Slevin (1942); Taylor (1951, 1954); Smith (1958); Auth (1994); Ibáñez et al. (1995); Martínez & Rodriguez (1994); Martínez et al. (1995).

Erythrolamprus aesculapii: Cope (1899: possibly); Barbour (1923); Dunn (1933); Wettstein (1934).

Erythrolamprus venustissimus: Cope (1876).

Syntypes. MHNG 464.30 as well as at MSNM and NMW, from Colombia.

Geographic distribution. Costa Rica to Colombia and Venezuela, 0–1910 m asl. In Panama, along the Pacific versant of western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, as well as along both versants of central and eastern Panama. In the Cordillera Central, reported from numerous sites along the Pacific versant up to ca. 1910 m asl.



Map 4.132: Distribution of *Erythrolamprus bizona.*

Diagnosis. This medium-sized snake (maximum TOL 1000 mm) with round pupils is unique among Panamanian tricolor (red-white or yellow-black) ringed snakes in having dyads of black rings in a way that broad red rings are separated by groups of narrow black-white-black rings, and smooth dorsals without apical pits arranged in 15—15—15 rows. It further differs from similarly ringed individuals of *Lampropeltis triangulum* in having the cloacal scute divided (vs. entire), and from *Erythrolamprus mimus* in having the first light ring behind the head bordered by two black rings and the posterior supralabials with black margins (vs. no black ring posterior to 1st white ring and posterior SPL without black margins).

Description. TOL to 1000 mm; tail short, TL/TOL = 0.10–0.13; D smooth, in 15—15—15 rows; V 180–204; SC 45–62; SPL 7; INL 7–9; loreal 1; Preoc 1–2; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Erythrolamprus bizona* is a bilobed organ with spines which are enlarged on the proximal portion and a terminal disk on each lobe.

Coloration in life. Body and tail with broad red rings separated by dyads of narrow black rings edging a narrow white or yellow ring; red and white or yellow scales with blackmarkings, black rings often edged by light-colored scales towards the red rings; D surface of head mostly black, light-colored parietal, labial, and snout regions with black scale margins; V surface of head light-colored with black markings; iris black.

Coloration in preservative. Similar to that in life, apart from that the red and possibly present yellow elements fade with time.

Natural history notes. Diurnal and terrestrial, feeding mainly on snakes which it usually swallows tail first, but also taking lizards. Defensive behavior includes dorsoventral flattening of the neck and anterior body. Bites can cause pain and swelling.

Remarks. My georeference for the records from "vicinity N of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is somewhat above the elevational maximum given as 1200 (Jaramillo et al. 2010) or 1250 m (Perez-Santos 1999) for Panama. A specimen photographed by Jeffrey Dietrich at Cerro Totuma, 1909 m, represents the highest record for this species so far (Solórzano 2004; Sasa et al. 2010). Together with this new upper elevational limit, the respective distances of less than 4 km between the records from Boquete and its vicinities (Perez-Santos 1999; CHP) as well as Cerro Totuma and the border of Bocas del Toro render the presence of *Erythrolamprus bizona* in this province plausible. Its occurrence in the Comarca Ngöbe-Buglé is rendered plausible by the records both E and W of it as well as the proximity of the records from La Fortuna and Cerro Mariposa to the Comarca's border.

***Erythrolamprus epinephelus* (Cope 1862)**

Fire-bellied Snake, Night Ground Snake, Northern Swampsnake; Falsa coral, Falsa coral de quebrada

Figure 4.108C; Map 4.133.

Leimadophis epinephalus or *L. e. juvenalis:* Swanson (1945); Dunn (1947); Smith (1958); Myers & Rand (1969); Myers (1977).

Leimadophis epinephelus: Breder (1946); Peters & Orejas-Miranda (1970).

Leimadophis taeniurus epinephalus: Dunn & Bailey (1939); Dunn (1937c).

Leimadophis taeniurus juvenalis: Dunn (1937c); Slevin (1942).

Leimadophis taeniurus juvenilis: Taylor (1951, 1954).

Liophis albiventris: Cope (1899).

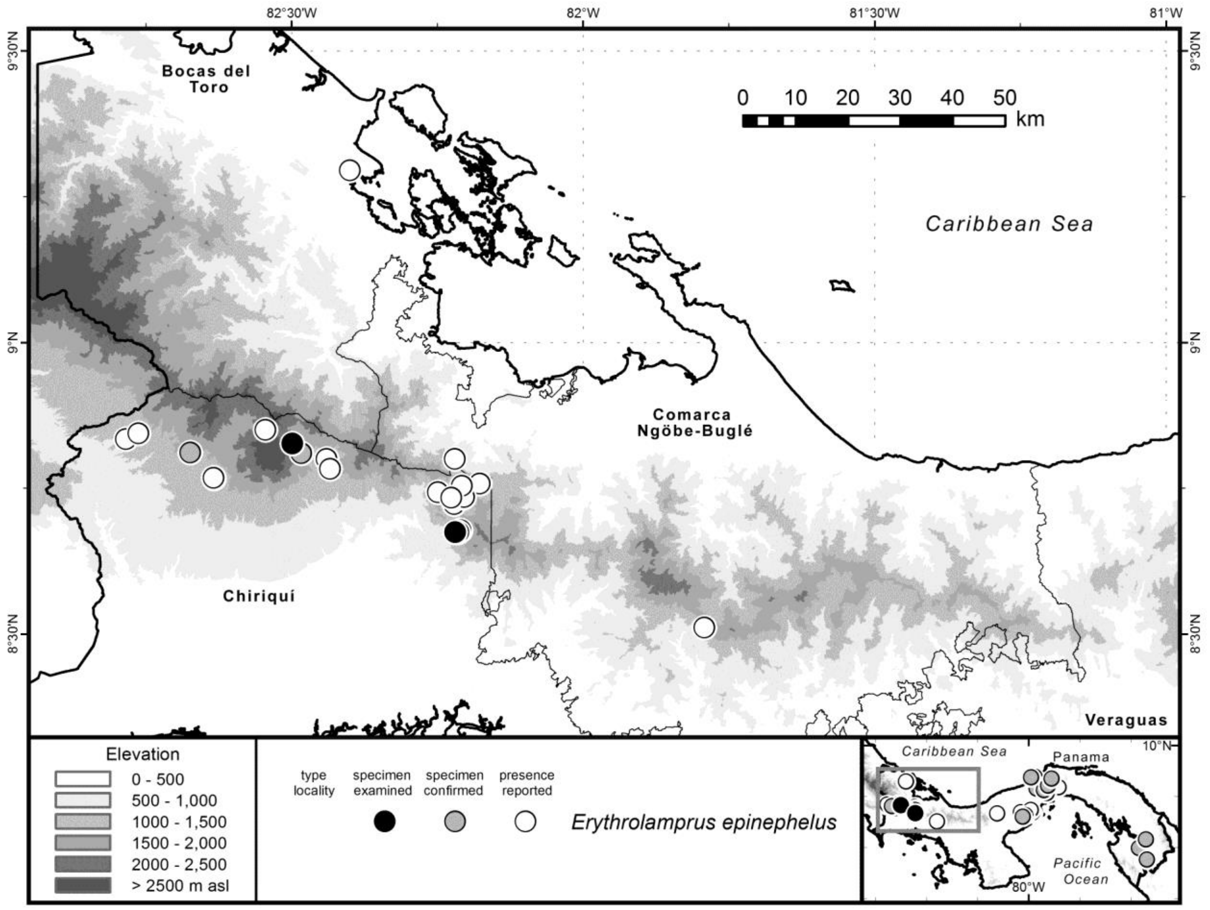
Liophis bimaculatus: Cope (1899).

Liophis cobella: Wettstein (1934); Taylor (1951, 1954).

Liophis epinephalus: Cope (1862a); Hofer & Bersier (2001); Savage (2002); McDiarmid & Savage (2005); Montero (2005); Ray (2009).

Liophis epinephelus: Cope (1862a); Boulenger (1894); Castillo et al. (1990); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1995, 1996, 1997, 2001); de Sousa (1999); Perez-Santos (1999); Young et al. (1999); Fundación PA.NA.M.A. (2007); Köhler (2008); Santos-Barrera et al. (2008); Savage & Watling (2009); Hamad (2009); Savage & Bolaños (2009); Carrizo (2010); Jaramillo et al. (2010); Köhler et al. (2010a); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010).

Holotype. ANSP 3688, from Truando, New Granada (= Río Truando, Colombia).



Map 4.133: Distribution of *Erythrolamprus epinephelus.*

Geographic distribution. Costa Rica to Colombia, Venezuela, and Peru, 0–2200 m asl (3500 m asl in South America). In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities chiefly along the Pacific versant up to ca. 2200 m asl.

Diagnosis. This medium-sized snake (maximum TOL 800 mm) with round pupils is readily distinguished from all other Panamanian snakes by its smooth dorsals arranged in 17—17—15 rows, divided cloacal scute, large eyes, and its olive dorsal coloration producing a coralsnake pattern of reddish and black bands when the body is bent or inflated, as well as its white or yellow lips and anterior ventral surfaces grading into bright orange posteriorly.

Description. TOL to 800 mm; SVL to 398 mm*; tail moderate, TL/TOL = 0.17–0.27; D smooth, in 17—17—15 rows; V 128–152; SC 44–80; SPL 7–10; INL 9–10; loreal 1; Preoc 1–2; Postoc 2; Tant 0–1, Tpost 1–3; cloacal scute divided; AP 1–2 at least on some anterior scales; eyes large, pupil round.

The hemipenis of *Erythrolamprus epinephelus* is a bilobed organ with a naked pedicel, spines along the truncus, and a terminal disk surrounded by a membranous flounce on each of the spinulate lobes.

Coloration in life. Apparently quite variable even within LCA. According to Savage (2002) and Solórzano (2004), Costa Rican individuals are reddish with black crossbands above, becoming darker with age, and below yellow green anteriorly grading into red with large black markings posteriorly (as shown in Plate 352 of Savage 2002; Fig. 112 and 113 of Solórzano 2004; Fig. 669 of Köhler 2008). All individuals which I have seen in Chiriquí had their D and upper L surfaces of body and tail olive with scale margins and skin between the scales exhibiting a conspicuous orange-black crossbanded pattern only when the animal is inflated or bent, their ventrolateral surfaces of body and tail rather uniformly lighter green, usually a dark L stripe along the tail, and their labials, chin, and throat region white to yellow grading into bright orange with very few to many large black markings posteriorly under body and tail (as shown in Plate 353 of Savage 2002; Fig. 670 of Köhler 2008).

The female SMF 89581 (Fig. 4.108C) was recorded as follows: D and upper portion of L surface of head Dark Brownish Olive (129), lower portion of L well as V surface of head white with Spectrum Yellow (55) pigment along the border of these two colors; D surface of body and tail Olive (30), bordered ventrolaterally by a Bunting Green (150) stripe occupying the 1st and 2nd row of D; edges of V scales Light Mauve (172D); central portion of V white on anterior part of body, grading into Burnt Orange (116) after 1st third of body; anterior margins of scales of anterior third of body between D scale rows 3–8 with alternating transverse bands (219A), upper third Chamois (123D).

Coloration in preservative. After 4–6 years in 70% ethanol, the D and L coloration of my examined specimens is largely brown dorsally but bluish gray on 1st and 2nd D row as well as where the oberhäutchen have been lost; the formerly orange venters are cream or white.

Natural history notes. Diurnal and terrestrial, feeding mainly on anurans. Defensive behavior includes dorsoventral flattening of the neck and anterior body which produces or emphasizes the coralsnake-like banded pattern. Five individuals were encountered active on the ground in forests or shade coffee plantations at daytime, a sixth under a rock at night.

Remarks. As the latest step in the taxonomic odyssey of this species, Grazziotin et al. (2012) transferred it to the genus *Erythrolamprus.* Savage & Bolaños (2009) clarified that the spelling *epinephalus* arose through a printer's error corrected on an errata sheet contained in the original issue, and that therefore *epinephelus* is the correct spelling of the specific epithet.

In 4 of the 6 individuals from which I recorded morphological data, the tail tips were missing. The specimen MHCH 2346 has only 7 SPL on the right side, which is the lowest number reported for this species so far.

The highest record from Panama which I could trace is CHP 5728 from "Sendero Los Quetzales, hacia Cerro Punta camino hacia Sitton" for which my georeference yields a SRTM elevation of 2198 m asl, which is well above the maximum elevation of 1980 m reported for Panama (Jaramillo et al. 2010). The records east and west of this political subdivision render the presence of *Erythrolamprus epinephelus* in Veraguas province plausible.

Another species traditionally placed in the genus *Liophis, Lygophis lineatus* (Linnaeus 1758), possibly ranges into my study area given that it occurs W to the lowlands of Veraguas and Cerro Hoya, as well as up to 550 or even 650 m asl (SRTM elevation for my georeference for CHP 3271) in Panama (Perez-Santos 1999; Jaramillo et al. 2010; CHP; see distribution map in Appendix 7).

Erythrolamprus mimus (Cope 1869)

Stripe-bellied False Coral, Central American False Coral; Coral falsa, Falsa coral de cabeza anillada

Figure 4.108D; Map 4.134.

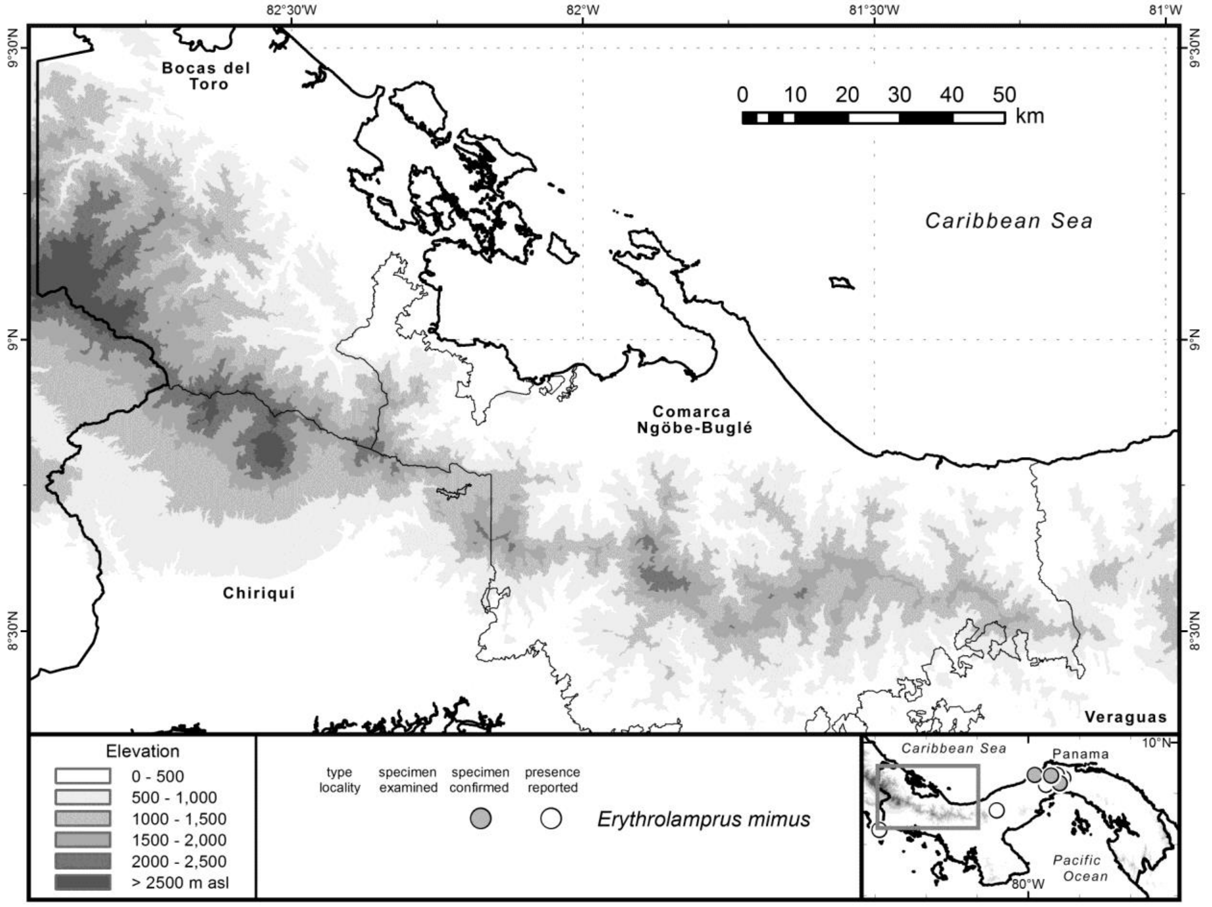
Opheomorphus mimus: Cope (1869).

Holotype. ANSP 3689, from "a mining district in the higher regions of Ecuador or New Grenada, but the exact locality I cannot fix" (Cope 1869).

Geographic distribution. Honduras to Colombia and Peru, 0–1460 m asl (2000 m asl in South America). In Panama, throughout the country along both versants including Bocas del

Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNGDOTH at 800 m asl.

Diagnosis. This medium-sized snake (maximum TOL 745 mm) with round pupils is unique among Panamanian tricolor (red-white or yellow-black) ringed snakes in having most or all black body rings somewhat divided by suffusions of light color, usually some to many black rings offset, and smooth dorsals without apical pits arranged in 15—15—15 rows. It further differs from *Erythrolamprus bizona* in having the first narrow light ring behind the head not bordered by a black ring posteriorly and the posterior supralabials without black margins (vs. a narrow black ring posterior to 1st white ring and posterior SPL with black margins).



Map 4.134: Distribution of *Erythrolamprus mimus.*

Description. TOL to 745 mm; SVL in Honduran specimens to 640 mm; tail short, TL/TOL = 0.10–0.16; D smooth, in 15—15—15 rows; V 171–199; SC 42–56; SPL 5–7; INL 7–10; loreal 1; Preoc 1–2; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Erythrolamprus mimus* is a bilobed organ; pedicel spinulate, truncus with enlarged spines and a naked asulcate area; apex with small spines and a terminal disk on each lobe.

Coloration in life. Body and tail with red rings separated by single black rings each edged by two narrow white or yellow rings; red and white or yellow scales with black markings; black rings usually suffused with light color dorsally and/or laterally in their centers; often at least some black rings offset on the two sides of the body; D surface of head mostly black anteriorly, light-colored parietal and posterior labial regions often suffused with red, may bear black markings but never with black scale margins; a single black nuchal collar bordered posteriorly by a narrow light ring; V surface of head immaculate light-colored; V surface of body and tail ringed as dorsum, but without light suffusions in black rings and often with a partially interrupted black stripe; iris black.

Coloration in preservative. Similar to that in life, apart from that the red and possibly present yellow elements fade with time.

Natural history notes. Diurnal and terrestrial, feeding mainly on snakes but also taking lizards. Defensive behavior includes dorsoventral flattening of the neck and anterior body as well as coiling up and displaying the tail. Bites can cause pain and swelling.

Remarks. Together with the presence on both versants in E Costa Rica (Savage 2002; Solórzano 2004), the records from central Panama and PNGDOTH render the presence of *Erythrolamprus mimus* in Bocas del Toro, Veraguas, and the Comarca Ngöbe-Buglé plausible.

***Geophis brachycephalus* (Cope 1871)**

Costa Rican Wormsnake, Earth Snake; Culebra de tierra, Culebra de tierra costarricense, Minadora

Figures 4.89A–B; 4.108E; Maps 4.18; 4.135.

Catastoma brachycephalum: Cope (1876).

Catostoma brachycephala: Wettstein (1934).

Catastoma dolichocephalum: Cope (1876).

Colobognathus brachycephalus: Cope (1871).

Colobognathus dolichocephalus: Cope (1871).

Dirosema brachycephalum: Boulenger (1894).

Elapoidis brachycephalus: Cope (1885).

Geophis bakeri: Taylor (1954).

Geophis brachycephala: Slevin (1942); Taylor (1951); Castillo et al. (1990: in part.); de Sousa (1999: in part.).

Geophis dolichocephala: Taylor (1951).

Geophis dolichocephalus: Taylor (1954).

Geophis hoffmanni: Boulenger (1894: in part.).

Geophis moesta: Taylor (1951).

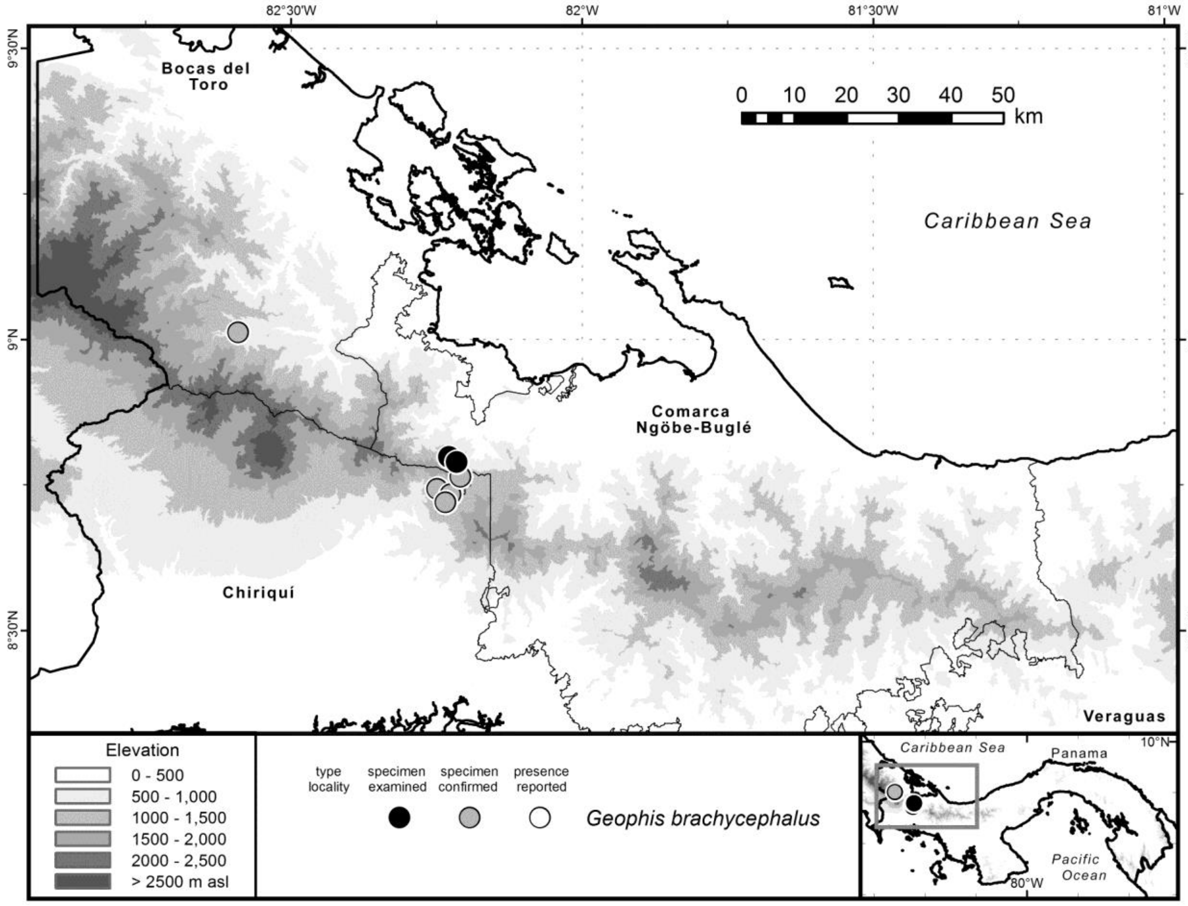
Geophis moestus: Taylor (1954).

Geophis nigroalbus: Downs (1967: in part.).

Geophis, species inquirenda: Myers (2003: in part.).

Holotype. ANSP 3337, juvenile male, from San José, Costa Rica (Savage & Watling 2008).

Geographic distribution. Endemic to Costa Rica and western Panama, 13–2230 m asl. In Panama, apparently restricted to the western portions of the country chiefly on the Caribbean versant, including Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from premontane elevations at Río Changena as well as from RFLF and surroundings up to ca. 1180 m asl.



Map 4.135: Distribution of *Geophis brachycephalus.*

Diagnosis. This small snake (maximum TOL 496 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis brachycephalus* differs from *G. championi* and *G. godmani* in having the supracaudal and at least the posterior dorsal scales keeled (vs. smooth), from *G. hoffmanni* in having 6 supralabials (vs. 5), from *G. talamancae* in having 169 or more total segmentals (vs. 171 or fewer) and in lacking blotched patterns in Panamanian specimens (vs. often present), from *G. tectus* in having a slightly bilobed hemipenis (vs. unilobed) as well as 48 or fewer subcaudals in males and 39 or fewer in females (vs. 44 or more in males, 42 or more in females), and from *Geophis* sp. in uncorrected p-distances of 0.6–1.2% in the 16S and 5.5–6% in the cyt-b fragment analyzed in chapter 4.1.9 (including data from Savage & Watling 2008).

Description. (including data from Savage & Watling 2008) TOL to 496 mm; SVL to 438 mm; tail short, TL/TOL = 0.12–0.22; D keeled at least on upper rows, keeling increasing posteriorly, striate, in 15—15—15 rows; supracaudals strongly keeled; V 129–149; SC 29–48; SPL 6; INL 6–7; loreal 1; Preoc 0; Postoc 1; Tant 0, Tpost 1; cloacal scute entire; AP 2, located subapically, barely distinct; eyes small to moderate, pupil vertically subelliptical.

The hemipenis of *Geophis brachycephalus* is a slightly bilobed organ; pedicel with spinules and two large spines distally; truncus with moderate spines; capitulum long and slender, about 2.5 times length of truncus on asulcate side, with spinulate calyces.

Coloration in life. For variability of blotched, banded, and striped D patterns in Costa Rican populations, see Savage (2002) and Savage & Watling (2008). Panamanian individuals dark brown to black above, some juveniles with a light nuchal collar, some adults with light tip of snout; chin and venter immaculate white to light gray; SC largely dark.

Coloration in preservative. Similar to that in life, often assuming a bluish or brownish hue.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; a "goo-eater" reported to feed chiefly on earthworms. The only individual in my collection referred to this species was found near the headwaters of Río Chiriquí Malí in BPPS, on the Caribbean versant just below the continental divide, upon the naked soil of a recent landslide around 23:00.

Remarks. In their revision of the *Geophis sieboldi* group in LCA, Savage & Watling redescribed *G. brachycephalus* and showed that most individuals formerly referred to this species from Chiriquí actually represent *G. talamancae,* while some others from western Panama were included in their new species, *G. tectus.* To my knowledge, no individuals of *G. brachycephalus* with red blotches or stripes are known from Panama. Still, the taxonomy and biogeography of the *G. brachycephalus* complex remain unsatisfactorily resolved as pointed out in chapter 4.1.9. As suggested by the repetitive use of the terms "usually" and "relatively" in the key of Savage & Watling (2008: p. 592), the assignment of a given individual from the Cordillera Central to one of the three nominal species on the basis of external morphology will remain guesswork in many cases, especially in young or otherwise unsexed individuals, or those with incomplete tails.

In view of the very uncertain taxonomy of specimens reported as *Geophis brachycephalus* in the past (e.g., records of Myers 1977, Castillo et al. 1990, and de Sousa 1999 from La Fortuna, that of Carrizo 2000 from Cerro Negro and that of Ray 2009 from Altos del María and PNGDOTH, as well as different MVUP specimens from La Fortuna and the Serranía de Talamanca), I classified all records and specimens which were not confirmed by Savage & Watling (2008) or examined by myself as *G.* cf. *brachycephalus* "reported" and omit them on Map 4.135. Considering the possibility that the records from Coclé and Veraguas mentioned above in parentheses might represent either *G. brachycephalus* or *G. tectus,* I include them in the synonymies of the latter species with the addition "probably" (see Appendix 6 for a full list of historic Panamanian records for *G. brachycephalus*).

As a consequence of their taxonomic revision, Savage & Watling (2008) restricted the distribution of *Geophis brachycephalus* to Costa Rica and western Panama. However, the point plotted for the specimen FMNH 130969 from "Río Changena" on their map of western Panama (Savage & Watling 2008: Fig. 15) lies on the lower Río Changuinola, a ubication which I consider erroneous. Rather, I assume this locality to be more or less synonymous with "Río Changena, ca 2400' (= ca. 732 m asl) specified in the FMNH catalogue for the specimens FMNH 130975–8 and 130979. If I am right, no lowland record of this species exists from Panama, while Savage and Watling (2008) presented doubts as if to the reliability of the Costa Rican lowland records, of which they already presented one less in their Costa Rican map (their Fig. 14) than did Savage (2002: Map 11.35). In view of the concentration of the Costa Rican records of this species in the Talamancan highlands (Savage & Watling 2008), one might suspect that *G. brachycephalus* actually is a species of premontane and higher elevations and that the few lowland records are based on somehow transported animals. Based on SMF 94577 collected at Volcán Barva, Costa Rica, Köhler et al. (2013) provided the highest elevation of 2230 m. Records of this species from Colombia go back to Downs' (1967) synonymization of *G. nigroalbus* with *G. brachycephalus* as clarified by Myers (2003), who confirmed the validity of the former species. Thus, the common name "Colombian Earth Snake" (Frank & Ramus 1995) should be avoided by all means.

I regard the presence of another species of the *Geophis sieboldi* group with 6 SPL, a supraocular, and D that are striate and keeled at least posteriorly, namely *G. bellus* Myers 2003, in Veraguas and my study area as possible in view of its distribution extending W to PNGDOTH and up to 855 m asl (Myers 2003; Ray 2009; see distribution map in Appendix 7). This species is unique among Panamanian *Geophis* and similar snakes in having the D and V surfaces entirely black except for a white nuchal band covering the parietals.

Geophis championi **Boulenger 1894**

Panamanian Earth Snake; Culebra de tierra, Minadora

Map 4.136.

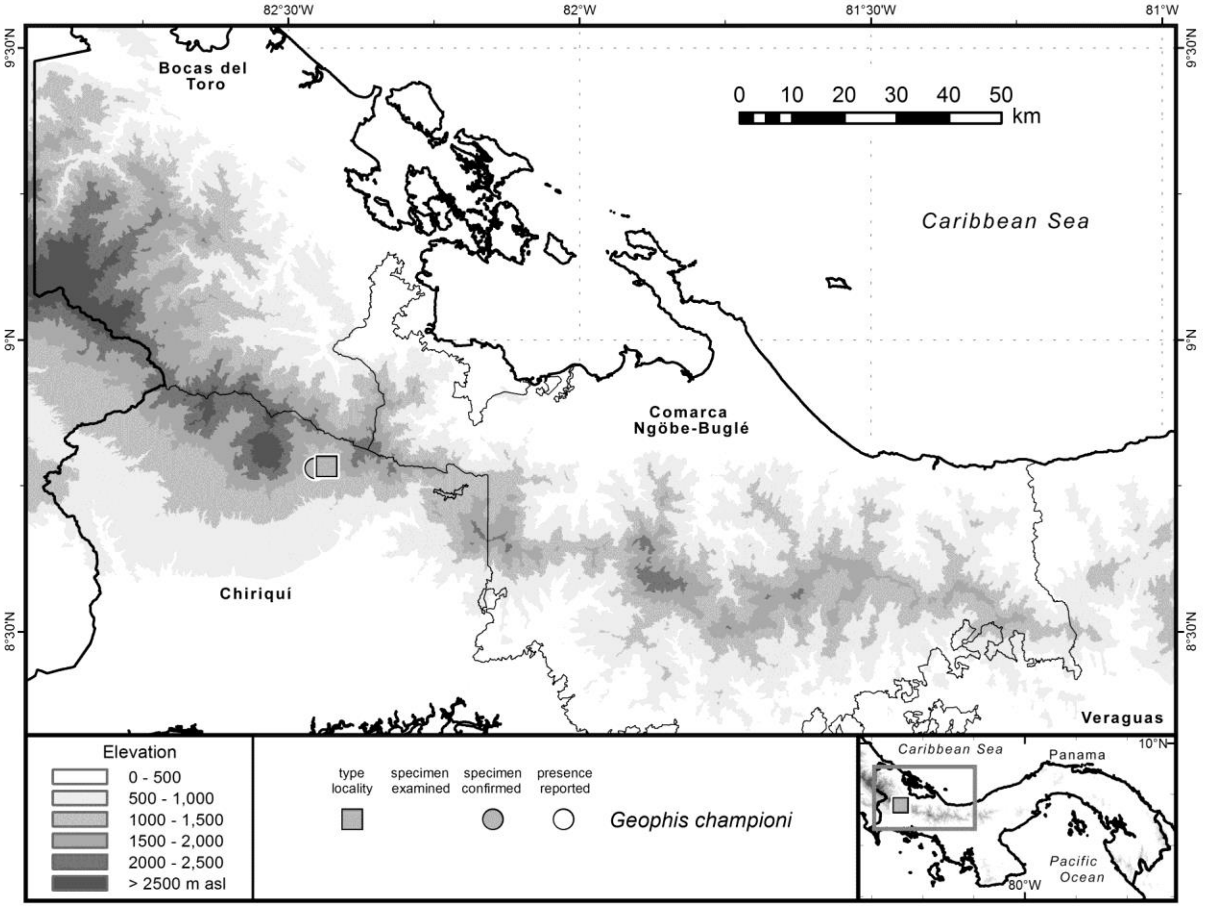
Geophis brachycephalus: Dunn (1942: in part., 1947: in part.).

Geophis brachycephala: Slevin (1942: in part., referring to CAS 78977)

Geophis champion: Smith (1958).

Holotype. BMNH 1946.1.1.77, male, from Chiriquí, Panama (Boquete according to Savage & Watling 2008).

Geographic distribution. Endemic to the Serranía de Talamanca of western Panama, where it is only known from Boquete and its vicinities at approximately 1100–1400 m asl.



Map 4.136: Distribution of *Geophis championi.*

Diagnosis. This small snake (maximum TOL 255 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis championi* is unique among *Geophis* in having smooth dorsal and supracaudal scales in combination with the presence of a supraocular, 156–158 total segmentals, a dark-banded venter, and the rostral projecting posteriorly so far between the internasals that it is almost in contact with the prefrontals in one of the known specimens (vs. rostral not or slightly projecting slightly between IN, separating them for at most half of their length) (including data from Downs 1967).

Description. (all data from Downs 1967) TOL to 255 mm; SVL to 224 mm; tail short, TL/TOL = 0.12–0.16; D smooth, striate above cloaca, in 15—15—15 rows; supracaudals smooth; V 125–130; SC 26–33; SPL 6; INL 6; loreal 1; Preoc 0; Postoc 1; Tant 0, Tpost 1; cloacal scute entire; AP 2 above cloaca; eyes small, pupil vertically subelliptical.

The hemipenis of *Geophis championi* is unknown.

Coloration in life. Probably similar to that in preservative.

Coloration in preservative. D and L surfaces brownish black, grading into lighter gray ventrolaterally and on head; scales of 1st D row partly dark and partly light; chin and gular region mostly light with scattered mottling; V surfaces of body and tail banded, with each V and anterior SC dark anteriorly and light posteriorly, and posterior SC completely dark.

Natural history notes. Probably similar habits as other *Geophis*.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Geophis championi,* and assigned that species to the IUCN category DD, in which it is also listed by the official IUCN Red List (IUCN 2014). *Geophis championi* is known from only two specimens probably representing two localities (see remarks), my georeferences for which lie ca. 2.2 km apart. That is, virtually nothing is known about the distribution, population, and natural history of this species, or any other aspect of its biology. Though the minimum convex polygon around my two georeferences allows for calculating an extent of occurrence (0.0044 km^2), this hardly makes any sense. Thus, I see no other option but to place it in the IUCN category "Data Deficient" (DD). Nevertheless, I calculated the EVS for *Geophis championi* as 6 (range) + 2 (persecution) + 5 (ecological distribution) = 13, indicating a high vulnerability.

Remarks. Though well distinguishable from all Panamanian congeners, this species is known from only two specimens, both of which were collected more than 70 years ago. Inhowfar this is the result of its special habitat requirements, unusual activity rhythms, pronounced fossoriality, low population density, or even of the fact that the two known specimens are actually very aberrant individuals of another species remains a matter of speculation.

The only documented elevational value for this species is 1370 m asl (Downs 1967), which was adhered to by Jaramillo et al. (2010). However, it is unclear to me how Downs (1967) obtained this value since the collector did not mention a discrete elevation for his sample of earthsnakes in his published report, referring only to "the vicinity" of Boquete and "the cafetals" (Slevin 1942: p. 474). My georeference set near the northern limits of the town yields a SRTM elevation of 1121 m. Savage & Watling (2008) give the locality for most of the CAS series collected by Joseph R. Slevin as "vic. Boquete, c. 1200 m". In my opinion, any elevation between 1100 and 1400 m makes sense for these vague locality denominators. In any case, the lower altitudinal limit of 750 m (Perez-Santos 1999) is clearly erroneous.

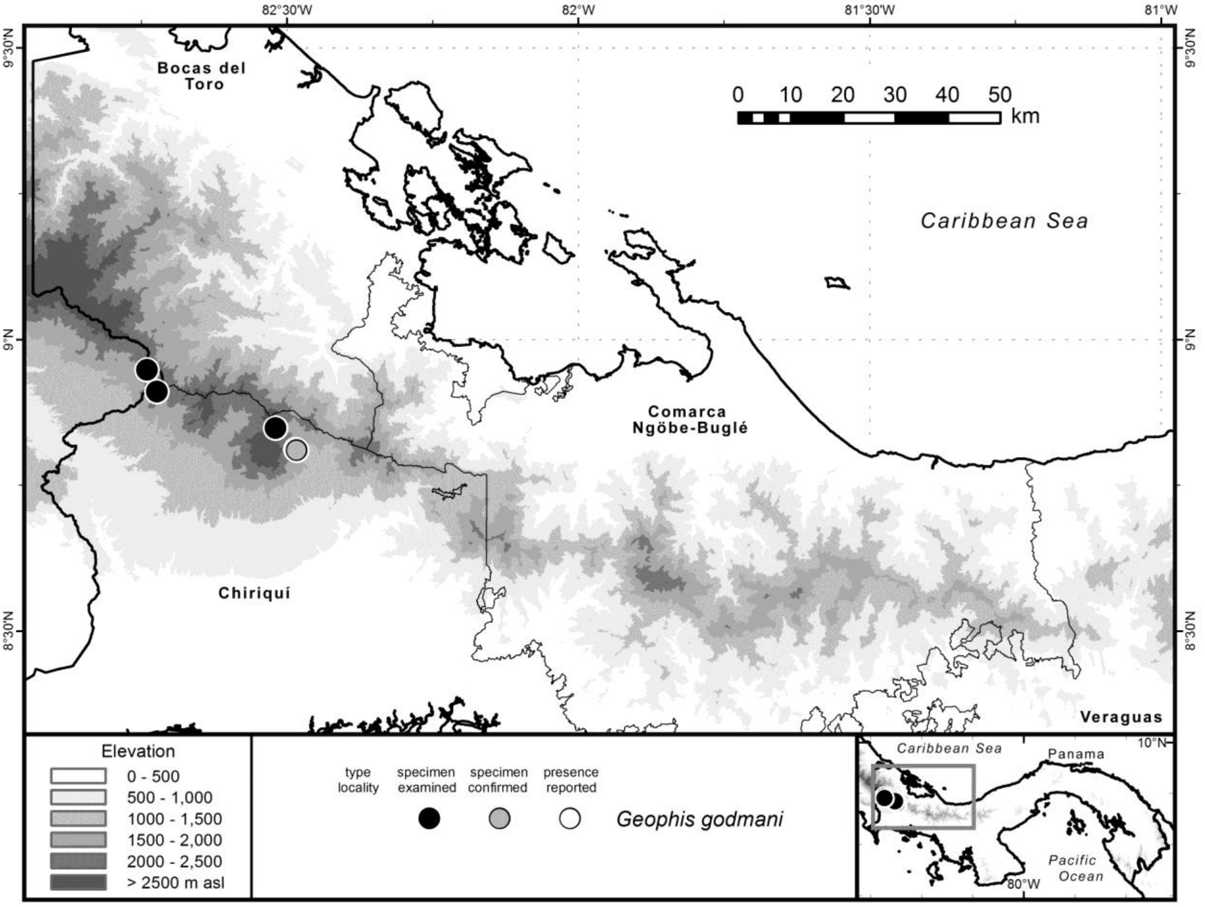
Geophis godmani Boulenger 1894

Godman's Earth Snake, Yellow-bellied Wormsnake; Culebra de tierra de vientre amarillo, Minadora

Figures 4.88A–D; 4.108F; Map 4.137.

Lectotype. BMNH 1946.1.6.41, from Irazú, Costa Rica (Downs 1967).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and western Panama, 1000–2350 m asl. In Panama, along the Serranía de Talamanca of Bocas del Toro and Chiriquí east to the Boquete area, reported from lower montane elevations of approximately 1600–2350 m asl.



Map 4.137: Distribution of *Geophis godmani.*

Diagnosis. This small snake (maximum TOL 450 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis godmani* is immediately distinguished from all other *Geophis* by the absence of a supraocular allowing the parietal to contact both the orbit and the prefrontal, in combination with smooth dorsal and supracaudal scales and a yellow ventral ground color in life.

Description. (including data from Downs 1967) TOL to 450 mm; SVL to 349 mm; tail short, TL/TOL = 0.13–0.18; D smooth, striate above cloaca, in 15—15—15 rows; supracaudals smooth; V 132–145; SC 24–38; SPL 6; INL 6–7; loreal 1; Preoc 0; Postoc 0–1; Tant 0, Tpost 1; cloacal scute entire; AP 0; eyes small, pupil vertically subelliptical.

The hemipenis of *Geophis godmani* is a unilobed organ with a naked pedicel; truncus with spines around distalmost portion, apex long, with spinulate calyces.

Coloration in life. D and L surfaces of head and body largely to completely black; V surfaces white in juveniles and yellow in adults, immaculate or with dark brown to black mottling that may fuse to form crossbands on the posterior portions of V and SC; light V ground color encroaching onto L and D portions of body and head in varying degrees, that is, especially rostral, nasal, and IN, as well as singular SPL and D, or margins of some to most D, often suffused with or entirely white or yellow; iris black.

The male SMF 89565 was recorded as follows: D ground color Jet Black (89) with irregularly pronounced Spectrum Yellow (55) scale margins and sparse mottling on body and tail; V ground color Spectrum Yellow (55) with a suggestion of Orange Yellow (18) increasing from about midbody towards the head; chin region and margins of V and SC scales mottled with Jet Black (89); snout Warm Buff (118) with a suggestion of Orange Yellow (18).

Coloration in preservative. After 4.5–6 years in 70% ethanol, the coloration is similar to that in life, except that the yellow tonaities of the adults have faded to cream or light brown.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; a "goo-eater" reported to feed chiefly on earthworms. In Costa Rica, Solórzano (2004) found an aggregation of 16 individuals together with one *Geophis brachycephalus* and one *Rhadinaea serperaster* in the soil. On 05.07.2008, the adult male SMF 89565 was found as it lay injured on the dirt road at Jurutungo, next to the finca of Porfírio Yangüez, at 17:00 after some rain. Six days later, the male SMF 89566 was rescued from a flock of chicken attacking it on the grounds of the finca around 09:30. The remaining 3 individuals of my Panamanian sample were discovered under dead wood. The female MHCH 2317 had 3 palpable eggs when caught on 22.04.2009.

Remarks. While Downs (1967) reported a small postocular posteroventral to orbit to be present in 5 of his 11 examined specimens, none of my six examined specimens has any.

Three of the 4 specimens from Jurutungo have 7 INL at least on one side, which is the highest number reported for this species so far. The extent of yellow coloration on the snout is very variable among my Panamanian specimens, ranging from bright yellow nasals, IN, and rostral in SMF 89565 over a mere suffusion with yellowish hues on these scales in SMF 89566 to the yellow suffusions restricted to anteroventral to nostrils in MHCH 2317. Considerable dark V mottling and banding is present in all my examined specimens. Apart from SMF 89770, all have the posterior edges of most V and SC, except near the head, with continuous dark borders that are broadest midventrally; MHCH 2318 even has almost the entire V surface black over the posterior two-thirds of its body.

The small distances between the border of Bocas del Toro and the respective records from Jurutungo (< 2 km) and Sendero Quetzales (< 3 km) render the occurrence of *Geophis godmani* in this province plausible. The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible. The specimen SMF 89770 was collected along Sendero Quetzales near Refugio Las Rocas at an elevation of 2354 m asl, which is more than 150 m higher than the maximum of 2200 m reported previously for this species (Solórzano 2004; Sasa et al. 2010). As detailed by Myers (2003) and Savage & Watling (2008), the lowland records from "Panama Sabanas" derive from specimens obtained in the course of the Panama snake census that were mislabeled and actually collected at Finca Lérida. This erroneous locality is likely to underly Perez-Santos' (1999) lower elevational limit of 100 m.

Another species of the *Geophis championi* group lacking supraoculars, *G. downsi* Savage 1981, occurs close to the Panamanian border in Costa Rica. It is hitherto only known from five specimens from around its type locality at Las Cruces, which is 5.6 airline km from the Panamanian border (Savage & Watling 2008; see map in Appendix 7). Thus, according to the criteria applied herein, its presence in Panama and my study area is merely judged "possible", though it seems highly likely that this snake will eventually be found in western Chiriquí next to Las Cruces, i.e., around Río Sereno and Santa Clara. *Geophis downsi* is readily distinguished from *G. godmani* by its keeled supracaudal and posterior D scales.

***Geophis hoffmanni* (Peters 1859)**

Hoffmann's Earthsnake, Plain Wormsnake; Culebra de tierra común, Minadora

Figures 4.88E–H; 4.108G; Map 4.138.

Colobognathus hoffmanni: Peters (1859).

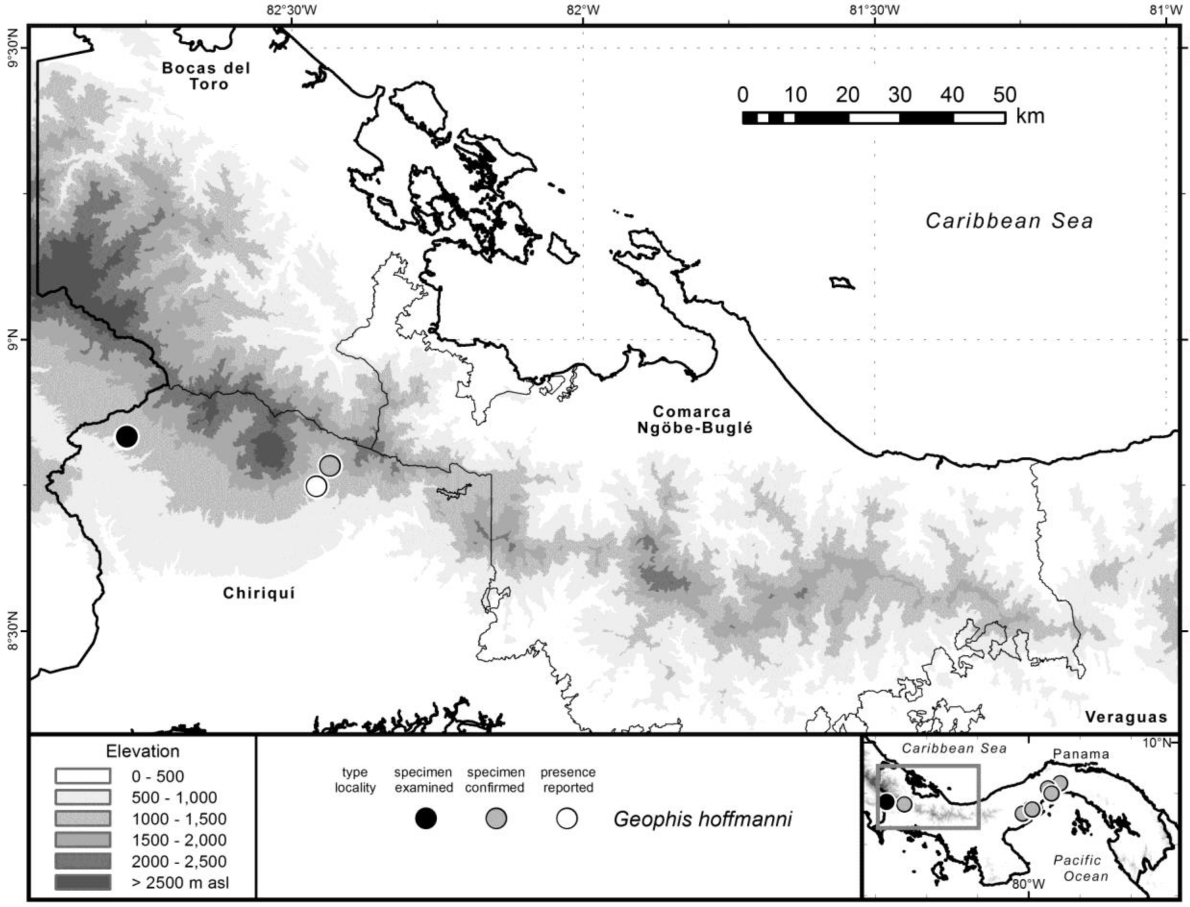
Geophis acutirostris: Taylor (1954).

Geophis brachycephalus: Slevin (1942: in part., referring to CAS 78976, 79033).

Rhabdosoma bicolor: Cope (1885).

Lectotype. ZMB 1870, adult female, from Costa Rica (Downs 1967).

Geographic distribution. Honduras to Colombia, 20–2100 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from Santa Clara and the Boquete area as well as Valle de Antón and PNAC, up to 1250 m asl.



Map 4.138: Distribution of *Geophis hoffmanni.*

Diagnosis. This small snake (maximum TOL 300 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis hoffmanni* differs from all other Panamanian *Geophis* in having only 5 supralabials (vs. 6) with a single very large one posterior to orbit that contacts the parietal (vs. two SPL posterior to orbit with the penultimate one enlarged and contacting the parietal) and smooth dorsals except above cloaca.

Description. (including data from Downs 1967) TOL to 300 mm; SVL to 260 mm; tail short, TL/TOL = 0.13–0.17; D smooth except some keeled above cloaca, in 15—15—15 rows;

supracaudals smooth; V 117–135; SC 23–37; SPL 5, rarely 4 by fusion of 3rd and 4th; INL 4–7; loreal 1; Preoc 0; Postoc 0–1; Tant 0, Tpost 0 or 1 (see remarks); cloacal scute entire; AP 0*–2 (see remarks); eyes moderate, pupil vertically subelliptical.

The hemipenis of *Geophis hoffmanni* is a slightly bilobed organ with a spiculate pedicel bearing 2–3 moderate spines distally; truncus with many spines, apex with spinulate calyces.

Coloration in life. D and L surfaces dark brown to black, becoming somewhat lighter on head; V surfaces unicolor white to gray, grading into darker gray or brown towards posteriorly under tail and on chin, immaculate or with dark anterior and/or L portions of V; a light nuchal collar in some juveniles; iris black.

The male SMF 91549 was recorded as follows: D ground color Jet Black (89), grading into Sepia (219) ventrolaterally; D and L surfaces of head Sepia (219); V surface of head Warm Sepia (221A), grading into Pale Neutral Gray (86) posteriorly; V ground color Pale Neutral Gray (86) with a suggestion of Light Neutral Gray (85), grading into Medium Neutral Gray (84) under tail; iris Jet Black (89); tongue Chestnut (32) with Pale Neutral Gray (86) tips.

The male SMF 91550, apparently about to shed its skin, was recorded as follows: D ground color Dark Neutral Gray (83) with a suggestion of Blackish Neutral Gray (82), grading into Medium Neutral Gray (84) ventrolaterally; D and L surfaces of head Medium Neutral Gray (84) with a suggestion of Dark Neutral Gray (83); V ground color Pale Neutral Gray (86), grading into Medium Neutral Gray (84) under tail and into Glaucous (79) on chin; iris Blackish Neutral Gray (82); tongue Antique Brown with Pale Neutral Gray (86) tips.

Coloration in preservative. After 4 years in 70% ethanol, the coloration of the 4 specimens from Santa Clara is similar to that in life, but has assumed a slightly bluish or lavender hue.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; a "goo-eater" reported to feed chiefly on earthworms. While two previous visits of several days each did not yield a single specimen, four individuals were found between 18.–20.06.2010 on the Finca Ecológica in Santa Clara. On an open meadow, the specimen SMF 91549 was found around 01:50 actively moving over loose soil, whereas SMF 91550 was dug out of nearby loose soil the next day around noon. Along the edge of a shade coffee plantation close to the Abarrotería La Sorpresa, SMF 91548 (containing 3 palpable eggs) was discovered beneath a large plastic bag filled with trash at 14:00, and MHCH 2319 beneath a fallen bromeliad around 20:00.

Remarks. Downs (1967: pp. 155–6) designated ZMB 1870 as the lectotype for this species, not ZMB 4003 as partially stated by Savage & Watling (2008: p. 588; in Appendix 4 on p. 598 the correct specimen is given). The enlarged scale bordering the 5th SPL and the parietal has variously been called a temporal (Solórzano 2004) or a postsupralabial (Savage & Watling 2008), probably owing to its position somewhat inserted between these two shields in some specimens. If it is called a postsupralabial, then there are no temporals at all in this species. Fusions of SPL or IN with PF occur in this species and in the latter variant were the motivation for Taylor (1954) to describe *Geophis acutirostris,* exclusion of loreals from the orbit and extensions of parietals to the orbit separating the supraocular and Postoc (if present) also occur with some frequency (Downs 1967; Savage 2002; Savage & Watling 2008). While Downs (1967: p. 156) stated this species to have paired AP above vent, I could not find any AP in none of my examined specimens.

Together with the distribution along the both versants of Costa Rica (Savage 2002; Solórzano 2004), the records from central Panama render the presence of *Geophis hoffmanni* in Bocas del Toro, Veraguas, and the Comarca Ngöbe-Buglé plausible. The specimens AH and I collected at Santa Clara up to 1209 m asl, as well as the ca. 1220 m I assigned to the Boquete record of Dunn (1947; elevation of "headquarters") document this species to occur at much higher elevations in Panama than the maximum of 750 m reported by Jaramillo et al. (2010) and render the maximum of 1250 m given by Perez-Santos (1999) plausible.

Geophis talamancae Lips & Savage 1994

Black-tailed Wormsnake, Talamancan Earthsnake; Culebra de tierra de cola negra, Minadora

Figures 4.89E–F; 4.108H; Maps 4.18; 4.139.

Geophis brachycephala: Slevin (1942: in part.).

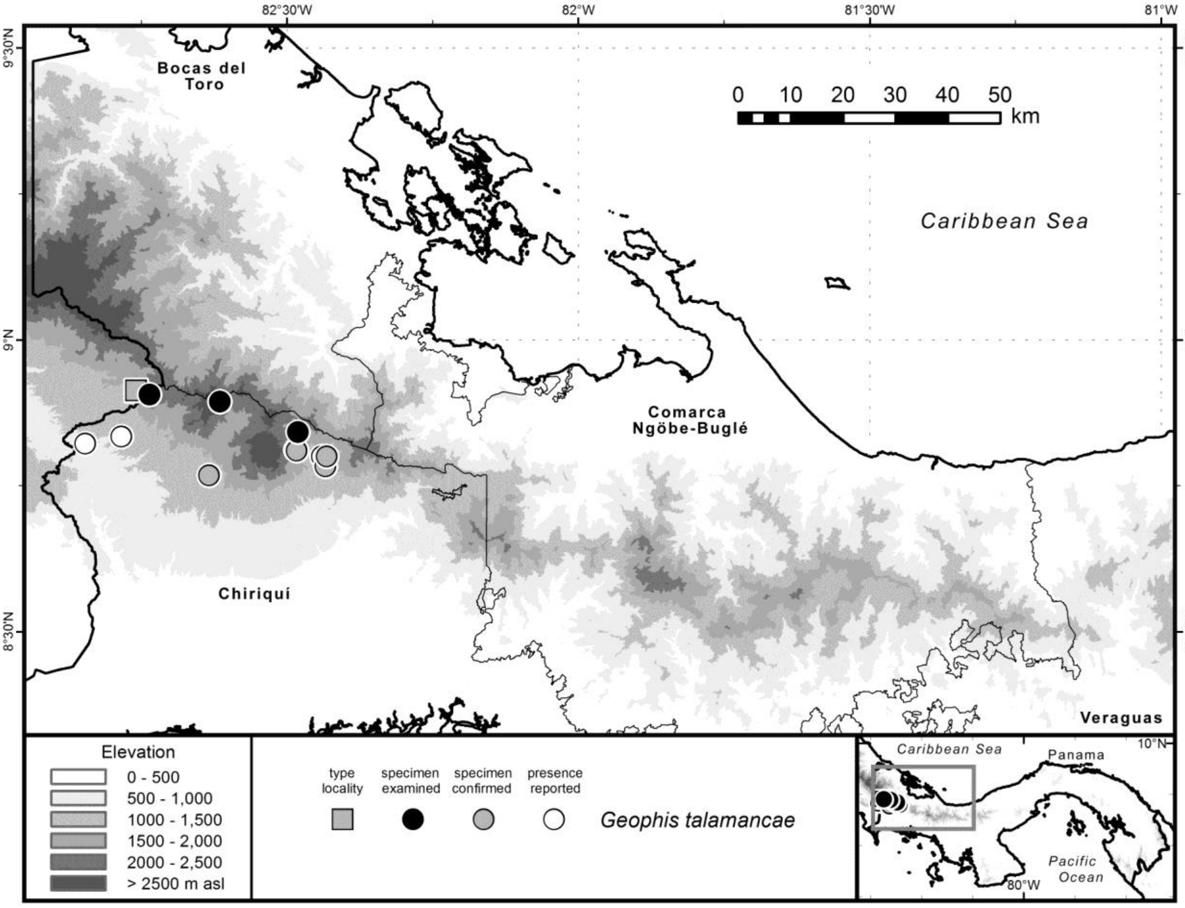
Geophis brachycephalus: Dunn (1942, 1947); Smith (1958); Downs (1967); Peters & Orejas-Miranda (1970); Auth (1994); Perez-Santos (1999); Young et al. (1999); Ibáñez et al. (2001); Savage (2002: in part.); Solórzano (2002: in part.); Myers (2003); Solórzano (2002: in part.); Fundación PA.NA.M.A. (2007); Köhler (2008); all in part.

Holotype. LACM 147169, subadult female, from "Costa Rica: Puntarenas Province: Cantón Coto Brus, Zona Protectora Las Tablas, Finca Jaguar, 1800 m" (Lips & Savage 1994).

Geographic distribution. Endemic to the Talamancan highlands of eastern Costa Rica and western Panama, 910–2120 m asl. In Panama, reported from numerous localities along the Pacific versant of the Serranía de Talamanca in Chiriquí (probably also present in Bocas del Toro), 910–2120 m asl.

Diagnosis. This small snake (maximum TOL 351 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis talamancae* differs from *G. championi* and *G. godmani* in having the supracaudal and at least the posterior dorsal scales keeled (vs.

smooth), from *G. hoffmanni* in having 6 supralabials (vs. 5), from *G. brachycephalus* in having 171 or fewer total segmentals (vs. 169 or more) and in often exhibiting a pattern of red lateral blotches on posterior portions of body (vs. not present in Panamanian specimens), from *G. tectus* in having a slightly bilobed hemipenis (vs. unilobed), 41 or fewer subcaudals in males and 38 or fewer in females (vs. 44 or more in males, 42 or more in females), as well as 171 or fewer total segmentals (vs. 175 or more), and from *Geophis* sp. in having 171 or fewer total segmentals (vs. usually 171 or more, 166 in one specimen) and in often exhibiting a pattern of red lateral blotches on posterior portions of body (vs. not present in examined specimens), as well as in uncorrected p-distances of 1.9–2.7% in the 16S fragment analyzed in chapter 4.1.9 (including data from Savage & Watling 2008).



Map 4.139: Distribution of *Geophis talamancae.*

Description. (including data from Savage & Watling 2008) TOL to 351 mm; SVL to 292 mm; tail short, TL/TOL = 0.10–0.20; D keeled at least on upper rows, keeling increasing posteriorly, striate, in 15—15—15 rows; supracaudals strongly keeled; V 118–139; SC 23–41; SPL 6; INL 6–7; loreal 1; Preoc 0; Postoc 1; Tant 0, Tpost 1; cloacal scute entire; AP 2, located subapically, barely distinct; eyes small, pupil vertically subelliptical.

The hemipenis of *Geophis talamancae* (Myers 2003: Fig. 20A) is a slightly bilobed organ; pedicel with spinules and two or three large spines distally; truncus with moderate spines; capitulum robust and relatively short, about 2 times length of truncus on asulcate side, with spinulate calyces.

Coloration in life. D and L surfaces dark brown to black, uniform or posterior portion of body with a pattern of partly offset red L blotches, at least some of which meet on middorsum, and some of which may fuse to form longitudinal bands on either or both sides; some juveniles with a light nuchal collar; V surfaces of head and body uniform white to cream or with dark spots, mottling, bands, or lines usually increasing posteriorly and under head towards chin; SC with dark banding or entirely black.

The female SMF 89567 (Fig. 4.108H) was recorded as follows: D and L ground color Sepia (119); L scales of body and tail with very narrow Pearl Gray (81) margins; body with 13 more or less offset pairs of Crimson (108) L blotches, most of which meet on middorsum to form transverse bands; V surfaces of body and head dirty white with a suggestion of Pearl Gray (81), locally with shadings of Pale Pinkish Buff (121D), with sparsely distributed fine Sepia (119) mottling on venter; chin region, infralabials and L edges of V mottled with Sepia (119); anal plate and subcaudals Sepia (119) with Pearl Gray Margins; iris Jet Black (89).

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 89567 is similar to that in life, apart from having assumed a slightly bluish hue and the red markings having faded to cream below and light brown above. After an unknown period of preservation in an unknown preservative, SMF 90182 is dark brown with cream light markings.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; a "goo-eater" probably feeding largely on earthworms. Slevin (1942) found "beetle remains" in stomach contents obtained from his sample from Boquete and surroundings that consisted mostly of *Geophis talamancae.* SMF 89567 was discovered coiled up under a log at 19:00.

Conservation. Jaramillo et al. (2010) calculated an EVS of 10 for *Geophis talamancae* and assigned that species to the IUCN category DD, while the official IUCN Red List (IUCN 2014) lists it as EN based on criterion B1ab(iii). I calculated the EVS for this *G. talamancae* as 4 (range) + 4 (persecution) + 4 (ecological distribution) = 12, indicating a high vulnerability. Though in the meantime more than 5 localities have become known (eliminating the subcriterion "a"), its extent of occurrence of just 449 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1b(iii).

Remarks. As discussed in chapter 4.1.9 and the remarks for *Geophis brachycephalus,* the taxonomy and biogeography of the *G. brachycephalus* complex remain unsatisfactorily resolved. Based exclusively on the holotype, Lips & Savage (1994) and consequently also Savage (2002) and Solórzano (2004) stated *G. talamancae* to lack apical pits, while the latter two authors noted 2 AP for *G. brachycephalus.* My examined specimens assigned to any of the species of the *G. brachycephalus* complex have 2 AP, though these are located somewhat subapically, i.e., about halfway between the apex and the broadest portion of a given dorsal scale, and rather wide and shallow what makes them difficultly discernible. However, in the specimen SMF 89567 which I collected at Jurutungo, close to the type locality of *G. talamancae,* I could only find extremely weak AP on singular scales, whereas the AP are also weakly but way better developed and more evenly distributed in the specimen JFB 055 from Las Nubes which I assigned to this species based on morphology only.

In view of the distribution of *Geophis talamancae* and *G. brachycephalus* as documented by Savage & Watling (2008) and herein, I assigned specimens UMMZ 147996 from "Finca Santa Clara" and UMMZ 147997 from "Río Candela valley", both reported by Perez-Santos (1999), to *G. talamancae.* For the latter, I used the georeference of UMMZ 147779 whose collection site is given as "Río Candela valley, on road from Sereno to Río Candela" by the same author. This georeference yields a SRTM elevation of 909 m asl, which is the lowest elevation reported for this species so far, while the specimen SMF 90182 given to JFB from the collection at Las Nubes (field no. JFB 055) comes from 2117 m, which is the highest elevation reported for this species so far (Savage & Watling 2008). Together with the altitudinal distribution as documented herein, the small distances between the border of Bocas del Toro and the respective records from Jurutungo (ca. 3 km), las Nubes (< 1.5 km), and Bajo Mono (< 3 km) render the occurrence of *Geophis talamancae* in this province plausible. The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible.

Geophis tectus **Savage & Watling 2008**

Earthsnake, Wormsnake; Culebra de tierra, Minadora

Figures 4.89G–H; 4.109A; Maps 4.18; 4.140.

Geophis brachycephala: Slevin (1942: in part.).

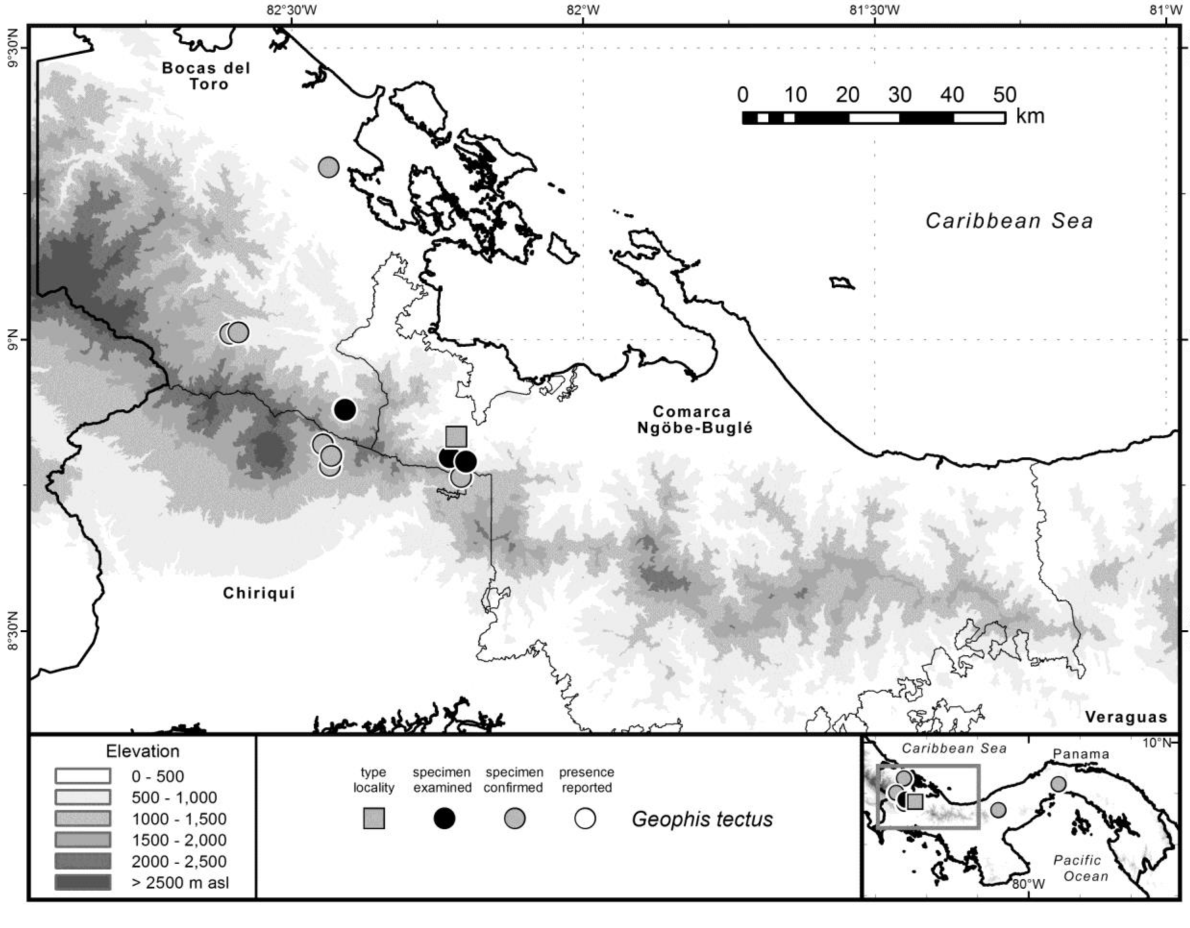
Geophis brachycephalus: Dunn (1942, 1947: all in part.); Smith (1958: in part.); Downs (1967: in part.); Peters & Orejas-Miranda (1970: in part.); Myers (1977, 2003: all in part.); Auth (1994: in part.); Perez-Santos (1999: in part.); Young et al. (1999: in part.); Carrizo (2000: probably); Ibáñez et al. (2001: in part.); Savage (2002: in part.); Solórzano (2004: in part.); Fundación PA.NA.M.A. (2007: in part.); Köhler (2008: in part.); Ray (2009: probably).

Geophis sp.: Perez-Santos (1999: in part., referring to KU 110701).

Geophis, species inquirenda: Myers (2003: in part.).

Holotype. MCZ 19326, male, from "La Loma (= Buena Vista), Distrito de Chiriquí Grande, Provincia de Bocas del Toro, Panama; c. 8°50'N, 82°13'W (300 m)" (Savage & Watling 2008; today this place pertains to the Comarca Ngöbe-Buglé).

Geographic distribution. Endemic to Panama, 40–1710 m asl. In Panama, along both versants of western Panama including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, as well as in Pacific versant central Panama. In the Cordillera Central, reported from PNGDOTH and several sites along both versants of the Serranía de Talamanca as well as the Fortuna area, up to ca. 1710 m asl.



Map 4.140: Distribution of *Geophis tectus.*

Diagnosis. This small snake (maximum TOL 381 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis tectus* differs from *G. championi* and *G. godmani* in having the supracaudal and at least the posterior dorsal scales keeled (vs. smooth), from *G. hoffmanni* in having 6 supralabials (vs. 5), from *G. brachycephalus* in having a unilobed hemipenis (vs. slightly bilobed) as well as 44 or more subcaudals in males and 42 or more in females (vs. 48 or fewer in males and 39 or fewer in females), from *G. talamancae* in having 175 or more total segmentals (vs. 171 or fewer), and from *Geophis* sp. in having 42 or more subcaudals in females (vs. 37 or fewer) as well as in uncorrected p-distances of 1.1–1.8% in the 16S, 3.1–3.3% in the COI, and 3.1–5.5% in the cyt-b fragment analyzed in chapter 4.1.9 (including data from Savage & Watling 2008).

Description. (including data from Savage & Watling 2008) TOL to 381 mm; SVL to 310 mm; tail short, TL/TOL = 0.17–0.22; D keeled at least on upper rows, keeling increasing posteriorly, striate, in 15—15—15 rows; supracaudals strongly keeled; V 133–140; SC 42–50; SPL 6; INL 6–8; loreal 1; Preoc 0; Postoc 1; Tant 0, Tpost 1; cloacal scute entire; AP 2, located subapically, barely distinct; eyes small to moderate, pupil vertically subelliptical.

The hemipenis of *Geophis tectus* (Myers 2003: Fig. 20B) is a unilobed organ; pedicel with spinules and two large spines distally; truncus with moderate spines; capitulum long and slender, about 2.5 times length of truncus on asulcate side, with spinulate calyces.

Coloration in life. All individuals from western Panama (for the blotched specimen from central Panama see Fig. 18 in Myers 2003) are dark brown to black above, some juveniles with a light nuchal collar, some adults with light tip of snout; V surfaces of head cream with dark pigmentation increasing towards INL and chin; venter immaculate white to light cream, in some individuals with a scarce dark mottling or with dark bands; SC white to cream, in many specimens banded with dark, then often becoming completely dark posteriorly.

Coloration in preservative. Similar to that in life, with a slight bluish hue.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; probably similar in its habits to other *Geophis*. The female SMF 91551 was encountered while it was moving through the leaf litter at 23:17. The animal was very close to shedding its skin and had small white globules (which I believe to be eggs) beneath some posterior ventrals.

Conservation. Jaramillo et al. (2010) calculated an EVS of 10 for *Geophis tectus* and assigned that species to the IUCN category DD, while the official IUCN Red List (IUCN 2014) lists it as LC. I calculated the EVS for this *G. tectus* as 5 (range) + 4 (persecution) + 3 (ecological distribution) = 12, indicating a high vulnerability. Its extent of occurrence of 8870 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category VU according to IUCN (2001) criterion B1b(iii).

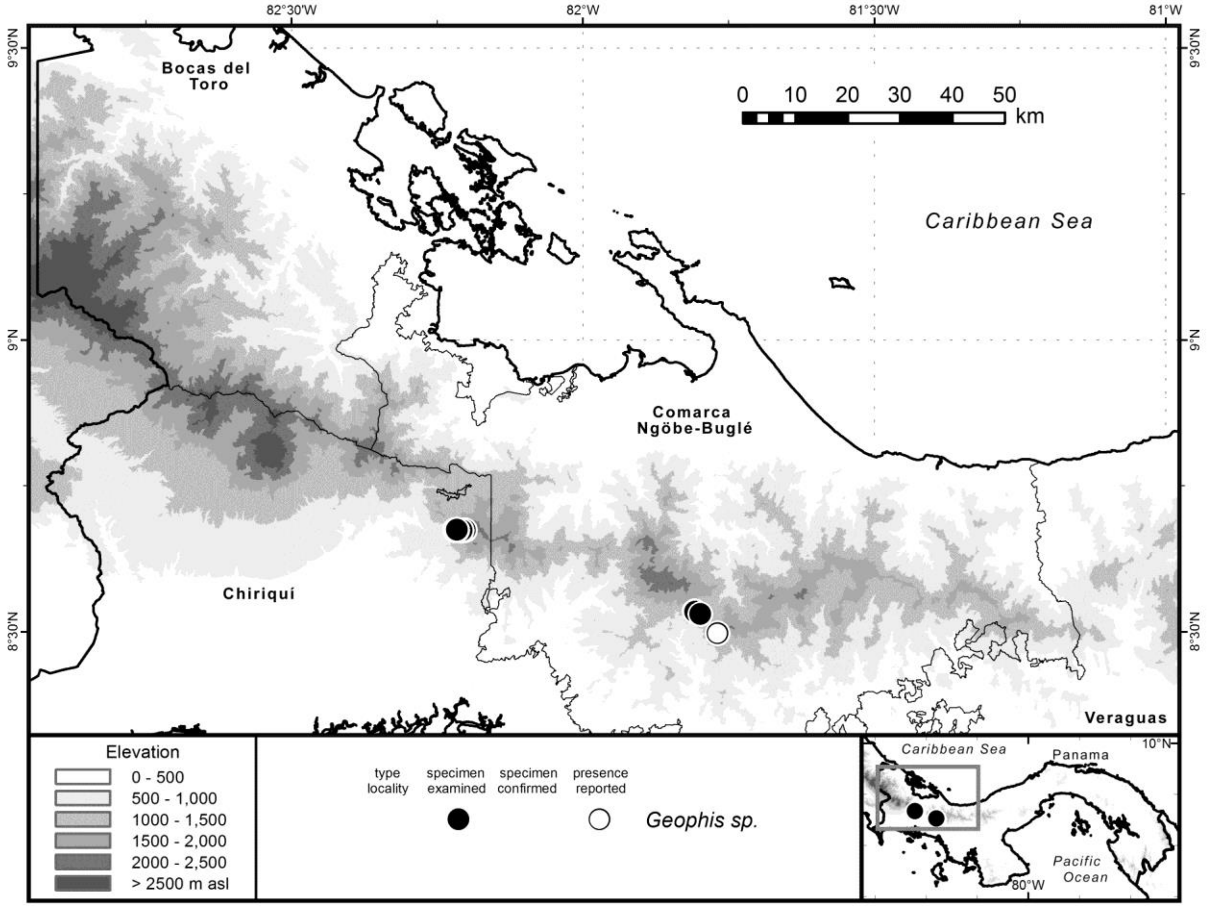
Remarks. The specimen SMF 91551 has 133 V + 42 SC = 175 total segmentals, all three being the lowest respective values reported for females of this species, and the species as a whole (Savage & Watling 2008), further increasing the overlap with *Geophis brachycephalus* in these features. Even without this further blurring of morphological distinctions, the taxonomy and biogeography of the *G. brachycephalus* complex remains unsatisfactorily resolved as discussed in chapter 4.1.9 and the remarks for the other members. The records from east and west of Veraguas render the presence of *G. tectus* in this province plausible, and the species a possible candidate for the records of *G. brachycephalus* from Cerro Negro (Carrizo 2000) and PNGDOTH (Ray 2009).

***Geophis* sp.**

Earthsnake, Wormsnake; Culebra de tierra, Minadora

Figures 4.89C–D; 4.109B; Maps 4.18; 4.141.

Geographic distribution. Only known from the western and central portions of the Serranía de Tabasará in western Panama, between Cerro Pata de Macho at RFLF and the Cerro Colorado area, 1250–1660 m asl.



Map 4.141: Distribution of *Geophis* sp.

Diagnosis. This small snake (maximum TOL 354 mm) with vertically subelliptical pupils is readily identified as a Panamanian member of the genus *Geophis* by its 15—15—15 dorsal rows, entire cloacal scute, presence of a loreal, lack of a preocular and anterior temporal allowing for loreal-orbit and supralabial-parietal contacts, short tail, and dark dorsal ground color without continuous longitudinal stripes. *Geophis* sp. differs from *G. championi* and *G. godmani* in having the supracaudal and at least the posterior dorsal scales keeled (vs. smooth), and from *G. hoffmanni* in having 6 supralabials (vs. 5). Among the very similar nominal species of the *G. brachycephalus* complex, it differs from *G. brachycephalus* in having 137 or fewer ventrals in females (vs. 136 or more) as well as in uncorrected p-distances of 0.6–1.2% in the 16S and 5.5–6% in the cyt-b fragment analyzed in chapter 4.1.9, from *G. talamancae* in usually having 171 or more (166 in one specimen) total segmentals (vs. 171 or fewer), in being unicolor dark above (vs. often with a pattern of red lateral blotches on posterior portions of body), as well as in uncorrected p-distances of 1.9–2.7% in the 16S fragment analyzed in chapter 4.1.9, and from *G. tectus* in having a slightly bilobed hemipenis (vs. unilobed), 37 or fewer subcaudals in females (vs. 42 or more), as well as uncorrected p-distances of 1.1–1.8% in the 16S, 3.1–3.3% in the COI, and 3.1–5.5% in the cyt-b fragment analyzed in chapter 4.1.9 (including data from Savage & Watling 2008).

Description. TOL to 354 mm*; SVL to 301 mm*; tail short, TL/TOL = 0.16–0.20 (0.16–0.18 in females, 0.18–0.20 in males); D keeled at least on upper rows, keeling increasing posteriorly, striate, in 15—15—15 rows; supracaudals strongly keeled; V 132–141 (132–137 in females, 132–141 in males); SC 34–48 (34–37 in females, 41–48 in males); total segmentals 166–187 (166–173 in females, 171–187 in males); SPL 6; INL 6–7; loreal 1; Preoc 0; Postoc 1–2; Tant 0, Tpost 1; cloacal scute entire; AP 2, located subapically, barely distinct; eyes moderate, pupil vertically subelliptical.

The hemipenis of *Geophis* sp. is a slightly bilobed organ; pedicel with spinules and a few large spines distally; truncus with moderate spines and a whorl of recurved hooks just below capitulum; capitulum moderately long and slender, about 2–2.5 times length of truncus on asulcate side, with spinulate calyces.

Coloration in life. D and L surfaces blackish brown to black; some individuals with a lighter snout; V surfaces white to cream, often with dark pigmentation on L tips of V, usually with dark mottling around chin and infralabials, SC always strongly marked or completely dark; iris black.

The male SMF 91543 was recorded as follows: D surfaces Blackish Neutral Gray (82); tips of V, SPL, and chin Blackish Neutral Gray (82); SC mottled with Blackish Neutral Gray (82); mottling becoming denser posteriorly; other V surfaces dirty white with a suggestion of Smoke Gray (44) and Cream Color (54). The female SMF 89563 was recorded as follows: D and L surfaces of head, body and tail as well as V surface of tail, cloacal shield, and chin Sepia (119); V surface of body Pearl Gray (81), grading into Sepia (119) at the head; iris Sepia (119). Nadim Hamad recorded a specimen from the surroundings of the Lost & Found

Ecohostel as follows: D and L surfaces Jet Black (89); V surfaces Pale Horn Color (92), with Jet Black (89) mottling under tail and chin; iris black.

Coloration in preservative. Similar to that in life, assuming a somewhat more bluish hue.

Natural history notes. Terrestrial and fossorial, primarily nocturnal; probably similar in its habits to other *Geophis.* Three of the 15 specimens collected at RFLF lack parts of their tails. One of these, the male SMF 89559, had its right hemipenis hanging out from the cloaca and necrotic when collected. Four of the 6 specimens collected in 2010 had orange globules (which I assume to be eggs of some arthropod) beneath some posterior ventrals. Of the specimens from RFLF, two were caught in pitfall traps and two discovered under a log and a rock, respectively. The remaining collected specimens and many more observed ones were spotted while actively moving over the ground or through the leaf litter. In the surroundings of the Lost & Found Ecohostel, *Geophis* sp. appeared extremely abundant in certain periods (e.g., around May–June 2008 or May–July 2010) with snakes crawling around openly at daytime, while only singular individuals were found at night or under cover in other periods (e.g., February–March and October–November 2009).

Conservation. I calculated the EVS for this *Geophis* sp. as 5 (range) + 2 (persecution) + 4 (ecological distribution) = 11, indicating a medium vulnerability. Its extent of occurrence of just 78 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category CR according to IUCN (2001) criterion B1b(iii).

Remarks. Concerning the specific distinctness of this taxon, see chapter 4.1.9. As discussed there and in the remarks for its other members, the taxonomy and biogeography of the *Geophis brachycephalus* complex remains unsatisfactorily resolved in any case. The specimen USNM 297710 from the Cerro Colorado region, said to most closely resemble the Costa Rican endemic *G. zeledoni* by Savage & Watling (2008; although they state that in this specimen the venter is "white and the subcaudals mostly white", whereas in *G. zeledoni* the venter is "uniformly dark gray to black or heavily marked with those colors" according to Savage 2002 and the subcaudals "mostly to entirely black" according to Savage & Watling 2008), is most likely to represent *Geophis* sp. in my opinion, since the "weak" keeling might be a preservation artefact and its segmental counts as reported by these authors closely resemble those of the four males collected by AH nearby and herein tentatively referred to *Geophis* sp.

Hydromorphus concolor Peters 1859

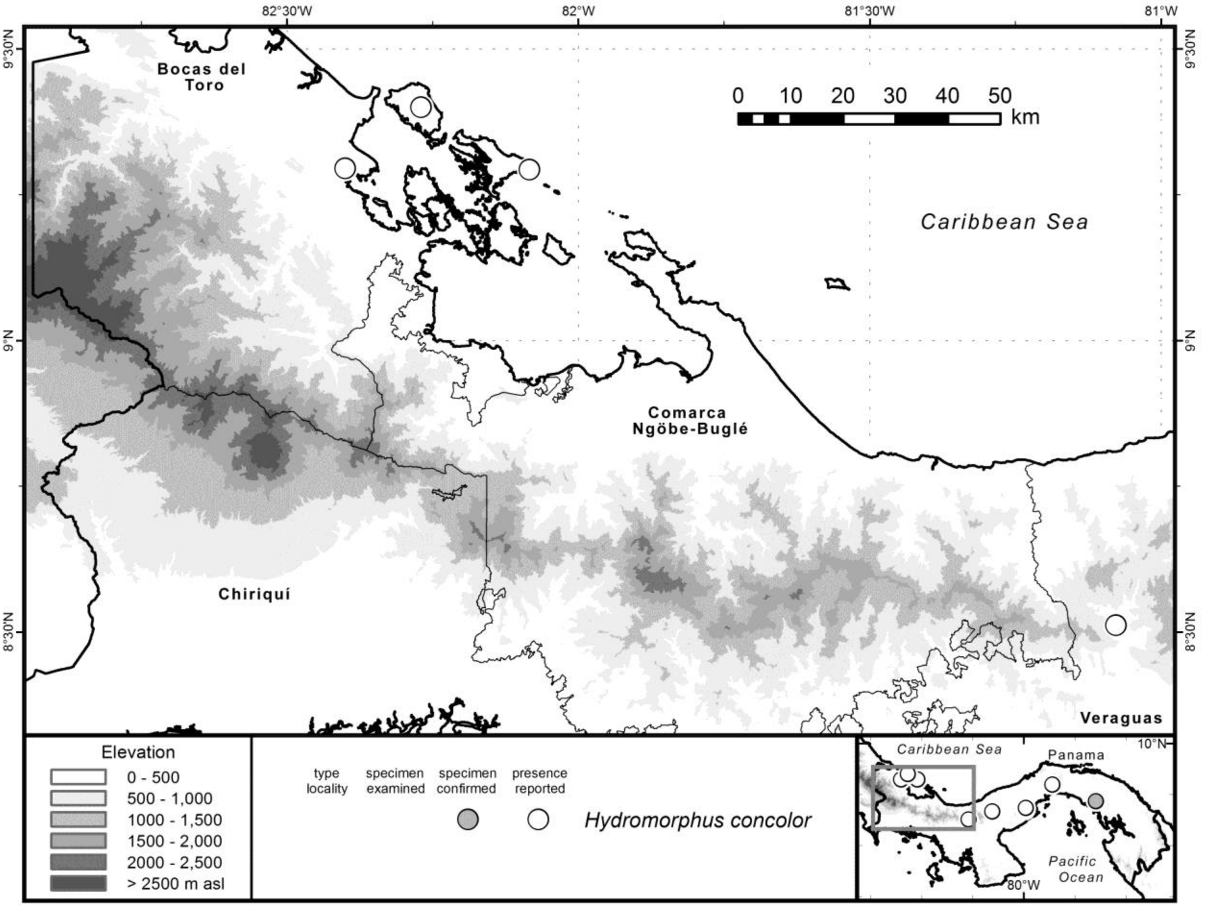
Costa Rica Water Snake, Prawn Snake, Tropical Seep Snake; Camaronera

Figure 4.109C; Map 4.142.

Hydromorphus clarki: Dunn (1942); Smith (1958); Peters & Orejas-Miranda (1970).

Holotype. ZMB 2493, from Costa Rica.

Geographic distribution. Guatemala to Panama, 0–1500 m asl. In Panama, throughout the western and central portions of the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and into Pacific eastern Panama. In the Cordillera Central, reported from Santa Fé, PNGDOTH, and PNAC, up to 800 m asl.



Map 4.142: Distribution of *Hydromorphus concolor.*

Diagnosis. This medium-sized snake (maximum TOL 850 mm) with vertically subelliptical pupils is unique among Panamanian snakes in having both the internasals and prefrontals fused into a single plate, respectively, its nostrils oriented dorsally, and smooth dorsals usually arranged in 19—17—15 rows.

Description. TOL to 850 mm; SVL in Honduran specimens to 615 mm; tail short to moderate, TL/TOL = 0.13–0.19; D smooth, in (15–21)—(15–17)—(15–17) rows; V 157–186; SC 31–54; SPL 5–7; INL 6–9; IN 1, very rarely 2; PF 1; loreal 1; Preoc 0–2; Postoc 1–3; Tant 1, Tpost 1–2; cloacal scute divided; AP 0–2; eyes small, pupil vertically subelliptical.

The hemipenis of *Hydromorphus concolor* is a distinctly bilobed organ; pedicel with spicules; truncus with large spines distally to two large basal hooks; apex with spines, calyculate distally.

Coloration in life. D and L surfaces grayish brown, unicolor or with darker dashes, spots, or blotches, rarely with paired dark L stripes; V surfaces cream to beige or orangish, usually with diffuse dark markings especially posteriorly; iris brown

Coloration in preservative. Similar to that in life, apart from that yellowish or orangish tonalities fade with time.

Natural history notes. Diurnal and nocturnal, semiaquatic, apparently feeding on freshwater crustaceans, frogs, and fish. Similar to the observations of McCranie (2011), the only individual which I have seen alive (at Dos Bocas de Bartola, Nicaragua; field no. JS 431) was active in a stream at night after heavy rainfall.

Remarks. *Hydromorphus concolor* is said to have 2 AP and a round pupil (Savage & Donnelly 1988; Savage 2002; Solórzano 2004), but I agree with McCranie (2011) in finding specimens of this species from Nicaragua to have no AP and a vertically subelliptical pupil.

The eastern distributional limit of this species, traditionally conceived to be in central Panama (Savage 2002; Köhler 2008), was recently extended to the Serranía de Majé in E Panama (Ponce et al. 2008a). Together with the distribution as documented in comprehensive works (Savage 2002; Köhler 2008), the records from Santa Fé, PNGDOTH, and PNAC render the distribution of this species in Chiriquí and the Comarca Ngöbe-Buglé plausible.

Hydromorphus dunni Slevin 1942

Dunn's Water Snake; Camaronera Chiricana

Map 4.143.

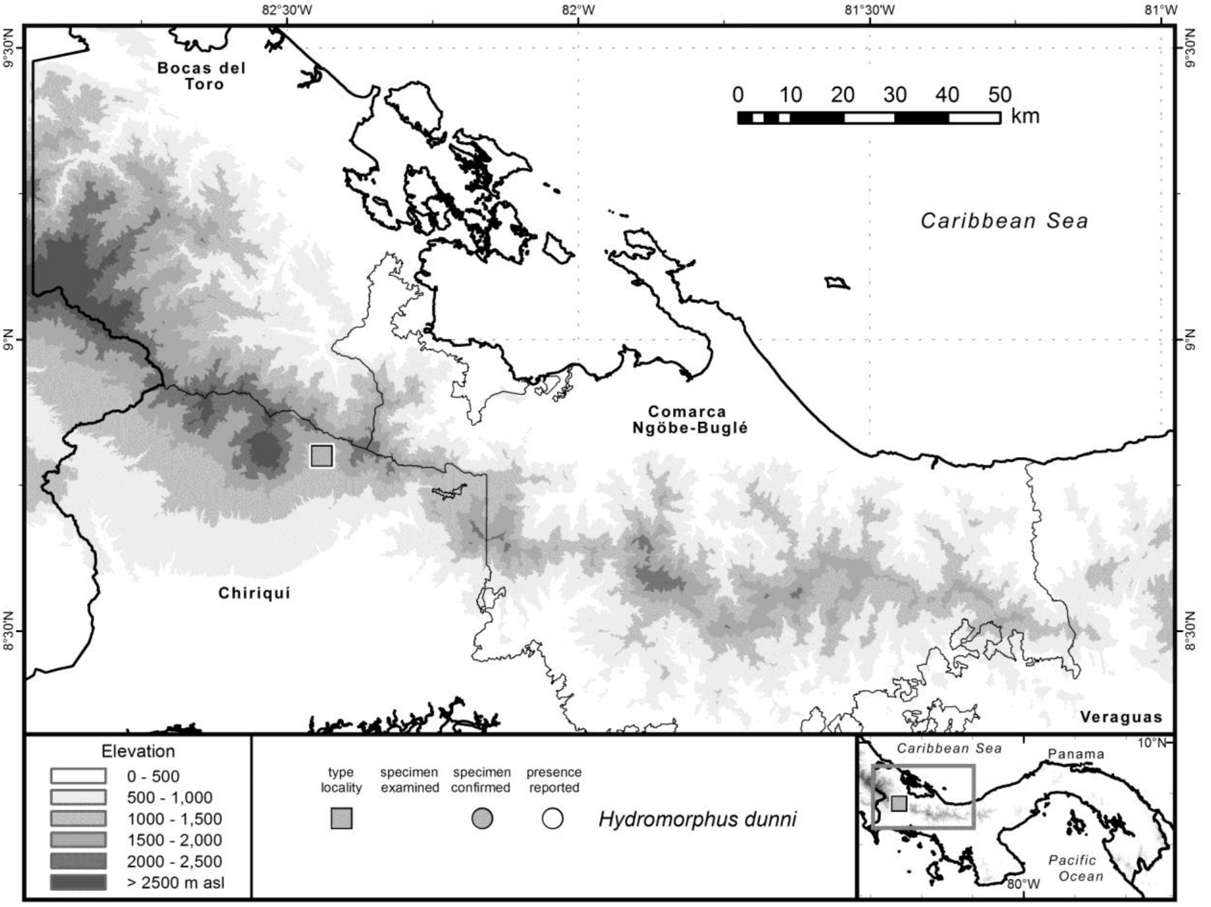
Holotype. CAS 78939, male, from "Vicinity North of Boquete, Chiriquí Province, Panama (Slevin 1942).

Geographic distribution. Only known from the type locality on the Pacific slopes of the Serranía de Talamanca in western Panama, around 1250–1300 m asl.

Diagnosis. This probably medium-sized snake (TOL of only known specimen 482 mm) with vertically subelliptical pupils is unique among Panamanian snakes in having two internasals and three prefrontals, the posterior chin shields slightly longer than the anterior ones, its nostrils oriented dorsally, and dorsals arranged in 15—15—13 rows that are smooth except for a few strongly keeled rows in the cloacal region.

Description. (including data from Slevin 1942 and Savage & Donnelly 1988) TOL 482 mm; SVL 390 mm; tail short to moderate, TL/TOL = 0.19; D smooth except for some strongly keeled rows above cloaca, in 15—15—13 rows; V 164; SC 53; SPL 6; INL 8; IN 2; PF 3, median one much smaller than lateral two; loreal 1; Preoc 1–2; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP ?; eyes moderate, pupil vertically subelliptical.

The hemipenis of *Hydromorphus dunni* is unknown.



Map 4.143: Distribution of *Hydromorphus dunni.*

Coloration in life. D and L surfaces uniformly olive, with suggestions of L lines; supracloacal keels white; V surfaces of body yellowish with dark mottling especially laterally, those of tail gray.

Coloration in preservative. D and L surfaces brownish, supracloacal keels yellow; V surfaces of body yellowish, those of tail nearly uniformly dark.

Natural history notes. The holotype was taken on the ground next to a trail bordered by dense vegetation.

Conservation. Jaramillo et al. (2010) calculated an EVS of 13 for *Hydromorphus dunni* and assigned that species to the IUCN category EN (which seems hard to understand given that they assessed *Geophis championi,* a "slightly better-known" species, to DD), while the official IUCN Red List (IUCN 2014) lists it as DD. *Hydromorphus dunni* is known from a single locality and a single specimen (see remarks). That is, virtually nothing is known about the distribution, population, and natural history of this species, or any other aspect of its biology, and the calculation of an extent of occurrence does not make sense. Thus, strictly adhering to the IUCN (2001) criteria, I see no other option but to place it in the IUCN category "Data Deficient" (DD) although the species will most probably be assignable to EN or CR once more data becomes available. Nevertheless, I calculated the EVS for *H. dunni* as 6 (range) + 4 (persecution) + 5 (ecological distribution) = 15, indicating a high vulnerability.

Remarks. Although it is perfectly diagnosable from all other Panamanian snakes, this species is still known only from the holotype which was collected by J.R. Slevin in 1939. In view of the numerous very pronounced differences to its only congener, I agree with Savage & Donnelly (1988) and Savage (2002) that the holotype of *Hydromorphus dunni* cannot be just an aberrant *H. concolor,* but instead is to be regarded as a distinct species. Just as for *Geophis championi,* which is known from only two specimens from the same general area, additional material of this species is sorely needed, not least as a basis to assess its IUCN category.

The type locality "vicinity N of Boquete" is quite vague, and Slevin (1942) did not specify the elevation at which the holotype was collected. Although there seems to be a general agreement among recent authors to give the elevation as 1250 m asl (Savage 2002; Köhler 2008; Jaramillo et al. 2010; Wilson & Johnson 2010), I could not find any hint to how exactly this value was obtained. Dunn (1947) states that "most collectors have had their headquarters at about 4000 feet [= ca. 1220 m asl], and worked up hill rather than down, and north towards the continental divide rather than west towards Lérida." According to these specifications, I placed my generalized georeference for the much cited "(vicinities) N of Boquete" slightly N of the town at 8.8°N, 82.44°W, yielding a SRTM elevation of 1323 m that might as well hold for the provenance of CAS 78939. The range of 1000–1500 m given by Perez-Santos (1999) seems a little too extrapolated. Again, additional specimens are needed to reveal the elevational distribution of this poorly known species.

Imantodes cenchoa **(Linnaeus 1758)**

Blunt-headed Vinesnake, Blunthead Tree Snake, Common Blunthead; Bejuquilla de cabeza redonda; Bejuquilla cabezona, Dormilona común, Sapera

Figure 4.109D; Map 4.144.

Dipsas cenchoa: Cope (1876).

Himantodes cenchoa: Cope (1860c: in part., 1861d, 1899); Barbour (1923).

Himantodes hemigenius: Cope (1899).

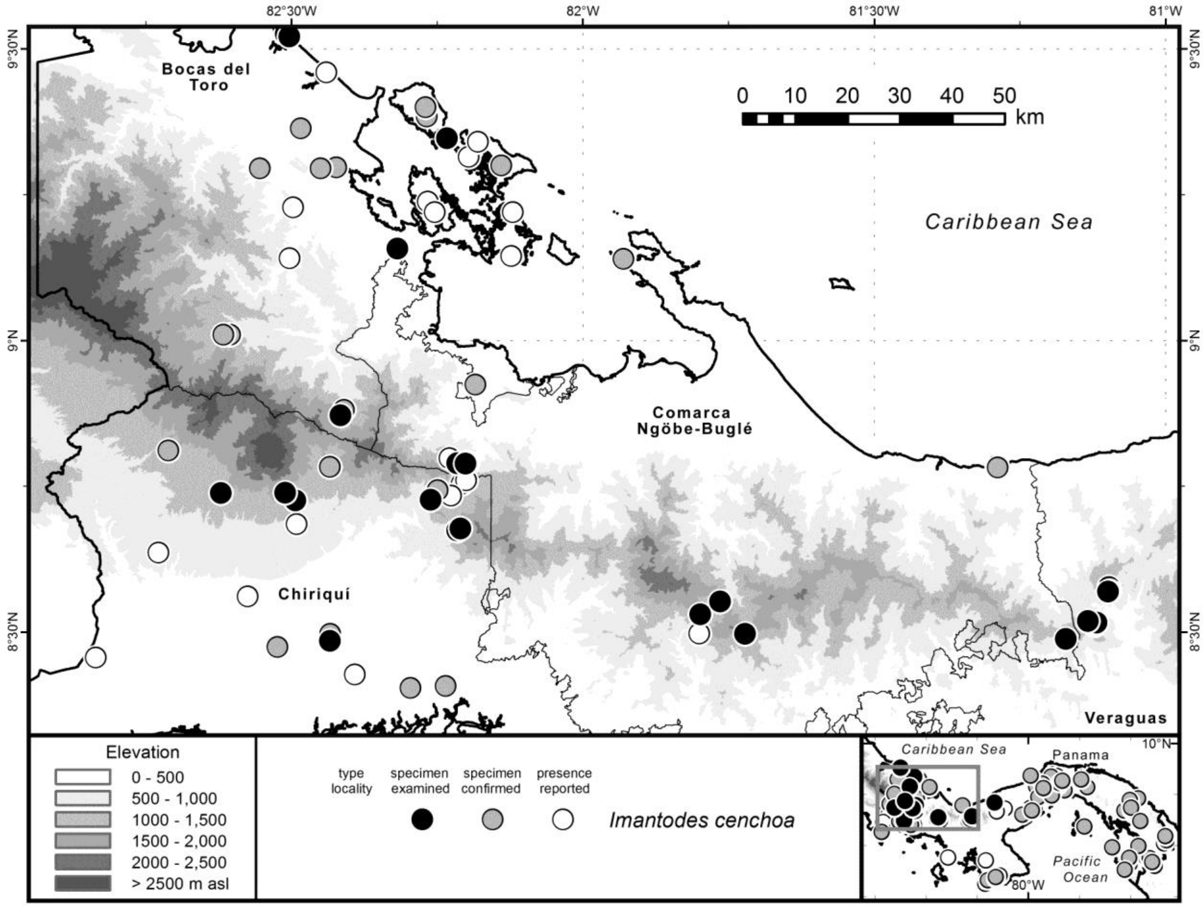
Himantodes leucomelas: Cope (1861d, 1899).

Himantodes platycephalus: Cope (1899).

Holotype. LinnMus 46, from America.

Geographic distribution. Mexico to Ecuador, Bolivia, Paraguay, and Argentina, 0–2060 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities up to 1660 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1480 mm) with vertically elliptical pupils is immediately recognized as a member of the genus *Imantodes* by its extremely elongate, slender body with a long tail in combination with its short, blunt head with large protruding eyes, the presence of a mental groove between its elongate chin shields, and smooth dorsals usually arranged in (17–19)—17—17 rows. *Imantodes cenchoa* is readily distinguished from its congeners ocurring in western Panama by the greatly enlarged scales of its vertebral row that are 3–5 times as wide as the adjacent dorsals (vs. at most 2.5 times as wide). It further differs from *I. inornatus* in having large, saddle-like dark dorsal blotches throughout the body in most specimens (vs. small spots and dashes) and 216 or more ventrals (vs. 218 or fewer), and from *I. gemmistratus* in having a and 31–52, usually 48 or fewer, dark dorsal body blotches (vs. 41–73, usually 49 or more) (including data from Myers 1982).



Map 4.144: Distribution of *Imantodes cenchoa.*

Description. TOL to 1480 mm; SVL to 1015 mm; tail long, TL/TOL = 0.27–0.35; D smooth, in (17–19)—17—(15–17) rows, vertebral row greatly enlarged, 3–5 times as wide as adjacent D; V 216–288; SC 134–195; SPL 7–9; INL 9–12; loreal 1; Preoc 1–3; Postoc 1–4; Tant 1–3, Tpost 2–4; cloacal scute divided, rarely entire; AP 0; eyes very large, protruding, pupil vertically elliptical (including data from Myers 1982).

The hemipenis of *Imantodes cenchoa* is a unilobed organ; pedicel with scattered spinules; truncus with basal hooks and enlarged spines; apex with papillate calyces.

Coloration in life. D and L surfaces brown, with a middorsal series of large rhomboid darker brown blotches; especially along posterior portions of body often a series of much smaller L blotches that may be connected to the D saddles or not; D surface of head with dark brown markings; V surfaces white to beige, with darker spotting or mottling of variable extent and intensity; iris silvery gray to brown, sometimes with a dark reticulum; juveniles often with a more contrasting pattern than adults.

The male SMF 89573 was recorded as follows: D ground color Ground Cinnamon (239) with Burnt Umber (22) saddles; venter Tawny Olive (223D) with Burnt Umber (22) mottling; iris Tawny Olive (223D). Leonhard Stadler recorded the adult male MHCH 2324 (Stadler 2010: Fig. A89) as follows (translated from Stadler 2010): D ground color Sayal Brown (223C) with Mars Brown (223A) saddles bordered by a fine Pale Pinkish Buff (121D) line; D surface of head Mars Brown (223A), L surface of head Sayal Brown (223C); V ground color Pale Horn Color (92) mottled with Mars Brown (223A); iris Tawny Olive (89).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is very similar to that in life, apart from that the reddish hues that once complemented the brown tonalities of several specimens have faded.

Natural history notes. Nocturnal and chiefly arboreal, feeding primarily on sleeping anole lizards and frogs. Of the 36 specimens I have seen alive in Panama, 3 were found active on the ground at night, one was discovered by AH at 16:00 hidden under the intact leaf sheath of a plaintain plant in a forest garden, and one was apparently inactive at night, being coiled up on branches about 3 m above ground at 00:30. The remaining specimens were spotted while moving about in vegetation 0.1–4 m above ground between 19:30 and 02:10. On the banks of Río Cochea, I caught SMF 89772 in the act of approaching an uncollected individual of *Norops polylepis* that was sleeping on a leaf of *Cyclanthus bipartitus* about 1.5 m above the riverbank around 20:20. As visible on Map 4.144, *Imantodes cenchoa* was the snake species most frequently encountered by our field parties, having been found in almost every single research locality of low and premontane elevations.

Remarks. The specimen MHCH 2332 has 216 V, MHCH 2336 has 221 V and 373 total segmentals, and SMF 91556 has 225 V, all values being inferior to the lowest counts (228 V, 383 total segmentals) reported for this species so far. SMF 89960 has 438 total segmentals, which is the highest value reported for this species so far. Of the 33 specimens from which I recorded morphological data, only one (SMF 91555) has the cloacal scute undivided. Based on SMF 89573 from the continental divide W of La Nevera, Lotzkat et al. (2010c) raised the highest documented elevation for this species in Panama to 1660 m asl.

Imantodes gemmistratus **(Cope 1861)**

Banded Blunthead, Blunt-headed Vinesnake, Central American Tree Snake; Bejuquilla de cabeza redonda; Bejuquilla cabezona, Dormilona de bandas

Figure 4.109E; Map 4.145.

Dipsas gemmistratus: Cope (1876).

Himantodes cenchoa: Cope (1860c: in part.).

Himantodes elegans: Barbour (1923).

Himantodes gemmistratus: Cope (1861d).

Leptognathus stratissima: Cope (1886).

Holotype. Originally at ANSP, now apparently lost, from "San Salvador, Central America" (Cope 1861d).

Geographic distribution. Mexico to Colombia, 0–1435 (or 1935) m asl. In Panama, along both versants throughout the western and central portions of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and into Pacific eastern Panama. In the Cordillera Central, reported from Volcán Barú and PNAC, up to at least 1000 m asl.

Diagnosis. This medium-sized snake (maximum TOL 880 mm) with vertically elliptical pupils is immediately recognized as a member of the genus *Imantodes* by its extremely elongate, slender body with a long tail in combination with its short, blunt head with large protruding eyes, the presence of a mental groove between its elongate chin shields, and smooth dorsals usually arranged in (17–19)—17—17 rows. It differs from *I. inornatus* in having large dark dorsal blotches or crossbands throughout the body in most specimens (vs. small spots and dashes), and from *I. cenchoa* in having a vertebral row of slightly enlarged scales that are at most 2.5 times as wide as the adjacent dorsals (vs. 3–5 times as wide) and 41–73, usually 49 or more, dark dorsal body blotches (vs. 31–52, usually 48 or fewer).

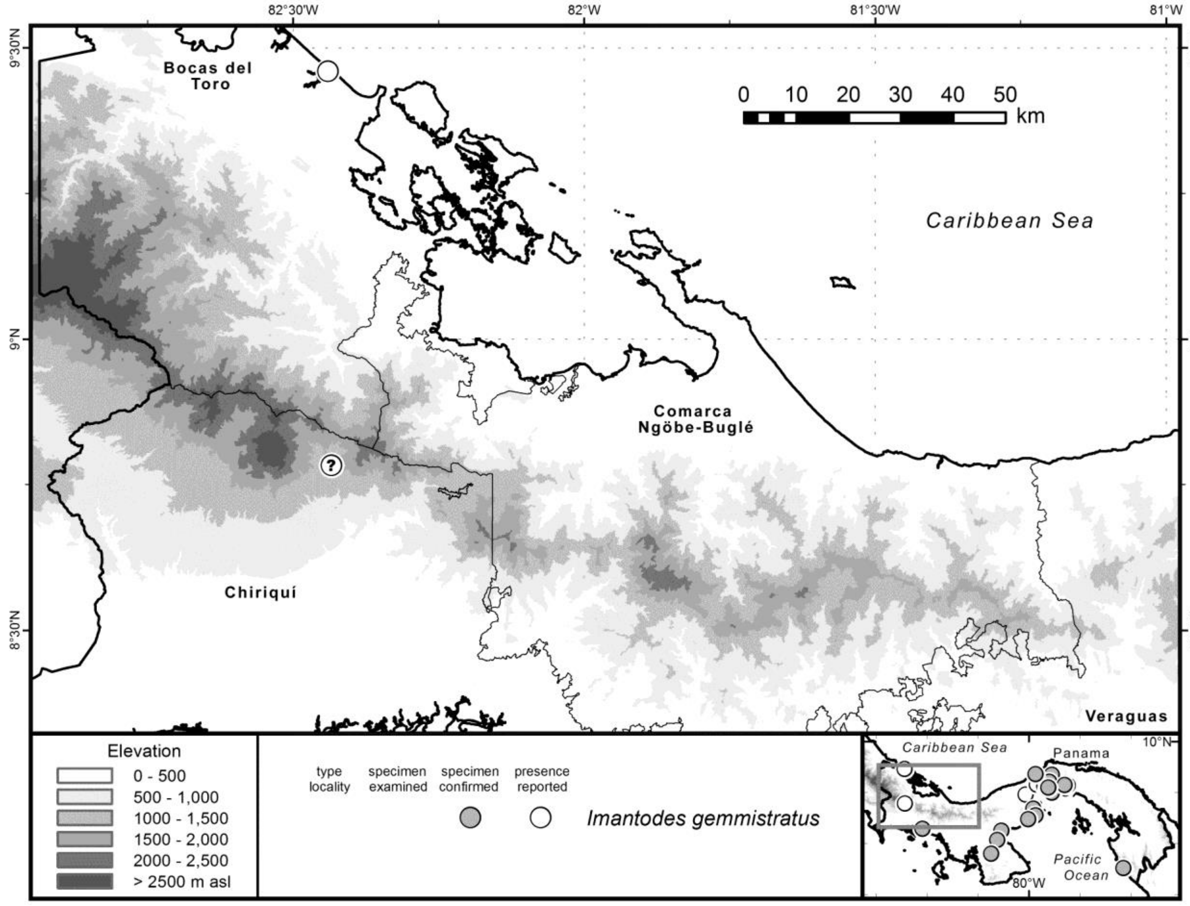
Description. TOL to 880 mm; SVL to 630 mm; tail long, TL/TOL = 0.24–0.30; D smooth, in (17–19)—17—(15–17) rows, vertebral row enlarged, 1.2–2.5 times as wide as adjacent D; V

195–278; SC 104–155; SPL 7–9; INL 9–11; loreal 1; Preoc 1–2; Postoc 1–3; Tant 1–2, Tpost 2–3; cloacal scute divided; AP 0; eyes very large, protruding, pupil vertically elliptical.

The hemipenis of *Imantodes gemmistratus* is a unilobed organ; pedicel with scattered spinules; truncus with basal hooks and enlarged spines; apex with papillate calyces.

Coloration in life. D and L surfaces light brown, rarely unicolor, usually with a middorsal series of large darker brown blotches or crossbands that may bear lighter centers giving an ocelli-like impression, and some of which may divided medially and offset; V surfaces white to beige, with darker spotting or mottling of variable extent and intensity; iris gray to brown; juveniles often with a more contrasting pattern than adults.

Coloration in preservative. Similar to that in life.



Map 4.145: Distribution of *Imantodes gemmistratus.*

Natural history notes. Nocturnal and arboreal, but often encountered on the ground, feeding chiefly on anoles and frogs. *Imantodes gemmistratus* is considered a species of more open and less humid environments than its congeners, but still co-occurs with *I. cenchoa* at several very humed forest sites.

Remarks. The presence of *Imantodes gemmistratus* in my study area is documented by the specimen MVUP 706 from "Volcán Barú, prov. Chiriquí". Since the MVUP catalogue does not further specify the specimen's collection locality, I arbitrarily placed (and therefore marked with a question mark in Map 4.145) my georeference at Boquete, where most herpetological collecting in the surroundings of Volcán Barú has taken place. My generalized coordinates for this settlement yield a SRTM elevation of 1121 m asl, which would constitute the highest record from Panama so far, more than 500 m above the maximum elevation given by Jaramillo et al. (2010). Notwithstanding the great uncertainty concerning the exact collection site, an elevation above 1000 m can confidently be assumed in view of the verbal locality descriptor. Moreover, on 31.05.2008 AH and I caught a specimen of *Imantodes* at Río Chilagres which I tentatively identified as *I. gemmistratus* upon capture in view of its comparably narrow middorsal scales. Lamentably, that animal had disappeared from its bag by the next morning. Taking into account the distribution documented for Costa Rica (Savage 2002; Solórzano 2004) and herein for Panama, especially the record from San San Pond Sak (ANAM 2004), a continuous distribution along the Caribbean lowlands of western Panama may be assumed for *I. gemmistratus.* This and the records from E and W of the Comarca Ngöbe-Buglé and Veraguas province along the Pacific versant render the species' occurrence in these political subdivisions plausible (Young et al. 1999 stated it to occur in the latter).

Savage (2002: p. 609) assumed that the allegedly highest record of this species (Varablanca, 1935 m) really came from a lower elevation, and that the next highest record (Cartago, 1435 m) might be closer to the real elevational maximum of this species. This notion was followed by various authors (Solórzano 2004; Köhler 2008; Wilson & Johnson 2010), while others retained the higher value (Sasa et al. 2010).

Imantodes inornatus **(Boulenger 1896)**

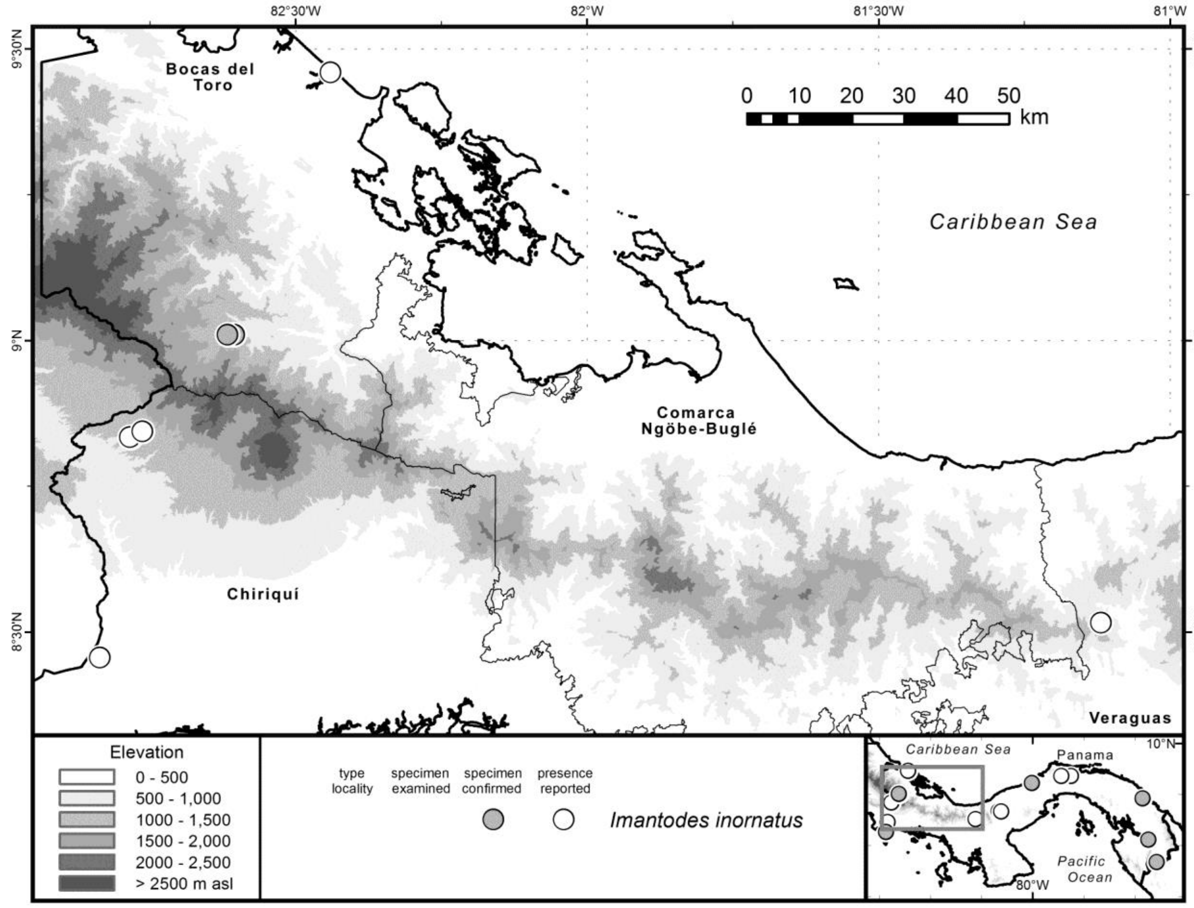
Yellow Blunt-headed Vinesnake, Plain Tree Snake, Speckled Blunthead, Western Tree Snake; Bejuquilla de cabeza redonda; Bejuquilla cabezona, Dormilona salpicada

Figure 4.109F; Map 4.146.

Imantades lentiferus: Martínez & Rodriguez (1994).

Syntypes. BMNH 1946.1.2.63A–B, from Hacienda Rosa de Jericho, 3250 ft (= ca. 991 m asl), Nicaragua.

Geographic distribution. Honduras to Colombia and Ecuador, 0–1600 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from Río Changena, Santa Clara, the Santa Fé area, and PNGDOTH, up to 1250 m asl.



Map 4.146: Distribution of *Imantodes inornatus.*

Diagnosis. This medium-sized snake (maximum TOL 1035 mm) with vertically elliptical pupils is immediately recognized as a member of the genus *Imantodes* by its extremely elongate, slender body with a long tail in combination with its short, blunt head with large protruding eyes, the presence of a mental groove between its elongate chin shields, and smooth dorsals usually arranged in 17—17—17 rows. *Imantodes inornatus* is readily distinguished from its congeners ocurring in western Panama by its dorsal pattern of small spots and dashes that usually aggregate to give the impression of diffuse crossbars (vs. large dark dorsal blotches or crossbands throughout the body in most specimens). It further differs from *I. cenchoa* in having 218 or fewer ventrals (vs. 216 or more) and the enlarged scales of the vertebral row at most 2 times as wide as the adjacent dorsals (vs. 3–5 times as wide).

Description. (including data from Myers 1982) TOL to 1035 mm; SVL to 690 mm; tail long, TL/TOL = 0.21–0.31; D smooth, in 17—(17–19)—(13–17) rows, vertebral row enlarged, 1.2–2 times as wide as adjacent D; V 196–218; SC 106–132; SPL 7–9; INL 8–11; loreal 1; Preoc 1–2; Postoc 2–3; Tant 1–2, Tpost 2–3; cloacal scute entire or divided; AP 0; eyes very large, protruding, pupil vertically elliptical.

The hemipenis of *Imantodes inornatus* is a unilobed organ; pedicel with scattered spinules; truncus with basal hooks and very large spines; apex with papillate calyces.

Coloration in life. D and L surfaces golden to light brown, with numerous dark spots, speckles, and dashes which usually aggregate to form series of diffuse, narrow, short transverse bars dorsally and laterally on body; D surface of head with dark speckles and sometimes a short dark longitudinal nuchal stripe; V surfaces white to yellow anteriorly grading into yellow to orange or orangish brown posteriorly, with darker spotting or mottling; iris gray to brown, often with yellow or orange hues.

Coloration in preservative. Similar to that in life.

Natural history notes. Nocturnal and arboreal, feeding primarily on frogs, anoles, and amphibian eggs. *Imantodes inornatus* is considered a mimic of the yellow "oropél" phase of *Bothriechis schlegelii.*

Remarks. In their species inventory of Cerro Tute, Martínez & Rodriguez (1994) listed "*Imantades lentiferus*" (sic). Since *I. lentiferus* has 15 D-HC, segmental counts similar to that of *I. inornatus,* and unblotched specimens are known (Myers 1982), I assume that this record is based on a misidentified *I. inornatus* with posterior reduction in D rows, further taking into consideration that these authors additionally listed *I. cenchoa.* The records E and W of the Comarca Ngöbe-Buglé render the species' presence therein plausible. My georeference for "Hartmann's Finca", the provenance of UMMZ 175753 (Perez-Santos 1999) yields a SRTM elevation of 1231 m asl, which is close to the maximum elevation of 1250 m given for Panama by Perez-Santos (1999) that is equally plausible for a specimen from that site.

Leptodeira annulata (Linnaeus 1758)

Banded Cat-eyed Snake, Common Cat-eye, Southern Cat-eyed Snake; Ojos de gato bandeada, Ojos de gato común, Ranera, Sapera

Figure 4.109G; Map 4.147.

Leptodeira maculata: Taylor (1951, 1954: all in part.).

Leptodeira ocellata: Wettstein (1934); Taylor (1951, 1954).

Leptodira annulata: Cope (1871).

Leptodira personata: Barbour (1906).

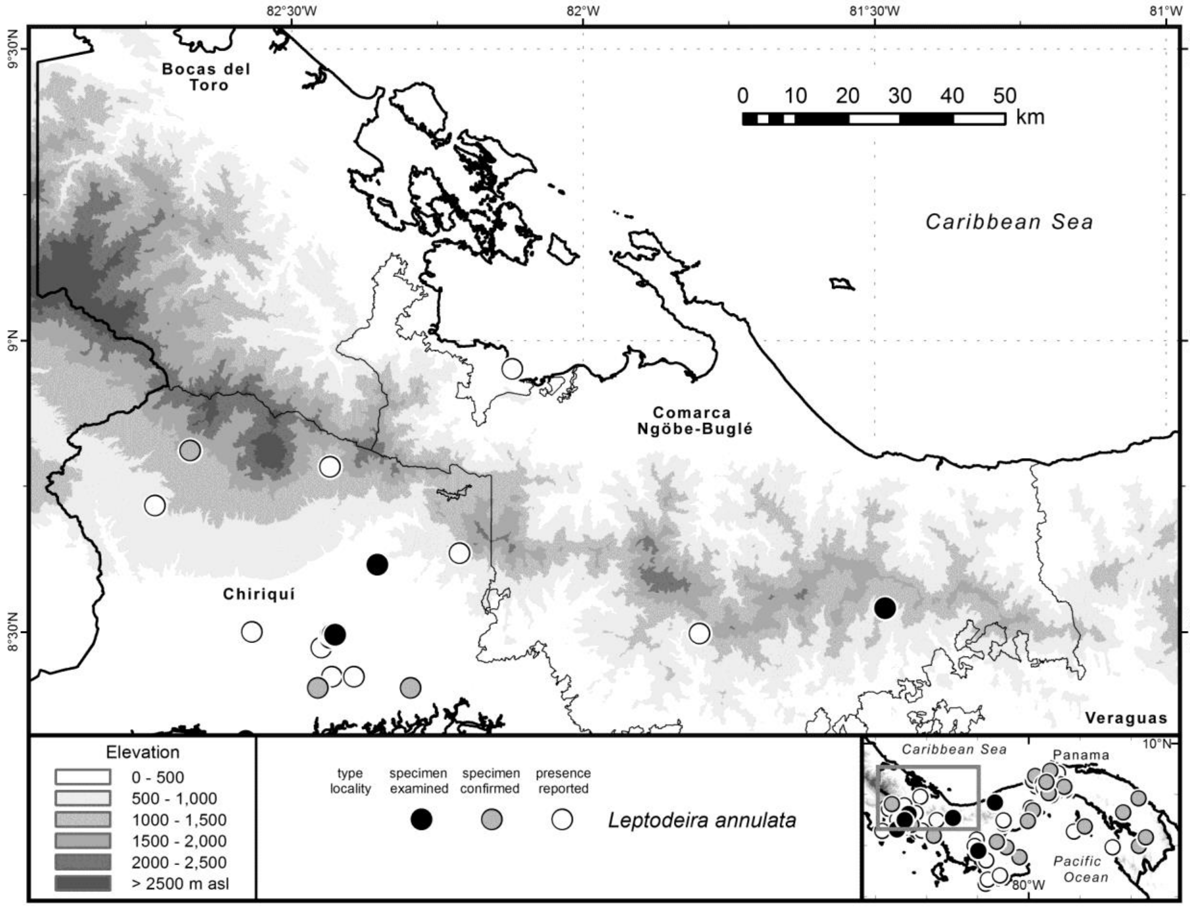
Leptodeira rhombifera: Dunn (1936: in part.); Dunn & Bailey (1939); Swanson (1945); Cochran (1946); Dunn (1947); Evans (1947); Taylor (1951, 1954); McCranie (2011).

Sibon annulatum: Cope (1876).

Sibon septentrionale rubricatum: Cope (1893).

Holotype. Zoologicka Institutionen Uppsala No. 9, from America; restricted to "lower Río Amazon, Pará, Brazil" by Duellman (1958).

Geographic distribution. Mexico to Ecuador, Bolivia, Paraguay, and Argentina, 0–2000 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites chiefly along the Pacific versant up to 1400 m asl.



Map 4.147: Distribution of *Leptodeira annulata.*

Diagnosis. This medium-sized snake (maximum TOL 790 mm) with vertically elliptical pupils is readily identified as a member of the genus *Leptodeira* by its brown dorsal coloration with rounded darker brown blotches in combination with a mostly or completely immaculate venter, and smooth dorsals with two apical pits arranged in 21 or more rows at midbody. It differs from *L. rubricata* in having a middorsal series of rounded blotches, some to many of which may connect to form a zig-zag pattern, on gray to brown ground color (vs. regular dark transverse bands on reddish brown ground color), and from *L. septentrionalis* in having 185 or fewer ventrals (vs. 185 or more in specimens from western Panama), the dark nape stripe usually connected to the 1st body blotch (vs. usually not connected, if present at all), and the dark body blotches usually with narrow light edges (vs. not light-edged).

Description. (including data from Duellman 1958) TOL to 790 mm; SVL to 630 mm; tail moderate to long, TL/TOL = 0.22–0.30; D smooth, in (17–25)—(21–25)—(15–19) rows, vertebral row may be very slightly enlarged; V 151–185; SC 54–89; SPL 7–9; INL 8–12; loreal 1–2; Preoc 1–4; Postoc 1–4; Tant 1–2, Tpost 1–3; cloacal scute divided; AP 2; eyes large, pupil vertically elliptical.

The hemipenis of *Leptodeira annulata* is a unilobed organ with a spinulate pedicel; truncus with enlarged spines; apical region calyculate, capitulum with a cup-shaped depression.

Coloration in life. D and L surfaces grayish brown to brown (reddish brown in the juveniles from W Panama which I have seen), with a middorsal series of large, rounded blotches usually bearing narrow light edges and sometimes somewhat lighter centers, some to many of which may connect to form an irregular zig-zag pattern; at least one series of smaller L blotches per side; a dark postorbital stripe; a dark median nape stripe usually extending from parietals posteriorly over several D scale rows and connecting to the 1st dark body blotch; V surfaces usually immaculate white to beige; iris gray to brown.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of the specimens in my collection is similar to that in life, apart from that reddish hues which had been present in the brown coloration of some specimens have disappeared; D scales whose oberhäutchen have been lost are grayish.

Natural history notes. Nocturnal and primarily terrestrial, chiefly feeding on anurans. Four individuals were encountered active on the ground at night, one moving around on a tree trunk about 1.2 m above ground, and another one crawling along a barbed wire fence ca. 0.5 m above ground. A gravid female was found dead on road with four eggs squeezed out of its body, and two specimens were brought to me after having been badly injured by local people in Los Algarrobos. When spotted by humans, this species regularly becomes the victim of its viper mimicry that includes head triangulation as a defensive posture. Bites have been reported to cause severe local symptoms in humans.

Remarks. Duellman (1958) presented a thorough morphological revision of the genus *Leptodeira* and recognized 5 subspecies of *L. annulata,* of which *L. annulata rhombifera* Günther 1872 occurs from Guatemala to Panama (holotype BMNH 1946.1.9.92 from banks of Río Chisoy, near the town of Cubulco, Guatemala). Recently, Daza et al. (2009) revealed the nominal species *L. annulata, L. bakeri, L. maculata, L. rubricata,* and *L. septentrionalis* to form a complex of at least 10 evolutionary lineages which they called "*L. annulata/septentrionalis* complex", with both *L. annulata* and *L. septentrionalis* being highly polyphyletic and each name comprising several genealogical lineages, some of which correspond to the subspecies recognized by Duellman (1958). Since all samples of "*L. annulata*" from Guatemala to Costa Rica analyzed by Daza et al. (2009) formed a distinct cluster, McCranie (2011) re-erected the name *L. rhombifera* for the populations formerly referred to *L. annulata rhombifera.* However, since Daza et al. (2009) did not include Panamanian "*L. annulata*" in their analyses, for now I refrain from following McCranie (2011) in applying this name to the Panamanian populations until they are genetically demonstrated to be conspecific with the sample of Daza et al. (2009), even though this is to be expected in view of the distribution of Duellman's (1958) "subspecies". Anticipating this confirmation, I have restricted the diagnosis and morphological description above to the data given for specimens from Costa Rica and western as well as central Panama, and/or referred to as *L. (annulata) rhombifera* (Duellman 1958; Savage 2002; McCranie 2011; own data). It should be noted that the only *L. rubricata* sampled by Daza et al. (2009; from Costa Rica) was inferred as the basal taxon in their cluster of *L. annulata rhombifera,* suggesting that the former nominal taxon, which has been reported from coastal W Chiriquí, is likewise in need of a taxonomic revision.

Though the dark nape stripe connects broadly to the first body blotch (which may be very small compared to the posteriorly subsequent blotches) in most of my examined specimens, it only narrowly does so in SMF 91560, and is separated by 1 D scale row in an uncollected juvenile from Los Algarrobos (as in the *Leptodeira septentrionalis* SMF 90194 from RFLF). The specimen FMNH 154481 from "Palo Santo, 4 mi NW El Hato, 4600 ft." (= ca. 1402 m asl; FMNH catalogue, examined by GK) raises the upper elevational limit for Panama from previously 1250 m (Jaramillo et al. 2010).

Leptodeira septentrionalis (Kennicott 1859)

Northern Cat-eyed Snake, Northern Cat-eye; Ojos de gato bandeada, Ojos de gato norteña, Ranera, Sapera

Figure 4.109H; Map 4.148.

Hypsiglena torquata torquata: Taylor (1954).

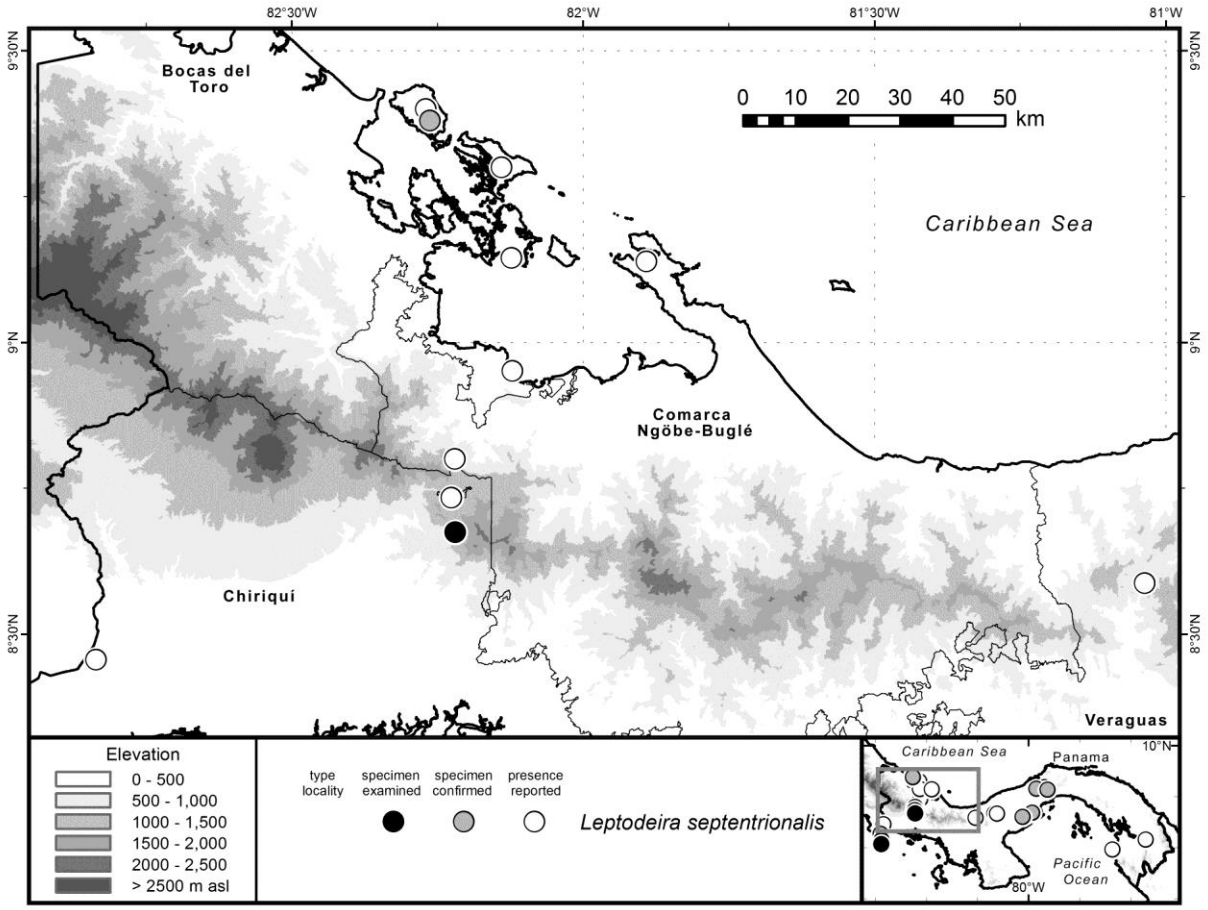
Leptodeira annulata annulata: Dunn (1936: in part.); Taylor (1951, 1954).

Leptodeira annulata polysticta: Dunn (1936: in part).

Leptodeira septemtrionalis: Martínez et al. (1995).

Syntypes. USNM 4267 (2 specimens) and 131739 (formerly 2288), from Matamoras, Tamaulipas, Mexico and Brownsville, Texas.

Geographic distribution. Southern USA to Venezuela, Colombia and Peru, 0–2000 m asl. In Panama, throughout the country along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Fortuna and Santa Fé areas, PNGDOTH, Valle de Antón, and PNAC, chiefly along the Pacific versant up to 1250 m asl.



Map 4.148: Distribution of *Leptodeira septentrionalis.*

Diagnosis. This medium-sized snake (maximum TOL 865 mm) with vertically elliptical pupils is readily identified as a member of the genus *Leptodeira* by its brown dorsal coloration with rounded darker brown blotches in combination with a mostly or completely immaculate venter, and smooth dorsals with two apical pits arranged in usually 21 or more rows at midbody. It differs from *L. rubricata* in having a middorsal series of rounded blotches, some to many of which may connect to form a zig-zag pattern, on gray to brown ground color (vs. regular dark transverse bands on reddish brown ground color), and from *L. annulata* in having 185 or more ventrals in specimens from western Panama (vs. 185 or fewer), the dark nape stripe, if present, usually not connected to the 1st body blotch (vs. usually connected), and the dark body blotches usually without light edges (vs. light-edged).

Description. (including data from Duellman 1958) TOL to 865 mm; SVL to 665 mm; tail long, TL/TOL = 0.26–0.40; D smooth, in (19–23)—(19–23)—(13–17) rows, vertebral and paravertebral rows slightly enlarged; V 181–211; SC 73–107; SPL 8–9; INL 9–12; loreal 1; Preoc 1–3; Postoc 1–3; Tant 1, Tpost 2–3; cloacal scute divided; AP 2; eyes large, pupil vertically elliptical.

The hemipenis of *Leptodeira septentrionalis* is a unilobed organ with a spinulate pedicel; truncus with enlarged spines; apical region calyculate, capitulum without a cup-shaped depression.

Coloration in life. D and L surfaces grayish brown to brown (with a suggestion reddish brown in the juveniles from W Panama which I have seen), with a middorsal series of rounded blotches usually without light edges but sometimes with somewhat lighter centers, several to most of which connect to form an irregular zig-zag pattern; a series of smaller L blotches per side; a usually diffuse dark postorbital stripe; a dark median nape stripe , if present, only extending over a few D scale rows posteriorly from parietals and usually not connecting to the 1st dark body blotch, but sometimes bifurcating around parietals; most juveniles with a broad white nuchal collar; V surfaces usually immaculate white to beige; iris gray to reddish brown.

The male SMF 90194 (Fig. 109H) was recorded as follows: D ground color Army Brown (219B) with a suggestion of Cinnamon Drab (219C), with Sepia (119) middorsal blotches partly fusing to form a zig-zag pattern; irregular Sepia (119) blotches and mottling throughout L surfaces of body and tail; a Vandyke Brown (221) postorbital stripe present; a Sepia (119) V-shaped marking, pointing posteriorly, on L margins of parietals continues as a longitudinal middorsal neck stripe on the first five D scales posterior to parietals; V surfaces of head and body Pale Horn Color (92) with a suggestion of Cream Color (54), grading into Cream Color (54) with a suggestion of Pale Pinkish Buff (121D) on posterior half of body; V surface of tail Beige (219D) with Dark Drab (119B) spots.

The juvenile SMF 91563 was recorded as follows: D ground color Raw Umber (23), grading into Sayal Brown (223C) ventrolaterally; a series of Sepia (119) L blotches turning into dots on tail; Sepia (119) vertebral markings partly as single blotches, partly forming a zig-zag pattern; D surface of head Sepia (219); a bright white nuchal collar extending from eye behind parietals until about seven scales behind parietals; lips and V surface of head dirty white; V surfaces of body and tail Tawny Olive (223D); iris Mars Brown (223A).

Coloration in preservative. After 4–4.5 years in 70% ethanol, the coloration of the specimens in my collection is similar to that in life.

Natural history notes. Nocturnal and semiarboreal, chiefly feeding on anurans. Four individuals were encountered active at night, three adults on the ground and one juvenile on vegetation above a swampy pond. A fourth specimen was found dead on road. When spotted by humans in western Panama, this species probably just as its congener becomes the victim of its viper mimicry which includes head triangulation as a defensive posture. Bites can cause painful local symptoms.

Remarks. Duellman (1958) presented a thorough morphological revision of the genus *Leptodeira* and recognized 5 subspecies of *L. septentrionalis,* of which *L. septentrionalis ornata* (Bocourt 1884) occurs from E Costa Rica to South America, and was said to intergrade with *L. s. polysticta* in Costa Rica. In the "*L. annulata/septentrionalis* complex" of Daza et al. (2009; see remarks for *L. annulata*), the samples from Costa Rica and Panama form a shared cluster that is only distantly related to the *L. s. ornata* of Colombia and Ecuador. Since Daza et al. (2009) did not include specimens of "*L. septentrionalis*" from the type localities of the nominal subspecies or *L. s. ornata* (the syntypes of the latter, MNHN 6201 (2 specimens), are from Isthmus of Darien, Panama) in their analyses, for now I follow McCranie (2011) in refraining from any taxonomic conclusions at this point. Yet, anticipating that the nominal taxon *L. septentrionalis* will be formally split into several species, one of which will include most or all LCA but few or no SA populations, I have restricted the diagnosis and morphological description above to the data given for specimens from Costa Rica and western as well as central Panama (Duellman 1958; Savage 2002; own data).

The specimen SMF 90194 from the Lost & Found Ecohostel at 1250 m asl raises the upper elevational limit for Panama from previously 1000 m (Jaramillo et al. 2010). A slender *Leptodeira* with reddish eyes which I encountered at Cerro Negro but could not secure probably represented this species and would have reconfirmed the record of Martínez et al. (1995) from the Santa Fé area.

Ninia celata McCranie & Wilson 1995

Costa Rican Coffee Snake; Culebra de café costarricense

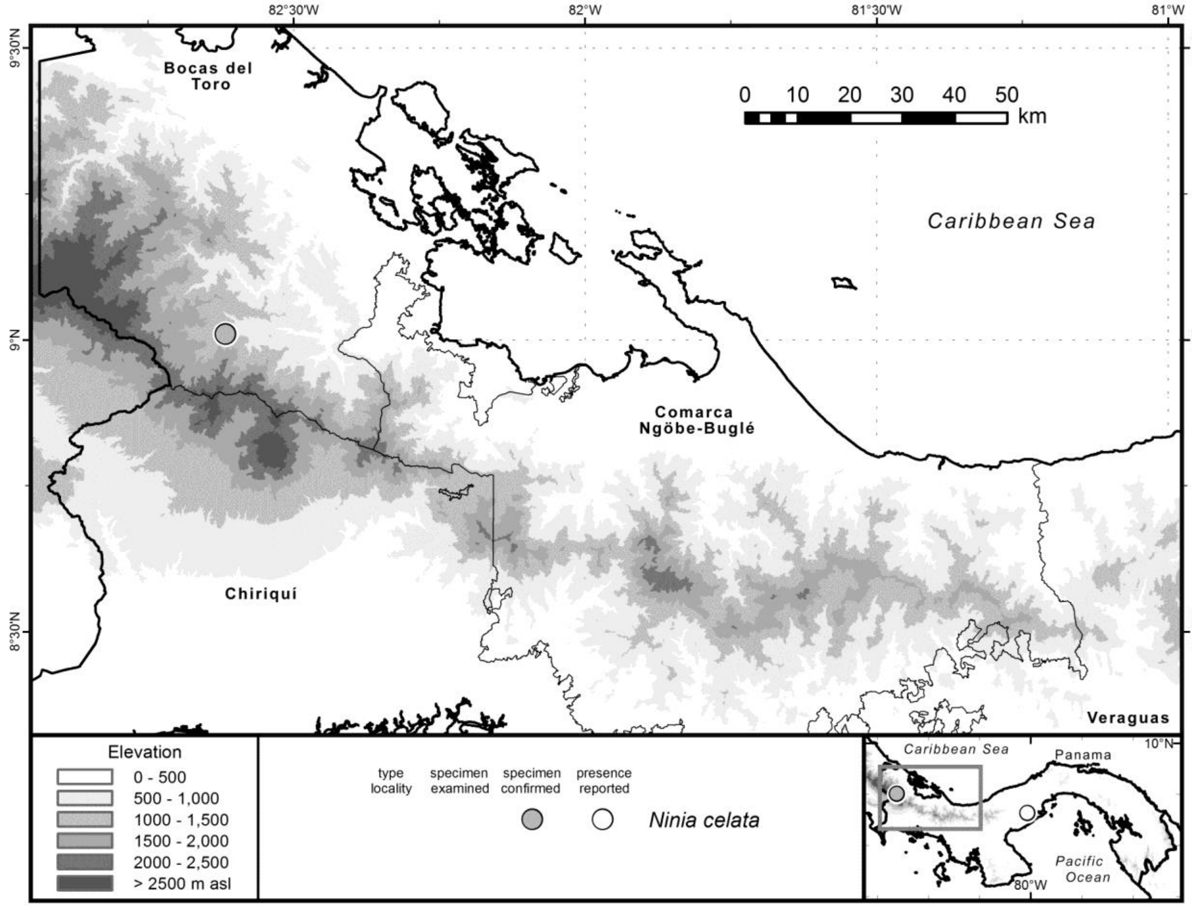
Map 4.149.

Ninia atrata: Cope (1876); Dunn & Bailey (1939: in part.); Taylor (1951, 1954); Peters & Orejas-Miranda (1970: in part.); Savage & Lahanas (1991); Auth (1994: in part.); Perez-Santos (1999: in part.).

Holotype. KU 31971, female, from Cinchona (Isla Bonita), Atlantic side of Volcan Poas, 1200 m elevation, Provincia de Alajuela, Costa Rica (McCranie & Wilson 1995).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and western Panama, 650–1600 m asl. In Panama, restricted to the Cordillera Central including Bocas del Toro, Comarca Ngöbe-Buglé, Veraguas, and possibly Chiriquí. In the Cordillera Central, only reported from Río Changena on the Caribbean and Valle de Antón on the Pacific versant, 850–910 m asl.

Diagnosis. This small snake (maximum TOL 450 mm) with vertically subelliptical pupils is readily identified as a member of the genus *Ninia* by its keeled dorsal scales without apical pits arranged in 19—19—19 rows, the presence of a loreal and paired prefrontals, and the absence of longitudinal stripes. *Ninia celata* differs from *N. psephota* in having 19 dorsal rows throughout (vs. 17), from *N. maculata* and *N. sebae* in having a unicolor blackish body (vs. brown with dark blotches or crossbands in the former, unicolor reddish in the latter) and a broad light nuchal collar or none at all (vs. a broad black nuchal collar or neck band in both), and from *N. atrata* of eastern Panama in having 130 or fewer ventrals (vs. 133 or more) and 171 or fewer total segmentals (vs. 177 or more).



Map 4.149: Distribution of *Ninia celata.*

Description. (including data from McCranie & Wilson 1995) TOL to 450 mm; SVL to 300 mm; tail short to moderate, TL/TOL = 0.15–0.20; D keeled, strongly striate, in 19—19—19 rows; V 123–130; SC 33–45; SPL 7; INL 8; loreal 1; Preoc 0–1; Postoc 1–2; Tant 1, Tpost 2; cloacal scute entire; AP 0; eyes small, pupil vertically subelliptical.

The hemipenis of *Ninia celata* remains undescribed, but is likely to be a unilobed organ with basal spines and a calyculate capitulum as in other members of the genus.

Coloration in life. D and L surfaces black, with or without a broad, yellow to red nuchal collar with dark spotting that involves large portions of the parietals and up to 5 adjacent D scale rows; V surfaces of body immaculate whitish, those of head and tail with varying amounts of dark mottling; SC at least with dark edges, sometimes almost completely dark.

Coloration in preservative. Similar to that in life, apart from that the black D coloration fades to dark brown and the nuchal collar fades to cream.

Natural history notes. Probably a terrestrial and semifossorial, largely nocturnal "goo-eater" like other members of the genus.

Remarks. McCranie & Wilson (1995) showed that all records of *Ninia atrata* from Costa Rica and W Panama were attributable to a different species, which they described as *N. celata.* Savage (2002) erroneously stated the species to have a very long tail (TL/TOL = 0.44–0.47), as did Solórzano (2004). The values for TL/SVL ranging between 0.189–0.257 (McCranie & Wilson 1995) can be translated to TL/TOL values in the range 0.158–0.204, which would be classifiable as short. However, the TL/SVL values from the original description of *N. celata* are also somewhat confusing, since the ratio for the holotype is given as 0.212, but according to the given measurements (240.5 mm SVL, 42 mm TL; TL/TOL = 0.149) should read 0.175.

Together with the records from Caribbean Costa Rica (McCranie & Wilson 1995; Savage 2002) and Río Changena (paratype KU 112621), the record from Altos del María at Valle de Antón (850 m asl; Ray 2009) renders the occurrence of *Ninia celata* in the Comarca Ngöbe-Buglé and Veraguas plausible. The presence in Chiriquí, at least at RFLF, as well as along the Pacific slopes of the Serranía de Tabasará appears possible in view of the species' altitudinal distribution (up to 1600 m according to McCranie & Wilson 1995 and Köhler 2008).

Another species of the genus with an immaculate whitish venter, *Ninia sebae* (Duméril, Bibron & Duméril 1854) was recently reported for Panama (Ponce et al. 2008) from lowland Bocas del Toro (see distribution map in Appendix 7). In view of its occurrence along both versants and up to premontane elevations in Costa Rica (Savage 2002; Solórzano 2004), its presence in my study area seems very likely, but following the criteria applied herein (see chapter 3.5.1) it is merely judged "possible".

Ninia maculata (Peters 1861)

Banded Coffee Snake, Spotted Coffee Snake, Spotted Woodsnake; Culebra de café bandeada

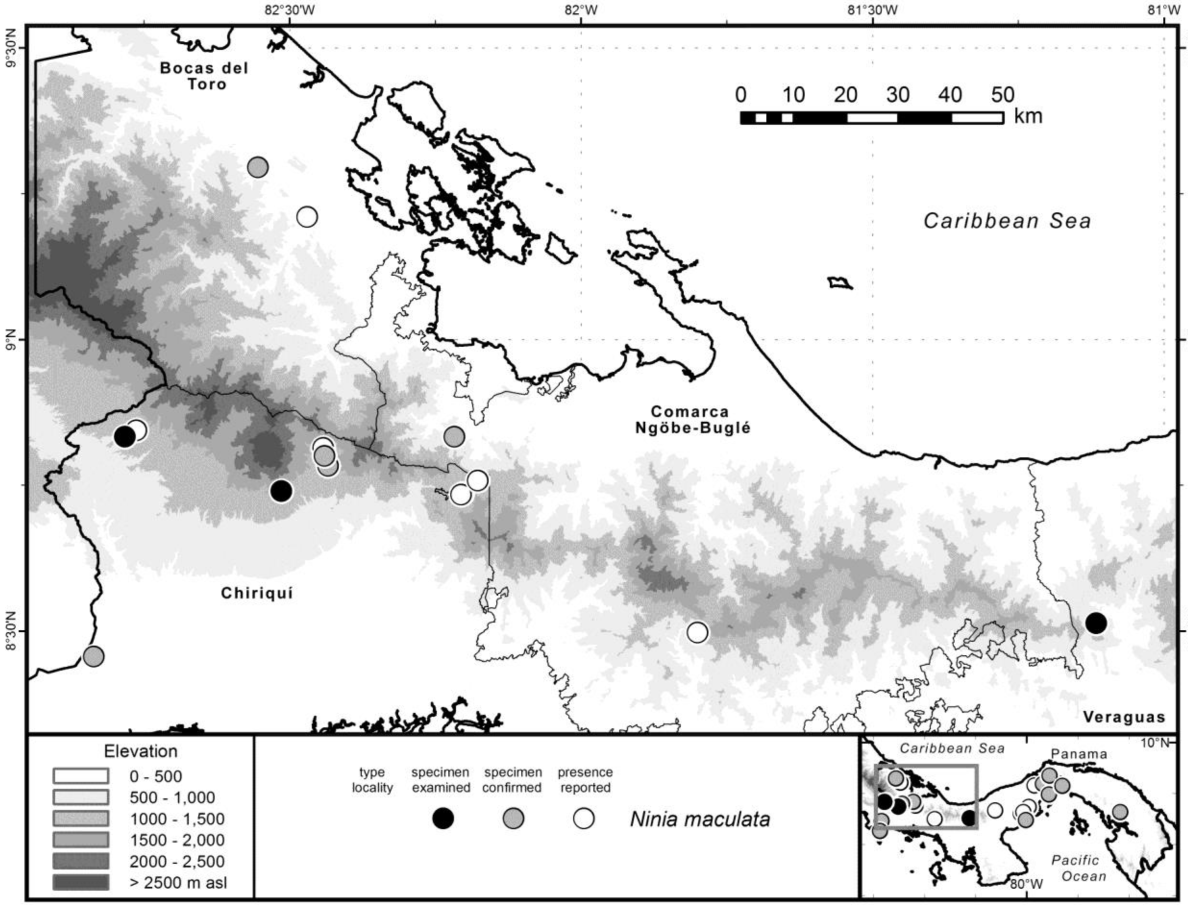
Figure 4.110A; Map 4.150.

Ninia tessellata: Taylor (1951, 1954).

Ninia sebae tesselatus: Cope (1876).

Syntypes. ZMB 1872, 1873 (2 specimens), and 1874 (2 specimens), from Costa Rica.

Geographic distribution. Honduras to eastern Panama, 0–1800 m asl. In Panama, along both versants in western and central, probably also eastern portions of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites along both versants, up to ca. 1420 m asl.



Map 4.150: Distribution of *Ninia maculata.*

Diagnosis. This small snake (maximum TOL 352 mm) with vertically subelliptical pupils is readily identified as a member of the genus *Ninia* by its keeled dorsal scales without apical pits arranged in 19—19—19 rows, the presence of a loreal and paired prefrontals, and the absence of longitudinal stripes. *Ninia maculata* differs from *N. psephota* in having 19 dorsal rows throughout (vs. 17) and dark dorsal blotches or crossbands (vs. unicolor or with light dorsal markings), and from *N. atrata, N. celata,* and *N. sebae* in having dark markings on both dorsum and venter (vs. dorsum typically unicolor, venter immaculate whitish).

Description. TOL to 352 mm; SVL to 233 mm*; tail moderate, TL/TOL = 0.20–0.25; D keeled, strongly striate, in 19—19—19 rows; V 124–155; SC 44–63; SPL 7–8; INL 6–8; loreal 1; Preoc 0–2; Postoc 2–3; Tant 1, Tpost 1–2; cloacal scute entire; AP 0; eyes small, pupil vertically subelliptical (including data from Slevin 1942).

The hemipenis of *Ninia maculata* is a unilobed organ; pedicel with some small spines; truncus with enlarged spines; spinulate calyces on the capitulum.

Coloration in life. D and L surfaces of body and tail reddish to dark brown with darker D markings that may form blotches, short L crossbars that are offset or opposed, or crossbands spanning dorsum and flanks, and usually become gradually smaller towards tail; usually with a dark nuchal collar posterior to parietals; D surface of head usually darker than ground color at least medially; V surfaces whitish to yellow, those of head with dark mottling, those of body with tri- or rectangular dark blotches that may be scattered or arranged in L or midventral lines; SC mostly or completely dark.

The specimen SMF 90203 (Fig. 4.110A) was recorded as follows: D and L surfaces of body Raw Umber (223), grading into Sepia (219) on posterior half of body; body with two series of Jet Black (89) L bars of irregular shape with fine Mars Brown (223A) edges, partly meeting each other on middorsum, becoming narrower and shorter posteriorly to continue as blotches onto anterior third of tail; outer edges of V and first D row with irregular Jet Black (89) mottling; D and L surfaces of tail Sepia (119); a Jet Black (89) neck band middorsally covering six transverse rows of D; D surface of head Raw Umber (223) with a Sepia (119) marking covering most of the parietals, the median scale posterior and all D head scales anterior to them; Sepia (119) vertical bars on lips and mottling on chin area; venter Pearl Gray (81) with a suggestion of dirty white; each V with one or two median or paramedian Sepia (119) blotches that form a median stripe on several portions of venter; V surface of tail Sepia (119) with fine Pearl Gray (81) mottling on anteroir third; iris Fuscous (21).

Leonhard Stadler recorded the adult female SMF 89583 (Stadler 2010: Fig. A90) as follows (translated from Stadler 2010): D surfaces Raw Umber (223), body and tail with regularly spaced, narrow Sepia (119) transverse stripes extending to venter; V surfaces Pale Horn Color (92) mottled with Raw Umber (223).

Coloration in preservative. After 4.5–6 years in 70% ethanol, the coloration of the two specimens mentioned above is similar to that in life, apart from that all reddish hues have faded.

Natural history notes. Diurnal and nocturnal, terrestrial and semifossorial, feeding on earthworms and slugs as well as soft-bodied arthropods. Defensive display includes dorsoventral flattening of head and body, and hiding the head while presenting the tail. SMF 90203 was found in a shade coffee plantation under dead wood in the early afternoon. SMF 89593 was spotted by LS and NH crossing a road at 20:15.

Remarks. SMF 90203 has 6 INL on both sides, which to my knowledge is the lowest value reported for this species so far. I have examined a photograph of a specimen collected by Juan

Castillo on Finca Los Mameyes, Potrerillos Arriba, at 1422 m asl, which is well above the highest elevation reported for Panama so far (1250 m according to Jaramillo et al. 2010).

Ninia psephota **(Cope 1876)**

Checkered Coffee Snake, Cope's Coffee Snake; Culebra de café cuadriculada

Map 4.151.

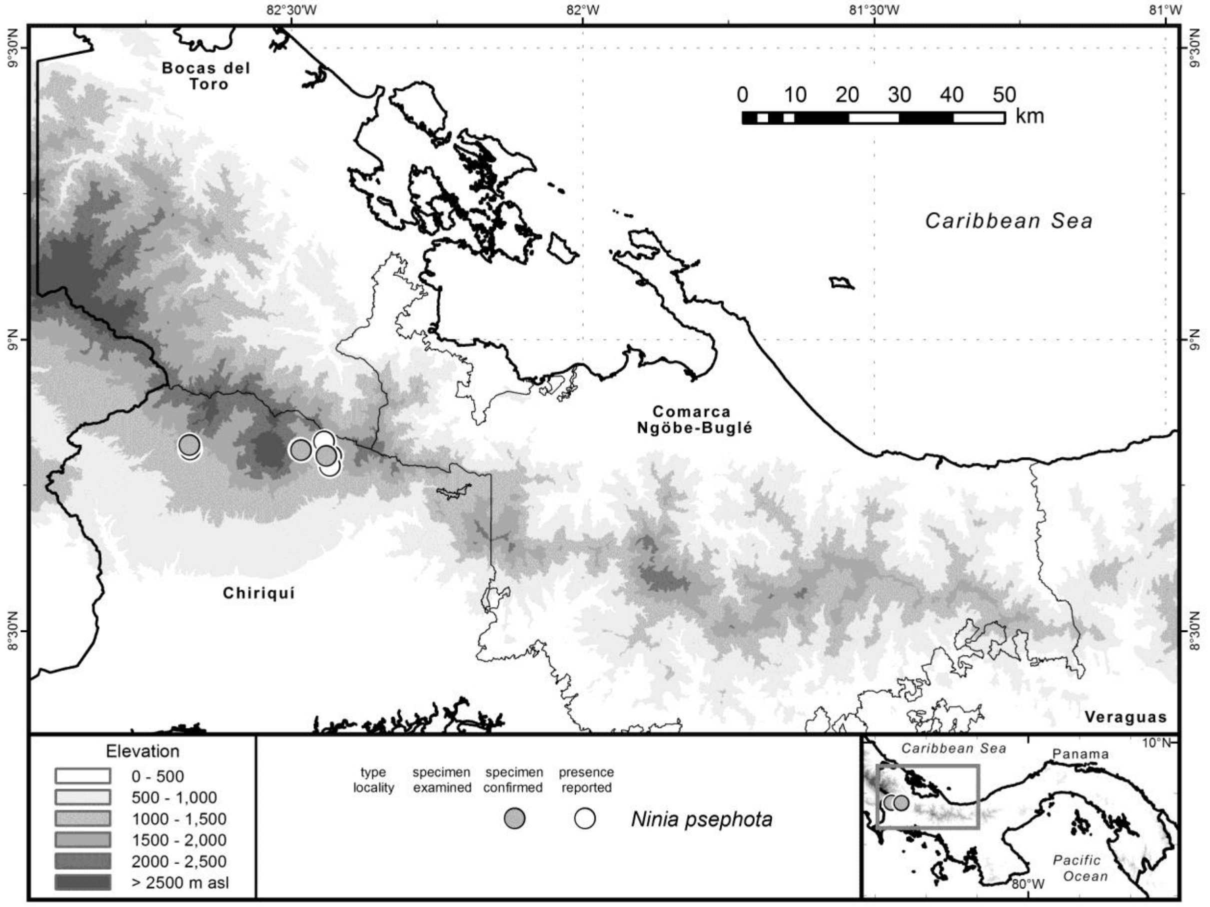
Catostoma psephotum: Cope (1876).

Ninia cerroensis: Taylor (1954); Peters & Orejas-Miranda (1970).

Ninia oxynota: Taylor (1951, 1954); Peters & Orejas-Miranda (1970).

Holotype. USNM 61971, male, from "higher points on Pico Blanco, 5000-7000 ft elevation, Costa Rica" (Cope 1876; = Limón: Cerro Utyum, 1523–2135 m asl fide Savage 2002).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and western Panama, 1000–2770 m asl. In Panama, only reported from the Pacific versant of the Serranía de Talamanca in Chiriquí east to the Boquete area, 1120–1870 m asl.



Map 4.151: Distribution of *Ninia psephota.*

Diagnosis. This small snake (maximum TOL 494 mm) with vertically subelliptical pupils is readily identified as a member of the genus *Ninia* by its keeled dorsal scales without apical pits arranged in 17—17—17 rows, the presence of a loreal and paired prefrontals, and the absence of longitudinal stripes. *Ninia psephota* differs from all its Panamanian congeners in having 17 dorsal rows throughout (vs. 19). It further differs from *N. maculata* in having a unicolor dorsum or light dorsal markings (vs. always with dark dorsal markings), and from *N. atrata, N. celata,* and *N. sebae* in having dark markings throughout the venter (vs. venter immaculate whitish).

Description. (including data from Cope 1876 and Slevin 1942) TOL to 494 mm; SVL to 352 mm; tail moderate, TL/TOL = 0.25–0.27; D keeled, strongly striate, in 17—17—17 rows; V 139–163; SC 51–77; SPL 6–7; INL 6; loreal 1; Preoc 0; Postoc 1–2; Tant 1–2, Tpost 1–2; cloacal scute entire; AP 0; eyes small, pupil vertically subelliptical.

The hemipenis of *Ninia psephota* remains undescribed to my knowledge, but is probably a unilobed organ with basal spines and a calyculate capitulum as in other members of the genus.

Coloration in life. D and L surfaces dark gray or brown to black, uniformly so or with light mottling or crossbands; often with the suggestion of an incomplete light nuchal ocllar; V surfaces white, yellow, pink, or red, with rectangular dark markings.

Coloration in preservative. Similar to that in life, apart from that yellow or red hues fade.

Natural history notes. Terrestrial and semifossorial, apparently largely nocturnal. Slevin (1942) noted *Ninia psephota* to be "a common species under debris in the cafetals, and occasionally found on open trails". He also found "a considerable quantity of beetle wingcovers" in the stomachs he examined.

Remarks. In describing the variation of his sample from Boquete and vicinities, Slevin (1942) treated the loreal as a preocular. My georeference for the specimen MVUP 422 from "Boquete" yields a SRTM elevation of 1121 m asl, which is slightly below the lowest elevation of 1200 m reported for Panama by Jaramillo et al. (2010). The lower limit of 750 m given by Perez-Santos (1999) seems to be far too low for this species. My georeference for the specimens MVUP 914 and 967 from "Cerro Horqueta" yields a SRTM elevation of 1866 m, which is well above the highest elevation reported for Panama (1600 m fide Jaramillo et al. 2010). The presence of *Ninia psephota* in Bocas del Toro is rendered plausible by the distance of less than 2 km between my georeference for these specimens and the provincial border. Likewise, my georeferences for numerous specimens from N of Boquete lie less than 5 km from the provincial border, and the species is known to occur on the Caribbean versant of the Talamancan highlands in Costa Rica (Savage 2002). The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible.

Nothopsis rugosus Cope 1871

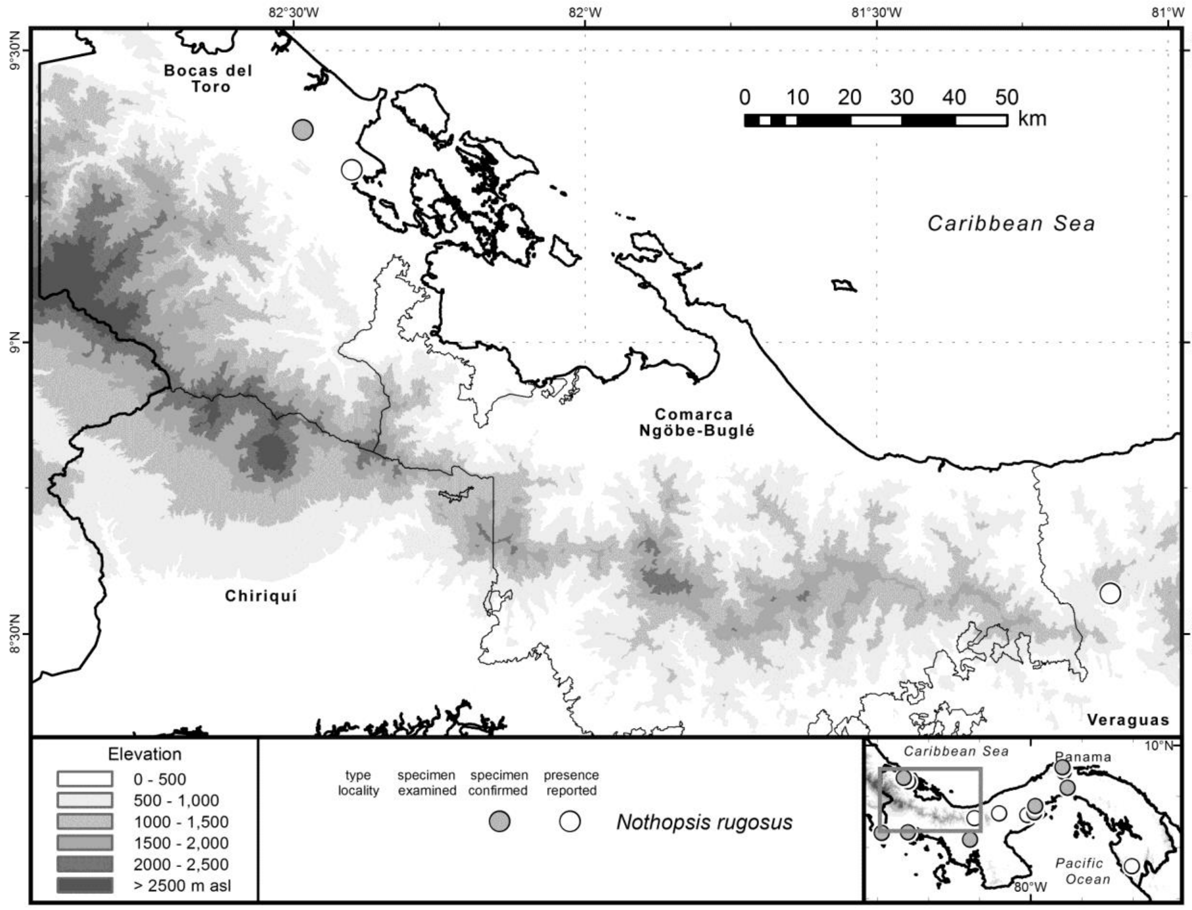
Pebble Snake, Rugose Littersnake; Culebra granosa

Figure 4.110B; Map 4.152.

Nothopsis torresi: Taylor (1951, 1954).

Holotype. USNM 12427, from "Isthmus of Darien", Panama (restricted to the Caribbean coast by Dunn & Dowling 1957).

Geographic distribution. Honduras to Colombia and Ecuador, 0–1000 m asl. In Panama, along both versants throughout the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to ca. 910 m asl.



Map 4.152: Distribution of *Nothopsis rugosus.*

Diagnosis. This small snake (maximum TOL 433 mm) with round pupils is the only snake in western Panama that has most of the upper head surfaces covered with small, tuberculate to keeled scales while lacking a loreal pit (distinguishing it from pitvipers) and having keeled dorsals paired subcaudals (distinguishing it from boas).

Description. (including data from Dunn & Dowling 1957) TOL to 433 mm; SVL to 320 mm; tail long, TL/TOL = 0.32–0.52; D strongly keeled, in (26–30)—(26–30)—(22–26) rows; V

146–162; SC 81–112; SPL 9–13; INL 11–16; D and L head scales (except for well-developed IN and "rudimentary" parietals and frontal) small and numerous, counts typically used for boas and vipers applicable: CO 14–23; SBO/SPL 0–1; cloacal scute entire; AP 0; eyes small, pupil round.

The hemipenis of *Nothopsis rugosus* is a short, unilobed organ; pedicel with small spicules; truncus short; sulcate side of truncus and apex calyculate, asulcate with enlarged spines on apex and distal most portion of truncus.

Coloration in life. D and L surfaces of body and tail cream to yellowish brown, with series of more or less diffuse dark D and L blotches producing at least partially a suggestion of butterfly-shaped markings and L zig-zag lines; D and L surfaces of head rather unicolor dark brown to black; V surfaces cream to yellowish brown with irregular darker spots or mottling.

Coloration in preservative. Similar to that in life.

Natural history notes. Diurnal and nocturnal, terrestrial and semifossorial, living in the leaf litter of forests and feeding on amphibians and lizards.

Remarks. I could not find any record to substantiate the upper elevational limit of 1000 m asl in Panama (Perez-Santos 1999), though this elevation appears plausible considering that Solórzano (2004) gave an identical value for Costa Rica. The highest Panamanian record is Dunn's (1940) "seventh known specimen of this genus" from "the damp forest on top of Cerro Campaña [sic], at about 3000 feet" (= ca. 914 m), though this specimen probably is identical with ANSP 24250, reported by Dunn & Dowling (1957) to have been collected on the same mountain at 2600 ft (= ca. 792 m asl), since these authors make no separate mention of a specimen from 3000 feet. The records from E and W of this political subdivision render the occurrence of *Nothopsis rugosus* in the Comarca Ngöbe-Buglé plausible.

***Oxyrhopus petolarius* (Linnaeus 1758)**

Banded Calico Snake, Banded False Coralsnake, Calico False Coral Snake, Calico Snake; Falsa coral, Gargantilla falsa

Figure 4.110C; Map 4.153.

Clelia petolaria: Taylor (1954)

Clelia petolarius: Taylor (1951)

Oxhyropus petolarius: Elizondo et al. (2007).

Oxyrhopus petola: Smith (1958); Rand & Myers (1969); Peters & Orejas-Miranda (1970); Myers & Rand (1990); Ibáñez et al. (1995, 2001); Young et al. (1999); Köhler (2001, 2008); Solórzano (2004); Sunyer (2009); Carrizo (2010); Jaramillo et al. (2010); Lotzkat et al.

(2010c); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); Lotzkat & Hertz (2011); McCranie (2011); Ray & Knight (2013).

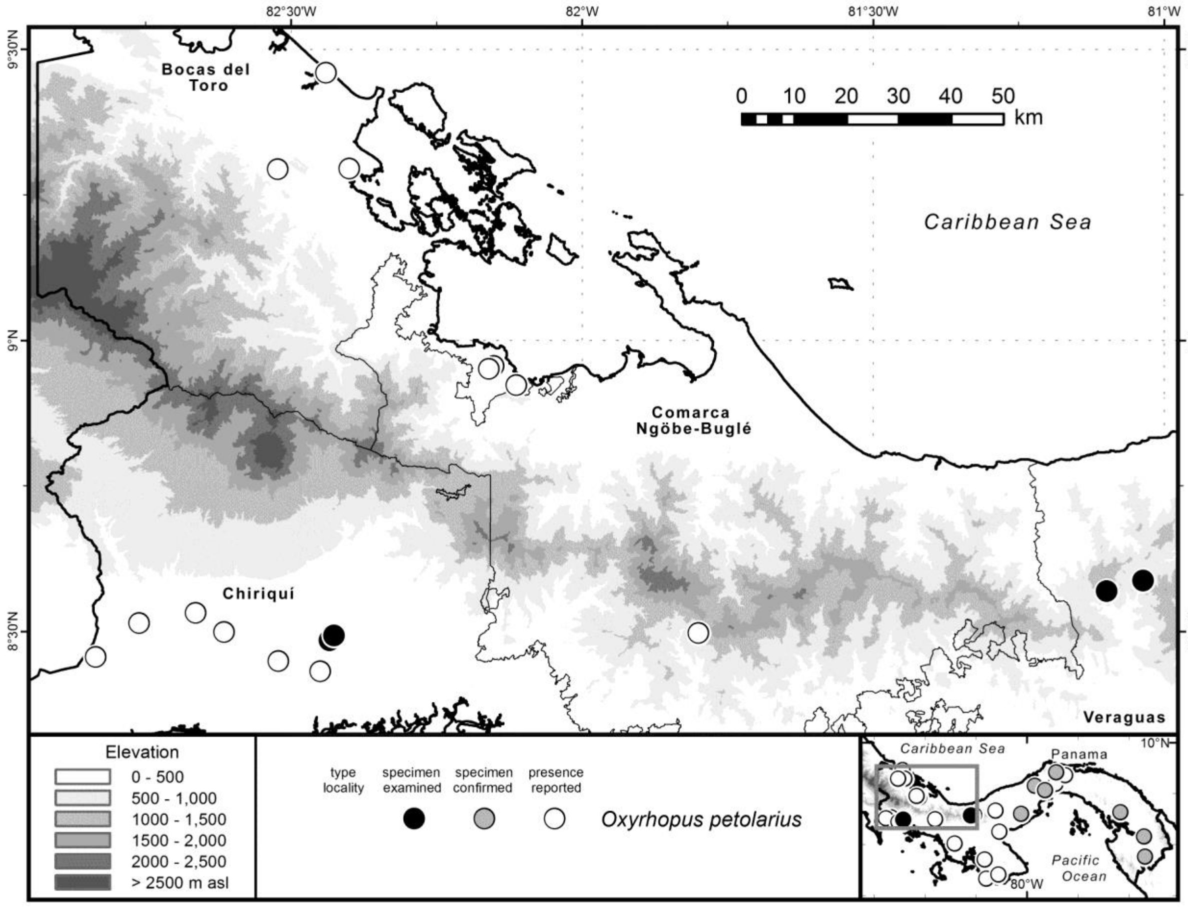
Oxyrrhopus petolarius: Cope (1876).

Oxyrhopus petolus: Ray (2009).

Pseudoboa petola: Dunn & Bailey (1939).

Syntypes. LinnMus 45 and 151, from Africa (in error).

Geographic distribution. Mexico to Peru, Bolivia, and Brazil, 0–1450 m asl. In Panama, along both versants throughout the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Cerro Colorado and Santa Fé areas, PNGDOTH, and Valle de Antón, up to ca. 910 m asl.



Map 4.153: Distribution of *Oxyrhopus petolarius.*

Diagnosis. This medium-sized snake (maximum TOL 1200 mm) with vertically elliptical pupils is unique among Panamanian bicolor (black-red or orange) coralsnake mimics in having an immaculate white to cream venter while the subcaudals present a continuatin of the banded dorsal pattern, smooth dorsals with two apical pits arranged in 19—19—17 rows, and no enlarged vertebral row. Melanistic adults differ from those of *Lampropeltis triangulum* in having in having 77 or more subcaudals (vs. 63 or fewer) and vertically elliptical pupils (vs.

round), and from members of the genus *Clelia* in having largely dark venters and subcaudals (vs. white to cream, some with scattered dark markings).

Description. TOL to 1200 mm; SVL to 903 mm*; tail moderate to long, TL/TOL = 0.19–0.40; D smooth, in 19—19—17 rows; V 186–244; SC 77–126; SPL 7–9; INL 9–11; loreal 1; Preoc 1–2; Postoc 2; Tant 2, Tpost 3; cloacal scute entire; AP 2 at least anteriorly; eyes moderate, pupil vertically elliptical.

The hemipenis of *Oxyrhopus petolarius* is a bilobed organ; pedicel naked proximally, spinulate distally; truncus with enlarged spines; apex calyculate with smooth cups.

Coloration in life. D and L surfaces with alternating transverse bands of black and red or orange, the latter grading over light orange to yellow or white towards head; bands mostly continuous over D and L surfaces, but some usually offset and meeting on midbody to produce a short zig-zag pattern; black bands as wide as (SMF 89702) or much wider than (SMF 89585) light ones; most or all of parietals and D as well as L surfaces of head anterior to these black, followed by a broad, white, yellow, or orange nuchal collar; light rings may have lighter borders and darken considerably in adults, which may become almost completely melanistic with age; V surfaces of head and body usually unicolor white to cream, those of tail at least with a faint continuation of the D and L pattern, and often with a midsubcaudal dark stripe; iris brown to black.

The juvenile SMF 89585 was recorded as follows: D and L ground color Sepia (119), extending onto the edges of V shields; transverse nuchal bar and transverse bands on neck (two complete, two left and one right laterally reaching onto middorsum) Warm Buff (118) with a suggestion of Salmon Color (106); body with a series of 22 transverse bands of Salmon Color (106) edged by Warm Buff (118), extending onto the edges of V shields and grading into Peach Red (94) edged by Salmon Color (106) posteriorly; the series of bands continues onto tail, where their left and right portions segregate on the distal half, to form L bars in a similar pattern to that on neck; V surfaces of head and body dirty white, with a suggestion of Drab-Gray (119D) in the mental region; distalmost portions of subcaudals Pearl Gray (81), the remaining portions exhibiting a continuum of the D and L coloration.

Coloration in preservative. After 5–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that the red bands of SMF 89702 have faded to light orangish brown and the orange bands of SMF 89585 have faded to white.

Natural history notes. Nocturnal, terrestrial and semiarboreal, feeding mainly on lizards, small mammals, and frogs. The juvenile SMF 89585 was found active on the forest floor at 20:30, an uncollected juvenile near Las Algarrobos was climbing around the trunk of a palm tree about 1 m above ground at 22:45. The juvenile SMF 89702 was given to me after having been found in a neighbor's garden during daytime. Just as this somewhat demolished specimen, conspecifics that attract the attention of humans often become victims of their coralsnake mimicry in western Panama.

Remarks. Savage (2011) clarified that the specific epithet should correctly read "*petolarius*". The maximum TOL of 2200 mm given by Köhler (2008) is either based on a typo or the erroneous record of Taylor (1954; McCranie 2011). The specimen SMF 89974 (903 mm SVL + 265+x mm TL = 1168+x mm TOL), collected by AC on Cerro Negro, is close to the maximum size of 1200 mm reported by other authors (e.g., Savage 2002).

I could not find any record to substantiate the upper elevational limit of 1250 m asl in Panama (Perez-Santos 1999), though this elevation appears plausible considering that Solórzano (2004) gave 1200 m for Costa Rica. The highest Panamanian record is FMNH 68097, examined by GK, from "El Valle de Anton, Finca Arce, 3000 ft" (= ca. 914 m), followed by USNM 297729 from "Cerro Colorado, Escopeta Camp, [...] ca. 900 m."

In view of its distribution along the Pacific versant of western Panama and up to about 500 m asl (Perez-Santos 1999; Köhler 2008; Wilson & Johnson 2010; MVUP; see distribution map in Appendix 7), I regard the presence of ***Phimophis guianensis*** **(Troschel 1848)** in my study area as possible. The records from Chiriquí also render its presence in Veraguas and the Comarca Ngöbe-Buglé plausible, and suggest that it might even range into Costa Rica.

Pliocercus euryzonus **Cope 1862**

Cope's False Coral Snake, Halloween Snake, Ringed Glasstail; Cola de vidrio anillada, Coral falsa

Figure 4.110D; Map 4.154.

Pliocercus annellatus: Taylor (1951, 1954); Peters & Orejas-Miranda (1970); Castillo et al. (1990); Martínez & Rodriguez (1994); Martínez et al. (1995); de Sousa (1999).

Pliocercus arubricus: Taylor (1954); Peters & Orejas-Miranda (1970).

Pliocercus dimidiatus: Cope (1876); Taylor (1951, 1954); Peters & Orejas-Miranda (1970); Castillo et al. (1990); de Sousa (1999).

Pliocercus euryzona: Ray & Knight (2013).

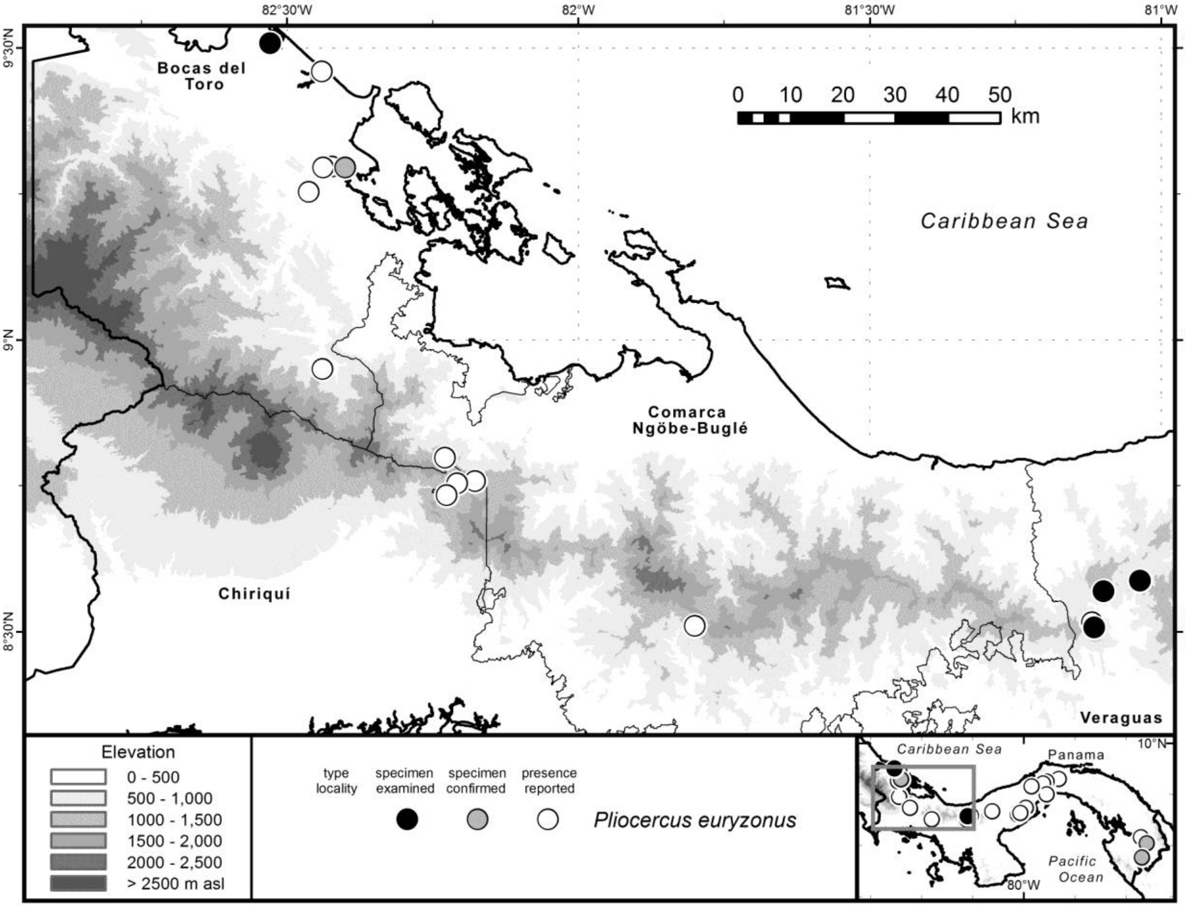
Urotheca elapoides: Wettstein (1934).

Urotheca euryzona: Dunn (1933); Ibáñez et al. (1996, 2001); Perez-Santos (1999); Young et al. (1999); Hofer & Bersier (2001); Savage (2002); ANAM (2004); Solórzano (2004);

Fundación PA.NA.M.A. (2007); Hamad (2009); Savage & Bolaños (2009); Ray (2009); Carrizo (2010).

Holotype. USNM 4303 (now lost), from region of the Truando, New Grenada (= Colombia).

Geographic distribution. Mexico to Colombia and Peru, 0–1600 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from various sites up to ca. 1140 m asl.



Map 4.154: Distribution of *Pliocercus euryzonus.*

Diagnosis. This medium-sized snake (maximum TOL 795 mm) with round pupils is unique among Panamanian bicolor (black-white or white and red) ringed snakes in having a very long tail (though frequently incomplete), most or all of the parietals and upper head surfaces anterior to them black, a loreal and usually two preoculars, smooth dorsals without apical pits arranged in 17—17—17 rows, 8–9 supralabils, and no enlarged vertebral row.

Description. TOL to 795 mm; SVL to 425 mm*; tail very long, TL/TOL = 0.38–0.47; D smooth, in 17—17—17 rows; V 118–142; SC 90–122; SPL 8–9; INL 9–11; loreal 1; Preoc 1–2; Postoc 2–3; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Pliocercus eryzonus* is a slightly bilobed organ; pedicel spinulate; truncus with many enlarged spines and basal hooks; apex with papillate calyces and a naked pocket.

Coloration in life. Body and tail with alternating broad black and narrow light rings, the latter being completely white or red, or white ventrally grading into red dorsally (as in 4 of the 5 Panamanian specimens I have seen) and becoming increasingly suffused with yellow and redd also on the V surfaces posteriorly. Most or all of parietals and D as well as L surfaces of head anterior to these black, with singular light blotches; a narrow nuchal collar covering covering parts of the parietals that may be interrupted medially or bear a medial extension along interparietal suture (broad and uninterrupted in Costa Rican specimens); iris black.

The male SMF 89587 was recorded as follows: D and V ground color Jet Black (89) with a suggestion of Sepia (119); a series of narrow (1-2 D wide) rings that continue throughout the V surfaces of body and tail, where they are broader (2-3 ventrals); dorsally, these rings are, apart from their irregular Sepia (119) mottling, dirty white with a suggestion of Pale Horn Color (92), grading into Rose Pink (108D) posteriorly and on tail; two dirty white nuchal bars extending from last SPL onto parietal scales; 6th and 7th INL, 2nd supralabial, mental, and most portions of the postmental and V neck scales dirty white.

Leonhard Stadler recorded the adult female SMF 89586 (Stadler 2010: Fig. A94) as follows (translated from Stadler 2010): Body with a pattern of alternating broad Sepia (119) and more narrow Flame Scarlet (15) rings; on the V surfaces, the Flame Scarlet (15) coloration grades into dirty white towards the head; head Sepia (119) with a postorbital transverse bar on each side, originating dirty white on the supralabials and grading into Flame Scarlet (15) toward their D limit on the parietals; a circular Flame Scarlet (15) blotch directly anterior to parietals; a small dirty white spot below th nasals.

Coloration in preservative. After 4.5–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that the red has faded to cream or light brown.

Natural history notes. Diurnal and nocturnal, terrestrial and semiarboreal, chiefly feeding on amphibians. Three of the 4 specimens in my collection, plus an uncollected individual at San San Pond Sak, were encountered while moving in low vegetation less than 1 m above ground. SMF 89587 was found on a sandbank in a small creek, and SMF 89586 was spotted by LS and NH while crawling out of a pond (Stadler 2010). All these specimens were active at night. In two of the 5, the tail is incomplete. *Pliocercus euryzonus* is famous for its rather perfect mimicry of *Micrurus mipartitus* and/or *M. multifasciatus* (see Savage 2002: p. 643 for a discussion of this mimicry complex). I found *P. euryzonus* to even exhibit the quick, seemingly nervous, often abrupt movements of *Micrurus.* Defensive behavior includes hiding the head under body coils.

Remarks. I follow recent comprehensive works (e.g., Köhler 2008; Wilson & Johnson 2010; McCranie 2011) in referring this species to the genus *Pliocercus,* while many other authors advocate its inclusion in *Urotheca.* See Savage (2002: p. 643–644) and references therein as well as McCranie (2011: p. 361) for a discussion of this issue and Sheehy (2012) for a first molecular perspective. Savage (2002) stated this species to "rarely" have 2 Tpost, but in the 4 specimens from which I recorded morphological data, this condition is present on 7 of 8 sides.

I was unable to trace any record to substantiate the upper elevational limit of 1600 m asl in Panama (Jaramillo et al. 2010), though this elevation appears plausible considering that Solórzano (2004) gave 1500 m for Costa Rica. The highest Panamanian record known to me is USNM 297730 from "San Felix, 24 km NNE of, Colorado Camp, Cerro Colorado", my georeference of which yields a SRTM elevation of 1136 m.

***Pseudoboa neuwiedii* (Duméril, Bibron & Duméril 1854)**

Neuwied's False Boa; Culebra (de sangre)

Figure 4.110E; Map 4.155.

Pseudoboa neuwiedi: Smith (1958); Busack (1966).

Scytale neuvidii: Cope (1899).

Scytale neuvidii: Brown (1893).

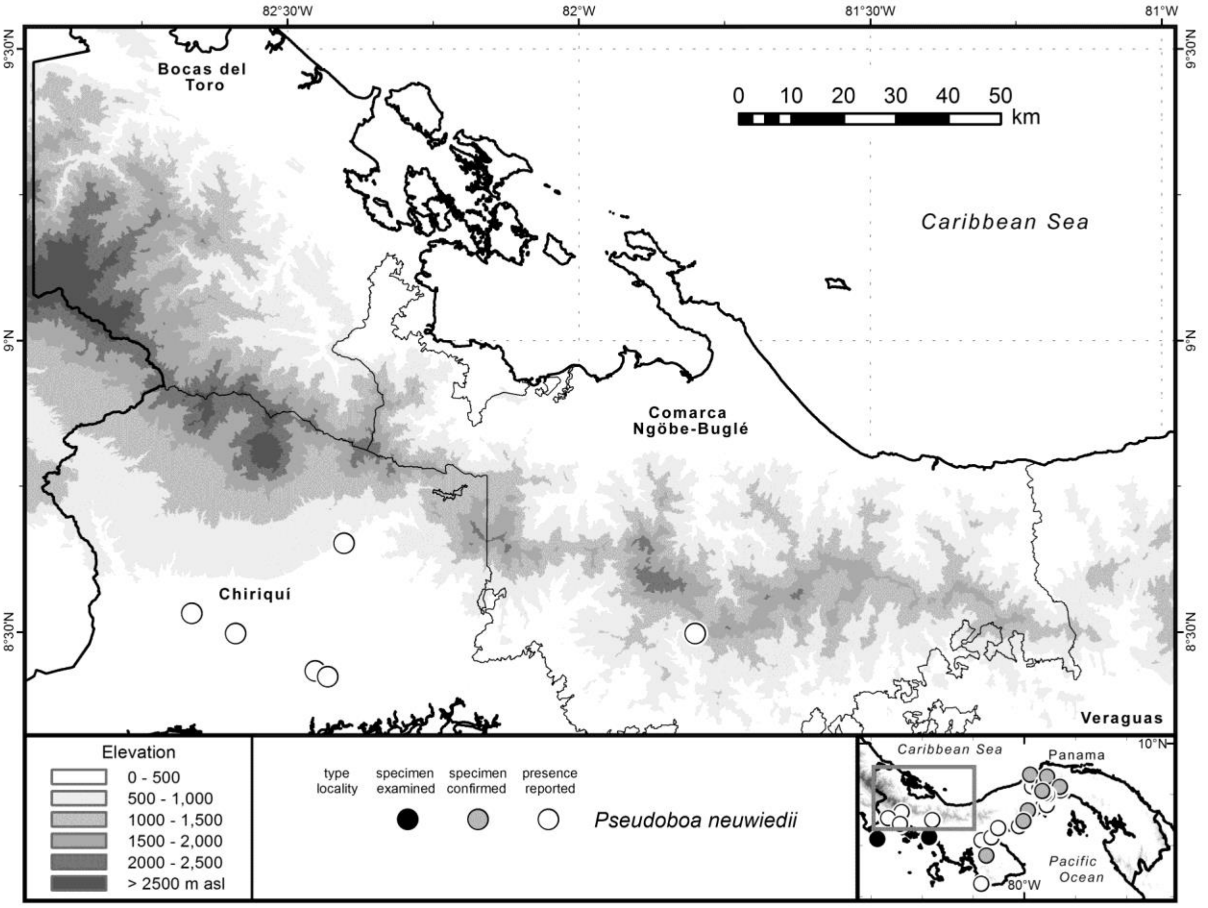
Lectotype. MNHN 2779, from Cote Ferme and Brasil, restricted to Cumaná, Venezuela.

Geographic distribution. Panama (and probably Costa Rica) to Peru and Brazil, 0–1000 m asl. In Panama, along both versants in central and eastern portions of the country and Pacific western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from Río Caldera, the Cerro Colorado area, and PNAC, up to ca. 900 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1200 mm) with vertically elliptical pupils is most unique among Panamanian snakes in having a red body and a black head with or without white nuchal collar, reddish eyes and an immaculate white venter, as well as unpaired subcaudals in combination with smooth dorsals arranged in 19—19—17 rows.

Description. TOL to 1200 mm; SVL to 631 mm*; tail moderate, TL/TOL = 0.28*; D smooth, striate*, in 19*—19—17 rows; V 177–203; SC 64–96; SPL 8*; INL 8*; loreal 1*; Preoc 1*; Postoc 1–2*; Tant 2*, Tpost 2–4*; cloacal scute entire; AP 2*; eyes moderate, pupil vertically elliptical.

The hemipenis of *Pseudoboa neuwiedii* is a deeply bilobed organ with a spinulate pedicel; truncus distally with enlarged spines, lobes with papillate calyces (Zaher 1999).



Map 4.155: Distribution of *Pseudoboa neuwiedii.*

Coloration in life. D and L surfaces of body and tail bright red in juveniles, changing to brownish red in large specimens; D and L surfaces of head and neck black, with a white nuchal collar in juveniles that increasingly darkens with age but usually remains indicated on the ventrolateral portions of head around the last SPL and posteriorly adjacent scales; V surfaces whitish, with dark pigment on INL and chin region, and reddish suffusions under tail that increase posteriorly; iris reddish brown.

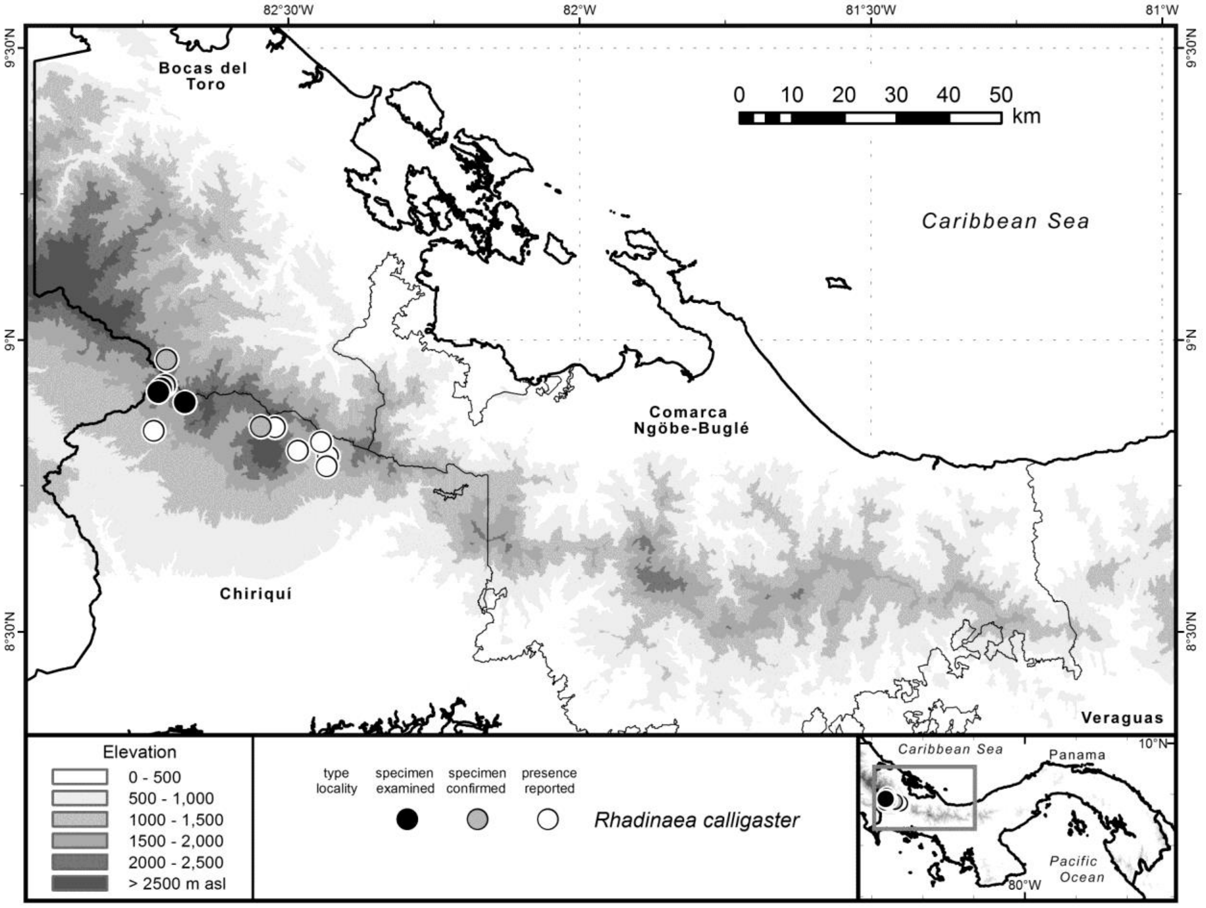
Coloration in preservative. After 4 years in 70% ethanol, the red body coloration of SMF 91572 has turned light brown middorsally, grading into white ventrolaterally.

Natural history notes. Nocturnal and terrestrial, feeding on lizards and other small vertebrates. The only individual which I found in western Panama, SMF 91572, had recently died on the road leading down the Peninsula Burica.

Remarks. A specimen photographed by AH at Las Lajas and handed to the Team Snake Panama collection had 203 V, which to my knowledge is the highest value reported for this species so far. The highest record for Panama is USNM 297731 from "Cerro Colorado, Escopeta Camp, [...] ca. 900 m", which is well above the maximum elevations documented for Panama (165 m asl according to Jaramillo et al. 2010; 300 m according to Perez-Santos 1999). The specimen SMF 91572 from the Peninsula Burica represents the westernmost record for this species, extending its documented distribution about 20 km further W than the previously westernmost record (KU 197807 from "4 1/2 km WNW Concepción near Río Escarrea", my georeference of which lies approximately 50 km NNE of the collection locality of SMF 91572). Moreover, the small distance of less than 2.5 km to the Costa Rican border renders the chance of this species being added to the reptile fauna of this country in the near future very probable.

Rhadinaea calligaster **(Cope 1876)**

Spot-lipped Littersnake, Thick Graceful Brown Snake; Hojarasquera de vientre manchado
Figure 4.110F; Map 4.156.
Contia calligaster: Cope (1876).
Liophis pulveriventris: Wettstein (1934).
Rhadinaea pulveriventris: Taylor (1951: in part., referring to Wettstein's specimen).
Lectotype. USNM 30679 from Pico Blanco (= Cerro Utyum, Cantón de Talamanca, Provincia de Limón fide Savage 1970, 1974), Costa Rica (Myers 1974).



Map 4.156: Distribution of *Rhadinaea calligaster.*

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 1200–2850 m asl. In Panama, along both versants of the Serranía de Talamanca including Bocas del Toro and Chiriquí (and possibly Comarca Ngöbe-Buglé), east to the Boquete area, 1220–2650 m asl.

Diagnosis. This small snake (maximum TOL 513 mm) with round pupils is readily recognized as a Panamanian member of the genus *Rhadinaea* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal, and a striped dorsal pattern. *Rhadinaea calligaster* differs from all its congeners in having bright yellow ventral surfaces with a midventral line of black markings and yellow labials with black borders, and in having more than 140 ventrals (vs. fewer than 135).

Description. (including data from Myers 1974) TOL to 513 mm; SVL to 411 mm; tail moderate, TL/TOL = 0.18–0.29; D smooth except for supracloacal keels in some adult males, striate*, in 17—17—17 rows; V 141–156; SC 46–68; SPL 7–9; INL 7–9; loreal 1; Preoc 1; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Rhadinaea calligaster* is a slightly bilobed organ; pedicel with small spinules; truncus with enlarged spines; apical region with papillate calyces.

Coloration in life. D and L surfaces of body and tail olive to brown, with some light and dark spotting or mottling; dark mottling forming a middorsal dark stripe at least anteriorly, or (as in my examined specimens) a middorsal, dorsolateral, and ventrolateral dark stripe, at least the latter continuing onto tail; D and L surfaces of head above SPL rather unicolor brown; Labials bright yellow with broad black sutures; V surfaces bright yellow with black markings forming a midventral line, more or less pronounced black V and SC margins, and black markings on chin region; iris brown.

The female SMF 89592 (Fig. 4.110F) was recorded as follows D ground color Dark Brownish Olive (129), grading into Yellowish Olive-Green (59) laterally and into Raw Umber (223) towards the head; scales of middorsal row basally with flecks of Sepia (119) with a suggestion of Jet Black (89) suggesting a middorsal longitudinal stripe best pronounced on the neck and anterior portions of body, where these scales have Sulphur Yellow (57) L margins, and disappearing on tail; L scales (1st–4th D rows) mottled with Sepia (119), the quite continuous mottling between 3rd and 4th row suggesting a L longitudinal stripe; D surface of head Raw Umber (223), finely spotted with, and with scale margins of, Sepia (119); V ground color Sulfur Yellow (157) with a suggestion of Spectrum Yellow (55); V and SC with Jet Black (89) basal and L margins, the latter forming ventrolateral longitudinal stripes along body and tail; centers of V with roughly triangular (pointing posteriorly) Jet Black (89) blotches; SPL Sulfur Yellow (157) with a suggestion of Sulphur Yellow (57), with Jet Black

(89) upper and posterior margins continuing onto INL; V surface of head with a few irregularly distributed Jet Black (89) spots and scale margins; iris Raw Sienna (136).

Coloration in preservative. After 6 years in 70% ethanol, the D coloration of my examined specimens has lost its greenish hue and the bright yellow V ground color has turned white.

Natural history notes. Diurnal and terrestrial, presumed to feed on small vertebrates and invertebrates. Myers (1974) reported the finding of several adults around a communal nest with 38 eggs at Cerro Pando. The female SMF 89592 was encountered moving across a trail at 18:40, as was the male SMF 89593 a day later at 17:45. Flattened remains of a colubrid snake in poor condition but identifiable as *Rhadinaea calligaster* by its yellow and black SC were found shortly after the latter specimen on the same trail. When disturbed, both specimens displayed at least parts of their contrasting V coloration.

Remarks. The highest record which I could trace from within my study area is that of MVZ 128688 from "SW flank Cerro Respingo, 4.8 km E (by air) Cerro Punta [...] 2645 m", which is far above the highest elevation documented for Panama (2260 fide Jaramillo et al. 2010). The distances of less than 10 km between the records from the Boquete area and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé possible. I cannot see where the "thick" in the common name "Thick Graceful Brown Snake" (Frank & Ramus 1995) might have been derived from.

Rhadinaea decorata (Günther 1858)

Adorned Graceful Brown Snake, Elegant Littersnake, Pink-bellied Littersnake, Red-bellied Littersnake; Hojarasquera de vientre rojo, Panza naranja

Figure 4.110G; Map 4.157.

Diadophis decoratus: Cope (1860c).

Dromicus ignitus: Cope (1871).

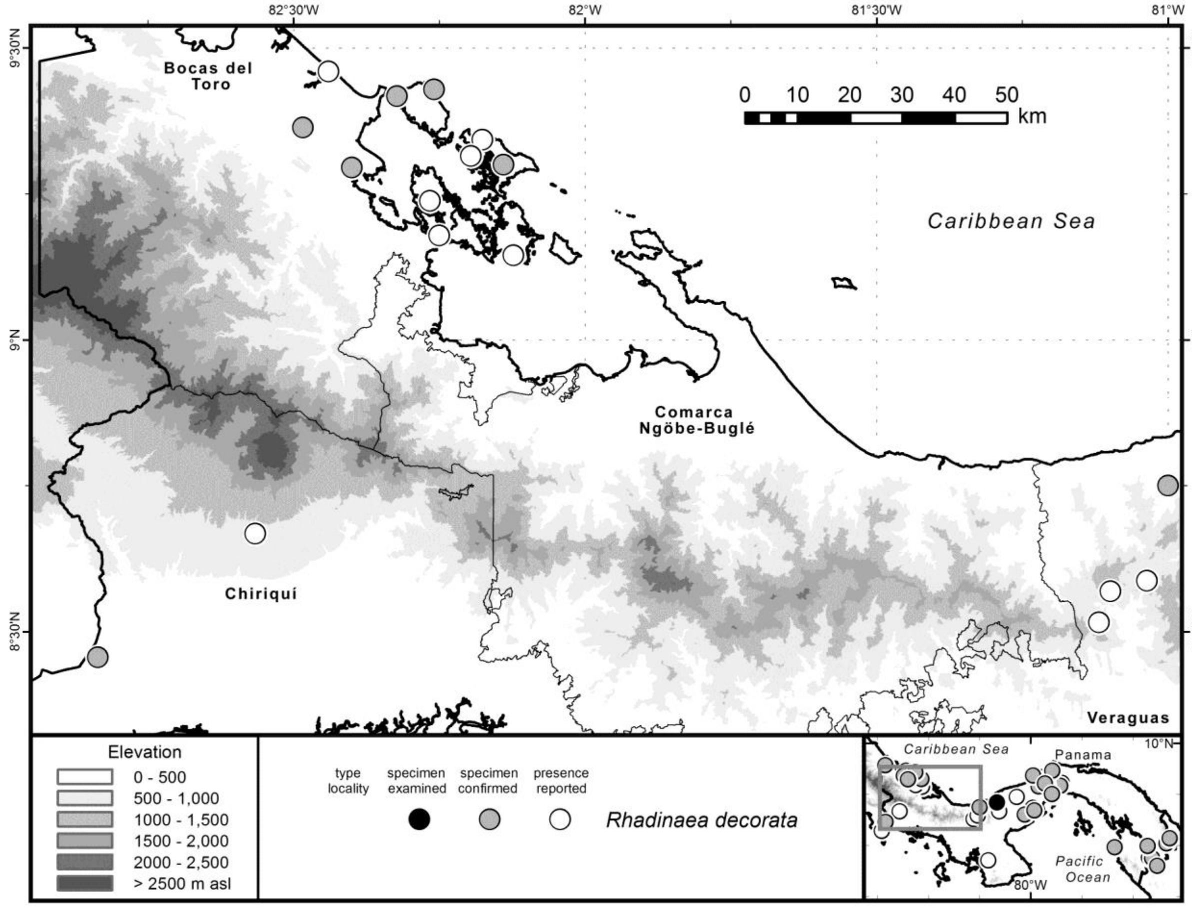
Rhadinaea ignita: Cope (1876).

Rhadinea decorata: Martínez & Rodriguez (1994).

Lectotype. BMNH 1946.1.9.4, from Mexico (Myers 1974).

Geographic distribution. Mexico to Colombia and Ecuador, 0–1400 m asl. In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the slopes of Volcán Barú, the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to ca. 880 m asl.

Diagnosis. This small snake (maximum TOL 470 mm) with round pupils is readily recognized as a Panamanian member of the genus *Rhadinaea* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal, and a striped dorsal pattern. *Rhadinaea decorata* differs from its Panamanian congeners in having a conspicuous light postocular marking that is continuous with or followed by a light dorsolateral stripe extending onto or throughout body, separating the lighter middorsal from the darker brown lateral coloration, as well as an immaculate yellow, orange, red, or white venter, light lips, and a long tail comprising 35% or more of the total length (vs. 35% or less).



Map 4.157: Distribution of *Rhadinaea decorata.*

Description. (including data from Myers 1974) TOL to 470 mm; SVL to 265 mm; tail long, TL/TOL = 0.35–0.47; D smooth except for supracloacal keels in many specimens and weak keels extending well anterior in about half of the Panamanian specimens, striate, in 17—17—17 rows (rarely 15 or 16 D-HH or D-HC); V 110–134; SC 85–122 (67 in one specimen from Ecuador); SPL 7–9; INL 8–11; loreal 1; Preoc 1–2; Postoc 1–3; Tant 1, Tpost 1–2; cloacal scute divided; AP 0 or in some specimens 1–2 anteriorly; eyes moderate, pupil round.

The hemipenis of *Rhadinaea decorata* is a unilobed organ; pedicel with small spinules; truncus with several small and a few enlarged spines; apical region with spinulate calyces proximally and papillate calyces distally.

Coloration in life. D surfaces medium brown, separated from the darker brown L surfaces by a light dorsolateral stripe with a dark lower edge; a conspicuous, often ocellus-like light (usually bright white) postorbital blotch or stripe connected to, or (in most Panamanian specimens) separated by a similar marking from, the light dorsolateral stripe that gradually becomes less contrasting posteriorly; sometimes with a more or less pronounced dark middorsal stripe; tail mostly unstriped; V surfaces of body and tail usually immaculate white, orange, or red, grading into white or yellow anteriorly and under head; SC sometimes with dark markings; iris brown to orange, with a lighter upper portion.

Coloration in preservative. Similar to that in life, apart from that the reddish and yellowish tonalities fade with time.

Natural history notes. Diurnal and terrestrial, feeding on frogs and their eggs as well as on other small vertebrates.

Remarks. The records from E and W of the Comarca Ngöbe-Buglé render the occurrence of *Rhadinaea decorata* in this political subdivision plausible.

Rhadinaea pulveriventris Boulenger 1896

Common Graceful Brown Snake, White-lipped littersnake; Hojarasquera de labios blancos

Map 4.158.

Liophis pulveriventris: Wettstein (1934).

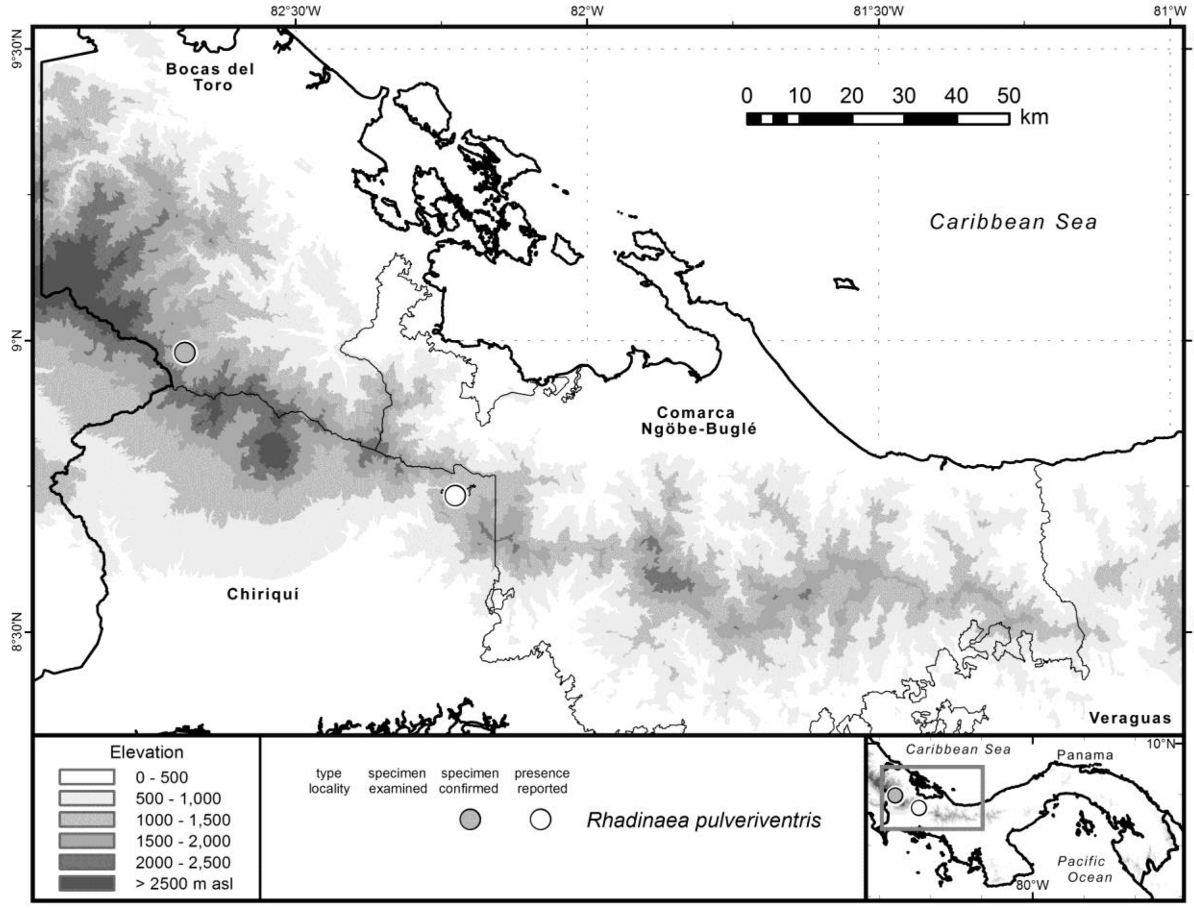
Holotype. BMNH 1946.1.9.6, female, from Azahar de Cartago, Costa Rica (Myers 1974).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 1000–1600 m asl. In Panama, along both versants of the Serranía de Talamanca including Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé, east to RFLF, 1000–1450 m asl.

Diagnosis. This small snake (maximum TOL 502 mm) with round pupils is readily recognized as a Panamanian member of the genus *Rhadinaea* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal, and a striped dorsal pattern. *Rhadinaea pulveriventris* differs from all its congeners in having a black longitudinal band on the neck that bifurcates in the nuchal area, and a black lateral stripe extending from rostral through eye and along body on each side.

Description. (including data from Myers 1974) TOL to 502 mm; SVL to 354 mm; tail long, TL/TOL = 0.26–0.32; D smooth except for weak supracloacal keels in few specimens, in 17—17—17 rows; V 119–134; SC 63–80; SPL 8; INL 8–11; loreal 1; Preoc 1; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Rhadinaea pulveriventris* remains undescribed to my knowledge, but it has recently become known that it lacks the "straight spines" on the truncus that are present in the other members of the *R. vermiculaticeps* group (Myers 2011).



Map 4.158: Distribution of *Rhadinaea pulveriventris.*

Coloration in life. D and L surfaces almost uniformly brown; a black L stripe originates at rostral and extends posteriorly through eye and onto body, where it becomes increasingly diffuse posteriorly, and is often bordered by a light line or dashes above; a more or less difuse, dark longitudinal middorsal band on anterior body bifurcates in the nuchal area to form a "Y"-shaped marking opening towards head; L surfaces of head below dark stripe as well as V surfaces whitish, immaculate or with more or less dense dark dotting or mottling; iris reddish in upper portion, brown below. Myers (1974) stated the specimen KU 112459 from Cerro Pando to have had the D brown tonalities with golden and yellowish hues, labials pinkish white, and posterior V surfaces yellowish.

Coloration in preservative. Similar to that in preservative, apart from that the yellowish and pinkish shades fade with time.

Natural history notes. Diurnal and terrestrial, probably with a similar diet as its congeners.

Remarks. The lower elevational limit of 750 m asl (Perez-Santos 1999) not substantiated by any record. This species has only been reported from two localities in my study area and Panama as a whole, the first of these being the N slope of Cerro Pando at 1450 m (KU 112459; Myers 1974). Later, Myers (1977) listed *Rhadinaea pulveriventris* for the area of the Fortuna dam without specific locality. While my generalized georeference for "Fortuna" yields a SRTM elevation of 1051 m, Perez-Santos (1999) stated this record to come from "Fortuna, 1000 m", which may be considered the lowest documented elevation in Panama (as understood by Jaramillo et al. 2010). Together with the record from the Caribbean slope of Cerro Pando, the distance of probably less than 5 km between the record from RFLF and the Comarca's border render the presence of this species in the Comarca Ngöbe-Buglé plausible.

***Rhadinaea sargenti* Dunn & Bailey 1939**

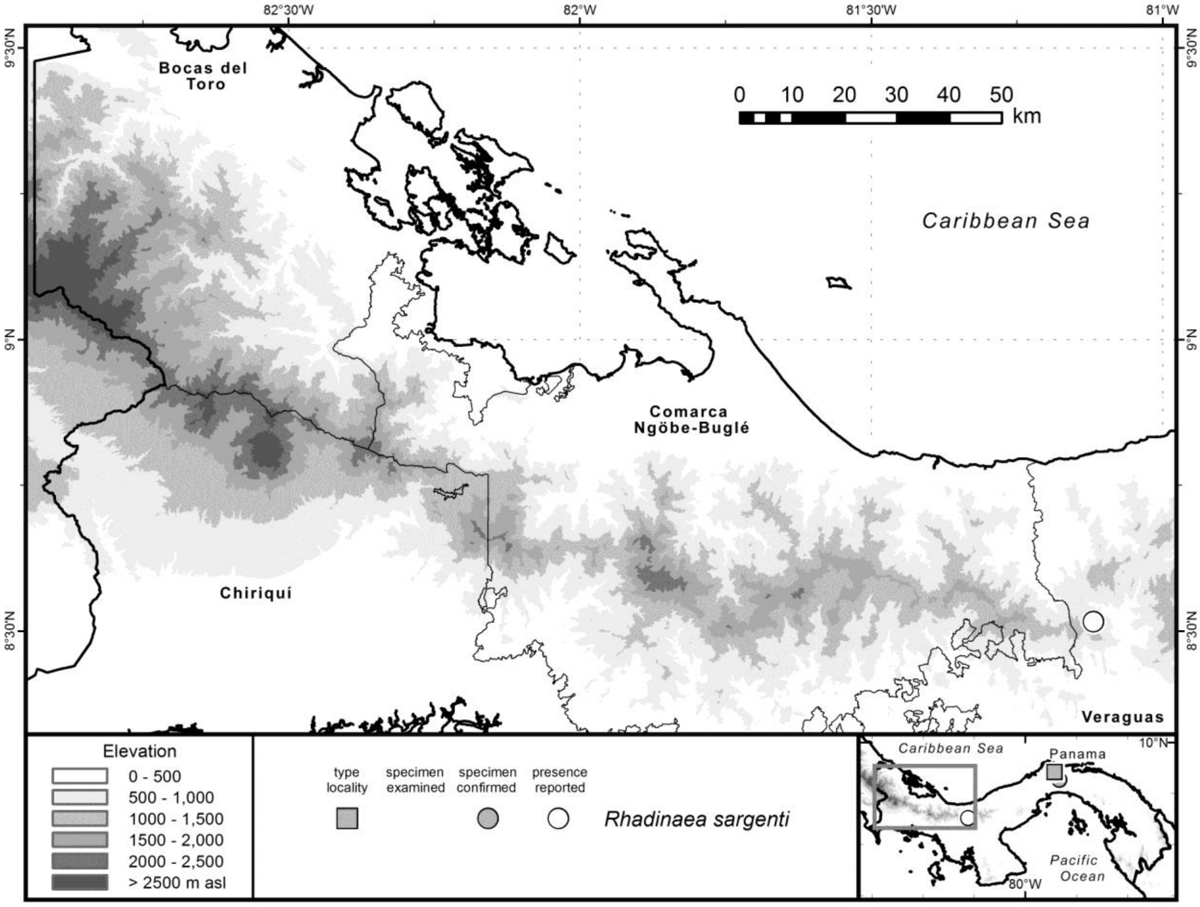
Littersnake, Sargent's Graceful Brown Snake; Hojarasquera

Figure 4.110H; Map 4.159.

Rhadinea sargenti: Martínez & Rodriguez (1994).

Holotype. MCZ 42788, adult male, from the Pequení-Esperanza ridge near head of [Río] Pequení, 1800 feet (= ca. 549 m asl).

Geographic distribution. Endemic to Panama, approximately 180–900 m asl. Apart from the records in Panama province E of the canal, reported from the Santa Fé area around 880 m asl.



Map 4.159: Distribution of *Rhadinaea sargenti.*

Diagnosis. This small snake (maximum TOL 310 mm) with round pupils is readily recognized as a Panamanian member of the genus *Rhadinaea* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal, and a striped dorsal pattern. *Rhadinaea sargenti* differs from all its congeners in having a light reticulum on the posterior dorsal head surfaces combined with a broad black lateral band throughout the body and a rather diffuse dark middorsal stripe (including data from Myers 1974).

Description. (including data from Myers 1974) TOL to 310 mm; SVL to 211 mm; tail long, TL/TOL = 0.32–0.35; D smooth except for supracloacal keels in one adult male, in 17—17—17 rows; V 117–122; SC 67–74; SPL 8; INL 9–10; loreal 1; Preoc 1; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Rhadinaea sargenti* is a unilobed organ; pedicel spinulate; truncus with two rows of large, straight spines and numerous small, recurved spines; apical region with papillate calyces.

Coloration in life. Similar to that in preservative, apart from that the V surfaces are red.

Coloration in preservative. D surfaces brown with a broad longitudinal black or blackish brown L band including the L tips of the ventrals, and a diffuse dark middorsal stripe that becomes more clear-cut on tail; D surfaces of head brown with a dark-edged whitish reticulum posterior to eyes; L surfaces of head with a broad dark stripe running from nostril through eye and connecting with the dark L body band, bordered above by a black-edged light stripe along head; SPL and INL light with black sutures and spotting; V surfaces white, with dark mottling often increasing under tail.

Natural history notes. Largely unknown, probably similar to its congeners.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Rhadinaea sargenti* and assigned the species to the IUCN category DD, while the official IUCN Red List (IUCN 2014) lists it as LC. I calculated the EVS for *R. sargenti* as 5 (range) + 4 (persecution) + 4 (ecological distribution) = 13, indicating a high vulnerability. The fact that it is known from only 5 localities, together with its extent of occurrence of 1859 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1ab(iii).

Remarks. Unfortunately, the specimens underlying the record of Martínez & Rodriguez (1994) from "Cerro Tute" (= Cerro Mariposa) have been lost (V. Martínez, pers. comm.), so that a verification of this most interesting distribution extension is impossible. Oddly enough, Martínez et al. (1994), in their subsequent inventory of the nearby Cerros Narices and La Anselma, which includes a somewhat altered version of the Cerro Tute species list of Martínez & Rodriguez (1994), do not list *Rhadinaea sargenti* for the latter mountain, without any commentary why the species was omitted. Thus, the presence of *R. sargenti* in my study area remains questionable. However, several species which for a long time were only known from the well-sampled surroundings of the former Canal Zone (e.g., *Dipsas nicholsi, Trimetopon barbouri*) have been reported from PNGDOTH and/or the Santa Fé area more or less recently, rendering the species' presence around Santa Fé not too improbable. If the record is correct as assumed herein, then the distance of ca. 4 km from Cerro Mariposa to the Comarca's border renders the species' occurrence in the Comarca Ngöbe-Buglé plausible. My georeference for "Río Pequení" (provenance of the "GML specimen" examined by Myers 1974), placed roughly in the middle of this river's course, yields a SRTM elevation of 178 m asl, which is somewhat below the lowest elevation given for this species, just as the approximate elevation of the record from Cerro Mariposa (880 m) is above the highest elevation given for this species (300 and 800 m fide Jaramillo et al. 2010). No record exists to substantiate the minimum elevation of 0 m given by Perez-Santos (1999).

***Rhadinaea vermiculaticeps* (Cope 1860)**

Littersnake, Vermiculate Graceful Brown Snake; Hojarasquera

Figure 4.111A; Map 4.160.

Rhadinea vermiculaticeps: Martínez & Rodriguez (1994).

Rhadinea vermiculuticeps: Martínez et al. (1995).

Taeniophis vermiculaticeps: Cope (1860c).

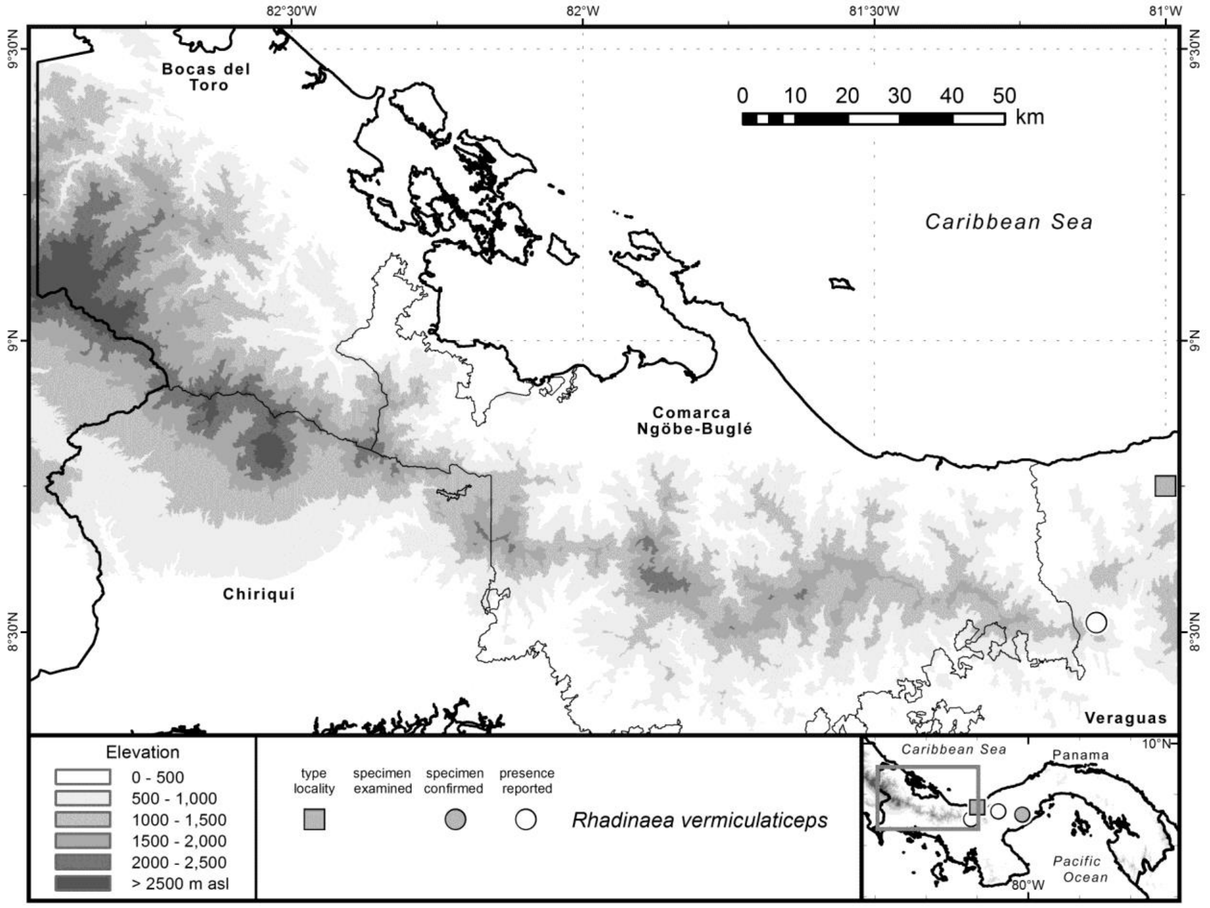
Lectotype. ANSP 3535, male, from "Veragua, New Grenada" (Cope 1860c; = Cocuyos de Veraguas, Panama, fide Myers 1974).

Geographic distribution. Endemic to west-central Panama, 200–990 m asl. In the Cordillera Central, reported from the Santa Fé area, PNGDOTH, and Valle de Antón, 590–990 m asl.

Diagnosis. This small snake (maximum TOL 374 mm) with round pupils is readily recognized as a Panamanian member of the genus *Rhadinaea* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal, and a striped dorsal pattern. *Rhadinaea vermiculaticeps* differs from all its congeners in having a light reticulum on the posterior dorsal head surfaces combined with a broad, light-centered dark middorsal stripe and one narrow dark lateral stripe per side (including data from Myers 1974).

Description. (largely based on Myers 1974) TOL to 374 mm; SVL to 268 mm; tail long, TL/TOL = 0.31–0.35; D smooth except for weak supracloacal keels in adult males, in 17—17—17 rows; V 117–121; SC 63–82; SPL 8–9; INL 9–10; loreal 1; Preoc 1; Postoc 2; Tant 1, Tpost 2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Rhadinaea vermiculaticeps* is a unilobed organ; pedicel spinulate; truncus with two rows of large, straight spines and numerous small, recurved spines; apical region papillate calyces.



Map 4.160: Distribution of *Rhadinaea vermiculaticeps.*

Coloration in life. The D and L coloration of the specimen photographed in life at Río Blanco, Coclé province, by Andrew Hein (Fig. 4.111A; V surfaces not visible) is very similar to the coloration in preservative described by Myers (1974) and observed by myself in a photograph of FMNH 47464 taken by GK: D and L ground color light yellowish brown; paravertebral and L stripes dark brown, the latter abruptly contrasting with the light ground color along its upper edge but slowly grading into it below over most of the L surfaces; paravertebral dark stripes fusing on tail to form a single middorsal dark stripe; iris orange; L surfaces of head above and below dark postocular stripe dirty white; dark borders of light reticulum on D head surfaces not very pronounced; anterior, unreticulated D head surface of a lighter brown then the posterior portion bearing the light reticulum. In the original description Cope (1860c) noted "chin and belly yellowish white", indicating that the V surfaces may have been yellow, orange, or even red in life as it is the case in the species' supposed close relative *Rhadinaea sargenti.*

Coloration in preservative. D and L surfaces brown, with a narrow dark L stripe on each side and a pair of dark paravertebral stripes enclosing a narrow light middorsal stripe on the vertebral scale row; D surfaces of head brown with a dark-edged whitish reticulum posterior to eyes that is connected to the light vertebral stripe; D and L stripes extending posteriorly onto, and over most of, tail; L surfaces of head with a broad dark stripe running from nostril through eye and connecting with the dark L body stripe, bordered above by a black-edged light stripe that grades into the brown D coloration posterior to head; SPL and INL light with black sutures and spotting; V surfaces white, sometimes with with dark mottling laterally that increaes under tail; L tips of V with dark spots fusing into a dark ventrolateral stripe on tail.

Natural history notes. Largely unknown, probably similar to its congeners.

Conservation. Jaramillo et al. (2010) calculated an EVS of 11 for *Rhadinaea vermiculaticeps* and assigned it to the IUCN category NT, in which it is also placed in the official IUCN Red List (IUCN 2014). I calculated the EVS for this species as 5 (range) + 4 (persecution) + 4 (ecological distribution) = 13, indicating a high vulnerability. Its extent of occurrence of 1362 km^2 and the continuing deforestation we observed in the region qualify the species for the IUCN category EN according to IUCN (2001) criterion B1ab(iii).

Remarks. The distance of ca. 4 km from Cerro Mariposa (Martínez & Rodriguez 1994) to the Comarca's border renders the species' occurrence in the Comarca Ngöbe-Buglé plausible. My georeference for the specimen CHP 5663 from "El Copé, Río Blanco (Parque NGDOTH)" yields a SRTM elevation of 986 m asl, which is somewhat above the highest elevation given for this species (850 m fide Jaramillo et al. 2010, 900 m fide Köhler 2008 and Wilson & Johnson 2010). No record exists to substantiate the minimum elevation of 0 m given by Perez-Santos (1999). As pointed out by Myers (1974), records of *Rhadinaea vermiculaticeps* from Costa Rica (see Taylor 1951) are not substantiated by specific records.

Rhadinella godmani **(Günther 1865)**

Godman's Graceful Brown Snake, Yellow-bellied Littersnake; Hojarasquera de vientre amarillo

Figure 4.111B; Map 4.161.

Rhadinaea altamontana: Taylor (1954); Perez-Santos (1999).

Rhadinaea godmani: Smith (1958); Peters & Orejas-Miranda (1970); Myers (1974); Auth (1994); Perez-Santos (1999); Young et al. (1999); Ibáñez et al. (2001); Savage (2002); Solórzano (2004); Fundación PA.NA.M.A. (2007); Köhler (2008); Savage & Bolaños (2009); Jaramillo et al. (2010); Sasa et al. (2010); Wilson & Johnson (2010).

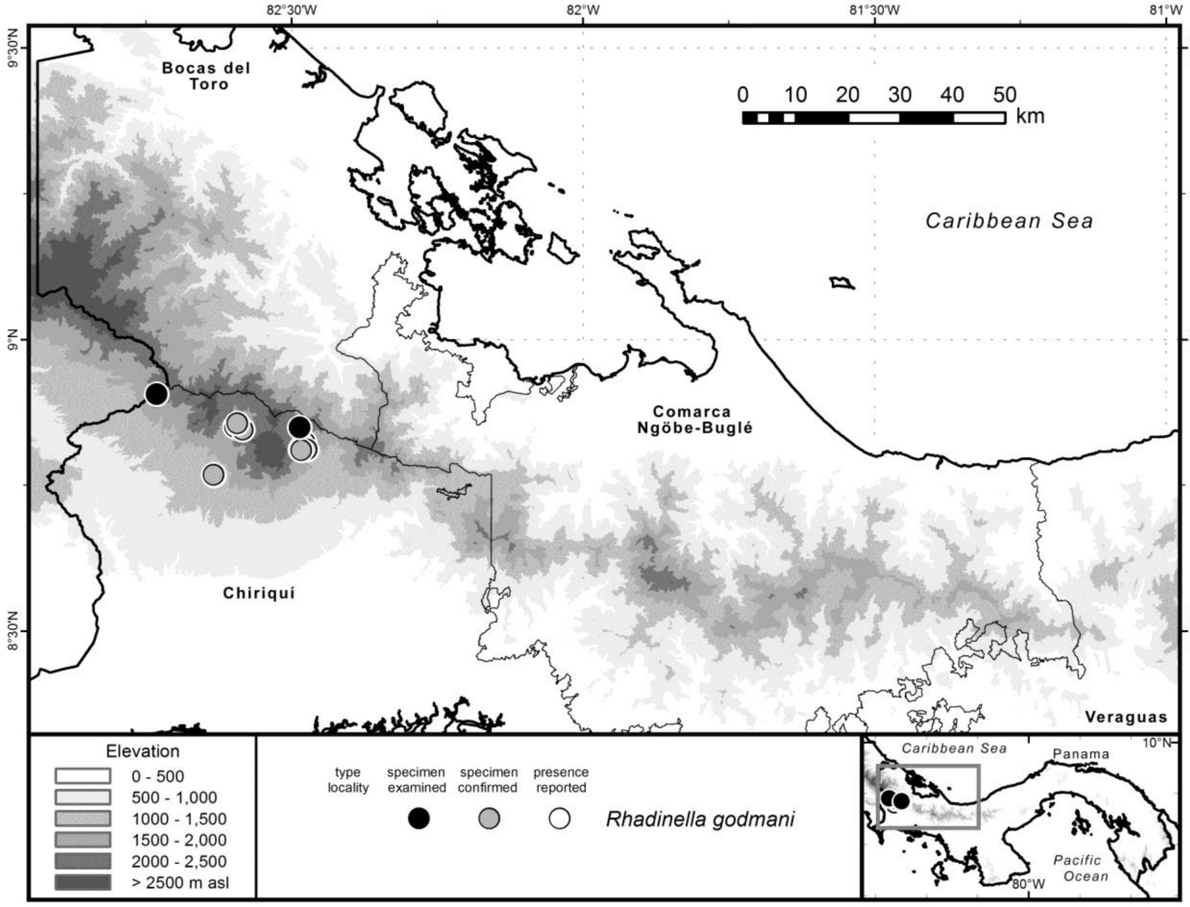
Rhadinaea godmanii: Cope (1876).

Rhadinaea serperaster: Peters & Orejas-Miranda (1970: in part.).

Rhadinaea serperastra: Dunn (1947); Smith (1958).

Lectotype. BMNH 1946.1.9.17, adult male, from Dueñas, Guatemala (Myers 1974).

Geographic distribution. Mexico to southeastern Honduras as well as Costa Rica and Panama, 1000–2650 m asl. In Panama, only reported from the Pacific versant of the Serranía de Talamanca in Chiriquí east to the Boquete area, approximately 1200–2130 m asl.



Map 4.161: Distribution of *Rhadinella godmani.*

Diagnosis. This small snake (maximum TOL 572 mm) with round pupils is readily distinguished from all other Panamanian snakes by its smooth dorsals arranged in 21—21—21 rows (very rarely 19 or 20 D-HC), divided cloacal scute, the presence of a loreal, its dorsal pattern comprising a dark middorsal and several dark lateral stripes on brown ground color, and its immaculate venter that is white in juveniles and yellow or orange in adults (including data from Myers 1974).

Description. (including data from Myers 1974) TOL to 572 mm*; SVL to 435 mm; tail moderate to long, TL/TOL = 0.23–0.32; D smooth except for supracloacal keels in some specimens, striate*, in 21—21—(19–21) rows; V 156–186; SC 71–95; SPL 7–9; INL 8–10; loreal 1; Preoc 1–2; Postoc 1–2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Rhadinella godmani* is a slightly bilobed organ; pedicel spinulate; truncus with numerous small to moderate spines; apical region with spinulate calyces proximally, distally with papillate calyces.

Coloration in life. D and L surfaces of body and tail brown, with a narrow dark middorsal sripe and a comparatively broad dark L stripe covering the 4th D row and at least adjacent portions of neighboring D rows, sometimes with a narrow light stripe in its center; 1–3 narrow ventrolateral stripes below L stripe, partially mergin on tail; often with a usually vague light nuchal collar that is usually interrupted by the anterior extreme of the dark middorsal stripe, and/or an elongate, whitish postocular marking obliquely extending towards penultimate SPL; anterior SPL to level of eye whitish with dark markings; D and L surfaces of head above SPL dark brown mottled with darker brown; V surfaces whitish in juveniles and yellow to orange in adults, mostly immaculate except for scattered dark spots on chin and L portions of V and SC, as well as dark mottling forming a midventral line under tail; iris brown.

The male SMF 89594 was recorded as follows: D ground color of body and tail Burnt Umber (22), grading into Sayal Brown (223C) laterally; scales of middorsal row Sepia (119), forming a longitudinal stripe that continues throughout the tail; a broad longitudinal Sepia (119) L stripe covering the scales from upper half of 3rd to lower edges of 6th D row, extending from head to tip of tail; a narrow longitudinal Sepia (119) L stripe covering the upper edges of 1st and lower edges of 2nd D row, extending from head to cloaca; fine, mostly merged Sepia (119) mottling between 2nd and 3rd D row as well as on common margins of V and 1st D row suggesting two more, very narrow L stripes extending from head to cloaca; L edges of SC mottled with Sepia (119), suggesting a caudal L stripe that merges with the continuous broad L stripe after anterior third of tail; neck with the faint suggestion of an interrupted Drab-Gray (119D) collar; D surface of head and adjacent D Dusky Brown (19); SPL Sepia (119) with Cream Color (54) blotches forming an interrupted supralabial stripe extending from 1st to 5th SPL, and a postocular stripe extending from 5th to 6th SPL; V surface of head Cream Color (54), grading into Trogon Yellow (153) towards the neck and finely mottled with Sepia (119), especially on chin region; V surfaces of body and tail Orange Yellow (18), grading into Trogon Yellow (153) towards the neck and with sparsely distributed Sepia (119) spots; median edges of subcaudals finely mottled with Sepia (119), suggesting a narrow, longitudinal subcaudal stripe; iris Cinnamon (123A).

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 89594 is similar to that in life, apart from that the yellow and orange V ground color has turned white.

Natural history notes. Diurnal and terrestrial, feeding on small vertebrates and their eggs as well as invertebrates. The adult male SMF 89594 was crossing the dirt road to Jurutungo around dusk at 18:30.

Conservation. Jaramillo et al. (2010) calculated an EVS of 9 for *Rhadinella godmani* and assigned the species to the IUCN category DD, while the official IUCN Red List (IUCN 2014) lists it as LC. However, the LCA populations of this nominal taxon have a rather restricted distribution, which might qualify them for one of the IUCN "Threatened" categories if they were eventually recognized as separate species.

Remarks. This species has been called *Rhadinaea godmani* by almost all authors until Myers (2011) resurrected the genus *Rhadinella* Smith 1941 for the *Rhadinaea godmani* species group of Myers (1974), including 14 additional species. As pointed out by Myers (1974) and Savage (2002), all records of *Rhadinaea serperaster* from Panama (e.g., Dunn 1947) are based on misidentified specimens of the similar *Rhadinella godmani,* whereas the former species appears to be endemic to Costa Rica.

As currently understood, *Rhadinella godmani* is one of the last montane reptile species inhabiting the highlands of both Nuclear and Lower Central America, that is, occurring across the wide hiatus of the Nicaraguan depression. Other such nominal species have been split up in the past (see remarks for *Cerrophidion sasai*), and I concur with McCranie (2011) in expecting the nominal taxon *R. godmani* to await a similar fate once a comprehensive molecular phylogeny of the various taxa once referred to *Rhadinaea* (Myers 1974) is constructed. In this case, the new combination *Rhadinella altamontana* (Taylor 1954) would become the name assignable to the taxon inhabiting the Talamancan highlands.

The female SMF 85091 (432 mm SVL + 140 mm TL = 572 mm TOL) is the largest specimen of *Rhadinella godmani* reported so far, and refutes the notion that males are larger than females in this species. Together with the maximum elevation of up to 2650 m asl as reported in recent comprehensive works (Köhler 2008; Sasa et al. 2010), the distance of less than 5 km between several records from the Boquete area (only 2 km in the case of SMF 85091) and the provincial border render the presence of *R. godmani* in Bocas del Toro plausible. Likewise, while I regard its presence in the Comarca Ngöbe-Buglé possible in view of the distance of less than 10 km between these records and the Comarca's border. The highest elevation given for Panama (2135 m; Jaramillo et al. 2010) seems to be derived from rounding up the upper limit of the elevational range given for MCZ 34369 by Myers (1974: "Boquete district, 6000-7000 ft" = ca. 1829-2134 m). The highest definite collection site in Panama known to me is that of SMF 89594 (1840 m), followed by that of FMNH from

"Nueva Suiza, 6000 ft (= ca. 1829 m). Nevertheless, I expect *R. godmani* to be collected at elevations well above 2130 m in the future.

Sibon annulatus (Günther 1872)

[in part modified from Lotzkat et al. (2012d); see Appendix 8 for original publication]

Red-ringed Snaileater, Ringed Snail-eater, Ringed Snail Sucker, Ringed Slugeater, Ringed Slug-eater; Caracolera, Caracolera de anillos rojos

Figures 4.80B; 4.87A–C; 4.111C; Maps 4.17; 4.162.

Dipsas annulata: Taylor (1951, 1954); Smith (1958).

Dipsas pictiventris: Taylor (1951, 1954).

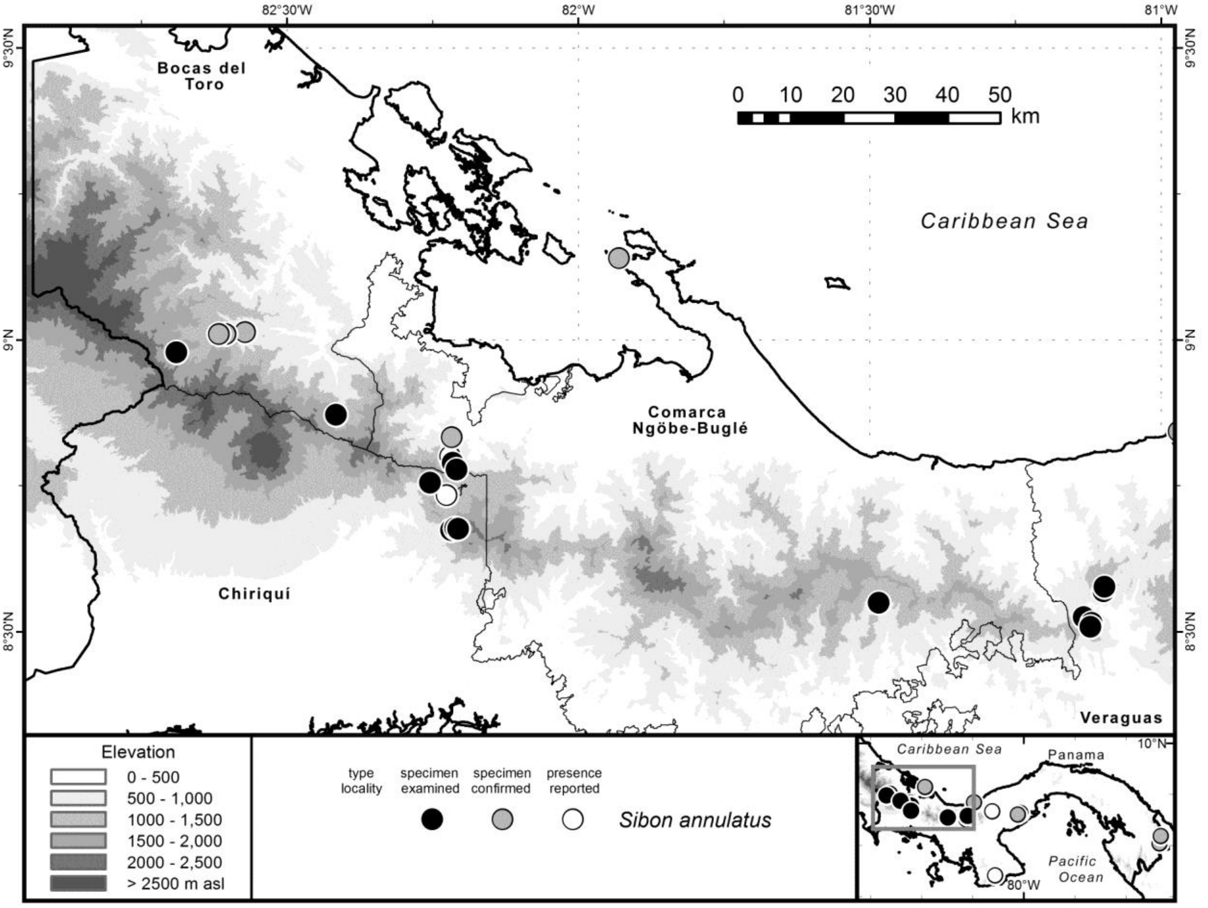
Leptognathus annulata: Cope (1876).

Leptognathus pictiventris: Cope (1876).

Sibon annulata: Dunn & Bailey (1939); Peters (1960); Peters & Orejas-Miranda (1970); Myers (1977).

Sibon dimidiatus: Hofer & Bersier (2001); Köhler (2008: in part.: Fig. 752).

Holotype. BMNH 1946.1.20.81, from the elevated country of Costa Rica, near Cartago.



Map 4.162: Distribution of *Sibon annulatus.*

Geographic distribution. Honduras to Panama, 0–1640 m asl. In Panama, along both versants throughout most of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites along both versants up to 1640 m asl.

Diagnosis. This medium-sized snake (maximum TOL 648 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. *Sibon annulatus* differs from *S. argus* in having 1–2 postmentals (vs. none, mental contacting 1st pair of chin shields) and a banded dorsal pattern (vs. blotched), from *S. lamari* in having comparably large and symmetrical dark brown markings on the upper head surface (vs. small, irregular white or yellow as well as green, red, and black speckles) and a brownish dorsal ground color (vs. greenish), from *S. longifrenis* in having a banded pattern (vs. blotched) and large and protruding eyes (vs. moderate, not protruding) as well as 277 or more total segmentals (vs. 275 or fewer), from *S. nebulatus* in having the 1st pair of infralabials separated by 1–2 postmentals (vs. in contact, no PM), from *S. noalamina* in having 2 supralabials posterior to eye (vs. one), and from *S. perissostichon* in having 15 straight dorsal rows at midbody (vs. 17 oblique rows).

Description. TOL to 648 mm*; SVL to 427 mm*; tail long, TL/TOL = 0.30–0.37; D smooth, striate*, in 15—15—15 rows, vertebral and paravertebral rows slightly enlarged; V 161–193; SC 103–135; SPL 6–9, enlarged penultimate one usually separated from orbit; INL 6–10, 1st pair separated by 1–2 PM; loreal 1; Preoc 0–2; Postoc 0–3; Tant 1–2, Tpost 2–3; cloacal scute entire; AP 0; eyes large, pupil vertically elliptical.

The hemipenis of *Sibon annulatus* is a very slightly bilobed organ; pedicel spinulate; truncus with enlarged spines; long apical region with spinulate calyces.

Coloration in life. D ground color pale olive to reddish brown, irregularly spotted and blotched with different shades of brown and green; body and tail with irregular darker (usually reddish) brown crossbands that may be offset and reach well onto venter (usually to midventer) or continuous and completely encircle body and tail, usually assuming darker tonalities ventrally, and often bear diffuse narrow light and/or dark borders on D and L surfaces; D surfaces of head, apart from variable mottling, with more or less symmetrical, large dark brown markings; V ground color white to yellow, immaculate or with darker mottling, usually extending onto ventrolateral surfaces of body between dark bands; iris reddish brown to red.

The male SMF 88715 was recorded as follows: D ground color Raw Umber (123) with Mars Brown (223A) pigment along vertebral line and Burnt Sienna (132) transverse bars which reach well onto V scales but do not meet at midventer and are edged by dirty white and Chamois (123D) scales; V surface of body Citrine (51) with Greenish Olive (49) speckling; V surface of tail Grayish Olive (43); D surface of head Mars Brown (223A) with Sepia (119) blotches; iris Burnt Sienna (132).

Leonhard Stadler recorded the adult female SMF 89596 as follows (translated from Stadler 2010): Body and tail with a continuous pattern of alternating crossbands extending around body: broader crossbands Burnt Umber (22) separated by more narrow crossbands that are Olive-Green (Auxiliary) (48) mottled with Ferruginous (41) and Burnt Umber (22) dorsally and dirty white ventrally; D surface of head with Burnt Umber (22), Olive-Green (Auxiliary) (48), and Ferruginous (41) blotches; iris Brick Red (132A).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that the reddish and greenish tonalities are reduced to different shades of brown, and the yellow venters of some individuals are white; the V continuations of the D bands are almost black.

Natural history notes. Nocturnal and arboreal, feeding on snails, slugs, and other soft-bodied invertebrates. Among the 6 dipsadine species whose diet they analyzed at PNGDOTH and Valle de Antón, Ray et al. (2012) found *Sibon annulatus* to be the only one whose fecal samples with identifiable prey items contained mollusc remains more often than oligochaete remains, and no amphibian eggs. These authors also observed an individual of this species feeding on a snail. All specimens collected in the course of my project were encountered active at night, and except for one juvenile that was crawling along a streambed while they were moving through vegetation 0.5–3 m above ground.

Remarks. The specimen SMF 91580 (427 mm SVL + 221 mm TL = 648 mm TOL) is the largest specimen reported for this species so far as specified by Lotzkat et al. (2012d), but has been overlooked by Lewis et al. (2013) who claimed a maximum size record for their apparently uncollected specimen of 611 mm TOL. As detailed in chapter 4.1.8.2, Panamanian *Sibon annulatus* may have the penultimate SPL in contact with the orbit and usually have only a single PM separating the 1st pair of chin shields. Furthermore, singular individuals in my sample have 1–2 Preoc on one or both sides (instead of the usual 0), and as few as 6 SPL or 6 INL, which are the lowest values reported for this species so far. About one-third of my examined specimens exhibit fusions of Postoc with adjacent scales on one or both sides of the head: Either the lower Postoc is fused with the 5th SPL, or the upper Postoc with the supraocular, or (in one specimen) both, so that no countable Postoc is left.

In his molecular phylogeny of the Dipsadinae, Sheehy (2012) found the population of *Sibon annulatus* from PNGDOTH to be more closely related to Costa Rican *S. lamari* than to *S. annulatus* from both Nicaragua and Costa Rica. Future studies will show to which (if to any) of these genealogical lineages the populations from throughout my study area are assignable (also see remarks for *S. perissostichon*).

Savage and McDiarmid (1992) assumed *Sibon annulatus* to be restricted to the Atlantic slope of the Cordillera Central in western Panama, with only one record from PNAC on the Pacific slope. However, SMF 88715 (Fig. 4.87B), SMF 91580, and in fact all our specimens from Veraguas, come from the Pacific drainage. These records indicate a continuous distribution of this taxon along the Pacific slope, at least at premontane elevations in the Serranía de Tabasará, where the continental divide drops below 1500 m asl repeatedly. The upper elevational limit of this species is given as 910 m for Panama (Jaramillo et al. 2010), 1300 m for Costa Rica (Savage 2002), and 1500 m for the species as a whole (Wilson & Johnson 2010). SMF 91580, an adult male found near Guayabito at 1510 m, now constitutes the highest record from the Pacific slope. The female SMF 91578 (Fig. 4.87A), from 1641 m on the Atlantic slope at Río Changena, is by far the highest record for this species.

***Sibon argus* (Cope 1876)**

Argus Snail Sucker, Blotched Snaileater, Blotched Snailsucker; Caracolera, Caracolera de cabeza chata

Figure 4.111D; Map 4.163.

Dipsas argus: Taylor (1951, 1954).

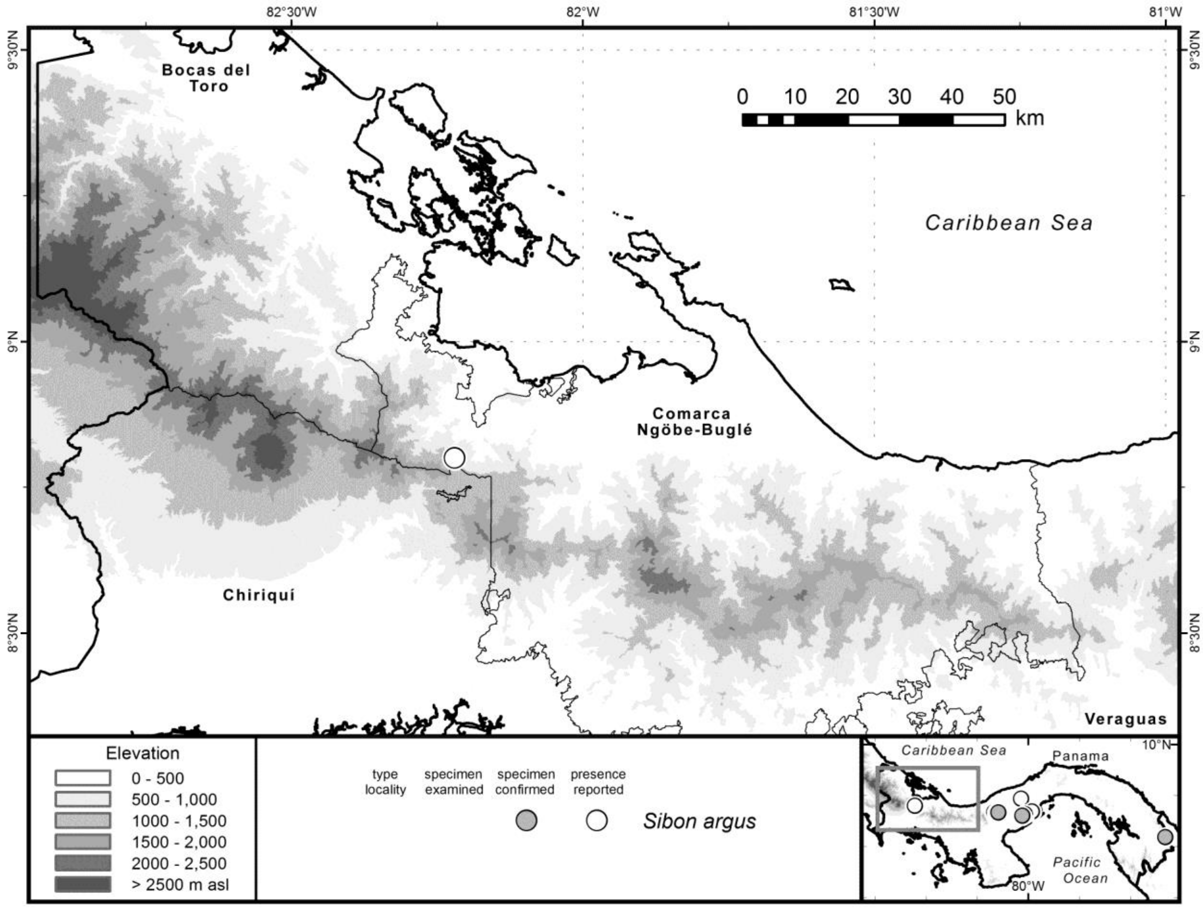
Leptognathus argus: Cope (1876); Stejneger (1909).

Holotype. USNM 30656, male, from Sipurio, Costa Rica.

Geographic distribution. Costa Rica and Panama, 0–1200 m asl. In Panama, along both versants throughout most of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from BPPS near RFLF, PNGDOTH, Valle de Antón, and PNAC, probably up to ca. 1200 m asl.

Diagnosis. This medium-sized snake (maximum TOL > 690 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. *Sibon argus* is readily distinguished from all other *Sibon* by its "*Imantodes*-like" habitus with a blunt head and very large, protruding eyes. It further differs from *S. annulatus, S. lamari, S.*

perissostichon, S. noalamina, and *S. nebulatus* in having a blotched dorsal pattern (vs. banded), from the former four species in lacking a postmental (vs. 1–2 PM present) and from the latter two in usually having the 1st pair of infralabials separated by contact between the mental and the 1st pair of chin shields (vs. 1st pair of INL in contact, separating mental from chin shields). *Sibon argus* shares the dorsal pattern of dark-edged ocelli or blotches with *S. longifrenis,* from which it differs in its "*Imantodes*-like" habitus (vs. head not very distinct from neck, eyes moderate) and in having 181 or more ventrals (vs. 173 or fewer) and 112 or more subcaudals (vs. 106 or fewer).



Map 4.163: Distribution of *Sibon argus.*

Description. (including data from Savage & McDiarmid 1992) TOL to > 690 mm; mean SVL in specimens from Valle de Antón 322–350 mm (Lewis et al. 2013); tail long, TL/TOL = 0.28–0.33; D smooth, in 15—15—15 rows, vertebral row not enlarged; V 181–201; SC 112–121; SPL 6–9, enlarged penultimate one bordering orbit; INL 6–9, 1st pair almost always separated by contact between chin shields and mental; loreal 1; Preoc 0; Postoc 2–3; Tant 1–2, Tpost 2–3; cloacal scute entire; AP 0; eyes very large and protruding, pupil vertically elliptical.

The hemipenis of *Sibon argus* is a unilobed organ; pedicel spinulate; truncus with 2 large basal hooks, moderate spines distally and large hooks proximally; apical region with spinulate calyces.

Coloration in life. D ground color greenish gray to brown with irregular spotting, each side with a series of dorsolateral dark-edged yellow to orange or reddish brown blotches or ocelli that extend to or across middorsum and are usually offset but may meet on middorsum; a L to ventrolateral series of similar blotches per side; V surfaces whitish to yellow, extending onto lower D rows between the blotches, with dark mottling usually increasing in density posteriorly and under tail; L blotches extending onto L portions of V, but not across venter; D surfaces of head with irregular green, reddish brown, and black mottling and reticulations; iris greenish gray with darker spotting or reticulations.

Coloration in preservative. As deduced from my examined *Sibon longifrenis* probably similar to that in life, apart from that the green and orange shadings can be expected to fade to different shades of brown with time, and yellow venters become white.

Natural history notes. Nocturnal and arboreal, feeding on soft-bodied prey. In their study of dipsadine diets at PNGDOTH and Valle de Antón, Ray et al. (2012) found *Sibon argus* to feed primarily on amphibian eggs in the vicinities of anuran breeding sites and on oligochaetes elsewhere, but to also consume mollusks.

Remarks. The enlarged penultimate SPL of *Sibon argus* always contacts the orbit. This condition is shared with *S. longifrenis* and has been used to distinguish these two species (that is, the *S. argus* group sensu Peters 1960 and Savage 2002) from other congeners. However, I found this condition to be present in a specimen of *S. annulatus* and absent in a specimen of *S. longifrenis*. Although these two incidences certainly are exceptional deviations from the general rule, they clearly show that such variation is to be expected and suggest that a "usually" should be slipped into future morphological descriptions and keys, as implemented in my key to LCA *Sibon* in chapter 4.1.8.2. Still, *S. argus* remains morphologically unique and unmistakably diagnosable among known members of the genus.

The records E and W of these provinces render the presence of *Sibon argus* in Bocas del Toro and Veraguas plausible. The occurrence of this species in Chiriquí, at least in the Fortuna area, is rendered plausible by the distance of < 2 km between the provincial border and the locality record of Hofer & Bersier (2001) from BPPS close to the continental divide. For this locality record, I arbitrarily applied the mean value (1200 m asl) of the given elevational range (800–1600 m). This elevation is well above the maximum elevation hitherto reported for this species (850 m according to Jaramillo et al. 2010; the 1000 m of Perez-Santos 1999 are likely to be based on extrapolation in steps of 250 m like most of his elevational values) but considered somewhat plausible. My georeference for the specimen CHP 5346 from "Río afluente del río Indio", Coclé province (using the coordinates given by Poe & Ibañez 2007 for "Rio Indio, La Mina, Manguesal"), yields a SRTM elevation of 35 m, which is far below the 550 m given as the lowest elevation recorded in Panama (Jaramillo et al. 2010), but appears plausible since the species is reported to occur down to near sea level (e.g., Savage 2002; Solórzano 2004; Wilson & Johnson 2010).

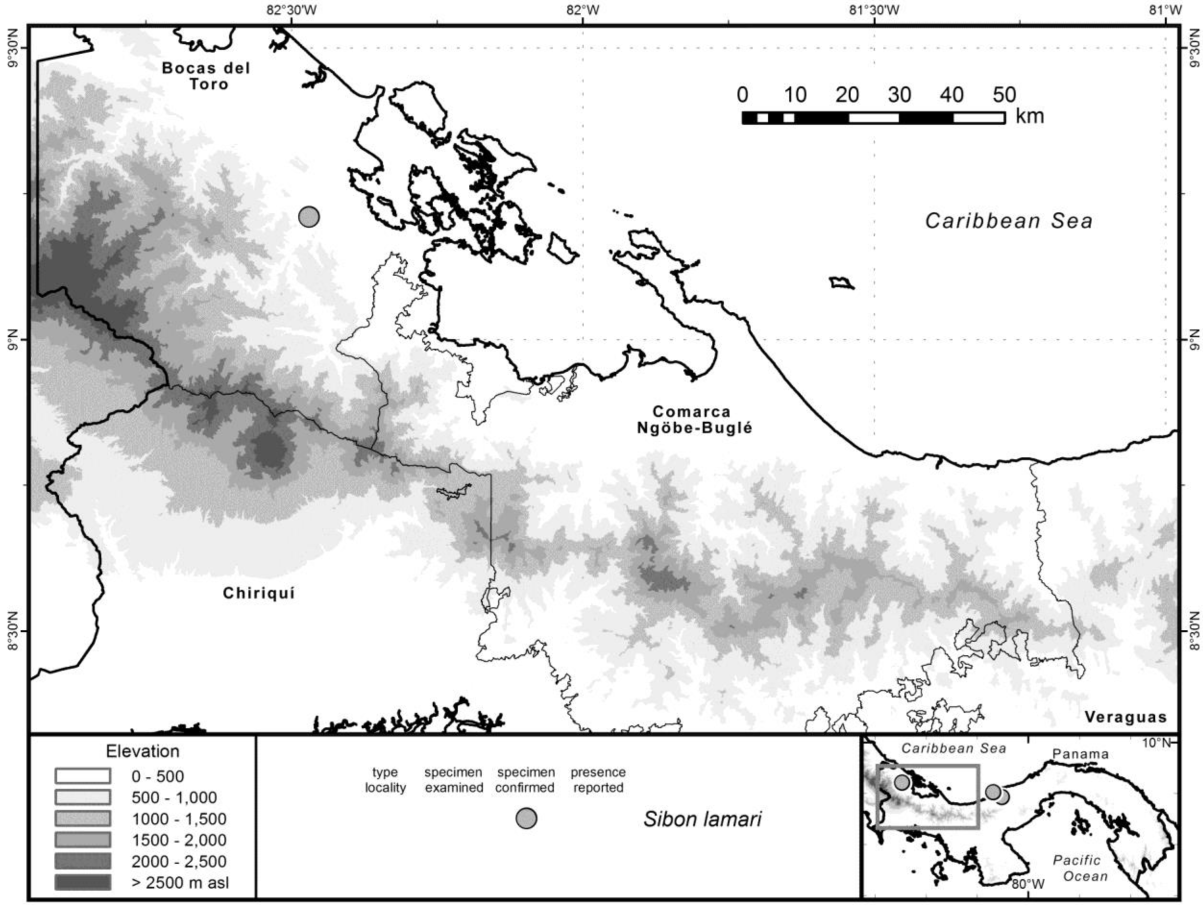
***Sibon lamari* Solórzano 2002**

Costa Rican Snailsucker, Lamar's Snaileater; Caracolera, Caracolera Costarricense

Figure 4.111E; Map 4.164.

Sibon sp.: Savage (2002: plate 395).

Holotype. UCR 13983, male, from "Guayacán de Siquirres, al noreste de la provincia de Limón (83 32'30"N y 10 02'10"NE)", Costa Rica (Solórzano 2002; the coordinates are clearly erroneous and probably should read 10°02'10"N, 83°32'30"W to be close to Guayacán).



Map 4.164: Distribution of *Sibon lamari.*

Geographic distribution. Costa Rica and Panama, 5–650 m asl. In Panama, along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, and

Veraguas. In the Cordillera Central, reported from the Caribbean foothills at El Guayabal in the Río Changuinola drainage, 150 m asl.

Diagnosis. This medium-sized snake (maximum TOL 591 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. *Sibon lamari* differs from *S. annulatus* in having small, irregular white or yellow as well as green, red, and black speckles on the upper head surface (vs. comparably large and symmetrical dark brown markings) and a greenish dorsal ground color (vs. brownish), from *S. argus* and *S. longifrenis* in having a banded dorsal pattern (vs. blotched) and 2 postmentals (vs. none, mental contacting 1st pair of chin shields in *S. argus* and some *S. longifrenis,* 1 PM in most *S. longifrenis*), from *S. nebulatus* in having the 1st pair of infralabials separated by 2 postmentals (vs. in contact, no PM), from *S. noalamina* in having 2 supralabials posterior to eye (vs. one), and from *S. perissostichon* in having 15 straight dorsal rows at midbody (vs. 17 oblique rows).

Description. (including data from Solórzano 2002) TOL to 591 mm; SVL to 389 mm; tail long, TL/TOL = 0.28–0.34; D smooth, in 15—15—15 rows, vertebral row slightly enlarged; V 162–171; SC 77–119; SPL 7–8, enlarged penultimate one separated from orbit; INL 8–10, 1st pair separated by 2 PM; loreal 1; Preoc 0–1 Postoc 2; Tant 1, Tpost 2–3; cloacal scute entire; AP 0; eyes large, pupil vertically elliptical.

The hemipenis of *Sibon annulatus* is a unilobed organ; pedicel spinulate, 2 large basal hooks; truncus with moderate spines distally and large hooks proximally; apical region with spinulate calyces.

Coloration in life. D ground color green to olive, irregularly spotted and blotched with dark and reddish pigment; body and tail with narrow, irregular reddish brown crossbands that may be offset and reach well onto venter (usually to midventer) or continuous and completely encircle body and tail, and usually bear diffuse dark borders suffused with singular light scales dorsally and laterally; D surfaces of head irregularly mottled or spotted with white or yellow as well as green, red or reddish brown, and black speckles; most of SPL and INL white or yellow with strong black markings; V ground color white to yellow, immaculate or with darker mottling, usually extending onto ventrolateral surfaces of body between dark bands; iris reddish brown to red.

Coloration in preservative. Probably similar to that in life, apart from that the reddish and greenish tonalities will presumably be reduced to different shades of brown, and the yellow venters of some individuals to cream or white.

Natural history notes. Nocturnal and arboreal, a "goo-eater" like other members of the genus. Solórzano (2002, 2004) reported that specimens were found at night in vegetation 2–8 m above ground, and that the holotype was eating a snail (*Helicinia funcki*) when captured.

Remarks. The presence of *Sibon lamari* in Panama was revealed by Jaramillo et al. (2008) based on two specimens (CHP 5402, MVUP 1892) from Colón province and one (CHP 6214) from Bocas del Toro. These records suggest a continuous distribution along the Caribbean lowlands of western Panama, rendering the presence of this species in Veraguas and the Comarca Ngöbe-Buglé plausible. This, together with the elevational maximum reported for Costa Rica (750 m asl fide Solórzano 2002, 650 m fide Solórzano 2004) and especially the distance of ca. 3 km between the collection site of CHP 6214 and my study area render the species' presence therein plausible.

Recently, Konrad Mebert provided me with photographs taken by Wouter Beukema that show specimens of *Sibon* from PNGDOTH which look quite like *S. lamari,* and others with an appearance that is somewhat intermediate between *S. lamari* and the Panamanian *S. annulatus* which I have seen. Since I cannot confidently determine whether these individuals are referable to *S. lamari* or rather represent the population of *S. annulatus* from PNGDOTH which was included in the phylogeny of Sheehy (2012; see remarks for that species), I refrain from plotting a corresponding point in Map 4.164.

Several pholidotic characters stated to distinguish *Sibon lamari* from *Sibon annulatus* in the original description lose their diagnostic value in the light of my Panamanian sample of the latter species. Among these are SPL eye (4–5 as stated to be diagnostic for *S. lamari* in most of my *S. annulatus*) and Preoc (stated to only occur in some *S. lamari,* but 1–2 present in two of my *S. annulatus*). The supposedly fewer SC of *S. lamari* might turn out to be an artefact in the case that the single individual with < 100 SC (female paratype UCR 13982 with 77 SC, next higher value 108) turns out to have an incomplete tail as I suspect it to have in view of the unusually high SC range in just 6 individuals underlying the original description (see remarks for *S. nebulatus*). Solórzano (2002) stated *S. lamari* to further differ from *S. annulatus* in relative head size, but did not explicitly compare values obtained from the two species. Moreover, he did neither mention how "head size" was measured, only indicating that head length was the measure referred to, nor present relative head sizes of the type series, or at least data that would permit to calculate these. Most of the available photos of *S. lamari* (Savage 2002: plate 359; Solórzano 2002: Figs. 1–2; Solórzano 2004: Figs. 163, 165;

McConnell 2014: Figs. 342–343) show animals with a very triangular head, but it is in no case clear if the animal photographed had assumed a defensive head triangulation during photography. Morphological data on the three Panamanian specimens reported by Jaramillo et al. (2008) would be highly desirable in this context. Notwithstanding the invalidity of the pholidotic as well as the irreproducibility of the mensural characters on which the original description was based, I continue to recognize *S. lamari* as a doubtlessly valid species based on the differences in coloration and the phylogeny of Sheehy (2012) in which the two sampled individuals referred to this species formed a clade perfectly separated from both clades of nominal *S. annulatus.*

The original description of *Sibon lamari* is a nice (or sad?) example how sloppy work can have lasting effects in the age of copy'n'paste: the coordinates of the type locality, which were given in a messily incorrect notation and are all but impossible for a point in Costa Rica, have made their way to at least two other publications (Köhler 2008; Uetz & Hošek 2014).

Sibon longifrenis **(Stejneger 1909)**

Drab Snaileater, Lichen-colored Snailsucker, Mottled Snailsucker; Caracolera, Caracolera de cabeza chata

Figures 4.87D–E; 4.111F; Maps 4.17; 4.165.

Dipsas costaricensis: Taylor (1951, 1954).

Dipsas longifrenis: Smith (1958).

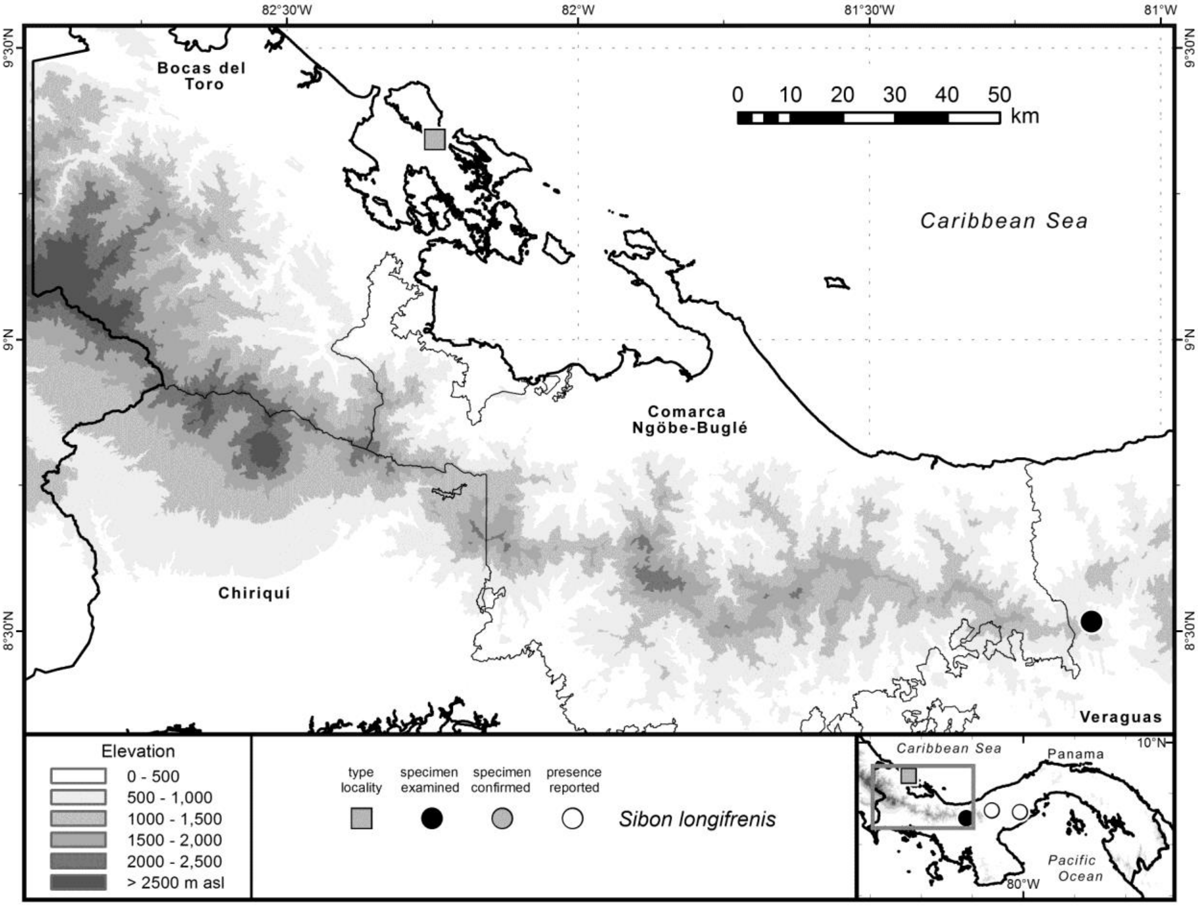
Mesopeltis longifrenis: Stejneger (1909).

Holotype. USNM 38750, female, from "Bocas del Toro, Republic of Panama" (Stejneger 1909).

Geographic distribution. Honduras to Panama, 0–1030 m asl. In Panama, from the Caribbean versant of extreme western to both versants in west-central portions of the country, including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Santa Fé area, PNGDOTH, and Valle de Antón, up to 900 m asl.

Diagnosis. This medium-sized snake (maximum TOL 624 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. *Sibon longifrenis* is differs from all other Panamanian *Sibon* in having the head only slightly distinct from the neck and merely moderate-sized, non-protruding eyes. It further differs from *S. annulatus, S. lamari, S. perissostichon, S. noalamina,* and *S. nebulatus* in having a blotched dorsal pattern (vs. banded) and in usually having the enlarged penultimate supralabial in contact with the orbit (vs. usually separated from orbit), and from the latter two in having the 1st pair of infralabials separated by a small postmental or contact between the mental and the 1st pair of chin shields (vs. no PM, 1st pair of INL in contact between mental and chin shields). *Sibon longifrenis* shares the dorsal pattern of dark-edged ocelli or blotches with *S. argus,* from which it differs in lacking that species' "*Imantodes*-like" habitus with a blunt head and very large, protruding eyes, as well as in having 173 or fewer ventrals (vs. 181 or more) and 106 or fewer subcaudals (vs. 112 or more).

Description. (including data from Savage & McDiarmid 1992) TOL to 624 mm; mean SVL in specimens from Coclé 337–383 mm (Lewis et al. 2013); tail long, TL/TOL = 0.28–0.35; D smooth, striate*, in 15—15—15 rows, vertebral and paravertebral rows slightly enlarged*; V 147–173; SC 80–106; SPL 7–9, enlarged penultimate one usually bordering orbit; INL 6–9, 1st pair separated by a small PM or contact between chin shields and mental; loreal 1; Preoc 0; Postoc 1–3; Tant 1–2, Tpost 1–3; cloacal scute entire; AP 0; eyes moderate, non-protruding, pupil vertically elliptical.



Map 4.165: Distribution of *Sibon longifrenis.*

The hemipenis of *Sibon longifrenis* is a unilobed organ; pedicel naked to spinulate; truncus with 2 large basal hooks, moderate spines distally and large hooks proximally; apical region with spinulate calyces.

Coloration in life. D ground color greenish with irregular dark spotting, each side with a series of dorsolateral dark-edged yellow to orange or reddish brown blotches or ocelli many to most of which extend far across middorsum giving the impression of a single middorsal series; a L to ventrolateral series of similar blotches per side, some to many of which may connect to the dorsolateral blotches; D surface of head with blotches similar to those on body; V surfaces of head and body whitish to yellow, extending onto lower D rows between blotches, with dark mottling usually increasing in density posteriorly; V surface of tail orange to olive with dense dark mottling; L blotches extending onto L portions of V, but not across venter; D surfaces of head with irregular green, reddish brown, and black mottling and reticulations; iris greenish gray with darker spotting or reticulations.

The female SMF 91581 was recorded as follows: D and L ground color Greenish Olive (49) with Sepia (119) spots and mottling; head, body, and tail with a series of rounded Tawny (38) markings with Hair Brown (119A) centers mottled with and bordered by Sepia (119), and becoming more and more diffuse towards, and throughout, tail; some of these markings fuse with the similar markings arranged in one ventrolateral series on each side of body and tail, encroaching onto tips of V; interspaces between the ventrolateral markings between lower tips of second D row and outer edges of V dirty white mottled with Sepia (119); L surface of head very densely mottled with Sepia (119); V surfaces of head and body Spectrum Yellow (55) mottled with Sepia (119); V surface of tail Tawny Olive (223D) mottled with Sepia (119); iris Pale Horn Color (92) mottled with Sepia (119); tongue Sepia (119).

Coloration in preservative. After 4 years in 70% ethanol, the coloration of SMF 91581 is similar to that in life, apart from that the greenish D ground color has turned grayish brown, the formerly rusty blotches are brown (white where the oberhäutchen has been lost), and the formerly yellow venter is white.

Natural history notes. Nocturnal and arboreal, feeding on soft-bodied prey. In their study of dipsadine diets at PNGDOTH and Valle de Antón, Ray et al. (2012) found *Sibon longifrenis* to feed primarily on amphibian eggs in the vicinities of anuran breeding sites and on oligochaetes elsewhere, but to also consume mollusks. SMF 91581 was encountered around 22:00 while moving over a fern frond about 0.7 m above ground.

Remarks. The female SMF 91581 has 147 ventrals, which is the lowest number of V reported so far for *Sibon longifrenis* (Savage & McDiarmid 1992; Köhler 2008). It lacks a PM, a condition known only from one specimen so far (KU 25703, the holotype of *Dipsas* *costaricensis* Taylor 1951, according to Savage & McDiarmid 1992), allowing contact between the mental and the first pair of chin shields. Most notably, its enlarged penultimate (6th) SPL is not in contact with the eye on both sides of the head. This condition is only known from one side of the head of one specimen (McCranie 2011), whereas all previous authors considered the contact between eye and the penultimate supralabial one of the key characteristics of *S. longifrenis.*

Köhler et al. (2013) recently provided a new elevational maximum based on SMF 94598 from Volcán Miravalles, Costa Rica, at 1030 m asl. Contrary to the values given by most recent authors, the lower distributional limit of this species is around sea level, since the type locality actually refers to the town Bocas del Toro itself (Stejneger 1909). The records E and W of the Comarca Ngöbe-Buglé render the presence of *Sibon longifrenis* therein plausible. I consider the occurrence of this species in Chiriquí, at least in the Fortuna area, possible in view of its altitudinal distribution. Perez-Santos (1999) lists a specimen from Darién ("KU 112480-1, Cerro Quía, 740 m(?)") which I could not trace elsewhere. Somewhat disturbingly, the holotype of *S. longifrenis* is listed as "*Sibon dimidiata*" in the USNM database records obtained via HerpNet.

Sibon nebulatus **(Linnaeus 1758)**

Common Snaileater, Cloudy Slugeater, Cloudy Snail Sucker; Caracolera, Caracolera común

Figures 4.87F–H; 4.111G; Maps 4.17; 4.166.

Dipsas nebulatus: Dunn (1947).

Leptognathus nebulata: Cope (1871, 1876).

Petalognathus nebulata: Cope (1899).

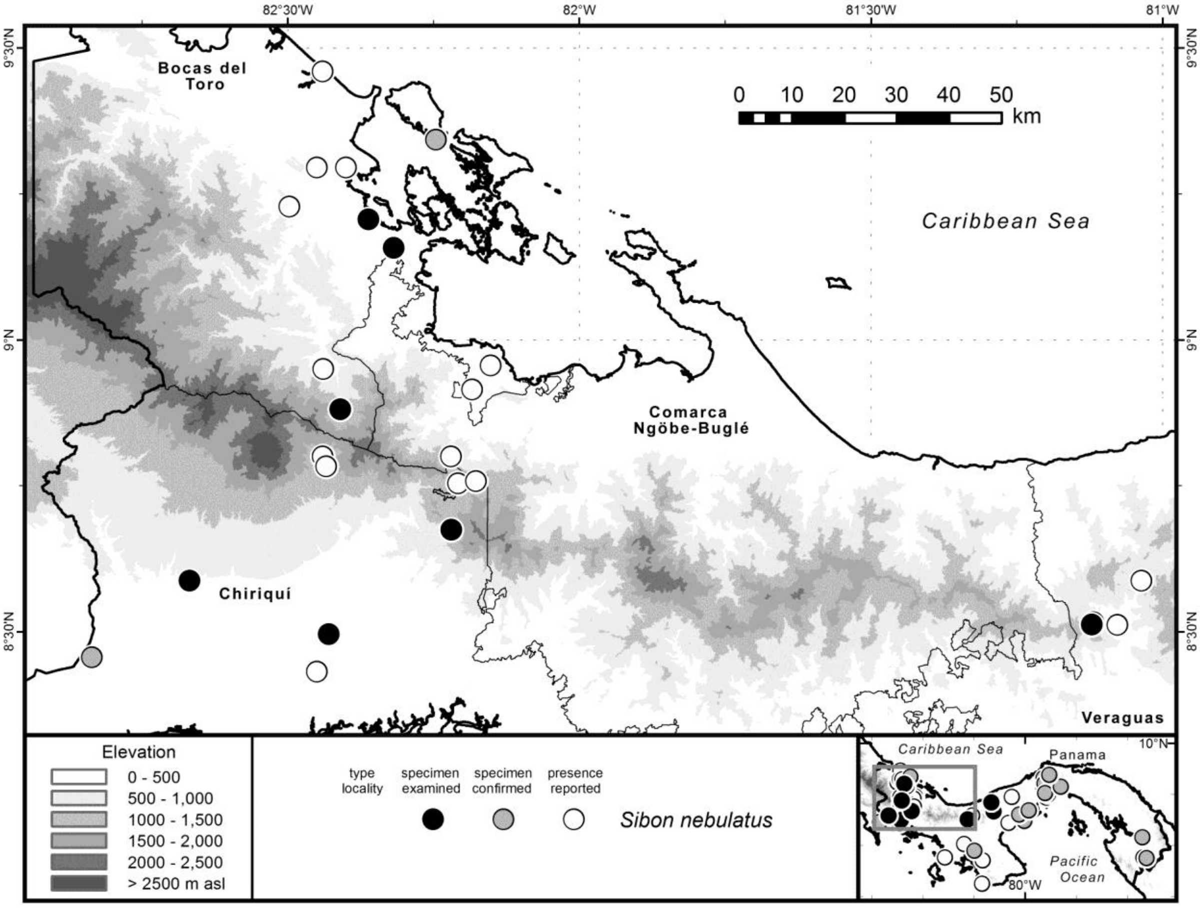
Sibon nebulata: Peters (1960); Peters & Orejas-Miranda (1970); Martínez & Rodriguez (1994); Martínez et al. (1995); de Sousa (1999); Myers et al. (2007).

Sibon sibon: Dunn & Bailey (1939); Slevin (1942).

Holotype. LinnMus 152, from America.

Geographic distribution. Mexico to Colombia, Ecuador, and Brazil, 0–1690 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities along both versants up to 1320 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1013 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. Western Panamanian *Sibon nebulatus* differ from all other Panamanian *Sibon* in having an overall grayish coloration, and from all other Panamanian *Sibon* except *S. noalamina* in having the 1st pair of infralabials in contact behind the mental (vs. separated by 1–2 postmentals or contact between mental and 1st pair of chin shields). It further differs from *S. noalamina* in having two supralabials posterior to orbit (vs. one) and in lacking a contrasting pattern of light and dark rings as well as slight keeling on the 3rd–5th dorsal row in adults.



Map 4.166: Distribution of *Sibon nebulatus.*

Description. TOL to 1013 mm; SVL to 612 mm*; tail moderate to long, TL/TOL = 0.22–0.29; D smooth, striate*, in 15—15—15 rows (occasionally 16 D-MB or 13 D-HC), vertebral and paravertebral rows slightly enlarged; V 159–200; SC 64–114; SPL 5–9, enlarged penultimate one separated from orbit; INL 6–10, 1st pair in contact behind mental, no PM; loreal 1; Preoc 0–2; Postoc 1–4; Tant 1, Tpost 1–2; cloacal scute entire; AP 0; eyes large, pupil vertically elliptical (including data from Peters 1960).

The hemipenis of *Sibon nebulatus* is a unilobed organ; pedicel with small spines; truncus with enlarged spines; apical region with spinulate calyces.

Coloration in life. D and L ground color gray or (usually grayish) brown, irregularly spotted and blotched with different darker gray, black, and white, cream, or pink; body and tail with irregular darker gray or black crossbands that are usually offset and reach well onto venter (usually to midventer) or rarely continuous and completely encircle body and tail, and often bear diffuse narrow light borders on D and L surfaces; D surfaces of head with dark mottling or blotches in variable density; V ground color white to cream, with darker mottling sparsely on body and densely on tail as well as dark blotches under head; iris gray to reddish brown with darker spotting or reticulations.

The female SMF 89599 was recorded as follows: D and L ground color Jet Black (89); D surfaces of body and tail spotted with Cream Color (54), causing a Glaucous (80) appearance when viewed from some distance, leaving unspotted areas forming Jet Black (89) mottles and a series of L offset (only in few cases opposed) transverse bands which extend from middorsum onto midventer and are irregularly bordered by Pink (7) mottling or stripes; D and L surface of head with fine Pink (7) mottling; V surface of head dirty white with Jet Black (89) spots and blotches on all scales; V surfaces of body and tail Cream Color (54) with a suggestion of Flesh Color (5), with the extensions of the Jet Black (89) transverse bands and some Jet Black (89) mottling that becomes very intense on, and covers most of, the SC; iris vinaceous (4) spotted with Jet Black (89).

Leonhard Stadler recorded the adult female SMF 89598 (Stadler 2010: Fig. A98) as follows (translated from Stadler 2010): D ground color Vandyke Brown (121); head with scattered dirty white blotches; body and tail with regular Neutral Gray (83) and dirty white transverse bars extending onto venter; V ground color dirty white mottled with Vandyke Brown (121); iris Vandyke Brown (121).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that the dark markings have become a little lighter to consist of different shades of gray and/or brown and the pink shades in SMF 89599 have faded to white.

Natural history notes. Nocturnal and arboreal, feeding on snails and slugs. In their study of dipsadine diets at PNGDOTH and Valle de Antón, Ray et al. (2012) found a large slug in an individual of *Sibon nebulatus.* Defensive behaviour includes head triangulation. Of the three individuals that were found active at night, one was moving along a barbed wire fence and two in vegetation up to 3 m above ground. Stadler (2010) found a large female (SVL 612 mm, TOL 809 mm) on the ground during heavy rain at night. The specimen from Los Algarrobos was found dead on road. Gabriel Palacios found a young male coiled up in the lower branches of a coffee bush around noon.

Remarks. In his molecular phylogeny of the Dipsadinae, Sheehy (2012) found the nominal taxon *Sibon nebulatus* to comprise two well-separated clades, a CA one including samples from Mexico to Nicaragua which would be attributable to the subspecies *S. n. nebulatus* (Köhler 2008)*,* and a SA one including genotypes from Colombia, Ecuador, Trinidad, and PNGDOTH that should correspond to the subspecies *S. n. leucomelas.* Since his phylogeny did not include samples from Costa Rica and Panama west of PNGDOTH, the question to which of these genealogical lineages the populations from my study area, among which I found the barcoded individuals from Veraguas and Chiriquí to be obviously conspecific in chapter 4.1.8, are assignable remains to be answered by future studies. My georeference for the specimens CAS 79002–3 from "Vicinity north of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is above the upper elevational limit of 1200 m provided for Panama by Jaramillo et al. (2010). The next highest Panamanian record is SMF 90209 from the Lost & Found Ecohostel at 1250 m.

The unusually broad range in the number of SC is chiefly owing to the low values found in populations from Colombia which Peters (1960) described as another subspecies, *S. n. popayanensis* (Peters 1960; Savage 2002). Peters (1960) pointed out that singular specimens of *S. nebulatus* have only 5 SPL and/or only 1 SPL posterior to orbit, a condition thought to be restricted to *S. noalamina* by Lotzkat et al. (2012d).

Sibon noalamina Lotzkat, Hertz & Köhler 2012

[in part modified from Lotzkat et al. (2012d); see Appendix 8 for original publication]

Tabasará Snail-sucker, Tabasará Snaileater; Caracolera, Caracolera de Tabasará

Figures 4.82, 4,83, 4.85; 4.111H; Maps 4.17; 4.167.

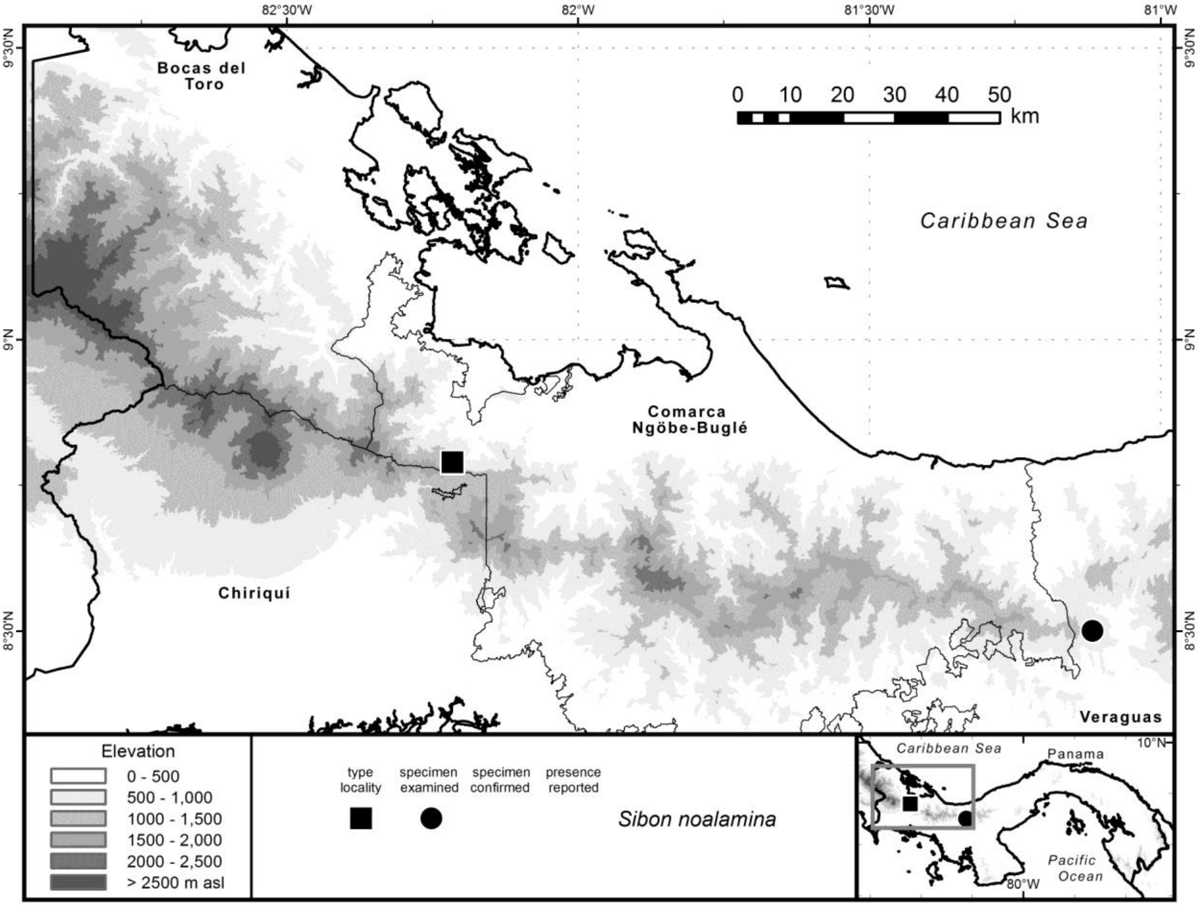
Dipsas articulata: Cope (1876), Köhler (2008: in part.: Fig. 592), Hamad (2009); Carrizo (2010: in part.: referring to Stadler 2010); Stadler (2010).

Holotype. SMF 91539, adult male, from from headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1050 m asl, Bosque Protector Palo Seco, Comarca Ngöbe-Buglé, Panama.

Geographic distribution. Endemic to the Cordillera Central of western Panama including Chiriquí, Comarca Ngöbe-Buglé, Veraguas, and possibly Bocas del Toro. Only reported from BPPS next to RFLF and Cerro Mariposa, 1050–1260 m asl.

Diagnosis. This medium-sized snake (maximum TOL 546 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, mostly smooth dorsals without apical pits arranged in 15—15—15 rows, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit.

Sibon noalamina is unique among Panamanian *Sibon* in exhibiting a contrasting pattern of alternating light and dark rings throughout body and tail. It further differs from all other *Sibon* as well as from all Panamanian bicolor (black and white) ringed or banded snakes in having only five supralabials, of which only the posteriormost is located posterior to orbit and has a higher anterior and a lower posterior portion (versus almost always 6 or more SPL, 2 posterior to orbit with the penultimate one enlarged in other *Sibon,* and 3 or more SPL, usually more than 2 posterior to orbit, all similarly high in *Dipsas*), as well as in having the 3rd–5th dorsal row slightly keeled at midbody in adults (vs. smooth).



Map 4.167: Distribution of *Sibon noalamina.*

Description. (see chapter 4.1.8.2 for a detailed description of the holotype) TOL to 546+x mm*; SVL to 385 mm*; incomplete tail long, TL/TOL = 0.27–0.29+x*; D smooth except for 3rd–5th row slightly keeled at midbody in adults, striate, in 15—15—15 rows, vertebral and paravertebral rows slightly enlarged*; V 164–177*; SC 80–96 on incomplete tails*; SPL 5, posteriormost one higher anteriorly and lower posteriorly*; INL 6–7, 1st pair in contact behind mental, no PM*; loreal 1*; Preoc 0*; Postoc 2*; Tant 1–2*, Tpost 1–2*; cloacal scute entire*; AP 0*; eyes large, pupil vertically elliptical*.

The hemipenis of *Sibon noalamina* is a unilobed organ; pedicel spinulate; truncus with enlarged spines; apical region with spinulate calyces.

Coloration in life. D and L ground color white to cream, with orange to brown suffusions and spotting most intense at middorsum; body and tail with complete dark rings whose V portions are narrower than their D and L portions which are about as broad or broader than the light interspaces; D and L surfaces of head largely dark, with a light nuchal collar narrowly or broadly interrupted middorsally and white to salmon mottling most intense around snout; V surfaces of head heavily, those of body and tail sparsely mottled with dark; dark rings and mottlings black in juveniles, brown in adults; suffusions and spotting on the light ground color orange in juveniles, brown in adults.

The color description of the holotype is provided in chapter 4.1.8.2. Leonhard Stadler recorded the juvenile paratype SMF 89550 (Fig. 4.85E) as follows (modified from Stadler 2010): Body and tail with alternating, complete dark and light rings; broader rings Jet Black (89), light rings Chamois (123D), about half as wide as, and becoming lighter toward, the dark rings; D and L ground color of head Jet Black (89); crescent-shaped L markings on posterior portion of head and small blotches on snout Chamois (123D); V surfaces of head and neck Chamois (123D) mottled with Jet Black (89); iris black.

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration is similar to that in life, apart from that all yellow and orange shades have faded and the formerly black elements of the juveniles have assumed a brown similar to that of the holotype's rings.

Natural history notes. Nocturnal and arboreal, presumably feeding on soft-bodied prey like its congeners. All three specimens were encountered at night on vegetation. The juvenile SMF 89550 from Cerro Mariposa was moving through epiphytic liverworts growing on a small tree-trunk about 0.5 m above ground at 18:40, after a rainy afternoon. The habitat may be characterized as ridgetop cloud forest with abundant epiphytic vegetation. Annual precipitation is approx. 2500 mm, mean annual temperature approx. 20.2°C, indicating the PMWF life zone. Other snail-eaters found at lower elevations on the slopes of Cerro Mariposa are *Dipsas temporalis, Sibon annulatus, S. longifrenis,* and *S. nebulatus.* Figure 4.85D shows the juvenile SMF 90180 as it was encountered at 19:40 and 19.1°C air temperature at the type locality: lying in loose coils upon a large leaf about 0.5 m above ground, in herbaceous secondary vegetation below the floodline of, and less than 10 m away from, a small stream. The holotype was found close to this stream while moving about in secondary forest, 2 m above ground at 23:00. The type locality is the valley of the mentioned stream, with rather undisturbed forest on the slope ascending northwards, minor clearings overgrown with grass and solitary trees directly by the riverside, and a more secondary forest on the slope ascending southward. The only additional snail-eater found at this site was *S. annulatus*. Annual total precipitation at the type locality is approx. 3000 mm, mean annual temperature approx. 20.6°C, indicating the PMWF life zone. Our datalogger recordings yielded a temperature range of 17.6–22.6°C (19.4 ± 1.3°C).

Conservation. The merely two localities from which *Sibon noalamina* has been reported do not allow for calculating a meaningful extent of occurrence (the value of 0.248 km^2 obtained from the minimum convex polygon does not make sense). However, based on current knowledge I have to assume a restricted distributional range for this Panamanian endemic. If one, for example, includes the entire Caribbean slope between the maximum elevation reported for the species and the longitudes of the two collection sites, and generously adds 10 km both north- and southwards, the resulting area would still amount to less than 5000 km^2. This small inferred extent of occurrence, together with only two known localities and the continuing deforestation we observed in the region and especially the mining threats in the Comarca Ngöbe-Buglé, qualify the species for the IUCN category EN according to IUCN (2001) criterion B1ab(iii). Moreover, I calculated the EVS for *S. noalamina* as 5 (range) + 2 (persecution) + 5 (ecological distribution) = 12, indicating a high vulnerability.

Remarks. The type locality of *Sibon noalamina* actually lies 6.4 km NNE (not NW as stated by Lotzkat et al. 2012d) of the Fortuna dam. The distance of less than 0.5 km between the type locality and the provincial border render the occurrence of *S. noalamina* in Chiriquí, at least around RFLF, plausible. I further regard its presence in Bocas del Toro as possible.

***Sibon perissostichon* Köhler, Lotzkat & Hertz 2010**

La Fortuna Snaileater; Caracolera, Caracolera de La Fortuna

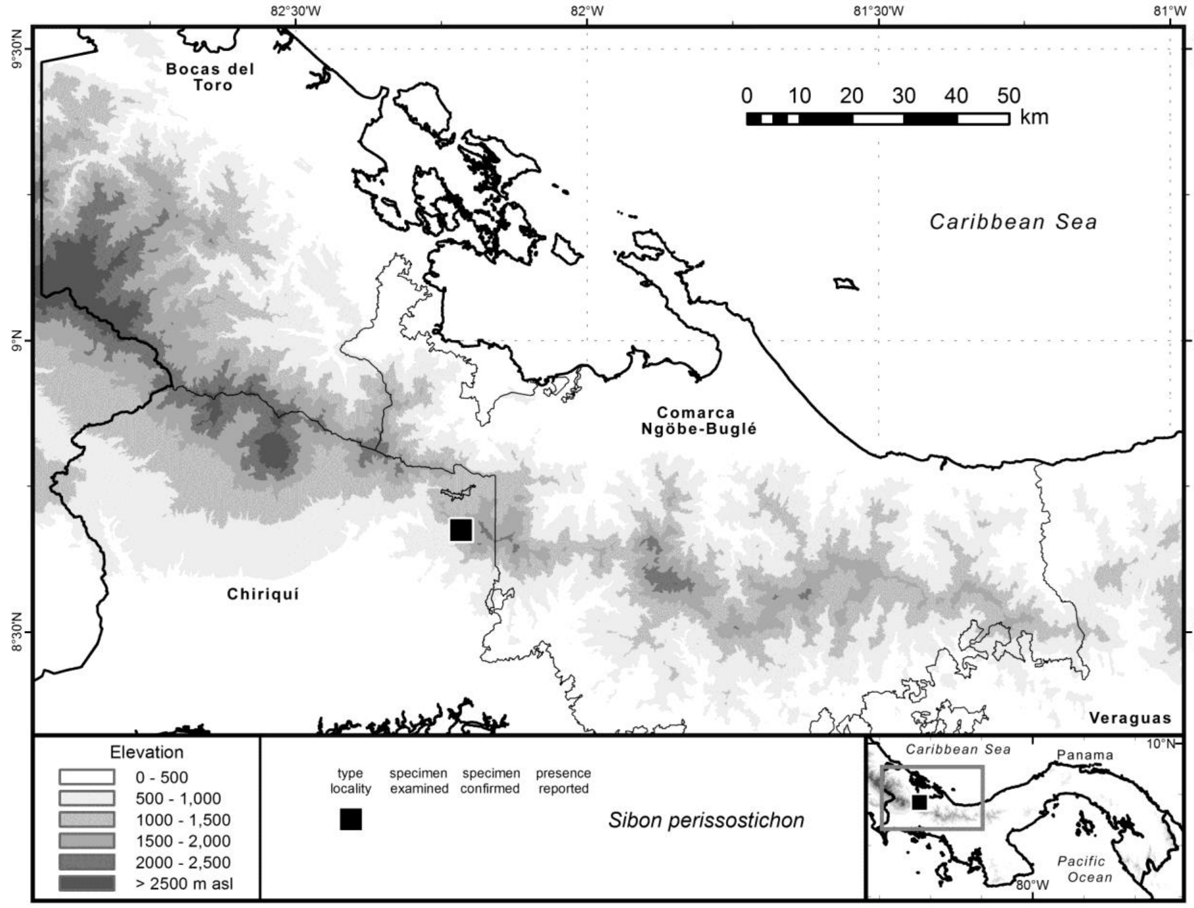
Figures 4.80A; 4.81; 4.84; 4.112A; Maps 4.17; 4.168.

Sibon perrisostichon: Rovito et al. (2012).

Holotype. SMF 88716, adult female, from near Lost and Found Ecohostel, 8.67443°N, 82.21611°W, 1434 m asl, Reserva Forestal La Fortuna, Chiriquí, Panama.

Geographic distribution. Endemic to the Cordillera Central of western Panama in Chiriquí. Only known from the type locality at RFLF, 1434 m asl.

Diagnosis. This medium-sized snake (maximum TOL 671 mm) with vertically elliptical pupils is readily identified as a member of the genus *Sibon* by its large eyes and large head that is distinct from the slender neck, enlarged supralabial immediately posterior to orbit, smooth dorsals without apical pits arranged in 15 rows anteriorly and posteriorly, crescent-shaped first chin shields enclosing a mental groove, entire cloacal scute, and loreal bordering the orbit. *Sibon perissostichon* differs from all other *Sibon* in having 17 oblique rows of dorsals at midbody (vs. 13, 15, or 17 straight rows). It further differs from *S. argus* and *S. longifrenis* in having a banded pattern (vs. blotched), from *S. nebulatus* and *S. noalamina* in having the 1st pair of chin shields separated by a postmental (vs. no PM, 1st pair of chin shields in contact behind the mental), and from *S. lamari* in having 186 ventrals (vs. 177 or fewer).



Map 4.168: Distribution of *Sibon perissostichon.*

Description. (see chapter 4.1.8.1 for a detailed description of the holotype) TOL to 671 mm*; SVL to 462 mm*; tail long, TL/TOL = 0.31*; D smooth, striate*, in 15—17—15 rows which are oblique at midbody, vertebral and paravertebral rows slightly enlarged anteriorly and posteriorly*; V 186*; SC 108*; SPL 6, enlarged penultimate one separated from orbit*; INL 7, 1st pair separated by 1 PM*; loreal 1*; Preoc 0*; Postoc 2–3*; Tant 1*, Tpost 3*; cloacal scute entire*; AP 0*; eyes large, pupil vertically elliptical*.

The hemipenis of *Sibon perissostichon* remains unknown.

Coloration in life. D ground color medium brown, irregularly spotted and blotched with darker and lighter brown; body and tail with irregular dark reddish brown crossbands that may be offset and reach well onto venter (usually to midventer) or continuous and completely encircle body and tail; D surfaces of head with more or less symmetrical, large dark brown markings; V ground color white with yellow hues and dark brown mottling, extending onto ventrolateral surfaces of body between dark bands; iris dark reddish brown.

Coloration in preservative. After 6 years in 70% ethanol, the coloration of the holotype is similar to that in life.

Natural history notes. The holotype was encountered at 20:53 in secondary premontane forest while it was active within the dense, fog-moistened undergrowth about 0.5 m above the forest floor (Fig. 4.84D). At the time of encounter, the snake was moving about on the inclined trunk of a young tree covered with folious hepatics. The undergrowth surrounding this trunk consisted of herbaceous as well as young woody plants, among which we could distinguish different ferns as well as members of the families Rubiaceae and Melastomataceae. The type locality is situated about 20 altitudinal meters below a narrow ridge on a very steep slope (approximately 45° inclination) facing the southern Pacific lowlands. Most trees' diameters at breast hight do not exceed 50 cm. The dense canopy layer extends from about 10 m above ground upwards. Detached rocks are scattered among the scenery, and there are no streams nearby. Air parameter measurements conducted after the capture showed a temperature of 17.7°C and 87% relative humidity.

Conservation. The official IUCN Red List (IUCN 2014) lists *Sibon perissostichon* as DD. This species is known from a single locality and a single specimen (see remarks). That is, virtually nothing is known about the distribution, population, and natural history of this species, or any other aspect of its biology, and the calculation of an extent of occurrence does not make sense. Thus, strictly adhering to the IUCN (2001) criteria, I see no other option but to place it in the IUCN category "Data Deficient" (DD) although the species will most probably be assignable to EN or CR once more data becomes available. Nevertheless, I calculated the EVS for *S. perissostichon* as 6 (range) + 2 (persecution) + 5 (ecological distribution) = 13, indicating a high vulnerability.

Remarks. In view of the distance of less than 10 km between the type locality and the Comarca's border, I regard the presence of *Sibon perissostichon* in the Comarca Ngöbe-Buglé as possible. The morphological distinction in SC numbers between *S. perissostichon* and its most similar congener, *S. annulatus,* as stated by Köhler et al. (2010a: 108 in the former vs. 113 or more in females of the latter) have lapsed in the light of my data, since the female *S. annulatus* SMF 91578 has merely 107 SC and unsexed specimens can have as few as 103 SC (McCranie 2011; juvenile SMF 90208). The only pholidotic distinction left for me to include in the modified diagnosis in chapter 4.1.8.1 (186 V in *S. perissostichon* vs. 171–185 in female *S. annulatus* from Panama) is very slight and does not take into account the unsexed juvenile

SMF 88713 with 187 V. This leaves the unusual arrangement of the D around midbody as the only pronounced morphological difference between these two species which are extremely similar in coloration and other pholidotic characters.

In his molecular phylogeny of the Dipsadinae, Sheehy (2012) found the holotype of *Sibon perissostichon* to form the sister group of his *S. annulatus* clade from Nicaragua and Costa Rica, both together forming the sister group to *S. annulatus* from PNGDOTH and Costa Rican *S. lamari.* The 16S barcode sequence which I obtained from the holotype of *S. perissostichon* clustered together with my sample of *S. annulatus* from throughout my study area (see Fig. 4.1). Assuming a contamination of the sample and recognizing the distinctness of *S. perissostichon* in the tree of Sheehy (2012), I regarded my barcoding attempt for *S. perissostichon* as failed, unfortunately being prevented from a second try by financial and temporal restrictions. Nevertheless, the possibility remains that the holotype of *S. perissostichon* merely represents an aberrant individual of the populations herein referred to *S. annulatus* from throughout my study area, which in turn might be conspecific with either or none of the clades referred to this nominal species that were recovered by Sheehy (2012) as is to be revealed by future studies.

***Trimetopon pliolepis* Cope 1894**

Collared Pygmy Snake, Cope's Tropical Ground Snake, Faded Dwarf Snake; Culebra enana de collar

Figure 4.112B; Map 4.169.

Trimetopon gracile: Dunn (1937c).

Holotype. AMNH 17302, from San José, Costa Rica.

Geographic distribution. Costa Rica and Panama, 60–1600 m asl. In Panama, possibly present in Bocas del Toro but to date only known from the Pacific slopes of the Serranía de Talamanca in extreme western Chiriquí around Santa Clara, 1200–1210 m asl.

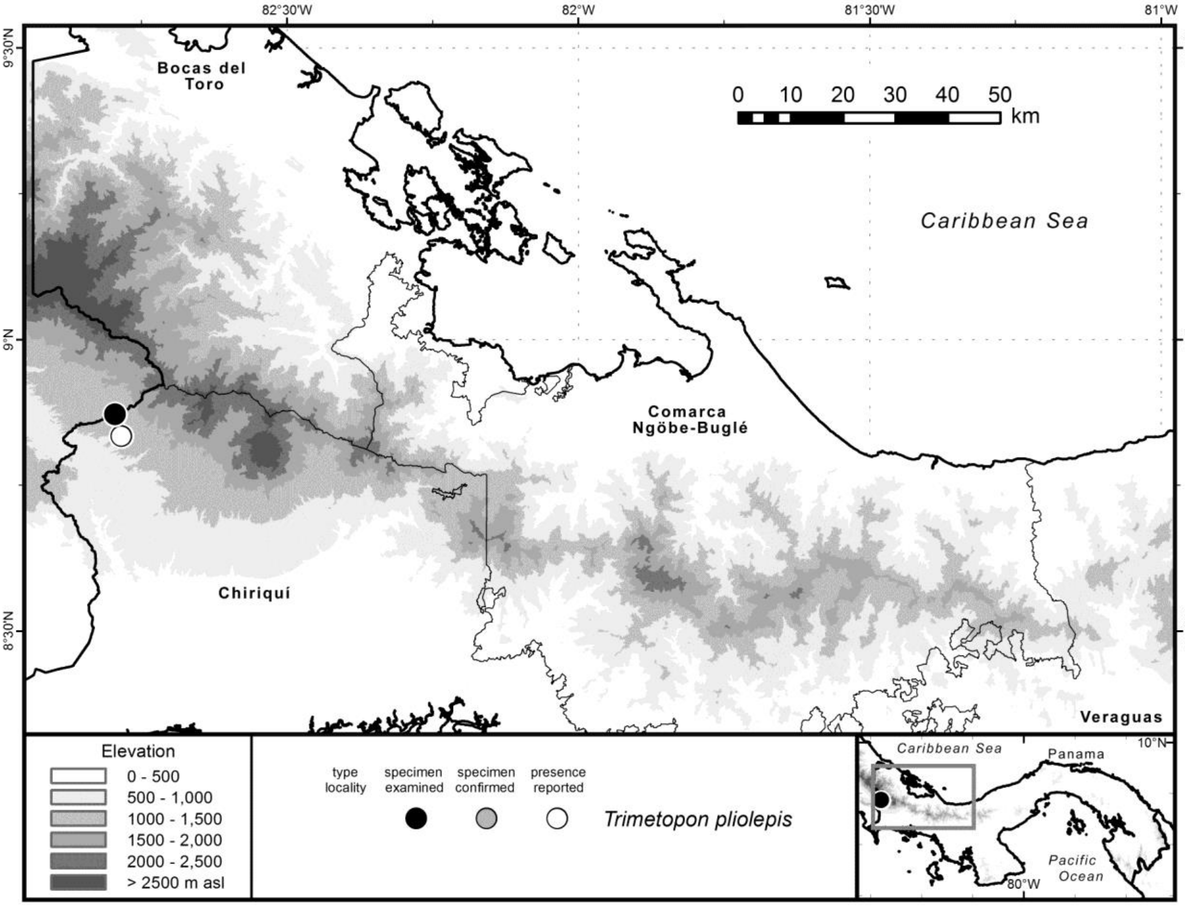
Diagnosis. This small snake (maximum TOL 287 mm) with round pupils is unique among Panamanian snakes in having the prefrontals fused into a single plate, dorsals without apical pits arranged in 17—17—17 rows, a loreal and a preocular, as well as a divided cloacal scute.

Description. (including data from Cope 1874) TOL to 287 mm; SVL to 211 mm; tail moderate, TL/TOL = 0.22–0.27; D smooth except for supracloacal keels in males, in 17—17—17 rows; V 137–157; SC 58–73; SPL 7–8; INL 7–8; PF 1; loreal 1; Preoc 1; Postoc 1; Tant 1–2, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Trimetopon pliolepis* is a unilobed organ; truncus with spines, apex calyculate.

Coloration in life. D and L ground color brown, with a middorsal dark stripe and 3–4 dark L stripes that may be discontinuous and/or unconspicuous; a yellowish nuchal collar usually interrupted by the middorsal stripe; head with more or less conspicuous yellow spotting and dark brown mottling as well as light areas on SPL usually including a post- and subocular light stripe; V surfaces white to yellow, immaculate or with sparse dark spotting that may form a midventral line under tail; iris brown.

Coloration in preservative. After 8 years in 70% ethanol, the coloration of SMF 85388 is similar to that in life, apart from that all yellow elements have faded to white.



Map 4.169: Distribution of *Trimetopon pliolepis.*

Natural history notes. Terrestrial and semifossorial, feeding on small lizards.

Remarks. Dunn's (1937c) placement of this species in the synonymy of *Trimetopon gracile* has been rejected by Taylor (1951) and all subsequent authors (Savage 2002). Savage's (2002) statement that maximum TOL of this species is 277 mm must be based on a typo, since the total length of the holotype is 287 mm (Cope 1894, Taylor 1951). To my knowledge, this species is known in Panama from only four specimens (KU 112504–6 from "Finca Santa Clara, 1200 m" according to Perez-Santos 1999, and SMF 85388 from "8 km NE Río Sereno, Finca C.A.S.A., 1210 m" examined by myself). Thus, the altitudinal range of 1000–1500 m asl in Panama given by Perez-Santos (1999) must be based on an extraordinarily wide extrapolation. The species' occurrence along the Caribbean slopes of northern Costa Rica (Savage 2002) lets its presence in Bocas del Toro appear possible.

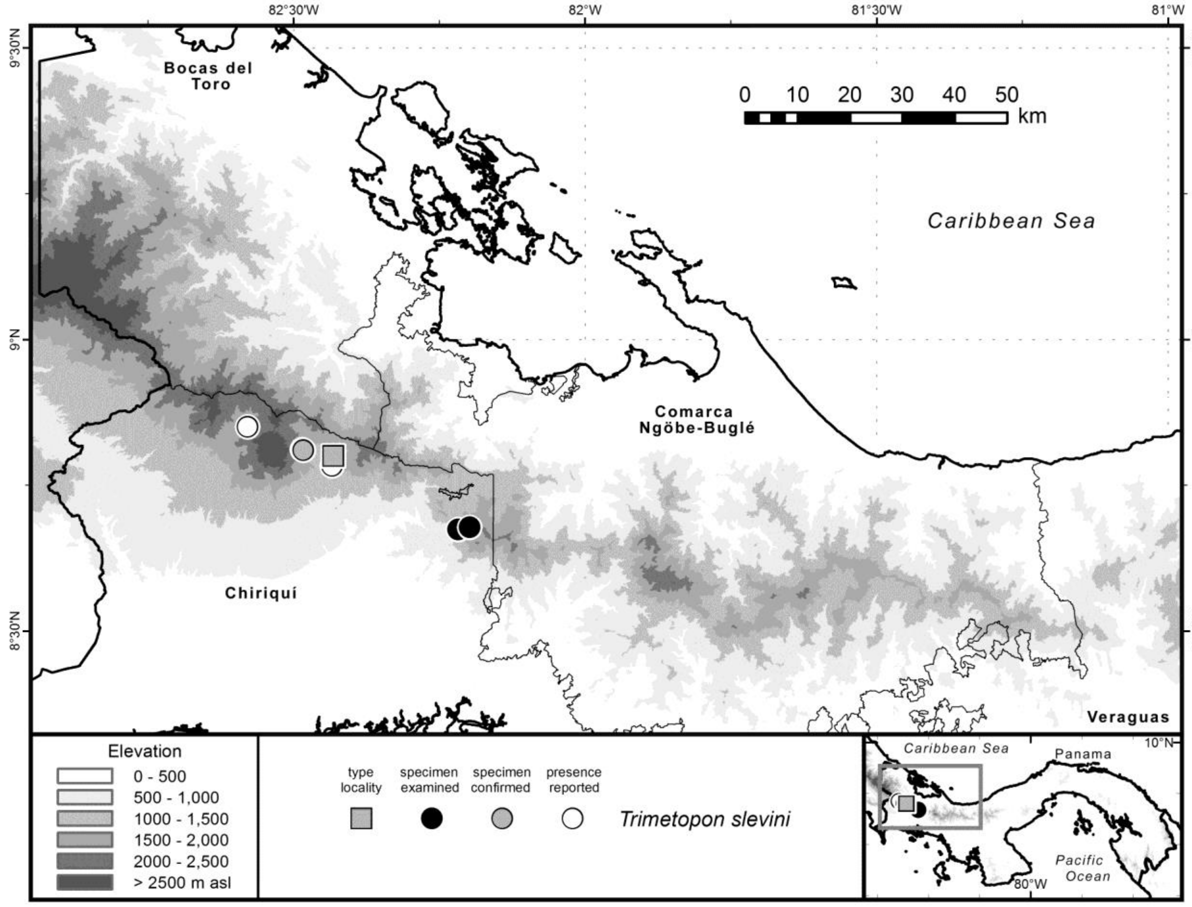
Trimetopon slevini Dunn 1940

Red-bellied Pygmy Snake, Slevin's Tropical Ground Snake; Culebra enana de vientre rojo

Figure 4.112C; Map 4.170.

Holotype. CAS 78938, young male, from "near Boquete, Chiriquí Prov. Panama, altitude 4000 feet" (Dunn 1940; = ca. 1219 m)

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 1200–1825 m asl. In Panama, known from the Pacific slopes of the Cordillera Central in Chiriquí, where it has been reported from Cerro Punta, the Boquete area, and east to Cerro Pata de Macho at RFLF, 1220–1825 m asl.



Map 4.170: Distribution of *Trimetopon slevini.*

Diagnosis. This small snake (maximum TOL 294 mm) with round pupils is unique among Panamanian snakes in having two separate prefrontals, dorsals without apical pits arranged in 17—17—17 rows that are smooth except for supracloacal keels in males, a preocular and usually a loreal, a divided cloacal scute, an immaculate reddish venter and two light nuchal spots, as well as 152 or more ventrals.

Description. (including data from Dunn 1940) TOL to 294 mm; SVL to 220 mm; tail moderate, TL/TOL = 0.19–0.27; D smooth except for supracloacal keels in males, striate laterally*, in 17—17—17 rows; V 152–167; SC 43–64; SPL 6–7; INL 7–8; PF 2; loreal 0–1; Preoc 1; Postoc 1; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Trimetopon slevini* is a unilobed organ; truncus with spines, apex calyculate.

Coloration in life. D and L ground color brown, with a middorsal dark stripe and 1 broad plus 2–3 narrow dark L stripes that may be discontinuous and/or unconspicuous; a pair of white to yellow nuchal spots posterior to parietals and a larger, oblique white marking laterally below each of these; head with more or less conspicuous light and/or dark mottling as well as light areas on snout and/or SPL, usually including a post- and subocular light stripe; V surfaces orange to red, grading into white under head, immaculate or sometimes with sparse dark spotting under tail; iris yellowish to dark brown.

The juvenile SMF 90211 (Fig. 4.112C) was recorded as follows: D surfaces of body and tail Raw Umber (223) with a Sepia (119) middorsal longitudinal stripe; L surfaces of body and tail Mars Brown (223A) with a Sepia (119) L longitudinal stripe; V surfaces of body and tail Ferruginous (41); D and L surfaces of head Sepia (119), with a dirty white blotch on the supralabial just posterior to eye and Yellow Ocher (123C) markings on snout; two Chamois (123D) paravertebral blotches on neck; dirty white markings on ventrolateral portion of neck; V surface of head Light Neutral Gray (85) with Pearl Gray (81) scale margins.

Nadim Hamad recorded the female SMF 89602 as follows (translated from Hamad 2009; animal pictured in Fig. 60 therein): Dorsum with a broad Raw Umber (223) longitudinal band bearing a black middorsal stripe and bordered laterally by narrow black lines; L surfaces Mars Brown (223A) with a black longitudinal stripe; D surface of head Raw Umber (223) with two Cinnamon (39) blotches posterior to parietals; L surfaces of head with two Pale Horn Color (92) blotches; venter Burnt Orange (116) with a suggestion of Pratt´s Rufous (140).

Coloration in preservative. After 4.5–6 years in preservative, the coloration of my examined specimens is similar to that in life, apart from that all yellow and orange elements have turned white.

Natural history notes. Terrestrial and semifossorial, probably feeding on small vertebrates as reported for its better-known congeners. The juvenile SMF 90211 (TOL 145 mm) was discovered by FO under a leaf on the ground along the ascent to an elfin forest ridge around

13:00. The female SMF 89602 was found by NH and LS as it was moving on the forest ground around 23:30 (Hamad 2009).

Remarks. The species' lower elevational limit given as 120 m asl by Savage (2002) for Panama and by Wilson & Johnson (2010), or even as being at sea level (Perez-Santos 1999) must be based on the specimens ANSP 23875, 24717–19, and 24770–72, which were originally labelled as coming from "Panama Sabanas". As detailed by Myers (2003) and Savage & Watling (2008), these lowland records from "Panama Sabanas" derive from specimens obtained in the course of the Panama snake census that were mislabeled and actually collected at Finca Lérida. I consider *Trimetopon slevini* to be a species of upper premontane and lower montane elevations and assume the lower elevational limit of 1200 m as given by Savage (2002) for Costa Rica and most other authors as being closer to reality, while coinciding nicely with the lowest Panamanian record which is the type locality at ca. 1220 m. The specimen KU 75760 from "Cerro Punta, 1825 m" (Perez-Santos 1999) represents the highest elevation reported for this species which is well above the elevational maximum of 1645 m given by Jaramillo et al. (2010).

The two specimens from RFLF, collected above the Lost & Found Ecohostel (SMF 89602) and on the W slope of Cerro Pata de Macho (SMF 90211) are the easternmost records of *Trimetopon slevini* and extend the species' distribution about 29 km ESE from the type locality near Boquete into the W Serranía de Tabasará. Together with the species' altitudinal range, the distances of < 5 km, respectively, from the type locality to the border of Bocas del Toro and from the collection site of SMF 90211 to the border of the Comarca Ngöbe-Buglé render the presence of *T. slevini* in these political subdivisions plausible.

Another species of *Trimetopon* with two separate PF and light nuchal spots posterior to the parietals, *T. barbouri* Dunn 1930, has recently been revealed to occur at Valle de Antón and PNGDOTH (Ray et al. 2013), and I regard its presence in my study area and Veraguas as possible (see distribution map in Appendix 7). It is readily distinguished from *T. slevini* by its 15—15—15 D rows and 138–153 V, as well as by its oblique white L nuchal marking extending anterodorsally to or even onto the parietals, that is, to well anterior of the light nuchal spots.

***Urotheca decipiens* (Günther 1893)**

Collared Glasstail, Long-tailed Littersnake; Cola de vidrio, Cola de vidrio de collar

Figures 4.112D, E; Map 4.171.

Liophis albiceps: Peters (1960); Peters & Orejas-Miranda (1970).

Rhadinacea decipiens: Castillo et al. (1990).

Rhadinaea decipiens: Taylor (1954); Smith (1958); Peters & Orejas-Miranda (1970); Myers (1974); Auth (1994); de Sousa (1999).

Rhadinaea pachyura decipiens: Dunn (1938b, 1942: in part., referring to Costa Rican specimens), Taylor (1951).

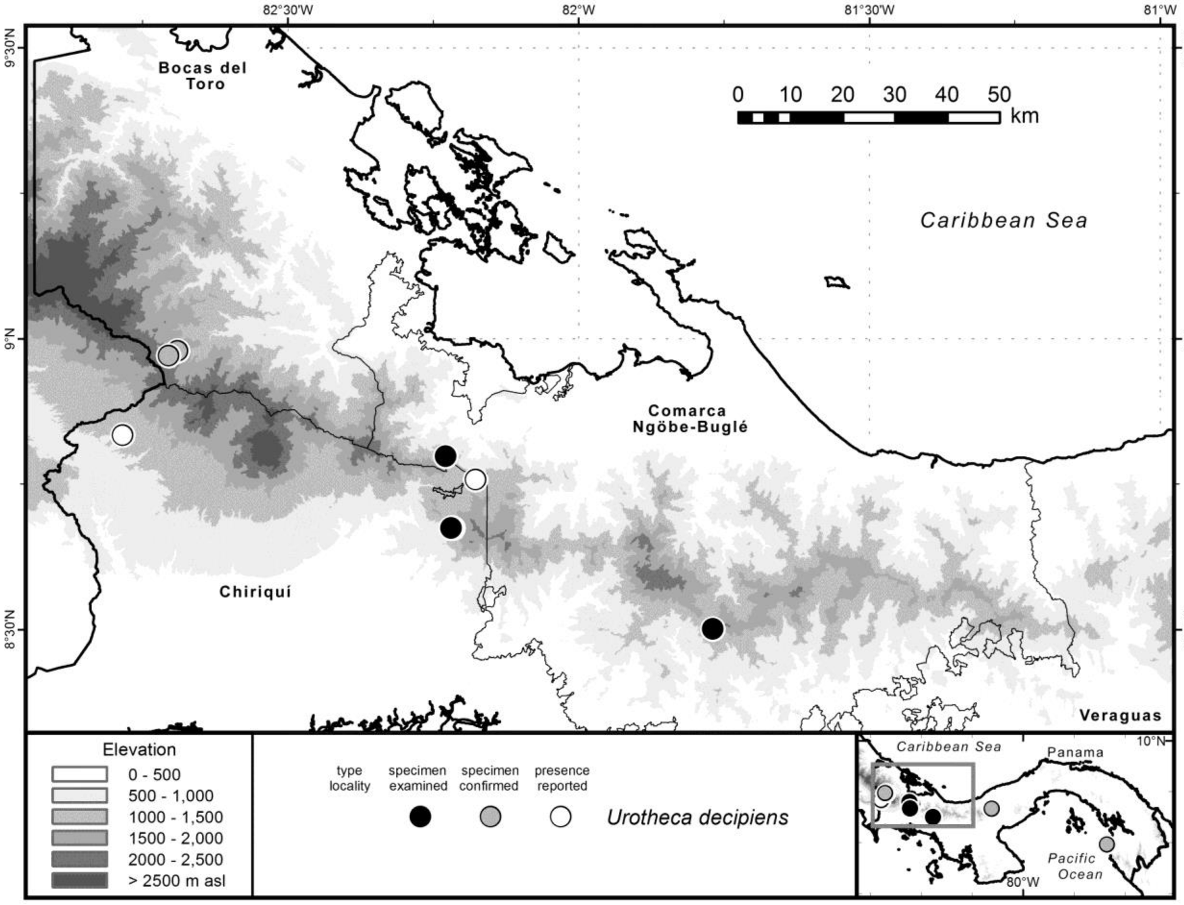
Urotheca dicipiens: Carrizo (2010).

Urotheca lateristriga: Boulenger (1894: in part.).

Urotheca sp.: Hamad (2009).

Syntypes. BMNH 1946.1.3.95–97 (3 specimens), from Irazú, Costa Rica (Myers 1974).

Geographic distribution. Honduras to Colombia (not recorded from Nicaragua), 0–1620 m asl (to 2740 m asl in Colombia). In Panama, along the Cordillera Central including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, and from the Serranía del Sapo in Pacific eastern Panama. In the Cordillera Central, reported from several sites along both versants east to PNGDOTH, 800–1620 m asl.



Map 4.171: Distribution of *Urotheca decipiens.*

Diagnosis. This small snake (maximum TOL 569 mm) with round pupils is recognized as a member of the genus *Urotheca* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal and at least one preocular, exceptionally long and thick tail that is incomplete in many specimens, and a striped dorsal pattern including a conspicuous white stripe on the 1st dorsal row. *Urotheca decipiens* differs from its LCA congeners in having a light supralabial stripe that is bordered above and below by dark pigment (vs. no such stripe or, if present, not bordered by dark pigment below on SPL). It further differs from *U. guentheri* in having a white to yellow venter that may be mottled with dark (vs. immaculate bright orange or red) and in lacking a distinct light postocular blotch or ocellus on each parietal (vs. present), and from *U. fulviceps, U. myersi,* and *U. pachyura* in having the head cap not conspicuously lighter than the body and not extending clearly behind parietals but grading into the dorsal coloration (vs. head cap lighter than body, sharply demarcated, extending 1–2 dorsal rows beyond parietals in the latter two and 3–4 rows in the former species).

Description. (including data from Myers 1974) TOL to 569 mm; SVL to 344 mm; tail long, TL/TOL = 0.35–0.47; D smooth, striate*, in 17—17—17 rows; V 122–143; SC 90–121; SPL 8–9; INL 9–10; loreal 1; Preoc 1–2; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Urotheca decipiens* is a slender, unilobed organ; pedicel spinulate; truncus with small spines proximally and enlarged spines distally; short apical region with papillate calyces on sulcate, and spinulate calyces and a deep naked pocket on asulcate side.

Coloration in life. Very variable. D and L surfaces greenish brown to black, with a white L stripe on 1st or 1st and 2nd D row usually continuing well onto tail; sometimes a second light L stripe on the 5th D row (absent in all specimens reported from W Panama); brown specimens often with a dark middorsal and several dark L stripes all of which may be very inconspicuous; often a yellow to orange or light brown nuchal collar touching or crossing the parietals and extending 1–4 D rows posterior to them, sometimes interrupted medially; D surface of head brown with dark mottling, or blackish; a conspicuous uninterrupted white supralabial stripe bordered above and below by dark pigment; V surfaces white to yellow, those of body and tail sometimes with dark mottling that may suggest a longitudinal line along V and/or SC, those of head nearly immaculate to heavily blotched with dark; iris reddish to dark brown; tongue dark with light tips.

The female SMF 90212 (Fig. 4.112E) was recorded as follows: D and L surfaces of body and tail Vandyke Brown (121) finely dotted with dirty white with a suggestion of Pearl Gray (81); a Sepia (119) vertebral stripe becoming less conspicuous towards posterior portion of body; a Sepia (119) dorsolateral longitudinal stripe barely discernable; dense dirty white with a suggestion of Pearl Gray (81) dotting suggesting a ventrolateral longitudinal stripe between 1st and 2nd D row that continues onto anterior portion of tail; edges of V Sepia (219), suggesting a dark ventrolateral longitudinal stripe that extends onto tail; D and L surfaces of head Raw Umber (223) mottled with Sepia (119); lips and chin area Pearl Gray (81) with a suggestion of dirty white, mottled with Raw Umber (223); V ground color dirty white with a suggestion of Pearl Gray (81); iris Brick Red (132A).

Nadim Hamad recorded the female SMF 89604 (Fig. 4.112D) as follows (translated from Hamad 2009): D ground color Jet Black (89), but each scale speckled with Grayish Olive (43); L surfaces Raw Umber (223), with a dirty white longitudinal stripe extending from neck to tip of tail along first D row; head Mars Brown (223A); supralabials dirty white with a fine Mars Brown (223A) line on their inferior borders, seeming like the beginning of the L stripe; venter Pale Horn Color (92); iris Mars Brown (223A).

Coloration in preservative. After 4.5–6 years in preservative, the coloration of SMF 89604 and SMF 90212 is similar to that in life, apart from that the yellow venter of the former has turned white and its greenish D hues have turned brown.

Natural history notes. Diurnal and nocturnal, terrestrial, feeding on amphibians and small lizards. Montgomery et al. (2006) reported a *Sphaerodactylus* in their specimen from PNGDOTH that was found moving through the leaf litter at night. At La Nevera, the female SMF 90212 containing palpable eggs crawled through our camp around 01:45. The female SMF 89604 was encountered by LS while it was active on the floor along the forest edge at the Lost & Found Ecohostel around 10:00.

Remarks. The high variability in coloration found in *Urotheca decipiens* somewhat complicates its identification and delimitation among the members of a genus that primarily differ in their respective color patterns. Especially the individuals from western Panama and adjacent Costa Rica lacking the nuchal collar and dorsolateral light line may be confused with *U. pachyura* as discussed by Myers (1974: p. 175), a problem experienced by myself during the identification of my examined specimens and corroborating the adequateness of the specific epithet meaning "deceiving". I tentatively assign the two specimens collected at RFLF and La Nevera (Figs. 4.112D and E), regarded to be conspecific with each other in view of their very low genetic differentiation (uncorrected p-distances of 0.2% in the 16S and 0.5% in the COI barcode), as well as the specimen MVUP 1753 collected by U. Hofer and colleagues at BPPS and reported as belonging to this species by Hofer & Bersier (2001), to *U. decipiens* based on current knowledge. All three specimens have immaculate venters, and none has a light nuchal collar or light dorsolateral line. The white ventrolateral stripe is well pronounced in SMF 89604 but less clear-cut and conspicuous in the other two specimens. The same applies to the white SPL stripe that is only sparsely bordered by scattered medium brown pigment in SMF 90212 and seems to have been similar (only posterior portion retained on right side, other SPL removed or decayed) in MVUP 1573. The dark mottling on the V head surfaces likewise is very pronounced in SMF 89604 and less dark and dense in the other two specimens. Another specimen from near the Lost & Found Ecohostel which I have only briefly checked, SMF 92009, is very similar to SMF 89604 at first glance and also referred to this species herein.

I could not find any record to substantiate the upper elevational limit of 1750 m asl in Panama as given by Perez-Santos (1999). I prefer to recognize the specimen KU 112439 from "north slope Cerro Pando, 1620 m" as representing the upper limit documented for Panama as apparently done by Jaramillo et al. (2010). The records from E and W of Veraguas render the occurrence of *Urotheca decipiens* in that province plausible, as suggested by Carrizo (2010) who cites an unpublished thesis to have listed the species for Alto de Piedra.

Urotheca guentheri **(Dunn 1938)**

Striped glasstail, Orange-bellied Littersnake, Günther's Graceful Brown Snake; Cola de vidrio, Cola de vidrio rayada

Figure 4.112F; Map 4.172.

Coniophanes decipiens: Dunn (1938b, 1942); Taylor (1951, 1954).

Rhadinaea persimilis: Dunn (1938b, 1942); Smith (1958); Taylor (1951, 1954); Peters & Orejas-Miranda (1970).

Rhadinaea guentheri: Peters & Orejas-Miranda (1970); Myers (1974); Auth (1994).

Rhadinaea güntheri: Dunn (1938b).

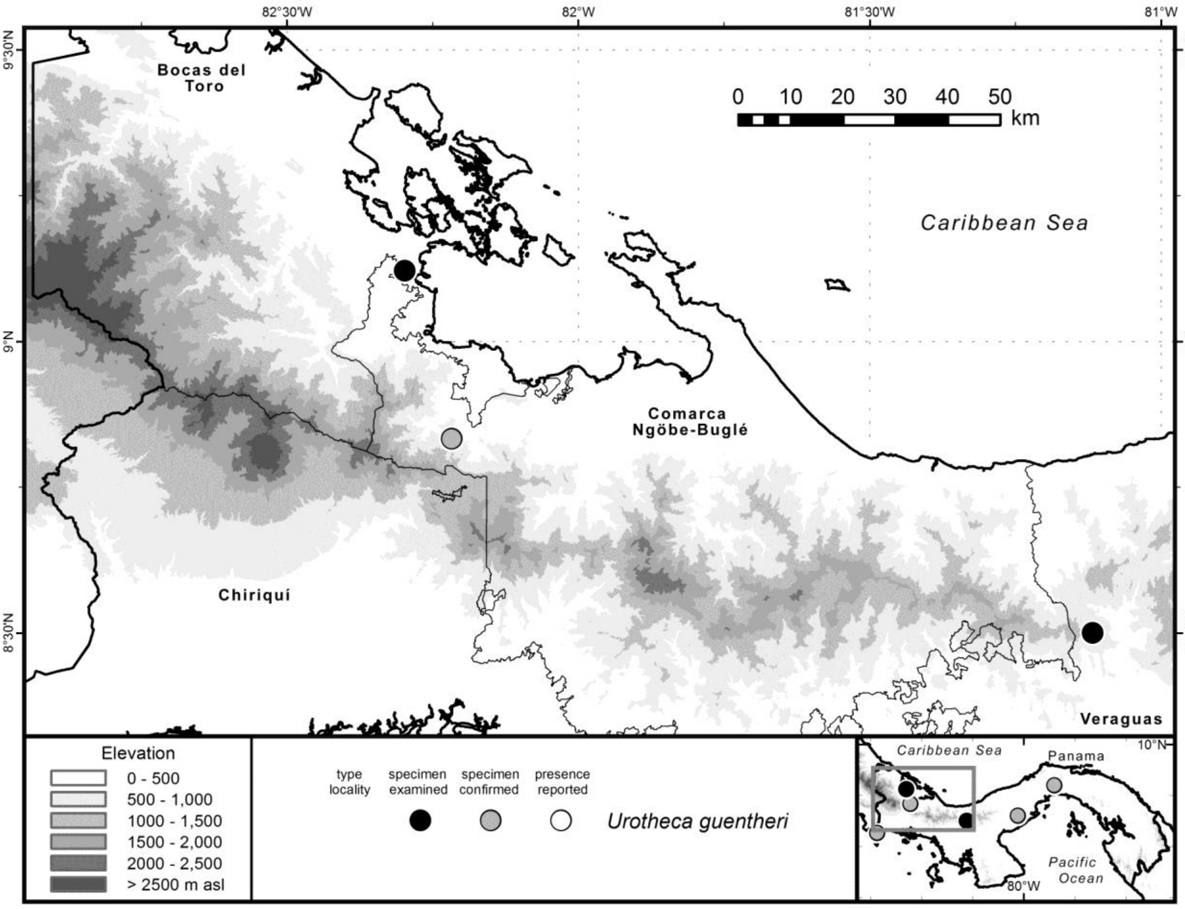
Holotype. BMNH 1946.1.8.15, from Irazú, Costa Rica (Myers 1974).

Geographic distribution. Honduras to Panama, 0–1800 m asl. In Panama, along both versants throughout western and central portions of the country, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from La Loma, the Santa Fé area, and Valle de Antón, up to 1250 m asl.

Diagnosis. This small to medium-sized snake (maximum TOL ca. 670 mm) with round pupils is recognized as a member of the genus *Urotheca* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal and at least one preocular, exceptionally long and thick tail that is incomplete in many specimens, and a striped dorsal pattern including a conspicuous white stripe on the 1st dorsal row. *Urotheca guentheri* is the only member of the genus, and actually unique among Panamanian snakes in, having two conspicuous light stripes on each side of the body and tail, a distinct light postocular blotch or ocellus on each parietal, and an immaculate bright orange to red venter.

Description. (including data from Myers 1974) TOL to about 670 mm; SVL to 399 or even 483 mm; tail long, TL/TOL = 0.36–0.44; D smooth except for supracloacal keels in some males, in 17—17—17 rows; V 135–176; SC 82–110; SPL 6–8; INL 6–8; loreal 1; Preoc 1–2; Postoc 2–3; Tant 0–1, Tpost 1; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Urotheca guentheri* is a unilobed organ; pedicel spinulate; truncus with enlarged spines that are largest on the asulcate side which bears a single basal hook; apical region with papillate calyces on sulcate and spinulate calyces as well as a deep naked pocket on asulcate side.



Map 4.172: Distribution of *Urotheca guentheri.*

Coloration in life. D and L surfaces brown to almost black, with a light (white, cream, or yellow) ventrolateral stripe on 1st or 1st and 2nd D row usually continuing well onto tail and a light dorsolateral stripe on the 5th or 5th and 6th D row always continuing onto tail; both light L stripes usually with dark borders; a grayish brown middorsal stripe usually very inconspicuous; anterior extreme of light dorsolateral stripe in most specimens widened to form a light nuchal blotch that may be separated from the stripe as a black-edged ocellus; a similar but smaller middorsal nuchal spot or ocellus usually present; a similar, distinct light postocular blotch or ocellus on each parietal; D surface of head usually with light markings anteriorly and on supraoculars; a conspicuous uninterrupted white supra- and infralabial stripe bordered above by blackish pigment; V surfaces immaculate orange to red; iris light brown above, dark brown to black below; tongue dark with light tips.

Leonhard Stadler recorded the adult female SMF 89603 (Fig. 4.112F; Stadler 2010: Fig. A99) as follows (translated from Stadler 2010): D surfaces Sepia (119) with two parallel L Raw Sienna (136) longitudinal stripes extending from back of head to tip of tail; a ventrolateral Chamois (123D) longitudinal line extending from snout to tip of tail; a postorbital Chamois (123D) blotch on each side; V surfaces Burnt Orange (116).

Coloration in preservative. After 5–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that the bright orange of their venters has turned white.

Natural history notes. Diurnal and nocturnal, terrestrial and semifossorial, feeding primarily on frogs. The female SMF 89603 was encountered by LS and NH around 12:45 moving through the leaf litter. The specimen SMF 89789 was found on the road to Almirante at 21:25, badly damaged with most of its tail torn off. The specimen must have died shortly before it was found, since it had not been there when we arrived at that site around 21:00.

Remarks. The rather complicated taxonomic history of this species, in large parts caused by Dunn (1938b) who proposed the replacement name *Rhadinaea güntheri* to avoid a secondary homonymy when transferring *Tachymenis decipiens* Günther 1895 to *Rhadinaea,* while in the same paper describing another specimen (MCZ 19345 from "La Loma, 1500 feet [= ca. 457 m] elevation, Atlantic slope on trail from Chiriquí Lagoon to Pacific side, Bocas del Toro, Panama"; today in the Comarca Ngöbe-Buglé) of the same species as *R. persimilis* and thus laying the foundations for another secondary homonymy, has been recounted in detail by Myers (1974) and Savage (2002).

As pointed out by Savage (2002: p. 645–646), the upper elevational limit of 2100 m asl as given by previous authors (Myers 1974; Köhler 2008) was based on a specimen with doubtlessly erroneous locality data. Thus, I adopt the next highest among the most recent values as the documented maximum elevation (1800 m fide Sasa et al. 2010). The specimen SMF 89603, collected by LS and NH on Cerro Mariposa at 1250 m, for the first time documents the species' presence in Veraguas, and moreover represents the highest record for Panama (Stadler 2010; Lotzkat et al. 2010c; Jaramillo et al. 2010). Recently, Sosa et al. (2012) extended the species' known distribution from Valle de Antón to Cerro Azul slightly E of the canal.

***Urotheca pachyura* (Cope 1876)**

Costa Rican Glasstail, Cope's Graceful Brown Snake; Cola de vidrio, Cola de vidrio costarricense

Figure 4.112G; Map 4.173.

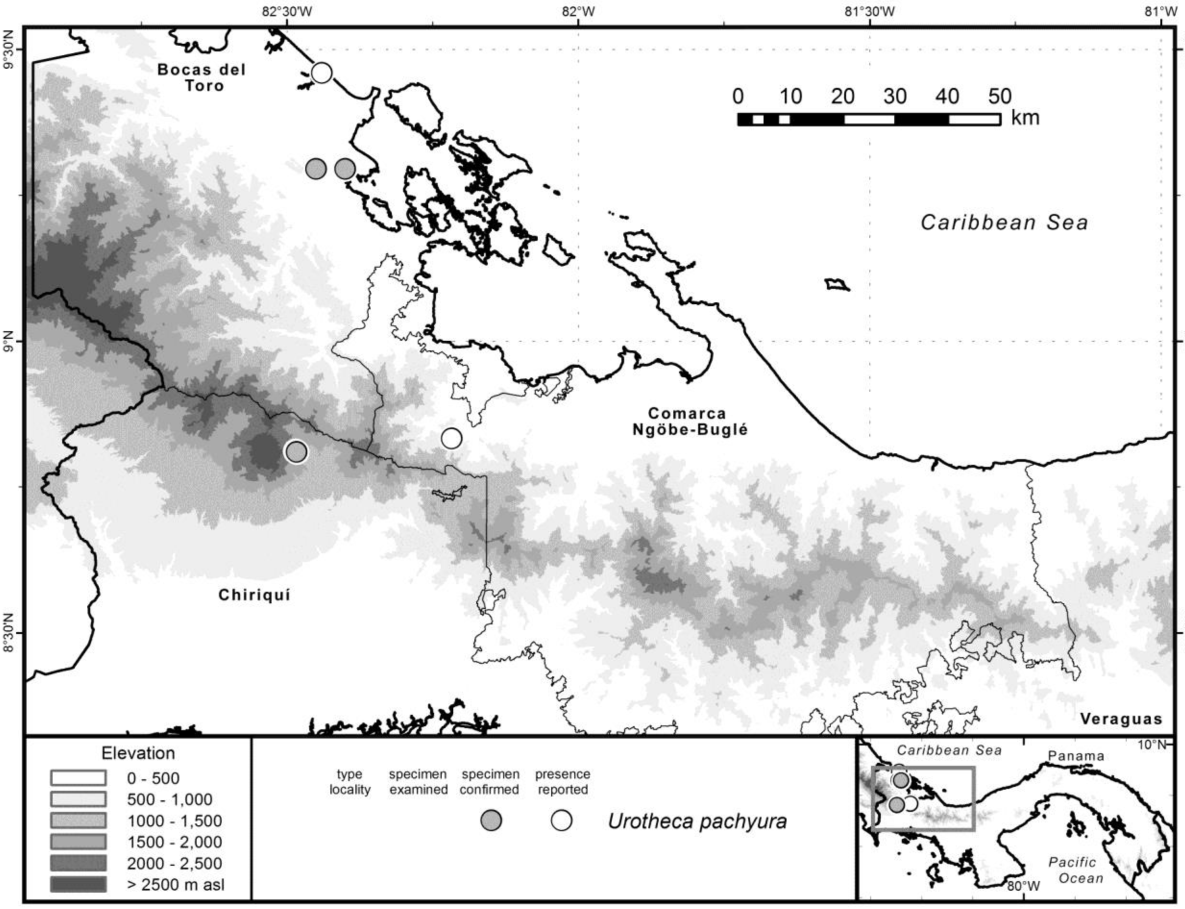
Contia pachyura: Cope (1876); Boulenger (1894).

Rhadinaea pachyura or *R. p. pachyura:* Dunn (1938b, 1942); Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970); Myers (1974); Auth (1994).

Rhadinaea pachyura decipiens: Dunn (1942: in part., referring to Finca Lérida specimens, 1947).

Rhadinaea decipiens rubricollis: Taylor (1954); Peters & Orejas-Miranda (1970).

Holotype. USNM 30618, adult male, from Sipurio (near Suretka, Limón province), Costa Rica (Myers 1974).



Map 4.173: Distribution of *Urotheca pachyura.*

Geographic distribution. Costa Rica and Panama, 0–1800 m asl. In Panama, predominantly along the western Caribbean versant including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas (see remarks). In the Cordillera Central, reported from La Loma and Finca Lérida up to 1800 m asl.

Diagnosis. This small to medium-sized snake (maximum TOL 725 mm) with round pupils is recognized as a member of the genus *Urotheca* by its smooth dorsal scales arranged in 17—17—17 rows, divided cloacal scute, presence of a loreal and at least one preocular, exceptionally long and thick tail that is incomplete in many specimens, and a striped dorsal pattern including a conspicuous white stripe on the 1st dorsal row. *Urotheca pachyura* differs from its LCA congeners in having a light reddish brown head cap that extends 1–2 dorsal rows posterior to parietals and sharply contrasts with the darker brown body, but is not delimited posteriorly by a narrow black nuchal collar. It further differs from *U. guentheri* and *U. myersi* in having a white venter (vs. bright orange or red in the former, yellow in the latter) and from the former also in lacking a distinct light postocular blotch or ocellus on each parietal as well as a light dorsolateral stripe (vs. present), from *U. decipiens* in having the light supralabial coloration not bordered by strong dark pigmentation below (vs. bordered below by dark), and from *U. fulviceps* in sometimes having dark supralabial sutures and singular spots on the supralabials, but lacking heavy black mottling or spotting on the light portions of the supralabials (vs. heavy mottling or spotting present).

Description. (including data from Myers 1974) TOL to 725 mm; SVL to 384 mm; tail long, TL/TOL = ca. 0.41; D smooth, in 17—17—17 rows; V 130–138; SC 104–124; SPL 8; INL 9–10; loreal 1; Preoc 1–2; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes moderate, pupil round.

The hemipenis of *Urotheca pachyura* is a unilobed organ; pedicel spinulate; truncus with small spinules proximally and enlarged spines, which are largest on the asulcate side, distally; short apical region with papillate calyces on sulcate and spinulate calyces on the asulcate side.

Coloration in life. D and L surfaces medium to blackish brown, with a white L stripe or series of dashes on 1st or 1st and 2nd D row continuing onto base of tail; sometimes with the indication of a second light L stripe around the 4th and 5th D row and/or several dark L stripes, all of which are very inconspicuous; hed cap of a lighter brown than D surfaces, usually reddish brown, extending 1–2 D scale rows posterior to parietals, in some examples 1–2 D further medially; a light nuchal collar crossing the parietals and extending 1–1.5 D rows posterior to them in juveniles; upper margins of SPL bordered with dark pigment, SPL largely white to yellowish, except for possibly present dark sutures and singular medial dark spots near their inferior border; V surfaces white, immaculate or with sparsely distributed dark spots, those of head yellowish; iris reddish brown.

Coloration in preservative. Similar to that in life, apart from that the head cap lightens up to yellow brown, sharpening the contrast to the darker brown body, and formerly yellowish SPL fade to white.

Natural history notes. Largely unknown, probably diurnal and nocturnal, terrestrial, and feeding on small vertebrates like its better-known congeners.

Remarks. Based on photos of individuals from the Caribbean lowlands of Colón province (by MP; Fig. 4.112G) and Coclé province (by Julie M. Ray), I regard *Urotheca pachyura* to evidently range much farther to the E than documented to date. Since the exact provenances of these photo records are unknown to me, neither of them is plotted on Map 4.173. Still, they render the species' occurrence in Veraguas plausible. I could not find any record to substantiate the upper elevational limit of 2000 m asl in Panama as given by Perez-Santos (1999). Though this value is close to the overall altitudinal range of Finca Lérida, I prefer to use the elevation given for that collection site by Perez-Santos (1999) as 1800 m for the specimens ANSP 23880 and 24774 (both examined by Myers 1974, previously reported as *Rhadinaea pachyura decipiens* by Dunn 1942, 1947) as the upper limit documented for Panama, which is somewhat above the value given by Jaramillo et al. (2010) and the highest specimen-based value reported for the species so far.

Two other species of *Urotheca* with a well-demarcated light head cap, *U. fulviceps* (Cope 1886) and *U. myersi* Savage & Lahanas 1989, possibly occur in my study area (see distribution maps in Appendix 7). The former species has been reported from numerous localities in central and eastern Panama as well as from Pacific lowland Costa Rica. The montane snake *Urotheca myersi* Savage & Lahanas 1989, the holotype of which was referred to as *Rhadinaea, species inquirenda* by Myers (1974), is only known from the Pacific versant of the Talamancan highlands in Costa Rica, but can definitely be expected to occur in Panama, at least in western Chiriquí. Lips (1993) reported the 3rd known specimen of this species from "Costa Rica: Puntarenas Province: Cantón Coto Brus: Finca Las Alturas, 15 km NNE of San Vito, 1500 m", which is the lowest elevation reported for this species and about 9 km from the Panamanian border. Apparently mislead my Lips' (1993) misspelling of "Chirripó Grande" (the provenance of the paratype CRE 10095) as "Chiriquí Grande" (a town in the Caribbean lowlands of Bocas del Toro), Savage (2002) erroneously stated *U. myersi* to have already been reported for Panama, which to my knowledge and according to Jaramillo et al. (2010) is not the case.

Xenodon rabdocephalus (Wied 1824)

False Fer-de-Lance, False Terciopelo; Equis falsa, Terciopelo falso

Figure 4.112H; Map 4.174.

Acanthophallus colubrinus: Cope (1899).

Ophis colubrinus: Wettstein (1934).

Xenodon angustirostris: Cope (1876).

Xenodon bertholdi: Taylor (1951, 1954).

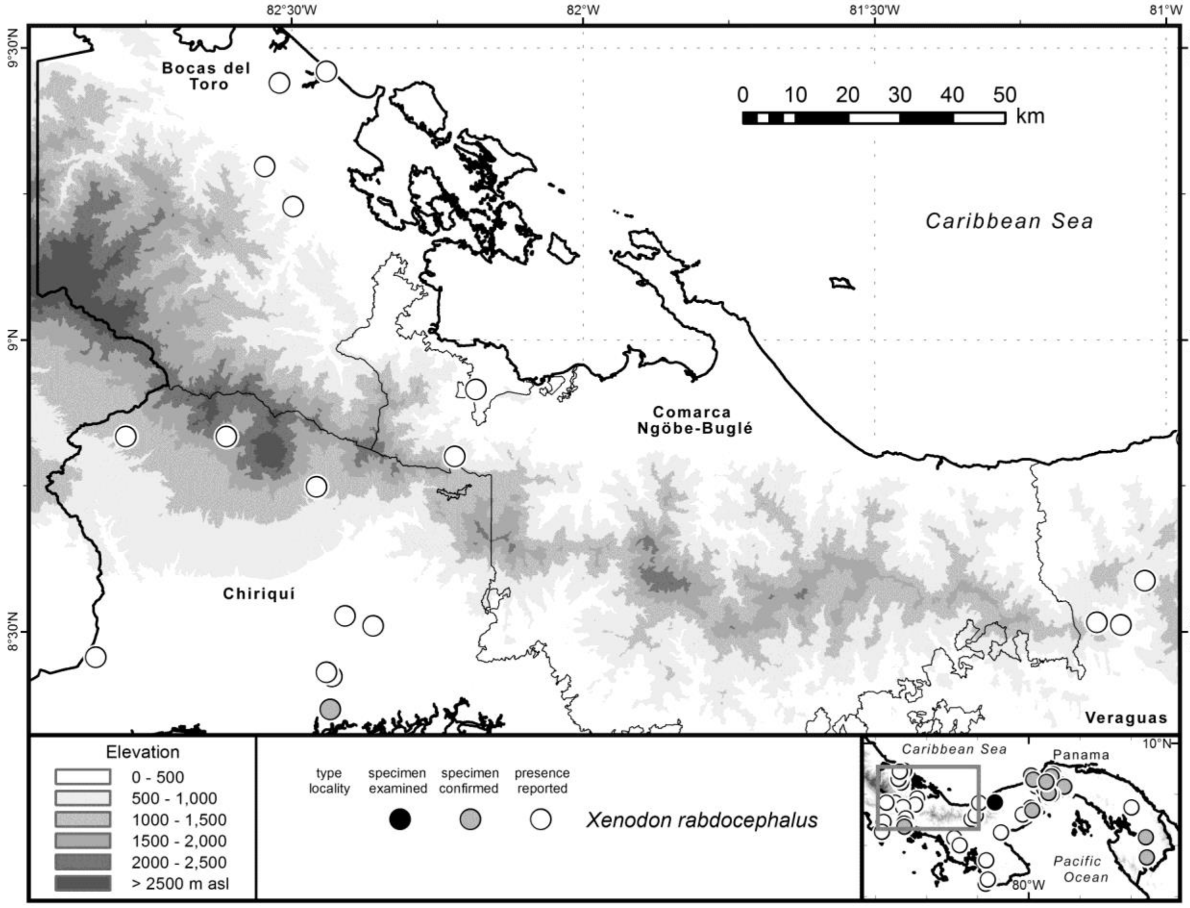
Xenodon colubrinus: Dunn & Bailey (1939); Smith (1958); Taylor (1951, 1954).

Xenodon rhabdocephalus: ANAM (2005).

Xenodon suspectus: Boulenger (1894); Peters & Orejas-Miranda (1970).

Holotype. Exact specimen assignment unclear, from Provinz Bahía, Brazil.

Geographic distribution. Mexico to Peru, Bolivia, and Brazil, 0–1610 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous sites on both versants, up to ca. 1610 m asl.



Map 4.174: Distribution of *Xenodon rabdocephalus.*

Diagnosis. This medium-sized snake (maximum TOL 800 mm) with round pupils is unique among Panamanian snakes in having smooth dorsals with one apical pit arranged in 19 oblique rows at midbody together with a viper-like triangular head and blotched pattern while lacking a loreal pit.

Description. TOL to 800 mm; SVL in Honduran specimens to 663 mm; tail short, TL/TOL = 0.14–0.18; D smooth, in 19—19—17 rows; V 124–153; SC 35–52; SPL 7–9; INL 9–12;

loreal 1; Preoc 1–2; Postoc 2–4; Tant 1, Tpost 2–3; cloacal scute entire; AP 1; eyes large, pupil round.

The hemipenis of *Xenodon rabdocephalus* is a bilobed organ with a naked pedicel; truncus and apex spinous, with or without terminal disk.

Coloration in life. D and L surfaces gray to brown, with light-edged oblique dark brown L bars at least partially arranged to produce butterfly-shaped markings; D surfaces of head dark brown surroundet by dark-outlined light dorsolateral lines; L surfaces of head light brown, with dark SPL sutures; V surfaces cream to light brown with darker spotting and/or mottling mainly on the venter; iris gray to brown.

Coloration in preservative. Similar to that in life.

Natural history notes. Diurnal and terrestrial, feeding mainly on toads which it deflates before swallowing them. Defensive behaviour includes dorsolateral flattening of the body, gaping, and biting which can result in painful local symptoms.

Remarks. My georeference for Bambito, Chiriquí, the provenance of the specimen MPM 18380, yields a SRTM elevation of 1614 m asl which is above the highest elevation reported for this species so far (1500 m according to Solórzano 2004 and Ray & Knight 2013). A specimen that escaped me above El Paredón must have been a *Xenodon rabdocephalus.*

Family Elapidae Boie 1827

Micrurus alleni Schmidt 1936

Allen's Coralsnake; Coral, Coral gigante de agua, Coral macho, Coralillo

Figure 4.113A; Map 4.175.

Micrurus alleni richardi: Taylor (1951).

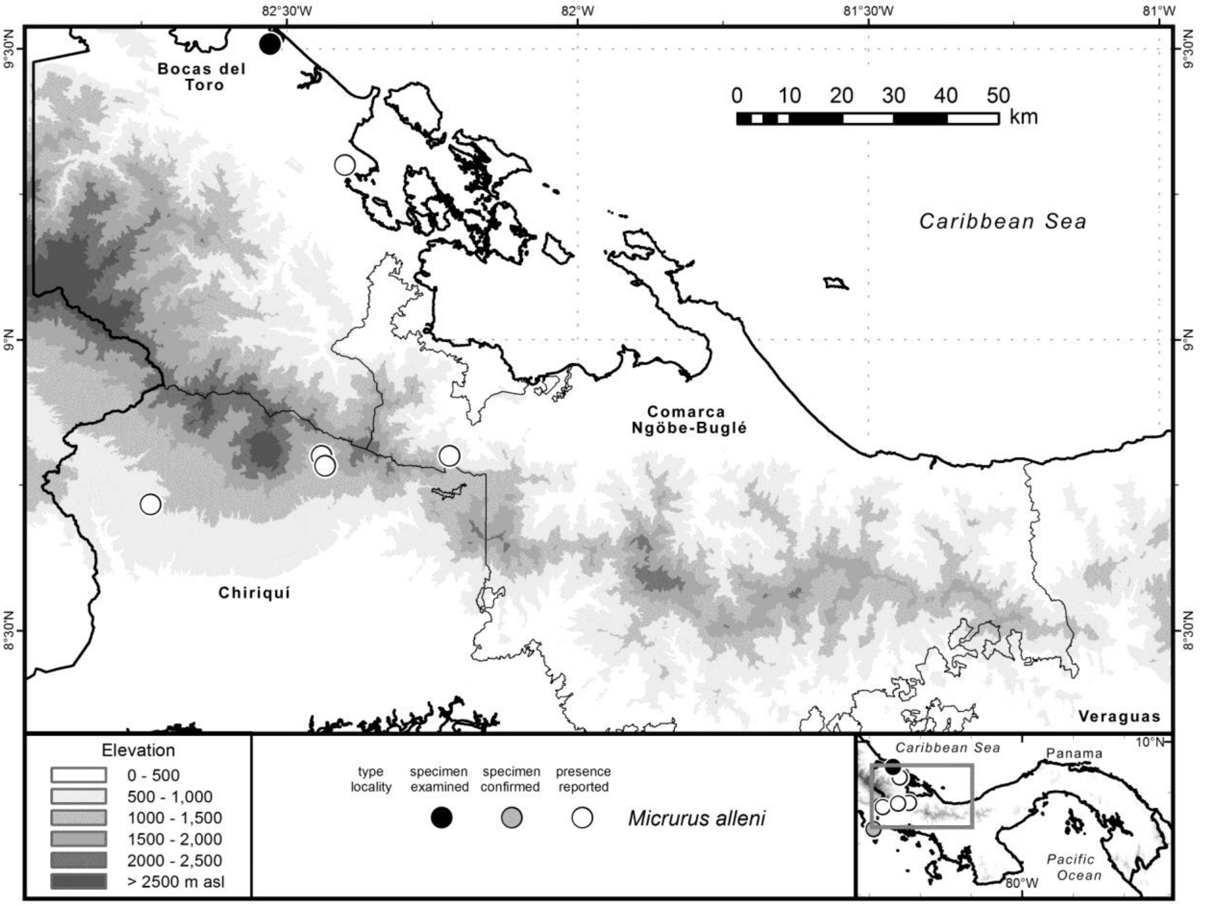
Micrurus nigrocinctus yatesi: Dunn (1942); Taylor (1954); Smith (1958).

Micrurus nigrocinctus alleni: Taylor (1951, 1954).

Micrurus richardi: Taylor (1954).

Holotype. UMMZ 79794, from Río Mico, 10 miles above Recero, Nicaragua.

Geographic distribution. Honduras to Panama, 0–1620 m asl. In Panama, on both versants of the westernmost portion of the country including Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from BPPS and the Pacific versant of the Serranía de Talamanca up to ca. 1320 m asl.



Map 4.175: Distribution of *Micrurus alleni.*

Diagnosis. This medium-sized snake (maximum TOL 1320 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings. *Micrurus alleni* is unique among Panamanian *Micrurus* in having a tricolor (white or yellow-black-white or yellow-red) monad pattern with the red rings usually less than two times the width of the black rings at midbody, and a more or less narrow extension of the black head cap posteriorly along the parietal suture.

Description. TOL to 1320 mm; SVL in Honduran specimens to 928 mm; tail short, TL/TOL = 0.08–0.19; D smooth except for supracloacal keels in adult males and large females, striate*, in 15—15—15 rows; V 205–244; SC 32–60; SPL 7; INL 6–7; loreal 0; Preoc 1; Postoc 2; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Micrurus alleni* is a bilobed organ; pedicel naked, truncus spinulate; apical region with enlarged spines and a long, spinelike awn on the tip of each lobe.

Coloration in life. Body tricolor, with narrow white or yellow rings separating the wide black and red rings; D scales of red rings marked with black, often turning completely black with age, but red retained ventrally; black head cap with a usually narrow posterior extension along parietal suture, rarely covering most of parietals, sometimes reaching to the wide black nuchal ring that does not touch parietals and is followed posteriorly by a white or yellow ring; tail with black and white or yellow rings.

Coloration in preservative. After 4.5 years in 70% ethanol, the coloration of SMF 90200 is similar to that in life, apart from that the yellow has faded to white and the red has faded to light brown dorsally and creamy white ventrally.

Natural history notes. Venomous. Primarily nocturnal, terrestrial and apparently semiaquatic, feeding largely on the swamp eel *Symbranchus marmoratus* but also on lizards. The juvenile SMF 90200 was found at night in the flooded Sangrito forest at San San Pond Sak, lying dead between the tabular roots of a large *Pterocarpus officinalis* tree with its head and especially the tail badly damaged.

Remarks. My georeference for the specimens CAS 79023–26 and 79028–29 from "vicinity north of Boquete" (Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is slightly above the highest elevations of 1000 (Jaramillo et al. 2010) or 1250 m (Perez-Santos 1999) reported for Panama. According to Campbell & Lamar (2004) and Ray & Knight (2013), the eastern limit of *Micrurus alleni* is situated in western Panama, with the records from eastern Panama (Auth 1994; Young et al. 1999; Savage 2002; Köhler 2008) probably being based on specimens of the similar *M. dumerilii.*

Micrurus clarki Schmidt 1936

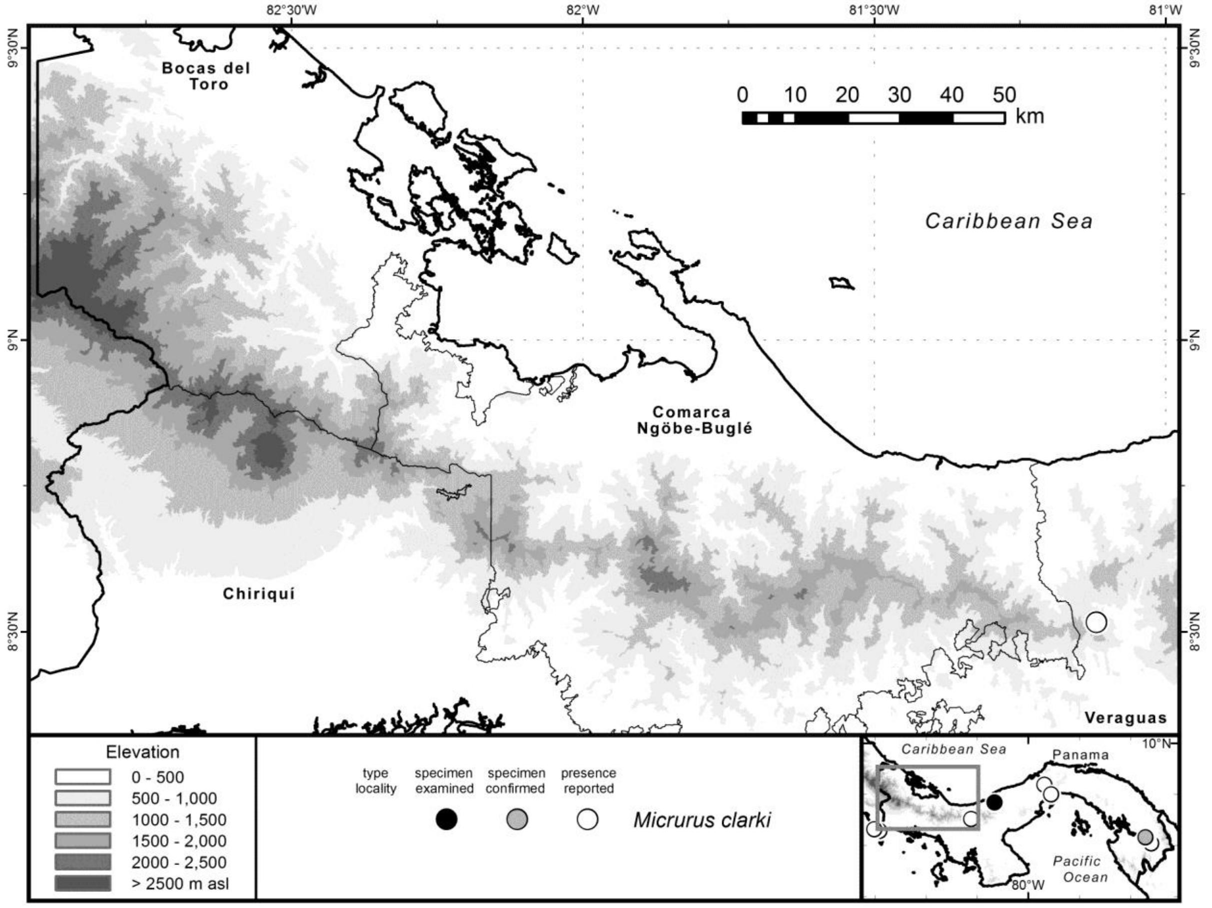
Clark's Coral Snake; Coral, Coral de labios manchados

Figure 4.113B; Map 4.176.

Holotype. MCZ 38390, from Yavisa, Darién, Panama.

Geographic distribution. Costa Rica to Colombia, 0–900 m asl. In Panama, along the Pacific versant of eastern and western Panama including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, as well as on both versants of central Panama. In the Cordillera Central, reported from Cerro Mariposa at approximately 880 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1320 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings. *Micrurus clarki* is unique among Panamanian *Micrurus* in having a tricolor (white or yellow-black-white or yellow-red) monad pattern with the red rings more than two times the width of the black rings at midbody, a black head cap that covers most or all of the parietals, and the light head scales edged with black.



Map 4.176: Distribution of *Micrurus clarki.*

Description. TOL to 919 mm; tail short, TL/TOL = 0.10–0.16; D smooth, in 15—15—15 rows; V 190–221; SC 33–58; SPL 7; INL 6–7; loreal 0; Preoc 1; Postoc 2; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Micrurus clarki* is a bilobed organ without terminal awns.

Coloration in life. Body tricolor, with narrow white or yellow rings separating the moderately wide black from the much wider red rings; D scales of red and white or yellow rings marked with black; black head cap extending far posteriorly to cover most or all of parietals, narrowly or not separated from the narrow black nuchal ring that does not touch parietals, may be reduced or absent, and is followed posteriorly by a red ring; light head scales including SPL and INL with black margins; tail with black and white or yellow rings, the latter of which may darken considerably.

Coloration in preservative. Similar to that in life, apart from that the yellow and red elements fade with time.

Natural history notes. Venomous. Primarily nocturnal and terrestrial, reported to feed on the swamp eel *Symbranchus marmoratus* as well as small snakes.

Remarks. The records east and west of this political subdivision as well as the distance of less than 5 km between the record from Cerro Mariposa (alias Cerro Tute; Martínez & Rodriguez 1994) to the Comarca's border render the presence of *Micrurus clarki* in the Comarca Ngöbe-Buglé plausible.

Micrurus mipartitus (Duméril, Bibron & Duméril 1854)

Bicolored Coralsnake, Many-banded Coralsnake, Red-tailed Coralsnake; Coral, Coral Gargantilla, Coralillo

Figure 4.113C; Map 4.177.

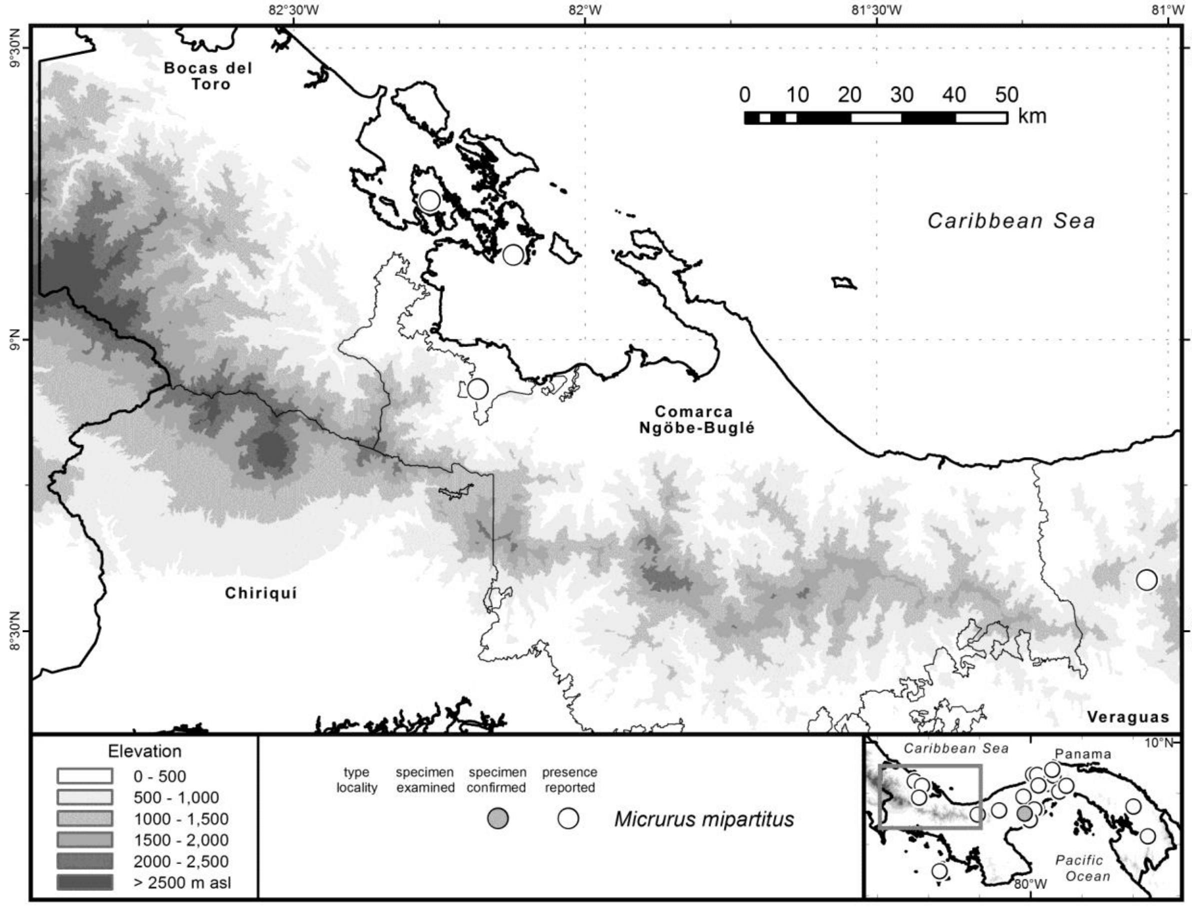
Holotype. MNHN 3915, from Río Sucio, Colombia.

Geographic distribution. Costa Rica to Colombia, Ecuador, and Venezuela, 0–1600 m asl (to 2410 m in Colombia). In Panama, along both versants throughout the country including Bocas del Toro, Comarca Ngöbe-Buglé, Veraguas, and possibly Chiriquí. In the Cordillera Central, reported from the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to 850 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1130 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings. Among Panamanian *Micrurus* with a bicolor (black and white, yellow, or red) body pattern, *M. mipartitus* differs from *M. stewarti* in having 34 or more black body rings which are of more or less equal width, each spanning 3–6 dorsals, and often whitish body rings combined with reddish parietal and tail rings (vs. 21 or fewer black body rings which are usually much wider and of two alternating widths, alternatingly spanning 3–8 and 8–14 dorsals, and all light rings either white or red), and from *M. multifasciatus* in lacking supracloacal keels in males (vs. present) and having the light body rings always white or yellow in Panamanian specimens (vs. white or red).

Description. TOL to 1130 mm; tail very short, TL/TOL = 0.05–0.08; D smooth, in 15—15—15 rows; V 197–326; SC 20–35; SPL 7; INL 6–8; loreal 0; Preoc 1; Postoc 2; Tant 0–1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Micrurus mipartitus* is a bilobed organ without terminal awns.



Map 4.177: Distribution of *Micrurus mipartitus.*

Coloration in life. Body bicolor, with narrow white or yellow rings separating the usually wider (3–6 D) black rings of which there are 34–84; D scales of light rings marked with black; black head cap usually extending to about level of eyes, separated by an immaculate orange to red parietal ring that usually covers all of the parietals from the black nuchal ring (2–9 D wide) that usually does not touch parietals (sometimes encroaches onto posterior tips) and is followed posteriorly by a white or yellow ring; tail with black and white or orange to red rings or blotches.

Coloration in preservative. Similar to that in life, apart from that yellow, orange and red shades fade over time.

Natural history notes. Venomous. Terrestrial and nocturnal, feeding on snakes, amphisbaenians, lizards, and caecilians.

Remarks. The taxonomic situation around *Micrurus mipartitus* and the very similar *M. multifasciatus* in Central America is utterly confusing and far from being resolved. Most recent authors (e.g., Campbell & Lamar 2004; Köhler 2008; Sasa et al. 2010; Wilson & Johnson 2010) recognize the former species as ranging from SA to central Panama, while the latter ranges from central Panama into CA. Others recognize a single species in CA (e.g., Savage 2002; Solórzano 2004). These latter authors usually refer to the taxon occurring in Costa Rica as *M. mipartitus,* while those representing the two-species view call the Costa Rican populations *M. multifasciatus* (as did McConnell 2014). Jaramillo et al. (2010) presented the most recent profound literature review and discussion of the problem and listed both species to occur in all their Panamanian ecoregions including the Cordillera Central. Ray & Knight (2013) go further and include both nominal taxa for both Panama and Costa Rica. Since the solution of this problem is far beyond the scope of my study, I somewhat adopt the position of the latter two teams of authors, regarding it to best acknowledge our uncertainties concerning this issue. The diagnosis and description presented herein for either species are taken from Campbell & Lamar (2004), while I adopted the verbatim species identification of all distributional records for the distribution maps (considering the presence in Chiriquí as stated by Ray & Knight 2013 possible) and left the synonymies blank. The matter has never been better summed up than by Campbell & Lamar (2004: p. 204): "...a confusing assemblage of bicolored coralsnakes that show considerable overlap in scale and pattern features. The validity of currently recognized forms can only be ascertained with additional material, accurate color descriptions of living specimens, and molecular analyses." Jaramillo et al. (2010) and Ray & Knight (2013) formulated similar statements.

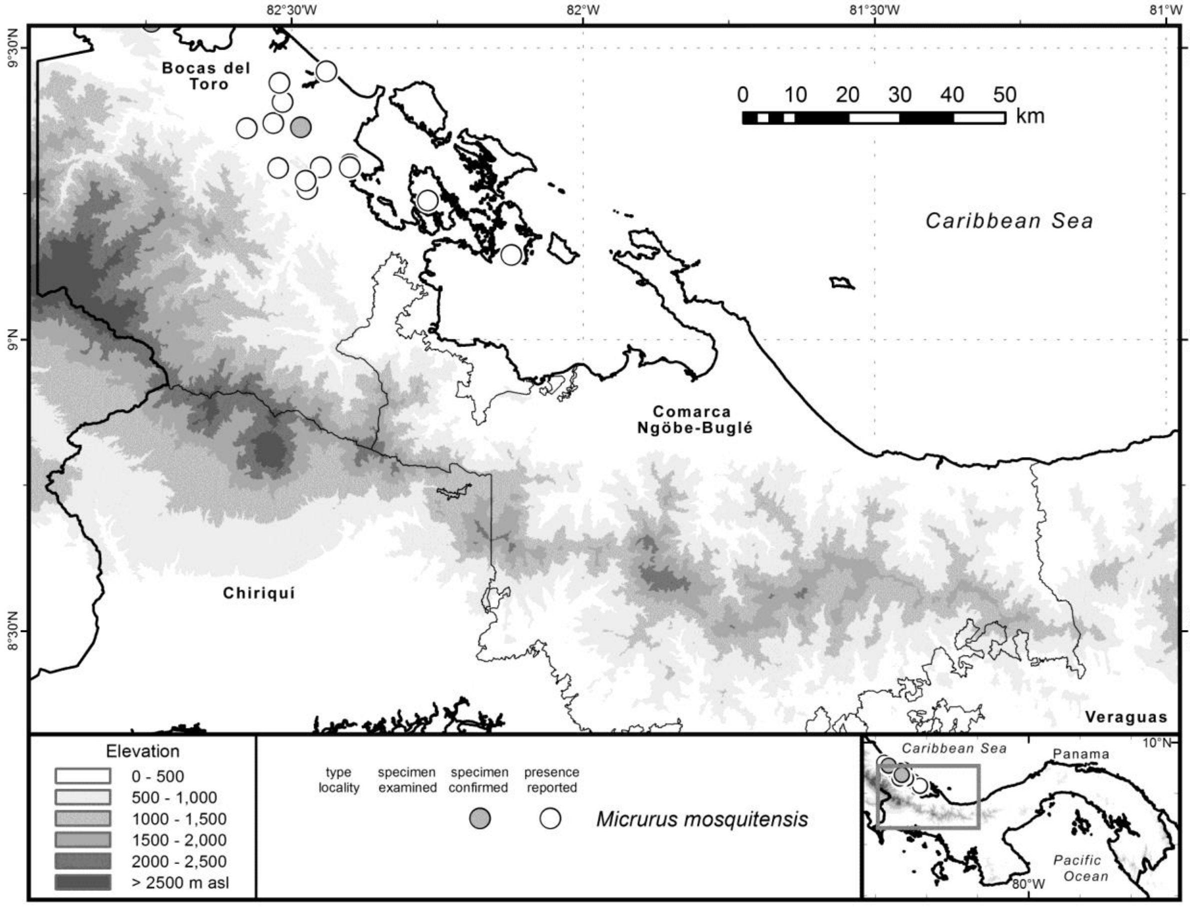
Another coralsnake with a bicolor pattern, the Panamanian endemic *Micrurus stewarti* Barbour & Amaral 1928, has been reported from Donoso (Colón; photo by Michael Castillo), PNAC (Ibáñez et al. 1996), Valle de Antón (the type series of *M. schmidti* Dunn 1940, a junior synonym of *M. stewarti*), PNGDOTH (Ray & Knight 2013), and Puerto Armuelles (FMNH 35906, examined by GK), and is possibly also present in my study area (see distribution map in Appendix 7; though its presence is quite likely, it is not included as "plausible" due to the criteria applied as specified in chapter 3.5.1). It is readily distinguished from *M. mipartitus* by its coloration which is entirely black and red or entirely black and white, with the black rings of alternating width as specified above. In comparing it to *M. mipartitus,* Campbell & Lamar (2004:p. 202) erroneously stated *M. stewarti* to always be black and white, while their species account for the latter species as well as their Figs. 178 and 179 clarify that black and red animals also exist. Ray & Knight (2013) stated the white variant of *M. stewarti* to occur on the Caribbean versant, while the red variant inhabits the Pacific versant according to these authors.

Micrurus mosquitensis Schmidt 1933

Costa Rican Coralsnake; Coral, Coral Costarricense

Figure 4.113D; Map 4.178.

Micrurus nigrocinctus or *M. n. mosquitensis:* Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970); Auth (1994: in part.); Ibáñez et al. (2001: in part.); Perez-Santos (1999: in part.); Young et al. (1999: in part.); Köhler (2001: in part., 2008); Savage (2002: in part.); ANAM (2004, 2009b); McDiarmid & Savage (2005: in part.); Fundación PA.NA.M.A. (2007: in part.); Sunyer (2009: in part.); McCranie (2011: in part.).



Map 4.178: Distribution of *Micrurus mosquitensis.*

Holotype. MCZ 19741, from Limón, Costa Rica.

Geographic distribution. Nicaragua to Panama, 0–1500 m asl. In Panama, along the Caribbean versant in Bocas del Toro and possibly into the Comarca Ngöbe-Buglé. In the Cordillera Central, reported from the Caribbean slopes up to 760 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1000 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings.

Micrurus mosquitensis is unique among Panamanian *Micrurus* in having a tricolor (yellow-black-yellow-red) monad pattern with the red rings usually wider than the black rings at midbody and a yellow parietal ring that extends from slightly anterior to 1–2 dorsals posterior to parietals, so that neither the black head cap nor the black nuchal ring touch the parietals. It further differs from the very similar *M. nigrocinctus* in having the black nuchal ring spanning 7–14 dorsal scales (vs. 8 or fewer).

Description. TOL to 1000 mm; tail short, TL/TOL = 0.10–0.16; D smooth except for supracloacal keels in adult males, in 15—15—15 rows; V 180–211; SC 32–52; SPL 7; INL 7; loreal 0; Preoc 1; Postoc 2; Tant 1, Tpost 1; cloacal scute divided; AP 0; eyes small, pupil round (including data from Taylor 1951).

The hemipenis of *Micrurus mosquitensis* is a bilobed organ with enlarged spines and terminal awns, similar to that of *M. nigrocinctus* but proportionally larger.

Coloration in life. Body tricolor, with narrow yellow rings separating the moderately wide black from the wider red rings; D scales of red rings marked with black; black head cap extending over anterior half or two-thirds of frontal and supraoculars; yellow parietal ring extending from anterior to 1–2 D scales posterior to parietals, but may be suffused with black; black nuchal ring not in touch with parietals, 7–14 D wide, followed posteriorly by a yellow ring; black body rings 9–15; tail with yellow and 3–5 black rings; light rings may become heavily suffused with black.

Coloration in preservative. Similar to that in life, apart from that the yellow and red elements fade with time.

Natural history notes. Venomous. Terrestrial and nocturnal, feeding principally on snakes but also reported to take caecilians, lizards, and the swamp eel *Symbranchus marmoratus.*

Remarks. Based on differences in segmental counts and coloration, Solórzano (2004) elevated the former subspecies of *Micrurus nigrocinctus* to species level. This notion was followed by some authors (e.g., Savage & Bolaños 2009; Jaramillo et al. 2010; Sasa et al. 2010; Wilson & Johnson 2010; Ray & Knight 2013), but not by others as for example Köhler (2008, without any mention of Solórzano's proposal) and Sunyer (2009, based on specimens with intermediate coloration characteristics). In view of the polymorphic populations in NE Honduras, McCranie (2011) did not accept the elevation of *M. mosquitensis* to species level, but believed just as Campbell & Lamar (2004) that several species are involved in what he treated as *M. nigrocinctus.*

The presence of *Micrurus mosquitensis* in my study area is rendered plausible by several specimens collected about 5 km from the study area together with the upper elevational limit reported as 500 m asl for Panama (Jaramillo et al. 2010) and 1500 m for Costa Cica and the species as a whole (Solórzano 2004; Wilson & Johnson 2010; Ray & Knight 2013). The specimen MCZ 22212, listed as *M. n. mosquitensis* and collected at "Bocas del Toro: Panama (Big Trail) [VERBATIM ELEVATION:2500ft]" (= ca. 762 m asl) according to the MCZ catalogue, indicates that the species does occur at premontane elevations in western Panama. Yet, the imprecise locality data prevented me from georeferencing this record, though I consider it to likely come from either the Pianista or Culebra trails, or a trail crossing the divide around La Fortuna.

The exact ubication of the eastern distributional limit of *Micrurus mosquitensis* remains to be identified. The specimens UMMZ 83526 from "Cocoplum, Penins. Valiente" and those collected by Martinez et al. (1995) at Cerro Narices (material now lost; V. Martínez, pers. comm.) were recorded as *M. n. nigrocinctus* and are thus treated as *M. nigrocinctus* herein, suggesting the areal border between the two close relatives to lie somewhere along the Laguna de Chiriquí. However, I regard the species' presence in the Comarca Ngöbe-Buglé (as stated by Ray & Knight 2013) possible, or very likely to be more specific, and can well imagine the species to range east into Veraguas or even further.

***Micrurus multifasciatus* (Jan 1858)**

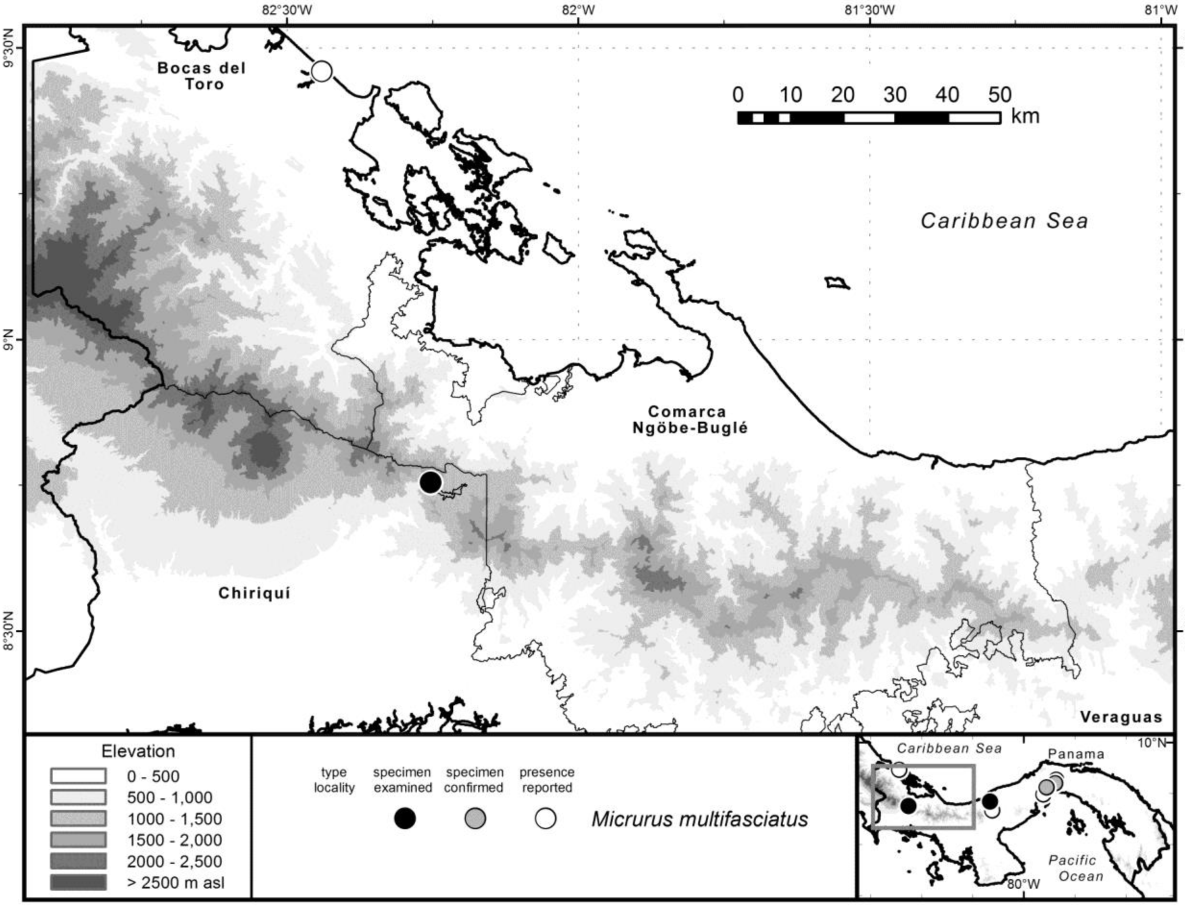
Many-banded Coralsnake; Coral, Coral roja y negra, Coralilla, Coral macho, Gargantilla

Figure 4.113E; Map 4.179.

Holotype. Once at MSNM, destroyed during 2nd World War; from Central America; ZSBS 2268 from Central America: holotype of *Micrurus multifasciatus hertwigi* Werner 1896.

Geographic distribution. Nicaragua to Panama, 0–1600 m asl. In Panama, along both versants in the central and maybe also eastern portions of the country as well as chiefly on the Caribbean versant in western Panama including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from RFLF and PNGDOTH, up to 1230 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1130 or 1200 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings. Among Panamanian *Micrurus* with a bicolor (black and white, yellow, or red) body pattern, *M. multifasciatus* differs from *M. stewarti* in having 40 or more black body rings which are of more or less equal width, each spanning 4–6 dorsals (vs. 21 or fewer black body rings which are usually much wider and of two alternating widths, alternatingly spanning 3–8 and 8–14 dorsals), and from *M. mipartitus* in having supracloacal keels in adult males (vs. absent) and having the light body rings white or red (vs. always white or yellow in Panamanian specimens).



Map 4.179: Distribution of *Micrurus multifasciatus.*

Description. TOL to 1130 or even 1200 mm; tail very short, TL/TOL = 0.06+x*; D smooth except for supracloacal keels in adult males, in 15—15—15 rows; V 233–311; SC 22–38; SPL 7; INL 6–8; loreal 0; Preoc 1; Postoc 2; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round (including data from Taylor 1951).

The hemipenis of *Micrurus multifasciatus* is a bilobed organ without terminal awns.

Coloration in life. Body bicolor, with narrow white, cream, pink, orange, or red rings separating the usually wider (4–6 D) black rings of which there are 40–73; D scales of light rings irregularly marked with black; black head cap usually extending to about level of eyes, separated by a white, cream, pink, orange, or usually red parietal ring that usually covers all of the parietals from the black nuchal ring (4–8 D wide) that does not touch the parietals and is followed posteriorly by a light ring; tail with black and white, cream, pink, orange, or red rings or blotches.

Coloration in preservative. Similar to that in life, apart from that yellow, orange and red shades fade over time. After 4.5 years in 70% ethanol, the formerly orange parietal and tail rings of SMF 90202 have faded to creamy white.

Natural history notes. Venomous. Terrestrial and nocturnal, probably feeding on snakes and/or other elongate vertebrates.

Remarks. This species has formerly been treated as a subspecies of *Micrurus mipartitus,* and accordingly called *M. mipartitus multifasciatus* by earlier authors. Concerning the taxonomic confusion surrounding these names and the CA populations to which they refer, as well as the possible occurrence of a 3rd coralsnake with bicolored body pattern in my study area, see remarks for *M. mipartitus.* As if to provide a nice example of the difficulties in separating these two nominal taxa, the juvenile SMF 90202, collected by FH and JFB on Cerro Guayabo at 1230 m asl, was tentatively identified as *Micrurus multifasciatus* by myself but pictured as *M. mipartitus* by Ray & Knight (2013: p. 100).

Micrurus nigrocinctus (Girard 1855)

Central American Coralsnake; Coral común, Coral centroamericana, Coralilla, Coral macho

Figure 4.113F; Map 4.180.

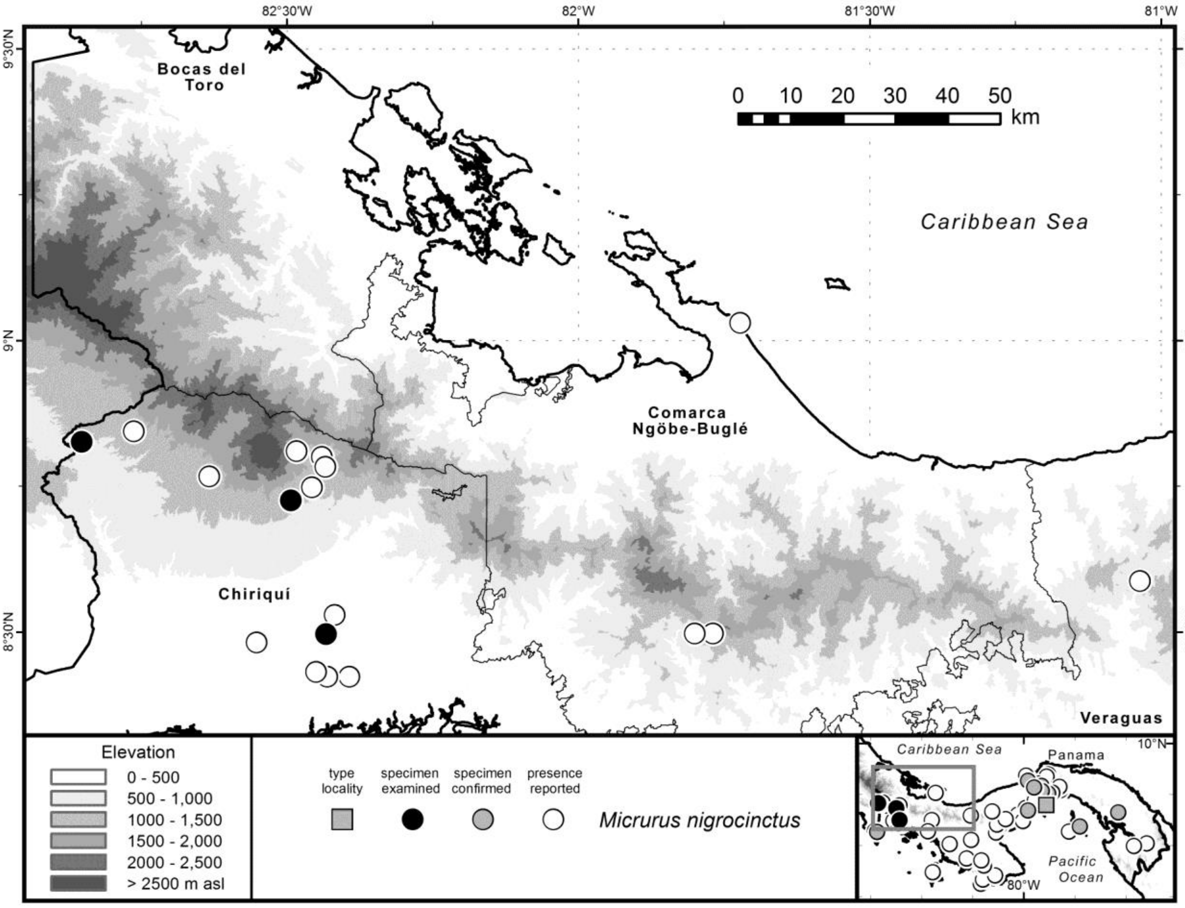
Elaps nigrocinctus: Cope (1860a, 1893).

Micrurus pachecoi: Taylor (1951, 1954).

Syntypes. USNM 7347 (2 specimens), from Taboga Island, Bay of Panama.

Geographic distribution. Mexico to Colombia, 0–2000 m asl. In Panama, along both versants throughout the country except for the extreme western Caribbean versant, including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities up to ca. 1830 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1194 mm) with round pupils is identified as a member of the elapid genus *Micrurus* by its cylindrical body and short tail, head not or only slightly distinct from neck, small black eyes barely discernible within the black head cap, short fangs anteriorly in upper jaw, smooth dorsals without apical pits arranged in 15—15—15 rows, divided cloacal scute, only two scales (postnasal and preocular) between nostril and orbit, and a contrasting pattern of black and light rings. *Micrurus nigrocinctus* is unique among Panamanian *Micrurus* in having a tricolor (white or yellow-black-white or yellow-red) monad pattern with the red rings usually wider than the black rings at midbody and a yellow parietal ring that does not cover all of the parietals, so that either the black head cap or the black nuchal ring or both extend onto parietals. It further differs from the very similar *M. mosquitensis* in having a more narrow black nuchal ring spanning 4–8 dorsal scales (vs. 7–14).



Map 4.180: Distribution of *Micrurus nigrocinctus.*

Description. TOL to 1194 mm; SVL in Honduran specimens to 1078 mm; tail short to moderate, TL/TOL = 0.08–0.17; D smooth except for supracloacal keels in adult males, striate*, in 15—15—15 rows; V 176–230; SC 29–58; SPL 7; INL 7; loreal 0; Preoc 1; Postoc 2–3; Tant 1, Tpost 1–2; cloacal scute divided; AP 0; eyes small, pupil round.

The hemipenis of *Micrurus nigrocinctus* is a bilobed organ with a naked pedicel and thin, enlarged spines; each lobe with a spinulate terminal awn bearing a spine at the tip.

Coloration in life. Body tricolor, with narrow white or yellow rings separating the moderately wide black from the wider red rings; scales of red rings marked with black, often also ventrally; black head cap extending to or onto anterior tips of parietals; narrow white or yellow parietal ring not extending over entire parietals; black nuchal ring often extending onto posterior portions of parietals, 4–8 D wide, followed posteriorly by a white or yellow ring; black body rings 9–24; tail with white or yellow and 3–8 black rings; white or yellow rings may become heavily suffused with red in some populations, may be interrupted on V surfaces of body.

Coloration in preservative. Similar to that in life, apart from that the yellow and red elements fade with time. After 4–4.5 years in 70% ethanol, the formerly red rings have faded to white suffused with light brown dorsally and white ventrally.

Natural history notes. Venomous. Terrestrial, diurnal and nocturnal, feeding largely on snakes but also on other reptiles and amphibians. The female MHCH 2351, found by AH dead on road at Los Algarrobos, contained a juvenile *Liotyphlops albirostris* (MHCH 2348).

Remarks. *Micrurus nigrocinctus* is the most commonly encountered coralsnake in Panama. Future elevations of subspecies to species level may be expected as indicated by Campbell & Lamar (2004).

My georeference for the specimen USNM 297738 from " Cerro Bollo, 3.5 km E of Escopeta Camp" yields a SRTM elevation of 1828 m asl, which is well above the highest elevation of 1600 m previously reported for Panama (Jaramillo et al. 2010).

Family Viperidae Oppel 1811

Atropoides mexicanus (Duméril, Bibron & Duméril 1854)

Central American Jumping Pitviper, Mexican Jumping Pitviper; Mano de piedra, Mano de piedra centroamericana, Toboba, Víbora mano de piedra, Víbora que salta

Figure 4.113G; Map 4.181.

Atropoide nummifer: Carrizo (2000).

Atropoides nummifer or *A. n. mexicanus:* Perez-Santos (1999); Young et al. (1999); Carrizo (2010); Ibáñez et al. (2001); Köhler (2001, 2008); Savage (2002); Castoe et al. (2003: in part.); Hamad (2009); Ray (2009); Stadler (2010).

Bothriopsis mexicanus: Cope (1871).

Bothrops nimmifera: de Sousa (1999).

Bothrops numifer: Myers (1977).

Bothrops nummifer or *B. n. mexicanus:* Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970); Martínez & Rodriguez (1994); Martínez et al. (1995).

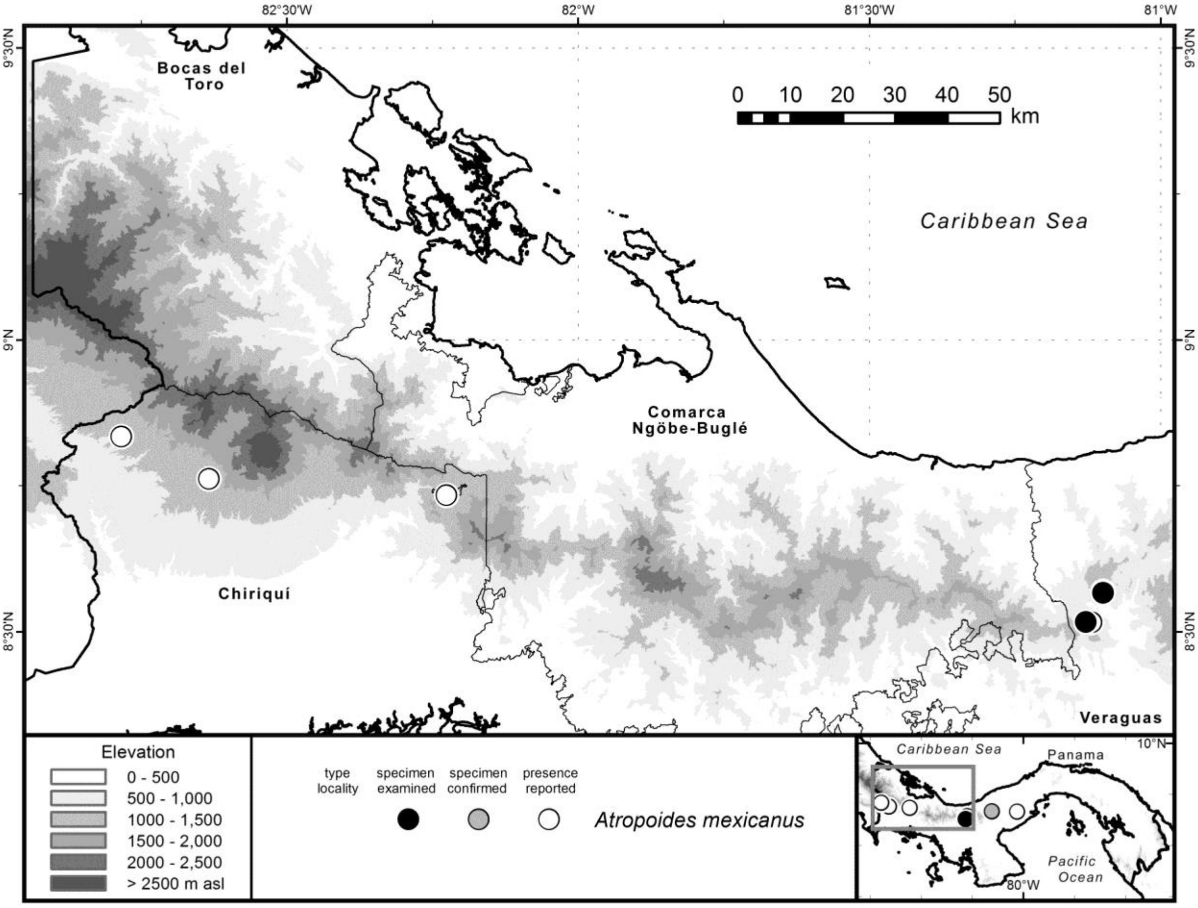
Porthidium nummifer: Auth (1994: in part.).

Trimeresurus nummifer: Dunn & Bailey (1939).

Holotype. MNHN 6712, from Coban, capitale de la province de la Véra-Paz (République de Guatemala, Amérique centrale).

Geographic distribution. Mexico to Panama, 0–1600 m asl. In Panama, along both versants to slightly east of the canal including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and

Veraguas. In the Cordillera Central, reported from the Pacific versant in Chiriquí, the Santa Fé area, PNGDOTH, and Valle de Antón, ca. 650–1390 m asl.



Map 4.181: Distribution of *Atropoides mexicanus.*

Diagnosis. This medium-sized snake (maximum TOL 979 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Atropoides* by its loreal pit, stout habitus, strongly keeled tuberculate dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small imbricate keeled scales and narrow or fragmented supraoculars on the dorsal head surface and a pronounced dark postorbital stripe and diamond-shaped middorsal markings. *Atropoides mexicanus* differs from its only Panamanian congener, *A. picadoi,* in having the rostral plate at least mostly separated from the prenasals by a row of small nasorostral scales (vs. in broad contact, no nasorostrals), the prelacunal separated from the supralabials by 2–3 rows of anterior subfoveals (vs. 1), 135 or fewer ventrals (vs. 138 or more), as well as in being still stouter (vs. not so exceedingly stout).

Description. TOL to 979 mm; SVL to 735 mm*; tail short, TL/TOL = 0.09–0.15; D strongly keeled and tuberculate, giving a very rugose appearance most pronounced on vertebral and paravertebral rows, in (25–33)—(23–31)—(17–23) rows; V 114–135; SC 22–37, most or all unidivided; SPL 8–12; INL 10–14; ISO 5–10; Canths 2–5; SF 2–4; SBO-SPL 2–4; cloacal scute entire; AP 0; eyes small, pupil vertically elliptical.

The hemipenis of *Atropoides mexicanus* is a deeply bilobed organ with long lobes; truncus with few small spinaes basally and many medium to large spines along lobes; apical regions with spinulate calyces.

Coloration in life. D and L surfaces yellow, beige, gray or light to reddish brown, with a middorsal series of rhomboid or diamond-shaped dark brown blotches pointing downwards that may fuse to form a zig-zag pattern and often fuse with the smaller dark brown L blotches or short transverse bars which are arranged below their L tips; still smaller L and ventrolateral blotches along body; dark brown postorbital stripe usually clear-cut, extending to last SPL; D and sometimes L surfaces of head with scattered small dark markings; L surface of head below postorbital stripe lighter gray to brown; V surfaces white to beige, almost immaculate or with heavy brown mottling; SC dark; yellow tail tip in juveniles; some individuals largely black; iris reddish to dark brown.

Leonhard Stadler recorded the adult female SMF 89529 (Fig. 4.113G; Stadler 2010: Fig. A100) as follows (translated from Stadler 2010): D ground color of body and tail Dark Drab (119C) with a pattern of regularly arranged diamond-shaped blotches that have Army Brown (219B) or Natal Brown (219A) centers and are bordered by Sepia (219), becoming darker towards anterior portion of body and tail; laterally, these diamonds are connected to Sepia (219) transverse bars; a Chestnut (32) blotch between each of these bars and the next one; L surface of head posteriorly with two Sepia (219) blotches and two Sepia (219) stripes, the latter extending to eye anteriorly; D surface of head Dark Drab (119C) with a series of four Sepia (219) blotches and mottled with Fawn Color (25), Mikado Brown (121C), and Tawny Olive (223D); V surfaces dirty white, with Chestnut (32) and Sepia (219) blotches below each of the aforementioned L Chestnut (32) blotches, and Chestnut (32) as well as Sepia (219) mottling becoming more dense posteriorly; V surface of head Cream Color (54).

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 89529 is similar to that in life, apart from that the brown diamonds have lost their reddish hue; scales without oberhäutchen in different shades of gray.

Natural history notes. Venomous. Adults obviously terrestrial, but juveniles have been found in arboreal situations. Diurnal and nocturnal, feeding mainly on rodents which it holds on to after striking, but as juveniles also on lizards, frogs, and invertebrates. The specimen SMF 89918 was encountered by AC while lying coiled up next to a treetrunk on a pasture at Cerro Negro, and SMF 89529 staged a strike when startled from beneath a prop root around 14:30 before being collected by LS and NH.

Remarks. This former subspecies of *Atropoides nummifer* was molecularly shown to comprise a distinct lineage by Castoe et al. (2003) and morphollogically confirmed by Jadin et al. (2010a). Campbell and Lamar (2004) and Solórzano (2004) were the first to explicitly use the combination *A. mexicanus,* which today is widely accepted.

My dataset lacks discrete locality records underlying the listings of this species for the former Canal Zone or the highlands of E Panama (Auth 1994; Campbell & Lamar 2004; probably all based on the head reported by Dunn & Bailey 1939 from the Pequení-Esperanza ridge) as well as the maximum elevation of 1600 m asl in Panama (Jaramillo et al. 2010), though the latter value seems plausible to me. Together with the distribution in Costa Rica (Savage 2002; Solorzano 2004), the records from Coclé and the Santa Fé area, especially from Cerro Mariposa about 4 km from the Comarca's border, render the species' presence in the Comarca Ngöbe-Buglé and Bocas del Toro plausible.

***Atropoides picadoi* (Dunn 1939)**

Picado's Jumping Pitviper; Víbora mano de piedra, Mano de piedra, Mano de piedra costarricense

Figure 4.113H; Map 4.182.

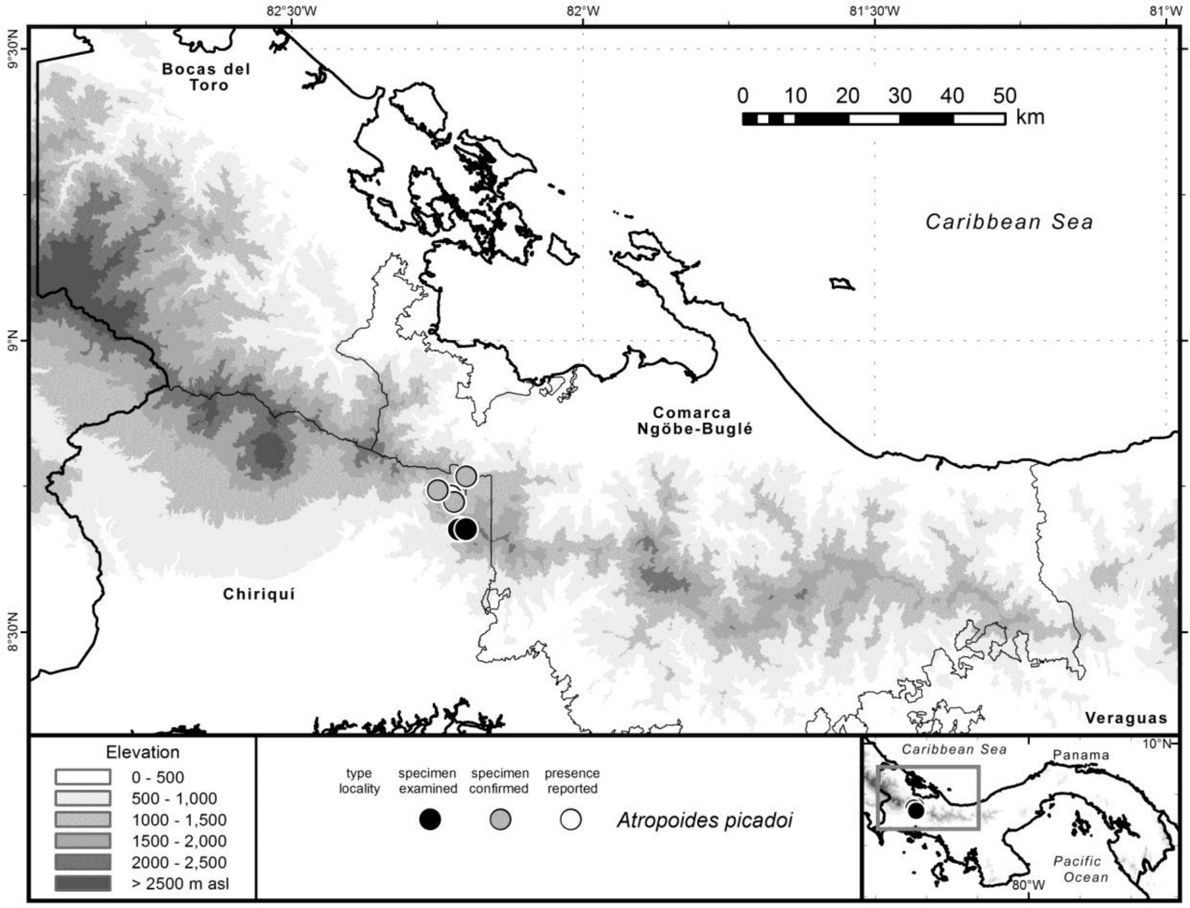
Bothrops picadoi: Taylor (1951, 1954); Peters & Orejas-Miranda (1970); Martínez (1983); Solís (1991); Martínez & Rodriguez (1994); de Sousa (1999).

Porthidium picadoi: Auth (1994).

Holotype. USNM 37753, from La Palma, Costa Rica, 4500 feet (= ca. 1372 m asl).

Geographic distribution. Costa Rica and Panama, 300–2000 m asl. In Panama, probably along both versants of at least extreme western Panama including Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé, but hitherto only reported from the Pacific versant of the Cordillera Central at RFLF, 1000–1650 m asl.

Diagnosis. This medium-sized snake (maximum TOL 1250 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Atropoides* by its loreal pit, stout habitus, strongly keeled tuberculate dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small imbricate keeled scales and narrow or fragmented supraoculars on the dorsal head surface and a pronounced dark postorbital stripe and diamond-shaped middorsal markings. *Atropoides mexicanus* differs from its only Panamanian congener, *A. mexicanus,* in lacking nasorostrals and thus having the rostral plate in broad contact with the prenasals (vs. at least mostly separated by a row of small nasorostrals), the prelacunal separated from the supralabials by 1 row of anterior subfoveals (vs. 2–3), 138 or more ventrals (vs. 135 or fewer), as well as in being less stout (vs. exceedingly stout).



Map 4.182: Distribution of *Atropoides picadoi.*

Description. TOL to 1250 mm; SVL to 1030 mm*; tail short, TL/TOL = 0.09–0.12; D strongly keeled, tuberculate, giving a very rugose appearance not more pronounced on vertebral and paravertebral rows, in (25–27)—(23–29)—(19–21) rows; V 138–155; SC 30–40, most undivided but some divided; SPL 8–12; INL 9–13; ISO 7–12; Canths 2*; SF 1; SBO-SPL 2*; cloacal scute entire; AP 0; eyes small, pupil vertically elliptical.

The hemipenis of *Atropoides picadoi* is a deeply bilobed organ with long lobes; truncus with few small spinaes basally and many medium to large spines along lobes; apical regions with spinulate calyces (Jadin et al. 2010a).

Coloration in life. D and L surfaces yellow, beige, gray or light to reddish brown, with a middorsal series of rhomboid or diamond-shaped dark brown blotches pointing downwards that may be partially light-edged, may fuse to form a zig-zag pattern, and are separated by light pigment from, or fuse with, the smaller dark brown L blotches or short transverse bars which are arranged below their L tips and may be partially light-edged; still smaller and less pronounced L and ventrolateral blotches along body; D surface of head dark brown with symmetrical dark nuchal markings; dark brown postorbital stripe usually clear-cut, extending to last SPL, often with a narrow light upper border posteriorly; L surface of head below postorbital stripe whitish to light gray or brown, often with more or less diffuse a dark subocular and a dark subfoveal blotch; yellow tail tip in juveniles; tail of some adults largely black; V surfaces white to yellow brown, except for diffuse dark blotches on chin almost immaculate anteriorly, with heavy dark brown mottling increasing towards tail; SC completely dark; iris reddish to dark brown.

Coloration in preservative. After 4.5–6 years in 70% ethanol, the coloration of my two examined specimens from RFLF is similar to that in life, apart from that scales which lost their oberhäutchen are gray rather than brown.

Natural history notes. Venomous. Terrestrial, diurnal and nocturnal, feeding mainly on rodents which it holds on to after striking, but as juveniles also on lizards, frogs, and invertebrates. The specimen SMF 89759 was moving over the forest ground at 17:00. An uncollected specimen was coiled up on a gravel bank in a small stream at 12:45. The large male SMF 90170 was found by FH and JFB lying on the ground around 13:40. *Atropoides picadoi* is quite common between the Lost & Found Ecohostel and Cerro Pata de Macho, and especially around Río Hornito frequently seen by hiking hostel guests.

Remarks. My dataset lacks discrete locality records underlying the listings of this species for western Bocas del Toro (Auth 1994), but I consider the species presence in this province and in the Comarca Ngöbe-Buglé plausible in view of the records from RFLF (partially < 1 km from the Comarca's border) and the records from the Caribbean slopes in Costa Rica (Savage 2002; Solórzano 2004; the Caribbean lowland records plotted on Map 11.122 of the former author as well as the corresponding lower elevational limit of 15 m asl are probably based on erroneous locality data according to the latter author). I could not trace any record substantiating the lower elevational limit of 750 in Panama given by Perez-Santos (1999), the lowest records being those from "Fortuna, 1000 m" (Perez-Santos 1999) and Quebrada Arena (Martínez 1983: 1050 m fide Solís 1991). SMF 89759 was collected at 1650 m, which is about 450 m above the highest record for this species in Panama given as 1200 m by Jaramillo et al. (2010) and inferred from the SRTM elevation corresponding to the coordinates of Solís (1991).

With a TOL of 1145+x mm (1030 mm SVL + 115+x mm TL), SMF 90170 is the largest individual of this species reported from Panama and one of the largest reported for the species (Solís 1991; Campbell & Lamar 2004). In the specimen SMF 89759, 13 of the 34 SC are divided.

Bothriechis lateralis Peters 1863

Side-striped Palm-Pitviper; Lora, Víbora

Figures 4.114A, B; Map 4.183.

Bothrops lateralis: Dunn (1947); Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970).

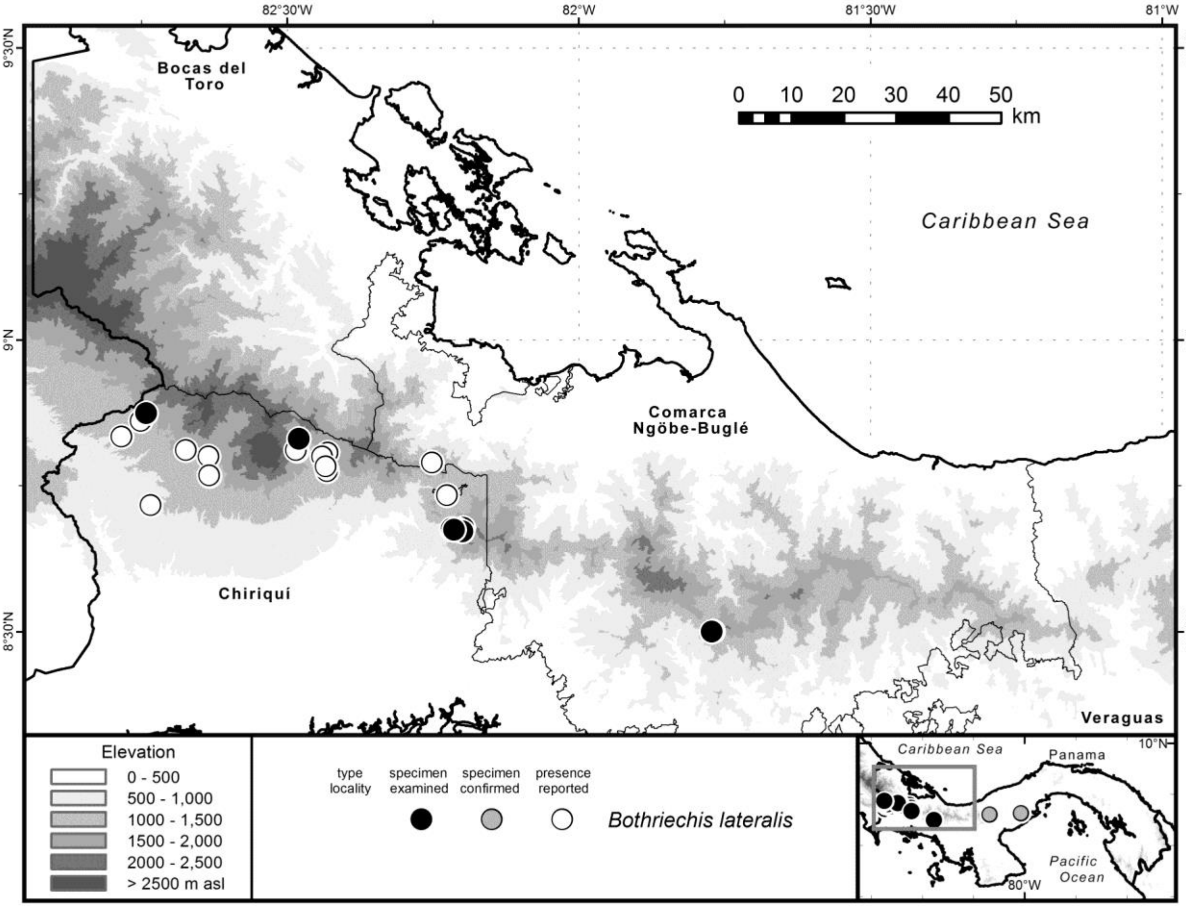
Bothrops bilineatus: Peters (1859).

Bothrops sp.: Myers (1977: possibly).

Trimeresurus lateralis: Dunn (1940); Slevin (1942).

Syntypes. ZMB 2979 (2 specimens), 2980, and 2981, from "Costa Rica vom Vulcan Barbo" and "Veragua" (Peters 1863c).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 500–2500 m asl. In Panama, throughout the Cordillera Central along both versants, including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, where it has been reported from the Pacific slopes of the Serranía de Talamanca, BPPS, RFLF, La Nevera, PNGDOTH, and Valle de Antón, 500–2130 m asl.



Map 4.183: Distribution of *Bothriechis lateralis.*

Diagnosis. This medium-sized snake (maximum TOL > 1000 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Bothriechis* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small imbricate keeled scales and enlarged smooth supraoculars on the dorsal head surface, and a prehensile tail. *Bothriechis lateralis* is unique among Panamanian pitvipers in having a conspicuous light ventrolateral stripe throughout the body at all ages.

Description. TOL to > 1000 mm; SVL to 735 mm*; tail moderate, TL/TOL = 0. 14–0.19; D keeled, in (21–25)*—(21–25*)—(16–19)* rows; V 155–173; SC 53–70, mostly undivided but some divided; SPL 8–12; INL 10–13; ISO 4–10; Canths 2; SF 0 due to fusion of 2nd SPL with prelacunal; SBO-SPL 0*; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Bothriechis lateralis* is a deeply bilobed organ with long lobes with enlarged basal spines and papillate calyces in the apical region.

Coloration in life. Adults (Fig. 4.114A): D and L surfaces yellowish, bluish, or bright green, unicolor or with irregular, often dark-edged, short white to yellow dorsolateral crossbars; a usually diffuse bluish postorbital stripe; V surfaces as well as L surfaces of head below postorbital stripe immaculate yellowish to light green; iris yellowish green, with dark spottings and/or reticulations; juveniles (Fig. 4.114B): D and L surfaces light to medium, reddish, or yellowish brown, unicolor or with irregular, often dark-edged, short white to yellow dorsolateral crossbars and/or irregular darker brown mottling; a usually diffuse darker brown postorbital stripe; V surfaces as well as L surfaces of head below postorbital stripe light brown spotted with darker brown; tail tip yellowish green; iris bronze, with dark spottings and/or reticulations; a conspicuous light (white, yellow, yellowish light green) ventrolateral stripe along and 1st D row, often including tips of V, present on each side at all ages.

The female MHCH 2298 was recorded as follows: D ground color Parrot Green (60), grading into Apple Green (61) laterally and into Shamrock Green (162) towards tip of tail; V surface of head Opaline Green (162D); a dirty white ventrolateral stripe covering the tips of V and 1st D row, respectively; a Spectrum Green (62) postorbital stripe present; iris Citrine (51).

Coloration in preservative. After 5–8 years in 70% ethanol, my examined specimens still retain their green coloration to a certain extent, though it has become variably suffused with blue and/or brownish hues.

Natural history notes. Venomous. Nocturnal and arboreal, juveniles presumedly terrestrial. Juveniles feed on lizards and frogs, adults chiefly on small mammals and birds. Also present in cultivated areas such as coffee plantations. All individuals were found at night in vegetation, either coiled up or moving along branches or fronds of tree ferns, between 0.5 (juvenile SMF 89762) and ca. 5 m (male SMF 89533) above ground.

Remarks. The specimen SMF 89532 has 25 D-MB, which is the highest value reported for this species so far.

I am unaware of any discrete record substantiating the upper elevational limit given as 2134 m asl for Panama (Jaramillo et al. 2010), but consider this value plausible in view of the altitudinal distribution as documented by recent authors (Sasa et al. 2010; Ray & Knight 2013). The highest Panamanian record which I can personally confirm is 1752 m on the W slope of Cerro Pata de Macho, where I found the specimen shown in Fig. 4.114A. Recently, Griffith et al. (2008) provided the easternmost as well as the lowest confirmed records (500 m) for the species.

In the original description (Peters 1863c), two localities are mentioned as the provenances of the type material: "Costa Rica vom Vulcan Barbo" can unequivocally be interpreted as Volcán Barva, Costa Rica. The other locality is merely given as "Veragua" and has been interpreted as "Veraguas, Panama" by Campbell & Lamar (2004) and Uetz & Hošek (2014). However, as depicted above (see chapter 1.3 and references therein), in the 19th century the term "Veragua" could mean any place in western Panama. I was unable to trace any record substantiating the presence of this species in Veraguas province as reported by Auth (1994), Campbell & Lamar (2004), and Griffith et al. (2008). I thus assume that these author's records are based on Peters' (1863c) imprecise locality name. Nevertheless, the records from E and W of Veraguas render the species' presence therein plausible, just as its presence in Bocas del Toro is rendered plausible by the records from Caribbean Costa Rica (Savage 2002) and the Comarca Ngöbe-Buglé (Hofer & Bersier 2001) as well as the distance of < 5 km of the numerous records from the Boquete area to the border of that province. According to Köhler (2001) and Sunyer (2009), there are no confirmed records to substantiate the presence of this species in Nicaragua, for which it is not listed by Wilson & Johnson (2010).

***Bothriechis nigroviridis* Peters 1859**

Black-speckled Palm-Pitviper; Toboba de árbol, Lora, Víbora

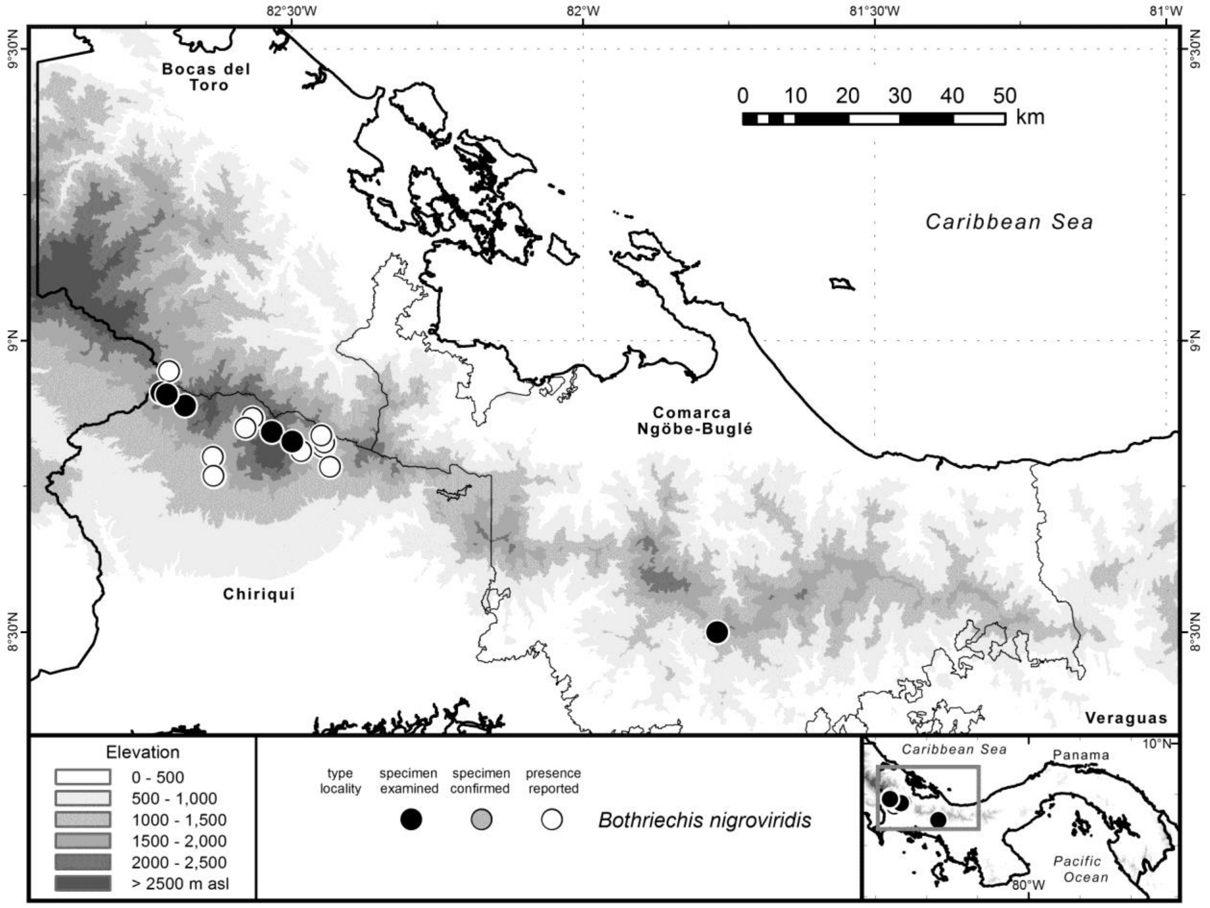
Figure 4.114C; Map 4.184.

Bothrops nigroviridis: Wettstein (1934); Dunn (1947); Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970: in part., referring to the nominal subspecies).

Trimeresurus nigroviridis: Dunn (1940).

Syntypes. ZMB 2986–2988, from "Vulcan von Barbo" (= Volcán Barva, Costa Rica) (Peters 1859).

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 700–3000 m asl. In Panama, along both versants of the Cordillera Central east to Cerro Santiago, including Bocas del Toro, Chiriquí, and the Comarca Ngöbe-Buglé. Reported from numerous sites along the Pacific slopes of the Serranía de Talamanca and from the Caribbean slopes at Cerro Pando and La Nevera, 1220–2540 m asl.



Map 4.184: Distribution of *Bothriechis nigroviridis.*

Diagnosis. This medium-sized snake (maximum TOL 950 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Bothriechis* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, enlarged smooth supraoculars, and a prehensile tail. *Bothriechis lateralis* is unique among Panamanian pitvipers in having the anterior dorsal head surface mostly covered by large smooth scales, as well as green upper surfaces heavily mottled with black.

Description. TOL to 937 mm; SVL to 457 mm*; tail moderate, TL/TOL = 0. 15–0.20; D keeled, in 21*—(17–21)—(15–17)* rows; V 134–162; SC 44–62, mostly undivided but often some divided; SPL 7–11; INL 8–12; ISO 3–9; Canths 2; SF 0, but 2nd SPL usually not fused with prelacunal; SBO-SPL 0–1*; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Bothriechis nigroviridis* is a deeply bilobed organ with long lobes, with enlarged basal spines and papillate calyces in the apical region.

Coloration in life. D and L surfaces yellowish green to dark green, heavily mottled and spotted with black, and with dark skin between the D scales; a black postorbital stripe sometimes diffuse and/or obscured by nearby mottling; D surface of head often with more or less symmetrical, large black markings; L surface of head and V surfaces green, similar to L ground color or somewhat lighter, with sparse black spotting; tail tip sometimes blackish; iris yellowish but usually so densely spotted and/or reticulated with black that it appears black.

Coloration in preservative. After 4.5–8 years in 70% ethanol, my examined specimens still retain their green coloration to a certain extent, though it has become variably suffused with blue.

Natural history notes. Venomous. Nocturnal and arboreal, feeding on small vertebrates. Usually absent from cultivated areas such as coffee plantations, but occasionally encountered on patches of open secondary vegetation between forest parcels. All specimens were encountered at night. The young male SMF 89534 was spotted by LS while lying on the petiolus of an aracean epiphyte about 3 m above ground, and the juvenile SMF 90174 was discovered by AU moving along vegetation about 0.7 m above ground. Marciano Montezuma found and killed MHCH 2299 on the dirt road just below the finca at Jurutungo, and FH and JFB almost stepped on SMF 90173 that was crossing a pasture at Paso Respingo.

Remarks. The male SMF 89534 has only 3 ISO, which is the lowest value reported for this species. Only 2 of the 5 specimens for which I recorded pholidotic data have all SC entire, while one has singular scattered, one only the distalmost, and one the distalmost 8 SC divided.

The minimum elevation of about 1220 m asl given by Dunn (1947) for the records from Boquete is somewhat below the elevational range of 1394–2000 m reported for this species in Panama (Jaramillo et al. 2010). The specimen SMF 90173 was collected slightly above Paso Respingo at 2538 m, which is the highest elevation reported for this species in Panama. The specimen from La Nevera extended the documented range of this species about 80 km ESE and into the Comarca Ngöbe-Buglé (Lotzkat et al. 2010c).

According to Sunyer (2009), there are no confirmed records to substantiate the presence of this species in Nicaragua, for which it is not listed by Wilson & Johnson (2010).

Bothriechis schlegelii **(Berthold 1845)**

Eyelash Viper, Eyelash Palm-Pitviper, Oropel; Bocaracá común, Oropél, Pestañosa, Tamagá, Toboba de pestañas, Víbora oropel, Víbora de pestañas

Figures 4.114D, E; Map 4.185.

Bothrops schlegeli: Smith (1958); Myers (1969a).

Bothrops schlegelii: Wettstein (1934); Taylor (1951, 1954); Smith (1958); Myers & Rand (1969); Peters & Orejas-Miranda (1970); Rand & Myers (1990); Martínez & Rodriguez (1994).

Bothrops schlegelli: de Sousa (1999).

Bothrops sp.: Myers (1977: possibly).

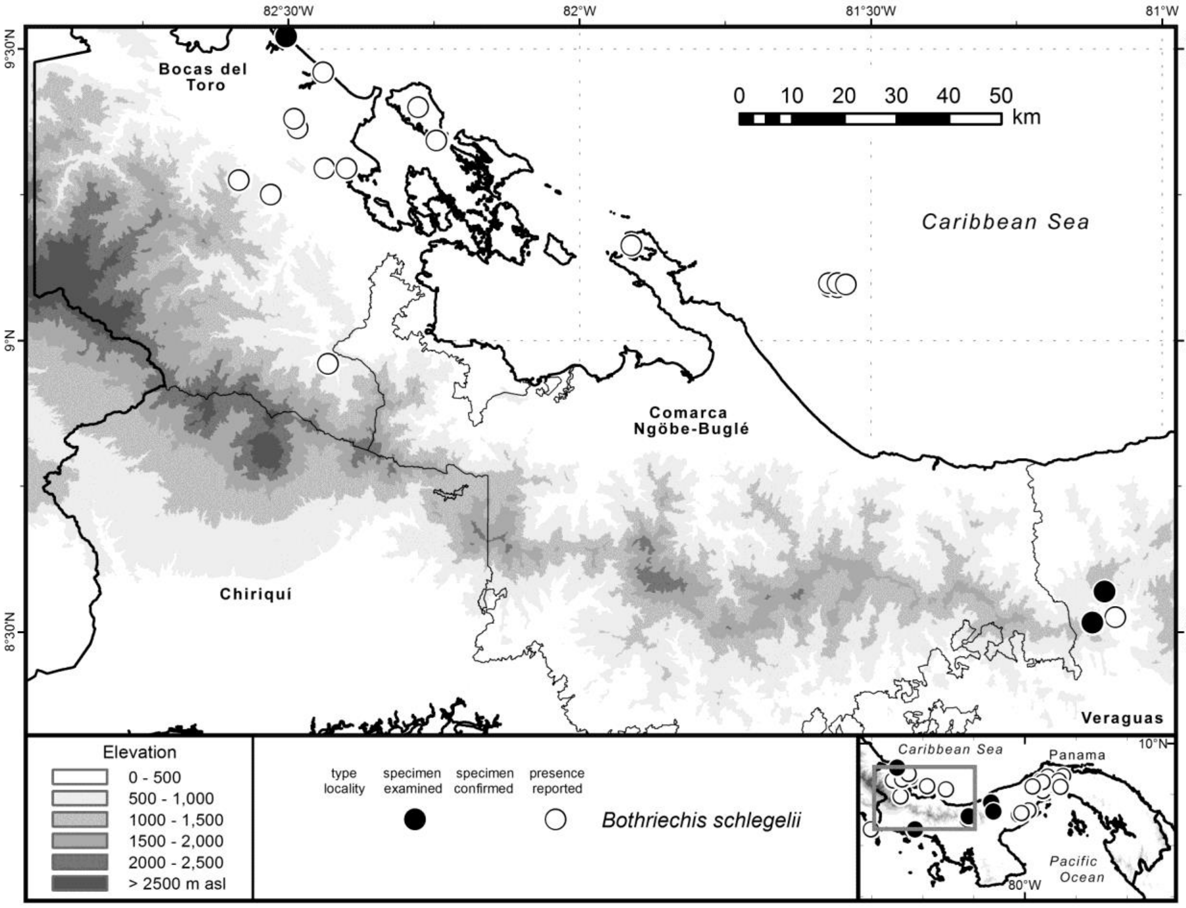
Teleurapsis schlegelii: Cope (1860a, 1876).

Trigonocephalus Schlegelii: Berthold (1845).

Trimeresurus schlegelii: Dunn & Bailey (1939).

Holotype. ZFMK 32554, from Popayan, western Colombia.

Geographic distribution. Mexico to Colombia, Peru, and Venezuela, 0–1530 m asl (to 2640 m asl in Colombia). In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, except for premontane elevations in Chiriquí. In the Cordillera Central, reported from the Caribbean foothils in Bocas del Toro, the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to ca. 910 m asl.



Map 4.185: Distribution of *Bothriechis schlegelii.*

Diagnosis. This medium-sized snake (maximum TOL 950 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Bothriechis* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small keeled scales and enlarged smooth supraoculars on the dorsal head surface, and a prehensile tail. *Bothriechis schlegelii* differs from all Panamanian pitvipers except *B. supraciliaris* in having 1–3 spine-like supraciliary scales above each eye. It differs from *B. supraciliaris* in being completely yellow ("oropél" morph) or having a pattern of diffuse mottling or of diffuse, irregularly shaped markings with usually extensive additional dark mottling and spotting (vs. oropél morph virtually absent, usually a pattern of well-defined dark paravertebral blotches that are partly offset but become opposed and fuse to form middorsal blotches at least posteriorly, with little or no additional dark mottling and spotting), and in having extensive dark pigmentation throughout the venter in adult specimens which are not of the oropél morph (vs. very little or no dark pigmentation on midventer at least anteriorly).

Description. TOL to 950 mm; SVL in Honduran specimens to 691 mm; tail moderate, TL/TOL = 0. 13–0.19; D keeled, in (21–27)—(21–25)—(17–21) rows; V 137–169; SC 42–64, mostly undivided but some divided; SPL 7–10; INL 8–13; ISO 3–8; Canths 2–3*; SF 0*, due to 2nd SPL fused with prelacunal; SBO-SPL 1–2*; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Bothriechis schlegelii* is a deeply bilobed organ with long lobes with enlarged basal spines and papillate calyces in the apical region.

Coloration in life. Exceedingly variable: Yellow, orange, or pink "oropél" morph immaculate or with scattered, usually diffuse darker mottling or suggestions of blotches; otherwise D and L ground color green, gray, olive, or brown (each in every possible shading) with irregular, often ill-defined and diffuse, paravertebral and/or L markings in the form of straight or curved short bars, and spotting and/or mottling in virtually any color; a sometimes diffuse postocular stripe; D surfaces of head usually with more or less symmetrical small dark markings similar to those on body, including two blotches on snout that may be in contact; V surfaces nearly immaculate in oropél morphs and juveniles, heavily marked with darker pigment otherwise; iris yellow to beige or brown, spotted with dark.

The juvenile SMF 90175 was recorded as follows: D and L ground color Spectrum Yellow (55) with a suggestion of Buff-Yellow (53), with two series of Clay Color (123B) paravertebral blotches extending from head to tip of tail; V surfaces Chamois (123D), edges of most V with Cinnamon (123A) blotches; iris Tawny Olive (223D).

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 90175 is very similar to that in life. After 4.5 years in 70% ethanol, the coloration of the oropél juveniles from San San Pond Sak, that were bright yellow in life, is almost unchanged.

Natural history notes. Venomous. Nocturnal and arboreal, feeding on small vertebrates. Three juveniles were encountered at night in vegetation, whereas AC found SMF 89922 in the leaf litter around 20:15.

Remarks. Singular SC are divided in 3 of the 5 specimens whose pholidotic data I recorded. I agree with Campbell & Lamar (2004) in that the value of 33 SC given by Solórzano et al.

(1998) must be based on a truncated tail, since it has not been reproduced by any other author including Solórzano (2004) himself.

This overwhelmingly variable snake is one of the most prominent, widely known species of CA herpetofauna. Simultaneously, the nominal taxon *Bothriechis schlegelii* is a typical case of a "well-known" species that is in fact surrounded by largely unsolved taxonomic incongruencies. The revalidation of *B. supraciliaris* (Solórzano et al. 1998; see remarks for that species.) has apparently just been the tip of the iceberg, since several studies (Wüster et al. 2002; Daza et al. 2010; Townsend et al. 2013) found deep genetic divergences between populations currently referred to *Bothriechis schlegelii* from CA (a single specimen in the case of the former two studies, three individuals from Honduras, Nicaragua, and Costa Rica in the case of the latter authors) and those from Ecuador. A range-wide integrative taxonomic analysis of this species complex involving as many specimens from throughout its range as possible is sorely needed. Since the type material of *B. schlegelii* is from Colombia, one result of such study might be the need for a new name to be applied to the CA populations.

Bothriechis supraciliaris **(Taylor 1954)**

Blotched Palm-Pitviper, Eyelash Palm-Pitviper, Eyelash Viper; Bocaracá manchada, Pestañosa, Toboba de pestañas, Víbora de pestañas

Figure 4.114F; Map 4.186.

Bothrops schlegelii or *B. s. supraciliaris:* Wettstein (1934); Taylor (1951, 1954); Smith (1958: in part.).

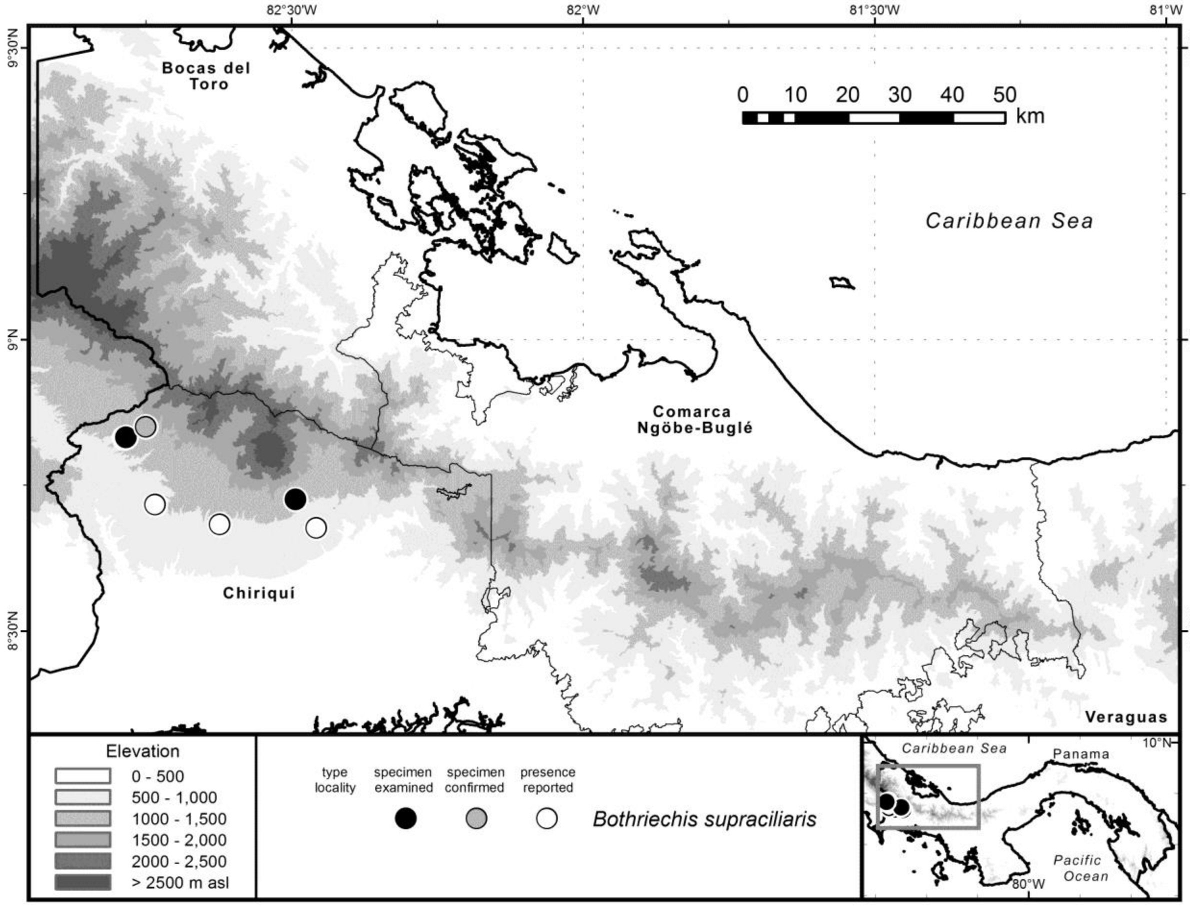
Bothriechis schlegelii or *B. s. supraciliaris:* Auth (1994: in part.); Perez-Santos (1999: in part.); Young et al. (1999: in part.); Ibáñez et al. (2001: in part.); Savage (2002: in part.); Fundación PA.NA.M.A. (2007: in part.); Santos-Barrera et al. (2008); Hamad (2009: in part.); Carrizo (2010: in part.); Stadler (2010: in part.).

Bothrops supraciliaris: Peters & Orejas-Miranda (1970).

Holotype. KU 31997, from "mountains near San Isidro del General, San José Province, Costa Rica (Taylor 1954).

Geographic distribution. Endemic to the Pacific slopes of the Talamancan highlands in Costa Rica and Panama, 610–1700 m asl. In Panama, reported from premontane elevations along the Pacific slopes of the Serranía de Talamanca in Chiriquí, 610–1300 m asl.

Diagnosis. This medium-sized snake (maximum TOL 800 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Bothriechis* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small keeled scales and enlarged smooth supraoculars on the dorsal head surface, and a prehensile tail. *Bothriechis supraciliaris* differs from all Panamanian pitvipers except *B. schlegelii* in having 1–3 spine-like supraciliary scales above each eye. It differs from *B. schlegelii* in usually exhibiting a pattern of well-defined dark paravertebral blotches that are partly offset but become opposed and fuse to form middorsal blotches at least posteriorly, with little or no additional dark mottling and spotting laterally (vs. a pattern of diffuse mottling or of diffuse, irregularly shaped markings with usually extensive additional dark mottling and spotting, or oropél morph being completely yellow), and in having very little or no dark pigmentation on midventer at least anteriorly in adult specimens (vs. extensive dark pigmentation throughout the venter which are not of the oropél morph).



Map 4.186: Distribution of *Bothriechis supraciliaris.*

Description. TOL to 800 mm; SVL to 514 mm*; tail moderate, TL/TOL = 0.15–0.16*; D keeled, in (23–26)—(21–23)—(18–19) rows; V 139–150; SC 45–54, mostly undivided but some divided; SPL 8–10; INL 10–12; ISO 4–8; Canths 3*; SF 0*, due to 2nd SPL fused with prelacunal; SBO-SPL 2*; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Bothriechis supraciliaris* remains undescribed, but probably is rather similar to that of *B. schlegelii.*

Coloration in life. Very variable. D and L surfaces yellow, orange, green, gray, bluish, olive, or brown; usually with rather regular, body and tail with well-defined and usually well-demarcated rounded, rhomboid, or elongate paravertebral blotches in any other color that are offset and/or (usually at least on posterior portions of body as well as on tail) opposed and fuse on middorsum to form middorsal blotches, with little or no additional dark mottling and spotting laterally; a sometimes diffuse postocular stripe; D surfaces of head usually with symmetrical large dark markings similar to those on body, including a single blotch on snout; V surfaces nearly immaculate in juveniles and with very little or no dark pigmentation on midventer at least anteriorly in adults; iris gray or brown to reddish brown, spotted with dark.

The juvenile SMF 89764 was recorded as follows: D ground color Sayal Brown (223C), grading into Tawny Olive (223D) laterally, with two series of Raw Umber (223) blotches diffusely bordered by Sepia (219), partly meeting on middorsum to suggest a zig-zag pattern; head dorsally with markings of the same color; V ground color Vinaceous Pink (221C), grading into Light Russet Vinaceous (221D) towards head and finely spotted with Sepia (119); 1st D row, tips of V and 2nd D row mottled with Walnut Brown (221B) and dirty white with a suggestion of Cream Color (54); iris Beige (219D).

Coloration in preservative. After 4–5 years in 70% ethanol, the coloration of the juvenile specimens is similar to that in life, apart from that both assumed a more grayish ground color; the formerly green ground color of the adult female SMF 89763 has changed to bluish gray, and its formerly reddish brown D blotches and postocular stripe have lost their reddish hue.

Natural history notes. Venomous. Nocturnal and largely arboreal, reported to feed on small rodents. Many individuals have been found on or near the ground. The female SMF 89763 was encountered around 23:15 a few meters from Río Cochea as it was hanging from low vegetation, the tail securing a sapling trunk about 0.5 m above ground and the head hanging at about half of that height and looking downwards. The two juveniles from Santa Clara were found on higher perches, MHCH 2301 while it was crawling over a Cyclanthacean leaf 2 m above ground, and SMF 89764 on the frond of a tree fern ca. 1 m above ground, next to a small creek. The latter juvenile was in the process of swallowing an already motionless, comparatively large *Craugastor fitzingeri* (field number AH 253) from behind, which it regurgitated in the collecting bag.

Remarks. *Bothriechis supraciliaris* has been reported for Panama by DeJesus (2007) from Finca Hartmann at 1300 m asl. The specimen SMF 89763 from Cochea extends the species' distribution slightly more than 30 km ESE from Finca Hartmann. The records of Batista et al. (in prep. b) come from about 23 km SE and 38 km ESE of Finca Hartmann, as well as from elevations down to 900 m. My georeference of the specimens MVZ 35569–80 from "16 mi W

Potrerillos", which I assume to represent this species rather than *B. schlegelii* as their catalogue entries suggest, yields a SRTM elevation of 610 m. This value is well below the lower elevational limit of 800 m reported by all authors since Solórzano (2004), far below the 1300 m given as the sole Panamanian elevation by Jaramillo et al. (2010), and further increases the theoretical range overlap between the two species. Still, the range of *B. supraciliaris* is only vaguely known and, just as the merely postulated allopatry of the two species, should be ascertained by targeted field surveys, if only for the benefit of evaluating the species' conservation status. However, its range map given by Ray & Knight (2013, range extending to Pacific ocean throughout E Puntarenas and W Chiriquí) strongly contradicts the notion that its sister species *B. schlegelii* inhabits the lowlands of the Golfo Dulce region (Campbell & Lamar 2004; Solórzano 2004).

While the genetic distinctness of *Bothriechis supraciliaris* from CA and SA populations referred to *B. schlegelii* has been confirmed by several authors (e.g., Wüster et al. 2002; Castoe et al. 2009; Townsend et al. 2013), the morphological distinctions between these species remain somewhat obscure. In my tiny sample from Panama, the 3 examined specimens of Panamanian *B. supraciliaris* (139–148 V; 46–50 SC; 185–198 V+SC), appear well separated from the 5 *B. schlegelii* (149–162 V; 55–61 SC; 204–217 V+SC). But these differences in segmental counts, just as those given by Solórzano et al. (1998), blur when compared with the more inclusive ranges given for *B. schlegelii* by other authors, while it is on the one hand not necessarily clear if these ranges might include specimens actually referable to *B. supraciliaris,* and on the other hand out of question that *B. schlegelii* as currently understood comprises at least 2 lineages meriting specific recognition whose distribution is unknown and morphology uncompaired. Only comprehensive study of the segmental counts in eyelash *Bothriechis* all around the LCA highlands can eventually assess how well these taxa are differentiable on the basis of these characters. A better tool for species identification seems to be the coloration, even though the overwhelming variation found in both nominal species around the Talamancan highlands (Fig. 4.114F; Campbell & Lamar 2004: plates 395–421; Solórzano 2004: Figs. 248–266; McConnell 2014: Figs. 478–519) requires some time to figure out the pattern differences which I regard to be most diagnostic in the specificity of the large D markings. Then, the common name "Blotched Palm-pitviper" makes sense for many or most individuals of *B. supraciliaris* as apposed to the rather mottled or streaked *B. schlegelii.* On the contrary, I found the differences in D and V mottling or "secondary pigmentation" (Solórzano et al. 1998; Solórzano 2004) not too helpful since the two oropél juveniles from San San Pond Sak have nearly immaculate V surfaces, MVUP 390 from coastal Chiriquí has a rather immaculate anterior venter, and the female *B. supraciliaris* from Cochea does have certain amounts of darker mottling or speckles on the D surfaces. Clutching at the straw of coloration, I could not help realizing that in the above mentioned figures as well as those of Solórzano et al. (1998), Savage (2002), Köhler (2008), and Ray & Knight (2013), as well as in my examined specimens, all contrastingly marked *B. supraciliaris* have a single anteriormost D blotch centrally on the snout, whereas all contrastingly marked *B. schlegelii* have two paramedian blotches that may touch each other or be fused to form a short transverse band, but nevertheless remain discernible. This difference also seems to hold between the *B. supraciliaris* and the rather similarly blotched *B. schlegelii* from South America pictured by Campbell & Lamar (2004: plates 404–421). Yet, its possible usefulness as a "countable" coloration character can only be confirmed in a much needed thorough integrative taxonomic study of the eyelashed pitvipers throughout their range.

Bothrops asper **(Garman 1884)**

Lancehead, Terciopelo, Fer-de-Lance; Bocaracá, Equis, Barba amarilla, Terciopelo, Toboba real, Rabo amarillo

Figure 4.114G; Map 4.187.

Bothrops atrox or *B. atrox asper:* Cope (1860a: in part., 1871, 1876); Dunn (1933); Swanson (1945); Breder (1946); Taylor (1951, 1954); Smith (1958); Myers & Rand (1969); Rand & Myers (1990)

Bothrops xanthogrammus: Peters & Orejas-Miranda (1970).

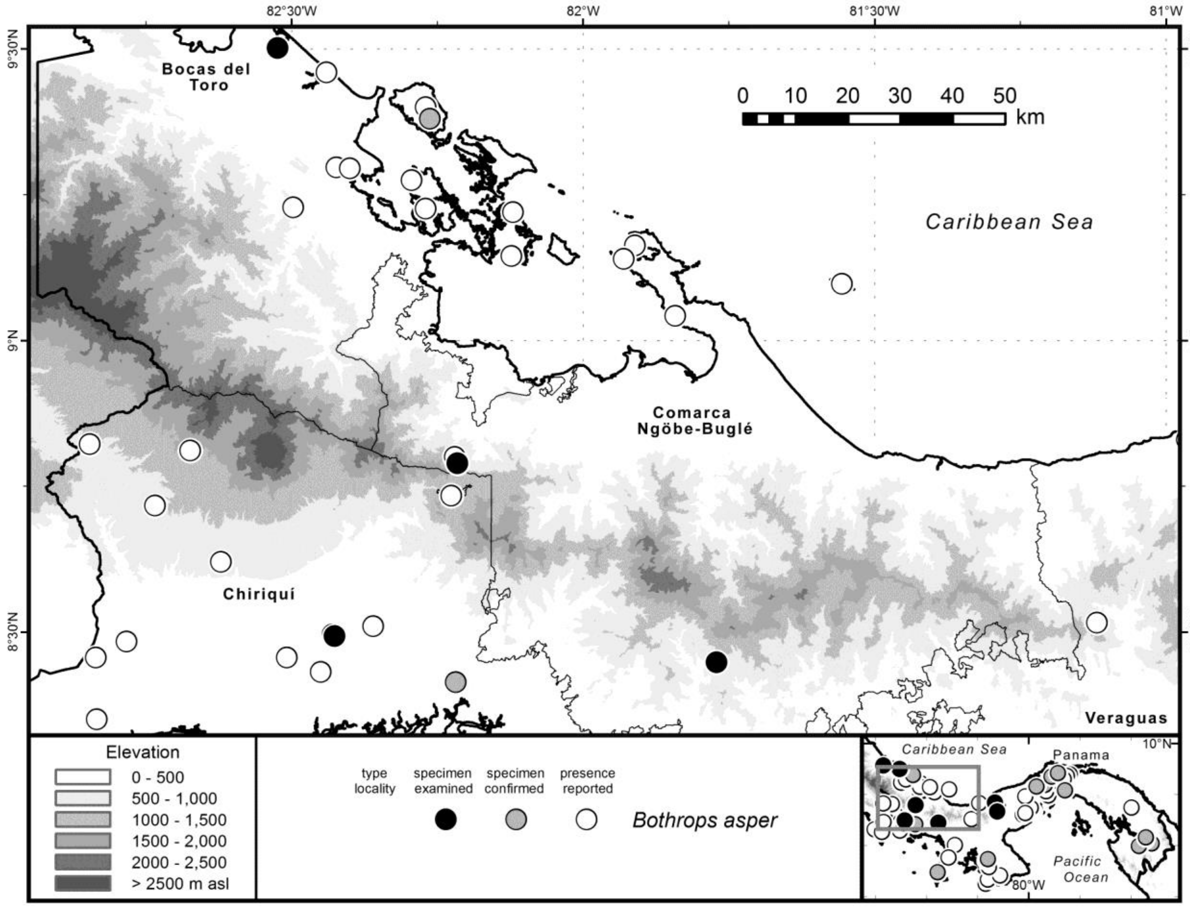
Trigonocephalus xanthogrammus: Cope (1869).

Trimeresurus atrox: Dunn & Bailey (1939).

Syntypes. MCZ 2718 (2 specimens), from Obispo on the Isthmus of Darién, Panama.

Geographic distribution. Mexico to Colombia, Ecuador, and Venezuela, 0–1500 m asl (to 2640 m asl in Colombia). In Panama, throughout the country along both versants including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from numerous localities along both versants up to 1400 m asl.

Diagnosis. This large snake (maximum TOL 2500 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Bothrops* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly divided subcaudals, small imbricate keeled scales and enlarged smooth supraoculars on the dorsal head surface, and a non-prehensile tail. *Bothrops asper* is unique among Panamanian pitvipers in having light-edged dark triangular dorsolateral markings pointing towards middorsum, at least some of which are opposed and fuse on middorsum to form butterfly-shaped markings.



Map 4.187: Distribution of *Bothrops asper*.

Description. TOL to 2500 mm; SVL in Honduran specimens to 1730 mm; tail short, TL/TOL = 0.12–0.15; D keeled, in (25–29)—(23–33)—(17*–21) rows; V 161–249; SC 46–86, at least mostly divided; SPL 7–9; INL 8–12; ISO 3–9; Canths 1–2; SF 0, due to 2nd SPL fused (rarely only in contact) with prelacunal; SBO-SPL 1–2; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Bothrops asper* is a deeply bilobed organ with long lobes; truncus and basal portion of lobes with enlarged spines, apical regions of lobes with papillate calyces.

Coloration in life. D and L ground color gray to dark brown; each side of body with a series of large, light-edged, roughly triangular or trapezoid darker L or dorsolateral markings pointing upwards that may be partially offset but at are least partially opposed and fuse along middorsum, creating butterfly-shaped markings; these large markings are accompanied by two dark blotches ventrolaterally, and usually become indistinct and unshaped on tail; a series of ventrolateral dark blotches between V and 1st D row as well as often diffuse paravertebral blotches between triangles; a dark postocular stripe; L surfaces of head below the postocular stripe usually rather immaculate gray to brown; V surfaces of head immaculate whitish to yellow; V surfaces of body and tail cream or yellow to gray or brown, immaculate anteriorly and mottled with dark at least on L portions posteriorly; tail tip white to yellow in young males, dark in females and older males; pattern usually more vivid in juveniles and in females, more blurred and with additional D mottling in males; iris gray to brown.

The male SMF 91533 was recorded as follows: D ground color Dusky Brown (19), grading into Raw Umber (223) laterally; body with a series of dorsolateral trapezoid Sepia (119) markings pointing upwards that are partly offset and partly meeting to fuse on middorsum, their anterior and posterior margins bordered by diffuse Cinnamon-Drab (219C) stripes, and becoming more and more diffuse towards, and on, tail; a Sepia (119) blotch ventrally to each lower corner of each trapezoid marking; L surfaces of body and tail irregularly mottled with Sepia (119); D surface of posterior third of tail Glaucous (79), grading into Drab-Gray (119D) laterally; L surface of head Raw Umber (123), grading into Clay Color (123B) on lips and chin area; a Dusky Brown (19) postocular stripe extending from eye to just behind last SPL; V ground color Beige (219D), grading into Orange-Rufous (132C) with a suggestion of Flesh Ocher (132D) on tips of V and 1st D row, into dirty white with a suggestion of Pale Horn Color (92) towards head and into Smoke Gray (44) on posterior third of tail; V surfaces of body and anterior two-thirds of tail mottled with Dark Drab (119B) grading into Sepia (119) laterally; iris Verona Brown (223B); tongue Sepia (119).

Coloration in preservative. After 4–6 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that scales which lost their oberhäutchen are gray rather than brown.

Natural history notes. Venomous. Primarily terrestrial, though juveniles are also found in vegetation and this agile snake can prove to be a good climber. Chiefly nocturnal, but also active at daytime. Feeding mostly on vertebrates. Two adult specimens were handed over to me after having been killed by neighbors in Los Algarrobos. The juvenile at San San Pond Sak was fleeing from a local worker. The male SMF 91533 was spotted crossing the road below Hato Chamí around 20:30. The very dark female SMF 91532 was coiled up next to a stream at BPPS around 20:50 and tried to escape by entering the stream. The two latter specimens proved to be very agile and fast when handled. This species is usually quite abundant in altered habitats as well as in the vicinities of settlements, and is involved in most serious cases of human envenomation in Costa Rica and Panama, causing far more deaths than any other species. Accordingly, it is pursued and killed whenever seen by local people in western Panama.

Remarks. The juvenile SMF 91533 has 17 D-HC, which is the lowest value reported for this species so far. The specimen FMNH 51689 from "Palo Santo, 4 miles NW of El Hato, 4600 pies" (= ca. 1402 m asl; Perez-Santos 1999 and FMNH catalogue) is the highest record of this species from the Cordillera Central which I am aware of, and well below the upper limit of 1100 m reported for Panama by Jaramillo et al. (2010).

Cerrophidion sasai **Jadin, Townsend, Castoe & Campbell 2012**

Costa Rica Montane Pitviper, Sasa's Montane Pitviper; Toboba de altura

Figure 4.114H; Map 4.188.

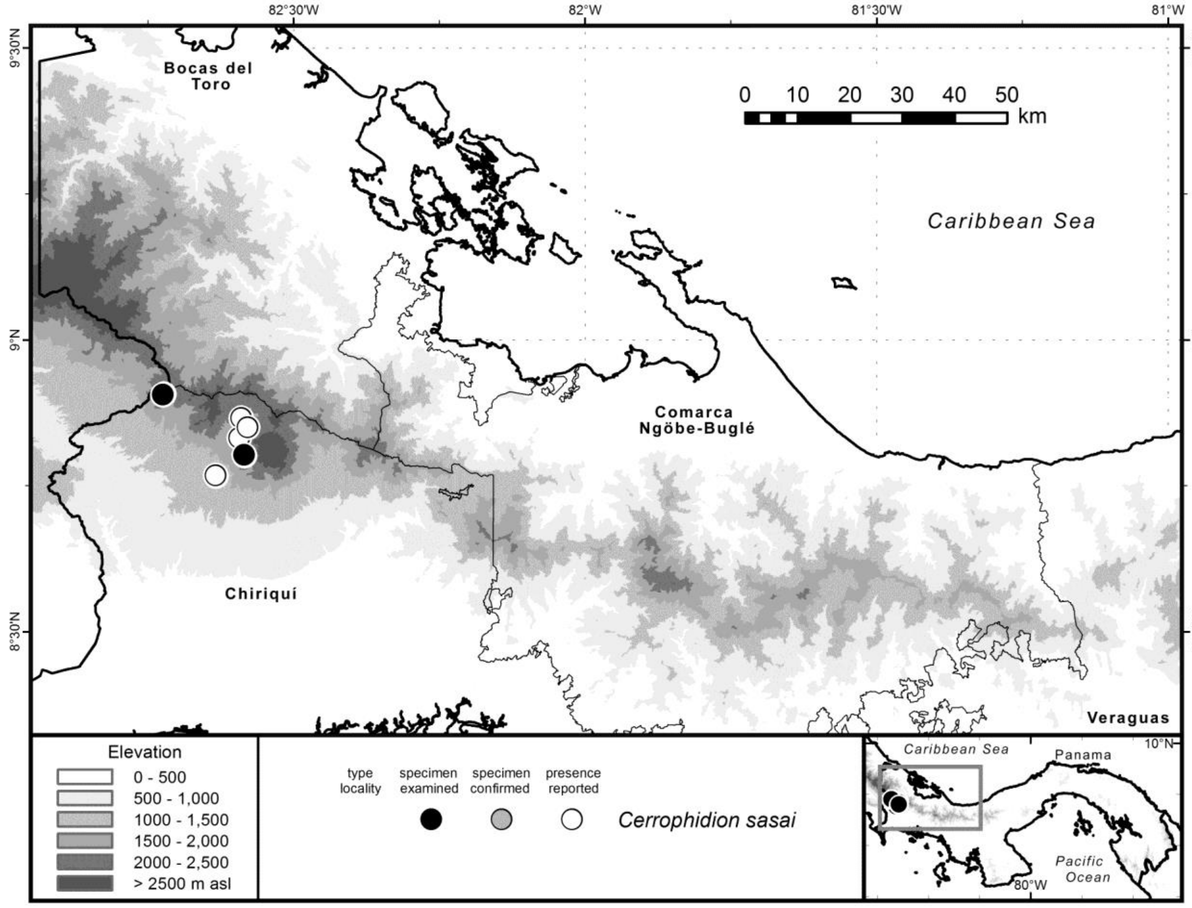
Cerrophidion godmani: Perez-Santos (1999); Young et al. (1999); Ibáñez et al. (2001); Savage (2002); Castoe et al. (2003, 2005, 2009: all in part.); Campbell & Lamar (2004: in part.) Solórzano (2004); Fundación PA.NA.M.A. (2007); Köhler (2008); Savage & Bolaños (2009); Sunyer (2009); Jaramillo et al. (2010); Sasa et al. (2010); Stadler (2010); Wilson & Johnson (2010); McCranie (2011: in part.).

Bothrops godmani: Dunn (1947); Taylor (1951, 1954); Smith (1958); Peters & Orejas-Miranda (1970).

Porthidium godmani: Auth (1994).

Trimeresurus godmanni: Dunn (1940).

Holotype. UTA R-51399, from "San Ramos de Tres Ríos, Departamento de San José, Costa Rica (Jadin et al. 2012).



Map 4.188: Distribution of *Cerrophidion sasai.*

Geographic distribution. Endemic to the Talamancan highlands of Costa Rica and Panama, 1360–3000 m asl. In Panama, probably along both versants of the Serranía de Talamanca in Bocas del Toro and Chiriquí, but hitherto only reported from the Pacific versant east to Volcán Barú, 1390–2010 m asl.

Diagnosis. This medium-sized snake (maximum TOL 822 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Cerrophidion,* and thus distinguished from all other Panamanian snakes, by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, several enlarged smooth plates in the frontal and parietal area as well as enlarged smooth supraoculars, a non-prehensile tail, as well as a pattern of often slightly elongate and vaguely hexagonal dark middorsal blotches, some to all of which are fused to form a zig-zag figure, coupled with smaller lateral blotches and a chiefly dark tail.

Description. (including data from Jadin et al. 2012) TOL to 713 mm (holotype); SVL to 635 mm (holotype); tail short, TL/TOL = 0.10–0.13; D keeled, in (21–25)—(21–23)—(17–21) rows; V 134–146; SC 25–34, most undivided but some divided; SPL 8–10; INL 9–12; ISO 3*; Canths 2*; SF 0–2; SBO-SPL 0–1*; cloacal scute usually entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Cerrophidion sasai* is a strongly bilobed organ; pedicel spinulate, truncus and basal portion of lobes with moderate spines increasing in size along lobes; apical region with scalloped calyces.

Coloration in life. D and L ground color gray to brown; body with a middorsal series of often slightly elongate and vaguely hexagonal dark brown middorsal blotches mostly with darker borders, some to all of which are fused to form a zig-zag figure; a series of smaller and usually more diffuse dark brown L blotches posterior to a L longitudinal neck band that (present in all examined specimens); blotched pattern becoming obscured by dark pigment on tail; D surface of head mor ore less unicolor brown; a dark brown postorbital stripe with a light inferior border; V surfaces cream to light brown anteriorly, with darker mottling increasing posteriorly to cover most or all of V and SC; iris gray to reddish brown; tongue dark brown with lighter tips.

The male SMF 89539 (Fig. 4.114H) was recorded about one hour after shedding its skin: D and L ground color Dark Drab (119B) with a suggestion of Light Drab (119C), grading into Natal Brown (219A) on the head; body with a series of middorsal Burnt Umber (22) blotches, grading into Dark Grayish Brown (20) posteriorly, interruptedly bordered by Sepia (119) and mostly merged to form a longitudinal band of partly zig-zag, partly chainlike appearance; L surface of body with a series of unmerged Burnt Umber (22) blotches grading into Dark

Grayish Brown (20) posteriorly, partly bordered by Sepia (119) as well as dirty white mottling (the latter especially on the inferior edges); D and L blotches fuse almost completely on tail; neck with a Burnt Umber (22) L band bordered by Sepia (1119) and, below, by dirty white mottling; L surface of head Light Drab (119C); a broad Burnt Umber (22) postorbital stripe descending until inferioposterior edge of mouth, bordered below by a narrow dirty white stripe; V surface of head dirty white with a suggestion of Pale Horn Color (92) with fine Light Drab (119C) mottling and Flesh Color (5) shadings on scale margins; V surface of body dirty white with a suggestion of Pale Horn Color (92), with heavy Verona Brown (223B) and Sepia (119) mottling that increases and merges posteriorly, in a way that 2nd half of body and tail appear almost completely Sepia (119) with fine Verona Brown (223B) and dirty white spots; iris Robin Rufous (340); tongue Dusky Brown (19), grading into Flesh Color (5) posteriorly.

Coloration in preservative. After 5–8 years in 70% ethanol, the coloration of my examined specimens is similar to that in life, apart from that scales which lost their oberhäutchen are gray rather than brown.

Natural history notes. Venomous. Terrestral and chiefly diurnal, apparently feeding on everything that passes by. At Jurutungo, SMF 89538 was moving on a trail on 15.07.2008 at 14:10, and 4 additional specimens (including SMF 89539 and MHCH 2303–4) were found until 15:00 around the construction site of a nearby building, all lying beneath 3 corrugated sheets that were distributed on the ground. Either by regurgitation or defecation, these four collected specimens revealed some of their recent prey including grasshoppers, subcaudal scales of a colubroid snake, mammal hair, and a large *Bolitoglossa sombra*. The 5th specimen from Jurutungo, SMF 90177, was found at night under a log.

Remarks. The genetic differentiation between different CA populations formerly referred to *Cerrophidion godmani* Günther 1863 was shown by several authors (Castoe et al. 2003, 2005, 2009; Daza et al. 2010), and Jadin et al. (2012) finally undertook taxonomic action, retaining the name *C. godmani* for populations in Mexico and Guatemala, while describing as separate species those from Honduras and El Salvador (*C. wilsoni*) and those from Costa Rica and Panama (*C. sasai*). Albeit their description was based exclusively on Costa Rican material, the Panamanian populations formerly referred to *C. godmani* must logically be included in *C. sasai.* The morphological data presented in the diagnosis and description is thus restricted to the original description of this species and my own examined material.

Five of the 6 specimens whose pholidotic characters I recorded have one to several proximal and/or distal SC divided. Three of these specimens have only 17 D-HC (another has 18), which is the lowest value reported for this species to my knowledge. SMF 89538 has a clearly divided cloacal scute.

SMF 86412 from Acuatal in PNVB was collected by AB ad MP at 2012 m asl, which is the highest Panamanian elevation reported for this species (Jaramillo et al. 2010). The lower elevational limit at sea level, as reported by Perez-Santos (1999) based on a supposed specimen from Puerto Armuelles is clearly erroneous, since the specimen in question (MCZ 42731) is a *Porthidium lansbergii* according to the MCZ catalogue and GK who examined it. The presence of *Cerrophidion sasai* in Bocas del Toro is rendered plausible by its altitudinal distribution (Solórzano 2004; Ray & Knight 2013) and the distance of < 3 km between the collection site at Jurutungo and the border of that province.

Lachesis melanocephala **Solórzano & Cerdas 1986**

Black-headed Bushmaster; Cascabel muda, Matabuey, Plato negro, Verrugosa plato negro
Map 4.189.

Lachesis muta or *L. m. stenophrys:* Taylor (1951, 1954: all in part.); Smith (1958: in part.); Peters & Orejas-Miranda (1970: in part.); Auth (1994: in part.); Perez-Santos (1999: in part.); *Lachesis muta melanocephala:* Solórzano & Cerdas (1986).

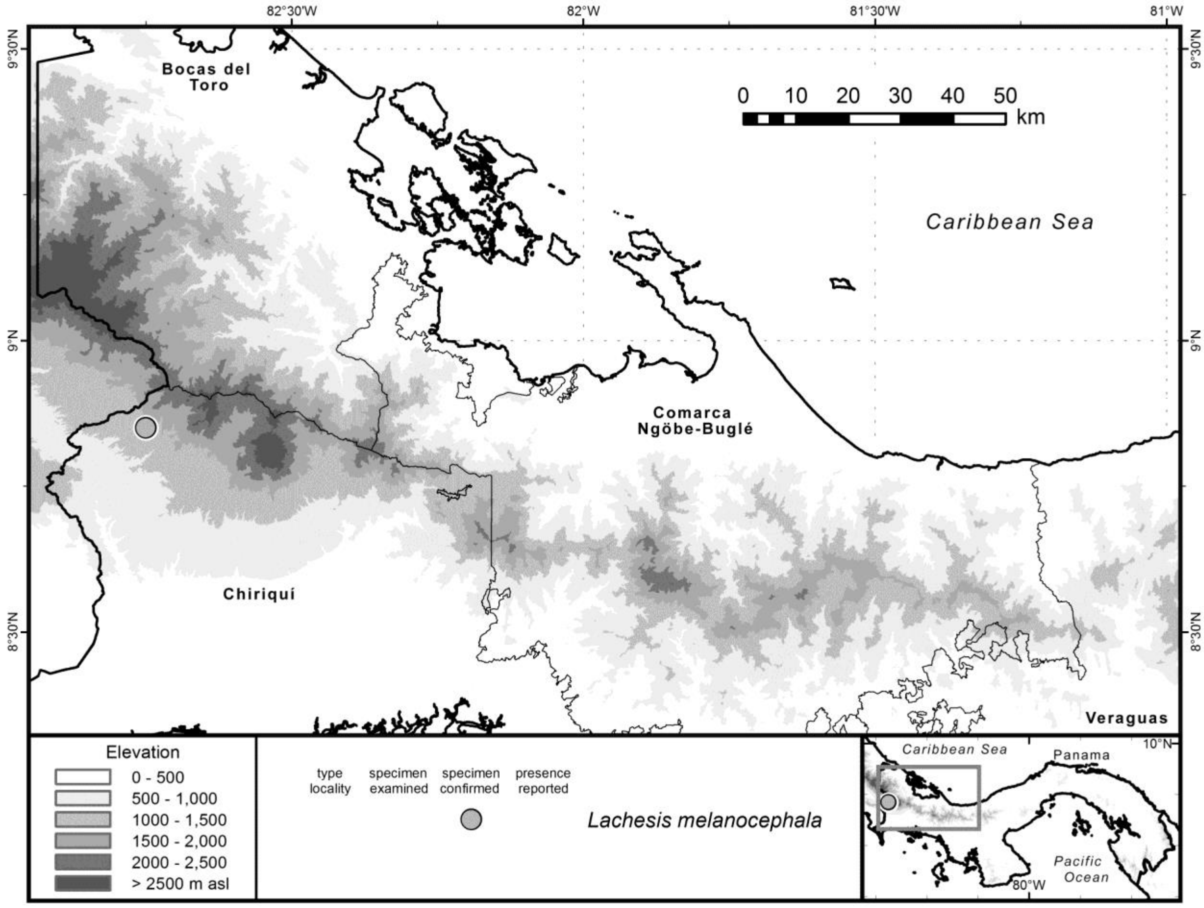
Holotype. Museo Instituto Clodomiro Picado 301, adult male, from "tropical rainforest 9 km northern of Ciudad Neily in southeastern Provincia de Puntarenas, Costa Rica" (Solórzano & Cerdas 1986).

Geographic distribution. Southern Pacific Costa Rica to western Panama, 0–1600 m asl. In Panama, apparently restricted to extreme western Chiriquí, with the only record being from Finca Hartmann at Santa Clara, ca. 1200 m asl.

Diagnosis. This large snake (maximum TOL 2400 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Lachesis* by its loreal pit, keeled dorsals arranged in more than 30 rows at midbody, head that is very distinct from neck, subcaudals that are arranged in two rows proximally and 4–5 rows distally, small smooth to tuberculate dorsal head scales and enlarged smooth supraoculars, as well as a non-prehensile tail with an elongated terminal spine at the tip and a pattern of dark diamonds whose lateral tips continue as transverse bars across the flanks. *Lachesis melanocephala* differs from its only congener in western Panama, *L. stenophrys,* in having a black head cap (vs. head brown above) and 209 or more ventrals (vs. 211 or fewer).

Description. (Including data from Solórzano & Cerdas 1986 and Fernandes et al. 2004) TOL to 2400 mm; recorded SVL to 1800 mm; tail short, TL/TOL = 0.08–0.10; D strongly keeled, tuberculate especially on vertebral and 2–3 paravertebral rows, in (36–42)—(34–41)—(25–26) rows; V 209–222; SC 35–56, including 12 or more of the smaller distal ones arranged in 4–5 longitudinal rows; SPL 7–9; INL 12–14; ISO 10–13; Canths 1–3; SF 0, due to 2nd SPL usually fused with prelacunal; SBO-SPL 4; cloacal scute entire; AP 2; eyes small, pupil vertically elliptical.

The hemipenis of *Lachesis melanocephala* is a deeply bilobed organ; pedicel spinulate, lobes proximally with moderate spines; apical region conical, calyculate.



Map 4.189: Distribution of *Lachesis melanocephala.*

Coloration in life. D and L surfaces yellow or yellowish brown, with a middorsal series of large black, more or less rhomboidal markings, often separated by light pigmentation along middorsum, whose laterally descending tips may be light-centered or broken up, but usually continue as transverse bands over most or all of flanks; D surfaces of head black, usually completely fused with dark postocular stripe; juveniles with a narrow light postocular stripe in head cap and orangish tail; L and V surfaces of head immaculate white to yellow, those of body white to cream; iris reddish to dark brown.

Coloration in preservative. Similar to that in life.

Natural history notes. Venomous. Terrestrial and nocturnal, feeding mainly on mammals. Oviparous.

Remarks. Zamudio & Greene (1997) elevated the subspecies *Lachesis muta stenophrys* Cope 1876 and *L. m. melanocephala* Solórzano & Cerdas 1986 to specific status. This action was confirmed by Fernandes et al. (2004), Cambell & Lamar (2004), and all subsequent authors.

After the presence of *L. melanocephala* in Panama had been suggested by the head-only *Lachesis* MVZ 27321 with the imprecise locality "Chiriquí" (Perez-Santos 1999; Campbell & Lamar 2004), its occurrence in Chiriquí was finally demonstrated by Dwyer & Perez (2009) based on UTADC 1039. Their collection site "Finca Hartmann" is clearly locatable, even though their locality data is highly erroneous: "Cantón Racimiento" should read "Distrito de Renacimiento", and their coordinates "ca. 8.51°N, 82.54°W" lie some 30 km SSE instead of the stated and plausible 20 km W of Volcán. If the two decimals were to be interpreted as minutes, the point would fall into Costa Rica. Thus, for my georeference, I used the approximate coordinates "8°51'N, 82°45'W" (= 8.85°N, 82.75°W) provided two years earlier by DeJesus (2007), which coincide well with the actual ubication of Finca Hartmann that is signposted at Santa Clara along the road leading from Volcán to Río Sereno.

***Lachesis stenophrys* Cope 1876**

Central American Bushmaster, Bushmaster; Verrugosa, Cascabel muda, Matabuey

Figure 4.115A; Map 4.190.

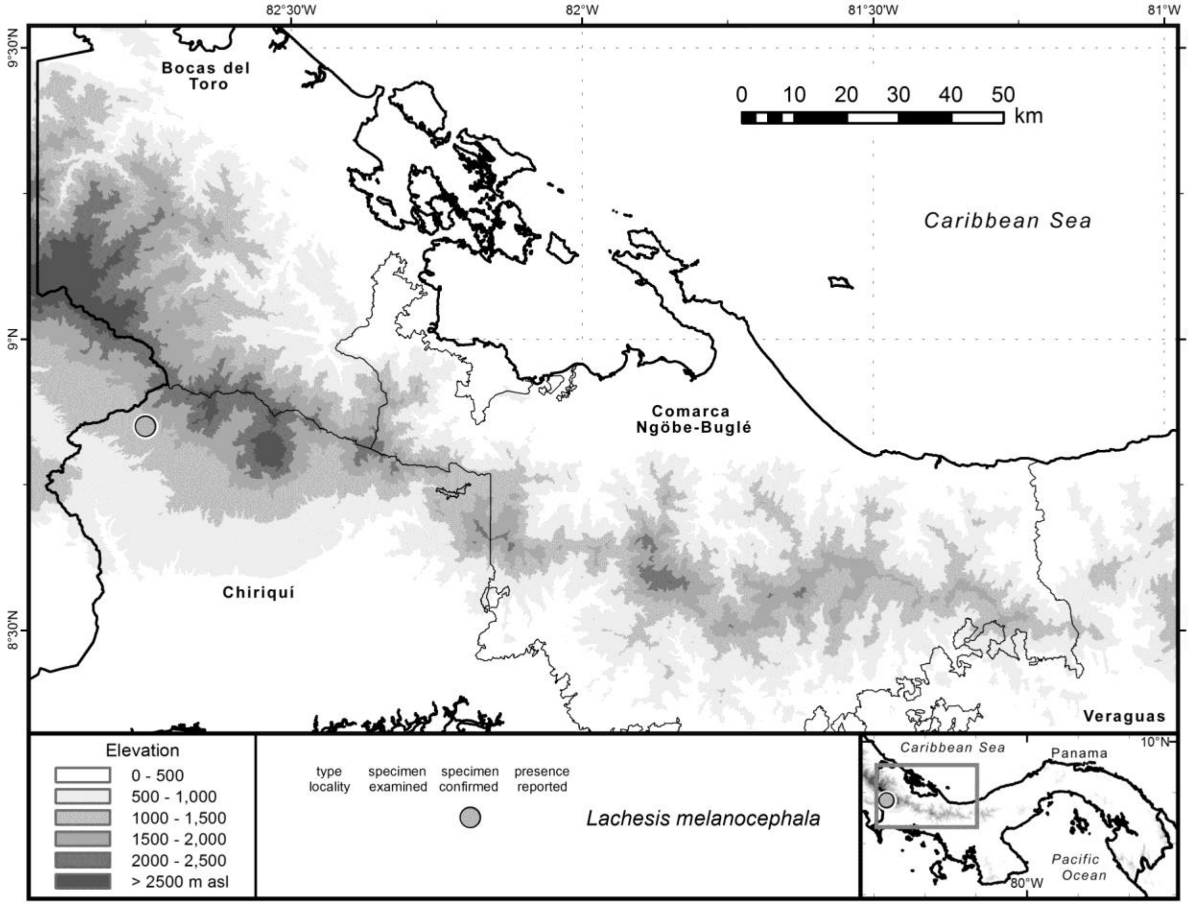
Lachesis muta or *L. m. stenophrys:* Dunn & Bailey (1939); Swanson (1945); Evans (1947); Taylor (1951, 1954: all in part.); Smith (1958: in part.); Myers & Rand (1969); Peters & Orejas-Miranda (1970: in part.); Myers (1977); Solórzano & Cerdas (1986); Rand & Myers (1990); Auth (1994: in part.); Ibáñez et al. (1995, 1996); Perez-Santos (1999: in part.); Young et al. (1999: in part.).

Lachessis muta: de Sousa (1999).

Holotype. USNM 32479, from Sipurio, Costa Rica.

Geographic distribution. Nicaragua to Panama, 0–1200 m asl In Panama, along the Caribbean versant of extreme western and both versants of west-central and central Panama including Bocas del Toro, Chiriquí, Comarca Ngöbe Buglé, and Veraguas. In the Cordillera Central, reported from RFLF and nearby BPPS, PNGDOTH, Valle de Antón, and PNAC, up to ca. 1200 m asl.

Diagnosis. This large snake (maximum TOL 3600 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Lachesis* by its loreal pit, keeled dorsals arranged in more than 30 rows at midbody, head that is very distinct from neck, subcaudals that are arranged in two rows proximally and 4–5 rows distally, small smooth to tuberculate dorsal head scales and enlarged smooth supraoculars, as well as a non-prehensile tail with an elongated terminal spine at the tip and a pattern of dark diamonds whose lateral tips continue as transverse bars across the flanks. *Lachesis stenophrys* differs from its only congener in western Panama, *L. melanocephala,* in having a brown dorsal head surfaces and a darker postocular stripe (vs. black head cap including postocular stripe) and 211 or fewer ventrals (vs. 209 or more).



Map 4.190: Distribution of *Lachesis stenophrys.*

Description. (Including data from Fernandes et al. 2004) TOL to 3600 mm; recorded SVL to 2050 mm; tail short, TL/TOL = 0.08–0.10; D strongly keeled, tuberculate especially on vertebral and 2–3 paravertebral rows, in (35–39)—(31–38)—(24–26) rows; V 191–211; SC 35–53, including 8 or more of smaller distal ones arranged in 4–5 longitudinal rows; SPL 7–9; INL 12–16; ISO 10–13; Canths 1–3; SF 0–1, 2nd SPL fused with prelacunal or not; SBO-SPL 3–4; cloacal scute entire; AP 2; eyes small, pupil vertically elliptical.

The hemipenis of *Lachesis melanocephala* is a deeply bilobed organ; pedicel spinulate, lobes proximally with moderate spines; apical region conical, calyculate.

Coloration in life. D and L surfaces gray to reddish brown, with a middorsal series of large black, more or less rhomboidal markings, often separated by light pigmentation along middorsum, whose laterally descending tips may be light-centered or broken up, but usually continue as transverse bands over most or all of flanks; D surfaces of head same color as dorsum or of a lighter or darker brown, unicolor or with sparse dark mottling; a conspicuous dark brown to black postocular stripe; L and V surfaces of head immaculate gray or white to yellow, those of body cream to orangish, sometimes with dark mottling posteriorly; juveniles with orangish tail; iris reddish to dark brown.

Coloration in preservative. Similar to that in life.

Natural history notes. Venomous. Terrestrial and nocturnal, feeding mainly on mammals. Oviparous, inhabiting primary forest.

Remarks. Zamudio & Greene (1997) elevated the subspecies *Lachesis muta stenophrys* Cope 1876 to specific status. This action was confirmed by Fernandes et al. (2004) as well as by Cambell & Lamar (2004), who additionally introduced the new combination *L. acrochorda* (García 1896) for the populations from E Panama, W Colombia, and W Ecuador (their map 81 clarifies that the statement that the latter species occurs on "both ... versants of western Panama..." is erroneous and should read "eastern Panama"). To my knowledge, this arrangement has been followed by all subsequent authors.

The records from E and W of this province render the occurrence of *Lachesis stenophrys* in Veraguas plausible. For the record of Hofer & Bersier (2001) from BPPS close to the continental divide, I arbitrarily applied the mean value (1200 m asl) of the given elevational range (800–1600 m), which is slightly above upper elevational limit of 1100 m given for this species in Panama and as a whole (Jaramillo et al. 2010, certainly based on the records from La Fortuna by Myers 1977). My georeference for a photograph of a juvenile *L. stenophrys* taken by Robert Maurer between RFLF and the transect of Hofer & Bersier (2001), close to the type locality of *Sibon noalamina,* yields a SRTM elevation of 1182 m that renders the species' occurrence around 1200 m plausible. *Lachesis stenophrys* has been reported from the Fortuna depression and may be expected along the Pacific slopes of the Serranía de Tabasará E of La Fortuna where forest persists. In view of putative contact zones between this species and its black-headed congener, it would be very interesting to verify the record of *L. stenophrys* from Refugio de Vida Silvestre Playa la Barqueta (Fuenmayor 2001 according to Ibáñez 2006; herein handled as *Lachesis* sp. and accordingly not plotted on Map 1.190), or whether individuals of *Lachesis* can be found in the rather isolated forest on Meseta de Chorcha.

Porthidium lansbergii (Schlegel 1841)

Lansberg's Hog-nosed Pitviper, Lansberg's Hognose Viper; Patoca, Tamagá, Toboba
Figure 4.115B; Map 4.191.

Bothriechis brachystoma: Cope (1861d).

Bothriopsis castelnaui: Cope (1871).

Bothrops lansbergi: Evans (1947); Smith (1958).

Bothrops lansbergii: Swanson (1945); Peters & Orejas-Miranda (1970).

Porthidium brachystoma: Cope (1871).

Porthidium lansbergi: Perez-Santos (1999).

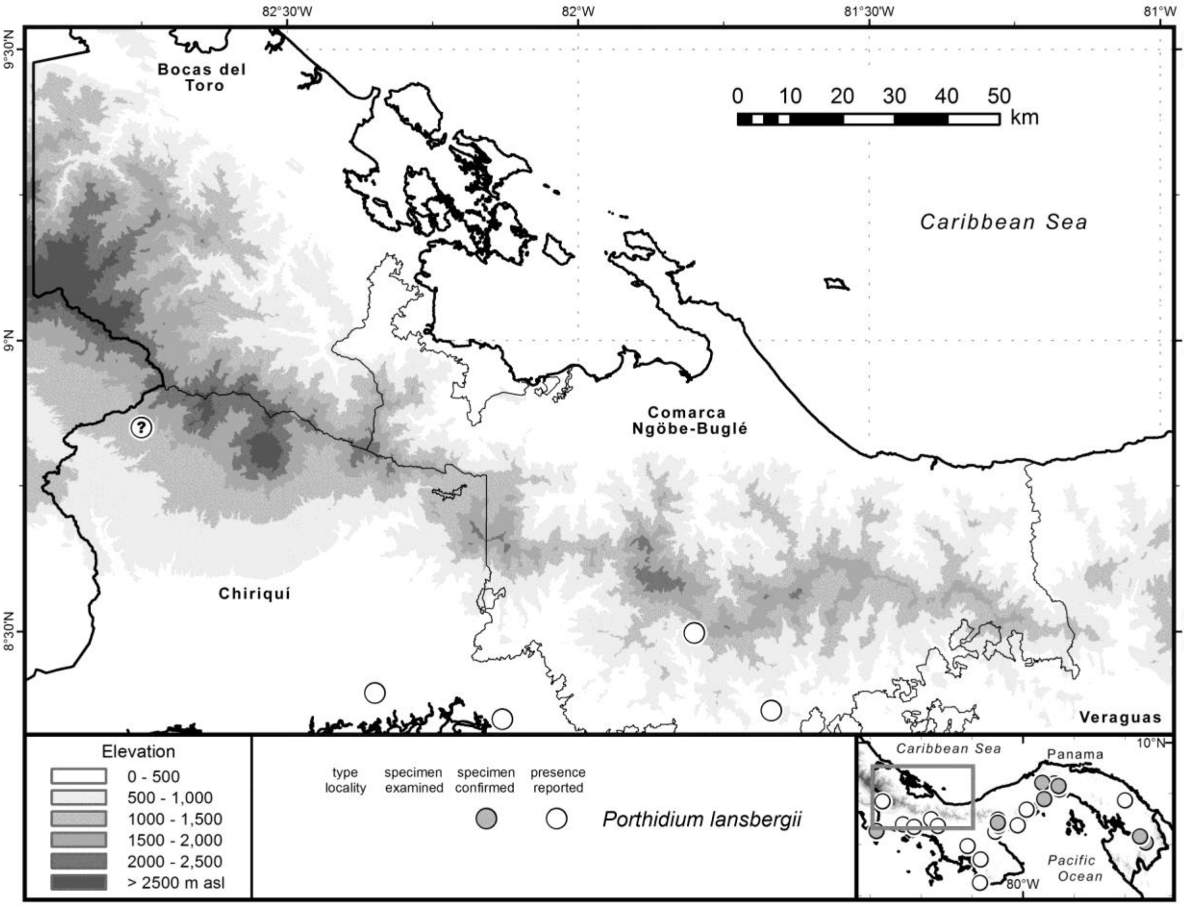
Teleuraspis castelnaui: Cope (1860a).

Teleuraspis lansbergii: Cope (1860a).

Trimeresurus lansbergi: Dunn & Bailey (1939).

Holotype. Unknown, from les environs de Turbaco, en Colombie (Departamento de Bolívar, Colombia).

Geographic distribution. Panama to Colombia and Venezuela, 0–1300 m asl. In Panama, along the Pacific versant including Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Cerro Colorado area and Santa Clara, up to ca. 1300 m asl (but see remarks).



Map 4.191: Distribution of *Porthidium lansbergii.*

Diagnosis. This medium-sized snake (maximum TOL 900 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Porthidium* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small keeled scales and enlarged smooth supraoculars on the dorsal head surface, a non-prehensile tail, and a dorsal pattern usually consisting of a vertebral stripe and paravertebral blotches. Among its Panamanian congeners, *Porthidium lansbergii* differs from *P. nasutum* in having the tip of the snout at most moderately upturned (vs. a conspicuously elongate and strongly upturned proboscis) and in having 139 or more ventrals (vs. 145 or fewer), and from *P. volcanicum* in lacking white ornamentations on the head, especially a contrasting light postocular stripe (vs. present), and in having a light venter mottled with dark (vs. mostly dark).

Description. (including data from two captive specimens photographed at the Serpentario of the Universidad de Panama) TOL to 900 mm; tail short; D keeled, in 21–27 rows at midbody; V 139–166; SC 27–41, at least mostly undivided; SPL 8–10; INL 8–13; ISO 5–7; Canths usually 1; SF 0–1*; SBO-SPL 1*; cloacal scute entire; AP 2 at least anteriorly; eyes moderate, pupil vertically elliptical.

The hemipenis of *Porthidium lansbergii* is a deeply bilobed organ; pedicel naked; proximal portion of lobes and adjacent base with small and large spines; apical regions calyculate, with a long awn containing a naked disk on the apex of each lobe.

Coloration in life. Very variable. D and L surfaces gray, yellow, or brown; body and tail with a narrow middorsal stripe that is bordered by usually paired paravertebral blotches, each pair usually marking the upper corners of a diffuse to merely suggested broad transverse crossband suffused with pigment that is slightly to conspicuously darker than ground color; a series of less contrasting L to ventrolateral blotches corresponding to the dorsolateral ones; sometimes 1–2 additional L and/or ventrolateral series of even less contrasting blotches; D surface of head often with diffuse dark markings; a more or less distinct postocular stripe usually present, often diffuse; V surfaces cream to light brown with darker mottling; iris gray.

Coloration in preservative. Similar to that in life, apart from that possibly present yellow, orange, and reddish shades fade with time.

Natural history notes. Venomous. Terrestrial, diurnal and nocturnal, feeding on small vertebrates or as juveniles on invertebrates.

Remarks. As suspected by Campbell & Lamar (2004) and Dwyer & van den Burgh (2012), certain records of *Porthidium lansbergii* from western Panama could actually be based on individuals of the somewhat similar *P. volcanicum* which the latter authors recently reported from Panama (also see remarks for the latter species). Regarding this suspicion to be very reasonable at least at premontane elevations in western Chiriquí, I marked the point corresponding to FMNH 152106 from Santa Clara (for which my georeference yields a SRTM elevation of 1300 m asl) with a questionmark in Map 4.191.

Having seen photos of putative *P. lansbergii* with somewhat light-colored postocular stripes from different sites in western Panama including lowland localities, I regard it as possible that *P. volcanicum* is even more widely distributed in Panama than assumed by Campbell & Lamar (2004). However, the specimen MCZ 42731 from Puerto Armuelles was confirmed by GK to represent *P. lansbergii* and constitutes the westernmost record for this species, which has been reported to range no further W than central Panama by some recent authors (Auth 1994; Campbell & Lamar 2004; Köhler 2008), whereas others (Young et al. 1999; Ray & Knight 2013) included Chiriquí in the species' distribution. At any rate, the taxonomy and distribution of *Porthidium* with a moderately upturned snout in Pacific western Panama is largely unresolved and requires geographically comprehensive studies preferably involving molecular data.

Likewise, the Costa Rican Golfo Dulce endemic *P. porrasi* which is very similar to *P. nasutum* (see remarks for that species) might well range into the lowlands of western Chiriquí, but is very distinct from *P. lansbergii* in having a strongly upturned snout tip, a white to yellow tail, and just 136–141 V. Yet another species of the genus, *P. ophryomegas,* has been stated to occur in Panama (Smith 1958; Peters & Orejas-Miranda 1970; Auth 1994; Young et al. 1999; Perez-Santos 1999; Fundación PA.NA.M.A. 2007). However, the underlying specimen MCZ 26873, thought to be from Progreso in Chiriquí, actually was collected in the Progreso district of Honduras (Campbell & Lamar 2004; McCranie 2011).

***Porthidium nasutum* (Bocourt 1868)**

Hog-nosed Pitviper, Rainforest Hog-nosed Pitviper, Rainforest Hognose Viper; Vibora narisona, Tamagá común, Tamagá, Toboba

Figure 4.115C; Map 4.192.

Bothrops lansbergii: Taylor (1951, 1954).

Bothrops nasuta: Dunn (1933); Wettstein (1934); Taylor (1951).

Bothrops nasutus: Taylor (1954); Peters & Orejas-Miranda (1970); Martínez et al. (1995).

Bothriopsis proboscideus: Cope (1876).

Bthrops nasutus: Martínez & Rodriguez (1994).

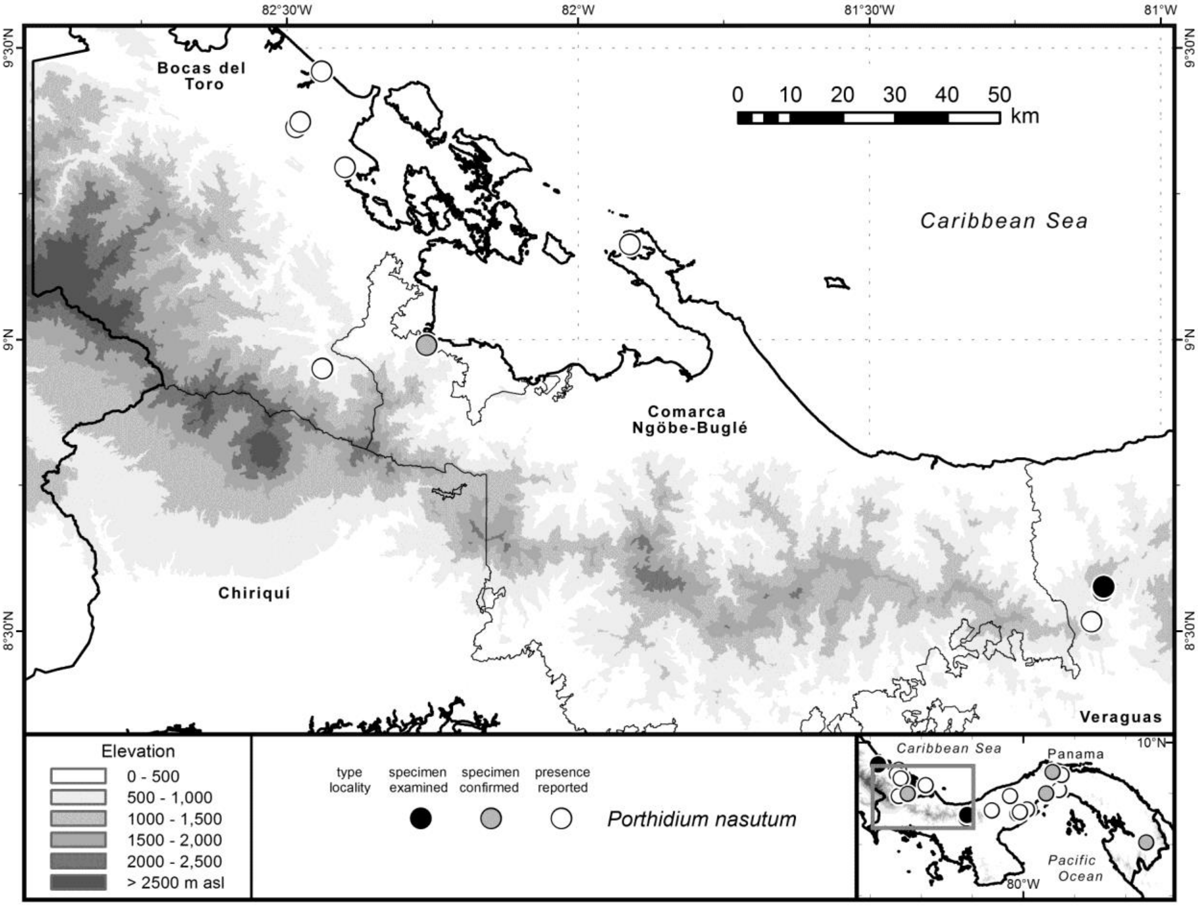
Porthidium nasutus: Cope (1871).

Prothidium nasutum: Carrizo (2000).

Trimeresurus nasutus: Dunn & Bailey (1939).

Holotype. MNHN 1592, from Pansos, sur les bords du Polochic, Guatemala.

Geographic distribution. Mexico to Colombia and Ecuador, 0–1700 m asl. In Panama, along the Caribbean versant of western Panama including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, as well as on both versants in central and probably also eastern Panama. In the Cordillera Central, reported from Culebra, the Santa Fé area, PNGDOTH, Valle de Antón, and PNAC, up to 1000 m asl.



Map 4.192: Distribution of *Porthidium nasutum.*

Diagnosis. This medium-sized snake (maximum TOL 635 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Porthidium* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small keeled scales and enlarged smooth supraoculars on the dorsal head surface, a non-prehensile tail, and a dorsal pattern usually consisting of a vertebral stripe and paravertebral blotches. *Porthidium nasutum* differs from its Panamanian congeners in having the tip of the snout with a conspicuously elongate and strongly upturned proboscis (vs. at most slightly upturned), as well as in having 145 or fewer ventrals (vs. 139 or more in *P. lansbergii* and 156 or more in *P. volcanicum*.

Description. TOL to 635 mm; tail short, TL/TOL = 0.09–0.14; D keeled, in (23–29)—(21–27)—(17–21) rows; V 123–145; SC 23–41, at least mostly undivided; SPL 8–11; INL 9–13; ISO 3–9; Canths 1; SF 0–1*; SBO-SPL 1–2*; cloacal scute entire; AP 2 at least anteriorly; eyes moderate, pupil vertically elliptical.

The hemipenis of *Porthidium nasutum* is a deeply bilobed organ; pedicel naked; proximal portion of lobes and adjacent base with small and large spines; apical regions calyculate, with a long awn containing a naked disk on the apex of each lobe.

Coloration in life. Very variable. D and L surfaces gray, yellow, or brown; body and tail often with a narrow middorsal stripe that is bordered by usually paired paravertebral blotches, each pair possibly marking the upper corners of a diffuse to merely suggested broad transverse crossband suffused with pigment that is slightly to conspicuously darker than ground color; a more or less pronounced series of less contrasting L to ventrolateral blotches corresponding to the dorsolateral ones often present, sometimes also an additional series of diffuse L to ventrolateral blotches; a more or less distinct light postocular stripe and supralabial usually present, often diffuse; V surfaces with dark mottling; juveniles with a light tail tip; some individuals unicolor dark; iris grayish.

Coloration in preservative. Similar to that in life, apart from that possibly present yellow, orange, and reddish shades fade with time.

Natural history notes. Venomous. Terrestrial, diurnal and nocturnal, feeding on small vertebrates or as juveniles on invertebrates.

Remarks. The specimen SMF 89975, collected by AC on Cerro Negro at 1000 m asl, raises the upper elevational limit reported for Panama from 850 m (Jaramillo et al. 2010). This specimen has 9 ISO, which is the highest number reported for the specis so far. Based on its altitudinal distribution, I regard the presence of this species in Chiriquí, at least around RFLF, as possible.

The Costa Rican Golfo Dulce endemic *Porthidium porrasi,* which resembles *P. nasutum* in having a conspicuously upturned proboscis on the tip of the snout, might well range into the lowlands of western Chiriquí, especially around the Peninsula Burica (that is, I regard its presence in Panama as possible). It differs from *P. nasutum* in having the tip of the tail white to yellow at all ages, in adults at least on the V surfaces (vs. light in juveniles, dark in adults) and usually 25–27 D-MB (vs. usually 23). However, historic records of *P. nasutum* from lowland western Chiriquí probably rather go back to the specimen MCZ 26872, which was thought to be from Progreso in Chiriquí but actually collected in the Progreso district of Honduras (Campbell & Lamar 2004; McCranie 2011).

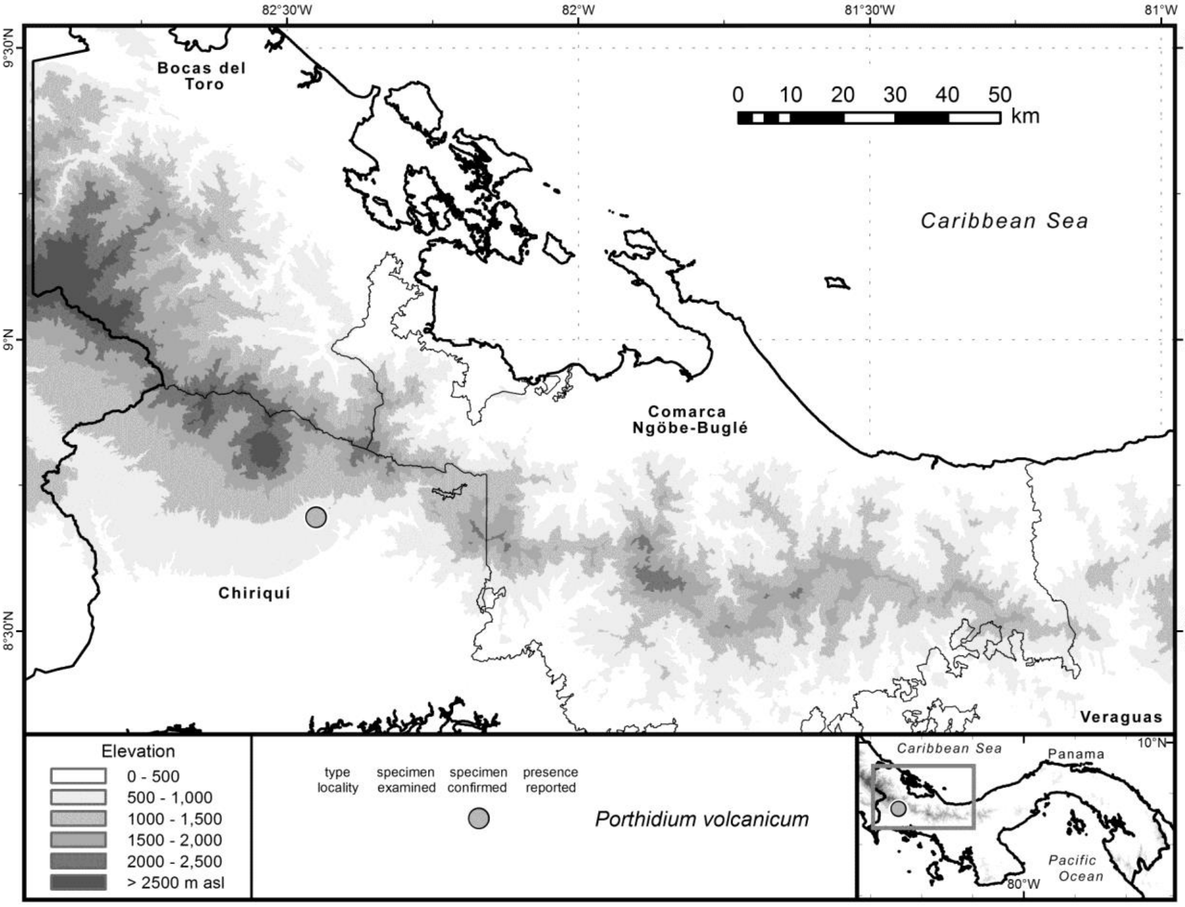
Porthidium volcanicum **Solórzano 1995**

Costa Rican Hog-nosed Pitviper, Hog-nosed Pitviper; Toboba Costarricense, Tamagá, Toboba

Figure 4.115D; Map 4.193.

Holotype. UCR 11642, from Ujarrás de Buenos Aires (Valle del General, suroeste de la provincia de Puntarenas, Costa Rica).

Geographic distribution. Endemic to the Pacific slopes of the Talamancan highlands in Costa Rica and Panama, 400–1000 m asl. In Panama, reported from the Serranía de Talamanca in Chiriquí near Boquete at 1000 m asl.



Map 4.193: Distribution of *Porthidium volcanicum.*

Diagnosis. This medium-sized snake (maximum TOL 536 mm) with vertically elliptical pupils is immediately recognized as a member of the pitviper genus *Porthidium* by its loreal pit, keeled dorsals, head that is very distinct from neck, at least mostly undivided subcaudals, small keeled scales and enlarged smooth supraoculars on the dorsal head surface, a non-prehensile tail, and a dorsal pattern usually consisting of a vertebral stripe and paravertebral blotches. *Porthidium volcanicum* differs from its Panamanian congeners in having a conspicuous, contrasting light postocular stripe (vs. not very contrasting if present, and usually dark). It further differs from *P. nasutum* in having the tip of the snout at most moderately upturned (vs. a conspicuously elongate and strongly upturned proboscis) and in having 159 or more ventrals (vs. 145 or fewer), and from *P. lansbergii* in having white ornamentations on and below the head (vs. absent), a mostly dark venter (vs. light mottled with dark), and 156 or more ventrals (vs. 166 or fewer).

Description. TOL to 536 mm; tail short, TL/TOL = 0.10–0.15; D keeled, in 19—(25–27)—19 rows; V 156–165; SC 25–35, at least mostly undivided; SPL 9–11; INL 11–13; ISO 6–8; Canths 1; SF 0; SBO-SPL 1; cloacal scute entire; AP 2; eyes moderate, pupil vertically elliptical.

The hemipenis of *Porthidium volcanicum* remains undescribed to my knowledge but probably is a deeply bilobed organ as in other species of the genus.

Coloration in life. Variable, but apparently generally more contrasting than in the other Panamanian specis. D and L surfaces gray to brown; body and tail with a narrow light middorsal stripe that is bordered by paired dark paravertebral blotches, each pair separated from the next by light pigmentation and usually marking the upper corners of a diffuse to merely suggested broad transverse crossband suffused with pigment that is slightly to conspicuously darker than ground color; a series of pronounced, light-edged dark L blotches usually well aligned with the dorsolateral ones; a L and a ventrolateral series off less contrasting dark blotches offset between the large paravertebral and L blotches; D surface of head dark with light markings posteriorly; a light stripe from rostral along canthus rostralis and supraocular, becoming most distinct as a light postocular stripe that bends down towards neck posterior to temporal region; 2–3 light vertical bars on SPL and INL, respectively; V surfaces of head dark with light mottling; V surfaces of body and tail chiefly dark brown, with darker and/or L light mottling; iris gray.

Coloration in preservative. Similar to that in life.

Natural history notes. Venomous. Terrestrial, diurnal and nocturnal, feeding on small vertebrates or as juveniles on invertebrates.

Remarks. *Porthidium volcanicum* was recently reported for Panama by Dwyer & van den Burgh (2012) based on UTADC 6801–6 from 15 km S of Boquete at 1000 m asl, which is the easternmost and highest record for this species. Just as Campbell & Lamar (2004), these authors suspected previous records of *P. lansbergii* from W Panama to be based on individuals of this species. Based on photos of uncollected individuals from as far E as Valle de Antón, I regard these suspicions as not too unsubstantiated, but recognize that a solution of this issue would require a comprehensive investigation which is far beyond the scope of the present study (also see remarks for *P. lansbergii*).

Based on analyses of mtDNA, Castoe et al. (2005) essentially reconfirmed the LCA arrangement of nominal taxa within *Porthidium* with the exception of *P. volcanicum,* which was not included in their sample and is apparently still known from only very few specimens, so that its variation probably is insufficiently known. In Savage's (2002: p. 734) paragraphs on diagnostics and similar species for *P. volcanicum,* data for this species are mixed up with that of *P. ophryomegas,* erroneously stating *P. volcanicum* to have 2 canthals, which is a character usually only found in *P. ophryomegas.* Campbell & Lamar (2004) pointed out that they could not reprodruce the high number of paravertebral blotches stated as diagnostic for this species (e.g., Savage 2002; Solórzano 2004) which therefore should not be relied upon as a diagnostic character given the confusions and uncertainties that can arise from the paired nature of these markings. The V counts used to distinguish *P. volcanicum* from *P. lansbergii* in the key of Campbell & Lamar (2004) lose their diagnostic value when the female maximum count of 166 V for *P. lansbergii,* not appearing in their species account or key but in their Table 44 and the paragraph on similar species for *P. volcanicum,* as well as in Köhler (2008: p. 341), is taken into account, since it causes the V range of *P. lansbergii* to overlap that of its congener completely. As in the case of the eyelash pitvipers, coloration seems by far to be the best character to separate these snakes.

Infraorder "Macrostomata" Ritgen 1828

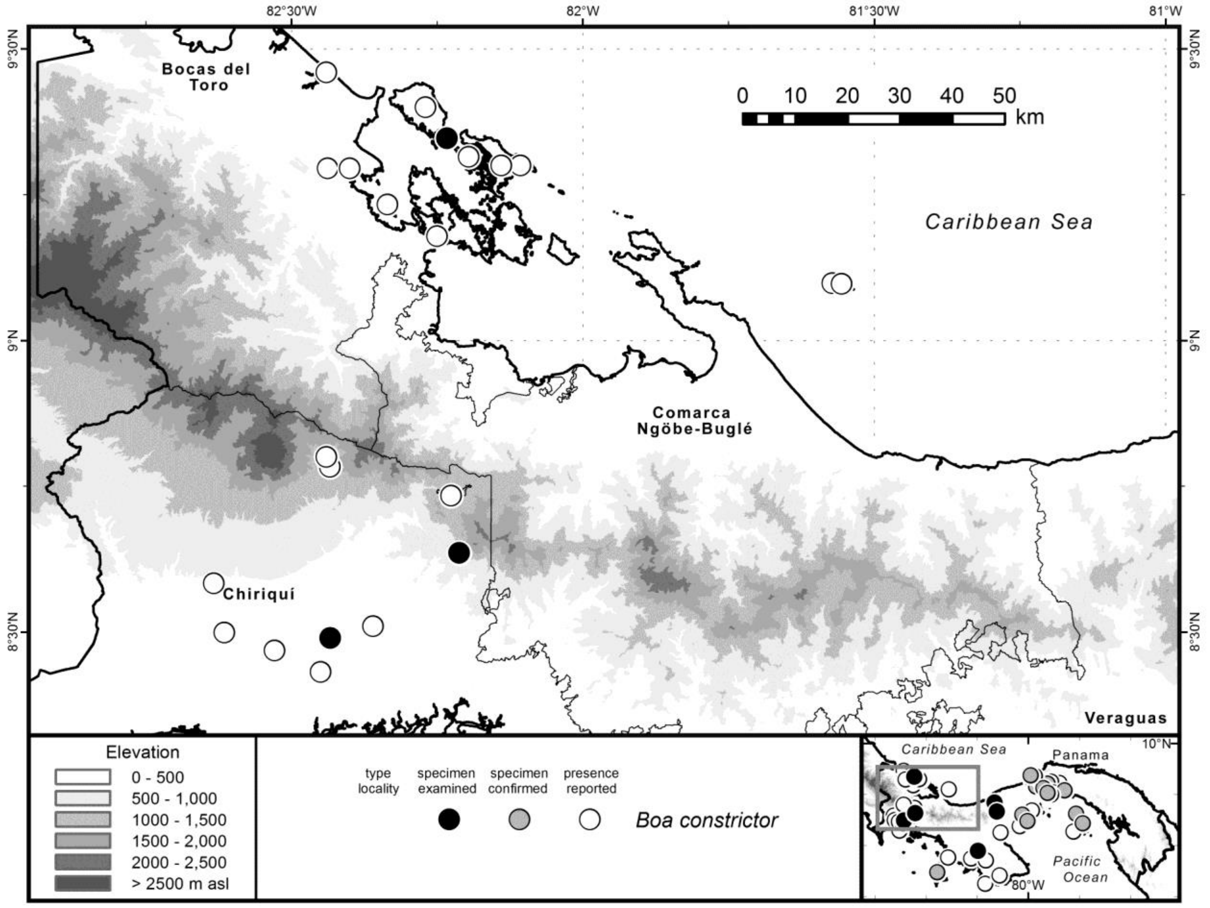
Family Boidae Gray 1825

Boa constrictor Linnaeus 1758

Boa Constrictor, Common Boa, Red-tailed Boa; Boa, Boa constrictora, Tragavenado, Bécquer
Figure 4.115E; Map 4.194.
Boa imperator: Cope (1876); Reynolds et al. (2013).
Constrictor constrictor: Dunn & Bailey (1939); Slevin (1942); Swanson (1945); Cochran (1946); Dunn (1947); Evans (1947); Taylor (1951, 1954).
Epicrates sabogae: Barbour (1906).

Syntypes. NHRM 10 and 20001, from Indiis (= South America).

Geographic distribution. Mexico to Peru, Bolivia, and Argentina, 0–1500 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from the Boquete and Fortuna areas, PNGDOTH, Valle de Antón, and PNAC, up to ca. 1320 m asl.



Map 4.194: Distribution of *Boa constrictor*.

Diagnosis. This very large snake (maximum TOL 4450 mm) with vertically elliptical pupils is unique among Panamanian snakes in having undivided subcaudals and the dorsal head surface entirely covered by numerous small smooth scales, smooth dorsals in 55 or more rows at midbody, 15 or more supralabials, as well as in lacking labial pits while having a conspicuous oblique dark postorbital stripe and usually also a dark middorsal stripe on the head.

Description. TOL to 4450 mm; SVL in Honduran specimens to 1568 mm; tail prehensile, short, TL/TOL = 0.10–0.17; D smooth, in (48–60)—(55–97)—(35–44) rows; V 225–283; SC 35–70, unidivided; SPL 15–25, separated from orbit; INL 17–28; ISO 14–18; SBO-SPL 0–1; cloacal scute entire; AP 0; eyes small, pupil vertically elliptical.

The hemipenis of *Boa constrictor* is a bilobed organ with a long naked pedicel; truncus naked proximally, flounced distally; apical regions mostly flounced but calyculate distally on asulcate side.

Coloration in life. D and L ground color gray to brown, with a series of large, rounded to rectangular dark middorsal blotches or transverse bars usually containing elongate light portions laterally and/or medially and becoming larger and differently shaped towards and on tail; a series of L blotches often with light centers; often D and/or L blotches variously fused among with D and/or L blotches; D surface of head usually with a median dark longitudinal stripe and possibly an interorbital bar; a conspicuous, oblique postocular stripe extending through eye and usually also a preocular stripe or blotch; frequently with dark bars on INL and below eye; V surfaces cream to gray with dark marikings; iris gray to brown except for dark horizontal bar.

The male SMF 89531 (Fig. 4.115E) was recorded as follows: D ground color Grayish Horn Color (91), grading into Olive-Gray (42) laterally and into Cream color (54) on tail; Sepia (119) saddles that contain Tawny Olive (123D) dorsolateral blotches and Grayish Horn Color (91) scales that become Mikado Brown (121C) on posterior portion of body and tail; tail often with reddish tonalities; venter Pearl Gray (81), grading into Cream Color (54) with Sepia (119) mottling on posterior part of body and tail.

Coloration in preservative. After 6 years in 70% ethanol, the coloration of SMF 89531 is similar to that in life, except that scales which lost their oberhäutchen are gray rather than brown.

Natural history notes. Primarily nocturnal but also diurnal, terrestrial and arboreal, feeding on vertebrates of different sizes. Between Los Planes and Valle de la Mina at about 997 m asl, SMF 89531 was crossing road to La Fortuna in the early afternoon. Two smaller specimens were encountered while moving along barbed wire fences delimiting pastures at night.

Remarks. Recently, Reynolds et al. (2013) proposed recognizing the CA subspecies *Boa constrictor imperator* (including *B. c. sabogae*) as a separate species. For now, I herein refrain from adopting this arrangement until a comprehensive study on the taxonomy and phylogeography of *B. constrictor* is available.

The records from E and W of the Comarca Ngöbe-Buglé render the presence of *Boa constrictor* therein plausible. My georeference for the specimens CAS 78816 from "vicinity north of Boquete" (Slevin 1942; Perez-Santos 1999) yields a SRTM elevation of 1323 m asl, which is slightly above the highest elevations of 1200 (Jaramillo et al. 2010) or 1250 m (Perez-Santos 1999) documented for Panama. Other than stated by Köhler (2008: p. 188), the subspecies *B. c. sabogae* (syntypes MCZ 6986, 2 specimens, from "Saboga Island"; Barbour 1906) does not occur on Taboga island near the mainland, but on the Archipiélago de las Perlas in the Gulf of Panama. It has further been reported from Isla Coiba (Perez-Santos & Martínez 1997; MCZ). Perez-Santos (1999: p. 54) stated it to occur "in the Pacific versant of the provinces of Panama and Veraguas" but only mapped it on Isla Coiba and Isla Saboga.

Even though it is quite a viper mimic, many people in western Panama recognize this snake to be nonvenomous and usually not harmful to humans. However, sympathy is forfeited as soon as it preys on a domestic animal. At least around Los Algarrobos, Panamanians of Chinese origin sometimes buy individuals of this species for food.

Corallus annulatus (Cope 1876)

Annulated Tree Boa; Boa arborícola, Boa arborícola anulada

Figure 4.115F; Map 4.195.

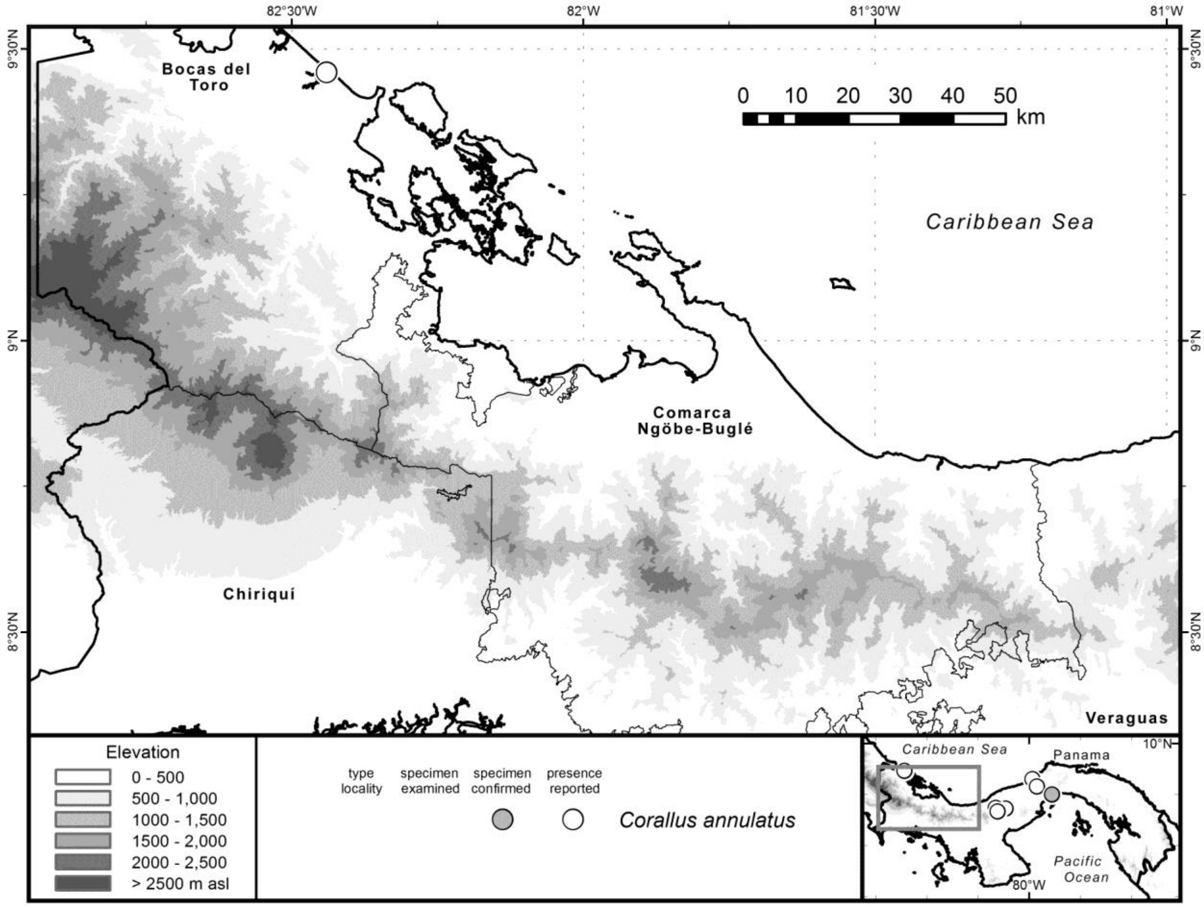
Boa annulata: Wettstein (1934); Taylor (1951, 1954).

Xiphosoma annulata: Brown (1893).

Xiphosoma annulatum: Cope (1876).

Holotype. USNM 32480, from Costa Rica as inferred by title of original publication.

Geographic distribution. Guatemala to Colombia and Ecuador, 0–1000 m asl. In Panama, along the western and central Caribbean versant including Bocas del Toro, Comarca Ngöbe-Buglé, and Veraguas, and the Pacific versant in central and eastern Panama. In the Cordillera Central, reported from PNGDOTH at ca. 800 m asl.



Map 4.195: Distribution of *Corallus annulatus.*

Diagnosis. This medium-sized to large snake (maximum TOL 1725 mm) with vertically elliptical pupils is readily recognized as a member of the genus *Corallus* by its undivided subcaudals, a laterally compressed body with smooth dorsals in 30 or more rows at midbody, the presence of conspicuous labial pits and 250 or more ventrals, enlarged smooth scales on snout and small smooth scales on the back of the head, as well as suboculars separating the supralabials from orbit. It differs from its only Panamanian congener, *C. ruschenbergerii,* in having 90 or fewer subcaudals (vs. 94 or more), the nasals separated from each other by contact between the rostral and internasals (vs. nasals in contact, separating rostral from IN), and in typically having rounded lateral markings (vs. typically rhomboid).

Description. TOL to 1725 mm; SVL in Honduran specimens to 1354 mm; tail prehensile, moderate, TL/TOL = 0.16–0.21; D smooth, in (40–41)—(47–57)—(25–30) rows; V 251–269; SC 76–90, unidivided; SPL 14–17, separated from orbit INL 16–21; ISO 10; SBO-SPL 0; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Corallus annulatus* is a slightly bilobed organ with a naked pedicel; truncus naked with a large papilla basally, with 4–5 fleshy flounces distally; apical region with papillate calyces.

Coloration in life. D and L ground color gray to brown, with a series of large, rounded to rectangular dark L blotches or transverse bars with large light centers that are offset or opposed and may be fused on middorsum; D surface of head usually without conspicuous markings; usually with 1–2 conspicuous, dark postocular and possibly a dark preocular stripe; labials usually lighter and unmarked; V surfaces beige, sometimes pinkish, with some dark mottling; iris gray to brown; darkening with age may obscure patterns very much; juveniles red, gray, or green.

Coloration in preservative. Similar to that in life, apart from that possibly present red tonalities fade with time.

Natural history notes. Nocturnal and arboreal, feeding on mammals, birds, and lizards.

Remarks. Together with the records from premontane elevations up to 1000 m asl in Costa Rica (Solorzano 2004, Sasa et al. 2010) and San San Pond Sak (ANAM 2004), the record from PNGDOTH (Ray 2009) renders the presence of *Corallus annulatus* in my study area as well as in the Comarca Ngöbe-Buglé and Veraguas plausible. In view of its altitudinal distributon, I regard its presence in Chiriquí around the Fortuna depression possible.

I further regard the presence of its congener *C. ruschenbergerii* (Cope 1876), called *C. hortulanus* by Savage (2002), in my study area as possible in view of its distribution all along the Pacific lowlands (also rendering its occurrence in the Comarca Ngöbe-Buglé plausible; see distribution map in Appendix 7) and its upper elevational limit reported as 525 m for Panama (Jaramillo et al. 2010) and 1000 m for the species as a whole (Köhler 2008).

Epicrates maurus Gray 1849

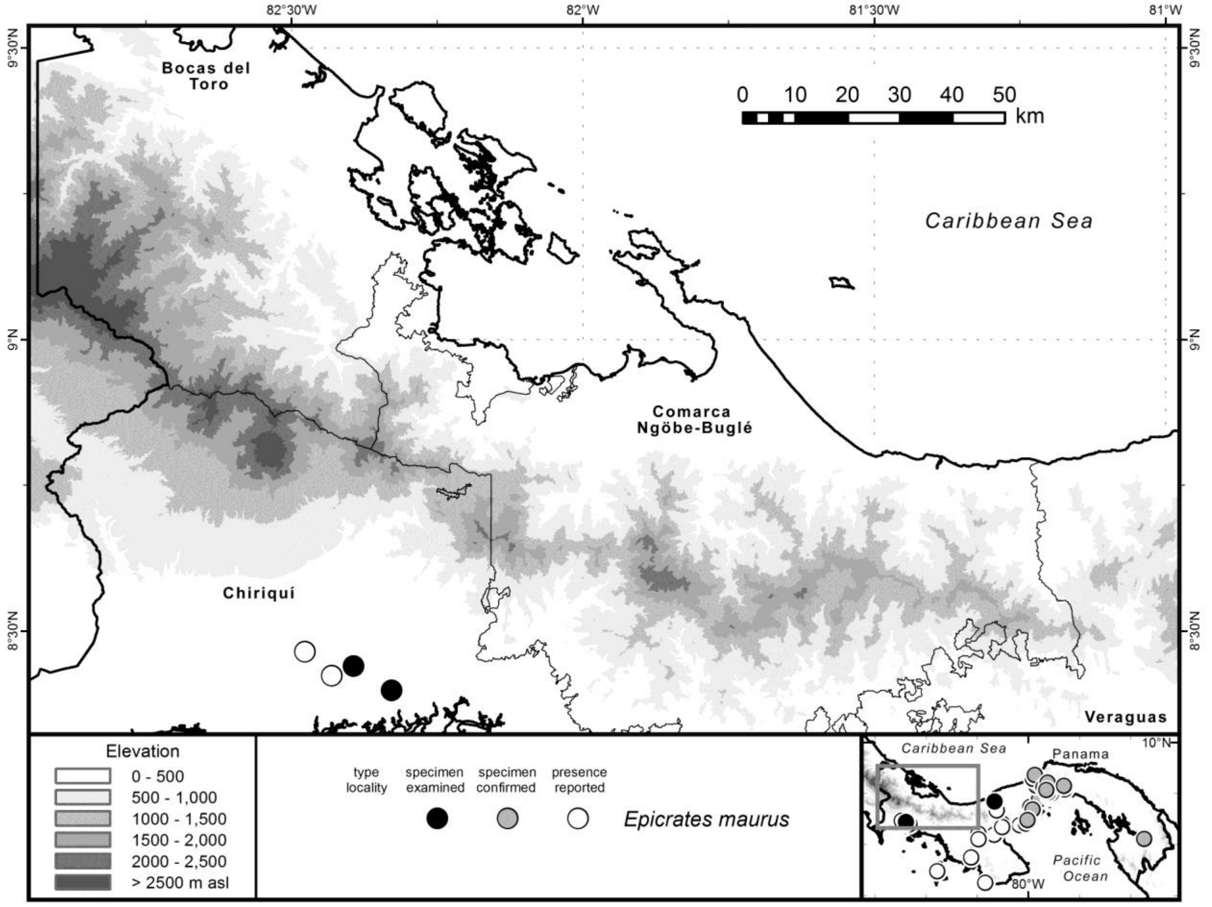
Brown Rainbow Boa, Rainbow Boa; Boa arcoiris, Boa tornasol

Figure 4.115G; Map 4.196.

Epicrates cenchria or *E. c. maurus:* Cope (1876); Dunn & Bailey (1939); Swanson (1945); Taylor (1951, 1954); Myers & Rand (1969); Peters & Orejas-Miranda (1970); Rand & Myers (1990); Auth (1994); Ibáñez et al. (1996, 2001); Perez-Santos & Martínez (1997); Martínez et al. (1999); Perez-Santos (1999); Young et al. (1999); Savage (2002); Solórzano (2004); ANAM (2005a); McDiarmid & Savage (2005); Fundación PA.NA.M.A. (2007); Köhler (2008); Hamad (2009); Ray (2009); Stadler (2010); McConnell (2014).

Epicrates cenchris: Cope (1899); Barbour (1906).

Holotype. BNHM 1946.1.10.40, adult male, from Venezuela (Passos & Fernandes 2008).



Map 4.196: Distribution of *Epicrates maurus.*

Geographic distribution. Nicaragua to Colombia, Venezuela, and Brazil, 0–1200 m asl. In Panama, along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas. In the Cordillera Central, reported from PNGDOTH and PNAC up to 800 m asl.

Diagnosis. This medium-sized to large snake (maximum TOL 1441 mm) with vertically elliptical pupils is readily recognized as a member of the genus *Epicrates,* and thus distinguished from all other Panamanian snakes, by its undivided subcaudals, a cylindrical body with smooth dorsals in 43 or more rows at midbody, the presence of shallow labial pits and fewer than 250 ventrals, enlarged smooth scales on snout and small smooth scales on the back of the head, as well as its supralabials bordering the orbit.

Description. (including data from Passos & Fernandes 2008) TOL to 1441 mm; SVL to 1280 mm; tail not prehensile, short, TL/TOL = 0.12; D smooth, in (30–39)—(43–53)—(24–31) rows; V 225–246; SC 40–61, unidivided; SPL 11–14, bordering orbit; INL 13–18; ISO 2–5; SBO 0; cloacal scute entire; AP 0; eyes moderate, pupil vertically elliptical.

The hemipenis of *Epicrates maurus* is a deeply bilobed organ with a naked pedicel; truncus with flounces; apical region papillate.

Coloration in life. D and L ground color yellow to light brown in juveniles, brown in adults; juvenile pattern contrasting, with a series of darker, large middorsal rings that may be broken up and their halves offset along the vertebral line; one to several series of dark L blotches or ocelli partly fused with each other and/or the middorsal markings or not; D surface of head usually with 3 dark longitudinal stripes (1 median, 2 L); usually with a dark postocular stripe extending from lower border of eye; labials lighter, SPL with dark markings; juvenile pattern gradually fades with age, elements becoming less contrasting and indistinct until large specimens appear mostly unicolor; V surfaces white except for ventrolateral continuations of L pattern; iris gray to brown.

Coloration in preservative. Similar to that in life.

Natural history notes. Nocturnal, terrestrial and semiarboreal, feeding on vertebrates.

Remarks. In a thorough morphological analysis of the *Epicrates cenchria* complex, Passos & Fernandes (2008) elevated the subspecies *E. cenchria maurus,* comprising all CA populations formerly referred to *E. cenchria,* to species level. The morphological data presented above is largely taken from their revision.

The presence of *Epicrates maurus* in my study area is rendered plausible by the record from PNGDOTH (Ray 2009) together with the species' upper elevational limit given as 820 m asl in Panama (Jaramillo et al. 2010) and 1200 m in Costa Rica (Savage 2002). Since the distribution in Costa Rica as mapped by the latter author and by Solórzano (2004) suggests a continuous occurrence of this species along the both versants of the Talamancan highlands, I regard its presence in Bocas del Toro and the Comarca Ngöbe-Buglé as plausible.

Ungaliophis panamensis **Schmidt 1933**

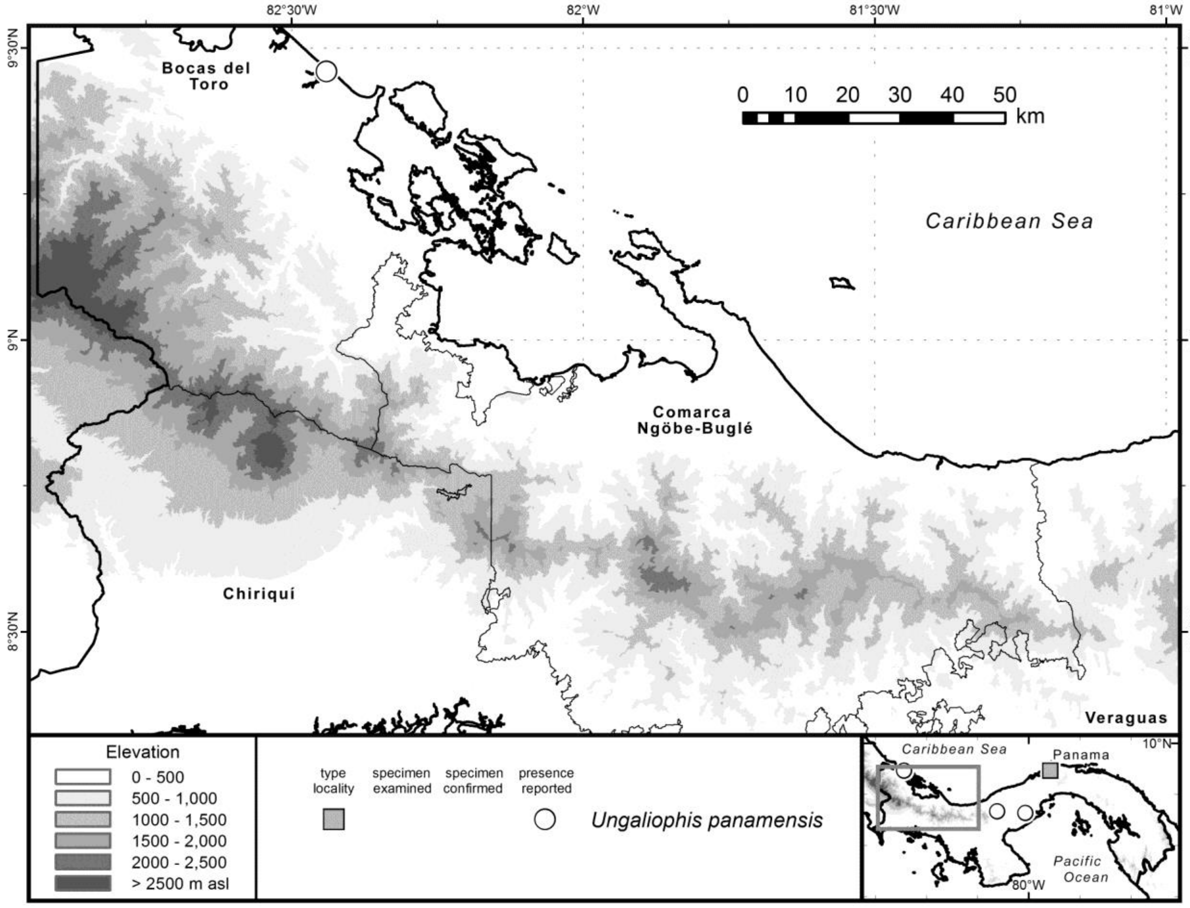
Panamanian Dwarf Boa, Central American Dwarf Boa, Southern Bromeliad Boa; Boa enana, Boa de las bromélias

Figure 4.115H; Map 4.197.

Ungaliophis panamansis: McConnell (2014).

Holotype. USNM 54059, from Cerro Brujo, Panama.

Geographic distribution. Nicaragua to Colombia, 0–2100 m asl. In Panama, probably along both versants throughout the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, but only recorded from scattered localities. In the Cordillera Central, reported from PNGDOTH and Valle de Antón, up to ca. 850 m asl.



Map 4.197: Distribution of *Ungaliophis panamensis.*

Diagnosis. This medium-sized snake (maximum TOL 850 mm) with vertically elliptical pupils is unique among Panamanian snakes in having undivided subcaudals, enlarged smooth plates on the anterior dorsal head surface including a single large prefrontal, smooth dorsals in 19–25 rows at midbody, and in having a dorsal pattern of alternating, rounded triangular, light-bordered dark paravertebral blotches.

Description. TOL to 850 mm; tail prehensile, short, TL/TOL = 0.08–0.10; D smooth, in ?—(19–25)—17 rows; V 226–254; SC 41–48, unidivided; SPL 7–9, bordering orbit; INL 8–11; PF 1; SBO 0; cloacal scute entire; AP 0; eyes small, pupil vertically elliptical.

The hemipenis of *Ungaliophis panamensis* is a bilobed organ that is naked basally and calyculate distally.

Coloration in life. D and L surfaces light gray to brown; body and tail with two series of light-bordered dark brown to black paravertebral blotches, most of which have more or less the shape of rounded triangles pointing upwards; blotches usually offset and alternating, but may fuse along or across body; flanks with several series of smaller, mostly light-bordered dark L blotches; irregular dark mottling and lines in interspaces between the blotches; D surface of head with a large dark marking bifurcating posteriorly to continue as 2 dorsolateral stripes somewhat onto neck; usually a dark internasal bar; a conspicuous broad, oblique postocular dark stripe and usually a narrow, horizontal upper dark stripe that extends onto neck; V surfaces light gray to brown, mottled with dark brown and with large portions of the ventrolateral series of dark blotches.

Coloration in preservative. Similar to that in life.

Natural history notes. Nocturnal and arboreal, but also found on the ground. While Savage (2002) attributed its rarity in collections to a strictly arboreal canopy-dwelling lifestyle in undisturbed forests, Solórzano reported finding specimens that were feeding on dead frogs on a paved road. In captivity accepting lizards and mice.

Remarks. *Ungaliophis panamensis* has been reported to occur at low and premontane elevations along both versants in Costa Rica (Savage 2002; Solórzano 2004). This, together with the records from PNGDOTH (Ray 2009; CHP), renders the species' presence my study area as well as in Chiriquí, the Comarca Ngöbe-Buglé, and Veraguas plausible.

Infraorder "Scolecophidia" Cope 1864

Family Anomalepididae Taylor 1939

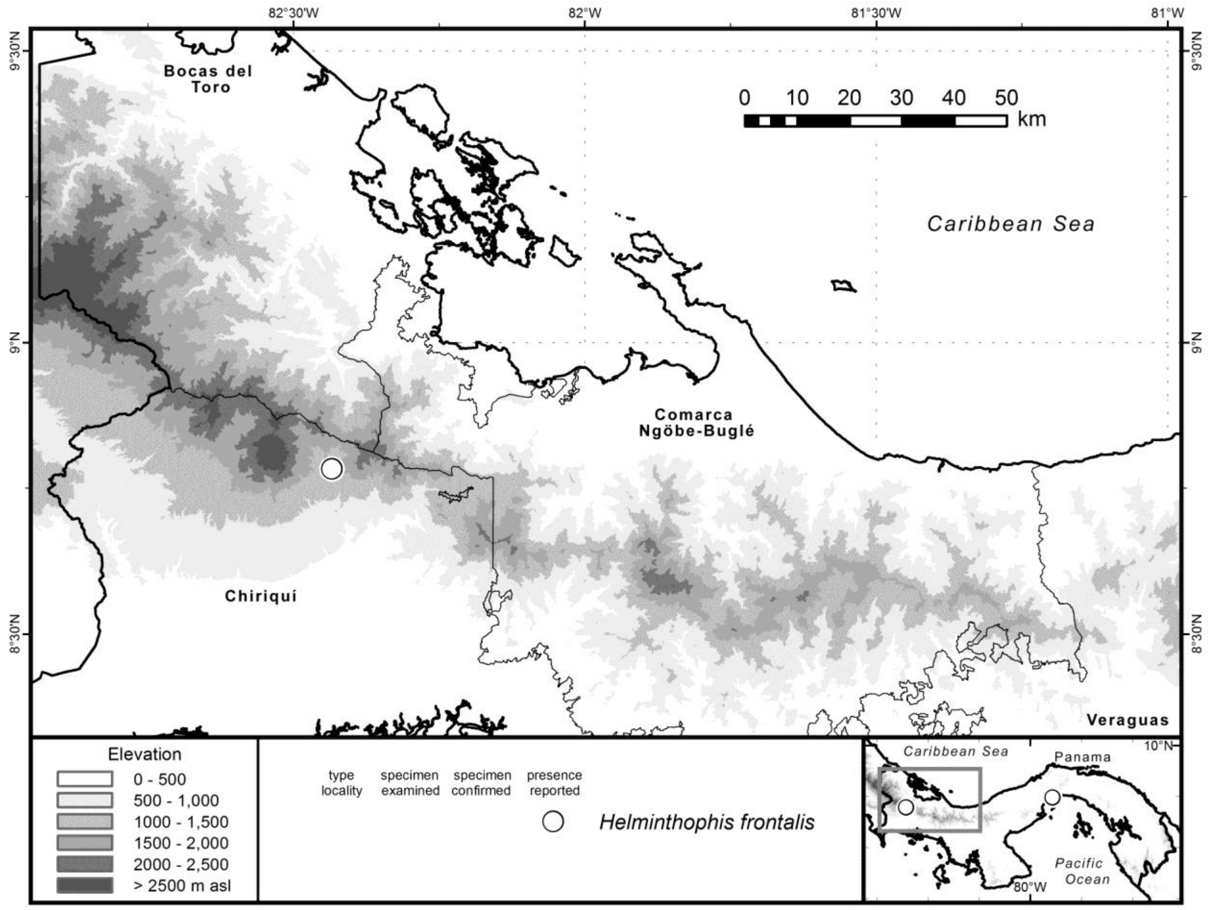
Helminthophis frontalis (Peters 1860)

Costa Rica Blindsnake, Northern Antsnake, Pink-headed Blindsnake; Culebrita ciega, Hormiguera

Map 4.198.

Syntypes. ZMB 3823 and 3925, from Costa Rica.

Geographic distribution. Costa Rica and Panama, 70–1440 m asl. In Panama, probably present throughout western and central portions of the country including Bocas del Toro, Chiriquí, Comarca Ngöbe-Buglé, and Veraguas, but only recorded from two localities. In the Cordillera Central, reported from Boquete around 1120–1220 m asl.



Map 4.198: Distribution of *Helminthophis frontalis.*

Diagnosis. This very small snake (maximum TOL 274 mm) is immediately recognized as a scolecophidian or blindsnake by its wormlike appearance, reduced eyes visible as dark spots under the cephalic scales, and homogenously cycloid scales all around body and tail. *Helminthophis frontalis* differs from Panamanian blindsnakes of the family Leptotyphlopidae in having 22 scales around midbody (vs. 14). It differs from the other two anomalepidid species occurring in Panama in having the light head cap extending well posterior to the enlarged head plates and usually rather sharply demarcated (vs. beginning to grade into darker body color near enlarged head plates), elongate prefrontals whose posterior contact separates the rostral from the cycloid frontal (vs. small PF separated by contact between rostral and frontal in *Liotyphlops albirostris,* large angular PF broadly in contact medially, separating rostral from frontal in *Anomalepis mexicanus*), and 470–480 dorsal scales from head to tail tip (vs. 267–272 in *A. mexicanus,* 370–455 in *L. albirostris*).

Description. TOL to 274 mm; tail very short, about as long as head, with terminal spine; supracephalic scales enlarged, with rounded posterior margins; PF 2, separating rostral from frontal; frontal enlarged, rounded, about twice the size of dorsals; D cycloid, smooth, in 22 rows at midbody; 470–480 transverse rows of D from head to tip of tail; no enlarged precloacal scales.

The hemipenis of *Helminthophis frontalis* remains undescribed to my knowledge.

Coloration in life. Body and tail uniform dark brown to black, glossy; head, neck, and usually cloacal region yellow to pink in life.

Coloration in preservative. Similar to that in life, apart from that the light tonalities fade to white or yellow with time

Natural history notes. Fossorial, probably feeding on ants and termites as well as their eggs and larvae, like some of its better studied relatives.

Remarks. The presence of *Helminthophis frontalis* in my study area is documented by the specimen UMMZ 57974 from "Boquete" (Dunn 1947; Perez-Santos 1999). My georeference for this specimen yields a SRTM elevation of 1121 m asl, while the elevation inferred from the "headquarters" mentioned by Dunn (1947) is 1220 m. Both values differ slightly from the value of 1200 m given by Jaramillo et al. (2010), which has probably been as arbitrarily chosen as mine. The only other record from Panama which I could trace is MCZ 17849 from Ancón, for which my georeference yields a SRTM elevation of 71 m which is the lowest elevation reported for this species (Wilson & Johnson 2010). The records from Ancón, Boquete, and the Caribbean versant of Costa Rica (Savage 2002) render the species' presence in Bocas del Toro, the Comarca Ngöbe-Buglé, and Veraguas plausible.

Other species of blindsnakes whose occurrence in my study area I consider possible in view of their altitudinal ranges are *Anomalepis mexicanus* which is thought to range along the Caribbean versant and *Liotyphlops albirostris* which has been recorded from several localities in Pacific western Panama as well as from PNGDOTH (Savage 2002; Ray 2009; see distribution maps in Appendix 7).

Figure 4.94: Non-squamate reptiles and anguid lizards of the study area. (A) *Trachemys grayi,* adult from Los Algarrobos; (B) *Rhinoclemmys annulata,* SMF 89034 from Dos Bocas de Bartola, Nicaragua; (C) *Cryptochelys leucostoma* from Greytown, Nicaragua; (D) *Kinosternon scorpioides* from Los Algarrobos; (E) *Caiman crocodilus,* juvenile from Finca La Providencia; (F) *Celestus* sp., SMF 90177 from Lost & Found Ecohostel, RFLF; (G, H) *Diploglossus bilobatus,* (G) female SMF 89547 and (H) juvenile MHCH 2310 from Cerro Mariposa.

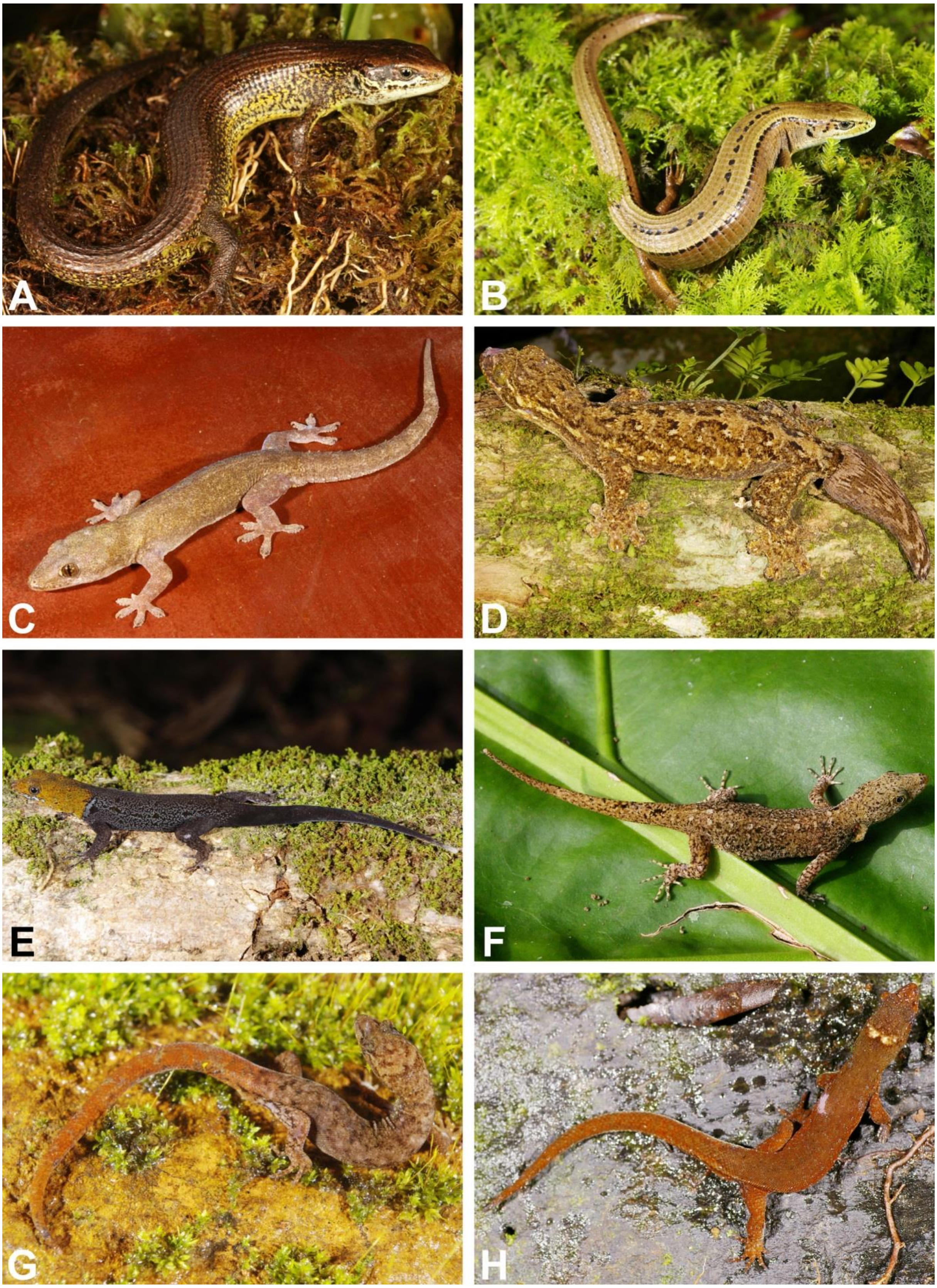


Figure 4.95: Lizards of the study area: Anguidae, Gekkonidae, Phyllodactylidae, and Sphaerodactylidae. (A, B) *Mesaspis monticola,* (A) male from Cerro Totuma, photo by AH, and (B) female SMF 90199 from Volcán Barú; (C) *Hemidactylus frenatus,* male from Los Algarrobos; (D) *Thecadactylus rapicauda,* female SMF 89601 from Volante; (E, F) *Gonatodes albogularis,* (E) male SMF 91552 from Finca La Providencia, and (F) female from Río Frío, Nicaragua; (G) *Lepidoblepharis xanthostigma,* male SMF 91558 from Alto Tólica; (H) *Lepidoblepharis* sp. 1, male SMF 89963 from Cerro Negro (dorsal skin on left side damaged).

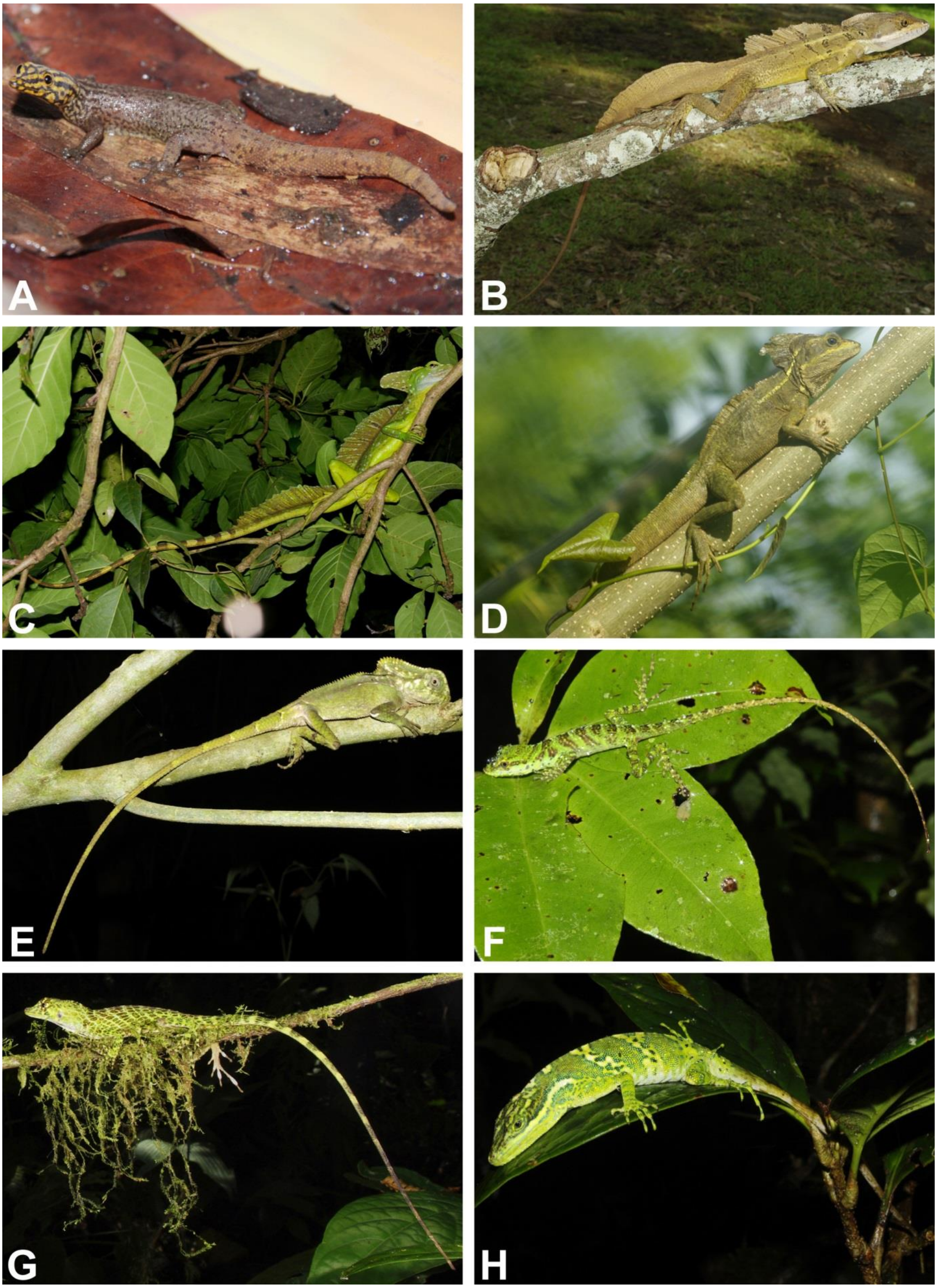


Figure 4.96: Lizards of the study area: Sphaerodactylidae, Corytophanidae, and Dactyloidae. (A) *Sphaerodactylus homolepis,* male from Costa Rica, photo by JV; (B) *Basiliscus basiliscus,* male SMF 90171 from Los Algarrobos; (C) *B. plumifrons,* male from Río Frío, Nicaragua; (D) *B. vittatus,* male from Bastimentos; (E) *Corytophanes cristatus,* male SMF 89767 from Cerro Negro; (F) *Dactyloa casildae,* juvenile from Cerro Pata de Macho, RFLF; (G) *D. frenata,* male SMF 91460 from Willie Mazú; (H) *D. ginaelisae,* adult from Cerro Saguí near type locality.

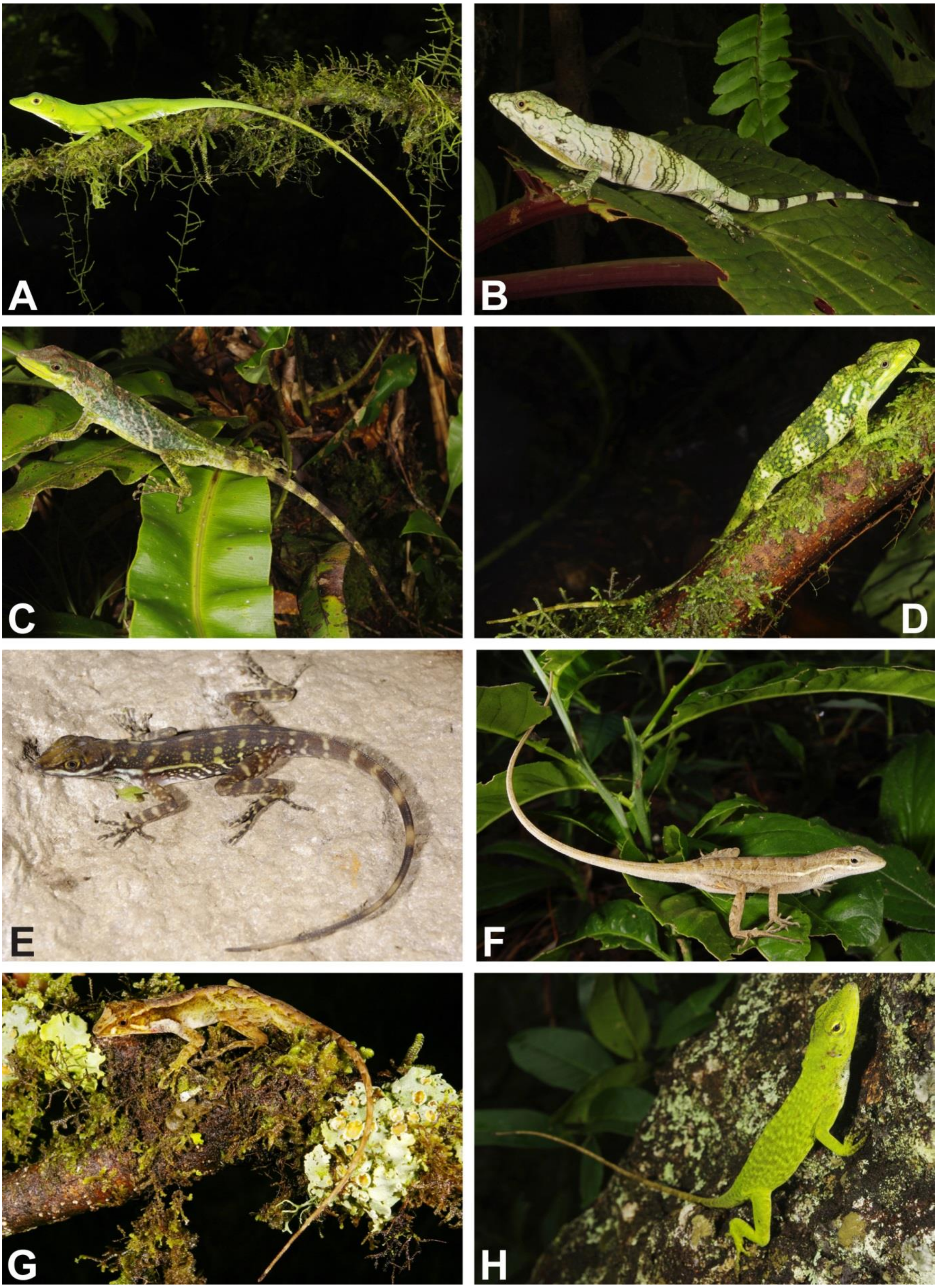


Figure 4.97: Lizards of the study area: Dactyloidae. (A) *Dactyloa ibanezi,* male SMF 91476 from Willie Mazú; (B) *D. insignis,* juvenile female SMF 91477 from Willie Mazú; (C) *D. kunayalae,* male SMF 91484 from headwaters of Río Chiriquí Malí; (D) *D. microtus,* young male SMF 91500 from Río Changena; (E) *Norops aquaticus,* male SMF 89667 from Santa Clara; (F) *N. auratus,* female SMF 89668 from Los Algarrobos; (G) *N. benedikti,* male paratype SMF 89507 from Jurutungo; (H) *N. biporcatus,* female SMF 91446 from Alto Tólica.

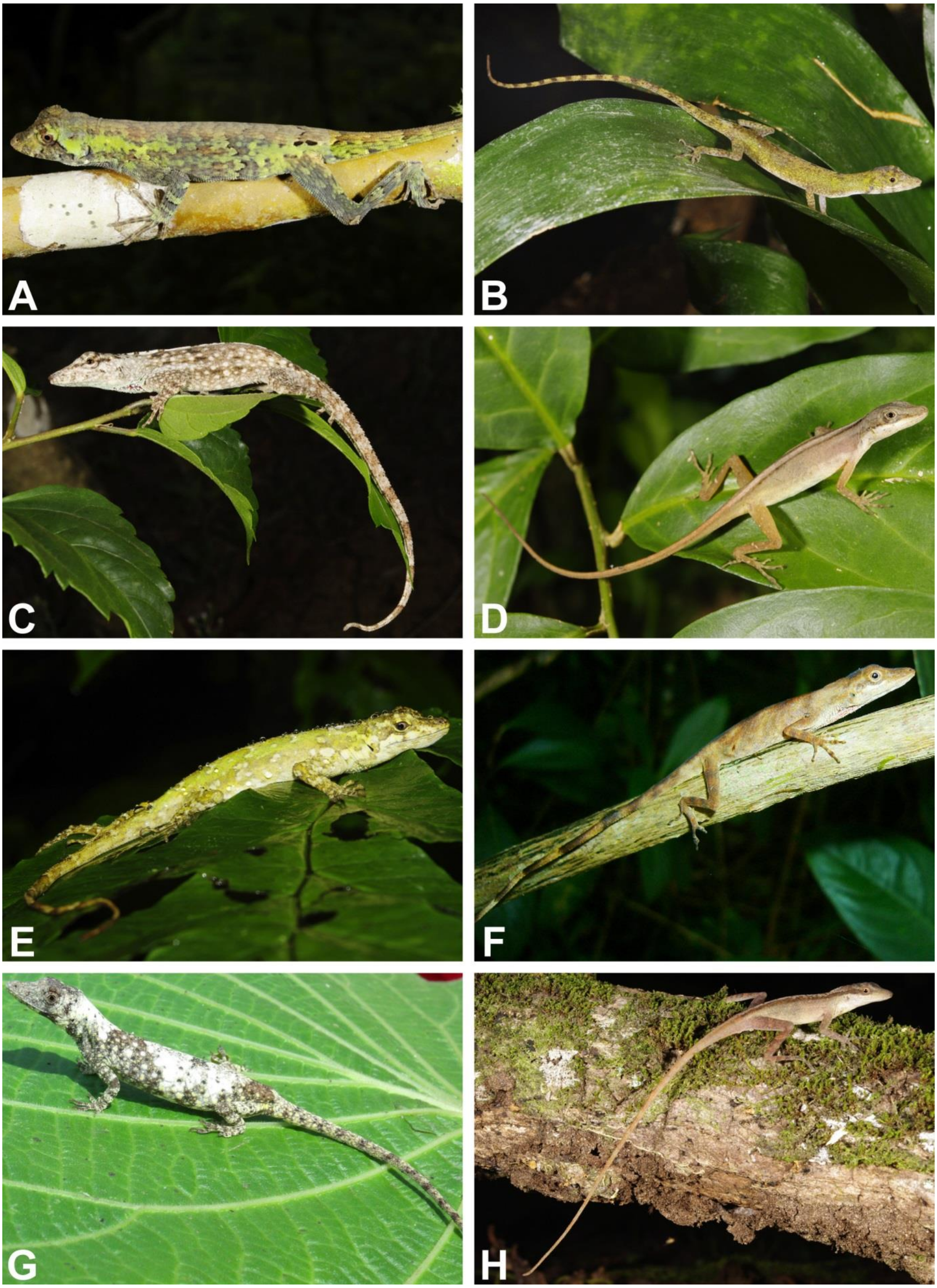


Figure 4.98: Lizards of the study area: Dactyloidae. (A) *Norops capito,* male MHCH 2117 from Potrerillos Arriba; (B) *N. carpenteri,* female from Costa Rica; (C) *N. charlesmyersi,* male holotype SMF 89688 from Los Algarrobos; (D) *N. cryptolimifrons,* female SMF 89689 from road to Almirante, km 24.5; (E) *N. datzorum,* female MHCH 2149 from La Nevera; (F) *N. fortunensis,* male SMF 86408 from RFLF, photo by MP; (G) *N. fungosus,* female MVUP 2095 from RFLF, photo by John Phillips; (H) *N. gaigei,* male SMF 91529 from Finca La Providencia.

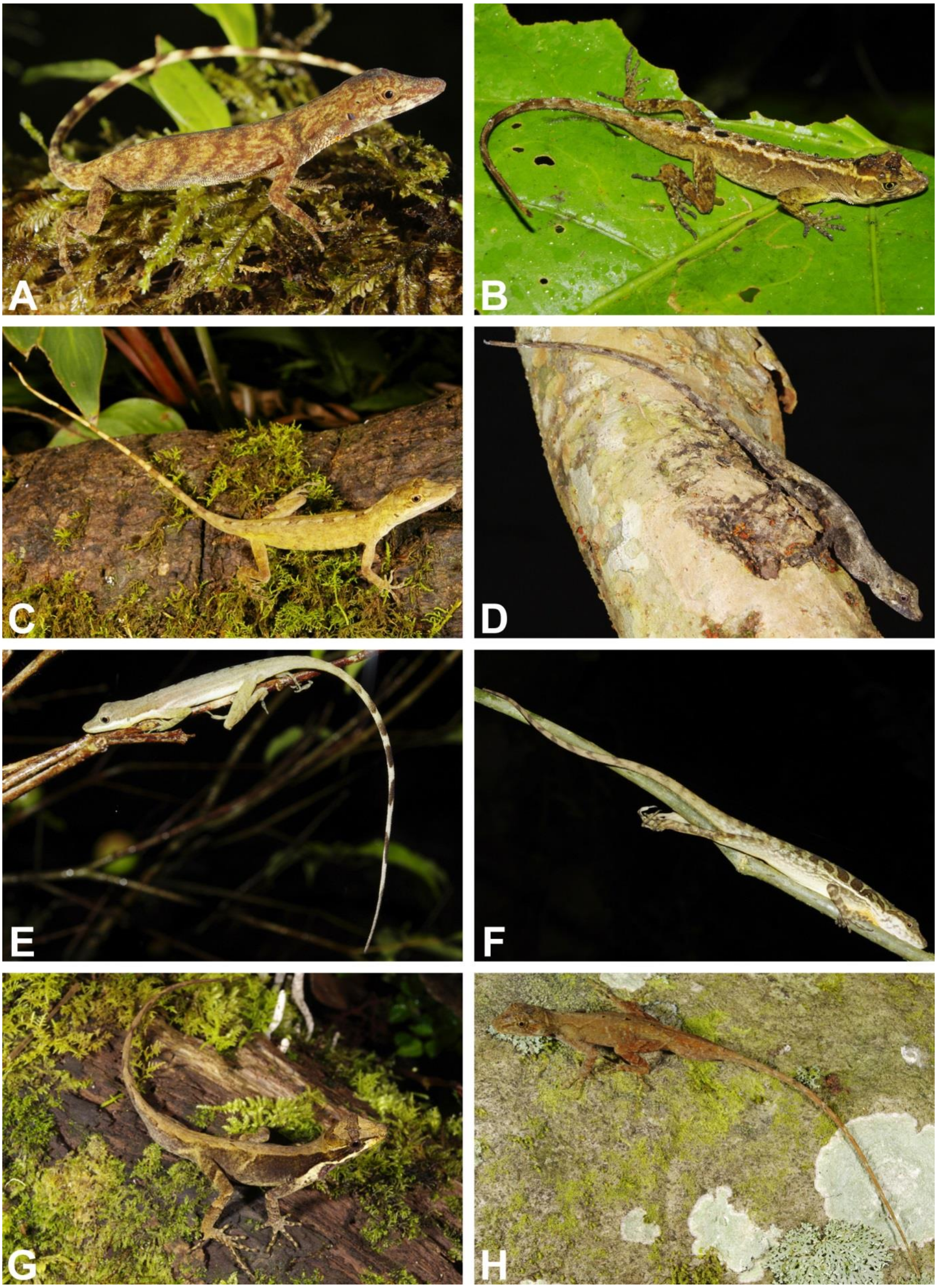


Figure 4.99: Lizards of the study area: Dactyloidae. (A) *Norops gruuo,* male MHCH 2162 from Cerro Mariposa; (B) *N. humilis,* male MHCH 2174 from Cerro Mariposa; (C) *N. kemptoni,* female SMF 89462 from Lost & Found Ecohostel; (D) *N. lemurinus,* male MHCH 2197 from San San Pond Sak; (E) *N. limifrons,* male MHCH 2206 from headwaters of Río Chiriquí Malí; (F) *N. lionotus,* male from Cerro Mariposa; (G) *N. magnaphallus,* male SMF 89731 from Sendero Los Quetzales; (H) *N. pachypus,* male MHCH 2251 from Jurutungo.

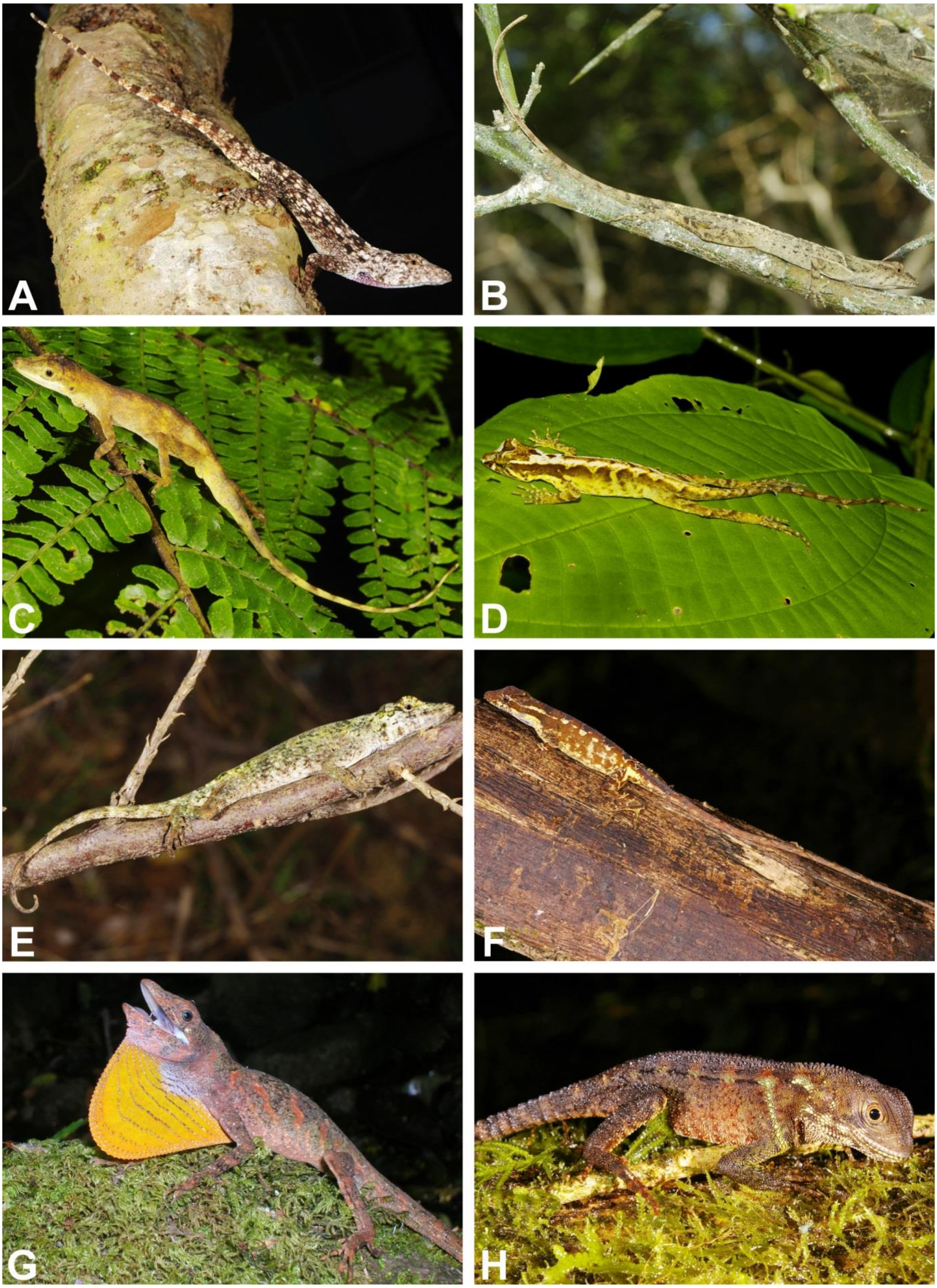


Figure 4.100: Lizards of the study area: Dactyloidae and Hoplocercidae. (A) *Norops pentaprion,* male SMF 90150 from San San Pond Sak; (B) *N. polylepis,* male MHCH 2260 from Cabecera de Cochea; (C) *N. pseudokemptoni,* male MHCH 2271 from Río Flor; (D) *N. pseudopachypus,* male from La Nevera; (E) *N. salvini,* female MHCH 2291 from Jurutungo; (F) *N. vittigerus,* female SMF 89528 from Río Chilagres; (G) *N. woodi,* male SMF 85435 from Río Chevo, photo by JS; (H) *Enyalioides heterolepis,* juvenile SMF 89558 from Cerro Negro.

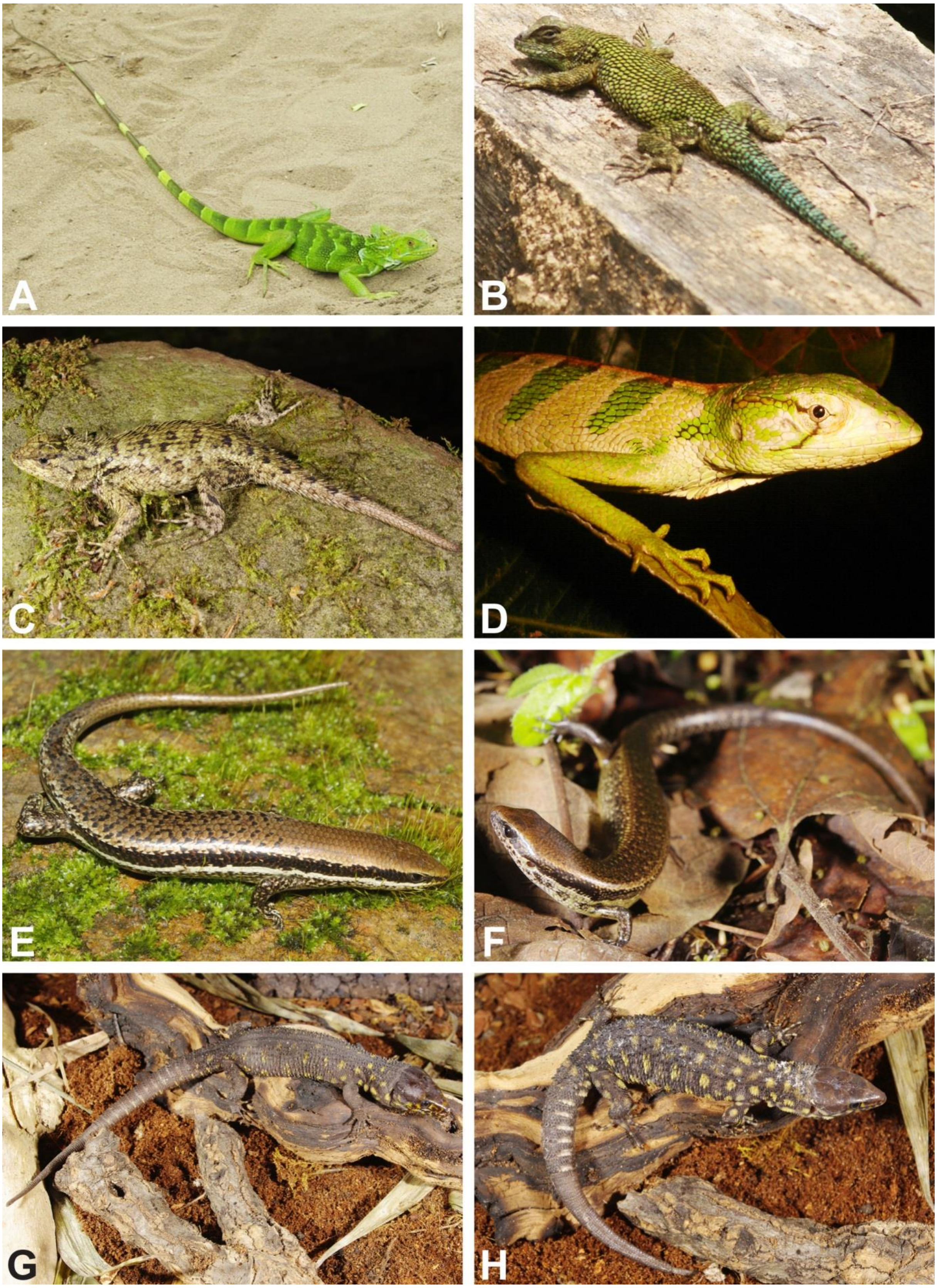


Figure 4.101: Lizards of the study area: Iguanidae, Phrynosomatidae, Polychrotidae, Mabuyidae, Sphenomorphidae, and Xantusiidae. (A) *Iguana iguana* from Peninsula Burica; (B, C) *Sceloporus malachiticus,* (B) male from Cerro Totuma, photo by AH, and (C) female SMF 89785 from Sendero La Cascada; (D) *Polychrus gutturosus* from RFLF, photo by AB; (E) *Marisora unimarginata* from Guayabito; (F) *Scincella cherriei,* MHCH 2368 from Santa Clara; (G) *Lepidophyma flavimaculatum,* captive animal from Costa Rica; (H) *L. reticulatum,* captive animal from Carara, Costa Rica.

Figure 4.102: Lizards of the study area: Gymnophthalmidae. (A) *Anadia ocellata,* male SMF 90095 from Santa Clara; (B) *Bachia blairi* from Río Chiriquí Viejo, photo by MP; (C) *Echinosaura panamensis,* SMF 89557 from Cerro Mariposa; (D) *Gymnophthalmus speciosus* from Cerro Platillón, Venezuela; (E) *Leposoma southi,* female SMF 90193 from San San Pond Sak; (F) *Potamites apodemus,* male SMF 89779 from Santa Clara; (G) *Ptychoglossus festae* from Serranía de Majé, photo by AB; (H) *P. plicatus,* male SMF 91576 from between Río Clarito and Ro Changena.

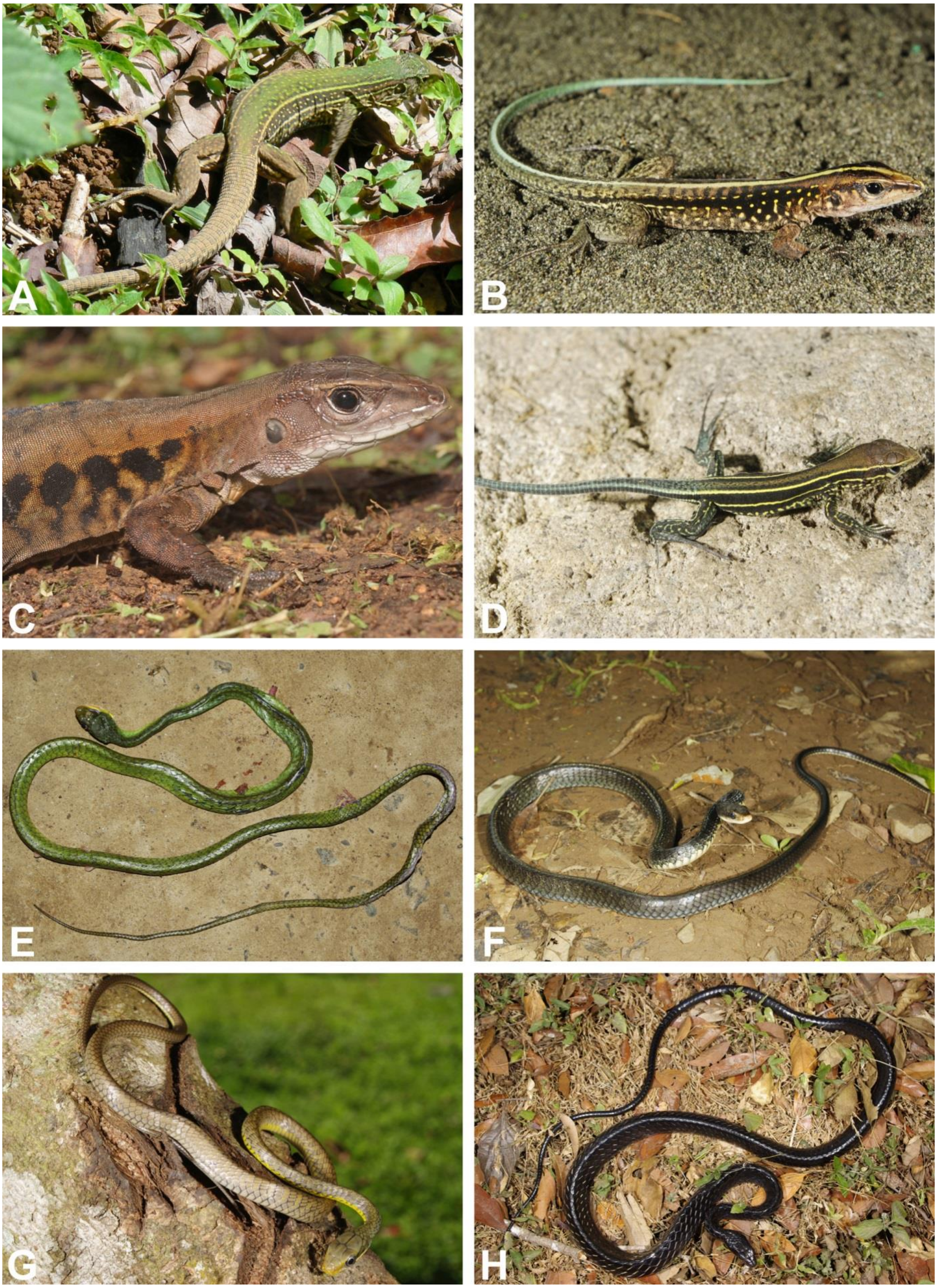


Figure 4.103: Lizards (Teiidae) and Snakes (Colubridae) of the study area. (A) *Ameiva praesignis* from Los Algarrobos, photo by Meike Piepenbring; (B) *Holcosus festivus,* juvenile SMF 90093 from San San Pond Sak; (C) *H. leptophrys* from Cana, Darién, photo by AB; (D) *H. quadrilineatus,* juvenile SMF 91444 from Santa Clara; (E) *Chironius exoletus,* SMF 91535 found dead on road at Valle de la Mina; (F, G) *C. flavopictus,* (F) female SMF 91534 from Los Valles, and (G) male juvenile SMF 89768 from road to Almirante, km 35.5; (H) *C. grandisquamis,* male SMF 89766 from Cabecera de Cochea.

Figure 4.104: Snakes of the study area: Colubridae. (A) *Dendrophidion apharocybe* from Altos del María, photo by Julie Ray; (B) *D. clarkii* from Serranía de Pirre, Darién, photo by AB; (C) *D. paucicarinatum,* female SMF 91538 from road Cerro Colorado – Raton; (D) *D. percarinatum,* SMF 88974 from Boca de San Carlos, Nicaragua; (E) *Drymarchon melanurus* from Bosawas, Nicaragua, photo by JS; (F) *Drymobius margaritiferus* from Davíd, photo by AB; (G) *D. rhombifer* from Río Squí, photo by AB; (H) *Lampropeltis triangulum,* male SMF 90188 from Santa Clara.

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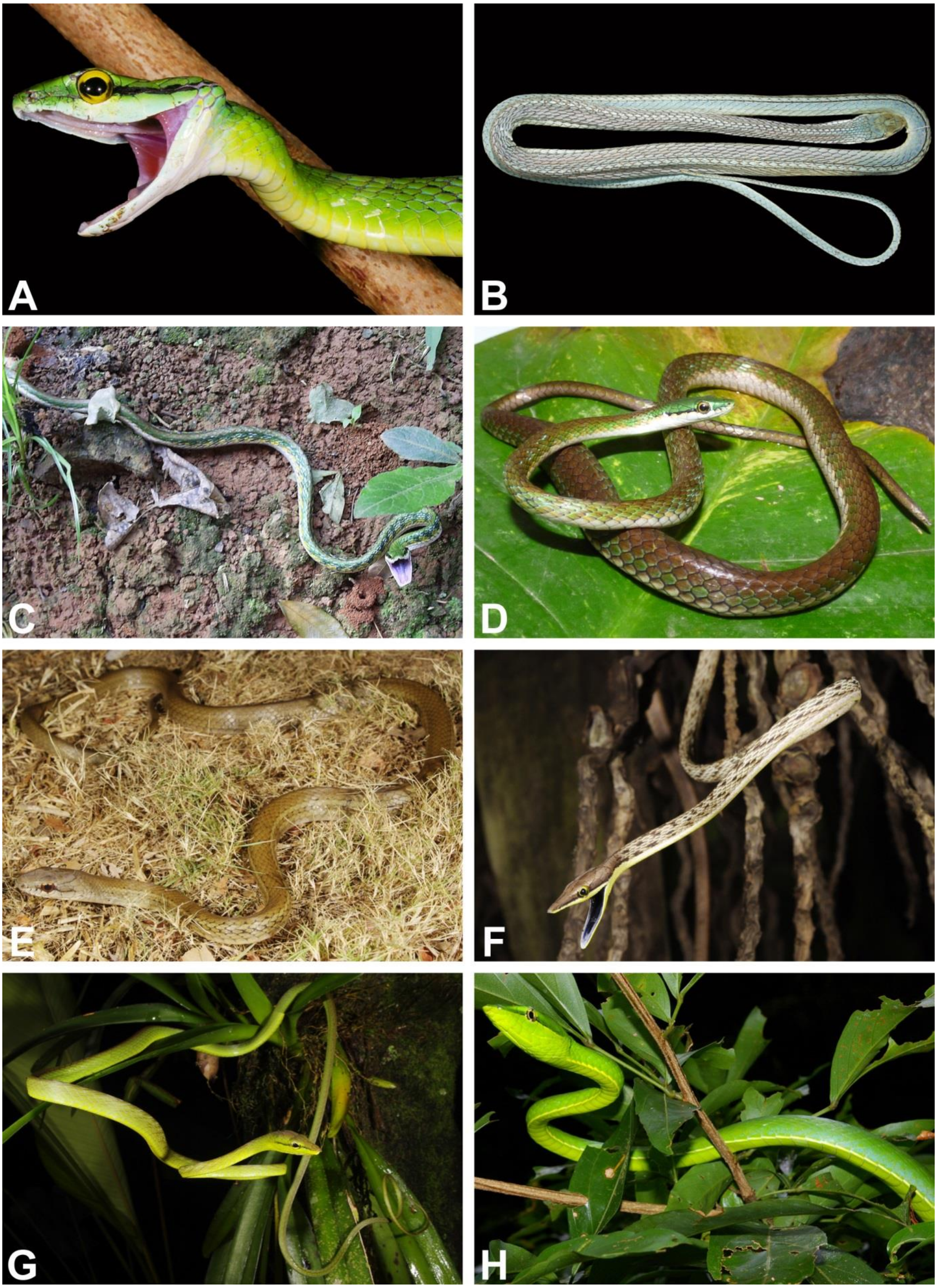

Figure 4.105: Snakes of the study area: Colubridae. (A) *Leptophis ahaetulla* from Los Algarrobos; (B) *L. depressirostris,* SMF 67350 from Costa Rica after 43 years in preservative; (C) *L. nebulosus* from PNGDOTH, photo by Julie Ray; (D) *L. riveti* from Donoso, Colón, photo by MP; (E) *Mastigodryas melanolomus,* male SMF 89777 from Lost & Found Ecohostel; (F) *Oxybelis aeneus,* male SMF 90204 from San San Pond Sak; (G) *O. brevirostris,* male 91571 from above El Paredón; (H) *O. fulgidus,* JS 422 from Dos Bocas de Bartola, Nicaragua.

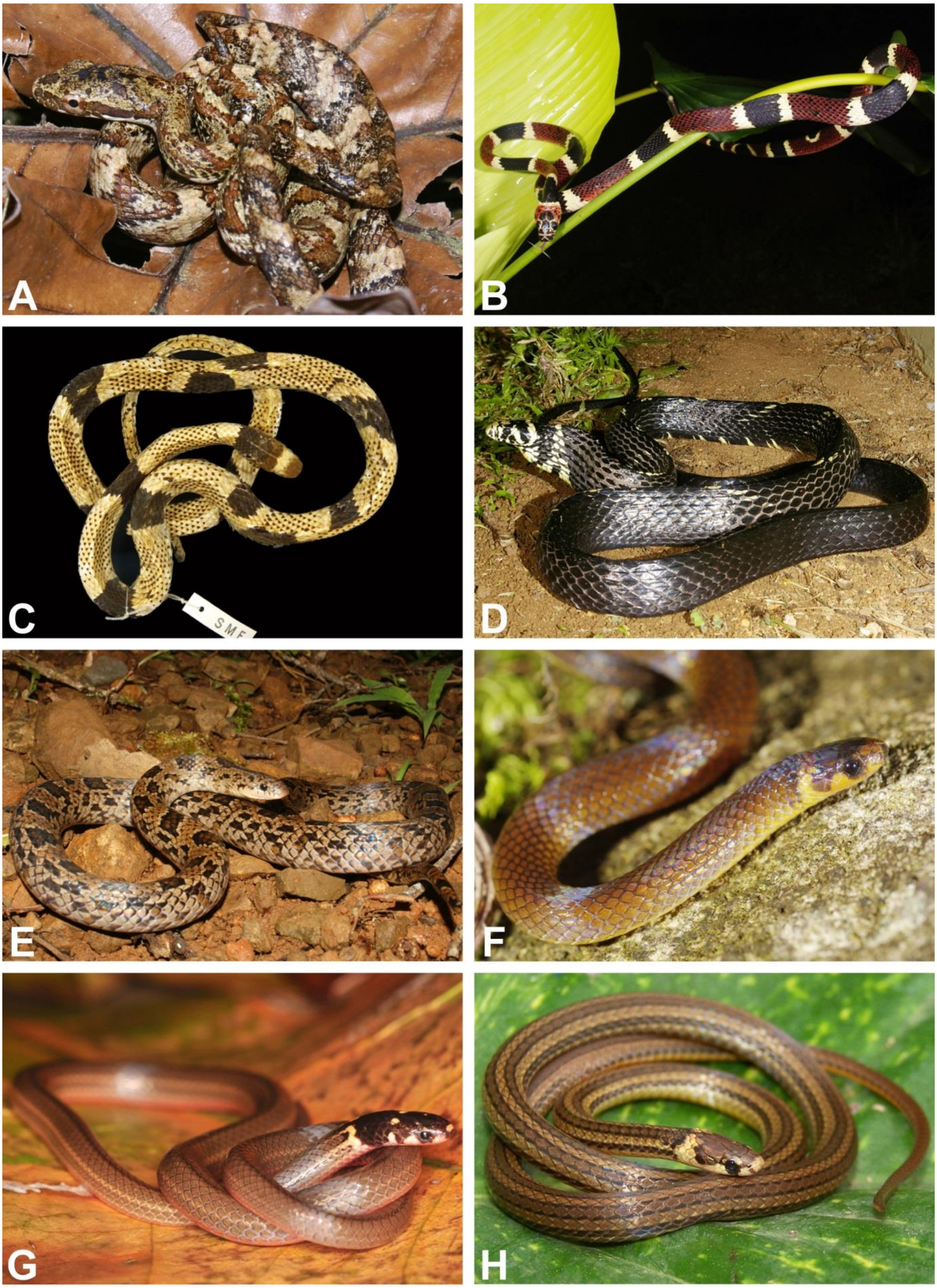

Figure 4.106: Snakes of the study area: Colubridae. (A) *Phrynonax poecilonotus,* juvenile from Petaquilla, Donoso, Colón, photo by AB; (B) *Rhinobothryum bovallii,* female SMF 91577 from above el Paredón; (C) *Scaphiodontophis venustissimus,* SMF 76284 from Penshurst, Costa Rica, after at least 43 years in preservative; (D) *Spilotes pullatus,* male SMF 89600 from Los Algarrobos; (E) *Stenorrhina degenhardtii,* AH 563 from Lost & Found Ecohostel, photo by AH; (F) *Tantilla alticola,* female SMF 91582 from Lost & Found Ecohostel; (G) *T. armillata* from Volcán Masaya, Nicaragua, photo by J. G. Martinez Fonseca; (H) *T. reticulata,* SMF 88191 from Greytown, Nicaragua, photo by Lenin Obando.

Figure 4.107: Snakes of the study area: Colubridae and Dipsadidae. (A) *Tantilla supracincta* from La Fortuna San Carlos, Costa Rica, photo by Cesar Barrio-Amorós; (B) *Amastridium veliferum,* SMF 90092 from RFLF; (C) *Clelia clelia* from Krin Krin, Nicaragua, photo by JS; (D) *C. equatoriana,* male SMF 89923 from Cerro Negro, photo by AC; (E) *Coniophanes fissidens,* SMF 88973 from Río Frío, Nicaragua; (F) *Dipsas articulata,* male SMF 89952 from Cerro Negro; (G) *D. temporalis* from Cerro Negro; (H) *Enuliophis sclateri* from Petaquilla, Colón, photo by AB.

Figure 4.108: Snakes of the study area: Dipsadidae. (A) *Enulius flavitorques* from Las Lomas near Davíd, photo by AB; (B) *Erythrolamprus bizona,* GK 3496 from Volcán Miravalles, Costa Rica, photo by GK; (C) *E. epinephelus,* female SMF 89581 from RFLF; (D) *E. mimus* from Boca San Carlos, Nicaragua, photo by JS; (E) *Geophis brachycephalus,* male SMF 90181 from headwaters of Río Chiriquí Malí; (F) *G. godmani,* male MHCH 2318 from Jurutungo; (G) *G. hoffmanni,* male SMF 91549 from Santa Clara; (H) *G. talamancae,* female SMF 89567 from Jurutungo.

Figure 4.109: Snakes of the study area: Dipsadidae. (A) *Geophis tectus,* female SMF 91551 from Willie Mazú; (B) *Geophis* sp., female SMF 89560 from RFLF; (C) *Hydromorphus concolor* from Costa Rica, photo by JV; (D) *Imantodes cenchoa,* male MHCH 2335 from Willie Mazú; (E) *I. gemmistratus* from Morgan's Rock, Nicaragua, photo by JS; (F) *I. inornatus*, photo by AB; (G) *Leptodeira annulata,* juvenile SMF 91561 from Guayabito; (H) *L. septentrionalis,* male SMF 90194 from Lost & Found Ecohostel.

Figure 4.110: Snakes of the study area: Dipsadidae. (A) *Ninia maculata,* SMF 90203 from Santa Clara; (B) *Nothopsis rugosus* from Nurra Madugandí, photo by AB; (C) *Oxyrhopus petolarius,* juvenile from Los Algarrobos; (D) *Pliocercus euryzonus,* SMF 89974 from Cerro Negro; (E) *Pseudoboa neuwiedii,* found dead on road at Las Lajas, photo by AH; (F) *Rhadinaea calligaster,* female SMF 89592 from Jurutungo; (G) *R. decorata,* GK 3444 from Isla Colón, photo by GK; (H) *R. sargenti,* holotype MCZ 42788 from Pequení-Esperanza ridge, photo by GK.

Figure 4.111: Snakes of the study area: Dipsadidae. (A) *Rhadinaea vermiculaticeps* from Río Blanco, Coclé, photo by Andrew Hein; (B) *Rhadinella godmani,* male SMF 89594 from Jurutungo; (C) *Sibon annulatus,* young male MHCH 2365 from Cerro Mariposa; (D) *S. argus* from BPPS, photo by MP; (E) *S. lamari* from Donoso, Colón, photo by MP; (F) *S. longifrenis,* female SMF 91581 from Cerro Mariposa; (G) *S. nebulatus,* juvenile MHCH 2367 from road to Almirante, km 53; (H) *S. noalamina,* male holotype SMF 91539 from headwaters of Río Chiriquí Malí.

Figure 4.112: Snakes of the study area: Dipsadidae. (A) *Sibon perissostichon,* female holotype SMF 88716 from RFLF; (B) *Trimetopon pliolepis,* female SMF 85388 from 8 km NE Río Sereno, photo by GK; (C) *T. slevini,* juvenile SMF 90211 from Cerro Pata de Macho, RFLF; (D, E) *Urotheca decipiens,* (D) female SMF 89604 from Lost & Found Ecohostel, and (E) female SMF 90212 from La Nevera; (F) *U. guentheri,* SMF 89603 from Cerro Mariposa; (G) *U. pachyura* from Colón, photo by MP; (H) *Xenodon rabdocephalus* from Costa Rica, photo by JV.

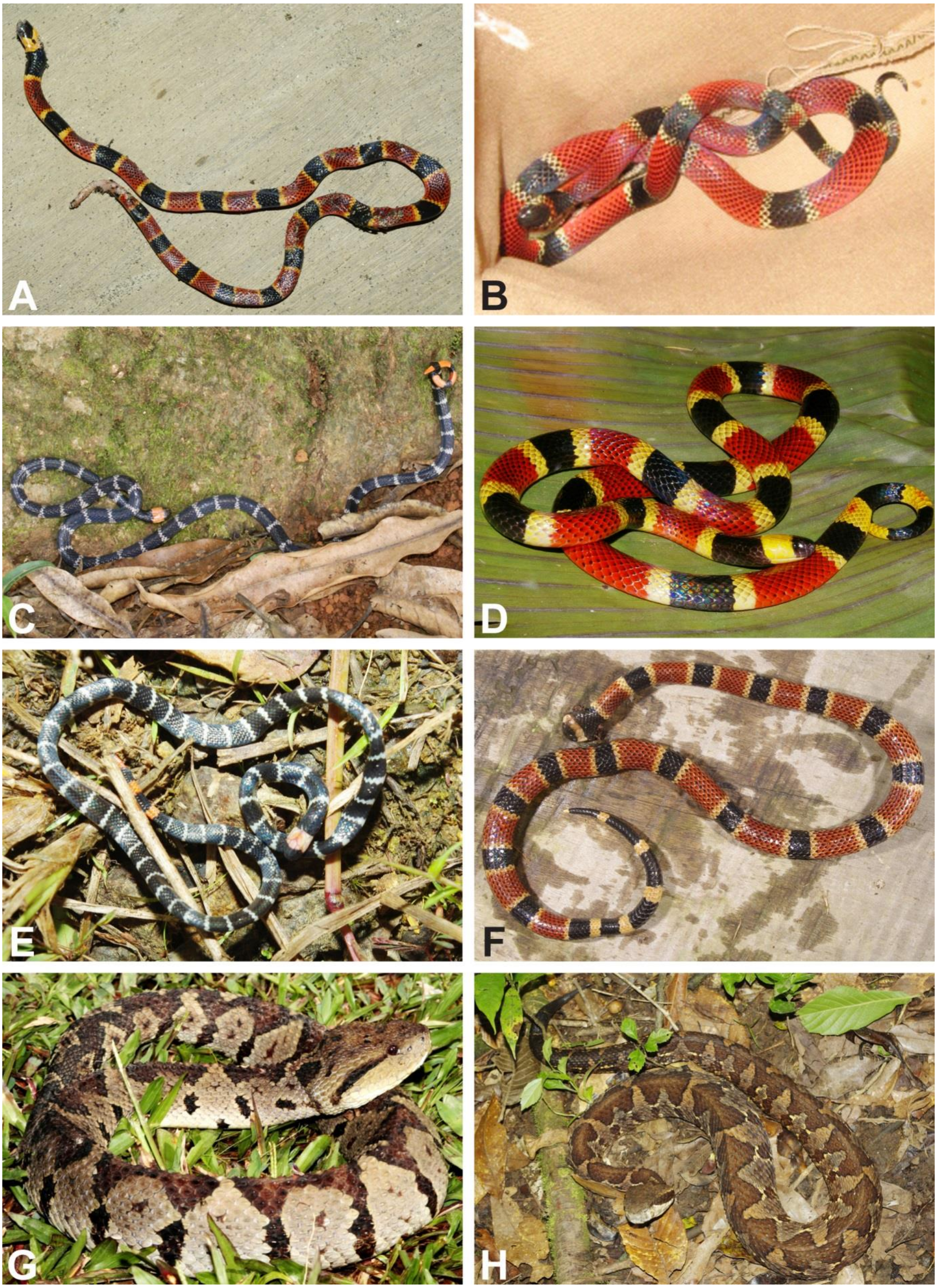

Figure 4.113: Snakes of the study area: Elapidae and Viperidae. (A) *Micrurus alleni,* juvenile SMF 90200 from San San Pond Sak; (B) *M. clarki* from Donoso, Colón, photo by Michael Castillo; (C) *M. mipartitus* from BPPS, photo by AB; (D) *M. mosquitensis,* SMF 89058 from Boca de San Carlos, Nicaragua; (E) *M. multifasciatus,* juvenile SMF 90202 from Cerro Guayabo, photo by JFB; (F) *M. nigrocinctus,* male SMF 90201 from Río Sereno; (G) *Atropoides mexicanus,* SMF 89529 from Cerro Mariposa, photo by NH; (H) *A. picadoi* from near Río Hornito.

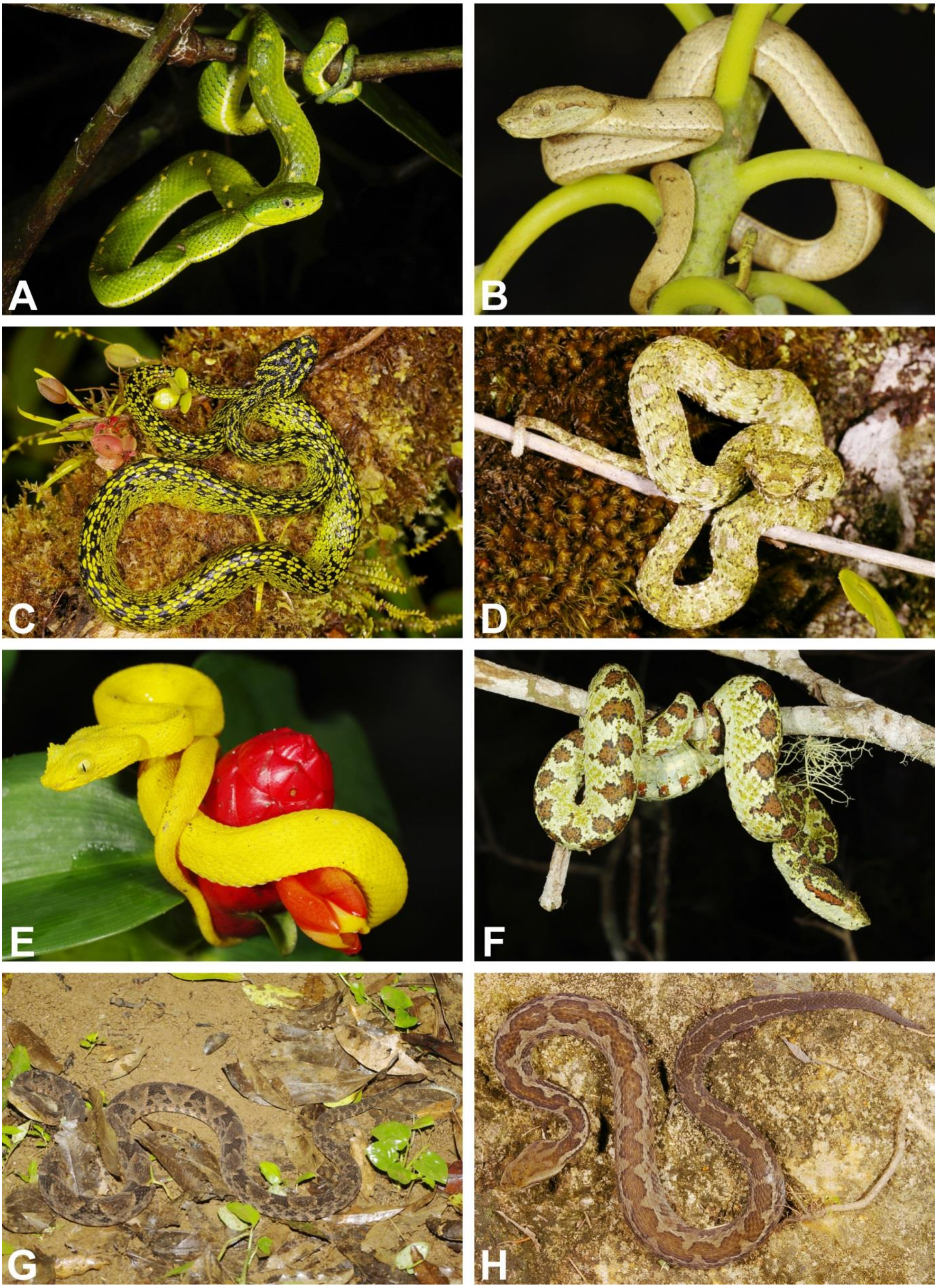

Figure 4.114: Snakes of the study area: Viperidae. (A, B) *Bothriechis lateralis,* (A) from Cerro Pata de Macho, RFLF, and (B) juvenile SMF 89762 from RFLF; (C) *B. nigroviridis,* male SMF 89534 from La Nevera; (D, E) *B. schlegelii,* juveniles (D) SMF 89535 from Cerro Mariposa, and (E) MHCH 2300 from San San Pond Sak; (F) *B. supraciliaris,* female SMF 89763 from Cabecera de Cochea; (G) *Bothrops asper,* male SMF 91533 from Hato Chamí; (H) *Cerrophidion sasai,* male SMF 89539 from Jurutungo.

Figure 4.115: Snakes of the study area: Viperidae and Boidae. (A) *Lachesis stenophrys,* juvenile from road above headwaters of Río Chiriquí Malí, photo by Robert Maurer; (B) *Porthidium lansbergii* captive specimen at Universidad de Panamá from Gorgona; (C) *Porthidium nasutum* from Kankintú, photo by AB; (D) *P. volcanicum* from Valle del General, Costa Rica, photo by Cesar Barrio-Amorós; (E) *Boa constrictor,* male SMF 89531 from Los Planes; (F) *Corallus annulatus* from Palma, Fortuna, Costa Rica, photo by JV; (G) *Epicrates maurus* from Las Lomas near Davíd; (H) *Ungaliophis panamensis* from Río Indio Lodge, Nicaragua, photo by JS.

4.3 Biogeography

In this section, I analyze the distribution of the 180 reptile species documented or inferred to occur along the Serranías de Talamanca and Tabasará in chapters 4.1 and 4.2 among physiographic regions, bioclimatic regimes, and elevation (chapter 4.3.1) as well as general patterns of their respective overall ranges (chapter 4.3.2), their occurrence in the study area's protected areas and conservation status (chapter 4.3.3), and pertinence to historical faunistic units (chapter 4.3.4). In chapter 4.3.5, I compare the range boundaries exhibited by clades of highland anoles to identify physiographic barriers that may have influenced their speciation. Last, I expand the focus to a Panamanian perspective and update the distribution of the country's reptile fauna as reported in chaper 4.2.1 among the country's four westernmost political subdivisions in chapter 4.3.6.

4.3.1 Ecological and physiographic distribution

Jaramillo et al. (2010) for the first time reviewed the distribution of the Panamanian herpetofauna among four generalized physiographic regions (Eastern Panamanian Highlands, Caribbean Lowlands, Pacific Lowlands, and Isthmian Central American Highlands) and five generalized Holdridge life zones (Lowland Wet/Moist Forest, Lowland Dry Forest, Premontane Rain/Wet Forest, Lower Montane Wet Forest, and Montane Wet Forest), as well as its elevational distribution. In this chapter, I present a partial update of the corresponding columns in their Table 4, only considering the 180 reptile species documented to occur in my study area (chapter 4.2.1) and their distribution in and along my study area, i.e., from 81°W westwards, but offering a more detailed perspective through refinment of regions and life zones as well as the additional consideration of Köppen climates and range-wide elevational distribution for each species.

Table 4.29 sums up my results for the occurrence of reptile species among the four physiographic regions, 7 Holdridge life zones (note that my processing of the WorldClim data yields the presence of PMMF and PMWF instead of PMWF and PMRF as stated by Jaramillo et al. 2010), 4 Köppen climates, and the elevational gradient. These results are visually summarized in Figures 4.116–120. Apart from the species which were newly described since 2010, many occurrences and elevational limits reported herein represent novelties or extensions with regard to the treatment of Jaramillo et al. (2010). These are explained and if necessary discussed in the respective species accounts in chapter 4.2.2.

Table 4.29: Distribution of the reptile fauna of the Serranías de Talamanca and Tabasará among physiographic regions, Holdridge life zones, Köppen climates, and elevation. X = presence documented; (x) = presence plausible; x? = presence possible. Occurrences (documented or plausible) in the Cordillera Central, adjacent lowland regions, and life zones not reported by Jaramillo et al. (2010) are in **bold** face. Elevational limits are in **bold** face if they are different from those reported by Jaramillo et al. (2010) for Panama (Cordillera Central) or the comprehensive works mentioned in chapter 3.5 (range-wide). Species endemic to Panama are marked with an asterisk (*).

	regions				**Holdridge life zones**							**Köppen climates**				**elevation**	
Taxon	**Talamanca**	**Tabasará**	**Caribbean Low**	**Pacific Low**	**LMF**	**LWF**	**PMMF**	**PMWF**	**LMMF**	**MWF**	**MRF**	**Am**	**Af**	**Cw**	**Cf**	**Cordillera Central**	**range-wide**
Order Testudines																	
Family Emydidae																	
Trachemys grayi	**X**	**X**	X	X	X	X	**X**	**(x)**				X	X			0–**1050**	0–**1050**
Family Geoemydidae																	
Rhinoclemmys annulata	(x)	(x)	X	x?	X	X	X	X				X	X			0–850	0–920
Family Kinosternidae																	
Cryptochelys leucostoma	**(x)**	**(x)**	X	(x)	X	X	(x)	X				X	X			0–230	0–1500
Kinosternon scorpioides	(x)	(x)	**X**	(x)	X	X	(x)	X				X	X			0–**850**	0–1500
Order Crocodylia																	
Family Alligatoridae																	
Caiman crocodilus	**(x)**	**(x)**	X	X	X	X						X	X			0–**430**	0–**430**
Order Squamata																	
Family Anguidae																	
Celestus sp.*	x?	**X**						**X**				(x)	X			**1250–1250**	**1250–1250**
Diploglossus bilobatus	X	X	X	x?	X	X	X	X				X	X			0–**1000**	0–1360
Mesaspis monticola	X	x?							X	(x)	X			X	X	**1850**–3420	1340–3820
Family Gekkonidae																	
Hemidactylus frenatus	(x)	X	X	X	X	X	X	X				X	X			0–**1000**	0–1230
Family Phyllodactylidae																	
Thecadactylus rapicauda	(x)	(x)	X	X	X	X	X	X				X	X			0–**990**	0–1050
Family Sphaerodactylidae																	
Gonatodes albogularis	X	(x)	X	X	X	X	X	X				X	X			0–600	0–1000
Lepidoblepharis xanthostigma	X	X	X	X	(x)	X	X	(x)				X	X			0–**1300**	0–1360
Lepidoblepharis sp. 1*		**X**	**(x)**		**X**	**X**	**X**	**X**				X	X			**100–700**	**100–700**
Sphaerodactylus homolepis	**(x)**	**(x)**	X		X	X	**(x)**	**X**				(x)	X			0–**610**	0–745
Family Corytophanidae																	
Basiliscus basiliscus	X	X		X	X	X	X	X				X	X			0–1140	0–1200
B. plumifrons	**X**	**(x)**	X	x?	X	X	**(x)**	**X**				X	X			0–**650**	0–1240
B. vittatus	**(x)**	**X**	X		X	X	**X**	**(x)**				X	X			0–**735**	0–1500
Corytophanes cristatus	X	X	X	X	X	X	X	X				X	X			0–**1100**	0–1640
Family Dactyloidae																	
*Dactyloa casildae**	X	X						X	**X**			X	X		X	**990–1720**	**990–1720**
D. frenata	X	X	X	(x)	X	X	X	X				X	X			0–**1170**	0–**1170**
*D. ginaelisae**	**X**	**X**						**X**	**X**					X	X	**1370–2130**	**1370–2130**
D. ibanezi	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**				X	X			**160–1070**	**160–1070**
D. insignis	X	X	X	**(x)**	X	X	X	X				X	X			0–1050	0–1820
*D. kunayalae**	X	X	X	**X**	X	(x)	X	X				X	X			**320–1050**	**320–1050**
D. microtus	X							(x)	X				(x)	X	(x)	**1640–1640**	**1100–2000**
Norops aquaticus	X			**X**	**(x)**	**X**		X				X				**380–1200**	30–**1200**
N. auratus	X	(x)	x?	X	X	X	X	X				X	(x)			0–1220	0–2000
N. benedikti	**X**							**(x)**	**X**					X	X	**1580–2390**	**1580–2390**

Table 4.29: continued.

	regions				**Holdridge life zones**							**Köppen climates**				**elevation**	
Taxon	**Talamanca**	**Tabasará**	**Caribbean Low**	**Pacific Low**	**LMF**	**LWF**	**PMMF**	**PMWF**	**LMMF**	**MWF**	**MRF**	**Am**	**Af**	**Cw**	**Cf**	**Cordillera Central**	**range-wide**
N. biporcatus	X	X	X	X	X	X	X	X				X	X			0–**1240**	0–2000
N. capito	X	X	X	X	X	X	X	X	**X**			X	X	X	X	0–**1640**	0–**1640**
N. carpenteri	**X**	**X**	X		X	X	**X**	**X**				X	X			0–**1050**	0–1570
N. charlesmyersi	**X**	**X**		**X**	**X**	**X**		**X**				X	X			**0–1050**	**0–1050**
N. cryptolimifrons	**X**		X		X	X		**X**					X			0–**1005**	0–**1005**
N. datzorum	X	X						x?	X					X	X	**1590**–2400	**1590**–2400
*N. fortunensis**	X	X						X				(x)	X			1050–**1200**	1000–1200
N. fungosus	X	X						X	**(x)**				X	X	(x)	**1030**–1450	1200–1600
N. gaigei		**X**		**X**	**X**	**X**	**X**	**X**				X				**0–640**	**0–900**
*N. gruuo**		X					X	X	**(x)**			X	X		X	**860–1530**	**860–1530**
N. humilis	X	X	X	X	X	X	X	X	**X**			X	X	X	X	0–**1750**	0–2000
N. kemptoni	X	X						X	X	**(x)**		X	X	X	X	**1000–2390**	1000–**2390**
N. lemurinus	(x)	X	X	X	X	X	X	X				X	X			0–**990**	0–2000
N. limifrons	X	X	X	X	X	X	X	X				X	X			0–**1360**	0–**1360**
*N. lionotus**	X	X	X	X	X	X	X	X				X	X			0–**1200**	0–1200
*N. magnaphallus**	X							X	**X**	**(x)**	**(x)**	X		X	X	1033–**2580**	1033–**2580**
N. pachypus	X							X	X	**(x)**	**(x)**	X		X	X	**1160–2555**	**1160–2555**
N. pentaprion	X	X	X	X	**X**	**X**	(x)	X				X	X			0–**620**	0–**900**
N. polylepis	X	X		X	X	X		X	X			X	X	X		0–**1615**	0–**1615**
*N. pseudokemptoni**		X						**X**	X				X		X	**1130–2010**	**1130–2010**
*N. pseudopachypus**	X	X						**X**	X			(x)	(x)		X	**1530–2030**	**1530–2030**
N. salvini	X	X						X	X			X	(x)	X	X	**1310–2050**	**1310–2050**
N. vittigerus		X	(x)	(x)	X	(x)	X	X				X				20–**890**	0–900
N. woodi	X							**X**	X			X		X		**1230–2060**	1150–2500
Family Hoplocercidae																	
Enyalioides heterolepis		X	(x)	(x)	X	X	X	X				X	X			0–860	0–900
Family Iguanidae																	
Iguana iguana	(x)	(x)	X	X	X	X	X	X				X	X			0–850	0–1000
Family Phrynosomatidae																	
Sceloporus malachiticus	X	x?						**X**	X	(x)	X	X	(x)	X	X	**1120**–3420	540–3800
Family Polychrotidae																	
Polychrus gutturosus	(x)	X	(x)	X	X	X	X	X				X	X			0–**880**	0–**1300**
Family Mabuyidae																	
Marisora unimarginata	X	X	X	X	X	X	X	X	**X**			X	X	X	(x)	0–**1960**	0–**1960**
Family Sphenomorphidae																	
Scincella cherriei	**X**		X	X	X	X		**X**				X	X			0–**1210**	0–1860
*S. rara**	X	X	X		**X**	**(x)**	(x)	X				(x)	X			**450–780**	**450**–780
Family Xantusiidae																	
Lepidophyma flavimaculatum	(x)	(x)	X	x?	X	X	X	X				X	X			0–820	0–1400
L. reticulatum	**X**			(x)		**(x)**		**X**				X	(x)			**515–515**	10–1250
Family Gymnophthalmidae																	
Anadia ocellata	X	X			X			X				X	X			**600–1310**	500–1530
Bachia blairi	**X**			X	X	X		**X**				X	(x)			**20–515**	0–**515**
*Echinosaura panamensis**	X	X	X	(x)	X	X	X	X				X	X			60–900	60–900
Gymnophthalmus speciosus	X	(x)	(x)	X	X	X	X	X	**X**			X	X	X		0–**1520**	0–**1520**
L. southi	(x)	X	X	X	X	X	X	X				X	X			0–**900**	0–900
Potamites apodemus	**X**			**X**	**(x)**	**X**		**X**				X	(x)			**30–1200**	**30**–1200

Table 4.29: continued.

	regions				Holdridge life zones							Köppen climates				elevation	
Taxon	**Talamanca**	**Tabasará**	**Caribbean Low**	**Pacific Low**	**LMF**	**LWF**	**PMMF**	**PMWF**	**LMMF**	**MWF**	**MRF**	**Am**	**Af**	**Cw**	**Cf**	**Cordillera Central**	**range-wide**
Ptychoglossus festae	X	X	X		X	X	X	X				X	X			0–**1050**	0–**1050**
P. plicatus	X	X	X	**(x)**	X	X	X	X	**X**			X	X	X	X	0–**1700**	0–1890
Family Teiidae																	
Ameiva praesignis	X	X		X	X	X	X	X				X	X			0–**1120**	0–**1120**
Holcosus festivus	X	X	X	(x)	X	X	X	X	**(x)**			X	X	(x)		0–**1470**	0–**1470**
H. leptophrys	X	X		X	X	X	X	X				X				0–850	0–900
H. quadrilineatus	X	X	X	X	X	X	X	X	**X**			X	X	X	(x)	0–**1680**	0–**1680**
Family Colubridae																	
Chironius exoletus	X	X	X	(x)	X	X	X	X	**(x)**			X	X	(x)	(x)	**10**–1130	20–2170
C. flavopictus	X	X	X	X	X	X	X	X	X			X	X	X	X	0–**1980**	0–**1980**
C. grandisquamis	X	X	X	X	X	X	X	X	**(x)**			X	X	(x)	(x)	0–**1220**	0–1600
Dendrophidion apharocybe	X	X	X	**(x)**	X	X	X	X				X	X			0–**1430**	0–**1430**
D. clarkii	X	X	X	X	X	X	X	X				X	X			**20**–910	0–**1800**
D. crybelum	**(x)**							**(x)**				(x)	(x)			?–?	**1100–1330**
D. paucicarinatum	X	X						X	X			X	X	X	X	**1020–1980**	1000–2000
D. percarinatum	X	X	X	X	X	X	X	X				X	X			0–**1160**	0–1200
Drymarchon melanurus	X	X	X	X	X	X	X	X	X			X	X	X	(x)	0–**1615**	0–2500
Drymobius margaritiferus	(x)	X	X	X	X	X	X	X	**(x)**			X	X	(x)	(x)	0–**1500**	0–2000
D. rhombifer	X	X	(x)	(x)	(x)	(x)	X	X				X	(x)			0–850	0–1200
Lampropeltis triangulum	X	X	(x)	(x)	X	(x)	X	X	X			X	X	X	(x)	0–2000	0–2500
Leptophis ahaetulla	X	X	X	X	X	X	X	X				X	X			0–**1320**	0–1680
L. depressirostris	X	X	X	X	X	X	X	X				X	X			0–**1000**	0–1300
L. nebulosus	**(x)**	**(x)**	(x)	**(x)**	X	(x)	**(x)**	**X**				X	(x)			130–**800**	0–1600
L. riveti	X	X		**(x)**	(x)	(x)	(x)	X				X	(x)			60–850	4–1800
Mastigodryas melanolomus	X	X	X	X	X	X	X	X	X			X	X	X	(x)	0–**1615**	0–1760
Oxybelis aeneus	X	X	X	X	X	X	X	X				X	X			0–**1320**	0–2500
O. brevirostris	X	X	X	**(x)**	X	X	X	X				X	X			**10–910**	0–910
O. fulgidus	X	X	X	X	X	X	X	X	**(x)**			X	X	(x)	(x)	10–**1050**	0–1600
Phrynonax poecilonotus	X	X	X	X	X	X	X	X	**(x)**			X	X	(x)	(x)	0–**1230**	0–**1610**
Rhinobothryum bovallii	X	X	X	X	X	X	X	X				X	X			0–**1120**	0–**1120**
Scaphiodontophis venustissimus	**(x)**	**(x)**	X	X	X	(x)	(x)	X				X	X			0–800	0–1300
Spilotes pullatus	X	X	X	X	X	X	X	X				X	X			0–**1320**	0–1500
Stenorrhina degenhardtii	X	X	X	X	X	X	X	X				X	X			0–**1320**	0–1900
Tantilla alticola	X	X					(x)	X	**X**			X	X	(x)	X	**740–1600**	40–2740
T. armillata	**(x)**	**(x)**		X	**X**	**(x)**	**X**	**X**				X	(x)			**380–800**	0–1435
T. reticulata	**X**	**(x)**	**X**		X	(x)	X	(x)				X	X			130–**850**	0–1430
T. ruficeps	X	(x)	**(x)**	X	X	X	X	X	**(x)**			X	X	(x)	(x)	0–1340	0–1600
T. schistosa	X	(x)	**(x)**	**X**	**X**	**(x)**	(x)	X	**(x)**			X	(x)	(x)	(x)	590–1370	0–1760
T. supracincta	(x)	(x)	**(x)**	(x)	X	(x)	(x)	X				X	X			10–850	0–970
Family Dipsadidae																	
Amastridium veliferum	X	X	X	(x)	X	(x)	(x)	X				X	X	X	(x)	26–**1434**	0–**1434**
Clelia clelia	X	X	X	X	X	X	(x)	X				X	X			0–**1050**	0–1200
C. equatoriana	**(x)**	**X**	x?	x?			X	(x)				X	(x)			**725**–725	60–1900
C. scytalina	X	X	x?	x?				**X**	X				X	(x)	(x)	**1050**–1783	0–2000
Coniophanes fissidens	X	(x)	X	X	X	X	(x)	X				X	X			**0–1320**	0–2200
Dipsas articulata	X	X	X	**X**	X	X	(x)	X				X	X			**10–1000**	0–1000
D. temporalis		**X**	x?	(x)	**(x)**	**X**	X	X				X				**700–990**	**500–1000**

Table 4.29: continued.

	regions				Holdridge life zones							Köppen climates				elevation	
Taxon	**Talamanca**	**Tabasará**	**Caribbean Low**	**Pacific Low**	**LMF**	**LWF**	**PMMF**	**PMWF**	**LMMF**	**MWF**	**MRF**	**Am**	**Af**	**Cw**	**Cf**	**Cordillera Central**	**range-wide**
Enuliophis sclateri	X	X	X	(x)	X	X	X	X				X	X			100–**1390**	0–1400
Enulius flavitorques	X	(x)	x?	X	X	X	(x)	X				X	(x)			0–**1000**	0–3000
Erythrolamprus bizona	X	X	x?	X	X	X	X	X	**X**			X	X	X	(x)	0–**1910**	0–**1910**
E. epinephelus	X	X	X	(x)	X	X	X	X	X			X	X	X	X	**0–2200**	0–2200
E. mimus	(x)	(x)	(x)	X	X	X	(x)	X				X	(x)			130–800	0–1460
Geophis brachycephalus	X	X					(x)	X	**(x)**			(x)	X	(x)	(x)	**730–1180**	13–**2230**
*G. championi**	X							X				X				**1100–1400**	**1100**–1400
G. godmani	X	x?						**(x)**	X					X	X	1600–**2350**	1000–**2350**
G. hoffmanni	X	(x)	(x)	(x)	X	(x)	(x)	X	**(x)**			X	(x)	(x)	(x)	**30–1250**	20–2100
G. talamancae	X	x?						X	X			X	X	X	X	**910–2120**	**910–2120**
*G. tectus**	X	X	X	x?	X	X	(x)	X	X			X	X	X	(x)	40–1710	40–1710
Geophis sp.*	x?	**X**						**X**	**X**			X	X		X	**1250–1660**	**1250–1660**
Hydromorphus concolor	(x)	X	X	(x)	X	X	(x)	X				X	X			0–**800**	0–1500
*H. dunni**	X							X				X		(x)		1250–**1300**	1250–**1300**
Imantodes cenchoa	X	X	X	X	X	X	X	X	**X**			X	X	(x)	X	0–**1660**	0–2060
I. gemmistratus	**X**	**(x)**	X	X	X	X	**X**	**X**				X	X			0–**1000**	0–**1435**
I. inornatus	X	X	X	X	X	X	X	X				X	X			0–**1250**	0–1600
Leptodeira annulata	X	X	X	X	X	X	X					X	X			0–**1400**	0–2000
L. septentrionalis	X	X	X	X	X	X	X					X	X			0–**1250**	0–2000
Ninia celata	X	(x)	x?	x?			(x)	X				X	X			**850**–910	650–1600
N. maculata	X	X	X	X	X	X	X	X	**(x)**			X	X	X	(x)	0–**1420**	0–1800
N. psephota	X	x?						X	X			X	(x)	X	(x)	**1120–1870**	1000–2770
Nothopsis rugosus	(x)	X	X	X	X	X	X	X				X	X			0–910	0–1000
Oxyrhopus petolarius	**(x)**	**X**	X	X	X	X	X	X				X	X			**0–910**	0–1450
Pliocercus euryzonus	X	X	X	X	X	(x)	X	X	(x)			X	X			0–**1140**	0–1600
Pseudoboa neuwiedii	**(x)**	**X**		X	X	X	**(x)**	**X**				X	X			0–**900**	0–1000
Rhadinaea calligaster	X	x?						X	X	**(x)**	**(x)**	X	(x)	X	X	**1220–2650**	1200–2850
R. decorata	X	X	X	X	X	X	X	X				X	X			0–880	0–1400
R. pulveriventris	X	X						X	**X**			(x)	X	X	(x)	1000–1450	1000–1600
*R. sargenti**		**X**	(x)	x?	X	X	X	X				X				**180–880**	**180–880**
*R. vermiculaticeps**		X	X	x?	X	(x)	X	X				X				200–**990**	200–**990**
Rhadinella godmani	X	x?						X	X	**(x)**	**(x)**	X		X	(x)	1200–2130	1000–2650
Sibon annulatus	X	X	X	X	X	X	X	X	**X**			X	X	X	X	0–**1640**	0–**1640**
S. argus	X	X	(x)	x?	X	(x)	X	X				X	X			**40–1200**	0–**1200**
S. lamari	**(x)**	**(x)**	X		X	X						(x)	X			5–150	5–650
S. longifrenis	**(x)**	**X**	X	x?	X	(x)	**X**	**X**				X	X			0–**900**	0–**1030**
S. nebulatus	X	X	X	X	X	X	X	X				X	X			0–**1320**	0–1690
*S. noalamina**	**X**	**X**					**(x)**	**X**				X	X			**1050–1260**	1050–1260
*S. perissostichon**		**X**						**X**				X				**1434–1434**	**1434–1434**
Trimetopon pliolepis	X			x?				X				X	(x)			1200–**1210**	60–1600
T. slevini	X	X						X	X			X	X	X	X	1220–**1825**	**1200**–1825
Urotheca decipiens	X	X	x?	x?	**(x)**	**(x)**	(x)	X	X			X	X	X	X	**800**–1620	0–1620
U. guentheri	X	X	X	X	X	X	(x)	X				X	X			0–**1250**	0–**1800**
U. pachyura	X	(x)	X		X	X	(x)	(x)	X			(x)	X	X	(x)	0–**1800**	0–**1800**
Xenodon rabdocephalus	X	X	X	X	X	X	X	X	**X**			X	X	X	(x)	0–**1610**	0–**1610**
Family Elapidae																	
Micrurus alleni	X	(x)	X	X	X	(x)	(x)	X	**(x)**			X	X	(x)	(x)	0–**1320**	0–1620

Table 4.29: continued.

	regions				Holdridge life zones							Köppen climates				elevation	
Taxon	**Talamanca**	**Tabasará**	**Caribbean Low**	**Pacific Low**	**LMF**	**LWF**	**PMMF**	**PMWF**	**LMMF**	**MWF**	**MRF**	**Am**	**Af**	**Cw**	**Cf**	**Cordillera Central**	**range-wide**
M. clarki	**x?**	**X**	x?	X	X	X	X	(x)				X	X			0–**880**	0–900
M. mipartitus	(x)	X	X	x?	X	X	X	X				X	X			**0**–850	0–1600
M. mosquitensis	**X**	x?	X		X	X	**(x)**	**(x)**					X			0–**760**	0–1500
M. multifasciatus	X	(x)	X		X	X	(x)	X				X	X			0–**1230**	0–1600
M. nigrocinctus	X	X	X	X	X	X	X	X	X			X	X	X	X	0–**1830**	0–2000
Family Viperidae																	
Atropoides mexicanus	X	X	x?	x?	(x)	(x)	X	X	(x)			X	X	(x)	(x)	650–1390	0–1600
A. picadoi	X	X	x?	x?				X	**(x)**			(x)	X	(x)	X	**1000–1650**	**300**–2000
Bothriechis lateralis	X	X	?	?		(x)	(x)	X	X			X	X	X	X	500–2130	450–2500
B. nigroviridis	X	X						X	X	**(x)**	**(x)**	X	(x)	X	X	**1220–2540**	700–3000
B. schlegelii	X	X	X	X	X	X	X	X				X	X			0–910	0–1530
B. supraciliaris	X	x?		x?				X	**(x)**			X	X	(x)		**610**–1300	**610**–1700
Bothrops asper	X	X	X	X	X	X	X	X	**(x)**			X	X	(x)		0–**1400**	0–1500
Cerrophidion sasai	X	x?						X	X	**(x)**	**(x)**	X		X	(x)	1390–**2010**	1300–**3000**
Lachesis melanocephala	X			**(x)**	**(x)**	**(x)**		X	**(x)**			X	(x)	(x)		1200–1200	0–1600
L. stenophrys	X	X	X	x?	X	X	(x)	X				X	X			0–**1200**	0–**1200**
Porthidium lansbergii	**X**	**X**		X	X	(x)	**X**	**X**				X	X	(x)		0–**1300**	0–**1300**
P. nasutum	X	X	X	**(x)**	X	X	X	X				X	X			**0–1000**	0–1700
P. volcanicum	**X**	x?		x?		**(x)**		**X**				(x)	X			**1000–1000**	400–**1000**
Family Boidae																	
Boa constrictor	X	X	X	X	X	X	X	X				X	X	(x)		0–**1320**	0–1500
Corallus annulatus	**(x)**	**(x)**	X	x?	X	(x)	**(x)**	**X**				X	X			0–**800**	0–1000
Epicrates maurus	(x)	(x)	(x)	(x)	X	X	(x)	X				X	X			0–800	0–1200
Ungaliophis panamensis	(x)	(x)	**(x)**	**(x)**	**X**	**(x)**	(x)	X	**(x)**			X	X	(x)	(x)	**10**–850	0–2100
Family Anomalepididae																	
Helminthophis frontalis	X	x?	x?	x?	**X**	**(x)**	(x)	X				X	(x)			**1120–1220**	**70**–1440
Total Lizards	**61**	**55**	**38**	**39**	**49**	**49**	**42**	**66**	**24**	**5**	**4**	**60**	**57**	**20**	**20**	0-3420	0-3820
documented	52	47	33	31	46	45	38	62	21	0	2	55	49	19	16		
plausible	9	8	5	8	3	4	4	4	3	5	2	5	8	1	4		
possible	1	2	1	3	0	0	0	1	0	0	0	0	0	0	0		
Total Snakes	**101**	**92**	**69**	**65**	**81**	**83**	**85**	**104**	**45**	**4**	**4**	**104**	**98**	**47**	**42**	0-**2650**	0-3000
documented	83	72	57	47	75	58	54	97	27	0	0	97	82	25	16		
plausible	18	20	12	18	6	25	31	7	18	4	4	7	16	22	26		
possible	2	10	11	18	0	0	0	0	0	0	0	0	0	0	0		
Total Reptilia	**167**	**152**	**112**	**108**	**135**	**137**	**131**	**174**	**69**	**9**	**8**	**169**	**160**	**67**	**62**	0-3420	0-3820
documented	136	120	95	80	126	108	94	162	48	0	2	157	136	44	32		
plausible	31	32	17	28	9	29	37	12	21	9	6	12	24	23	30		
possible	3	12	12	22	0	0	0	1	0	0	0	0	0	0	0		

Figure 4.116 summarizes the distribution of my study area's reptiles among the 4 physiographic regions. As the most speciose region, the Serranía de Talamanca holds about 93% of my study area's reptile species, while 60% occur along the Pacific lowlands. Generally, the mountain ranges are home to more species-rich faunas, each holding between

40–59 more species than any of the lowland regions, or 20–35 more than both together (132). Snakes outnumber lizards in every region. Twenty-five species (14%) occur in a single region, while 85 (47%) are found in all four.

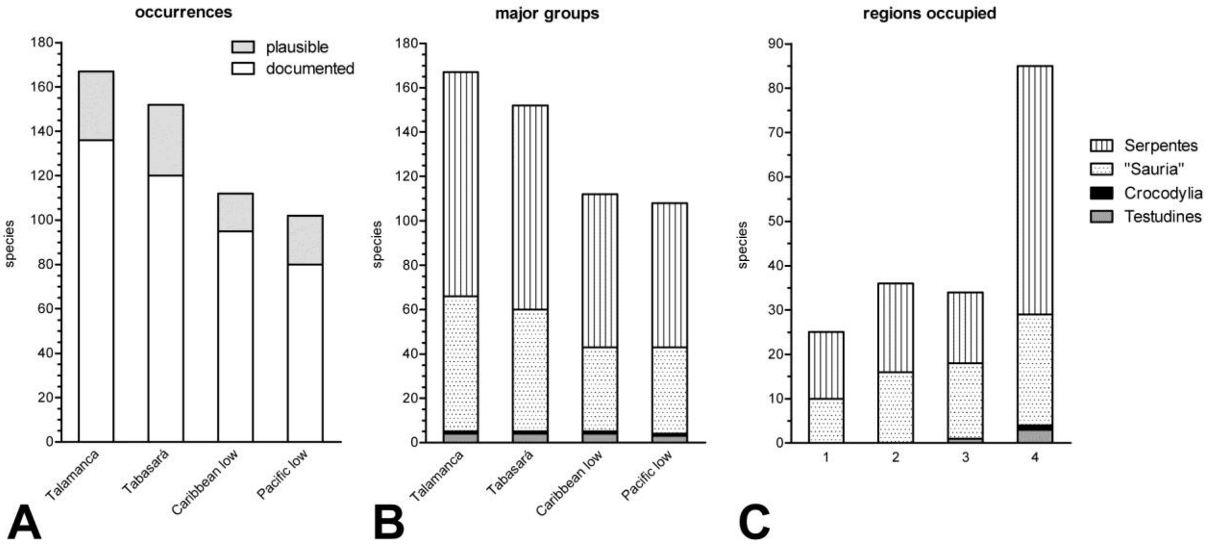

Figure 4.116: Distribution of the study area's reptile species among physiographic regions. (A) Species per region, subdivided by documented and plausible occurrences; (B) species per region, subdivided by reptile orders and squamate suborders; (C) regions per speices, subdivided by reptile orders and squamate suborders.

The distribution among Holdridge life zones is shown in Figure 4.117. Each of the Lowland and Premontane life zones holds well more than two-thirds of the study area's total reptile species. The most speciose life zone is PMWF with 174 species (97%), while MWF and MRF are the least speciose with 9 and 8 species (5 and 4.4%), respectively. Interestingly, the latter two are the only life zones where lizards species numbers are equal to (MRF) or even higher than (MWF) those of snakes. From Lower Montane climates upwards, all reptiles belong to the order Squamata. Eight species are restricted to a single life zone (7 to PMWF, 1 to LMWF) and 9 occur in six, while 125 species (69%) occur in 4 or 5 life zones and none is found in all seven. The distribution of my dataset's georeferenced records from west of 81°W is very heterogeneous: while I have more than 2000 records each for LMF and PMWF and well above 1000 each for LWF and LMWF, only 378 come from PMMF, 33 from MRF, and none is situated within MWF. If the respective humidity provinces are lumped together for each temperature regime as done in Fig. 4.117E, the resulting bioclimatic belts are equivalent to four of the generalized life zones employed by Jaramillo et al. (2010; LDF is not considered here). With a total of 176 species (98%), almost every species reported from my study area occurs in Premontane climates. While Lowland climates hold 138 species (77%), Lower Montane climates are only half as speciose with 69 species (38%), and Montane climates appear species-poor with 9 species. Only 13 species are restricted to a single bioclimatic belt (2 to L, 10 to PM, 1 to LM), whereas 122 (68%) are found in two (99 in L +

PM, 22 in PM + LM, 1 in LM + M), and 45 (25%) occur in three belts (37 in L + PM + LM, 8 in PM + LM + M).

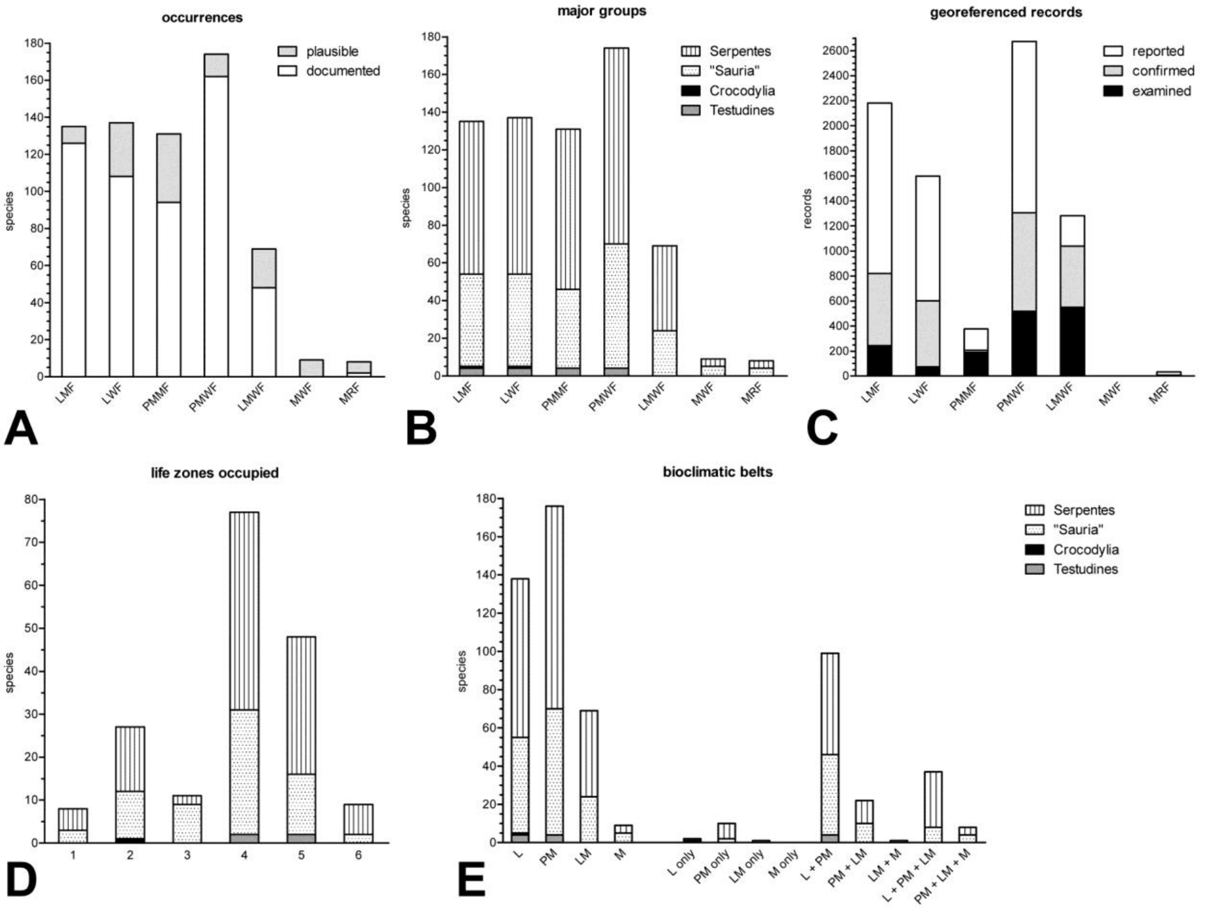

Figure 4.117: Distribution of the study area's reptile species among Holdridge life zones. (A, B) Species per life zone, subdivided by (A) documented and plausible occurrences, and (B) reptile orders and squamate suborders; (C) total georeferenced records per life zone west of 81°W, subdivided by quality of evidence; (D) number of life zones per species, subdivided by reptile orders and squamate suborders; (E) distribution among bioclimatic belts, subdivided by reptile orders and squamate suborders.

Analogously to the Holdridge life zones, Fig. 4.118 summarizes the distribution among the four Köppen climates found west of 81°W. The most speciose climate is Am with 169 species (94%), closely followed by Aw with 160 species (89%). Each of the C climates is home to slightly more than one-third of the study area's reptile fauna, and only inhabited by squamates. Most of my georeferenced records lie within Am (2886) and Af (3787) areas, with much fewer coming from Cw (967) or Cf (510) climates. Only 8 species are restricted to a single Köppen climate (6 to Am, 2 to Af), whereas 50 or more occur in 2, 3, or all 4 climates, respectively. When lumping together the different rainfall seasonalities, the resulting A climate zone holding 175 species (97%) roughly corresponds to the L and PM bioclimatic belts, while the C climate zone holding 72 species (40%) roughly corresponds to the LM and

M belts. 108 species (60%) are restricted to A climates and a mere 5 (3%) to C climates, while 67 species (37%) occur in both.

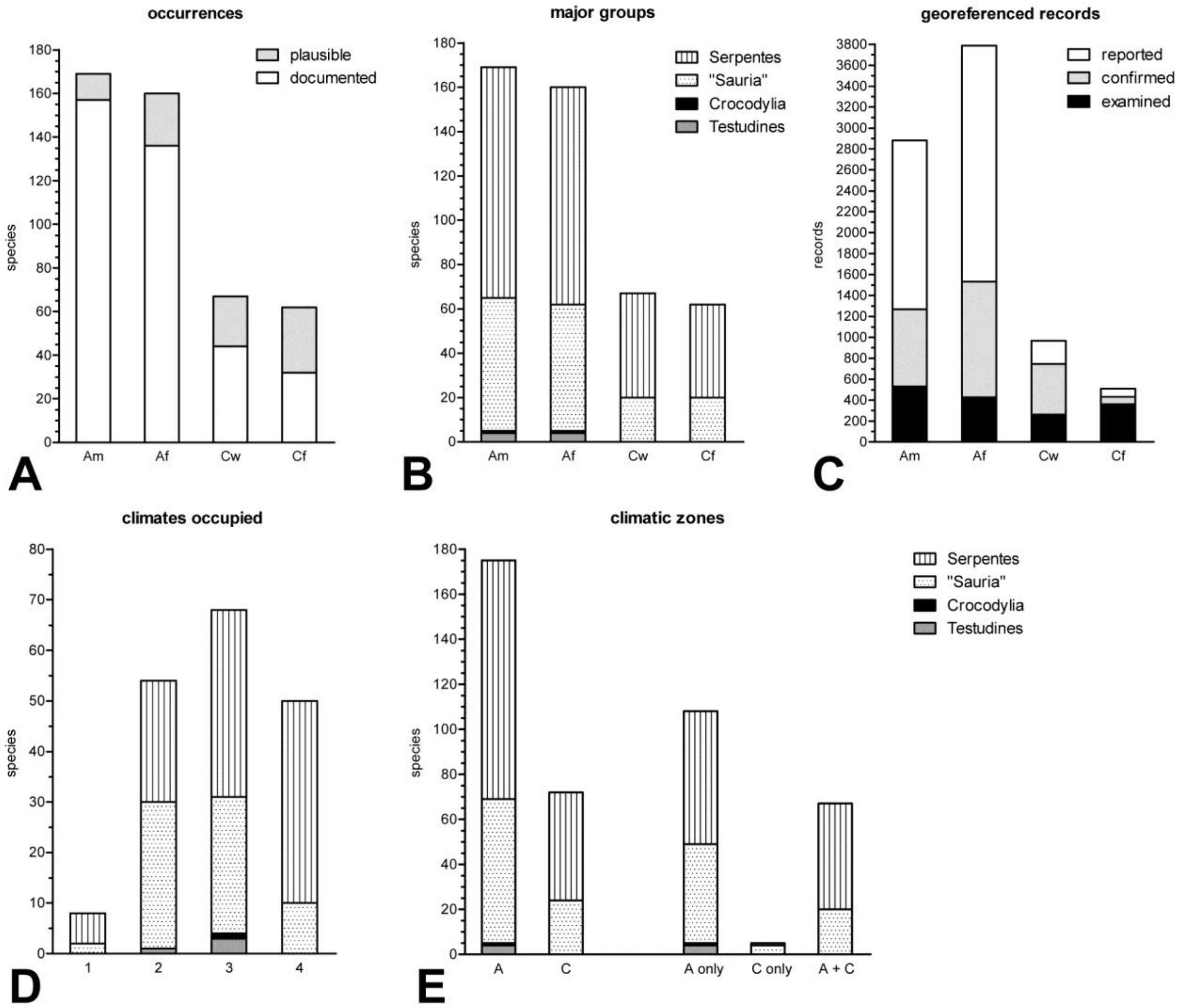

Figure 4.118: Distribution of the study area's reptile species among Köppen climates. (A, B) Species per climate, subdivided by (A) documented and plausible occurrences, and (B) reptile orders and squamate suborders; (C) total georeferenced records per climate west of 81°W, subdivided by quality of evidence; (D) number of climates per species, subdivided by reptile orders and squamate suborders; (E) distribution among climatic zones, subdivided by reptile orders and squamate suborders.

Regarding elevational distribution, a fundamental aspect of my results is the multitude of extensions of both upper and lower elevational limits for several species (highlighted in **bold** face in Tab. 4.29, detailed and discussed in the respective species accounts) compared with previous comprehensive works, range-wide as well as for western Panama, resulting from the broad range of literature considered as well as own collections. If only extensions of 50 or more vertical meters are considered, my combined dataset extends the range-wide upper limit for 42 species by a total of 11919 m, an average of 283.8 m, and up to 980 m for a single species (*Norops magnaphallus*). Considerable downward corrections for range-wide upper elevational limits, like -930 m for *N. pentaprion* or -1000 m for *N. aquaticus,* also exist. The same applies to the range-wide lower limits of many species, which are for example corrected downward by at least 50 m for 12 species, the greatest extension being -470 m for *N. pseudokemptoni.* Concerning the elevational distributions along the Cordillera Central, which in many cases (especially for the upper limits) equate to those throughout Panama and are thus compared to the ranges provided by Jaramillo et al. (2010), the extensions documented herein are even more significant. Upper limits along the Cordillera Central (usually equal to those throughout Panama) are herein raised over at least 50 m for 105 species (58% of my study area's and almost 40% Panama's reptile fauna) by a total of 35629 m, an average of 339.3 m, and by up to 1010 m for a single species (*Scincella cherriei*). The inferior elevational limits along the Cordillera Central derived from my dataset are lowered by 50 m or more for 29 species by a total of 8832 m, an average of 305 m, and by as much as 1130 m for a single species (*Helminthophis frontalis*).

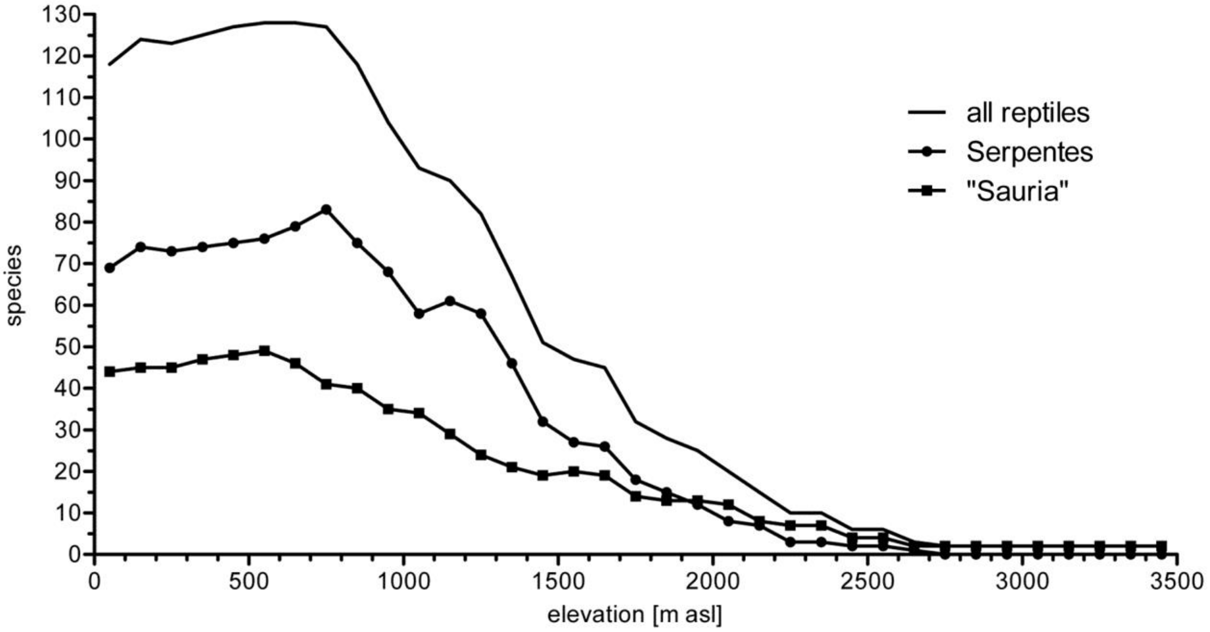

Figure 4.119: Distribution of the study area's reptile species among altitudinal 100 m segments: interpolated numbers of lizard, snake, and total reptile species derived from the altitudinal ranges given for the Cordillera Central in Tab. 4.29.

Figure 4.119 illustrates the numbers of snake, lizard, and total reptile species among elevational segments of 100 m as interpolated from each species' elevational limits along my study area. Below 1000 m asl, more than 100 species (i.e., > 56% of the total fauna) are inferred to inhabit each given segment. With more than 120 species, respectively, each of the segments between 100 and 800 m holds more than two-thirds of my study area's reptile fauna. Above 800 m, species numbers of snakes and total reptiles decrease, as they do for lizards above 500 m. Around 2000 m asl, lizard species begin to outnumber snake species, and constitute the only recorded reptile group with just two representatives above 2700 m up to the summit of Volcán Barú.

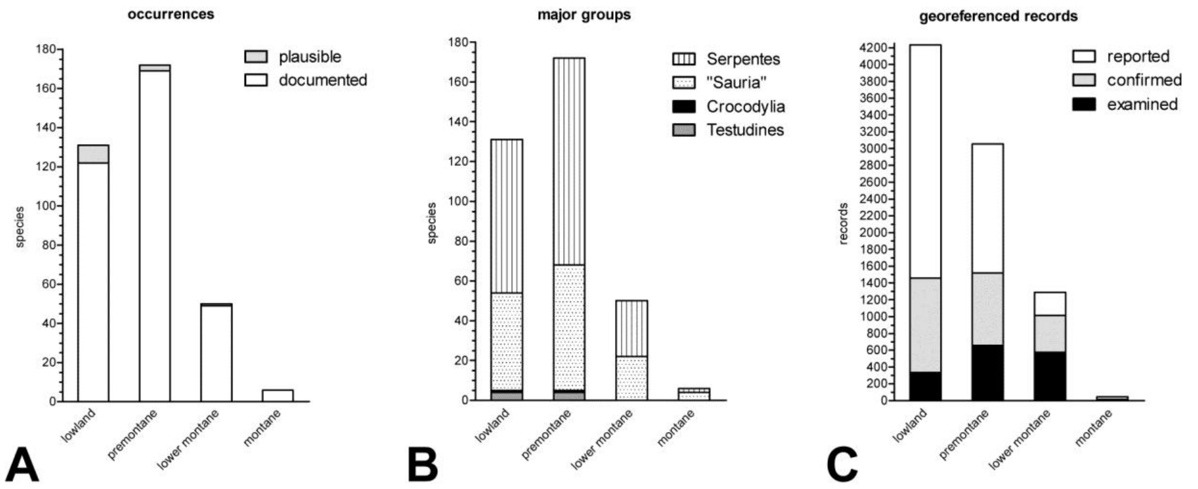

Figure 4.120: Distribution of the study area's reptile species among altitudinal belts. (A) Species per belt, subdivided by documented and plausible occurrences; (B) species per belt, subdivided by reptile orders and squamate suborders; (C) total of georeferenced records per belt west of 81°W, subdivided by quality of evidence.

Showing the distribution among the four principal altitudinal belts based on actual elevational values associated with my georeferenced records, Figure 4.120 offers a different perspective on elevational distribution. Yet, the overall picture is similar and logically also closely resembles the distribution among the bioclimatic belts (Fig. 4.117E): With 172 documented (169) and plausible (3) occurrences, premontane elevations of 500–1500 m asl house the highest species number (96%) of any elevational belt, followed by lower elevations with 131 species (73%). Lower montane elevations of 1500–2500 m asl are home to 50 species (28%), and devoid of turtles and crocodiles just as the highest belt accomodating a mere 6 species (3.3%), of which 4 are lizards. The number of georeferenced records from along my study area gradually decreases along the elevational belts, from 4240 below 500 m to 44 above 2500 m.

4.3.2 Distribution patterns and endemism

The distribution patterns exhibited by the reptile species of my study area, based on each species' respective overall distributional range, are tabulated in Table 4.30 and visualized in Figure 4.121. The documented range of 28 species (16%; 11 snakes + 17 lizards) reaches its western/northern extreme in or along my study area, and 52 species present in my study area (29%; 24 snakes + 28 lizards) do not occur east of 81°W according to current knowledge. Of these, 14 species (8%; 5 snakes + 9 lizards) have both their respective E and W range limits between the Costa Rica-Panama border and 81°W, i.e., are endemic to the westernmost portion of Panama.

Table 4.30: Generalized distribution patterns of the study area's reptile species. CA = Central America, COL = Colombia, CRI = Costa Rica, LCA = Lower Central America, SA = South America. Species endemic to Panama are marked with an asterisk (*).

	widespread species							**LCA endemics**							
Taxon	**widespread all**	**CA**	**CA + COL**	**LCA + COL**	**CA + SA**	**SA + CRI**	**SA**	**LCA endemic all**	**low + premontane**	**low + premontane Caribbean**	**low + premontane Pacific**	**Talamancan highland**	**Talamancan highland small-scale**	**western limit along study area**	**eastern limit along study area**
Order Testudines															
Family Emydidae															
Trachemys grayi	X		X												
Family Geoemydidae															
Rhinoclemmys annulata	X				X										
Family Kinosternidae															
Cryptochelys leucostoma	X				X										
Kinosternon scorpioides	X				X										
Order Crocodylia															
Family Alligatoridae															
Caiman crocodilus	X				X										
Order Squamata															
Family Anguidae															
Celestus sp.*								X				X	X	X	X
Diploglossus bilobatus	X	X													
Mesaspis monticola								X				X			X
Family Gekkonidae															
Hemidactylus frenatus	X				X										
Family Phyllodactylidae															
Thecadactylus rapicauda	X				X										
Family Sphaerodactylidae															
Gonatodes albogularis	X				X										
Lepidoblepharis xanthostigma	X		X												
Lepidoblepharis sp. 1*								X	X					X	
Sphaerodactylus homolepis	X	X													
Family Corytophanidae															
Basiliscus basiliscus	X				X										
B. plumifrons	X	X													
B. vittatus	X	X													X
Corytophanes cristatus	X		X												
Family Dactyloidae															
*Dactyloa casildae**								X				X	X	X	X
D. frenata	X			X											
*D. ginaelisae**								X				X	X	X	X
D. ibanezi								X	X	X					
D. insignis								X	X						
*D. kunayalae**								X	X					X	
D. microtus								X				X			X
Norops aquaticus								X	X		X				X
N. auratus	X					X									
N. benedikti								X				X	X		X
N. biporcatus	X				X										
N. capito	X	X													

Table 4.30: continued.

	widespread species							LCA endemics							
Taxon	**widespread all**	**CA**	**CA + COL**	**LCA + COL**	**CA + SA**	**SA + CRI**	**SA**	**LCA endemic all**	**low + premontane**	**low + premontane Caribbean**	**low + premontane Pacific**	**Talamancan highland**	**Talamancan highland small-scale**	**western limit along study area**	**eastern limit along study area**
N. carpenteri	X	X													
N. charlesmyersi								X	X		X				X
N. cryptolimifrons								X	X	X					X
N. datzorum								X				X			X
*N. fortunensis**								X				X	X	X	X
N. fungosus								X				X			X
N. gaigei	X						X							X	
*N. gruuo**								X				X	X	X	X
N. humilis								X	X						
N. kemptoni								X				X			X
N. lemurinus	X	X													
N. limifrons	X	X													
*N. lionotus**								X	X	X				X	
*N. magnaphallus**								X				X	X	X	X
N. pachypus								X				X			X
N. pentaprion	X		X												
N. polylepis								X	X		X				X
*N. pseudokemptoni**								X				X	X	X	X
*N. pseudopachypus**								X				X	X	X	X
N. salvini								X				X			X
N. vittigerus	X			X										X	
N. woodi								X				X			X
Family Hoplocercidae															
Enyalioides heterolepis	X						X							X	
Family Iguanidae															
Iguana iguana	X				X										
Family Phrynosomatidae															
Sceloporus malachiticus	X	X													X
Family Polychrotidae															
Polychrus gutturosus	X				X										
Family Mabuyidae															
Marisora unimarginata								X	X						
Family Sphenomorphidae															
Scincella cherriei	X	X													X
*S. rara**								X				X	X	X	X
Family Xantusiidae															
Lepidophyma flavimaculatum	X	X													
L. reticulatum								X	X		X				X
Family Gymnophthalmidae															
Anadia ocellata								X				X			
Bachia blairi								X	X		X				X
*Echinosaura panamensis**								X	X					X	
Gymnophthalmus speciosus	X				X										
L. southi	X			X											
Potamites apodemus								X	X		X				X

Table 4.30: continued.

	widespread species							LCA endemics							
Taxon	**widespread all**	**CA**	**CA + COL**	**LCA + COL**	**CA + SA**	**SA + CRI**	**SA**	**LCA endemic all**	**low + premontane**	**low + premontane Caribbean**	**low + premontane Pacific**	**Talamancan highland**	**Talamancan highland small-scale**	**western limit along study area**	**eastern limit along study area**
Ptychoglossus festae	X			X										X	
P. plicatus	X			X											
Family Teiidae															
Ameiva praesignis	X					X									
Holcosus festivus	X		X												
H. leptophrys								X	X						
H. quadrilineatus	X	X													
Family Colubridae															
Chironius exoletus	X					X									
C. flavopictus	X					X									
C. grandisquamis	X				X										
Dendrophidion apharocybe	X	X													
D. clarkii	X					X									
D. crybelum								X				X	X		X
D. paucicarinatum								X				X			X
D. percarinatum	X				X										
Drymarchon melanurus	X				X										
Drymobius margaritiferus	X		X												
D. rhombifer	X				X										
Lampropeltis triangulum	X				X										
Leptophis ahaetulla	X				X										
L. depressirostris	X				X										
L. nebulosus	X	X													
L. riveti	X					X									
Mastigodryas melanolomus	X	X													
Oxybelis aeneus	X				X										
O. brevirostris	X				X										
O. fulgidus	X				X										
Phrynonax poecilonotus	X				X										
Rhinobothryum bovallii	X				X										
Scaphiodontophis venustissimus	X		X												
Spilotes pullatus	X				X										
Stenorrhina degenhardtii	X				X										
Tantilla alticola	X		X												
T. armillata	X	X													
T. reticulata	X		X												
T. ruficeps	X	X													
T. schistosa	X	X													
T. supracincta	X				X										
Family Dipsadidae															
Amastridium veliferum	X		X												
Clelia clelia	X				X										
C. equatoriana	X					X									
C. scytalina	X	X													
Coniophanes fissidens	X				X										

Table 4.30: continued.

	widespread species							LCA endemics							
Taxon	**widespread all**	**CA**	**CA + COL**	**LCA + COL**	**CA + SA**	**SA + CRI**	**SA**	**LCA endemic all**	**low + premontane**	**low + premontane Caribbean**	**low + premontane Pacific**	**Talamancan highland**	**Talamancan highland small-scale**	**western limit along study area**	**eastern limit along study area**
Dipsas articulata	X	X													
D. temporalis	X						X							X	
Enuliophis sclateri	X		X												
Enulius flavitorques	X		X												
Erythrolamprus bizona	X					X									
E. epinephelus	X					X									
E. mimus	X				X										
Geophis brachycephalus								X				X			X
*G. championi**								X				X	X	X	X
G. godmani								X				X			X
G. hoffmanni	X		X												
G. talamancae								X				X	X		X
*G. tectus**								X				X		X	
Geophis sp.*								X				X	X	X	X
Hydromorphus concolor	X	X													
*H. dunni**								X				X	X	X	X
Imantodes cenchoa	X				X										
I. gemmistratus	X		X												
I. inornatus	X				X										
Leptodeira annulata	X				X										
L. septentrionalis	X				X										
Ninia celata								X				X			
N. maculata	X	X													
N. psephota								X				X			X
Nothopsis rugosus	X				X										
Oxyrhopus petolarius	X				X										
Pliocercus euryzonus	X				X										
Pseudoboa neuwiedii	X						X							X	
Rhadinaea calligaster								X				X			X
R. decorata	X				X										
R. pulveriventris								X				X			X
*R. sargenti**								X	X					X	
*R. vermiculaticeps**								X				X		X	
Rhadinella godmani	X	X													X
Sibon annulatus	X	X													
S. argus								X	X						
S. lamari								X	X	X					
S. longifrenis	X	X													
S. nebulatus	X				X										
*S. noalamina**								X				X		X	X
*S. perissostichon**								X				X	X	X	X
Trimetopon pliolepis								X				X			X
T. slevini								X				X			X
Urotheca decipiens	X		X												
U. guentheri	X	X													

Table 4.30: continued.

Taxon	widespread species							LCA endemics							
	widespread all	**CA**	**CA + COL**	**LCA + COL**	**CA + SA**	**SA + CRI**	**SA**	**LCA endemic all**	**low + premontane**	**low + premontane Caribbean**	**low + premontane Pacific**	**Talamancan highland**	**Talamancan highland small-scale**	**western limit along study area**	**eastern limit along study area**
U. pachyura								X	X						
Xenodon rabdocephalus	X				X										
Family Elapidae															
Micrurus alleni	X	X													X
M. clarki	X			X											
M. mipartitus	X					X									
M. mosquitensis	X	X													X
M. multifasciatus	X	X													
M. nigrocinctus	X		X												
Family Viperidae															
Atropoides mexicanus	X	X													
A. picadoi								X				X			X
Bothriechis lateralis								X				X			
B. nigroviridis								X				X			X
B. schlegelii	X				X										
B. supraciliaris								X				X			X
Bothrops asper	X				X										
Cerrophidion sasai								X				X			X
Lachesis melanocephala								X	X		X				X
L. stenophrys	X	X													
Porthidium lansbergii	X						X							X	
P. nasutum	X				X										
P. volcanicum								X	X		X				X
Family Boidae															
Boa constrictor	X				X										
Corallus annulatus	X				X										
Epicrates maurus	X				X										
Ungaliophis panamensis	X		X												
Family Anomalepididae															
Helminthophis frontalis								X	X						
Total Lizards	**33**	**12**	**4**	**5**	**8**	**2**	**2**	**35**	**16**	**3**	**6**	**19**	**10**	**17**	**28**
Total Snakes	**77**	**19**	**12**	**1**	**34**	**8**	**3**	**30**	**7**	**1**	**2**	**23**	**6**	**11**	**24**
Total Reptilia	**115**	**31**	**17**	**6**	**46**	**10**	**5**	**65**	**23**	**4**	**8**	**42**	**16**	**28**	**52**

As shown in Figure 4.121, almost two-thirds (115 species, 64%) of my study area's reptile fauna are made up by widespread species. Among these are many more snakes than lizards, and all five non-squamate species. A little more than one-third (65 species, 36%) of the reptile species inhabiting in my study area are restricted to Lower Central America, i.e., do not occur outside of Costa Rica and Panama. These LCA endemics include slightly more lizard than snake species, and 21 species (13 lizards + 8 snakes; 32% of the LCA endemics and 12% of the study area's total reptile fauna) which are endemic to Panama.

Most of the widespread species are either widespread in Central America (42% of the widespread species and 27% of the study area's fauna, including those ranging S into Colombia but not further) or in Central as well as South America (40% and 26%), while comparably few which are widespread in SA do not reach further N than to Panama or Costa Rica (13% and 8%), or range only through LCA and Colombia (5% and 3%).

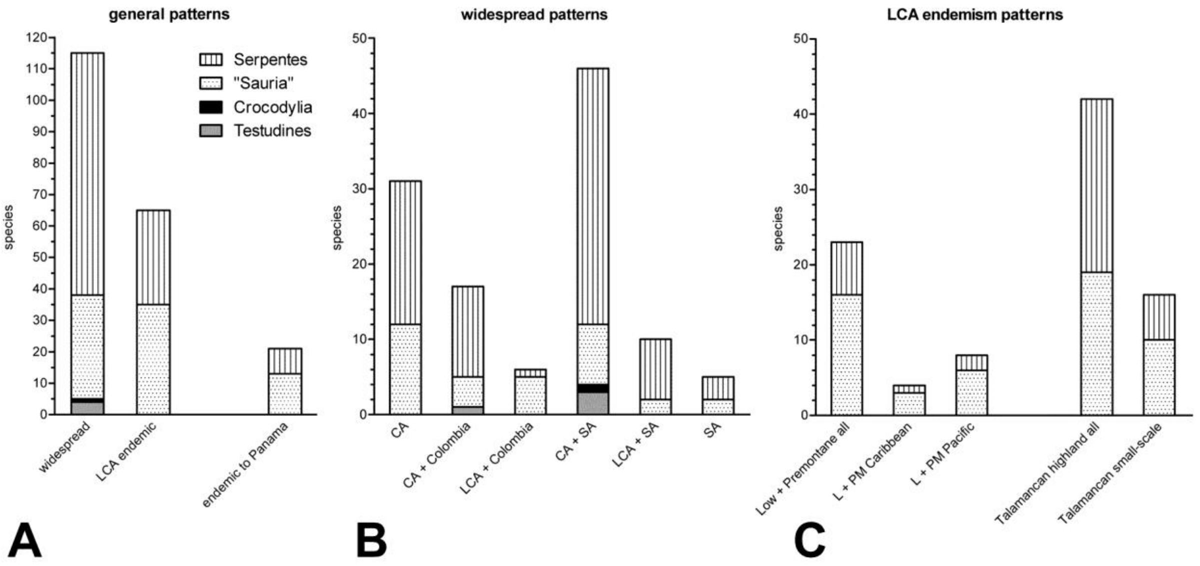

Figure 4.121: General distribution patterns of the study area's reptile species, subdivided by reptile orders and squamate suborders: (A) widespread species, LCA endemics, and Panamanian national endemics; (B) range patterns of widespread species; (C) range patterns of LCA endemics.

Among the 65 LCA endemics, 23 species (35% of the LCA endemics and 13% of the study area's total reptile fauna, including many more lizards than snakes) predominantly occur at elevations below 500 m asl but range into premontane elevations. More than a third of these are "Golfo Dulce endemics" (McDiarmid & Savage 2005; Lotzkat et al. 2012a) restricted to the Pacific versant of the Talamancan highlands, that is, twice as many as those restricted to the Caribbean versant. The bulk of the LCA endemics (65%, that is 23% of the total fauna) occur chiefly above 500 m asl and only along the Talamancan highlands, i.e., are Talamancan highland endemics. Sixteen of these species (25% and 9%; 10 lizards + 6 snakes) have documented ranges spanning 100 km or less and are thus classified as Talamancan small-scale endemics. With three exceptions, these are also endemic to Panama. Every second small-scale highland endemic is an anole (2 *Dactyloa* + 6 *Norops,* 1 + 5 of which have been described during the past 10 years), and every second snake in this category is a member of the genus *Geophis*.

4.3.3 Distribution among protected areas and conservation

Jaramillo et al. (2010) assigned IUCN categories and EVS values for 237 native non-marine reptile species, including 165 that occur in my study area. For 70 species (including 32 occurring in my study area) which these authors identified as "threatened" in view of their endemicity to Panama, high EVS value, or assignment to an IUCN Threatened category, they assessed the presence in protected areas. In this chapter, I review the occurrence in protected areas and conservation status of my study area's reptile fauna and present a partial update and extension of the corresponding analyses carried out by Jaramillo et al. (2010). Table 4.31 sums up my results and compares them to existing conservation status assessments. The subsequent figures 4.122–124 graphically summarize my results and integrate them with the distribution patterns inferred in the previous chapter.

Table 4.31: Distribution among highland protected areas and conservation status of the study area's reptiles. X = presence documented; (x) = presence plausible; x? = presence possible. Occurrences (documented or plausible) in protected areas not reported by Jaramillo et al. (2010) as well as the resulting IUCN categories and EVS values used for the summations below and further analyses are in **bold** face. Species endemic to Panama are marked with an asterisk (*).

	occurrence in protected areas							**IUCN category**			**EVS**	
Taxon	**PILA**	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Order Testudines												
Family Emydidae												
Trachemys grayi	**(x)**	**(x)**			**X**	**(x)**	1/3/0	NE	**NT**		**11**	
Family Geoemydidae												
Rhinoclemmys annulata	**(x)**	**(x)**				**(x)**	0/3/0	**NT**	**NT**		**8**	
Family Kinosternidae												
Cryptochelys leucostoma	**X**	**(x)**				**(x)**	1/2/0	NE	**LC**		**7**	
Kinosternon scorpioides	**(x)**	**(x)**				**(x)**	0/3/0	NE	**LC**		**7**	
Order Crocodylia												
Family Alligatoridae												
Caiman crocodilus	**(x)**	**(x)**				**(x)**	0/3/0	**LC**	**LC**		**11**	
Order Squamata												
Family Anguidae												
Celestus sp.*					**X**		1/0/0			**DD**		**14**
Diploglossus bilobatus	**X**	**X**			**(x)**	**X**	3/1/0	LC	**DD**		**9**	
Mesaspis monticola	**(x)**	**X**		**X**	x?		2/1/1	**LC**	**LC**		**11**	
Family Gekkonidae												
Hemidactylus frenatus	**(x)**	**(x)**				**(x)**	0/3/0	**LC**	-		-	
Family Phyllodactylidae												
Thecadactylus rapicauda	**X**	**(x)**			x?	**(x)**	1/2/1	NE	**LC**		**8**	
Family Sphaerodactylidae												
Gonatodes albogularis	**(x)**	**(x)**				**(x)**	0/3/0	NE	**LC**		**7**	
Lepidoblepharis xanthostigma	**X**	**(x)**		x?	**X**	**X**	3/1/1	**LC**	**LC**		**8**	
Lepidoblepharis sp. 1*						**X**	1/0/0			**EN**		**12**
Sphaerodactylus homolepis	**X**	**(x)**				x?	1/1/1	**LC**	**LC**		**9**	

Table 4.31: continued.

Taxon	occurrence in protected areas							IUCN category			EVS	
	PILA	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Family Corytophanidae												
Basiliscus basiliscus					**(x)**	**X**	1/1/0	NE	**LC**		**7**	
B. plumifrons	**X**	**(x)**				x?	1/1/1	**LC**	**LC**		**11**	
B. vittatus	**(x)**	**(x)**				**X**	1/2/0	NE	**LC**		**11**	
Corytophanes cristatus	**X**	**(x)**			**(x)**	**X**	2/2/0	NE	**LC**		**8**	
Family Dactyloidae												
*Dactyloa casildae**	X				X		2/0/0	NE	NT	**EN**	13	**12**
D. frenata	**X**	**(x)**			**X**	**X**	3/1/0	NE	LC	**NT**	**8**	**8**
*D. ginaelisae**	**(x)**	**X**		**X**	**X**		3/1/0	NE		**EN**		**12**
D. ibanezi	**X**	**X**			**(x)**	**X**	3/1/0	NE		**VU**		**11**
D. insignis	**X**	**(x)**			**X**	**(x)**	2/2/0	NE	LC	**NT**	**11**	**11**
*D. kunayalae**	**X**	x?			**X**	**X**	3/0/1	NE	LC	**VU**	**12**	**12**
D. microtus	**X**	**X**					2/0/0	NE	LC	**EN**	11	**12**
Norops aquaticus			**(x)**	x?			0/1/1	NE	**DD**		**11**	
N. auratus			x?	x?	**(x)**		0/1/2	NE	**LC**		**7**	
N. benedikti	**X**	**X**		**X**			3/0/0	NE		**EN**		**11**
N. biporcatus	**X**	**X**		x?	**X**	**X**	4/0/1	NE	**LC**		**8**	
N. capito	**X**	**X**	**(x)**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**8**	
N. carpenteri	**X**	**X**			**X**	**X**	4/0/0	**LC**	**LC**		**9**	
N. charlesmyersi					**X**		1/0/0	**NE**				
N. cryptolimifrons	X	**X**					2/0/0	NE	**LC**		**12**	
N. datzorum	**X**	X		**(x)**	**X**		3/1/0	NE	**LC**		**13**	
*N. fortunensis**	**X**				X		2/0/0	DD	DD	**CR**	13	**14**
N. fungosus	**X**	**X**		x?	**X**		3/0/1	NE	**DD**		**12**	
N. gaigei						x?	0/0/1	NE				
*N. gruuo**						**X**	1/0/0	NE	VU	**EN**	14	**12**
N. humilis	**X**	**X**	**(x)**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**11**	
N. kemptoni	**X**	**X**	x?	**X**	**X**		4/0/1	NE	**LC**		**11**	
N. lemurinus	**(x)**	**(x)**			**(x)**	**X**	1/3/0	NE	**LC**		**8**	
N. limifrons	**X**	**(x)**	**X**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**8**	
*N. lionotus**	X	**(x)**			**X**	X	3/1/0	LC	LC	**VU**	**12**	**12**
*N. magnaphallus**	**(x)**	X		X			2/1/0	NE	LC	**CR**	13	**12**
N. pachypus		**X**	**(x)**	**X**			2/1/0	**LC**	**LC**		**11**	
N. pentaprion	**X**	**(x)**				**(x)**	1/2/0	NE	**LC**		**7**	
N. polylepis			**X**	**(x)**	**X**		2/1/0	NE	**LC**		**10**	
*N. pseudokemptoni**							0/0/0	NE	VU	**CR**	14	**13**
*N. pseudopachypus**	**X**				**X**		2/0/0	NE	VU	**EN**	13	**12**
N. salvini	**(x)**	**X**	**x?**	**X**	**(x)**		2/2/1	NE	**DD**		**11**	
N. vittigerus						**X**	1/0/0	NE	**LC**		**8**	
N. woodi		**(x)**	**X**	x?			1/1/1	NE	**DD**		**12**	
Family Hoplocercidae												
Enyalioides heterolepis						**X**	1/0/0	NE	**LC**		**8**	
Family Iguanidae												
Iguana iguana	**(x)**	**(x)**				**(x)**	0/3/0	NE	**LC**		**10**	
Family Phrynosomatidae												
Sceloporus malachiticus	**(x)**	**X**	**(x)**	**X**	x?		2/2/1	**LC**	**LC**		**10**	
Family Polychrotidae												

Table 4.31: continued.

	occurrence in protected areas							**IUCN category**			**EVS**	
Taxon	**PILA**	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Polychrus gutturosus	**(x)**	**(x)**			x?	**X**	1/2/1	NE	**LC**		**7**	
Family Mabuyidae												
Marisora unimarginata	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	0/6/0	**LC**	**LC**		**7**	
Family Sphenomorphidae												
Scincella cherriei	**X**	**(x)**	x?				1/1/1	NE	**DD**		**11**	
*S. rara**	X	**(x)**					1/1/0	DD	VU	**EN**	14	**12**
Family Xantusiidae												
Lepidophyma flavimaculatum	**X**	**(x)**				**(x)**	1/2/0	**LC**	DD		**9**	
L. reticulatum			x?				0/0/1	**LC**				
Family Gymnophthalmidae												
Anadia ocellata	**X**	**(x)**	**(x)**	**(x)**	**X**	**(x)**	2/4/0	NE	**DD**		**11**	
Bachia blairi							0/0/0	**NT**	DD		**11**	
*Echinosaura panamensis**	**X**	x?			x?	X	2/0/2	LC	LC	**VU**	11	**12**
Gymnophthalmus speciosus	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	0/6/0	NE	**LC**		**8**	
L. southi	**(x)**	**(x)**			x?	**X**	1/2/1	NE	**LC**		**8**	
Potamites apodemus			x?				0/0/1	LC		**VU**		**11**
Ptychoglossus festae	**(x)**	**(x)**			**X**	**(x)**	1/3/0	NE	**LC**		**8**	
P. plicatus	**X**	**X**	**(x)**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**8**	
Family Teiidae												
Ameiva praesignis			x?	x?	**(x)**	**X**	1/1/2	NE	**LC**		**7**	
Holcosus festivus	**X**	**(x)**	**(x)**	**(x)**	**(x)**	**X**	2/4/0	NE	**LC**		**8**	
H. leptophrys					x?	**X**	1/0/1	NE	**LC**		**11**	
H. quadrilineatus	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**X**	1/5/0	**LC**	**LC**		**9**	
Family Colubridae												
Chironius exoletus	**(x)**	**(x)**	x?	x?	**X**	**(x)**	1/3/2	NE	**LC**		**9**	
C. flavopictus	**(x)**	**(x)**	**(x)**	**(x)**	**X**	**X**	2/4/0	DD	**LC**		**7**	
C. grandisquamis	**X**	**X**	**(x)**	**(x)**	**X**	**(x)**	3/3/0	NE	**LC**		**9**	
Dendrophidion apharocybe	**X**	**(x)**			x?	**X**	2/1/1	NE	**LC**		**9**	
D. clarkii	**X**	**(x)**			x?	**X**	2/1/1	NE	**LC**		**9**	
D. crybelum			x?				0/0/1	NE		**EN**		**13**
D. paucicarinatum	X	X	**(x)**	X	X		4/1/0	**LC**	DD		**12**	
D. percarinatum	**(x)**	**(x)**		x?	**(x)**	**X**	1/3/1	NE	**LC**		**9**	
Drymarchon melanurus	**(x)**	**(x)**	**(x)**	**(x)**	**X**	**(x)**	1/5/0	**LC**	DD		**7**	
Drymobius margaritiferus	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**X**	1/5/0	NE	**LC**		**8**	
D. rhombifer	**(x)**	**(x)**			x?	**X**	1/2/1	**LC**	DD		**8**	
Lampropeltis triangulum	**X**	**(x)**	**(x)**	**(x)**	**X**	**X**	3/3/0	NE	**LC**		**8**	
Leptophis ahaetulla	**(x)**	**(x)**	x?	**(x)**	**X**	**X**	2/3/1	NE	**LC**		**8**	
L. depressirostris	**(x)**	**(x)**		x?	**(x)**	**X**	1/3/1	NE	**LC**		**9**	
L. nebulosus	**(x)**	**(x)**				**(x)**	0/3/0	**LC**	DD		**12**	
L. riveti			x?	x?	x?	**(x)**	0/1/3	NE	**DD**		**9**	
Mastigodryas melanolomus	**X**	**(x)**	**(x)**	**(x)**	**X**	**X**	3/3/0	**LC**	**LC**		**9**	
Oxybelis aeneus	**X**	**X**	x?	**(x)**	**X**	**X**	4/1/1	NE	**LC**		**8**	
O. brevirostris	**X**	**(x)**				**X**	2/1/0	NE	**LC**		**9**	
O. fulgidus	**(x)**	**(x)**			**X**	**(x)**	1/3/0	NE	**LC**		**8**	
Phrynonax poecilonotus	**(x)**	**(x)**		**(x)**		**X**	1/3/0	**LC**	**LC**		**8**	
Rhinobothryum bovallii	**X**	**(x)**			**(x)**	**(x)**	1/3/0	**LC**	**LC**		**9**	
Scaphiodontophis venustissimus	**(x)**	**(x)**			x?	(x)	0/3/1	**LC**	DD		**9**	

Table 4.31: continued.

Taxon	occurrence in protected areas							IUCN category			EVS	
	PILA	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Spilotes pullatus	**X**	**X**	x?	**(x)**	**(x)**	**X**	3/2/1	NE	**LC**		**8**	
Stenorrhina degenhardtii	**(x)**	**(x)**	x?	**(x)**	**X**	**(x)**	1/4/1	NE	**LC**		**8**	
Tantilla alticola	**(x)**	**(x)**	**(x)**	**(x)**	**X**	**(x)**	1/5/0	NE	**LC**		**10**	
T. armillata						**(x)**	0/1/0	**LC**				
T. reticulata	**(x)**	**X**				**(x)**	1/2/0	NE	**DD**		**7**	
T. ruficeps			**(x)**	**(x)**	**(x)**	**(x)**	0/4/0	**LC**	DD		**10**	
T. schistosa	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	0/6/0	**LC**	**LC**		**8**	
T. supracincta	**(x)**	**(x)**			x?	**(x)**	0/3/1	NE	**DD**		**10**	
Family Dipsadidae												
Amastridium veliferum	**X**	**X**	**(x)**	**(x)**	**X**	**(x)**	3/3/0	**LC**	**LC**		**7**	
Clelia clelia	**(x)**	**(x)**			**X**	**(x)**	1/3/0	NE	**LC**		**8**	
C. equatoriana	**(x)**	**(x)**	x?	x?	x?	**X**	1/2/3	NE	**DD**		**10**	
C. scytalina	**(x)**	**(x)**	x?	x?	(x)		0/3/2	**LC**	DD		**12**	
Coniophanes fissidens	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	0/6/0	NE	**LC**		**9**	
Dipsas articulata	**X**	**(x)**			**(x)**	**X**	2/2/0	**LC**	**LC**		**10**	
D. temporalis						**X**	1/0/0	NE	**DD**		**8**	
Enuliophis sclateri	**X**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	1/5/0	NE	**DD**		**7**	
Enulius flavitorques			x?	**(x)**	x?	**(x)**	0/2/2	NE	**LC**		**6**	
Erythrolamprus bizona	**(x)**	**(x)**	**(x)**	**(x)**	**X**	**X**	2/4/0	**LC**	**LC**		**9**	
E. epinephelus	**X**	**(x)**	**(x)**	**X**	**X**	**(x)**	3/3/0	NE	**LC**		**9**	
E. mimus	**(x)**	**(x)**	x?	x?	x?	**(x)**	0/3/3	**LC**	**LC**		**10**	
Geophis brachycephalus	**X**	**(x)**			**X**		2/1/0	**LC**	**LC**		**10**	
*G. championi**				(x)			0/1/0	**DD**	**DD**	**DD**	**13**	**13**
G. godmani	**(x)**	**(x)**	x?	**X**	x?		1/2/2	**LC**	DD		**11**	
G. hoffmanni	**(x)**	**(x)**	x?	**(x)**	**(x)**	**(x)**	0/5/1	NE	**DD**		**7**	
G. talamancae	**(x)**	**X**	**(x)**	**(x)**	x?		1/3/1	**EN**	DD	**EN**	10	**12**
*G. tectus**	X	X	x?	**(x)**	X	**(x)**	3/2/1	LC	DD	**VU**	10	**12**
Geophis sp.*	x?				**X**		1/0/1			**CR**		**11**
Hydromorphus concolor	**(x)**	**(x)**			x?	**(x)**	0/3/1	**LC**	**LC**		**7**	
*H. dunni**				**(x)**			0/1/0	**DD**	EN	**DD**	13	**15**
Imantodes cenchoa	**X**	**X**	**(x)**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**6**	
I. gemmistratus	**(x)**	**(x)**	x?	**(x)**	x?	**(x)**	0/4/2	NE	**LC**		**7**	
I. inornatus	**X**	**(x)**		**(x)**	x?	**(x)**	1/3/1	**LC**	**LC**		**7**	
Leptodeira annulata	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	**(x)**	0/6/0	NE	**LC**		**8**	
L. septentrionalis	**X**	**(x)**	x?	x?	**X**	**X**	3/1/2	NE	**LC**		**9**	
Ninia celata	**X**	**(x)**				**(x)**	1/2/0	**NT**	DD		**11**	
N. maculata	**X**	**(x)**	**(x)**	**(x)**	**X**	**(x)**	2/4/0	**LC**	**LC**		**7**	
N. psephota	**(x)**	**X**	**(x)**	**(x)**	x?		1/3/1	**LC**	DD		**10**	
Nothopsis rugosus	**(x)**	**(x)**			x?	**X**	1/2/1	**LC**	**LC**		**7**	
Oxyrhopus petolarius	**X**	**(x)**			x?	**X**	2/1/1	NE	**LC**		**9**	
Pliocercus euryzonus	**X**	**(x)**	x?	x?	X	**X**	3/1/2	**LC**	**LC**		**9**	
Pseudoboa neuwiedii					x?	**(x)**	0/1/1	NE	**LC**		**10**	
Rhadinaea calligaster	**(x)**	**X**	**(x)**	**X**	x?		2/2/1	**LC**	DD		**10**	
R. decorata	**(x)**	**(x)**			x?	**X**	1/2/1	NE	**LC**		**7**	
R. pulveriventris	**X**	**X**	**(x)**	**(x)**	**X**		3/2/0	NE	**DD**		**11**	
*R. sargenti**					**(x)**		0/1/0	LC	DD	**EN**	11	**13**
*R. vermiculaticeps**					**(x)**		0/1/0	NT	NT	**EN**	11	**13**

Table 4.31: continued.

Taxon	occurrence in protected areas							IUCN category			EVS	
	PILA	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Rhadinella godmani	**(x)**	**(x)**	**(x)**	**(x)**	x?		0/4/1	**LC**	DD		**9**	
Sibon annulatus	**X**	**X**			**X**	**X**	4/0/0	**LC**	**LC**		**9**	
S. argus	X	**(x)**			**(x)**	**(x)**	1/3/0	**LC**	**LC**		**12**	
S. lamari	X	**(x)**				**(x)**	1/2/0	**EN**	DD		**13**	
S. longifrenis	**(x)**	**(x)**			x?	**(x)**	0/3/1	**LC**	DD		**10**	
S. nebulatus	**X**	**X**	**(x)**	**(x)**	**X**	**X**	4/2/0	NE	**LC**		**8**	
*S. noalamina**	**X**	x?			x?	**X**	2/0/2	NE		**EN**		**12**
*S. perissostichon**	x?				**X**		1/0/1	**DD**		**DD**		**13**
Trimetopon pliolepis	x?	x?	x?	x?			0/0/4	**LC**	DD		**11**	
T. slevini	**(x)**	**(x)**	**(x)**	**(x)**	**X**		1/4/0	**LC**	DD		**10**	
Urotheca decipiens	**X**	**X**	**(x)**	**(x)**	**X**	**(x)**	3/3/0	NE	**DD**		**7**	
U. guentheri	**X**	**(x)**	x?	x?	**(x)**	**X**	2/2/2	**LC**	DD		**7**	
U. pachyura	**X**	**(x)**	x?	**(x)**	**(x)**	**(x)**	1/4/1	**LC**	DD		**9**	
Xenodon rabdocephalus	**X**	**(x)**	**(x)**	**(x)**	**(x)**	**X**	2/4/0	NE	**LC**		**9**	
Family Elapidae												
Micrurus alleni	**X**	**(x)**	**(x)**	**(x)**	**(x)**		1/4/0	**LC**	DD		**9**	
M. clarki					x?	**X**	1/0/1	NE	**DD**		**9**	
M. mipartitus	**(x)**	**(x)**			x?	**X**	1/2/1	NE	**LC**		**12**	
M. mosquitensis	**X**	**(x)**					1/1/0	**LC**	DD		**14**	
M. multifasciatus	**(x)**	**(x)**			**X**	**(x)**	1/3/0	**LC**	**LC**		**10**	
M. nigrocinctus		x?	**(x)**	**(x)**	**(x)**	**X**	1/3/1	NE	**LC**		**8**	
Family Viperidae												
Atropoides mexicanus	**(x)**	**(x)**	**(x)**	**(x)**	**X**	**X**	2/4/0	**LC**	DD		**9**	
A. picadoi	**(x)**	**(x)**	**(x)**	**(x)**	X		1/4/0	**LC**	DD		**14**	
Bothriechis lateralis	X	**(x)**	**(x)**	(x)	X	(x)	2/4/0	**LC**	**LC**		**12**	
B. nigroviridis	**(x)**	X	**(x)**	X	**(x)**		2/3/0	NE	**NT**		**13**	
B. schlegelii	**X**	**X**			x?	**X**	3/0/1	NE	**LC**		**10**	
B. supraciliaris			**(x)**	**(x)**			0/2/0	NE	**DD**		**14**	
Bothrops asper	**X**	**(x)**	**(x)**	**(x)**	**X**	**(x)**	2/4/0	NE	**LC**		**9**	
Cerrophidion sasai	x?	**(x)**	**(x)**	X	x?		1/2/2	NE	**DD**		**12**	
Lachesis melanocephala			x?	x?			0/0/2	NE	**CR**		**14**	
L. stenophrys	**X**	**(x)**			**X**	**(x)**	2/2/0	NE	**NT**		**10**	
Porthidium lansbergii			x?	x?	x?	**(x)**	0/1/3	NE	**NT**		**8**	
P. nasutum	**X**	**(x)**			**(x)**	**X**	2/2/0	**LC**	**LC**		**8**	
P. volcanicum			x?	x?			0/0/2	**DD**				
Family Boidae												
Boa constrictor	**(x)**	**(x)**			**X**	**(x)**	1/3/0	NE	**VU**		**8**	
Corallus annulatus	**(x)**	**(x)**			x?	**(x)**	0/3/1	NE	**DD**		**7**	
Epicrates maurus	**(x)**	**(x)**			x?	**(x)**	0/3/1	NE	**LC**		**6**	
Ungaliophis panamensis	**(x)**	**(x)**	x?	x?	x?	**(x)**	0/3/3	NE	**DD**		**8**	
Family Anomalepididae												
Helminthophis frontalis	x?	x?	x?	x?	x?	x?	0/0/6	**DD**	**DD**		**10**	
Total Lizards	**49**	**46**	**14**	**19**	**35**	**38**		**evaluated**		**66**		**64**
documented	33	19	3	8	23	27		LC		40	low	22
plausible	16	27	11	11	12	11		DD or NT		10	medium	24
possible	0	2	7	7	7	3		Threatened		16	high	18

Table 4.31: continued.

Taxon		occurrence in protected areas							IUCN category			EVS	
		PILA	**BPPS**	**HIILV**	**PNVB**	**RFLF**	**PNSF**	**total X/(x)/x?**	**IUCN (2014)**	**Jaramillo et al. (2010)**	**this work**	**Jaramillo et al. (2010)**	**this work**
Total Snakes		**85**	**85**	**36**	**50**	**59**	**80**		**evaluated**		**107**		**105**
	documented	40	17	0	6	36	35		LC		74	low	37
	plausible	45	68	36	44	23	45		DD or NT		23	medium	46
	possible	5	4	25	16	32	1		Threatened		10	high	22
Total Reptilia		**139**	**136**	**50**	**69**	**95**	**123**		**evaluated**		**178**		**174**
	documented	74	36	3	14	60	62		LC		117	low	62
	plausible	65	100	47	55	35	61		DD or NT		35	medium	72
	possible	5	6	32	23	39	4		Threatened		26	high	40

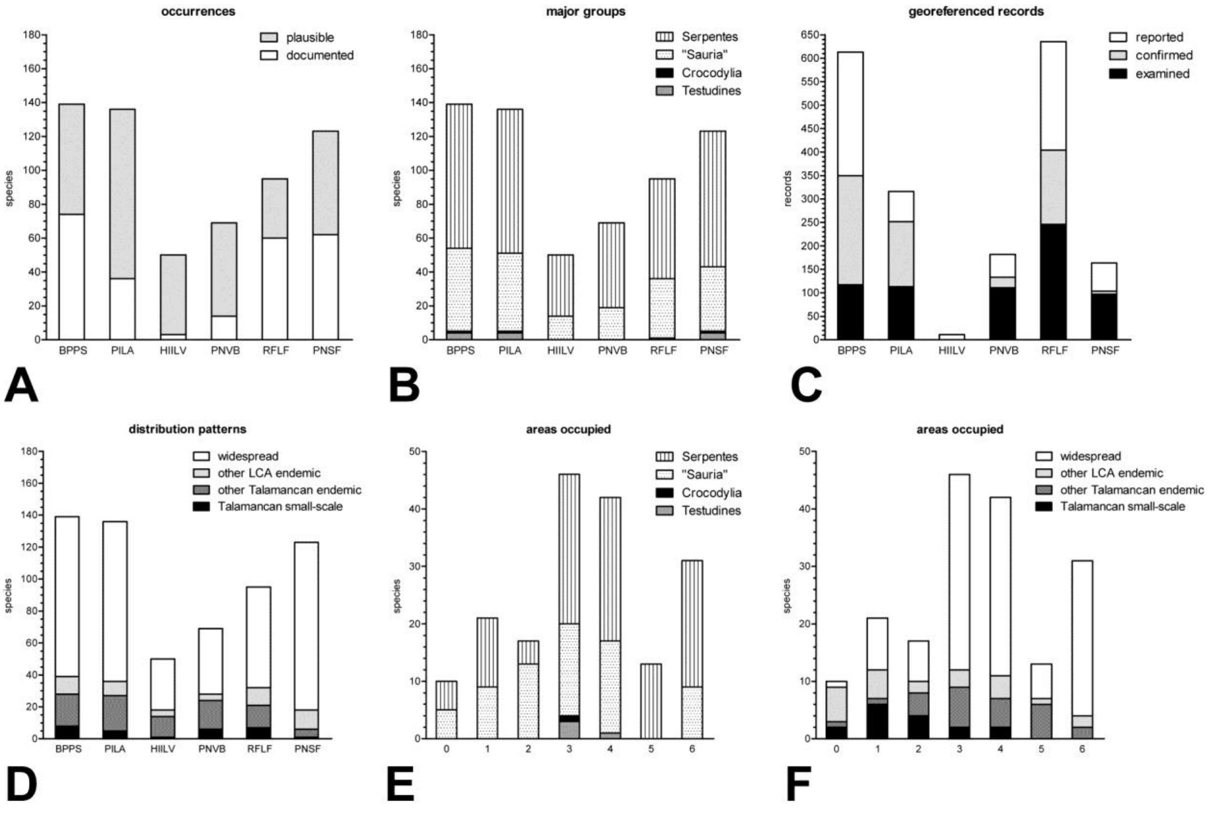

Figure 4.122: Occurrence of reptile species in the protected areas established within the study area. (A, B) Species per protected area, subdivided by (A) documented and plausible occurrences and (B) reptile orders and squamate suborders; (C) total of georeferenced records per protected area west of 81°W, subdivided by quality of evidence; (D) species per protected area, subdivided by distribution pattern; (E, F) protected areas per species, subdivided by (E) reptile orders and squamate suborders and (F) distribution pattern.

Figure 4.122 illustrates the distribution of my study area's reptile fauna among the six protected areas established along the Talamanca and Tabasará ranges. The large areas BPPS and PILA are inferred to each accomodate more than three-fourths (77% and 76%, respectively), and RFLF and PNSF to each hold more than half (53% and 68%, respectively) of the study area's total reptile species. However, it must be noted that these figures contain a much higher proportion of plausible occurrences than most species numbers reported in preceding analyses, in a way that the documented occurrences only account for between 6% (HIILV) and 63% (RFLF) of the totals. This is reflected by the total number of georeferenced records for each area with a minimum of just 11 from HIILV. With up to 85% (PNSF), widespread species account for a larger proportion of most protected areas' total species than they do within the entire study area, except for PNVB (59%) and HIILV (64%). The highest numbers of LCA endemics, Talamancan highland endemics, and Talamancan small-scale endemics are found in BPPS (39 LCA / 28 Talamancan / 8 small-scale) and PILA (36/27/5), each of which houses more than half of the study area's LCA endemics, followed by RFLF (32/21/7) and PNVB (28/24/6), that house slightly less than half of the study area's LCA endemics each. HIILV (18/14/1) and RFLF (18/6/1) each hold a single Talamancan small-scale endemic.

While almost three-fourths (132 species, 73%) of the study area's reptile species occur in 3 or more protected areas, 21 (12%) are inferred to occur in a single and 10 (almost 6%; 5 lizards + 5 snakes) to occur in none of the protected areas along my study area. Nine of these ten species are endemic to LCA, including two small-scale endemics (*Norops pseudokemptoni* and *Dendrophidion crybelum*). Six other Talamancan small-scale endemics are inferred to occur in a single protected area. Only considering documented occurrences, 47 species (26%) have not been documented from any of the six areas analyzed. Among these are 10 inferred to occur in 1, 16 inferred to occur in 3, and 5 inferred to occur in 6 areas.

Different perspectives on the conservation status of my study area's reptile fauna are given in Fig. 4.123. In the official IUCN Red List (IUCN 2014; Fig. 4.123A), way less than half of the species (73 species; 41%) have been evaluated, most of them as LC (59 spp.; 33%) or DD (8 spp., including 5 Talamancan small-scale endemics). Only two species (including the small-scale endemic *Geophis talamancae*) are accomodated in a Threatened category, and 33 (i.e., about half of the) LCA endemics including the undescribed *Lepidoblepharis* sp. 1 and 10 Talamancan small-scale endemics (*Celestus* sp., *Geophis* sp., and 8 described species) are among the 107 NE species.

The IUCN assessments resulting from the synthesis of the two previous (IUCN 2014; Jaramillo et al. 2010) and my own assessments (Fig. 4.123B, C) present a very different picture. Only two species (the LCA endemic *Norops charlesmyersi* and the widespread *N. gaigei*) are left NE, and 117 (65%) are classified as LC (including 13 Talamancan and 8 other, that is, about 32% of the LCA endemics). Nine species are NT and 26 others (14%) in one of the Threatened categories, including 25 (that is, 38% of the) LCA endemics. Eight

Talamancan small-scale endemics are EN and 4 are CR. In other words, two out of three small-scale endemics are assessed as Threatened according to IUCN guidelines herein. The remaining 4, together with 10 other LCA endemics and 12 widespread species, are DD. Snakes account for large portions of the DD and LC species (73 and 63%, respectively), whereas there are more lizards (62%) among the Threatened species.

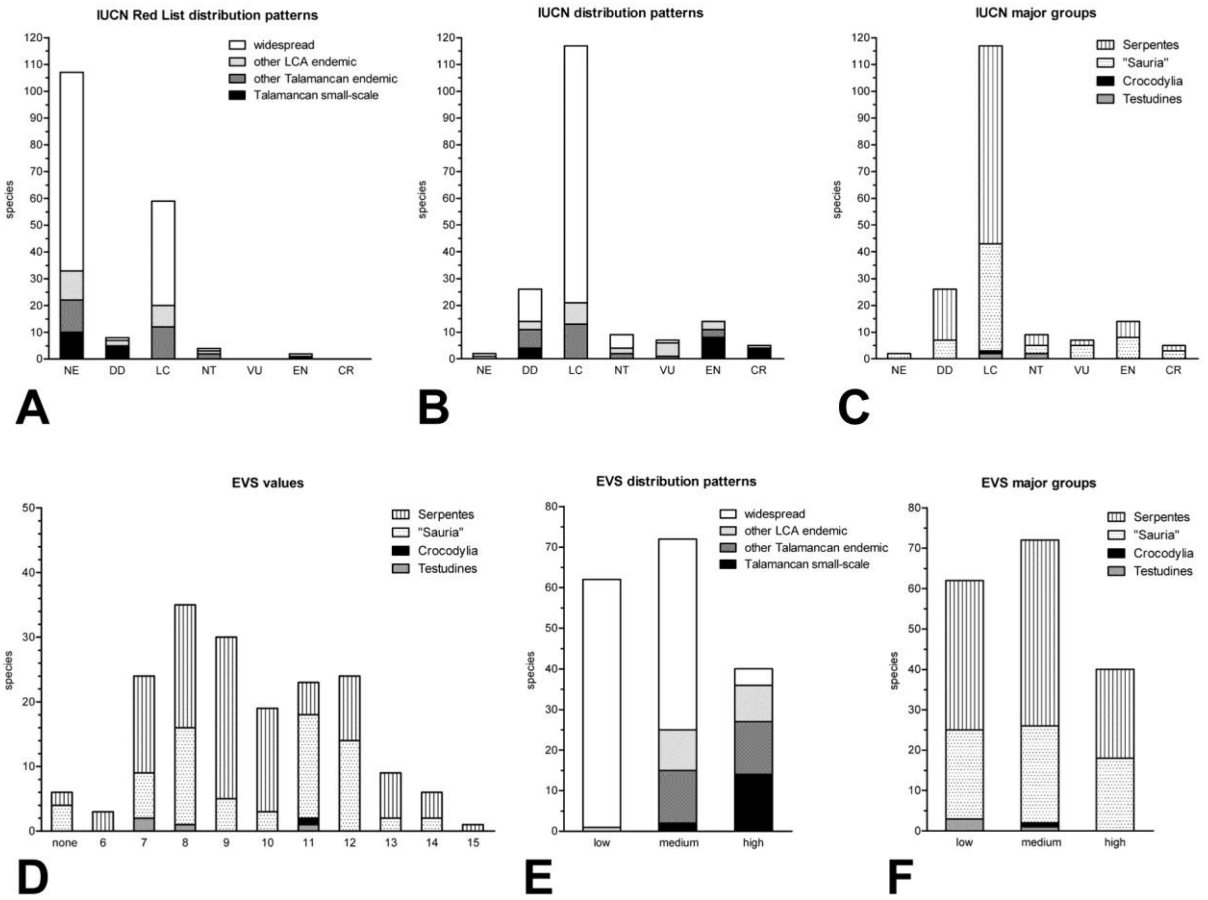

Figure 4.123: Conservation status of the reptile species occurring within the study area. (A) Species per category in the IUCN (2014) Red List, subdivided by distribution patterns; (B, C) species per IUCN category based on Jaramillo et al. (2010) and own assessments, subdivided by (B) distribution patterns and (C) reptile orders and squamate suborders; (D) species per EVS value based on Jaramillo et al. (2010) and own assessments, subdivided by reptile orders and squamate suborders; (E, F) species per EVS category, subdivided by (E) distribution patterns, and (F) reptile orders and squamate suborders.

The combined Environmental Vulnerability Scores of Jaramillo et al. (2010) and my own assessments (Fig. 4.123D–F) leave 6 species unassessed (4 lizards + 2 snakes; the LCA endemics *Norops charlesmyersi, Lepidophyma reticulatum,* and *Porthidium volcanicum* as well as 3 widespread species). For the 174 (97%) scored species, the individual EVS values range from 6–15. About 34% of the study area's species have received values of 8 or lower and are thus considered to exhibit a low vulnerability. With the exception of the LCA endemic *Marisora unimarginata,* these are all widespread. Among the 72 species (40%) inferred to exhibit medium vulnerability, the 25 LCA endemics (15 of which are highland endemics, including the small-scale endemics *Norops benedikti* and *Geophis* sp.) account for a considerable portion. The 40 exclusively squamate species (22%) scored as highly vulnerable with EVS > 11 include more than half (36 species; 55%) of the study area's LCA endemics, among these 27 (that is, 64% of all) Talamancan highland endemics including the remaining 14 small-scale endemics.

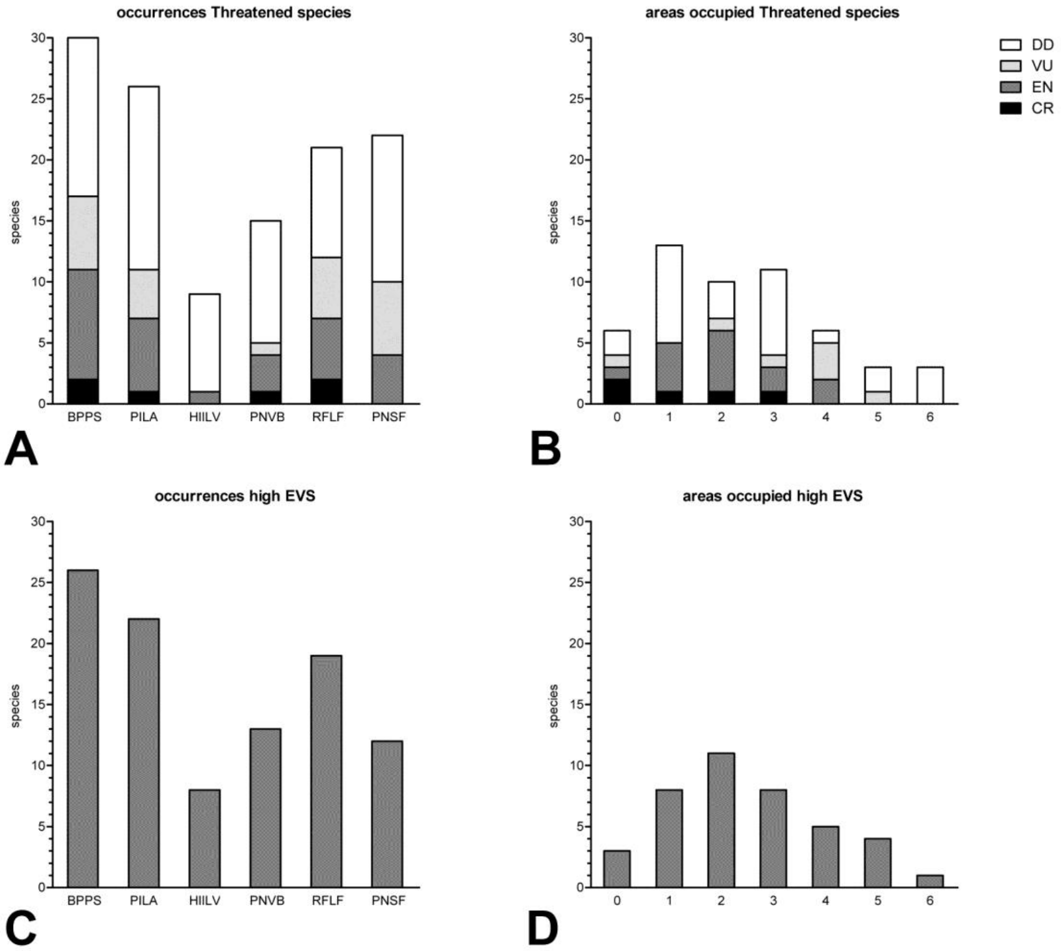

Figure 4.124: Occurrence of Threatened and high vulnerability species in the protected areas established within the study area. (A, B) Species assigned to the IUCN Threatened categories according to Jaramillo et al. (2010) and own assessments (A) per protected area, and (B) protected areas per species; (C, D) species with high EVS values of 12–15 according to Jaramillo et al. (2010) and own assessments (C) per protected area, and (D) protected areas per species.

Finally, Figure 4.124 shows the distribution among protected areas of the species assigned to the IUCN Threatened (7 VU + 14 EN + 5 CR = 26 species) or DD (26 species) categories, as well as of the 40 species assessed to exhibit a high vulnerability. Four Threatened (including the CR *Norops pseudokemptoni* and *Lachesis melanocephala*) and 2 DD species do not occur in any of the 6 protected areas considered herein, while 5 Threatened and 8 DD species are found in a single area. With 17 Threatened and 13 DD species, BPPS is the only reserve along my study area that holds 50% or more of the species assigned to either of these categories, followed by RFLF with 12 Threatened + 9 DD, PILA with 11 + 15, and PNSF with 10 + 12. The 3 CR species which occur in 1, 2, or 3 protected areas are found in BPPS, PILA, PNVB, and RFLF. Concerning species with high EVS, three (*N. pseudokemptoni, Dendrophidion crybelum,* and *L. melanocephala*) are absent from the protected areas along my study area, and 8 others occur in a single one. The large BPPS and PILA each hold more than half of the high EVS species, followed by RFLF with slightly fewer than half.

4.3.4 Historical source units

Savage (2002) assigned all native genera of the Costa Rican herpetofauna to his three major historical source units. My assignment of the 80 native reptile genera containing 179 native species (excluding the introduced *Hemidactylus*) inhabiting my study area to the North, Middle, and South American Elements as defined by Savage (2002) is detailed in Table 4.32 and summarized in the subsequent Figure 4.125.

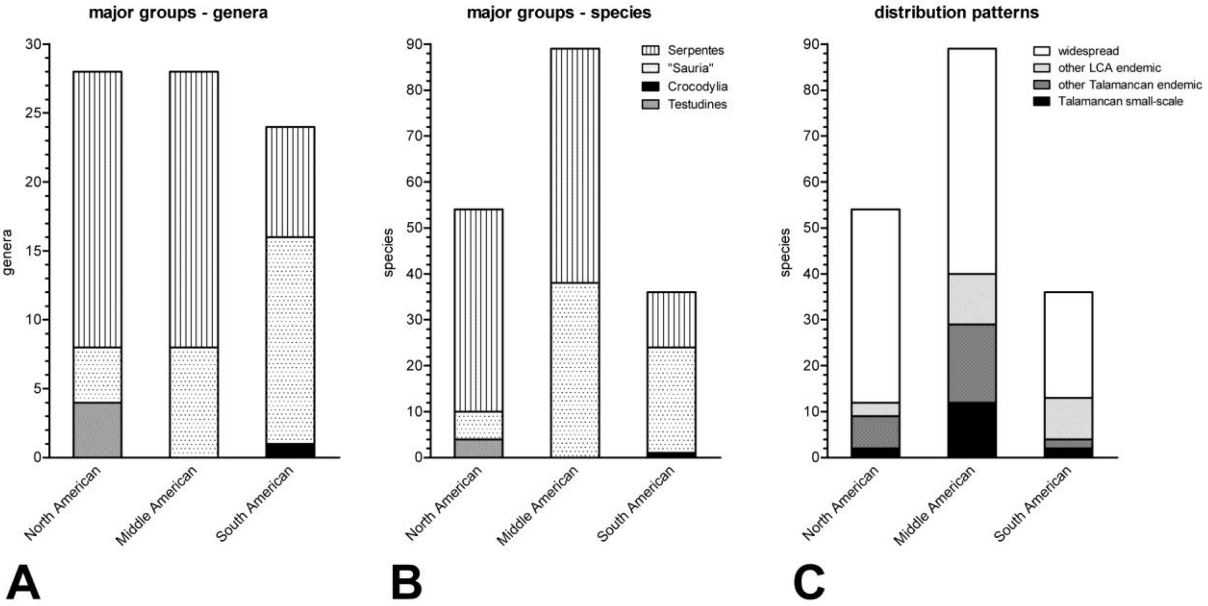

Figure 4.125: Composition of the study area's reptile fauna by historical elements. (A) genera and (B) species per unit, both subdivided by reptile orders and squamate suborders; (C) species per unit, subdivided by distribution pattern.

At the generic level, the contribution of the three historical source units appears quite balanced: both the North American and the Middle American Element are represented by 28 genera, respectively, while 24 genera are assigned to the South American Element. Contrary to the former two which hold 2.5–5 times as many snake as lizard genera, the South American Element contributes almost twice as many lizard as snake genera to my study area's fauna, almost half of which are gymnophthalmids. The evolutionary origin of all four turtle genera lies in NA, that of the only crocodilian in SA.

Table 4.32: Generic composition and species numbers of the historical units accounting for the study area's reptile fauna. The number of Panamanian endemics per genus in the study area is indicated by asterisks (*).

	North American Element	Middle American Element	South American Element
Order Testudines			
	Trachemys (1)		
	Rhinoclemmys (1)		
	Cryptochelys (1)		
	Kinosternon (1)		
Order Crocodylia			
			Caiman (1)
Order Squamata			
Suborder "Sauria"	*Mesaspis* (1)	*Celestus* (1*)	*Thecadactylus* (1)
	Sceloporus (1)	*Diploglossus* (1)	*Gonatodes* (1)
	Scincella (2*)	*Sphaerodactylus* (1)	*Lepidoblepharis* (2*)
	Lepidophyma (2)	*Basiliscus* (3)	*Dactyloa* (7***)
		Corytophanes (1)	*Enyalioides* (1)
		Norops (27******)	*Polychrus* (1)
		Iguana (1)	*Marisora* (1)
		Holcosus (3)	*Anadia* (1)
			Bachia (1)
			Echinosaura (1*)
			Gymnophthalmus (1)
			Leposoma (1)
			Potamites (1)
			Ptychoglossus (2)
			Ameiva (1)
Suborder Serpentes	*Chironius* (3)	*Amastridium* (1)	*Clelia* (3)
	Dendrophidion (5)	*Coniophanes* (1)	*Erythrolamprus* (3)
	Drymarchon (1)	*Dipsas* (2)	*Oxyrhopus* (1)
	Drymobius (2)	*Enuliophis* (1)	*Pseudoboa* (1)
	Lampropeltis (1)	*Enulius* (1)	*Xenodon* (1)
	Leptophis (4)	*Geophis* (7***)	*Corallus* (1)
	Mastigodryas (1)	*Hydromorphus* (2*)	*Epicrates* (1)
	Oxybelis (3)	*Imantodes* (3)	*Helminthophis* (1)
	Phrynonax (1)	*Leptodeira* (2)	
	Rhinobothryum (1)	*Ninia* (3)	
	Scaphiodontophis (1)	*Nothopsis* (1)	
	Spilotes (1)	*Pliocercus* (1)	
	Stenorrhina (1)	*Rhadinaea* (5**)	
	Tantilla (6)	*Rhadinella* (1)	
	Atropoides (2)	*Sibon* (7**)	
	Bothriechis (4)	*Trimetopon* (2)	
	Bothrops (1)	*Urotheca* (3)	
	Cerrophidion (1)	*Micrurus* (6)	
	Lachesis (2)	*Boa* (1)	
	Porthidium (3)	*Ungaliophis* (1)	
Total Lizards	4 genera, 6 species	8 genera, 38 species	15 genera, 23 species
Total Snakes	20 genera, 44 species	20 genera, 51 species	8 genera, 12 species
Total Reptilia	**28 genera, 54 species**	**28 genera, 89 species**	**24 genera, 36 species**

At the species level, the picture is a different one: Owing not least to the speciose genus *Norops,* the Middle American Element contributes 56% of the study area's lizard species and almost half of its total species. Among snakes, the genera *Geophis, Sibon, Micrurus,* and *Rhadinaea* have the largest share in this lead. While another third of the lizard species belong to lineages that originated in SA, only 6 lizard species have their origins in NA. Forty LCA endemics (62% of all 65 LCA endemics), including 29 Talamancan highland endemics (69% of the total 42) among which 12 have a small-scale distribution (75% of the total 16), are found in the Middle American Element. The remaining 25 LCA endemics are almost equally distributed between the NA (12, including 9 highland endemics 2 of which are small-scale) and SA (13/4/2) elements, but the number and percentage (17%) of Talamancan highland endemics among the species of the former is well above those of the latter (11%). Each of these two source units bears a higher percentage of widespread species (78 and 63%, respectively) among its members than the Middle American Element (55%).

4.3.5 Phylogeographic boundaries as suggested by highland anoles

In chapters 4.2.3–4.2.6, I have reviewed the taxonomy and specific distributions along my study area for several highland species of anoles. Some of these species are members of true highland species complexes whose members are restricted to premontane and higher elevations in the Central American highlands. Besides *Norops datzorum,* which is assumed to be most closely related to a CA group of highland anoles including the Costa Rican endemic *N. intermedius* and several species from Nuclear CA, these are the four respective Panamanian members of the *N. kemptoni* and *N. pachypus* complexes which are even restricted to the LCA highlands without exception. On the contrary, the *N. pentaprion* group and the genus *Dactyloa* each have several members with chiefly lowland distributions but also include a few species which are not found below premontane elevations. In an attempt to identify patterns of geographic distribution that are shared among the five mentioned groups of highland anoles, and thus possibly bear implications for common vicariance events induced by the region's physiography, Figure 4.126 aligns the respective distribution maps with the corresponding branches of the ML trees (shown in full in Fig. 4.1) obtained from 16S and COI barcodes. Generalized boundaries between neighboring genealogical lineages (DCLs or species) which might correspond to physiographic barriers are indicated by black bars in the maps. These putative physiographic barriers are coherently numbered throughout the maps, roughly according to the frequency with which they appear on the different maps. Next to the gray bars delimiting the barcoded lineages, their numbers are used to indicate their correspondence to the respective phylogenetic divergences.

On all four maps, the putative barrier 1 lies across the western Tabasará range somewhere between the Cerros Pata de Macho and Chorcha to the west and Cerro Saguí to the east, separating the western two species of the *Norops kemptoni* complex from the eastern two as

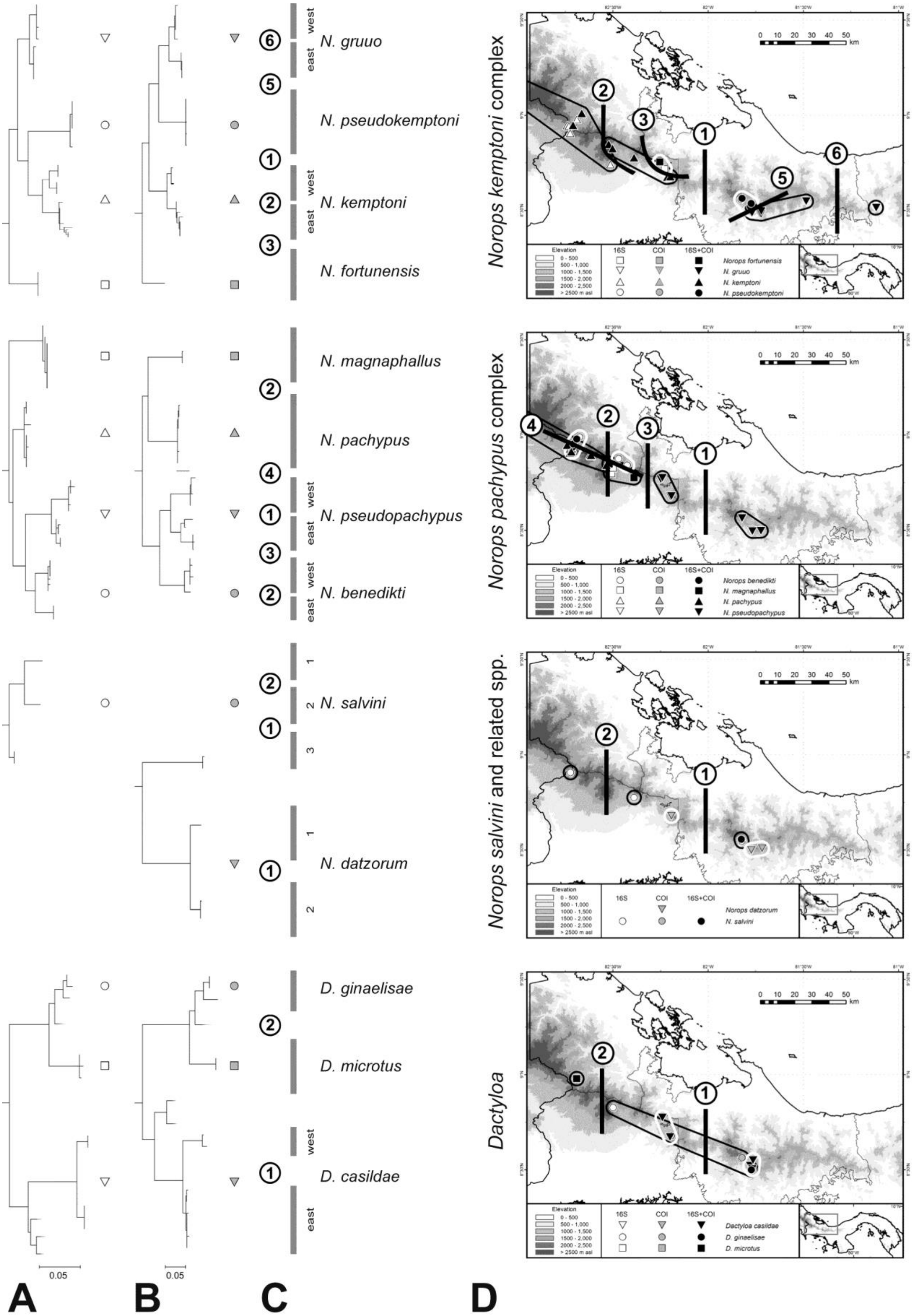

Figure 4.126: Phylogeographic boundaries exhibited by highland anoles. (A, B) Details from the ML trees provided in full in Fig. 4.1, showing the four clades of highland anoles as inferred from the analyses of (A) 16S and (B) COI barcodes; (C) genealogical lineages within each clade as inferred in chapters 4.1.3–6, with encircled numbers indicating the corresponding boundaries; (D) distribution of the genealogical lineages within each of the four clades of highland anoles along the study area; Approximate ranges as deducible from barcoded specimens are encircled by black or white lines, numbered bars indicate inferred phylogeographic boundaries.

well as the respective DCLs found within *Dactyloa casildae, N. datzorum, N. salvini,* and *N. pseudopachypus.* I believe that the series of low passes around 82°W, where the continental divide drops down to at least 1240 m asl, is the physiographic feature constituting this barrier. The putative barrier 2 is also present on all maps, though not always as clear-cut as the former. It is situated across the Talamanca range at Volcán Barú, and separates *Norops pachypus* from its possible sister species *N. magnaphallus* as well as possibly *Dactyloa ginaelisae* from *D. microtus,* and respective DCLs found within *N. kemptoni, N. benedikti,* and *N. salvini.* I believe this barrier to be associated with Volcán Barú and Cerro as well as Paso Respingo, which together form a continuum above 2500 m asl. The third possible barrier is inferred to lie across the continental divide just W of the Fortuna depression separating *Norops benedikti* from its sister species *N. pseudopachypus,* or in a modified version more parallel to the divide separating *N. kemptoni* from *N. fortunensis.*

Each of the remaining three boundaries is obvious only for a single pair of lineages, respectively. The putative barrier 4 stretches along the continental divide of the Serranía de Talamanca and separates the Pacific versant species pair *Norops magnaphallus* and *N. pachypus* from the more Caribbean *N. benedikti.* It could also be applicable to the species pairs *Dactyloa ginaelisae* and *D. microtus* (instead of or together with barrier 2) or *N. kemptoni* and *N. fortunensis* (instead of or together with barrier 2). Likewise, number 5 separating the possible sister species *N. gruuo* and *N. pseudokemptoni,* based on the distribution of these two species, appears to parallel the continental divide, though along a much lower portion in the central Serranía de Tabasará. Last, the deeply divergent DCLs west and east found in *N. gruuo* are separated by a boundary which I placed more than everything arbitrarily across the eastern Serranía de Tabasará.

4.3.6 Distribution of Panamanian reptiles among the western provinces

In the only attempt ever made to break down the distribution of the entire Panamanian herpetofauna among the republic's political subdivisions, Young et al. (1999) listed 169 of their total 228 reptile species for the western Provinces Bocas del Toro (115 species), Chiriquí (130), and Veraguas (55), leaving 59 species to only occur east of Veraguas. Fifteen years after the treatment by these authors, the Panamanian reptile fauna is reported herein to be composed of 265 species. Taking into account my combined dataset, Table 4.33 presents a partial update and extension of the list of Young et al. (1999), namely for the three western provinces mentioned above as well as the Comarca Ngöbe-Buglé which was not considered by these authors. The updated occurrences are graphically summarized in Figure 1.127.

From Veraguas and the three political subdivisions west of it, 207 species have to my knowledge been documented, and I regard the occurrence of four additional species (*Dendrophidion crybelum, Leptophis nebulosus, L. riveti, Tantilla armillata*) within this area as plausible. The resulting 211 species represent an increment of 42 species (or 25%) over the number of Young et al. (1999) and comprise almost 80% of Panama's reptile fauna. Of the merely 54 Panamanian reptile species (20%) hitherto exclusively reported from east of Veraguas, six species known to occur in Coclé and/or Colón (*Amphisbaena varia, Celestus adercus, Lepidoblepharis sanctaemartae, Dipsas nicholsi, Geophis bellus, Trimetopon barbouri*) possibly range into Veraguas. Last, four species known from eastern Costa Rica not too far from the Panamanian border possibly occur in Bocas del Toro (*Drymobius melanotropis*) or Chiriquí (*G. downsi, Urotheca myersi, Porthidium porrasi*).

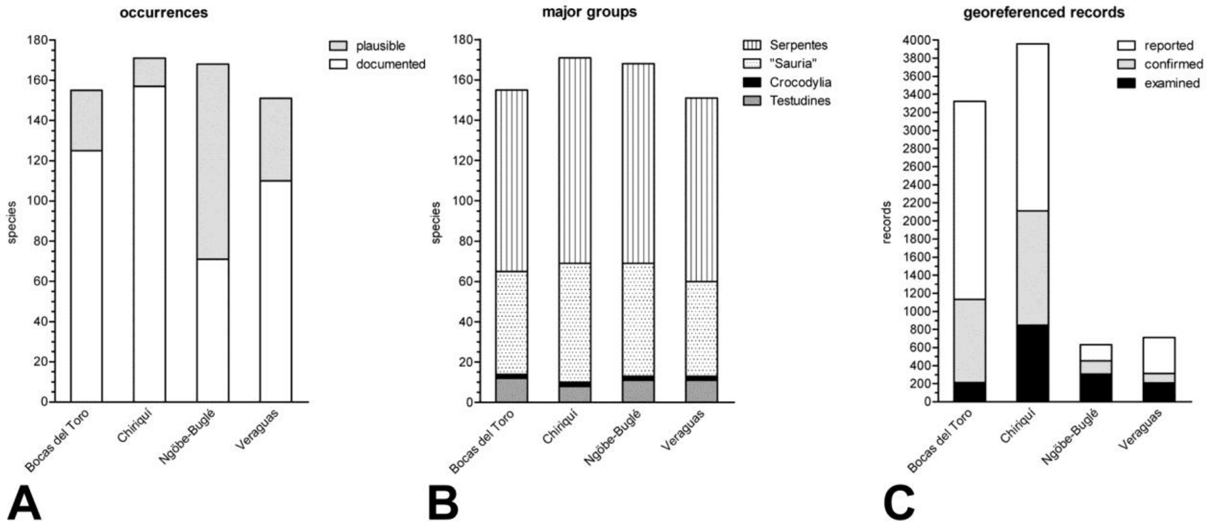

Figure 4.127: Distribution of reptile species among the country's four westernmost political subdivisions. (A) Species per province or comarca, subdivided by documented and plausible occurrences; (B) species per province or comarca, subdivided by reptile orders and squamate suborders; (C) total of georeferenced records per province or comarca, subdivided by quality of evidence.

Each of the political subdivisions overlapping my study area is home to between 151 and 171 reptile species (57–65% of Panama's 265) whose occurrence is either documented or considered plausible. Chiriquí appears as the most speciose province with 171 species (157 documented + 14 plausible; 65% of Panama's total reptile fauna and 81% of the reptile fauna from Veraguas westwards), closely followed by the Comarca Ngöbe-Buglé with 168 species (71 + 97; 63 and 80%). Somewhat fewer species are found in Bocas del Toro with 155 species (125 + 30; 58 and 73%) and Veraguas with 151 species (110 + 41; 57 and 72%). For each of the three provinces, the increments over the respective species numbers reported by Young et al. (1999) are considerable with 40 species for Bocas del Toro (35% more), 41 (32%) for Chiriquí, and 96 (175%) for Veraguas.

Table 4.33: Distribution of Panamanian reptiles among the four westernmost political subdivisions. X = presence documented; (x) = presence plausible; x? = presence possible. Occurrences (documented or plausible) not reported by Young et al. (1999) are in **bold** face. Species endemic to Panama are marked with an asterisk (*).

Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas	Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas
Order Testudines					*H. turcicus*				
Family Cheloniidae					*Lepidodactylus lugubris*	**X**	**(x)**	**(x)**	**X**
Caretta caretta	X	**X**	**(x)**	**X**	**Family Phyllodactylidae**				
Chelonia mydas	X	**X**	**(x)**	**(x)**	*Thecadactylus rapicauda*	X	X	**(x)**	**X**
Eretmochelys imbricata	X	**X**	**(x)**	X	**Family Sphaerodactylidae**				
Lepidochelys olivacea	**X**	X	**(x)**	X	*Gonatodes albogularis*	X	X	**(x)**	X
Family Chelydridae					*Lepidoblepharis sanctaemartae*				x?
Chelydra acutirostris	X		**(x)**	**(x)**	*L. xanthostigma*	X	X	**X**	**X**
Family Dermochelyidae					*Lepidoblepharis* sp. 1*			x?	**X**
Dermochelys coriacea	X	**X**	**(x)**	X	*Lepidoblepharis* sp. 2*				
Family Emydidae					*Sphaerodactylus argus*	X		x?	x?
Trachemys grayi	X	X	**(x)**	X	*S. graptolaemus*		X		
Family Geoemydidae					*S. homolepis*	X		**(x)**	(x)
Rhinoclemmys annulata	X		**(x)**	**(x)**	*S. lineolatus*		X	x?	X
R. funerea	X		**(x)**	**(x)**	**Family Corytophanidae**				
R. melanosterna					*Basiliscus basiliscus*		X	**X**	**X**
Family Kinosternidae					*B. galeritus*				
Cryptochelys angustipons	X		x?		*B. plumifrons*	X		**X**	**(x)**
C. leucostoma	X	X	**X**	X	*B. vittatus*	X		**(x)**	**X**
Kinosternon scorpioides	**X**	X	**(x)**	**X**	*Corytophanes cristatus*	X	**X**	**(x)**	X
Family Testudinidae					**Family Dactyloidae**				
Chelonoidis carbonaria					*Dactyloa casildae**	x?	X	**X**	
Order Crocodylia					*D. chloris*				
Family Alligatoridae					*D. chocorum*				
Caiman crocodilus	X	X	**(x)**	**X**	*D. frenata*	X	**X**	**X**	X
Family Crocodylidae					*D. ginaelisae**	**(x)**	**X**	**X**	
Crocodylus acutus	X	X	**(x)**	X	*D. ibanezi*	**X**	**(x)**	**X**	**X**
Order Squamata					*D. insignis*	X	X	**X**	**X**
Family Amphisbaenidae					*D. kunayalae**	x?	**X**	**X**	**X**
Amphisbaena spurelli					*D. latifrons*				
A. varia				x?	*D. microtus*	**X**			
Family Anguidae					*Norops apletophallus**				
*Celestus adercus**				x?	*N. aquaticus*		X		
Celestus sp.*		**X**			*N. auratus*		X	**(x)**	**X**
Coloptychon rhombifer		X			*N. benedikti*	X	**X**	x?	
Diploglossus bilobatus	X		**(x)**	**X**	*N. biporcatus*	X	X	**X**	X
D. monotropis	X		**(x)**	**(x)**	*N. capito*	X	X	**X**	**X**
*D. montisilvestris**					*N. carpenteri*	X	X	**(x)**	X
Mesaspis monticola	**X**	X	x?		*N. charlesmyersi*		**X**	**(x)**	x?
Family Gekkonidae					*N. cryptolimifrons*	**X**		**X**	
Hemidactylus brooki					*N. datzorum*	**X**	**X**	**X**	
H. frenatus	**X**	X	**(x)**	**X**	*N. fortunensis**		X	**X**	
H. mabouia					*N. fungosus*	X	X	**(x)**	

Table 4.33: continued.

Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas	Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas
N. cf. *fuscoauratus*					*E. panamensis**	**(x)**	**(x)**	**X**	**X**
N. gaigei		**X**	**(x)**	**X**	*Gymnophthalmus speciosus*	X	X	**(x)**	X
*N. gruuo**			**X**	**X**	*Leposoma rugiceps*	**X**		**(x)**	**(x)**
N. humilis	X	X	**X**	**X**	*L. southi*	X	X	**(x)**	**X**
N. kemptoni	**X**	X	**(x)**		*Potamites apodemus*		**X**		
N. lemurinus	X	X	**X**	**X**	*Ptychoglossus festae*	X	**X**	**(x)**	**(x)**
N. limifrons	X	X	**X**	X	*P. myersi**				
*N. lionotus**	X	**X**	**X**	**X**	*P. plicatus*	X	X	**X**	X
*N. magnaphallus**	**(x)**	**X**	**(x)**		**Family Teiidae**				
N. oxylophus	X				*Ameiva praesignis*		X	**(x)**	X
N. pachypus	**(x)**	X			*Cnemidophorus duellmani*				
N. pentaprion	X		**X**	X	*Holcosus festivus*	X	X	**X**	X
N. poecilopus					*H. leptophrys*		X	x?	X
N. polylepis		X	**(x)**		*H. quadrilineatus*	X	X	**(x)**	X
*N. pseudokemptoni**			**X**		**Family Colubridae**				
*N. pseudopachypus**		**X**	**X**		*Chironius exoletus*	X	X	**(x)**	**(x)**
N. salvini		X	**X**		*C. flavopictus*	X	X	**(x)**	**X**
N. tropidogaster					*C. grandisquamis*	X	X	**X**	**X**
N. vittigerus			x?	**X**	*Coluber mentovarius*				
N. woodi		X			*Dendrophidion apharocybe*	X		**X**	X
Family Hoplocercidae					*D. crybelum*	X	(x)	**X**	**X**
Enyalioides heterolepis			x?	**X**	*D. clarkii*		**(x)**		
Morunasaurus groi					*D. paucicarinatum*	X	X	**X**	
Family Iguanidae					*D. percarinatum*	X	X	**(x)**	X
Ctenosaura similis	X	X	**(x)**	**X**	*Drymarchon melanurus*	X	X	**(x)**	X
Iguana iguana	X	X	**(x)**	X	*Drymobius margaritiferus*	X	X	**X**	X
Family Phrynosomatidae					*D. melanotropis*	x?			
Sceloporus malachiticus	**(x)**	X	x?		*D. rhombifer*	(x)	**X**	**(x)**	**X**
Family Polychrotidae					*Lampropeltis triangulum*	X	X	**(x)**	X
Polychrus gutturosus	**(x)**	**X**	**(x)**	**X**	*Leptophis ahaetulla*	X	X	**(x)**	X
Family Mabuyidae					*L. depressirostris*	X	X	**(x)**	X
Marisora unimarginata	X	X	**X**	**X**	*L. nebulosus*	**(x)**	**(x)**	**(x)**	**(x)**
Family Sphenomorphidae					*L. riveti*		(x)	**(x)**	**(x)**
Scincella cherriei	X	X			*Mastigodryas melanolomus*	X	X	**(x)**	X
*S. rara**	X		**X**		*M. pleei*			x?	**X**
Family Xantusiidae					*Oxybelis aeneus*	X	X	**X**	X
Lepidophyma flavimaculatum	X		**(x)**	**(x)**	*O. brevirostris*	(x)	X	**X**	X
L. reticulatum		**X**			*O. fulgidus*	**X**	X	**(x)**	**X**
Family Gymnophthalmidae					*Phrynonax poecilonotus*	X	X	**X**	X
Anadia ocellata	X	X	**(x)**	**(x)**	*Rhinobothryum bovallii*	X	(x)	**X**	X
A. vittata					*Scaphiodontophis venustissimus*	**X**	**X**	**(x)**	(x)
Bachia blairi		X			*Spilotes pullatus*	X	X	**(x)**	**X**
B. pallidiceps					*Stenorrhina degenhardtii*	(x)	X	**X**	X
Cercosaura vertebralis					*Tantilla albiceps**				
Echinosaura palmeri					*T. alticola*		X	**X**	**(x)**

Table 4.33: continued.

Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas	Taxon	Bocas del Toro	Chiriquí	Comarca Ngöbe-Buglé	Veraguas
T. armillata		**(x)**	**(x)**	**(x)**	*Leptodeira annulata*	X	X	**X**	X
T. melanocephala					*L. rubricata*		**X**		
T. reticulata	**X**		**(x)**	X	*L. septentrionalis*	X	X	**X**	X
T. ruficeps		X	**(x)**	X	*Lygophis lineatus*				**X**
T. schistosa	**(x)**	**X**	**(x)**	**(x)**	*Ninia atrata*				
T. supracincta	(x)	X	**(x)**	(x)	*N. celata*	X	x?	**(x)**	**(x)**
Family Dipsadidae					*N. maculata*	X	X	**X**	X
Amastridium veliferum	X	X	**X**	**X**	*N. psephota*	**(x)**	X	x?	
Atractus clarki					*N. sebae*	**X**			
*A. darienensis**					*Nothopsis rugosus*	X	**X**	**(x)**	**X**
*A. depressiocellus**					*Oxyrhopus petolarius*	X	X	**X**	**X**
*A. hostilitractus**					*Phimophis guianensis*		X	**(x)**	**(x)**
*A. imperfectus**					*Pliocercus euryzonus*	X	X	**X**	X
Clelia clelia	X	X	**(x)**	**X**	*Pseudoboa neuwiedii*		X	**X**	**X**
C. equatoriana	**(x)**	**(x)**	**(x)**	**X**	*Rhadinaea calligaster*	X	X	x?	
C. scytalina	**(x)**	X	**(x)**	x?	*R. decorata*	X	X	**(x)**	X
Coniophanes bipunctatus	X		**(x)**		*R. pulveriventris*	**X**	X	**(x)**	
C. fissidens	X	X	**(x)**	**(x)**	*R. sargenti**			**(x)**	**X**
*C. joanae**					*R. vermiculaticeps**			**(x)**	X
Diaphorolepis wagneri					*Rhadinella godmani*	**(x)**	X	x?	
Dipsas articulata	X	X	**X**	**X**	*Sibon annulatus*	X	X	**X**	X
*D. nicholsi**				x?	*S. argus*	**(x)**	**(x)**	**X**	**(x)**
D. temporalis			**(x)**	**X**	*S. lamari*	**X**		**(x)**	**(x)**
D. tenuissima		X			*S. longifrenis*	X	x?	**(x)**	**X**
*D. viguieri**					*S. nebulatus*	X	X	X	X
Enuliophis sclateri	X	**X**	**(x)**	**X**	*S. noalamina**	x?	**(x)**	**X**	**X**
Enulius flavitorques		X	**(x)**	X	*S. perissostichon**		**X**	x?	
Erythrolamprus bizona	**(x)**	**X**	**(x)**	**X**	*Siphlophis cervinus*				
E. epinephelus	**X**	X	**X**	**(x)**	*S. compressus*		**X**		
E. mimus	**(x)**	X	**(x)**	(x)	*Tretanorhinus mocquardi**				
*Geophis bellus**				x?	*T. nigroluteus*	X		**(x)**	**(x)**
G. brachycephalus	X	X	**X**		*Trimetopon barbouri**				x?
*G. championi**		X			*T. pliolepis*	x?	**X**		
G. downsi		x?			*T. slevini*	**(x)**	X	**(x)**	
G. godmani	(x)	X	x?		*Urotheca decipiens*	X	X	**X**	**(x)**
G. hoffmanni	(x)	X	**(x)**	(x)	*U. fulviceps*				
G. talamancae	**(x)**	**X**	x?		*U. guentheri*	X	X	**X**	**X**
*G. tectus**	**X**	**X**	**X**	**(x)**	*U. myersi*		x?		
Geophis sp.*		**X**	**X**		*U. pachyura*	X	X	**X**	**(x)**
Hydromorphus concolor	X	**(x)**	**(x)**	**X**	*Xenodon rabdocephalus*	X	**X**	**X**	**X**
*H. dunni**		X			**Family Elapidae**				
Imantodes cenchoa	X	X	**X**	X	*Hydrophis platurus*				
I. gemmistratus	X	X	**(x)**	(x)	*Micrurus alleni*	X	X	**X**	
I. inornatus	X	X	**(x)**	X	*M. ancoralis*				
*I. phantasma**					*M. clarki*		X	**(x)**	**X**

Table 4.33: continued.

Taxon	**Bocas del Toro**	**Chiriquí**	**Comarca Ngöbe-Buglé**	**Veraguas**	**Taxon**	**Bocas del Toro**	**Chiriquí**	**Comarca Ngöbe-Buglé**	**Veraguas**
M. dissoleucus					*C. ruschenbergerii*		**X**	**(x)**	**X**
M. dumerilii					*Epicrates maurus*	**(x)**	X	**(x)**	**X**
M. mipartitus	X	x?	**X**	**X**	*Ungaliophis panamensis*	**X**	**(x)**	**(x)**	**(x)**
M. mosquitensis	**X**		x?		**Family Tropidophiidae**				
M. multifasciatus	**X**	**X**	**(x)**	**(x)**	*Trachyboa boulengeri*				
M. nigrocinctus		X	**X**	X	**Family Anomalepididae**				
*M. stewarti**		**X**	**(x)**	**(x)**	*Anomalepis mexicanus*	X		**(x)**	**(x)**
Family Viperidae					*Helminthophis frontalis*	**(x)**	X	**(x)**	**(x)**
Atropoides mexicanus	**(x)**	X	**(x)**	**X**	*Liotyphlops albirostris*	**(x)**	X	**(x)**	(x)
A. picadoi	**(x)**	X	**(x)**		**Family Leptotyphlopidae**				
Bothriechis lateralis	**(x)**	X	**X**	**(x)**	*Epictia goudotii*				
B. nigroviridis	**X**	X	**X**		*Trilepida macrolepis*				
B. schlegelii	X	X	**X**	**X**					
B. supraciliaris		**X**							
Bothrops asper	X	X	**X**	X	**Total Lizards**	**51**	**59**	**56**	**47**
B. punctatus					documented	45	56	28	40
Cerrophidion sasai	**(x)**	X	x?		plausible	(6)	(3)	(28)	(7)
Lachesis acrochorda					possible	2?	0?	9?	4?
Lachesis melanocephala		**X**			**Total Snakes**	**90**	**102**	**99**	**91**
Lachesis stenophrys	X	X	**X**	**(x)**	documented	66	91	42	61
Porthidium lansbergii		X	**X**	**X**	plausible	(24)	(11)	(57)	(30)
P. nasutum	X	x?	**X**	**X**	possible	3?	8?	9?	4?
P. porrasi		x?			**Total Reptilia**	**154**	**171**	**168**	**151**
P. volcanicum		**X**			documented	125	157	71	110
Family Boidae					plausible	(30)	(14)	(97)	(41)
Boa constrictor	X	X	**(x)**	**X**	possible	5?	8?	19?	9?
Corallus annulatus	X	x?	**(x)**	**(x)**					

While these inferred total species richnesses are rather similar among the four areas, the proportion of species occurrences actually documented by available records varies greatly, from 92% for Chiriquí over 81% for Bocas del Toro and 73% for Veraguas down to a mere 42% for the Comarca Ngöbe-Buglé. Likewise, the number of georeferenced records per subdivision shows a very uneven distribution: While 3954 and 3328 records come from Chiriquí and Bocas del Toro, respectively, only 710 are located within Veraguas and just 633 inside the Comarca Ngöbe-Buglé.

5. Discussion

In the following, I review the core findings of my results presented in the preceding section and discuss them in the context of reptile diversity research in- and outside Panama. Many aspects concerning the variation, taxonomy, and distribution of single species and species groups have been discussed in the respective taxonomic treatments (4.1.1–4.1.9) and species accounts (4.2.2) and are not repeated in this section.

5.1 Taxonomy

Taxonomy is the biological discipline occupied with distinguishing and naming natural groups. While the delineation, ranking, and nomenclature of groups at the generic and higher level might in many cases be regarded somewhat more arbitrary, the recognition of biological species as fundamental ecological and evolutionary units (Simpson 1961; Wiley 1978; de Queiroz 2005a, b, 2007) should leave less room for interpretation. The reliable identification of species is especially important considering that this alpha taxonomy, which is the facette of taxonomy focused on in the present work, has binding implications for most other biological disciplines. Though the evolutionary distinctness and reproductive isolation of reptile species are often reflected in their outer appearance, this is not necessarily the case, and rather not or not at all applies to several reptile groups containing complexes of so-called cryptic species. In the figurative sense "hiding" their distinctness, these cryptospecies bear little or no differentiations in external morphology, be it as a result of ecological equivalence or of recent phylogenetic separation, while in contrast the members of other species, often termed polymorphic, exhibit profound variability in external characters among each other. Thus, besides the discrimination of intra- from interspecific variation, the principal task of species-level taxonomy is the recognition, evaluation, and reasonable application of diagnostic characters and the correct assignment of the appropriate names to the taxa thus distinguished.

Until recently, alpha taxonomists have largely to entirely relied on morphology to distinguish between species, and in the field are still bound to do so. While the members of several reptile groups are readily separable by the application of traditional standard characters that were already established in the 19th century, the characters useful to distinguish species in other groups have long been unrecognized. The small members of the family Sphaerodactylidae dealt with in chapter 4.1.2 are a nice example for the evolution of taxonomy's understanding of pholidotic characters. While the first species now assigned to the genus *Lepidoblepharis* were described in the 1890s (Uetz & Hošek 2014), it was not until the 1920s that the presence and condition of the claw sheath was first applied to distinguish between this genus and its allies (Noble 1921) and the number of subdigital lamellae shown to be of primordial importance in distinguishing the species within the genus (Parker 1926). Original descriptions of *Lepidoblepharis* species preceding the review of Parker (1926) usually omitted lamellar counts and relied on other characters thought to be diagnostic, like scales across snout or postrostrals. However, most of these characters have been shown to be of less diagnostic value than first assumed in more recent species descriptions and the present study, owing to the in some cases great overlap between species as also revealed by better understanding of intraspecific variability in the light of larger sample sizes. Nevertheless, still no comprehensive overview of the respective lamellar count ranges of all described *Lepidoblepharis* has been published. Continuing the discovery of key characters for this group, the present study to my knowledge is the first to employ the configuration of the ventral and subfemoral escutcheon scale patches as a diagnostic character among species of *Lepidoblepharis,* thus establishing a novel diagnostic trait whose applicability to most congenerics of the species focused on herein (and furthermore to other sphaerodactylid genera) is yet to be tested.

As indicated above, the taxonomic value of a given morphological character can easily be misjudged, especially when few specimens are available to provide a reasonable notion of their intraspecific variability. Several historic species authorities have based the bulk of their species descriptions on single specimens, respectively. Some of these authors, the perhaps most noteworthy in this context being the incredibly productive E.D. Cope, apparently had the habit to accept every minor deviation in scale counts or structure as a proof of specific distinctness warranting a new name. As more material from these specimens' respective provenances became available during the 20th century, many names erected this way have been sunk into the synonymies of previously described species. Potentially problematic single-specimen issues also exist among my sample: While the unique specimens of *Celestus* sp. and *Sibon perissostichon* exhibit profound pholidotic differences to their congenerics, additional material of either taxon is urgently required for a sound understanding of their respective intraspecific morphological variability, and to preclude the imaginable possibility that these specimens are just aberrant individuals of previously described species. In the case of *Celestus* sp., material other than the single or few respective type specimen(s) of the geographically surrounding members of the genus are equally needed to address this issue.

One of the taxonomically most challenging groups of CA reptiles, the anoles, provide brilliant examples of character discovery and application as well as the issue of intraspecific versus interspecific variability, i.e., character state interpretation. Exemplary for both issues, a comparison of the reviews of the *Norops kemptoni* complex presented by Ponce & Köhler (2008) and myself (this work; results largely congruent with those of Gutpelet 2012) reveals that the increment in examined specimens from 4 to 23 for *N. gruuo* and from 3 to 22 for *N. pseudokemptoni* has resulted in the discovery of large overlaps in all pholidotic characters regarded as diagnostic by the former authors, precluding their usefulness for a doubtless species identification. Additionally, the exclusively qualitative characters thus left for confidently assigning a name to a given representative of this cryptic species group also had to be partially relativized and redefined in the light of my increased sample size. The other way round, exuberant variation within "long and well" known nominal species can obscure their composition of several distinct evolutionary units as exemplified by the case of *Dactyloa ginaelisae* and *D. microtus,* whose polymorphic coloration and pattern including a drastic potential for metachrosis, along with the small sample sizes available prior to the assembly of my collection, have long overshadowed the consistent differences in coloration pattern and morphometrics between these two species. Multivariate statistics and morphological phylogenetics involving a multitude of characters can help to recognize subtle morphological differentiations between not obviously distinguished taxa as well as to clarify their relationships (Jadin et al. 2010a; Castañeda & de Queiroz 2013, chapters 4.1.3 and 4.1.4 of this work), but the actual straightforward species identification in practice requires a manageable amount of preferably external diagnostic characters allowing to draw taxonomic conclusions with reasonable effort and timing.

While many species of *Norops* are often considered notoriously difficult to identify, and some are indeed virtually undistinguishable from each other even when observed from short distances or counting scales (see chapters 4.1.4–4.1.7), my taxonomic studies demonstrate that all nominal species present in my study area can readily be diagnosed using just two characteristics, if necessary in combination: the hemipenis and the (mostly male) dewlap. The taxonomic value of the former character among this lizard group has largely been established by GK and colleagues (see Köhler 2008, 2009, 2011; Köhler & Sunyer 2008; Köhler et al. 2006, 2007, 2010b, 2012a, b, and references therein) and is confirmed herein to distinguish some otherwise really cryptic species pairs of *Norops* found along my study area, such as *N. kemptoni* and *N. pseudokemptoni,* or *N. cryptolimifrons* and *N. limifrons*. Lamentably, hemipenial morphology as a taxonomic tool is burdened with the major drawback that the eversion and preparation of these delicate organs requires the animal in question to be sacrificed and is often difficult, and thus can only be satisfactorily performed by trained people with corresponding permits, adequate equipment, and some experience. Nevertheless, in most of the cases in which the hemipenis is the crucial character for the discrimination of cryptic species (such as in the two species pairs mentioned above), the reproductive organ does not have to be everted, since its relative size and the resulting bulging of the tail base can be sufficiently judged from the outer appearance of a given adult male.

Interestingly, unlike in other anoline radiations, the hemipenis does not serve as a distinctive feature among the cryptic species in the *N. pachypus* complex. Instead, species in this complex are only reliably diagnosable by their dewlaps. Directly linked to mate recognition within evolutionary entities, the size, coloration, and scalation of the male dewlap has been used for decades to characterize anoles and constitutes the paramount key character for any species identification in this group (see Fitch & Hillis 1984, Savage 2002; Lotzkat et al. 2011, Ng et al. 2013, and references therein). Indeed, it is the only character that reliably separates several species pairs which are truly cryptic concerning their scalation and even hemipenes, such as *N. benedikti* and *N. pseudopachypus, N. magnaphallus* and *N. pachypus, N. fortunensis* and *N. kemptoni,* or *N. charlesmyersi* and *N. pentaprion*. However, to fulfill this purpose, the dewlap coloration in life must be recorded. While this obvious truth sounds all too trivial, the taxonomic history of the *N. pachypus* complex illustrates how the ignorance of dewlap color can entail a blatant underestimation of species diversity: As noted by Lotzkat et al. (2011) for *N. benedikti,* the previous failures to recognize the specific distinctness of the otherwise mostly cryptic and only recently described *N. benedikti, N. magnaphallus,* and *N. pseudopachypus* can most probably and parsimoniously be attributed to the lack of dewlap coloration data associated with long collected specimens of either of these "new" species – or to the ignorance of such information as in the case of *N. magnaphallus,* for which a "rich blood-red" male dewlap has been explicitly stated (Slevin 1942). The fact that the yellow, orange, or red pigmentation of most *Norops* dewlaps fades quite rapidly in alcoholic preservatives, preventing the a posteriori determination of the dewlap color in preserved material, emphasizes the importance of recording the dewlap color of any anole directly in the field, as otherwise this character of utmost taxonomic significance is lost (Lotzkat et al. 2011). Fortunately, in the era of digital cameras, doing so is nowadays more practible than ever. Still, the manifold inquiries I have received from conservation staff as well as from trained biologists to provide species identifications for small brown anoles that were accompanied by photos of the handheld animal in question, but not of the extended dewlap (or verbal information on its color) have tought me that the taxonomic importance of the dewlap has not yet been realized by everyone working with anoles. Yet, since anoles constitute a large fraction of the Panamanian reptile fauna including numerous national and/or small-scale endemics, the reliable identification of species in this group is highly warranted. The present work provides an unprecedented overview of the variability in dewlap coloration and other morphological characters found in 37 Panamanian species of anoles, including all nominal species known from western Panama. I sincerely hope that this colorful compilation will promote better supported identifications of these "difficult" species in the future.

Overlapping variabilities in quantitative as well as qualitative characteristic and the often subjective nature of taxonomic interpretation of morphological traits make the application of additional lines of evidence desirable, and frequently necessary, to achieve well-supported taxonomies. In principle, molecular data allows approaches applicable to all organisms regardless of their specific morphology and facilitates a more objective and thus highly welcomed perspective on the evolutionary divergence among organisms. DNA barcoding using fragments of the mitochondrial COI (e.g., Hebert et al. 2003; Hajibabaei et al. 2006) and/or 16S (Vences et al. 2005a) genes has been demonstrated to be a powerful tool for deciphering cryptic diversity in amphibians and reptiles (e.g., Vieites et al. 2009; Miralles et al. 2011; Jansen et al. 2011; Hertz et al. 2012b; Köhler et al. 2012b; Nagy et al. 2012; Lotzkat et al. 2013; Batista et al. 2014). Yet, while the approximate phylogenetic position of a given individual to another can usually be inferred rather unambiguously with one or two of the above mentioned fragments, the degrees of genetic divergence within and between species are by no means fixed but may overlap just as morphological characters do, and vary considerably between different groups (e.g., Vences et al. 2005b; Nagy et al. 2012; this work). In addition, several analysis parameters such as the number and relative position of bases contained in the employed gene fragments, alignment procedures, and distance calculation parameters can considerably influence the resulting pairwise distance values (e.g., Vences et al. 2005a; Nagy et al. 2012) as experienced by myself, especially for the non-coding 16S barcode with its highly variable loop regions. Moreover, only a tiny fraction of all reptile species has been barcoded to date, as exemplified by the reptile fauna of my study area of which only very few species were represented by 16S and/or sufficiently long COI fragments from Panama or the surrounding countries available on GenBank when I began with my barcoding efforts in 2010. Since many of the hitherto published COI and 16S sequences were generated for studies on supraspecific phylogenetics rather than for taxonomic studies, the correct identification of the respective specimens may in some cases be considered questionable (see remarks in the species account of *Dactyloa insignis*). Thus, we are still far from automatic species recognition through the mere sequencing of some base pairs, or automated species inventories based on barcoding only. To ultimately assemble the comprehensive barcode reference libraries necessary for such identification approaches, ideally comprising 16S and COI barcodes of all described reptile species, reptile taxonomists still have to go down a very long road of thorough integrative analyses of selected species groups. While barcode clusters whose differentiation from others surpasses a certain threshold or not can be automatically recognized, the paramount question of whether an observed divergence is to be interpreted as intra- or interspecific remains unanswered even by the most witty software application running on the fastest processor. Thus, a reasonable evaluation of any degree of divergence, identification of meaningful group-specific threshold values, as well as most importantly the correct assignment of available or new names to inferred clades, can only be achieved through creating a well-substantiated consensus of classical and DNA taxonomy via the identification of congruences between the phylogenetic signals provided by morphological and molecular traits and the integration of the existing taxonomic knowledge in these results. In this process of integrative taxonomy, DNA barcoding may corroborate (as in chapters 4.1.4–4.1.5) or dismiss (as in chapters 4.1.7.2 and 4.1.7.5) taxonomic hypotheses initially formulated in view of morphology, and often even be indispensable to initially recognize cryptic diversity (as for *Dactyloa ginaelisae* or the *Norops limifrons* complex).

Together with the published 16S barcode analyses incorporated in the present work (Köhler et al. 2012b; Lotzkat et al. 2013), this study is the first DNA barcoding study on Lower Central American reptiles to be compiled. Based on just 300 squamate specimens representing 65 species recognized herein (including the undescribed *Celestus* sp., *Lepidoblepharis* sp. 1 and 2, and *Geophis* sp.) for which I had 16S and/or COI barcodes available, it obviously lags behind other barcoding studies on tropical herpetofauna (e.g., Vieites et al. 2009; Nagy et al. 2012) both in terms of specimen and species numbers. Still, apart from corroborating the usefulness of the 16S barcode to distinguish species in several LCA reptile groups, it provides an important starting point for more comprehensive assessments of reptile diversity in LCA and the Neotropics in general by generating an initial set of reference barcodes. Moreover, for the principle barcoded groups, my results provide a first estimation of uncorrected p-distances typical of intra- and interspecific barcode pairs in the respective groups. As was to be expected from the results obtained for Madagascan reptiles by Nagy et al. (2012), the genetic divergences typically found between species vary considerably among the Panamanian reptile groups which I barcoded. This holds for both the 16S and the COI barcode, the latter of which generally yields higher values of uncorrected p-distances. While different methods have recently been used to assess which magnitude of sequence divergence is indicative of a possible specific status of barcoded lineages (compare, e.g., Miralles et al. 2011, Nagy et al. 2012, and Batista et al. 2014), my results further attest a certain usefulness to haplotype networks in this regard. With the exception of highly divergent DCLs and very closely related sibling species, the 16S haplotypes of most of my barcoded species form separate parsimony networks at the 95% connection limit. While this threshold was suggested by Hart & Sunday (2007) for the COI barcode, my results suggest that the higher divergences found in this fragment among my barcoded species almost invariably require a lower connection limit of at least 90%, and often even twice the number of substitusional steps required for a 95% parsimony probability, to yield separate networks for each species. While this and other algorithms may provide somewhat objective perspectives on divergences and thus assist in evaluating the evolutionary distinctness of populations, they must by no means be relied upon blindly, as it is the case with "typical" mean and/or threshold values for pairwise genetic distances. Instead, the extreme cases of mtDNA divergence within certain species (e.g., *Norops pseudopachypus* DCLs east and west) and similarity between others (e.g., *N. pachypus* and *N. tropidolepis*), as evidenced by the overlaps between the intraspecific p-distances and those of closely related species found in the 16S barcodes of certain lineages (see Tab. 4.23), once more illustrate the necessity of integrative taxonomic approaches combining separate lines of evidence for a robust evaluation of barcoding results, or generally speaking of any taxonomy. After all, the delineations and names that we apply to sets of organisms which we perceive to represent evolutionary entities distinct from other such entities, i.e., our specific taxonomies, are just hypotheses of evolutionary reality that are very difficult to profoundly verify in practice. All we can do is rule out as many imaginable falsifications as possible by testing our alpha-taxonomic hypotheses against as many lines of evidence as possible. The more supporting lines of evidence we have, the more robust we may regard our hypotheses to be. In this context, the analysis of nuclear DNA to obtain a second molecular perspective that in any case will complement, and may be slightly to strongly discordant to, the somewhat biased picture provided by the maternally inherited mitochondrial barcode fragments (e.g., Vences et al. 2005b and references therein) appears highly warranted to draw substantiated conclusions on the putative specific distinctness of many lineages identified through DNA barcoding in this study.

Apart from the establishment of a first barcode reference frame for Panamanian and other LCA reptiles, my taxonomic analyses accompanied by comprehensive illustrations of morphological variability, coupled with the wherever possible standardized descriptions and diagnoses in the species accounts that are augmented with color photographs of all but 12 species, constitute the hitherto most ample basis for the identification of a large portion of the Panamanian reptile fauna. This is especially important in view of the several species which have only very recently been described from, or reported for, western Panama and to date have at most been partially compared among each other or to the previously known fauna. Indeed, the present study is the first to outline the variability and provide profound identification groundwork for all 16 reptile species described during the past 10 years from type localities in Panama and the three species newly reported for the country since Jaramillo et al. (2010). In this context, my results' utility for the differentiation of anoles, which account for 12 of the 16 new species mentioned above, may once more be highlighted.

Yet, even with this recent boost in species descriptions, the Linnean shortfall for Panamanian reptiles is unlikely to be overcome soon, as many secretive, fossorial, or highly arboreal species can be assumed to still await discovery, and cryptic diversity around the species level must be expected among numerous nominal taxa, as exemplarily demonstrated for several groups of *Norops* in this work. Dedicated surveys both filling geographical sampling gaps and re-visiting "well-sampled sites" are needed to profoundly unravel this unrecognized diversity, as well as to address different issues of unclear taxonomic status pointed out in this work. However, regardless of any good intentions in this respect, the taxonomic impediment is also active in Panamanian reptile research, as exemplified by my single specimen of *Celestus* sp. that has been residing in a jar for five years now, still awaiting its formal description for which I simply did not have time. Not to speak of cryptic species or the secretive ones never collected to date, I seriously wonder how many potential type specimens of well-diagnosable reptile species share the fate of this juvenile lizard, especially in jars currently located in the Republic of Panama.

Last, even established and well-substantiated taxonomy does not promote itself but depends on consistent implementation by the herpetological community in general to duely fulfill its purpose as the cornerstone of biological knowledge. This is especially true for the locality records classified herein as "reported", each of which may technically be considered to be questionable in terms of specific identity. While this obviously applies to mere listings not citing any voucher specimens, it also holds for a possibly not too low percentage of voucher specimens long housed in public collections. Two sad examples of unrealized thorough implementation of taxonomical changes in collection catalogues and the like are the holotype (USNM 38750) of *Sibon longifrenis* (Stejneger 1909) which some 105 years after the species' formal description is still catalogued as *S. dimidiata,* or the holotype (MCZ 42788) of *Rhadinaea sargenti* Dunn & Bailey 1939, which according to the label in its jar (photographed by GK) is a representative of the similar *R. vermiculaticeps.*

5.2 Diversity

Biological diversity is the sum of life's variability, from the molecular over the species to the ecosystem level, throughout the biosphere, through all times (Streit 2007). Non-biologists usually perceive the term biodiversity as species diversity, given that the multitude of species is the most intuitively intellegible aspect of biodiversity, and that this species or alpha diversity is the level of biodiversity that has the broadest significance and application in political, socioeconomic, and conservation contexts. Recognizing this prominence and importance, species diversity is also the level of diversity focused on in the present work. Yet, while a comprehensive study of all aspects of diversity concerning such a diverse assemblage as the reptile fauna of my study area can never be completed, the voluminous species accounts presented in chapter 4.2.2, complemented by the taxonomic analyses in section 4.1, offer at least a fragmentary glimpse at the morphological, genetic, phylogenetic, behavioural, and ecological diversity among the species concerned. As an example, my DNA barcoding results reveal considerable degrees of genetic diversity within several nominal species (e.g., between the DCLs of *Dactyloa casildae* and *Norops pseudopachypus,* or the UGLs found within several other *Norops*) which may have implications for conservation and/or taxonomy, while my biogeographical analyses presented in chapter 4.3.1 link species with habitat diversity.

Within the species level of diversity, building mostly on my alpha-taxonomic studies and combined species occurrence datasets, my work furthermore concentrates on species richness as the most fundamental measure of species diversity. Its second standard measure, the species' relative abundances, are usually not provided in the faunistic works which I chiefly consulted. I also had to neglect it during my own field surveys, after initial attempts to record relative abundances had shown that the required survey protocols would severely decrease the effectiveness of the species inventory work (especially by reducing the time available for the "patient cruising" highlighted as the optimal approach for this task by Myers 1972) which I considered more important. Moreover, throughout my field work I found the detectability, that is, the population density percieved by myself, of many species to vary considerably over time within a single place for unknown reasons that would be worth a proper study themselves. Examples are mentioned in the species accounts of *N. charlesmyersi, N. datzorum, N. salvini,* and *Geophis* sp., and were detailed for *Diploglossus bilobatus* by Lotzkat et al. (2010b). Thus, abundance data is merely mentioned, more than anything anecdotically for species which I found to occur very abundantly, in selected species accounts.

Logically, any information on the species richness of a given area is dependent on the underlying inventory work in two ways. First, the completeness of the species inventory, i.e., the detected portion of the species actually present, heavily depends on survey techniques, duration, and staff, as well as on climatic and other natural factors which cannot be controlled by the surveyors. Concerning the inventory work carried out in and around my study area by myself and coworkers, I am convinced that everyone involved applied the maximum effort possible through most of the respective survey time. However, looking at the list of collected and observed specimens and species, one is bound to notice that my collections (including those of AC, JFB, LS, and NH) appear heavily biased towards anoles, whereas comparably few snake specimens and species were found. This is on the one hand due to the high detectability of sleeping anoles at night and the fact that anoles constitute a large portion of my study area's total species as well as to the high population densities perceived by us for many anole species. In contrast, many snake species are far less detectable, possibly because they occur in lower densities and definitely because they are less conspicuous owing to their habits. On the other hand, the low representation of snakes goes along with that for fossorial or strictly arboreal taxa as exemplified by the single specimens collected alive of each *Celestus* sp. and *Anadia ocellata,* respectively. Due to their habitat preferences, species with completely fossorial or arboreal lifestyles are largely outside the surveyor's range of vision, requiring digging and climbing techniques far beyond the microhabitat searches performed by us for an adequate sampling of their diversity. Similar constraints apply to the numerous species of small "leaf litter snakes", whose in general low representation in collections tells a tale of their low detectability in the field (Ray et al. 2013). In retrospective, I furthermore regard the fact that most of our searching was performed at night as a constraint to the completeness of my inventories, since more sampling at daytime would have increased the probabilities of casual encounters with actively moving diurnal animals, again especially snakes, some common and widespread species of which I have never seen in life. Independent of survey techniques, the time spent at a given locality logically has a major influence on the species richness detected, in a way that it is not surprising to find our collection from Cerro Mariposa (92 man-nights spent, 33 species) containing more species than those from nearby Cerro Negro (18 man-nights, 24 species) or above El Paredón (2 man-nights, 6 species). Last but not least, the success of any reptile sampling effort is to a considerable extent subjected to "the fortuitous nature of most herpetological collecting" pointed out by Noble (1916), particularly in the diversely structured tropical habitats whose ecology we do not yet sufficiently understand.

Apart from the representativity of the species number recorded for a given area, the second constraint that greatly influences resulting diversity assessments is the taxonomy applied, i.e., the issue of correct identifications and/or catalogings already addressed in the preceding chapter. Apart from the always assumable outdated name listed for a specimen in the corresponding collection catalogue, many reptile inventories for sites in Panama are mere lists of names which are either completely unsubstantiated (that is, the authors do not even mention if they collected voucher specimens, or on which basis they identified species) or do not list the collected voucher specimens on which one could verify their identifications. Thus, a multitude of doubtful identifications appearing in many inventories which I consulted for this study can never be confirmed nor corrected as discussed in the respective species accounts. Whenever I considered such unsubstantiated identifications as completely impossible and senseless (such as the bulk of montane species reported for HIISSPS by ANAM 2004, which I presume to be the result of these authors uncritically adopting for this coastal lowland area all species listed for Bocas del Toro province by Young et al. 1999), I removed it from the respective list. Yet, I left such doubtful occurrences in my dataset whenever I regarded the occurrence of a listed species somewhat imaginable, even if the possibility seemed rather remote to me. As an example, this was the case for *Ptychoglossus festae* (see remarks in species account), considering that the distribution of *Leposoma rugiceps,* a lizard species with a presumably not too different ecology, has recently been extended from the previously known localities in central Panama throughout western Panama (Lotzkat et al. 2012b). In the end, my three categories reflecting different quality levels of taxonomic evidence (reported, confirmed, and examined) were established to reflect the uncertainties surrounding many records. This way, any highly cautious reader may choose to simply disregard any white symbol plotted on any of my maps.

Concerning the species richness of my study area and other assessed areas, I chose to include in my total counts the species which have not yet been documented but whose presence I regard as plausible (not to say evident) based on their overall distribution. I did so with the purpose of approximating the real species richness as closely as possible. Again, the more conservative reader may choose to disregard the plausible occurrences and instead stick to the documented ones, which are always separately specified throughout the results sections. The distance of 5 km from a given area as a threshold between "plausible" and "possible" occurrences was somewhat arbitrarily chosen. Although this value is supposed to reflect a more cautious and not too inclusive approach and thus to add weighting to any categorization as "plausible", my strict adherance to the accordingly defined occurrence criteria has left out some species which most probably range into my study area, such as *Norops oxylophus* and *Leposoma rugiceps.* However, the species of possible occurrences are specified and their distribution maps provided in Appendix 7, so that readers can draw their own conclusions regarding their presence in the study area (or other areas dealt with in section 4.3). Nevertheless, I am convinced that my approach of including in my total counts the species of plausible occurrence with those that have been documented, while leaving out the species of merely possible occurrence, results in the hitherto closest approximation to real species richness throughout my lists for Panama, the Cordillera Central, and my study area (just as those for other areas dealt with in section 4.3), while at the same time not venturing too far into mere assumptions and extrapolations of areals. That is, I am utterly confident that future surveys will certainly document the occurrence of the species whose presence I have classifed as plausible in the respective areas – provided that their biogeographic framework is not severely altered by justified changes in alpha taxonomy.

The reptile species richness of Panama is outstanding in any context. The 265 species considered herein to occur in the country correspond to more than 20 times the number found in Germany (13 authochthonous species, Uetz & Hošek 2014), which is five times larger than Panama, and are in the order of magnitude of the total herpetofauna of Europe (Glandt 2010). While the USA hold about twice as many species (Uetz & Hošek 2014), the relative species richness in Panama is way higher with a SRI of 286 (or 34.9 species per 10000 km^2) compared to 18861 (or 0.53 species per 10000 km^2). Turning to the Neotropical realm, Panama's southern neighbor Colombia holds more than twice as many species, but likewise is way behind Panama in terms of relative species richness (SRI = 1937; 5.2 spp. / 10000 km^2). Within the Mesoamerican biodiversity hotspot (all comparative values from Wilson & Johnson 2010), Panama is ranked second in absolute reptile species richness after Mexico (which in turn has a lower relative species richness owing to its large size), and thus the most reptile species-rich country in Central America. Only the smaller countries Costa Rica (SRI = 226; 44.2 spp. / 10000 km^2), El Salvador (SRI = 219; 45.6 spp. / 10000 km^2), and Belize (SRI = 187; 53.6 spp. / 10000 km^2) exhibit higher species densities than the 1.5–3.7 times larger Panama. On a global scale, the Panamanian reptile fauna comprises 2.64% of the currently known 10038 reptile species (Uetz & Hošek 2014, re-accessed on 30.09.2014).

Even against the Panamanian yardstick, my study area is extremely species-rich. Already the 160 species of documented occurrence are more than reported by Jaramillo et al. (2010) for the entire Cordillera Central. The 180 reptile species resulting from the inclusion of the plausible occurrences, comprising almost 1.8% of the globally known reptile species, represent most of the entire Cordillera's as well as more than two-thirds of the Panamanian reptile fauna, and are more than reported by Wilson & Johnson (2010) for the entire Talamancan highlands of LCA. Stretching over approximately 10065 km^2, the relative species richness of my study area (SRI = 56; 178.8 spp. / 10000 km^2) by far exceeds those of even the smallest CA countries. In view of these numbers, and even more when taking into account the high degree of endemism, the study area (or alternatively the Cordillera Central, or the Talamancan highlands of LCA) constitutes a reptile diversity hotspot of its own.

An extreme case of diversity is the family Dactyloidae. Containing the two genera with the highest numbers of described species, it accounts for almost a fifth of my study area's total species richness (34 spp., 18.8%). The most speciose genus, *Norops,* alone makes up 15% of the reptile species reported herein for the Talamanca and Tabasará ranges. At least with members of this latter genus, dactyloid lizards are not only present in all environments of the Cordillera Central and adjacent lowlands except the highest peaks, but also constitute a very (if not the most) prominent element of the reptile fauna wherever they occur. This holds both in terms of species numbers and population densities. As an extreme example for the latter, I have personally found several individuals of *Norops humilis, N. limifrons,* or *N. pseudokemptoni* sleeping within a single square meter in certain places along the Ríos Flor and Hacha. Talking about species densities, Poe et al. (2009) reported PNGDOTH to be the place with the highest known anole species richness, recounting 12 (described, +2 undescribed) documented species and mentioning another of possible occurrence. For the area around Santa Fé de Veraguas, I count 13 documented species and another of plausible occurrence. Both areas are outnumbered in terms of anoline fauna by RFLF, where numerous Talamancan highland endemics restricted to altitudes above 1000 m asl add to the already high counts that are apparently typical for premontane localities in Panama. For the Reserva Forestal La Fortuna, my dataset contains documented occurrences of 15 anole species and renders the presence of 3 more plausible. Adopting the wording of Poe et al. (2009), the Cordillera Central of western Panama clearly is an outstanding place for anole diversity.

The species numbers presented here represent considerable increments over the correspondent figures published by previous authors with two exceptions. The first of these is the higher number of snake species reported for Panama by Ray & Knight (2013: 153 spp. vs. 148 reported herein), on which I cannot comment since this number is not accompanied by a list. The second exception is the Reptile Database (Uetz & Hošek 2014), whose higher species number for Panama chiefly results from the persistence of old records considered dubious herein, and in a few cases from hitherto not implemented changes in taxonomy and distribution. The abrupt rise in reptile species numbers from just 229 (Ibáñez et al. 2001) to 265 (this work; almost 16% higher) within this century is the manifestation of a recent renaissance of herpetodiversity research in Panama, which has to date largely concentrated on the western portion of the country. While only the six snakes described by Myers (2003) have their type localities east of the Canal and their respective type specimens collected in the past century, all other 16 descriptions of new species from Panama after the year 2000 were at least largely based on material collected within this century, and almost exclusively in western Panama. The fact that most of the remaining additions (chiefly in the form of first country records for species theretofore known from Costa Rica) also resulted from contemporary expeditions underlines the importance of continuous, geographically comprehensive field surveys producing quality vouchers for the complementation of Panama's reptile inventory. The latter will certainly be further augmented, both from the biogeographical side through new distributional records for known species as well as from the taxonomic side through the discovery and recognition of undescribed species, be they cryptic with their recognition requiring profound taxonomic work or rather cryptozoic demanding intensive field surveys as well as a good share of luck to spot a single specimen.

5.3 Biogeography

[Paragraphs dealing with conservation in part modified from Lotzkat et al. 2012a, c, d, 2013, 2014; see Appendix 8 for original publications]

Biogeography is the discipline occupied with the distribution of organisms in space. While taxonomic issues and uncertainties as well as the representativeness of species inventories as discussed in the preceding chapters equally exert an influence on any biogeographical dataset, another source of concern arises from the quality of the associated geographical data. Concerning my dataset, the multitude of sources from which I collected occurrence records as well as the sheer number of these records posed a major challenge in their processing, and entails a broad range of exactness and credibility levels.

Since comparably few records were accompanied by more or less exact coordinates, most of the localities specified in the respective publications or databases had to be georeferenced. As defined in section 3.6, in many cases the assigned coordinates are very approximate estimates of the ubication of some loosely defined locality. This holds especially for inventories of larger areas, or verbal locality denominators specifying linear or two-dimensional features such as rivers and roads or districts and communities. In many of these cases, even three decimals make the corresponding coordinates look much more exact than they actually are. Nevertheless, taking into account that the diameter of the circular symbol used for most records on most maps corresponds to ca. 5 km on the species distribution maps centered on my study area (more on maps showing larger portions of Panama) and to about 44 km on the overview map insets, I am confident that for by far most of my georeferences the symbols plotted on the maps should cover the actual locality. Logically, far less doubts about the exactness of coordinates exist with recently collected specimens for which GPS data was taken. However, it must be noted that geographical coordinates are frequently presented in an erroneous and/or misleading manner in recent literature (see species accounts), be it through the confusion of minutes and seconds with decimals or longitude with latitude, and in some cases just unreproducibly mistaken. I am assured that my verification of any georeference has relativized by far most of these cases. Also beyond sheer coordinates, the geographical data is prone to errors and, above all, generalizations. As an example, the elevations around 1200 m asl often specified for specimens from Boquete almost certainly derive from Dunn's (1947: p. 156) statement that "most collectors have had their headquarters at about 4000 feet" (= 1220 m asl), just as the 1620 m asl associated with many specimens from Finca Lérida appear to be based on his information that "Finca Lérida is at an elevation of 5300 feet" (= ca. 1615 m asl). Yet, while at the times of Dunn a term like "Boquete" was a comparably exact locality denominator, anyone seeing the terrain around Boquete and the nearby Finca Lérida is bound to realize that these general elevation values will be exactly corresponding to the collection sites of only very few, if any, of the specimens with which they are associated. Even elevational values based on more modern technology must be treated with caution for many reasons. To mention just one of these, especially barometric altimeters can considerably deviate from the actual elevation depending on changes in air pressure, that is, weather conditions, as experienced by myself using a GPS unit built in 2006. While I had the option of calibrating my altimeter using the GPS altitude, altimeters in pre-GPS times were calibrated according to values believed to be true. The fact that certain elevations specified in William E. Duellman's field notes of the 1966 Duellman, Trueb, and Myers expedition across Cerro Pando are up to 200 m lower than the values independently obtained by myself and AH at the corresponding, unequivocally attributable localities shows the possible magnitude of such deviations. Similarly, the elevation and climatic values extracted from SRTM and WorldCim data, respectively, must be treated with care and judged in view of the resolution of the underlying raster data, i.e., regarded as approximate values, especially in the steeper portions of my study area. Yet, in both cases the underlying raster datasets are the best respective datasets currently available, and thus may be considered as representing the current state of knowledge and technology as good as possible.

Containing over 14600 georeferenced records, my combined occurrence dataset is rather large. While I regard it to contain by far most reptile locality records that have been published for western Panama, and moreover many unpublished records associated with specimens in different collections or extracted from unpublished reports, its completeness drastically decreases east of Veraguas province. That is, the picture of any species' distribution in central and eastern Panama as given by the respective overview map inset into the distribution map in many cases is a rather fragmentary one and does not accurately reflect the complete biogeographical record for this species. Exceptions are species taxonomically analyzed herein (e.g., *Dactyloa kunayalae* or *Norops gaigei*) as well as those for which recent comprehensive revisions have provided extensive, georeferenced species lists (e.g., *Dendrophidion* owing to Cadle 2012a, b, and Cadle & Savage 2012). Even with all the above discussed uncertainties, possible error sources, and its eastward increasing incompleteness, I am convinced that my combined occurrence dataset represents the most encyclopedic and exact point dataset of western Panamanian reptiles assembled so far, and consider the derivation of my analyses from it to not only make sense, but moreover to result in the most comprehensive, substantiated, and reproducible picture drawn of the biogeography of this reptile fauna to date. Though in part also owing to novel taxonomic findings and locality records, the numerous distribution extensions and especially the increments in species numbers as presented herein for any area, climate, or elevation, over the correspondent results of Jaramillo et al. (2010) can be regarded as a reassurance of this opinion. Furthermore, my results stand out from previous biogeographic listings (e.g., Young et al. 1999; Jaramillo et al. 2010), none of which specified whether a given species was listed for a given area based on evidence or assumption, by being perfectly reproducible and revisable in every respect through the differentiation of taxonomic and biogeographic evidence categories and, most crucially as well as highly desirable in the era of open access, through the provision of all underlying datasets in the Appendices.

The distribution of my study area's reptile species among physiographic regions clearly reveals the mountainous backbone of western Panama to be more species-rich than the adjacent lowlands on any of the two versants. This confirms the notion that tropical montane areas exhibit a higher species-level diversity than tropical lowlands (Savage 2002; Wilson & Johnson 2010). Indeed, of the five physiographic regions in Mesoamerica for which Wilson & Johnson (2010) listed more species than the 180 reported herein for my study area, only two are lowland regions, and both of these extend over incomparably large areas. The distribution among Holdridge life zones is inferred herein at a much finer resolution than that of Jaramillo et al. (2010), but still yields higher species numbers than presented by these authors when simplified to climatic belts according to their methodology. The distribution of Panamanian reptiles among Köppen climates is herein analyzed for the first time and basically yields results similar to those obtained for the Holdridge life zones, though from a slightly different perspective. Both analyses nicely show that species richness is highest below some 1500 m asl, and that comparably few species are restricted to the Lower Montane and Montane belts, or C climates to which the former are largely congruent in their extent. However, these pictures presumably bear a certain distortion in view of the paucity of records from high elevations. The elevational distribution of the reptile fauna presented herein contains manifold, often remarkable extensions or restrictions of their respective elevational range for numerous species that considerably complement the picture of their elevational, and thus also ecological, distribution. Yet, when comparing the range-wide upper limits of different LCA highland taxa, which are often based on records from Costa Rica (e.g., *Bothriechis nigroviridis*), to those recorded from my study area, it becomes apparent that still higher locality records from Panama can be expected for several montane species in the future. Only dedicated surveys at high altitude can fulfill this purpose, as anticipated by Walters (1953) for the crater of Volcán Barú, in stating that "it is likely that future investigators of this highly interesting area will record more species". The fact that we still only know the two species already reported by this author to occur in the crater is probably best explained by assuming that not many thorough searches have been performed there in the 60 years since he wrote these lines.

Looking at the distribution patterns exhibited by the members of the study area's reptile fauna, one is struck with the high number of endemics. Regardless of the numerous widespread species reaching up along the Cordillera Central's slopes, more than a third of the species does not occur outside LCA, almost a fourth is restricted to the Talamancan highlands, and almost every tenth species has a documented total range of less than 100 km along these highlands. However, I consider only a minor portion of these ranges to be as near-completely documented by now as for instance that of *Norops magnaphallus*. For this species, the contact zones with two of its three close congeners (which I assume to ecologically exclude each other in view of these contact zones' narrowness) are rather exactly known and the ubication of the third can be anticipated within an uncertainty range of about 10 km. In contrast, the total geographic ranges of many species dealt with herein will certainly be expanded by future fieldwork that fills geographical collection gaps and/or increases sampling at sites where little collecting has been performed. For example, I am confident that dedicated searches in suitable habitat around the Cerros Saguí and Santiago will produce eastward extensions to the central Serranía de Tabasará for several Talamancan highland endemics whose currently documented eastern distribution limits lie around Volcán Barú, Boquete, or the Fortuna area (e.g., *Mesaspis monticola, Norops fungosus, Sceloporus malachiticus, Geophis godmani,* or *Rhadinaea calligaster*), as exemplified by those already published for *N. salvini* (Bienentreu et al. 2013) and the frogs *Agalychnis annae* (Hertz et al. 2011), *Isthmohyla picadoi* (Hertz & Lotzkat 2012), and *I. zeteki* (Köhler et al. 2008). Such distributional ranges of Talamancan endemics extending to the Central Serranía de Tabasará nicely concur with the geological history of the westernmore, northwesterly-southeasterly oriented, and older portion of the Cordillera Central (IGNTG 2008).

While the overall low number of locality records from high altitudes renders considerable distribution extensions on the horizontal scale most likely to be revealed for such montane taxa, several cases that I came across in the course of this PhD project (e.g., *Dactyloa kunayalae* or *Leposoma rugiceps*) demonstrate that even common and/or widespread lowland taxa can be found far from their documented range. In this context, I especially expect records from within or along the Serranía de Tabasará for several species whose currently documented range has its W extreme around PNGDOTH, western Colón province, or Valle de Antón and PNAC. Given that recent publications have extended the known ranges of several species from these areas further to the W (e.g., Lotzkat et al. 2012b; Ray et al. 2013) and the multitude of species shared between PNGDOTH and the Santa Fé area as partly revealed by own collections (e.g., Lotzkat et al. 2010c), I herein classified the presence of many corresponding taxa in my study area as possible (see distribution maps in Appendix 7). Unlike the species numbers for my study area, or those for other sites within and W of Veraguas province, that will be increased by such range extensions, the high degree of endemism found among the reptiles of my study area is unlikely to be relativized through a more comprehensive notion of each species' distribution. On the contrary, I expect the recognition of cryptic diversity as begun herein for several reptile genera and the possibly ensuing formal descriptions of often all but wide-ranging nominal species to drive the number of endemic species, and especially of small-scale or microendemics, further up. Naturally, these unique biota have strong implications for conservation plans.

Besides the "Talamancan Herpetofauna" which obviously constitutes the principal assemblage, two more of the 7 major herpetofaunal assemblages delineated by Savage (2002) for Central America are found in my study area: the "Eastern and Western Lowlands Herpetofauna" including most lowland species adapted to humid conditions found along both versants, and marginally also the "Panamanian Herpetofauna" of subhumid lowland habitats accounting for a few species peripherally ranging into my study area, like *Norops gaigei*. A more detailed view on shared distribution patterns of LCA herpetofauna was offered by Savage (2002: p. 814, Fig. 5.17) in his Costa Rican faunal areas, which are perfectly extendable to western Panama and my study area. Endemism to the Talamancan highlands, corresponding to the "Cordillera de Talamanca" faunal area, is by far the most prominent and originary distribution pattern among the non-widespread species of my study area. Along the premontane slopes of my study area (corresponding to the "Montane Slopes and Cordillera Central" faunal area), Talamancan endemics increasingly mix with widespread species and those exhibiting other patterns of endemism, most of which reach well into my study area but are primarily distributed at lower elevations. Here, the Caribbean lowlands and the eastern portion of the Pacific lowlands (continuing Savage's "Atlantic Lowlands" faunal area to the east and marking the "upper left" branch of the "Panamanian X" sensu Myers 1972) and the western Pacific lowlands (at least throughout present-day Chiriquí forming the eastern extension of Savage's "Southwest Pacific Lowlands"), share many widespread species but each have their own set of endemics. Comparably few LCA endemics are completely (*Norops cryptolimifrons*) or chiefly (*Dactyloa ibanezi, N. lionotus, Sibon lamari*) restricted to the Atlantic versant of the LCA highlands, owing to the "leaking" of Caribbean climatic conditions and biota across the eastwards lowering passes of the Tabasará range beginning at the Fortuna depression. Around this first "Caribbean leak" along the course of the Cordillera Central, also many widespread taxa of otherwise mostly Caribbean distribution are found on the unusually perhumid Pacific slopes, as it is the case for the Santa Fé area with its much lower cuts in the continental divide. I expect many of these taxa to be also found, though maybe patchily, along the Pacific slopes of the entire Tabasará range, as exemplified by the record of *Sibon annulatus* from Guayabito. In contrast to their less catholic Caribbean counterparts, over one-third of the non-highland LCA endemics are exclusively found along the Pacific versant. This number is bound to increase as the uniqueness of the humid Pacific lowlands of LCA is increasingly being manifested through recent species descriptions (Köhler 2010; Köhler et al. 2010b; Cadle 2012a) and the recognition of accordant divergences within nominal species (Daza et al. 2010, Köhler et al. 2012a, chapters 4.1.7.1 and 4.1.7.4 of this work) some of which will most likely have taxonomic consequences. These so-called Golfo Dulce endemics (McDiarmid & Savage 2005; Lotzkat et al. 2012a) strongly advocate the function of the Talamancan range as a physiographic barrier triggering speciation events along with other climatic barriers acting on the Pacific versant (as opposed to the Caribbean versant) around its eastern and western extremes, as also reflected in the biogeographic schemes of Morrone (2006) and the conclusions of Daza et al. (2010) and Cadle (2012a).

Apart from obviously having played a major role in vicariant speciation events among taxa of low and premontane elevations, I regard the crest of the LCA highlands to also have exerted a similar influence, most likely acting as a "cold" barrier during glacial periods in the Pleistocene, on certain highland taxa. As illustrated in Figure 4.126, the continental divide roughly parallels the present range boundaries of *Norops benedikti* with both *N. magnaphallus* and *N. pachypus,* as well as to a less obvious extent those of *N. kemptoni* with *N. fortunensis* and *N. pseudokemptoni* with *N. gruuo,* and could even have played a role in the split between *Dactyloa ginaelisae* and *D. microtus* (though not indicated in Fig. 4.126). While the high, uninterrupted Talamancan ridge is an obvious candidate for a historic phylogeographic barrier, other potential barriers that apparently have not acted along, but across the divide are not so blatant, but evidently shared at least among the highland *Norops* species complexes as adumbrated by their current distribution patterns. Of these, one of the two most palpable ones appearing in each of the four maps in Fig. 4.126 is that around Volcán Barú. While it is plain to see that the 2500 m high Respingo pass between the volcano and the continental divide would have acted as a "cold" barrier during glacials similar to the divide itself, the barrier effect on the Carribean (separating the DCLs of *N. benedikti*) and Pacific (separating the DCLs of *N. kemptoni* and *N. magnaphallus* from *N. pachypus*) cannot be explained so easily. Here, I rather assume possible separation mechanisms to be directly connected to Volcán Barú itself, potentially in the form of its Pacific rain shadow, or even major eruptions creating unviable terrain. All other physiographic barriers oriented across the continental divide appear to be situated around depressions and thus may be assumed to have acted as "hot" barriers during warm periods, when the high massifs constituted climatic refuges for montane organisms. The most prominent of these (barrier 1), separating the respective DCLs of *D. casildae, N. datzorum, N. pseudopachypus,* and *N. salvini* as well as the species with unilobed hemipenes (*N. fortunensis* and *N. kemptoni*) from those with bilobed hemipenes (*N. gruuo* and *N. pseudokemptoni*) within the *N. kemptoni* complex, lies halfway between the Fortuna and Cerro Colorado areas. Here, elevations drop well below 1300 m asl which makes me believe that this "hot" barrier is still active between the DCLs of *N. pseudopachypus,* which I consider to be restricted to elevations above 1500 m since I could not find it at lower elevations despite intensive searches. The ubication of the next most frequently inferred transverse barrier (no. 3) is somewhat blurred around the Fortuna depression which drops even lower than the passes in the western Tabasará, and barrier 5 is more than anything arbitrarily placed between the DCLs of *N. gruuo.* While I am convinced that these barriers have existed and caused vicariance events during Pleistocene temperature fluctuations, I recognize that their exact positions in the meantime have probably been blurred by subsequent dispersals, as indicated Fig. 4.126 by the bending of some correspondent bars and overlaps of the simplified hulls around certain species ranges currently found in the *N. kemptoni* and *N. pachypus* complexes. Even though the phylogeographical barriers as identified herein obviously are mere approximations based on current distributions that are derived from a patchy specimen record, together with the corresponding mitochondrial phylogenies they provide first hints on spatial settings of in situ speciation within lineages endemic to the Talamancan highlands, and serve as a starting point for ongoing phylogeographic studies on these species groups. A first conclusion to be drawn from the relationships inferred within *D. casildae, N. gruuo,* and *N.*

pseudopachypus is that the high massifs of the central Tabasará range, i.e., Cerro Saguí and/or Cerro Santiago, housing the respective basal subclade within each of these three species, apparently have acted as isolated climatic refuges for montane species during warm periods and thus constitute phylogeographically important physiographic features of the Cordillera Central. Venturing a little further into speculation, one could expect that they might reassume a similar significance in the course of ongoing global warming.

The affiliation of the study area's reptile species with the three historical source units shows rather balanced contributions of the three historical elements at the genus level. Though roughly concordant with the pictures presented for Costa Rica (Savage 2002) and Nicaragua (Sunyer 2009), the SA element has a smaller share in the fauna of these countries than in that of my study area at both the generic and species levels. These discrepancies increase northwards and become evident when comparing the study area's faunal origins with those of montane sites in Nuclear Central America: As an example, the reptile fauna of Parque Nacional Cusuco in Honduras (Townsend & Wilson 2008) completely lacks members of the SA element. At the species level, the Middle American Element by far surpasses the other two units in species numbers and has given rise to most of the LCA, and especially the Talamancan, endemics. This predominance of species of Middle American origin, amounting to almost half of my study areas total species richness and more than two-thirds of its highland endemics, nicely illustrates the significance of in situ speciation for the diversity and composition of the Talamancan herpetofauna.

More than any other of the analyses presented in section 4.3, the distribution among protected areas is heavily based on occurrences inferred as plausible. While the presence in any of the six analyzed protected areas is not even inferred as plausible for a mere 10 species, a total of 47 species (about 26% of the study area's reptile fauna) is actually not documented to occur in any. This, together with the relative paucity of records from most areas, indicates that much inventory work remains to be done within each of the six areas. Yet, even when just considering the documented occurrences, my results are far more comprehensive than those Jaramillo et al. (2010). This is, on the one hand, a logical consequence of my including plausible occurrences, and moreover all species present in the study area instead of just the threatened ones as done by these authors, but on the other hand also owes to a more scrutinous approach eliminating most if not all of the sometimes irreproduceable gaps in the correspondent tables of Jaramillo et al. (2010), such as their ignoring the ubication within protected areas of the type localites of *Dactyloa kunayalae* and *Norops fungosus,* both which they stated to be absent from protected areas, and in the case of the latter taxon even to be "not expected in any".

Similarly, I am confident that my conservation status assessments, though only performed for a few species, are somewhat more reliable, and in any case far more reproducible, than those of Jaramillo et al. (2010), whose IUCN assessments lack any specifications on the applied criteria or underlying data and assumptions. This fact precludes any logical explanation for the numerous discrepancies already noted for the species of *Dactyloa* in the revision of Lotzkat et al. (2013), for which I calculated EVS values similar to those of Jaramillo et al. (2010) but elaborated IUCN assessments differing profoundly from those of the latter authors, who classified *D. casildae* as NT and all other species of *Dactyloa* as LC. With the exception of *D. insignis* and *D. frenata,* who, when applying range-based IUCN criteria, fall out of the Threatened categories owing to their large geographical ranges, I assign all other species to one of the Threatened categories VU or EN. Partially, these seemingly more pessimistic assessments are due to taxonomic changes resulting in smaller extents of occurrence (*D. ginaelisae, D. ibanezi,* and *D. microtus*). On the other hand, I place *D. kunayalae* in a higher risk category although the range as documented by Lotzkat et al. (2013) and accordingly herein is much larger than that known to Jaramillo et al. (2010). Whatever reasons might account for these differences in conservation status assessments, I am convinced that, in view of their arboreal lifestyle and the forest environments in which they are exclusively encountered, all species of *Dactyloa* should be considered to be higly susceptible to habitat loss or alteration, and thus not be assessed as LC taxa in this era of rapid socioeconomic development fueling the degradation of natural habitats in Panama and its neighboring countries.

Apart from often appearing too optimistic to me, the conservation status assessments of Jaramillo et al. (2010) sometimes differ profoundly for species bearing the same baseline distributional data (especially *Hydromorphus dunni* vs. *Geophis championi*). In this context, I feel the need to emphasize that the IUCN category DD is by no means indicative of a status other than Threatened, as exemplified by the two aforementioned taxa: Although I felt the technical necessity to evaluate both species as DD in view of their singular (*H. dunni*) or two very nearby (*G. championi*) locality records precluding any meaningful calculation of an extent of occurrence, small to very small ranges may be presumed for both taxa, and the absence of additional specimens from the rather well-sampled Boquete region might be interpreted as an indication of low population densities. If both assumptions were true, either species is subject to a high risk of extinction by natural catastrophy as well as anthropogenic actions. Aditionally, notwithstanding that I regard their presence in PNVB as plausible, neither of these two species has been recorded from any protected area. They share this fate with several other small-scale highland endemics, which may in principle be regarded as potentially threatened species as reflected by the assignment of IUCN Threatened categories and/or high EVS scores to most of them. For two of these microendemics, I do not even expect their occurrence in any of the six protected areas along my study area. Additionaly, more than 10 species of Talamancan highland and other LCA endemics are documentedly or plausibly present in just one or none of the protected areas analyzed. While the conservation of any LCA endemic shared with Costa Rica could optimistically be regarded a task to be shared between the two countries, the Panamanian endemics and especially the small-scale highland endemics (even if shared with Costa Rica as in the case of *Norops benedikti* or *Dendrophidion crybelum*) must be given special attention by Panamanian decision-makers. In this context, the mere occurrence of a nominal species in one protected area must not be equated with effective conservation measures being in place for two reasons. First, most protected areas in Panama lack appropriate demarcation and staff numbers to ensure the adequate enforcement of protective measures (Jaramillo et al. 2010; Lotzkat et al. 2011; Hertz et al. 2012a) against a population that largely lacks awareness of environmental issues in general and the intrinsic value of biodiversity in particular. Second, both the low genetic diversity over short geographical distances (e.g., among the populations living within RFLF) and the high genetic divergences over larger geographical distances (e.g., between the populations living within RFLF and those of the Cerro Colorado region) which are exemplarily revealed by my barcode analyses for several dactyloid highland endemics clearly demonstrate the evolutionary uniqueness of the DCLs found within these species, and thus entail strong implications for the conservation of these genealogical lineages.

Among the endemic reptile species which I regard as seriously threatened (that is, for which my EVS values indicate a high vulnerability and which I assigned to a IUCN Threatened category), the most alarming case is that of the CR *Norops pseudokemptoni* as pointed out by Lotzkat et al. (2014). Of all evaluated species for which the existence of more than two locality records allowed me to calculate a well-substantiated two-dimensional extent of occurrence, this lizard with a documented range spanning a mere 13 airline km is the species with the smallest resulting value of just 32 km^2. Even worse, it occurs far from any protected area in the Cerro Colorado region of the central Serranía de Tabasará in the Comarca Ngöbe-Buglé. A similar and largely congruent, yet even smaller range is documented for the recently discovered rainfrog *Diasporus igneus* Batista, Ponce & Hertz 2012 that is only known from La Nevera and near Río Rey (Batista et al. 2012). Both species are presumed to be primarily forest-dwellers and thus highly susceptible to habitat degradation, while deforestation occurs at an alarming pace within the Comarca (ANAM 2009) owing to a desastrous socioeconomic setting largely evoked by extreme poverty and population growth (IGNTG 2008; www.contraloria.gob.pa/inec). Moreover, its mountains' enormous mineral deposits and high suitability for hydroelectric dams pose major threats to the Comarca's natural environments (Nakoneczny & Whysner 2010; Simms & Moolji 2011). If, for example, the exploitation of the Cerro Colorado copper deposit eventually was undertaken, both species easily might be driven to extinction. Apart from these two extreme cases, other species that are endemic to the Cordillera Central or even restricted to the Serranía de Tabasará according to current knowledge would share their fate or at least be gravely affected by such highly destructive exploitation measures. As recounted in several publications by our group (Batista et al. 2012; Hertz et al. 2012a, b, 2013; Lotzkat et al. 2012 c, d, 2013, 2014), among these are *Dactyloa casildae, D. ginaelisae, N. datzorum, N. gruuo, N. pseudopachypus, Sibon noalamina,* and presumably also *Celestus* sp., *Geophis* sp., and *S. perissostichon,* as well as *Diasporus citrinobapheus* Hertz, Hauenschild, Lotzkat & Köhler 2012, *Bolitoglossa jugivagans* Hertz, Lotzkat & Köhler 2013 and several amphibian species whose populations have suffered serious declines by chytridiomycosis. All these taxa, with one exception discovered only during the last seven years, remain very poorly known, while many more unknown organisms can confidently be expected to await discovery in the blatantly underexplored forests of the Tabasará range. If the survival of the vital forest environments along the Serranía de Tabasará is not seriously pursued soon, we might never come to know their true diversity.

A similar reasoning applies to the Serranía de Talamanca. While its lower montane and montane elevations as well as the Caribbean slopes retain considerable forest cover and are at least theoretically protected through the seamless coverage with the reserves BPPS, PILA, and PNVB, the Pacific slopes below these parks are almost completely deforested by now, and no legal protection exists for the last remaining patches of lowland and premontane Pacific rainforests in western Panama with their proper set of unique species. As pointed out by Lotzkat et al. (2012a), these Golfo Dulce endemics have only a few minor retreats left since most of the lowland and adjacent premontane areas in western Chiriquí and eastern Puntarenas (Costa Rica) provinces are densely populated and occupied by agriculture and infrastructure, while not a single conservation area exists on the Panamanian side.

Thus, the establishment of expediently placed and thoroughly enforced additional protected areas along my study area appears utterly warranted. Promising candidates for sheltering Golfo Dulce endemics in the lowlands are the forest remnants around Chorogo and Meseta de Chorcha. For the montane forests of the Serranía de Tabasará, such an area has been proposed by Hertz et al. (2012a) comprising the entire Cerro Colorado region around the massifs of Cerro Saguí and Cerro Santiago. The polygon suggested by these authors would include all known populations of *Norops pseudokemptoni* as well as genealogical lineages of *N. gruuo, N. pseudopachypus, N. salvini, N. datzorum,* and *Dactyloa casildae* that must be regarded as evolutionarily significant considering their high genetic divergence from their respective sister DCLs. At any rate, serious conservation action should be undertaken in the central Serranía de Tabasará for a number of reasons, one of which is the existence of a multitude of reptile and amphibian endemics, in order to protect these and many other unique species, as well as the economically deprived indigenous population that heavily depends on the area's natural resources for subsistence, from becoming victims of human greed disguised as socioeconomic development. I am assured that my results constitute an unprecedented groundwork for our understanding of the spatial patterns of reptile diversity in my study area, and hope that they will serve as a basis for appropriate conservation actions that are so sorely needed. Likewise, increased study of the herpetofauna and other biota of this region, as well as of the entire Cordillera Central, clearly is warranted. Ironically, such studies can often greatly benefit from roads and other infrastructure originally built for resource exploitation such as ore mining or hydroelectricity to access formerly remote areas. A brilliant example is the case of RFLF, which, in view of its small size versus the largest number of reptile records of any of the six protected areas analyzed herein, must be regarded as the best-studied of these areas. Here, practically all 20th century inventory work was performed in the course of the initial creation and subsequent extension of the Fortuna reservoir. A similar but more recent case is the Cerro Colorado region, whose endemic and endangered highland anoles would probably not have had their respective type series secured by Senckenbergian researchers if there had not been a road to La Nevera constructed for prospection and test drill purposes.

Apart from revealing how few locality records are available from the Comarca Ngöbe-Buglé and Veraguas province, the faunal lists presented for the four political subdivisions along my study area fulfill a similar purpose. With the species lists for each of the three provinces considerably lengthened and most importantly containing the first reptile list ever assembled for the Comarca Ngöbe-Buglé, they provide a last example of how my studies complement the existing knowledge on the distribution of reptiles in western Panama through the combination of own collections and examined specimens with critically filtered locality records from a multitude different sources and careful interpolation of documented occurrences. Not in the least owing to the differential presentation of occurrences in separate quality categories, they constitute a solid reference framework for future studies, biodiversity management, and conservation.

5.4 Conclusions

Though limited to a comparably small area in western Panama, the present work is the largest study on Panamanian reptile diversity assembled to date. Including the published descriptions of four species new to science (*Norops benedikti, Dactyloa ginaelisae, Sibon noalamina,* and *S. perissostichon*), the delineation of three genealogical lineages which are in the process of formal description (*Celestus* sp., *Lepidoblepharis* sp. 1 and 2), and the identification numerous mitochondrial lineages (including *Geophis* sp.) awaiting morphological corroboration, it considerably increases our knowledge on reptile alpha diversity both along the Cordillera Central and in Panama as a whole. Moreover, my taxonomic studies on selected groups, including the re-evaluations of many diagnostic characters, amount to an unprecedented, lavishly illustrated overview of their variability, and together with the standardized species accounts provide a solid basis for the identification of any of the 180 species considered herein to be present in my study area. The analyses of my biogeographical dataset yield numerous considerable range extensions and result in the hitherto most detailed, reproducible, and comprehensive assessments of these species' geographical and ecological distribution as well as their occurrence in political subdivisions and protected areas, and conservation status, thus increasing our knowledge of these species also from a biogeographical perspective.

Yet, in this era of unprecedented progress in biodiversity research owing to the application of novel molecular tools in taxonomy as well as to an apparent renaissance of field expeditions especially among younger colleagues who actually publish their findings instead of jealously sitting on them for decades as certain established colleagues do, attempts like this work to compile a larger picture are inevitably doomed to result in an ephemeral snapshot of a momentary state of knowledge which has already been overcome before the picture is fully assembled. As a nice example, AB's barcoding of the sole specimen from eastern Panama referred herein to *Lepidoblepharis xanthostigma* has resulted in the discovery that it represents a different, hitherto undescribed species of dwarf gecko, which appears to be morphologically separable from *L. xanthostigma* only by the configuration of the ventral escutcheon. Apart from nicely confirming the postulated diagnostic value of this scalation character and raising my species count of Panamanian reptiles to 266, this finding has lead us to the conclusion that *L. xanthostigma* is actually absent from eastern Panama as well as from Colombia, and would have to be classified as widespread in CA instead of CA + COL, thus overall changing the figures presented in chapters 4.1.2, 4.2.1, 4.2.2, and 4.3.2 of the present work. Similarly, without effect for the Panamanian reptile richness but directly affecting that of my study area, Duran Geiger et al. (2014) recently reported *Ninia sebae* (one of the 27 species whose occurrence I classified as "possible") from Boquete, thus increasing the number of reptile species known to occur within my study area to 181.

This rapid succession of novel findings shows that much work remains to be done, be it in the field, laboratories, or libraries. Since the present study extends over a broad range of topics and taxa, I was unable to exhaust all arising questions with the necessary thoroughness and adequate methodological sophistication, but rather had to restrict myself to outlining identified problems in many cases. Several issues that require further studies have been pinpointed in the results and preceding discussion sections, such as the verification of numerous locality records and specimen IDs as well as the pending integrative studies on the UGLs identified in this study. Indispensable for such comprehensive taxonomic studies, but equally important to complement our knowledge on the reptile fauna's diversity and biogeography, is the completion of the patchy pictures of several species' distributions caused by the widely scattered, singular specimen records. Only additional sampling and publication also of "minor" results can fill these gaps. Likewise, the many occurrences inferred as plausible in the sections 4.2 and 4.3 require confirmation through well-documented voucher specimens. This is especially important for the putative presences of endemic and/or threatened species in protected areas, in order to draw substantiated conclusions about the effectiveness of these areas. After all, the ultimate task is the conservation of this diverse fauna, which can only be achieved via a sound and comprehensive knowledge of their ecology, life histories, diversity, and distribution. At least for the latter two aspects, the present work should to constitute a broad and solid basis.

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Appendices

On the following pages:

On enclosed DVD-ROM:

Appendix 4: Morphological data

Appendix 5: Molecular data: Alignments and distance matrices

Appendix 6: Occurrence datasets

Appendix 7: Distribution maps for species possibly occurring in the study area

Appendix 8: Original publications incorporated in this work

Appendix 9: Visual identification guide for reptiles in western Panama

Appendix 1: Waypoints taken in the field

Waypoint	Province	Name	Latitude North	Longitude West	Elevation [m asl]	General locality
1	Chiriquí	Los Algarrobos: Casa de la Alemana	8.49591	82.43268	141	29
2	Chiriquí	Los Algarrobos: Casa Culebra	8.49533	82.42942	134	29
3	Chiriquí	Davíd: UNACHI	8.43318	82.45190	55	–
4	Comarca Ngöbe-Buglé	Boca del Monte	8.41317	81.76610	849	–
5	Comarca Ngöbe-Buglé	Hato Chamí	8.44788	81.77095	1007	–
6	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: camp on road	8.49971	81.77237	1699	19
7	Comarca Ngöbe-Buglé	road to Cerro Colorado: along continental divide	8.50609	81.77849	1569	19
8	Comarca Ngöbe-Buglé	road to Cerro Colorado: along continental divide	8.50836	81.78044	1511	19
9	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.51136	81.79238	1472	17
10	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.52889	81.79832	1647	17
11	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.53869	81.81354	1570	17
12	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.53529	81.80805	1600	17
13	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón: camp on road	8.53034	81.79866	1662	17
14	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.51726	81.79340	1501	17
15	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: confluence of intermittent creeks	8.49960	81.76995	1638	19
16	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: slope with secondary growth	8.50039	81.76996	1644	19
17	Veraguas	Cerro Mariposa: Alto de Piedra, Restaurante	8.51453	81.11765	867	23
18	Veraguas	Cerro Mariposa: water supply hut near Alto de Piedra	8.51607	81.11849	883	23
19	Veraguas	PNSF: Cerro Mariposa: trail meets creek at water supply	8.51166	81.12163	855	23
20	Veraguas	road Santiago - Santa Fé, halfway between Santiago and San Francisco	8.17955	80.95105	76	–
21	Chiriquí	road to La Fortuna, between Los Planes and Valle de la Mina	8.63576	82.21208	997	–
22	Chiriquí	RFLF: Lost & Found Ecohostel	8.67462	82.21958	1250	16
23	Chiriquí	RFLF: Río Hornito	8.67797	82.21023	1274	16
24	Chiriquí	RFLF: near Lost & Found Ecohostel: trail to Río Hornito	8.67447	82.21392	1400	16
25	Chiriquí	RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge	8.67403	82.21543	1455	16
26	Chiriquí	RFLF: near Lost & Found Ecohostel: trail to Río Hornito	8.67385	82.21845	1320	16
27	Chiriquí	Santa Clara: road from Volcán to Río Sereno	8.83437	82.77412	1157	1
28	Chiriquí	Río Sereno: Casa de Porfirio Yanguez	8.82573	82.85245	945	–
29	Chiriquí	Hacienda Café de Eleta: camp next to workshop/utility shed	8.88044	82.75997	1437	2
30	Chiriquí	Hacienda Café de Eleta: citrus plantation between utility shed and Río Candela	8.88288	82.75945	1464	2
31	Chiriquí	Hacienda Café de Eleta: creek	8.87157	82.77099	1380	2
32	Chiriquí	RFLF: near Lost & Found Ecohostel: trail to Río Hornito, just below ridge	8.67443	82.21611	1434	16
33	Chiriquí	Dam "Represa de Caldera"	8.61505	82.35294	257	–
34	Chiriquí	RFLF: Finca La Suiza	8.66025	82.20900	1221	–
35	Veraguas	PNSF: Cerro Mariposa: southern summit according to NASA SRTM	8.49026	81.11540	1417	23
36	Veraguas	PNSF: Cerro Mariposa: trail towards summit: large clearing	8.49786	81.11627	1303	23
37	Veraguas	PNSF: Cerro Mariposa: northern summit	8.49536	81.11642	1437	23
38	Veraguas	PNSF: Cerro Mariposa: trail towards summit just below large clearing	8.49819	81.11643	1348	23
39	Veraguas	PNSF: Cerro Mariposa: trail towards summit	8.50007	81.11696	1255	23
40	Veraguas	PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María	8.58724	81.03634	476	25
41	Veraguas	trail to Río Chilagres along Río Santa María: rancho with plantations	8.56933	81.04222	437	25
42	Veraguas	trail to Río Chilagres along Río Santa María: river crossing	8.55466	81.04621	406	25
43	Veraguas	near Río Santa María: end of road, beginning of trail to Río Santa María and Río Chilagres	8.54811	81.04818	387	25
44	Veraguas	Casa de Don Roberto	8.54468	81.05185	382	–
45	Chiriquí	Los Algarrobos: trail enters Río Majagua	8.48456	82.43417	109	29
46	Chiriquí	Playa La Barqueta: road to Davíd	8.31277	82.57817	18	–
47	Chiriquí	RFLF: near Lost & Found Ecohostel: antenna and lookout on small peak	8.67275	82.21596	1515	16
48	Chiriquí	RFLF: near Lost & Found Ecohostel	8.67362	82.21224	1438	16
49	Chiriquí	RFLF: W slope Cerro Pata de Macho: lower limit of bamboo ridge	8.67567	82.20667	1388	16
50	Chiriquí	RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge	8.67546	82.20574	1419	16
51	Chiriquí	RFLF: W slope Cerro Pata de Macho: traps	8.67399	82.20220	1521	16
52	Chiriquí	RFLF: W slope Cerro Pata de Macho: crossing Río Hornito before ascent	8.67581	82.20789	1304	16
53	Chiriquí	RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket"	8.67612	82.20064	1657	16
54	Chiriquí	RFLF: W slope Cerro Pata de Macho: provisional camp at creek	8.67189	82.19971	1421	16
55	Chiriquí	RFLF: W slope Cerro Pata de Macho: elfin forest ridge	8.67755	82.19811	1752	16

Waypoint	Province	Name	Latitude North	Longitude West	Elevation [m asl]	General locality
56	Chiriquí	RFLF: W slope Cerro Pata de Macho: 1800 m asl	8.67930	82.19299	1800	16
57	Chiriquí	PILA: road to Jurutungo: sign "Bienvenidos al PILA"	8.89102	82.74480	1596	3
58	Chiriquí	PILA: road to Jurutungo: above crossing of Río Candela	8.90056	82.73740	1722	3
59	Chiriquí	PILA: Jurutungo: Finca of Porfirio Yangüez	8.91059	82.72312	1996	3
60	Chiriquí	PILA: Jurutungo: W slope Cerro without name: lookout onto Cerro Pando and Jurutungo	8.91337	82.70999	2312	3
61	Chiriquí	PILA: Jurutungo: summit of Cerro without name	8.91467	82.70784	2463	3
62	Chiriquí	PILA: Jurutungo: W slope Cerro without name: branch to summit or top of waterfall	8.91188	82.70954	2250	3
63	Chiriquí	PILA: Jurutungo: W slope Cerro without name: shortly after last clearing	8.91140	82.71288	2068	3
64	Chiriquí	PILA: Jurutungo: W slope Cerro without name: entrance to ascent	8.91114	82.71586	2018	3
65	Chiriquí	PILA: Jurutungo: S slope Cerro Pando	8.91494	82.72340	2222	3
66	Chiriquí	PILA: Jurutungo: S slope Cerro Pando	8.91624	82.72399	2316	3
67	Chiriquí	PILA: Jurutungo: summit of Cerro Pando	8.91944	82.72258	2464	3
68	Chiriquí	PILA: Jurutungo: W slope Cerro without name: branch to first waterfall	8.91164	82.71049	2133	3
69	Chiriquí	PILA: Jurutungo: W slope Cerro without name: shortly above branch to second waterfall	8.91209	82.70964	2202	3
70	Chiriquí	PILA: Jurutungo: W slope Cerro without name: ascent to summit	8.91393	82.70863	2403	3
71	Chiriquí	PILA: Jurutungo: W slope Cerro without name	8.91202	82.71820	1977	3
72	Chiriquí	PILA: road to Jurutungo: branch to the right, towards building at WP 86	8.90665	82.72587	1891	3
73	Chiriquí	PILA: Jurutungo: ascent towards border trail on divide: sign "Limite del Parque"	8.91482	82.71825	2014	3
74	Chiriquí	PILA: Jurutungo: ascent towards border trail on divide: lookout	8.91687	82.71648	2170	3
75	Chiriquí	PILA: Jurutungo: ascent towards border trail on divide: lookout	8.91928	82.71681	2308	3
76	Chiriquí	PILA: Jurutungo: ascent towards border trail on divide: arrival at divide and border trail	8.92115	82.71745	2402	3
77	Bocas del Toro	PILA: N slope Cerro Pando, border trail on divide: border monument	8.92217	82.71225	2447	4
78	Bocas del Toro	PILA: N slope Cerro Pando, border trail on divide	8.93068	82.71373	2405	4
79	Chiriquí	PILA: Jurutungo: ascent towards border trail on divide: shortly after sign "Limite del Parque"	8.91671	82.71838	2099	3
80	Chiriquí	PILA: road to Jurutungo: branch to the right	8.90554	82.72889	1827	3
81	Chiriquí	PILA: road to Jurutungo	8.90631	82.73175	1840	3
82	Chiriquí	PILA: road to Jurutungo: upper limit of large clearing	8.90633	82.73571	1834	3
83	Chiriquí	PILA: road to Jurutungo: pond and coffee plantation	8.90211	82.73781	1782	3
84	Chiriquí	PILA: road to Jurutungo: crossing of Río Candela	8.89950	82.73878	1704	3
85	Chiriquí	PILA: Jurutungo: path to building at WP 86	8.90601	82.72420	1930	3
86	Chiriquí	PILA: Jurutungo: building under construction	8.90694	82.72291	1954	3
87	Chiriquí	Volante	8.58662	82.66704	480	5
88	Chiriquí	Volante: camp	8.58698	82.66833	481	5
89	Chiriquí	Volante: Río Escárrea	8.58830	82.67332	430	5
90	Veraguas	Cerro Negro: dirt road, beginning of trail to camp	8.53801	81.08703	448	24
91	Veraguas	PNSF: Cerro Negro: trail to camp, upper limit of Lomita de Felicidad	8.54894	81.09214	603	24
92	Veraguas	PNSF: Cerro Negro: trail to camp, clearing	8.55481	81.09463	609	24
93	Veraguas	PNSF: Cerro Negro: trail to camp, rancho with chicken	8.55679	81.09964	610	24
94	Veraguas	PNSF: Cerro Negro: trail to camp, rancho	8.56638	81.09885	722	24
95	Veraguas	PNSF: Cerro Negro: camp	8.56901	81.09894	700	24
96	Veraguas	PNSF: Cerro Negro: ridge above camp: small clearing	8.57555	81.09756	1083	24
97	Veraguas	PNSF: Cerro Negro: ridge above camp	8.57697	81.09705	1115	24
98	Chiriquí	Río Sereno: next to border	8.81823	82.86160	986	–
99	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: first confluence of creeks below camp	8.50178	81.76894	1555	19
100	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: camp	8.50112	81.76936	1580	19
101	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: small summit just above camp	8.50091	81.76845	1644	19
102	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: second confluence of creeks below camp	8.50323	81.76749	1533	19
103	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: ascent creek	8.49887	81.76823	1602	19
104	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: ascent creek	8.49612	81.76768	1761	19
105	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: elfin forest summit on continental divide	8.49535	81.76727	1814	19
106	Bocas del Toro	road from divide to caribbean coast, near Chiriquí Grande	8.89978	82.18374	72	27
107	Chiriquí	Cabecera de Cochea: village	8.71625	82.49619	1090	11
108	Chiriquí	Cabecera de Cochea: gate just before parking	8.72338	82.49400	1135	11
109	Chiriquí	Cabecera de Cochea: Rancho de Rodrigo	8.72656	82.49154	1174	11
110	Chiriquí	Cabecera de Cochea: crossing Río Cochea	8.72550	82.49305	1090	11
111	Chiriquí	Cabecera de Cochea: Río Cochea above crossing	8.72717	82.49368	1140	11
112	Chiriquí	Los Algarrobos: Casa de Mair	8.49276	82.42633	147	29

Waypoint	Province	Name	Latitude North	Longitude West	Elevation [m asl]	General locality
113	Chiriquí	RFLF: Dam	8.74286	82.25054	1071	–
114	Bocas del Toro	road from Chiriquí Grande to Almirante: km 0, branch to Almirante	8.94213	82.17727	27	27
115	Bocas del Toro	road from Chiriquí Grande to Almirante: km 13	9.00108	82.25920	23	27
116	Bocas del Toro	road from Chiriquí Grande to Almirante: shortly after km 23, branch to Palma Real and Punta Róbalo	9.03932	82.30119	46	27
117	Bocas del Toro	road from Chiriquí Grande to Almirante: shortly after km 33	9.11072	82.28856	38	27
118	Bocas del Toro	road from Chiriquí Grande to Almirante: shortly after km 43	9.15717	82.31816	53	27
119	Bocas del Toro	road from Chiriquí Grande to Almirante: shortly after km 53	9.20612	82.36156	50	27
120	Bocas del Toro	road from Chiriquí Grande to Almirante: shortly after km 63	9.26613	82.40875	85	27
121	Bocas del Toro	Almirante: gas station and bus stop	9.29649	82.40959	17	27
122	Bocas del Toro	road from Chiriquí Grande to Almirante: km 13.5	9.00193	82.26385	54	27
123	Comarca Ngöbe-Buglé	road from Chiriquí Grande to Almirante: km 15.5	9.00987	82.27359	29	27
124	Bocas del Toro	road from Chiriquí Grande to Almirante: km 24.5	9.05476	82.30319	34	27
125	Bocas del Toro	road from Chiriquí Grande to Almirante: km 35.5, bus stop	9.12116	82.29782	35	27
126	Bocas del Toro	Punta Peña: casa de Elisabeth Gomez	8.91636	82.18438	33	27
127	Chiriquí	Carretera Interamericana: branch to San Félix	8.27775	81.87171	89	–
128	Comarca Ngöbe-Buglé	Sabanita: regional office of ANAM Comarcal	8.34127	81.83298	132	–
129	Chiriquí	Carretera Interamericana: branch to Tolé	8.22622	81.67046	242	–
130	Chiriquí	Tolé	8.24376	81.67245	326	–
131	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: limit of Comarca Ngöbe-Buglé	8.27814	81.66654	500	–
132	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: Alto Caballero, escuela	8.29571	81.67311	469	–
133	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: Cerro Sombrero	8.30657	81.67668	525	–
134	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: Alto Sardaña	8.33415	81.68636	412	–
135	Comarca Ngöbe-Buglé	Chichica	8.36437	81.66720	537	–
136	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: take branch to the left	8.37106	81.65904	563	–
137	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: take branch to the right	8.40291	81.67330	718	–
138	Comarca Ngöbe-Buglé	road to Buabidí alias Alto/Llano/Hato Tugrí: Peña Blanca, escuela	8.47058	81.68824	879	–
139	Comarca Ngöbe-Buglé	Buabidí alias Alto/Llano/Hato Tugrí: community building	8.47985	81.71207	1191	20
140	Comarca Ngöbe-Buglé	Buabidí alias Alto/Llano/Hato Tugrí: Casa de Amado	8.48169	81.71594	1241	20
141	Comarca Ngöbe-Buglé	Buabidí alias Alto/Llano/Hato Tugrí: hilltop along way to Laguna	8.48195	81.72097	1251	20
142	Comarca Ngöbe-Buglé	Buabidí alias Alto/Llano/Hato Tugrí: Laguna	8.48550	81.72852	1313	20
143	Comarca Ngöbe-Buglé	E slope Cerro Santiago: Quebrada Ardilla: camp	8.49644	81.72028	1532	20
144	Comarca Ngöbe-Buglé	E slope Cerro Santiago: Quebrada Ardilla	8.49678	81.72163	1570	20
145	Comarca Ngöbe-Buglé	E slope Cerro Santiago: Quebrada Ardilla	8.49677	81.72208	1576	20
146	Comarca Ngöbe-Buglé	E slope Cerro Santiago: Quebrada Ardilla	8.49744	81.72275	1598	20
147	Comarca Ngöbe-Buglé	E slope Cerro Santiago: Río Rey	8.50442	81.71958	1546	20
148	Comarca Ngöbe-Buglé	E slope Cerro Santiago: continental divide above Río Rey	8.50822	81.71618	1718	20
149	Comarca Ngöbe-Buglé	E slope Cerro Santiago: secondary vegetation above Río Rey	8.50642	81.71862	1564	20
150	Veraguas	Santa Fé	8.51169	81.07726	441	–
151	Veraguas	PNSF: Cerro Negro: trail to camp, creek crossing	8.56333	81.09794	675	24
152	Veraguas	PNSF: Cerro Negro: creek above camp	8.57022	81.09629	778	24
153	Veraguas	PNSF: Cerro Negro: ridge above camp	8.57886	81.09619	1145	24
154	Veraguas	PNSF: Cerro Negro: ridge above camp	8.57991	81.09509	1163	24
155	Chiriquí	Cerro Punta: branch to Bajo Grande	8.85909	82.56667	1980	7
156	Chiriquí	PNVB: Bajo Grande: sign "Limite del Parque Nacional Volcán Barú"	8.85005	82.54479	2195	7
157	Chiriquí	PNVB: Sendero Los Quetzales: Estación de Guardaparques Alto Respingo	8.84439	82.53379	2500	7
158	Chiriquí	PNVB: Sendero Los Quetzales: Refugio Las Rocas	8.84796	82.51964	2393	7
159	Chiriquí	PNVB: Sendero Los Quetzales: creek below Refugio Las Rocas	8.84769	82.52312	2268	7
160	Chiriquí	PNVB: Sendero Los Quetzales: Quebrada El Silencio, Refugio	8.84944	82.51538	2130	7
161	Chiriquí	PNVB: Sendero Los Quetzales: crossing Río Caldera	8.85292	82.50271	1953	7
162	Chiriquí	PNVB: Sendero Los Quetzales: crossing Río Caldera	8.85237	82.49881	1911	7
163	Chiriquí	PNVB: Sendero Los Quetzales: trail enters dirt road	8.85248	82.49591	1867	7
164	Chiriquí	PNVB: Sendero Los Quetzales: Estación de Guardaparques Alto Chiquero	8.84674	82.48824	1873	7
165	Chiriquí	Sendero Los Quetzales: branch to Bajo Mono	8.84175	82.48121	1688	7
166	Chiriquí	private beach without name near Playa Hermosa	8.20071	82.13966	2	–
167	Chiriquí	Los Algarrobos: old railway bridge over Río Majagua	8.48092	82.42795	88	29
168	Chiriquí	road Davíd-Boquete: Portachuelo	8.46471	82.42007	67	29
169	Chiriquí	Bajo Mono: bus stop at branching Alto Quiel/Alto Chiquero/Boquete/Sendero la Cascada	8.83013	82.48029	1585	8
170	Chiriquí	PNVB: Bajo Mono: Sendero La Cascada: waterfall	8.82504	82.50206	1866	8
171	Chiriquí	PNVB: Bajo Mono: Sendero La Cascada: camp	8.82634	82.49894	1822	8
172	Chiriquí	PNVB: Bajo Mono: Sendero La Cascada: water-supply installation below Camp	8.82733	82.49639	1778	8
173	Chiriquí	PNVB: Bajo Mono: Sendero La Cascada: last clearing with hut before forest	8.82811	82.48928	1679	8

Waypoint	Province	Name	Latitude North	Longitude West	Elevation [m asl]	General locality
174	Chiriquí	Santa Clara: Finca Ecológica: Abarrotería La Sorpresa	8.83305	82.78241	1209	1
175	Chiriquí	Santa Clara: Finca Ecológica: southern border creek	8.83092	82.78420	1125	1
176	Chiriquí	Santa Clara: Finca Ecológica: junction of border creeks	8.83064	82.78698	1088	1
177	Chiriquí	Santa Clara: Finca Ecológica: northern extreme of finca on road to Río Sereno	8.83552	82.78267	1220	1
178	Chiriquí	Santa Clara: Finca Ecológica: southern extreme of finca on dirt road	8.83000	82.78241	1205	1
179	Bocas del Toro	PILA: N slope Cerro Pando, near border trail on divide: camp	8.93138	82.71370	2389	4
180	Bocas del Toro	PILA: N slope Cerro Pando, border trail on divide	8.93606	82.71361	2303	4
181	Bocas del Toro	PILA: N slope Cerro Pando, near border trail on divide: creek below camp	8.93329	82.71307	2305	4
182	Chiriquí	Los Algarrobos: trail to Río Majagua	8.48927	82.43333	128	29
183	Chiriquí	RFLF: W slope Cerro Pata de Macho: ridge at 1876 m asl	8.67929	82.19137	1876	16
184	Chiriquí	Los Algarrobos: Bar El Corte	8.49520	82.42525	154	29
185	Chiriquí	Los Algarrobos: Residencial Las Lajas	8.50470	82.41720	162	29
186	Chiriquí	Potrerillos Arriba: Finca Los Mameyes: Rancho	8.74000	82.51418	1422	10
187	Chiriquí	Potrerillos Arriba: Finca Los Mameyes: Río Pedro	8.74181	82.51337	1355	10
188	Chiriquí	Potrerillos Arriba: Finca Los Mameyes: Río Pedro: bridge	8.74087	82.51183	1320	10
189	Chiriquí	Potrerillos Arriba: Finca Los Mameyes: Río Pedro below bridge	8.73855	82.51073	1300	10
190	Chiriquí	Potrerillos Arriba: Finca Los Mameyes: pasture above Río Pedro	8.73858	82.51396	1361	10
191	Chiriquí	Potrerillos Arriba: Avenida Central: Casa Familia Castillo	8.69127	82.49451	960	10
192	Veraguas	PNSF: Cerro Mariposa: creek above water supply	8.50815	81.12104	899	23
193	Chiriquí	RFLF: Continental divide on road to Bocas	8.77875	82.20788	1090	14
194	Comarca Ngöbe-Buglé	BPPS: headwaters of Río Chiriquí Malí	8.78906	82.21547	1054	14
195	Chiriquí	El Salto above Boquete: branch to Volcán Barú	8.79343	82.47821	1618	9
196	Chiriquí	PNVB: road to summit of Volcán Barú: sign "Limite del Parque Nacional Volcán Barú"	8.79672	82.48911	1791	9
197	Chiriquí	PNVB: road to summit of Volcán Barú: just below "Las Zarzamora"	8.79720	82.50677	2326	9
198	Chiriquí	PNVB: road to summit of Volcán Barú: area de acampar Mamecillos	8.80151	82.51303	2580	9
199	Chiriquí	PNVB: road to summit of Volcán Barú: ca. 3000 m asl	8.80441	82.52469	3006	9
200	Chiriquí	PNVB: summit of Volcán Barú	8.80902	82.54241	3475	9
201	Chiriquí	PNVB: road to summit of Volcán Barú: area de acampar Los Fogones	8.80744	82.53503	3321	9
202	Chiriquí	PNVB: road to summit of Volcán Barú: "La Nevera"	8.81369	82.52938	3146	9
203	Chiriquí	PNVB: road to summit of Volcán Barú: lookout over crater	8.80930	82.52718	3065	9
204	Chiriquí	PNVB: Volcán Barú: floor of crater	8.80556	82.52688	2972	9
205	Comarca Ngöbe-Buglé	W slope Cerro Santiago, below La Nevera: Río Flor	8.50767	81.76683	1507	19
206	Comarca Ngöbe-Buglé	W slope Cerro Santiago, La Nevera: above ascent creek	8.49587	81.76778	1789	19
207	Bocas del Toro	PILA: N slope Cerro Pando, near border trail on divide: creek below camp	8.93542	82.71282	2284	4
208	Bocas del Toro	Changuinola: Puente San San: oficinas ANAM, AAMVECONA	9.46617	82.54928	24	26
209	Bocas del Toro	HIISSPS: Boca San San, Centro AAMVECONA	9.52587	82.50993	1	26
210	Bocas del Toro	HIISSPS: beach east of Boca San San	9.52116	82.50354	2	26
211	Bocas del Toro	HIISSPS: finca GTZ, vivero on N bank Río San San	9.50167	82.52428	11	26
212	Bocas del Toro	HIISSPS: finca GTZ, mangrove on S bank of Río Negro	9.50312	82.52399	6	26
213	Bocas del Toro	HIISSPS: Río Negro: flooded forest on N bank	9.50476	82.52467	8	26
214	Bocas del Toro	HIISSPS: Río Negro: flooded forest on N bank	9.50797	82.52885	12	26
215	Chiriquí	RFLF: Río Hornito: "Tuna's cave"	8.67361	82.20778	1317	16
216	Chiriquí	RFLF: W slope Cerro Pata de Macho: confluence of Río Hornito and "Río Perdido"	8.67134	82.20491	1350	16
217	Veraguas	Finca La Providencia: houses	7.89731	80.98654	53	30
218	Veraguas	Finca La Providencia: forest patch	7.89769	81.00072	56	30
219	Veraguas	Finca La Providencia: creek	7.89269	80.98440	41	30
220	Chiriquí	Peninsula de Burica: road to Puerto Limones	8.15188	82.87821	20	28
221	Chiriquí	Peninsula de Burica: road to Puerto Limones	8.12746	82.87363	26	28
222	Chiriquí	Peninsula de Burica: Puerto Limones	8.10278	82.86489	2	28
223	Chiriquí	Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek	8.08582	82.87432	62	28
224	Chiriquí	Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek	8.06767	82.88668	61	28
225	Chiriquí	Peninsula de Burica: dirt road from Puerto Limones to Bella Vista	8.07324	82.88573	74	28
226	Chiriquí	RFLF: near Lost & Found Ecohostel: "on/off-lake"	8.67513	82.21429	1377	16
227	Chiriquí	RFLF: upper limit of Valle de la Mina on road	8.66710	82.21705	1125	16
228	Chiriquí	Santa Clara: Finca Ecológica: clearing with plaintain and coffe on descent to western border creek	8.83223	82.78435	1179	1
229	Comarca Ngöbe-Buglé	road to Cerro Colorado, above Hato Chamí: Camp	8.48732	81.76855	1478	19
230	Comarca Ngöbe-Buglé	above Hato Chamí: creek next to road to Cerro Colorado	8.48768	81.76944	1431	19
231	Comarca Ngöbe-Buglé	Chumí: branch to Guayabito	8.40443	81.50157	396	21
232	Comarca Ngöbe-Buglé	Alto Tólica: escuela	8.47447	81.50341	1053	21
233	Comarca Ngöbe-Buglé	Alto Tólica: creek near escuela	8.47429	81.50536	1048	21

Waypoint	Province	Name	Latitude North	Longitude West	Elevation [m asl]	General locality
234	Comarca Ngöbe-Buglé	road to Guayabito: pass above Alto Tólica	8.48292	81.50399	1317	21
235	Comarca Ngöbe-Buglé	road to Guayabito: Alto Galera: escuela	8.51756	81.49294	1131	21
236	Comarca Ngöbe-Buglé	Guayabito	8.53909	81.48239	1139	21
237	Comarca Ngöbe-Buglé	above Guayabito: entering forest	8.54820	81.48496	1496	21
238	Comarca Ngöbe-Buglé	above Guayabito: forest	8.54939	81.48467	1527	21
239	Comarca Ngöbe-Buglé	above Guayabito: shade coffee plantation	8.54703	81.48384	1417	21
240	Veraguas	Los Valles: ANAM station	8.44807	81.19825	402	22
241	Veraguas	Los Valles: creek above ANAM station	8.44857	81.20083	404	22
242	Comarca Ngöbe-Buglé	El Paredón	8.45480	81.19377	432	22
243	Comarca Ngöbe-Buglé	El Paredón: Piedra pintada	8.46009	81.18893	454	22
244	Comarca Ngöbe-Buglé	above El Paredón: valley of Río Rasca: clearing with lookout	8.48294	81.17804	719	22
245	Comarca Ngöbe-Buglé	above El Paredón: valley of Río Rasca	8.48653	81.17214	779	22
246	Comarca Ngöbe-Buglé	above El Paredón: valley of Río Rasca	8.48776	81.17121	805	22
247	Comarca Ngöbe-Buglé	above El Paredón: Río Rasca	8.49100	81.16937	786	22
248	Comarca Ngöbe-Buglé	above El Paredón: valley of Río Rasca	8.48507	81.17273	788	22
249	Comarca Ngöbe-Buglé	above El Paredón: valley of Río Rasca: clearing	8.48158	81.18100	744	22
250	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: houses	8.79327	82.19285	510	15
251	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: camp	8.79009	82.19728	643	15
252	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: trail above camp	8.78853	82.20158	739	15
253	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: trail above camp, branch	8.79016	82.20105	730	15
254	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: trail above camp	8.79030	82.20032	718	15
255	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: trail above camp	8.79028	82.19893	681	15
256	Comarca Ngöbe-Buglé	road to Cerro Colorado: Terminal de Hacha	8.51095	81.78822	1393	18
257	Comarca Ngöbe-Buglé	road Cerro Colorado - Ratón	8.53355	81.80349	1636	17
258	Comarca Ngöbe-Buglé	SE slope Cerro Saguí: Ratón	8.54075	81.82070	1540	17
259	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Ratón: camp on pasture	8.54601	81.82247	1643	17
260	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Ratón: corn plantation	8.54661	81.82160	1680	17
261	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Ratón: corn plantation	8.54727	81.82100	1729	17
262	Comarca Ngöbe-Buglé	SE slope Cerro Saguí: Alto Cedro: upper limit of pasture	8.55775	81.82951	1858	17
263	Comarca Ngöbe-Buglé	SE slope Cerro Saguí: Alto Cedro: camp at Quebrada Juglí	8.55612	81.82517	1700	17
264	Comarca Ngöbe-Buglé	SE slope Cerro Saguí: Alto Cedro: Quebrada Juglí above camp	8.55757	81.82618	1708	17
265	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Quebrada Juglí: small clearing on path	8.55855	81.82322	1856	17
266	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Quebrada Juglí: crossing ridge	8.55958	81.82150	1892	17
267	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Quebrada Juglí: clearing with grass, creek	8.56125	81.82137	1874	17
268	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge	8.56357	81.82166	1971	17
269	Comarca Ngöbe-Buglé	SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge: elfin forest	8.56422	81.82209	2033	17
270	Bocas del Toro	PILA: N slope Cerro Pando, border trail on divide: branch to Changena trail	8.93900	82.71450	2253	4
271	Bocas del Toro	PILA: N slope Cerro Pando, tributary to Río Changena: "upper" camp 1, on highest pasture	8.95240	82.70929	1955	4
272	Bocas del Toro	PILA: N slope Cerro Pando, tributary to Río Changena: above "upper" camp 1	8.94736	82.70983	1995	4
273	Bocas del Toro	PILA: N slope Cerro Pando, tributary to Río Changena: pasture	8.96691	82.70334	1814	4
274	Bocas del Toro	PILA: N slope Cerro Pando, ridge between tributary and Río Changena	8.97784	82.69349	1715	4
275	Bocas del Toro	PILA: N slope Cerro Pando, Río Changena: "middle" camp 2	8.97850	82.69005	1641	4
276	Bocas del Toro	PILA: N slope Cerro Pando, pasture above Río Changena	8.98241	82.68904	1754	4
277	Bocas del Toro	PILA: N slope Cerro Pando, upper limit of pasture above Río Changena	8.98805	82.68602	1873	4
278	Bocas del Toro	PILA: N slope Cerro Pando, ridge between Río Changena and Río Clarito	8.99109	82.67118	1752	4
279	Bocas del Toro	PILA: N slope Cerro Pando, upper limit of pasture above Río Clarito	8.99207	82.66598	1641	4
280	Bocas del Toro	PILA: N slope Cerro Pando, Río Clarito: "lower" camp 3	9.00976	82.66400	1240	4
281	Bocas del Toro	PILA: N slope Cerro Pando, pasture above Río Clarito	8.99821	82.66774	1538	4
282	Bocas del Toro	PILA: N slope Cerro Pando, ridge between Río Changena and Río Clarito	8.98873	82.67490	1819	4
283	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: creek	8.78910	82.19936	704	15
284	Comarca Ngöbe-Buglé	BPPS: Willie Mazú: upper end of trail	8.78811	82.20174	778	15
285	Comarca Ngöbe-Buglé	Hacha trail: Río Marabí	8.51923	81.78307	1256	18
286	Comarca Ngöbe-Buglé	Hacha trail: Río Flor: camp at bridge	8.52090	81.77847	1216	18
287	Comarca Ngöbe-Buglé	Hacha trail: Río Flor: tree bridge	8.51835	81.77827	1254	18
288	Comarca Ngöbe-Buglé	Hacha trail: confluence of Río Marabí and Río Flor	8.52242	81.77831	1197	18
289	Comarca Ngöbe-Buglé	Hacha trail: Hacha	8.53615	81.77387	1125	18
290	Comarca Ngöbe-Buglé	Hacha trail: bridge to Suiche	8.54435	81.77195	1045	18
291	Comarca Ngöbe-Buglé	Hacha trail: Río Hacha: camp at creek	8.55028	81.76375	986	18
292	Comarca Ngöbe-Buglé	Hacha trail: Río Hacha: stairs	8.55218	81.76448	953	18
293	Comarca Ngöbe-Buglé	Alto Tólica: creek near escuela	8.47472	81.50548	1055	21
294	Comarca Ngöbe-Buglé	Guayabito: central soccer field	8.54043	81.48163	1130	21
295	Comarca Ngöbe-Buglé	above Guayabito: forest	8.55210	81.48314	1522	21
296	Veraguas	Santiago: Casa Carrizo	8.12465	80.96139	127	–

Appendix 2: Examined specimens

In the following list of my examined specimens, observations of uncollected but unequivocally identified specimens ("obs.") are only listed if they constitute the only record of a given species from a given locality, or if additional specimens other than those constituting an exclusively photographic record ("photo"; photographed by myself if no other photographer is specified) have been observed at the same locality. The complete dataset of examined specimens including all observations is provided in Appendix 6. When known to me, field numbers are given in parentheses, following the collection number where applicable.

Order Testudines

Family Dermochelyidae

Dermochelys coriacea.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: obs., photo.

Family Emydidae

Trachemys grayi.— PANAMA: Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo.

Family Kinosternidae

Kinosternon scorpioides.— PANAMA: Chiriquí: Los Algarrobos: near Río Majagua, 8.4851°N, 82.4345°W, 106 m: MHCH 2337 (JFB 12); Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: obs, photo; Veraguas: Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: photo; road Santiago - Santa Fé, halfway between Santiago and San Francisco, 8.1796°N, 80.9511°W, 76 m: SMF 89574 (SL 139).

Order Crocodylia

Family Alligatoridae

Caiman crocodilus.— PANAMA: Bocas del Toro: HIISSPS: beach east of Boca San San, 9.5212°N, 82.5035°W, 3 m: obs., photo; Chiriquí: Volante: Río Escárrea, 8.5883°N, 82.6733°W, 430 m: obs.; Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: obs., photo; Veraguas: Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: obs., photo.

Order Squamata

Family Amphisbaenidae

Amphisbaena varia.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Anguidae

Celestus sp.— PANAMA: Chiriquí: RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 90177 (SL 449)$^{\mathrm{COI}}$.

Diploglossus bilobatus.— PANAMA: Veraguas: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: obs.; Cerro Mariposa, 8.5152°N, 81.1203°W, 933 m: MHCH 2309 (LSt 89); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: MHCH 2310 (SL 482), SMF 89546 (SL 124)$^{\mathrm{COI}}$, 89547–49 (SL 125–27); PNSF: Cerro Negro: ridge above camp, 8.5756°N, 81.0976°W, 1000 m: SMF 89951 (AC 84).

Diploglossus monotropis.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Mesaspis monticola.— PANAMA: Chiriquí: Cerro Totuma, 8.8877°N, 82.6824°W, 1987 m: photo by Andreas Hertz; PNVB, Aguacatal, 8.803°N, 82.5849°W, 2012 m: SMF 86386 (MHCH 376); PNVB: road to summit of Volcán Barú: area de acampar Los Fogones, 8.8074°N, 82.535°W, 3321 m: obs.; PNVB: Volcán Barú: floor of crater, 8.8056°N, 82.5269°W, 2972 m: photo, SMF 90198–9 (SL 506–7); PNVB: Sendero Los Quetzales: Refugio Las Rocas, 8.848°N, 82.5196°W, 2420 m: obs.; PNVB: Alto Chiquero, Ranger-Station, 8.8464°N, 82.4871°W, 1850 m: SMF 85439–40 (GK 1249–50).

Family Gekkonidae

Hemidactylus frenatus.— PANAMA: Bocas del Toro: HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: SMF 90185 (SL 549); HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: SMF 90184 (SL 562); Chiriquí: Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: MHCH 2323 (SL 164); Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: SMF 89568 (SL 174); Los Algarrobos: Bar El Corte, 8.4954°N, 82.4253°W, 150 m: MHCH 2320–1 (JFB 79–80); Veraguas: Cerro Mariposa, 8.512°N, 81.1203°W, 1004 m: MHCH 2322 (LSt 122); Finca La Providencia: houses, 7.8973°N, 80.9865°W, 53 m: photo.

Lepidodactylus lugubris.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: MHCH 2339 (SL 532), SMF 90191 (SL 554), photo; road from Chiriquí Grande to Almirante: shortly after km 63, 9.2661°N, 82.4088°W, 85 m: SMF 89775 (SL 318).

Family Phyllodactylidae

Thecadactylus rapicauda.— PANAMA: Bocas del Toro: Cerro Tebata, 9.5659°N, 82.8475°W, 491 m: SMF xxxxx (MHCH 583); Chiriquí: Volante: camp, 8.587°N, 82.6683°W, 481 m: SMF 89601 (SL 228).

Family Sphaerodactylidae

Gonatodes albogularis.— PANAMA: Chiriquí: Peninsula de Burica: Puerto Limones, 8.1028°N, 82.8649°W, 2 m: obs.; Los Algarrobos, Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: photo; Veraguas: Finca La Providencia: forest patch, 7.8977°N, 81.0007°W, 56 m: SMF 91553 (SL 574)$^{\mathrm{COI}}$; Finca La Providencia: houses, 7.8973°N, 80.9865°W, 53 m: SMF 91552 (SL 573); NICARAGUA: Río San Juan: Boca de San Carlos, 10.7905°N, 84.1938°W, 40 m: SMF 86745 (JS 525).

Lepidoblepharis buchwaldi.— ECUADOR: Los Ríos: Pichincha: Centro Cientifico Río Palenque, 0.55°S, 79.3667°W: MCZ 151697, 151710; Pichincha: 1 km N Buena Fe, 0.88781°S, 79.48896°W: MCZ 151709.

Lepidoblepharis duolepis.— COLOMBIA: Valle: Valle Río Pance: MCZ 159596–7.

Lepidoblepharis festae.— COLOMBIA: Antioquia: Urrao, 2030 m: MCZ 166521.

Lepidoblepharis grandis.— ECUADOR: Pichincha: Pichincha: FMNH 177434–5.

Lepidoblepharis heyerorum.— BRAZIL: Pará: Urua (Parque Nacional de Amazonia, Río Tapajos), 4.6°S, 56.2333°W: MCZ 172927–8.

Lepidoblepharis intermedius.— COLOMBIA: Cauca: Isla Gorgona: MCZ 159595; Isla Gorgona, beach in front of Gorganilla: MCZ 160150; Valle del Cauca: Valle Río Sabaletas, Sabaletas Piedras: MCZ 160199.

Lepidoblepharis microlepis.— COLOMBIA: Antioquia: Laguna Quesada, Puerto Limón (near Murindo) [Rio Quesado, Atrato River region according to original description (Noble 1923)], 6.95°N, 76.75°W, 34 m: AMNH R-18229.

Lepidoblepharis miyatai.— COLOMBIA: Magdalena: Ancon Guairaca (=Bahia Gairaca+Ensenada de Bayraca): MCZ 154447–9; Ancon Guairacal-Bahia Gairaca=Ensenada de Gayraca: MCZ 156973–4.

Lepidoblepharis montecanoensis.— VENEZUELA: Falcón: Paraguana Penninsula, 6km W Pueblo Nuevo, in the Monte Cano Biological Reserve, ca. 11.95°N, 69.975°W, 150 m: MCZ 175913.

Lepidoblepharis peraccae.— COLOMBIA: Los Mangos, S.W. Colombia, 300 m: BMNH 1908.5.29.46B.

Lepidoblepharis sanctaemartae.— COLOMBIA: Magdalena: Fundacion: MCZ 11304; PANAMA: Comarca Emberá: Comunidad de Villa Caleta, 8.4507°N, 77.7258°W, 30 m: SMF 85371 (MHCH 304); Darién: Distrito de Sambú, Garachine, Finca del Pana de Gustavo Dogirama, 1 hora SO del pueblo, 8.0482°N, 78.3567°W, 45 m: (AB 385); Distrito de Chepigana, Río San Antonio, Cerro Sapo, Camp 2, 7.9794°N, 78.3551°W, 834 m: (AB 594–5); Distrito de Sambú, Río San Antonio, Cerro Sapo, 8.0038°N, 78.3485°W, 200 m: (AB 448); Sante Fe, Cuipo site, 8.6833°N, 78.1167°W, 70 m: FMNH 170124; Distrito de Chepigana, toma de agua, Meteti, 8.4614°N, 77.989°W, 132 m: (AB 250); Distrito de Pinogana, 1km to Rancho Frío Field station, 8.0168°N, 77.7297°W, 133 m: (AB 1216); Río Pita: FMNH 68156; Panamá: cliffs to west of Cerro Campana, 8.685°N, 79.924°W, 366 m: FMNH 60196; Barro Colorado Island, 9.155°N, 79.848°W, 178 m: FMNH 13306, 177051–2; Distrito de Chepo, Wacuco, Padre Pablo Kasuboski Fram. toma de agua, 8.9435°N, 78.4699°W, 262 m: (AB 997).

Lepidoblepharis sp. 1.— PANAMA: Colón: Distrito de Donoso, Petaquilla, 8.8553°N, 80.6556°W, 107 m: (AB 018$^{\mathrm{16S}}$, 1251–2); Distrito de Donoso, Chicheme, Donoso, Mina de cobre panama, 8.8653°N, 80.6438°W, 100 m: (AB 1241); Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89963 (AC 79).

Lepidoblepharis sp. 2.— PANAMA: Comarca Emberá: Distrito de Cémaco, Bajo pequeño, camp3 Pechito parao- quebrada muestreo entre 730-850, 8.4791°N, 77.528°W, 718 m: (AB 887); Comarca Kuna Yala: Distrito de Narganá, Burbayar la cascada trail, 9.3184°N, 79.0027°W, 360 m: (AB 963); Nusagandí, Umgebung Feldstation, 9.3417°N, 78.994°W, 350 m: SMF 81950 (GK 12)–SMF 81952; Nusagandí, Sendero Nusagandi, 9.3417°N, 78.9917°W, 280 m: SMF 81954; Nusagandí, Sendero Nusagandi, 9.3417°N, 78.9917°W, 290 m: SMF 81953; Distrito de Wargandi, way back from Yarculup to Taintidu river, 9.0345°N, 78.0221°W, 227 m: (AB 786); border of Darien, Summit camp, 8.92°N, 77.85°W, 350 m: FMNH 170042; border of Darien, Summit site, 8.92°N, 77.85°W, 320 m: FMNH 170029, 170043; Darién: Distrito de Sambú, Camino hacia Cerro Sapo, 7.9801°N, 78.3556°W, 773 m: (AB 415)$^{\mathrm{16S}}$; border of Darien, Summit site, 8.92°N, 77.85°W, 320 m: FMNH 170044, 170045; Distrito de Pinogana, Río Cana, Cana field station, Chimenea trail, 7.756°N, 77.6857°W, 515 m: (AB 245); Panamá: Distrito de Chepo, Río Terable, 9.284°N, 78.9838°W, 322 m: (AB 989).

Lepidoblepharis williamsi.— COLOMBIA: Antioquia: San Vicente (La Honda): MCZ 1170640, 170643.

Lepidoblepharis xanthostigma.— COSTA RICA: no specific locality: SMF 78437; Heredia: Schutzgebiet Rara Avis, Catarata, 10.2819°N, 84.0457°W, 675 m: SMF 81816 (CR 49); Limón: Zent, near Puerto Limón, Costa Rica, 10.033°N, 83.283°W, 13 m: MCZ 11658; no specific locality: FMNH 176918, 176919; NICARAGUA: Río San Juan: Bartola, 10.9728°N, 84.3392°W, 30 m: SMF 80998 (GK 303); Bartola, Orange Trail 8, 10.9728°N, 84.3392°W, 30 m: SMF 82559 (GK 367); Cerro El Bolívar, near Río Machado, 10.8672°N, 84.1695°W, 280 m: SMF 84817 (GP 095); Dos Bocas de Río Indio, 11.0486°N, 83.8801°W, 20 m: (JS 564, 585, 603, 606, 621), SMF 86741–4 (JS 605, 602, 604, 569); PANAMA: Bocas del Toro: HIISSPS: Río Negro: flooded forest on N bank, 9.508°N, 82.5289°W, 13 m: SMF 90190 (SL 558)$^{\mathrm{16S}}$; HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: MHCH 2338 (SL 563); Isla Bastimento, Wizard, 9.351°N, 82.197°W, 10 m: SMF 86389 (MHCH 396); Isla Popa, 9.2206°N, 82.1411°W, 4 m: photo by Konrad Mebert; Chiriquí: Cordillera Central, Reserva Forestal Fortuna, Pfad von Finca nach Dam Site, 8.7311°N, 82.2534°W, 1300 m: SMF 85006 (GK 1494); Meseta de Chorcha, 8.4139°N, 82.2183°W, 260 m: SMF 85005 (GK 1400); Coclé: El Valle de Antón, 8.6°N, 80.1167°W, 594 m: FMNH 177522–3; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Distrito de Donoso, Petaquilla, 8.8553°N, 80.6556°W, 107 m: (AB 1249–50); Cerro Santa Rita, ca 800', 9.324°N, 79.787°W, 244 m: FMNH 68157; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: SMF 90189 (SL 489); Alto Tólica: creek near escuela, 8.4747°N, 81.5055°W, 1055 m: SMF 91558 (SL 750)$^{\mathrm{16S}}$; Darién: Distrito de Pinogana, camp. 4 arriba de Río Pucuro, 8.0575°N, 77.3702°W, 1043 m: (AB 527); Panamá: Cerro de La Victoria, Quebrada Buenos Aires, along stream, 2000', 9.2°N, 79.3833°W, 610 m: FMNH 153600; La Victoria, 2200', 9.2°N, 79.3833°W, 722 m: FMNH 154549; Veraguas: Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: SMF 89576 (SL 129), 91559 (SL 760)$^{\mathrm{16S}}$.

Family Corytophanidae

Basiliscus basiliscus.— PANAMA: Chiriquí: Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek, 8.0858°N, 82.8743°W, 62 m: obs.; Cabecera de Cochea: Río Cochea above crossing, 8.7272°N, 82.4937°W, 1140 m: SMF 89760 (SL 279); Los Algarrobos: near Río Majagua, 8.4854°N, 82.4349°W, 110 m: SMF 90171 (JFB 13); Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo, MHCH 2296 (SL 461); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: obs.; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: obs.; Los Algarrobos: old railway bridge over Río Majagua, 8.4809°N, 82.428°W, 88 m: MHCH 2295 (SL 395); Veraguas: Los Valles: creek above ANAM station, 8.4486°N, 81.2008°W, 404 m: SMF 91531 (SL 627)$^{\mathrm{COI}}$; Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: obs.; PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: SMF 89530 (SL 168); Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: photo.

Basiliscus vittatus.— PANAMA: Bocas del Toro: HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: MHCH 2297 (SL 551); HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: photo, SMF 90172 (SL 531); HIISSPS: beach east of Boca San San, 9.5212°N, 82.5035°W, 3 m: photo; road from Chiriquí Grande to Almirante: shortly after km 63, 9.2661°N, 82.4088°W, 85 m: SMF 89761 (SL 317); Isla Bastimentos: Hostal Bastimentos, 9.3485°N, 82.209°W, 10 m: photo;

Corytophanes cristatus.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: junction of border creeks, 8.8306°N, 82.787°W, 1100 m: MHCH 2306–7 (SL 473, 608), SMF 91537 (SL 607); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Cerro Mariposa, 8.5148°N, 81.1192°W, 937 m: SMF 89542 (LSt 125); Alto de Piedra, 8.5161°N, 81.1185°W, 864 m: photo by Konrad Mebert; PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 800 m: SMF 89930 (AC 88); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: (AC 80); PNSF: Cerro Negro: ridge above camp: small clearing, 8.5756°N, 81.0976°W, 1000 m: obs.; PNSF: Cerro Negro: creek above camp, 8.5702°N, 81.0963°W, 782 m: SMF 89767 (SL 373).

Family Dactyloidae

Dactyloa casildae.— PANAMA: Chiriquí: RFLF: Cerro Guayabo, 8.7744°N, 82.2398°W, 1723 m: SMF 90098 (JFB 44)$^{16S, COI}$; RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1419 m: MHCH 2124 (SL 263), SMF 89673 (SL 262); RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1440 m: SMF 89674 (SL 354); RFLF: W slope Cerro Pata de Macho, 8.6745°N, 82.2044°W, 1437 m: SMF 89455–6 (NH 42–3); RFLF: W slope Cerro Pata de Macho, 8.6745°N, 82.204°W, 1454 m: SMF 89457 (NH 44); RFLF: W slope Cerro Pata de Macho: traps, 8.674°N, 82.2022°W, 1500 m: MHCH 2125 (SL 353); RFLF: W slope Cerro Pata de Macho: traps, 8.674°N, 82.2022°W, 1521 m: MHCH 2123 (SL 261); SMF 89672 (SL 260); RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1657 m: photo; RFLF: W slope Cerro Pata de Macho: camp at "Río Perdido", 8.6719°N, 82.1997°W, 1421 m: photo, MHCH 2120 (SL 182)$^{16S, COI}$, 2121 (SL 183), 2127 (SL 568), SMF 89458 (SL 184); Comarca Ngöbe-Buglé: Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1216 m: photo, MHCH 2128 (SL 712), 2129 (SL 714)^{COI}, SMF 91453 (SL 713)$^{16S, COI}$; Hacha trail: confluence of Río Marabí and Río Flor, 8.5224°N, 81.7783°W, 1197 m: photo; Hacha trail: Río Flor: tree bridge, 8.5184°N, 81.7783°W, 1254 m: SMF 91454 (SL 727)^{COI}; "Cerro Nevera" = La Nevera, 8.5°N, 81.7722°W, 1600 m: SMF 85370 (MHCH 063); W slope Cerro Santiago, La Nevera: first confluence of creeks below camp, 8.5018°N, 81.7689°W, 1555 m: MHCH 2122 (SL 241); W slope Cerro Santiago, La Nevera: second confluence of creeks below camp, 8.5032°N, 81.7675°W, 1533 m: MHCH 2126 (SL 521), SMF 89452 (SL 240), 89453 (SL 242)$^{16S, COI}$, 89454 (SL 243)^{COI}; Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: SMF 91455 (SL 730)$^{16S, COI}$.

Dactyloa frenata.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: Willie Mazú: creek, 8.7891°N, 82.1994°W, 704 m: SMF 91460 (SL 706)$^{16S, COI}$; Veraguas: PNSF: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: SMF 91459 (SL 757)^{16S}; Cerro Mariposa, 8.507°N, 81.1139°W, 869 m: SMF 89467 (LSt 94)^{COI}; PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 844 m: SMF 89897 (AC 221).

Dactyloa ginaelisae.— PANAMA: Chiriquí: PNVB: Bajo Mono: Sendero La Cascada: camp, 8.8263°N, 82.4989°W, 1831 m: SMF 89737 (SL 399)^{16S}; Parque Nacional Volcán Barú, Alto Chiquero, Ranger-Station, 8.8464°N, 82.4871°W, 1870 m: SMF 85070 (GK 1636); Chiriquí: Sendero el Pianista, 8.8222°N, 82.4217°W, 1498 m: SMF 86381 (MHCH 484); RFLF: Cerro Guayabo, 8.7715°N, 82.2427°W, 1660 m: SMF 90135 (JFB 45); RFLF: Cerro Guayabo, 8.7732°N, 82.2412°W, 1662 m: SMF 90134 (JFB 43); RFLF: W slope Cerro Pata de Macho: camp at "Río Perdido", 8.6719°N, 82.1997°W, 1430 m: SMF 90136 (SL 453); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1752 m: photo, SMF 89501 (SL 197); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1725 m: photo; RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1740 m: MHCH 2237 (SL 267); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1727 m: SMF 89500 (SL 188)^{COI}; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1740 m: photo, MHCH 2236 (SL 266), SMF 89499 (SL 187), 89738 (SL 352); Comarca Ngöbe-Buglé: SE slope Cerro Saguí: Alto Cedro: Quebrada Juglí above camp, 8.5576°N, 81.8262°W, 1708 m: MHCH 2240 (SL 665), SMF 91504 (SL 660)^{16S}; SE slope Cerro Saguí: Alto Cedro: camp at Quebrada Juglí, 8.5561°N, 81.8252°W, 1700 m: photo, MHCH 2239 (SL 658), SMF 91503 (SL 659); SE slope Cerro Saguí above Quebrada Juglí: small clearing on path, 8.5586°N, 81.8232°W, 1856 m: photo; SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1956 m: SMF 91502 (SL 666)^{COI}; W slope Cerro Santiago, La Nevera: camp on road, 8.4997°N, 81.7724°W, 1699 m: SMF 89496 (SL 121)$^{16S, COI}$; SMF 89497 (SL 248); "Cerro Nevera" = La Nevera, 8.5°N, 81.7722°W, 1600 m: SMF 85069 (GK 1597); W slope Cerro Santiago, La Nevera: camp, 8.5011°N, 81.7694°W, 1580 m: SMF 89498 (SL 247); W slope Cerro Santiago, La Nevera: first confluence of creeks below camp, 8.5018°N, 81.7689°W, 1555 m: photo, MHCH 2235 (SL 245); W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1620 m: MHCH 2238 (SL 512); W slope Cerro Santiago, La Nevera: ascent creek, 8.4961°N, 81.7677°W, 1761 m: photo; W slope Cerro Santiago, La Nevera: second confluence of creeks below camp, 8.5032°N, 81.7675°W, 1533 m: photo, MHCH 2234 (SL 244); W slope Cerro Santiago, La Nevera: elfin forest summit on continental divide, 8.4954°N, 81.7673°W, 1814 m: photo, SMF 90133 (SL 515); E slope Cerro Santiago: Quebrada Ardilla, 8.4974°N, 81.7228°W, 1598 m: MHCH 1338.

Dactyloa ibanezi.— PANAMA: Bocas del Toro: Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: MHCH 1059; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: Willie Mazú: trail above camp, branch, 8.7902°N, 82.2011°W, 730 m: SMF 91475 (SL 708), 91476 (SL 711)^{16S}; Veraguas: PNSF: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: MHCH 2184 (SL 758)^{COI}; Cerro Mariposa, 8.51°N, 81.1166°W, 878 m: SMF 89459 (LSt 49)$^{16S, COI}$; PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: photo.

Dactyloa insignis.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 748 m: SMF 91477 (SL 646)$^{16S, COI}$; Veraguas: Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: SMF 89482 (SL 131)^{16S}.

Dactyloa kunayalae.— PANAMA: Chiriquí: Reserva Forestal la Fortuna, Quebrada Arena, 8.7774°N, 82.2088°W, 1030 m: SMF 86355 (MHCH 506); Comarca Kuna Yala: border of Darien, Summit site, 8.92°N, 77.85°W, 320 m: FMNH 170034 (photo); Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: SMF 91484 (SL 600); Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 970 m: SMF 91485 (SL 737)^{16S}; Veraguas: Alto de Piedra, 8.5152°N, 81.1202°W, 865 m: SMF 96009 (GK 2518); PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: photo.

Dactyloa microtus.— COSTA RICA: Cartago: Parque Nacional Tapantí, 9.73°N, 83.79°W, 1773 m: photo by Mason Ryan; Heredia: Cerro Dantas, 10.1°N, 84.06°W, 2113 m: photo by Daniel Cascante; San Jose: near San Jose, probably La Palma, 10.0358°N, 83.9807°W, 1497 m: USNM 31282; PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1641 m: SMF 91499 (SL 697)$^{16S, COI}$, 91500 (SL 698)^{16S}, 91501 (SL 701)$^{16S, COI}$.

Norops apletophallus.— PANAMA: Darién: Majé (Fila Chacon), Río Ambroya, 8.9417°N, 78.5333°W, 188 m: SMF 89360 (MHCH 1082)^{COI}; Panamá: Parque Metropolitano, 8.9833°N, 79.5461°W, 45 m: photo, SMF 85310, 85314^{COI}.

Norops aquaticus.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: junction of border creeks, 8.8306°N, 82.787°W, 1088 m: MHCH 2100 (SL 411), SMF 89667 (SL 420); Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1108 m: SMF 89666 (SL 415); Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1125 m: MHCH 2101–2 (SL 475, 615), SMF 91445 (SL 614)^{COI}; Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1200 m: obs.; Nacimiento Quebrada Chevo, 8.841°N, 82.7721°W, 1160 m: SMF 85438 (GK 1657); Quebrada Chevo, 8.8421°N, 82.7711°W, 1170 m: SMF 85437 (GK 1656); Chiriquí: Cordillera (pueblo), 4 km SSE El Hato del Volcan, 8.7383°N, 82.6211°W, 1160 m: SMF 89281–3 (MHCH 1026, 1028, 1029).

Norops auratus.— PANAMA: Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: MHCH 2104 (SL 585); Los Algarrobos: Casa de Mair, 8.4928°N, 82.4263°W, 147 m: MHCH 2103 (SL 421), SMF 89668 (SL 414); Veraguas: road Santiago - Santa Fé, halfway between Santiago and San Francisco, 8.1796°N, 80.9511°W, 76 m: SMF 89444 (SL 140)^{COI}.

Norops benedikti.— COSTA RICA: Puntarenas: Las Tablas, 8.9407°N, 82.728°W, 1960 m: SMF 92134 (GK 2557), xxxxx (GK 2559); PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, border trail on divide, 8.9307°N, 82.7137°W, 2400 m: obs.; PILA: N slope Cerro Pando, near border trail on divide: camp, 8.9314°N, 82.7137°W, 2389 m: SMF 89744 (SL 433)^{16S}; PILA: N slope Cerro Pando, near border trail on divide: creek below camp, 8.9333°N, 82.7131°W, 2305 m: SMF 89746 (SL 435), 90149 (SL 529)$^{16S, COI}$; PILA: N slope Cerro Pando, near border trail on divide: creek below camp, 8.9333°N, 82.7131°W, 2332 m: SMF 89745 (SL 434); PILA: N slope Cerro Pando, near border trail on divide: creek below camp, 8.9354°N, 82.7128°W, 2284 m: SMF 90148 (SL 528)$^{16S, COI}$; PILA: N slope Cerro Pando, tributary to Río Changena: above "upper" camp 1, 8.9474°N, 82.7098°W, 1980 m: SMF 91508 (SL 679)^{16S}; PILA: N slope Cerro Pando, tributary to Río Changena: above "upper" camp 1, 8.9474°N, 82.7098°W, 1995 m: MHCH 2106 (SL 677), 2107 (SL 678)^{16S}; PILA: N slope Cerro Pando, tributary to Río Changena: "upper" camp 1, on highest pasture, 8.9524°N, 82.7093°W, 1955 m: SMF 91507 (SL 681)$^{16S, COI}$; PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1641 m: MHCH 2109 (SL 695)^{16S}, SMF 91505 (SL 696)$^{16S, COI}$; PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1650 m: SMF 91506 (SL 682); PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1655 m: MHCH 2108 (SL 686); PILA: N slope Cerro Pando, ridge between Río Changena and Río Clarito, 8.9887°N, 82.6749°W, 1819 m: SMF 91509 (SL 694)^{16S}; Sendero Culebra, Bajo Mono, 8.876°N, 82.4696°W, 1736 m: SMF 86374 (MHCH 494)^{16S}, 86375 (MHCH 496), 89274 (MHCH 495)^{16S}; Sendero el Pianista, 8.8411°N, 82.4246°W, 1652 m: SMF 86370 (MHCH 429)^{16S}, 86371–3 (MHCH 430–2); Chiriquí: Jurutungo, 8.9083°N, 82.7168°W, 2055 m: SMF 85275–7 (GK 1352–4); PILA: Jurutungo: ascent towards border trail on divide: lookout, 8.9193°N, 82.7168°W, 2308 m: obs.; PILA: Jurutungo: W slope Cerro without name: entrance to ascent, 8.9111°N, 82.7159°W, 2018 m: SMF 89505 (SL 206)$^{16S, COI}$; Jurutungo, 8.9109°N, 82.7144°W, 2060 m: SMF 85272–3 (GK 1320–1); PILA: Jurutungo: W slope Cerro without name: shortly after last clearing, 8.9114°N, 82.7129°W, 2068 m: SMF 89507 (SL 224)^{16S}; PILA: Jurutungo: W slope Cerro without name: shortly above branch to second waterfall, 8.9121°N, 82.7096°W, 2202 m: photo, SMF 89506 (SL 207); PILA: Jurutungo: W slope Cerro without name: branch to summit or top of waterfall, 8.9119°N, 82.7095°W, 2250 m: MHCH 2105 (SL 202); PNVB: Alto Chiquero, 1,0 km S Ranger-Station, 8.8453°N, 82.4958°W, 1915 m: SMF 85264–7 (GK 1257–60); PNVB: Alto Chiquero, 0.4 km S Ranger-Station, 8.8333°N, 82.4833°W, 1820 m: SMF 85268 (GK 1261).

Norops biporcatus.— PANAMA: Bocas del Toro: Sendero el Pianista, 8.8714°N, 82.4159°W, 1005 m: SMF 86388 (MHCH 421); road from Chiriquí Grande to Almirante: shortly after km 43, 9.1572°N, 82.3182°W, 53 m: MHCH 2111 (SL 306); Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo, SMF 89448 (SL 175); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: obs.; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: photo by Meike Piepenbring, photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: obs.; Los Algarrobos: Casa de Mair, 8.4928°N, 82.4263°W, 147 m: SMF 89671 (SL 369); Los Algarrobos: Bar El Corte, 8.4952°N, 82.4253°W, 154 m: obs.; Los Algarrobos: Residencial Las Lajas, 8.5047°N, 82.4172°W, 162 m: MHCH 2112 (SL 458); private beach without name near Playa Hermosa, 8.2007°N, 82.1397°W, 2 m: obs.; Coclé: PNGDOTH: 8.6667°N, 80.6167°W, 800 m: photo by Andreas Hertz; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: Hacha trail: bridge to Suiche, 8.5444°N, 81.772°W, 1026 m: SMF 91449 (SL 742); Buabidí alias Alto/Llano/Hato Tugrí: Casa de Amado, 8.4817°N, 81.7159°W, 1241 m: photo, SMF 89669 (SL 361); Alto Tólica: creek near escuela, 8.4743°N, 81.5054°W, 1048 m: SMF 91446 (SL 749); Guayabito: central soccer field, 8.5404°N, 81.4816°W, 1130 m: SMF 91447 (SL 753)^{COI}; above El Paredón: valley of Río Rasca: clearing, 8.4816°N, 81.181°W, 744 m: MHCH 2113 (SL 638)^{COI}, SMF 91448 (SL 637); Veraguas: PNSF: Cerro Mariposa, 8.5237°N, 81.1335°W, 717 m: SMF 89447 (LSt 113); PNSF: Cerro Mariposa, 8.5255°N, 81.1311°W, 645 m: SMF 89446 (LSt 106); Cerro Mariposa, 8.5156°N, 81.1171°W, 852 m: SMF 89445 (LSt 82); Cerro Mariposa, 8.5053°N, 81.1089°W, 825 m: MHCH 2110 (LSt 105); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89670 (SL 383); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 800 m: SMF 89895 (AC 82).

Norops capito.— PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, upper limit of pasture above Río Clarito, 8.9921°N, 82.666°W, 1641 m: SMF 91452 (SL 692); PILA: N slope Cerro Pando, Río Clarito: "lower" camp 3, 9.0098°N, 82.664°W, 1254 m: SMF 91450 (SL 689)^{COI}; Isla Colon - Caremero, 9.347°N, 82.233°W, 9 m: photo by Konrad Mebert; Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85196 (GK 1273); Potrerillos Arriba: Finca Los Mameyes: Río Pedro: bridge, 8.7409°N, 82.5118°W, 1321 m: SMF 90097 (SL 469)^{COI}; Potrerillos Arriba: Finca Los Mameyes: Río Pedro below bridge, 8.7386°N, 82.5107°W, 1301 m: photo, MHCH 2117 (SL 470); Fortuna, Trail from Finca to Dam site, 8.734°N, 82.2494°W, 1200 m: SMF 85200 (GK 1531); RFLF: Lost & Found Ecohostel, 8.6745°N, 82.2201°W, 1246 m: MHCH 2116 (NH 39); RFLF: Lost & Found Ecohostel, 8.6744°N, 82.2192°W, 1283 m: SMF 89450 (NH 13); RFLF: near Lost & Found Ecohostel, 8.6744°N, 82.2161°W, 1265 m: MHCH 2115 (JFB 49)^{COI}; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge, 8.674°N, 82.2154°W, 1455 m: SMF 89449 (NH 5); RFLF: near Lost & Found Ecohostel: "on/off-lake", 8.6751°N, 82.2143°W, 1377 m: MHCH 2119 (SL 591)^{COI}; Palo Seco, Sendero los tucanes, 8.7815°N, 82.2122°W, 1120 m: SMF 85197–8 (GK 1455–6); RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1419 m: SMF 89451 (SL 181); RFLF: W slope Cerro Pata de Macho, 8.6719°N, 82.1997°W, 1427 m: MHCH 2114 (JFB 07); RFLF: W slope Cerro Pata de Macho: camp at "Río Perdido", 8.6719°N, 82.1997°W, 1421 m: MHCH 2118 (SL 567); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1055 m: SMF 90096 (SL 500)^{COI}; behind finca Celestine road to Bocas del Toro, 8.8025°N, 82.1842°W, 610 m: photo by Ralph Mangelsdorff; above El Paredón: valley of Río Rasca, 8.4851°N, 81.1727°W, 788 m: SMF 91451 (SL 636)^{COI}; Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 850 m: SMF 89896 (AC 201).

Norops carpenteri.— PANAMA: Bocas del Toro: Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: SMF 89356–7 (MHCH 1058, 1057).

Norops charlesmyersi.— PANAMA: Chiriquí: Progreso - Chiriquí, 8.456°N, 82.836°W, 27 m: MVUP 319; Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo, MHCH 2137 (SL 176), SMF 89508 (SL 177); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: MHCH 2138 (SL 459), SMF 89688 (SL 445), 90099 (SL 460); Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: obs.; Las Lomas - Chiriquí, 8.427°N, 82.391°W, 57 m: MVUP 306A, 306B; Loma del silencio, Prov. Chiriquí, 8.734°N, 82.226°W, 1051 m: MVUP 799.

Norops cryptolimifrons.— PANAMA: Bocas del Toro: Sendero el Pianista, 8.8714°N, 82.4159°W, 1005 m: SMF 86376–9 (MHCH 424–7), 86388 (MHCH 428); Sendero El Pianista, Casa de Ancon, 8.8714°N, 82.4159°W, 1005 m: SMF 89366 (MHCH 1055), 89368 (MHCH 1054)^{COI}, 89370 (MHCH 1053), 89371 (MHCH 1075)^{COI}; road from Chiriquí Grande to Almirante: shortly after km 63, 9.2661°N, 82.4088°W, 85 m: MHCH 2143 (SL 315)$^{\text{16S}}$, SMF 89700–1 (SL 313–4); road from Chiriquí Grande to Almirante: shortly after km 53, 9.2061°N, 82.3616°W, 50 m: MHCH 2141 (SL 307)$^{\text{16S, COI}}$, SMF 89697 (SL 308)$^{\text{16S}}$, 89698–9 (SL 309–10); road from Chiriquí Grande to Almirante: shortly after km 43, 9.1572°N, 82.3182°W, 53 m: MHCH 2139–40 (SL 297, 301), SMF 89694 (SL 298)$^{\text{16S}}$, 89695–6 (SL 299–300); road from Chiriquí Grande to Almirante: km 24.5, 9.0548°N, 82.3032°W, 34 m: MHCH 2144–6 (SL 332–4), SMF 89689–91 (SL 330, 331, 335); road from Chiriquí Grande to Almirante: shortly after km 23, branch to Palma Real and Punta Róbalo, 9.0393°N, 82.3012°W, 46 m: MHCH 2130 (SL 289), SMF 89683–5 (SL 288, 290, 291); road from Chiriquí Grande to Almirante: km 35.5, bus stop, 9.1212°N, 82.2978°W, 35 m: MHCH 2147 (SL 336)$^{\text{16S}}$, 2148 (SL 339), SMF 89692–3 (SL 337–8); road from Chiriquí Grande to Almirante: shortly after km 33, 9.1107°N, 82.2886°W, 38 m: MHCH 2131 (SL 292)$^{\text{16S}}$, 2132 (SL 294), SMF 89686 (SL 293)$^{\text{16S}}$, 89687 (SL 295); Comarca Ngöbe-Buglé: road from Chiriquí Grande to Almirante: km 15.5, 9.0099°N, 82.2736°W, 29 m: MHCH 2133 (SL 320)$^{\text{16S, COI}}$, 2134–5 (SL 322, 324), SMF 89679–82 (SL 321, 323, 325, 342).

Norops cf. cryptolimifrons.— PANAMA: Bocas del Toro: road from Chiriquí Grande to Almirante: shortly after km 63, 9.2661°N, 82.4088°W, 85 m: MHCH 2142 (SL 312)$^{\text{16S, COI}}$, SMF 89702 (SL 316)$^{\text{16S}}$; road from Chiriquí Grande to Almirante: km 13.5, 9.0019°N, 82.2639°W, 54 m: MHCH 2136 (SL 329), SMF 89675 (SL 319)$^{\text{16S, COI}}$, 89676–8 (SL 326–8).

Norops cupreus.— COSTA RICA: Alajuela: San Miguel de Turrucares, 9.9446°N, 84.3223°W, 550 m: SMF 93897 (GK 2301)$^{\text{16S, COI}}$; Puntarenas: Quebrada Ganado, 9.7272°N, 84.6263°W, 60 m: SMF xxxxx (GK 2235)$^{\text{16S, COI}}$; Puente Río Tarcoles, 9.8021°N, 84.6065°W, 45 m: SMF 93873 (GK 2233)$^{\text{16S, COI}}$.

Norops datzorum.— PANAMA: Bocas del Toro: Sendero El Pianista, 8.8467°N, 82.4244°W, 1656 m: SMF 86380 (MHCH 479); Chiriquí: PILA, near Estacion de Guardaparques Las Nubes, 1800 m, 8.894°N, 82.615°W, 1800 m: SMF 86642 (MHCH 064); PILA, near Estacion de Guardaparques Las Nubes, Sendero La Cascada, 2400 m, 8.894°N, 82.615°W, 2400 m: MHCH 065; RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1752 m: SMF 89704 (SL 345); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1739 m: MHCH 2150 (SL 572)$^{\text{COI}}$; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1830 m: SMF 90102 (SL 451); Comarca Ngöbe-Buglé: SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge: elfin forest, 8.5642°N, 81.8221°W, 2033 m: SMF 91456 (SL 667); W slope Cerro Santiago, La Nevera: camp on road, 8.4997°N, 81.7724°W, 1699 m: SMF 89460 (SL 250)$^{\text{COI}}$; La Nevera, 8.5°N, 81.7722°W, 1600 m: SMF 85067 (GK 1585), 85093 (GK 1581), 89114 (MHCH 611); W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1592 m: MHCH 2149 (SL 509); W slope Cerro Santiago, La Nevera: ascent creek, 8.4961°N, 81.7677°W, 1761 m: SMF 89461 (SL 252); W slope Cerro Santiago, La Nevera: elfin forest summit on continental divide, 8.4954°N, 81.7673°W, 1814 m: photo, SMF 90100–1 (SL 516–7); E slope Cerro Santiago: continental divide above Río Rey, 8.5082°N, 81.7162°W, 1649 m: SMF 89703 (SL 366)$^{\text{COI}}$.

Norops fortunensis.— PANAMA: Chiriquí: RFLF: Cerro Guayabo, 8.7548°N, 82.2534°W, 1200 m: SMF 90103 (JFB 33)$^{\text{16S, COI}}$; RFLF, Cable car, 8.718°N, 82.2284°W, 1074 m: SMF 86405 (MHCH 512), 86406 (MHCH 513)$^{\text{16S}}$, 86407 (MHCH 514)$^{\text{16S}}$, 86408 (MHCH 515).

Norops fungosus.— PANAMA: Chiriquí: Fortuna, STRI station, 8.7346°N, 82.2401°W, 1216 m: MVUP 2095; RFLF, Cable car, 8.718°N, 82.2284°W, 1074 m: SMF 86385 (MHCH 519); RFLF, Quebrada Arena, 8.7763°N, 82.208°W, 1030 m: MHCH 509.

Norops gaigei.— PANAMA: Chiriquí: road btw. La Pita and Chiriquí, 8.4038°N, 82.2955°W, 34 m: SMF 91916 (GK 3184)$^{\text{16S, COI}}$; road from Interamericana to Horconcitos, 8.3218°N, 82.1344°W, 70 m: SMF 91917 (GK 3201)$^{\text{COI}}$; Los Santos: near Playa Venao, 7.4351°N, 80.1913°W, 31 m: SMF 91918 (GK 3202)$^{\text{16S, COI}}$; Playita Resort, 7.4204°N, 80.18°W, 37 m: SMF 91906 (GK 3115)$^{\text{COI}}$, 91907 (GK 3116)$^{\text{16S, COI}}$; Panamá: Panama City, Metroplitan National Park, 8.9833°N, 79.5461°W, 45 m: SMF 85304 (SMF 85304)$^{\text{16S}}$; Panama City, Barrio San Miguelito, 9.0389°N, 79.5206°W, 80 m: SMF 85303 (SMF 85303)$^{\text{16S}}$; Veraguas: Los Valles: creek above ANAM station, 8.4486°N, 81.2008°W, 404 m: SMF 91530 (SL 628)$^{\text{16S, COI}}$; Finca La Providencia: forest patch, 7.8977°N, 81.0007°W, 56 m: SMF 91529 (SL 575)$^{\text{16S, COI}}$; Finca La Providencia: houses, 7.8973°N, 80.9865°W, 53 m: MHCH 2294 (SL 576)$^{\text{COI}}$; Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: photo; Finca La Providencia, near Ponuga, 7.8928°N, 80.9843°W, 30 m: SMF 91956 (GK 2506)$^{\text{COI}}$; San Francisco, 8.2533°N, 80.9709°W, 150 m: SMF 91961 (GK 2521)$^{\text{COI}}$.

Norops gruuo.— PANAMA: Comarca Ngöbe-Buglé: near the headwaters of Río San Felix, ca. 2 km N Escopeta Camp, 8.5333°N, 81.8333°W, 900 m: SMF 85416–9 (GK 1607–10); above Hato Chamí: creek next to road to Cerro Colorado, 8.4877°N, 81.7694°W, 1431 m: MHCH 2161 (SL 623), SMF 91461 (SL 624)$^{\text{16S, COI}}$; above Hato Chamí: creek next to road to Cerro Colorado, 8.4877°N, 81.7694°W, 1445 m: SMF 91462 (SL 621)$^{\text{16S, COI}}$, 91463 (SL 622); road to Cerro Colorado, above Hato Chamí: Camp, 8.4873°N, 81.7686°W, 1478 m: obs.; Buabidí alias Alto/Llano/Hato Tugrí: Laguna, 8.4855°N, 81.7285°W, 1313 m: MHCH 1315–18, 2159–60 (SL 357, 359), SMF 89710–11 (SL 356, 358), 89712 (SL 360)$^{\text{16S}}$; Buabidí alias Alto/Llano/Hato Tugrí: hilltop along way to Laguna, 8.482°N, 81.721°W, 1251 m: SMF 89709 (SL 355)$^{\text{16S, COI}}$; E slope Cerro Santiago: Quebrada Ardilla: camp, 8.4964°N, 81.7203°W, 1532 m: SMF 89713 (SL 368)$^{\text{16S, COI}}$; above Guayabito: entering forest, 8.5482°N, 81.485°W, 1496 m: SMF 91464 (SL 751)$^{\text{16S, COI}}$; Veraguas: Cerro Mariposa, 8.5142°N, 81.121°W, 900 m: SMF 89469 (LSt 23)$^{\text{16S, COI}}$; Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: MHCH 2162 (SL 761)$^{\text{16S, COI}}$, 2163 (SL 762)$^{\text{16S, COI}}$; PNSF: Cerro Mariposa, 8.5007°N, 81.1182°W, 1218 m: SMF 89470 (LSt 66); Cerro Mariposa, 8.5174°N, 81.1179°W, 856 m: SMF 89471 (LSt 88); PNSF: Cerro Mariposa: trail towards summit, 8.5001°N, 81.117°W, 1260 m: SMF 90104 (SL 484); Cerro Mariposa, 8.5144°N, 81.1169°W, 863 m: SMF 89468 (LSt 1)$^{\text{16S, COI}}$.

Norops humilis.— PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, ridge between Río Changena and Río Clarito, 8.9911°N, 82.6712°W, 1752 m: SMF 91474 (SL 687)$^{\text{16S, COI}}$; PILA: N slope Cerro Pando, upper limit of pasture above Río Clarito, 8.9921°N, 82.666°W, 1665 m: SMF 91473 (SL 693)$^{\text{16S, COI}}$; Sendero el Pianista, 8.8736°N, 82.4116°W, 1001 m: SMF 89276–7 (MHCH 435–6); Sendero el Pianista, 8.8815°N, 82.4019°W, 819 m: SMF 89278 (MHCH 437); road from Chiriquí Grande to Almirante: shortly after km 33, 9.1107°N, 82.2886°W, 38 m: MHCH 2172 (SL 296)$^{\text{16S, COI}}$; Chiriquí: Fortuna, 8.7264°N, 82.2614°W, 1100 m: SMF 85103–09 (GK 1436–42); Fortuna, Laguna, 8.7264°N, 82.2614°W, 1000 m: SMF 85101–2 (GK 1431, 1435); Fortuna, Trail from Finca to Dam site, 8.7318°N, 82.2567°W, 1075 m: SMF 85113–4 (GK 1525–6); RFLF: Cerro Guayabo, 8.7658°N, 82.2517°W, 1577 m: MHCH 2164 (JFB 36); RFLF: Cerro Guayabo, 8.7683°N, 82.2484°W, 1557 m: SMF 90107–8 (JFB 41–2); RFLF: Cerro Guayabo, 8.7746°N, 82.2395°W, 1701 m: SMF 90106 (JFB 39); RFLF near Lost&Found, 8.6746°N, 82.2196°W, 1250 m: photo by Konrad Mebert; RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: MHCH 2178 (SL 598); RFLF: near Lost & Found Ecohostel, 8.6746°N, 82.2186°W, 1331 m: SMF 89475 (NH 15); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, just below ridge, 8.6744°N, 82.2161°W, 1434 m: SMF 89477 (SL 146); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge, 8.674°N, 82.2154°W, 1455 m: obs.; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6746°N, 82.215°W, 1451 m: MHCH 2167 (NH 22); RFLF: near Lost & Found Ecohostel: "on/off-lake", 8.6751°N, 82.2143°W, 1350 m: SMF 91466 (SL 597)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel: "on/off-lake", 8.6751°N, 82.2143°W, 1377 m: MHCH 2177 (SL 592); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6746°N, 82.2143°W, 1430 m: SMF 89476 (NH 23); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: photo; RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: SMF 89478 (SL 161); SMF 89479 (SL 162); RFLF: near Río Hornito, 8.676°N, 82.2092°W, 1308 m: SMF xxxxx (AH 578); RFLF: Finca La Suiza, 8.6603°N, 82.209°W, 1221 m: MHCH 2169 (SL 159); RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1419 m: obs., photo; RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1420 m: MHCH 2173 (SL 452); RFLF: W slope Cerro Pata de Macho: traps, 8.674°N, 82.2022°W, 1520 m: SMF 90109 (SL 454); RFLF: W slope Cerro Pata de Macho: traps, 8.674°N, 82.2022°W, 1521 m: MHCH 2170 (SL 193); RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1657 m: SMF 89480 (SL 192); RFLF: W slope Cerro Pata de Macho: camp at "Río Perdido", 8.6719°N, 82.1997°W, 1421 m: MHCH 2171 (SL 270), 2176 (SL 569); Colón: Petaquilla, Distrito de Donoso, 8.8191°N, 80.658°W, 181 m:

photo by Victor Martinez; Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: MHCH 2175 (SL 492); SMF 90105 (SL 498)$^{\text{COI}}$; BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 739 m: MHCH 2179 (SL 645); BPPS: Willie Mazú: trail above camp, 8.7903°N, 82.1989°W, 681 m: SMF 91471 (SL 709)$^{\text{16S, COI}}$, 91472 (SL 710); BPPS: Willie Mazú: camp, 8.7901°N, 82.1973°W, 643 m: obs.; BPPS: Willie Mazú: houses, 8.7933°N, 82.1929°W, 510 m: MHCH 2180 (SL 649); nördlich Laguna Fortuna, Straße nach Chiriquí Grande, Celentine, 8.7858°N, 82.1881°W, 610 m: SMF 85110 (GK 1479); road to Cerro Colorado: along continental divide, 8.5061°N, 81.7785°W, 1569 m: SMF 89481 (SL 120)$^{\text{COI}}$; Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1216 m: SMF 91467 (SL 723), 91468 (SL 726)$^{\text{COI}}$; Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1230 m: photo, MHCH 2181–2 (SL 724–5); Hacha trail: Río Flor: tree bridge, 8.5184°N, 81.7783°W, 1254 m: obs.; Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 970 m: SMF 91469 (SL 738); Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: SMF 91470 (SL 735)$^{\text{COI}}$; Veraguas: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: photo; Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: obs.; PNSF: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: MHCH 2168 (SL 133), 2174 (SL 486), SMF 89474 (SL 136); PNSF: Cerro Mariposa, 8.5133°N, 81.1216°W, 910 m: SMF 89472 (LSt 22); Cerro Mariposa, 8.5102°N, 81.1202°W, 1018 m: MHCH 2165 (LSt 50); Cerro Mariposa, 8.5159°N, 81.1198°W, 879 m: MHCH 2166 (LSt 67); Cerro Mariposa, 8.5154°N, 81.1193°W, 909 m: SMF 89473 (LSt 53); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: MHCH 2183 (SL 764), SMF 91465 (SL 763); PNSF: Cerro Tute, 8.4881°N, 81.1098°W, 1100 m: SMF 89901 (AC 166); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: photo, SMF 89715 (SL 380)$^{\text{16S}}$; PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 800 m: SMF 89898–9 (AC 115, 213); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 850 m: SMF 89900 (AC 214); PNSF: Cerro Negro: ridge above camp: small clearing, 8.5756°N, 81.0976°W, 1083 m: SMF 89714 (SL 377); PNSF: Río Narices, 8.5702°N, 81.066°W, 441 m: SMF 89902 (AC 192).

Norops kemptoni.— COSTA RICA: Puntarenas: N of Buenos Aires, 9.2674°N, 83.2298°W, 1834 m: SMF 92547 (GK 2372)$^{\text{16S}}$; Las Tablas, 8.9474°N, 82.7412°W, 1830 m: SMF 92549 (GK 2544)$^{\text{16S}}$; Las Tablas, 8.9446°N, 82.7318°W, 1915 m: SMF 92548 (GK 2553)$^{\text{16S}}$; PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, tributary to Río Changena: above "upper" camp 1, 8.9474°N, 82.7098°W, 1970 m: SMF 91482 (SL 680)$^{\text{16S, COI}}$; PILA: N slope Cerro Pando, tributary to Río Changena: "upper" camp 1, on highest pasture, 8.9524°N, 82.7093°W, 1955 m: SMF 91481 (SL 676); PILA: N slope Cerro Pando, tributary to Río Changena: pasture, 8.9669°N, 82.7033°W, 1814 m: MHCH 2195 (SL 703), SMF 91483 (SL 702); PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1641 m: SMF 91479 (SL 699)$^{\text{16S}}$; PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1670 m: MHCH 2193 (SL 683); PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1677 m: MHCH 2194 (SL 684); PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1684 m: SMF 91480 (SL 685); PILA: N slope Cerro Pando, Río Clarito: "lower" camp 3, 9.0098°N, 82.664°W, 1268 m: SMF 91478 (SL 688)$^{\text{16S, COI}}$; Sendero el Pianista, 8.855°N, 82.4259°W, 1569 m: SMF 86369 (MHCH 478), 86402–3 (MHCH 474, 473); Sendero el Pianista, 8.8466°N, 82.4245°W, 1656 m: SMF 86404 (MHCH 471); Chiriquí: PILA: road to Jurutungo: crossing of Río Candela, 8.8995°N, 82.7388°W, 1704 m: photo; PILA: road to Jurutungo: pond and coffee plantation, 8.9021°N, 82.7378°W, 1782 m: photo, SMF 89485 (SL 219); PILA: road to Jurutungo: branch to the right, towards building at WP 86, 8.9067°N, 82.7259°W, 1891 m: photo, MHCH 2187 (SL 211), SMF 89484 (SL 210)$^{\text{16S}}$; PILA: Jurutungo: path to building at WP 86, 8.906°N, 82.7242°W, 1930 m: SMF 89720 (SL 428)$^{\text{16S}}$; PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1959 m: SMF 89483 (SL 209); PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1960 m: photo; PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1970 m: obs., photo; PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: photo; PILA: Jurutungo: W slope Cerro without name, 8.912°N, 82.7182°W, 1977 m: obs., photo; PILA: Jurutungo: W slope Cerro without name: entrance to ascent, 8.9111°N, 82.7159°W, 2018 m: MHCH 2190 (SL 438); PILA: Jurutungo: W slope Cerro without name: shortly after last clearing, 8.9114°N, 82.7129°W, 2068 m: photo; Cordillera de Talamanca, nahe Cerro Pelota, "WP sila", 8.8356°N, 82.6106°W, 1600 m: SMF 85413 (GK 1413); PNVB: Sendero Los Quetzales: creek below Refugio Las Rocas, 8.8477°N, 82.5231°W, 2268 m: SMF 89721 (SL 385)$^{\text{16S, COI}}$; Potrerillos Arriba: Finca Los Mameyes: Río Pedro, 8.7418°N, 82.5134°W, 1355 m: SMF 90112 (SL 467), 90113 (SL 468)$^{\text{16S}}$; Potrerillos Arriba: Finca Los Mameyes: Río Pedro: bridge, 8.7409°N, 82.5118°W, 1320 m: photo; Potrerillos Arriba: Finca Los Mameyes: Río Pedro, 8.7389°N, 82.5102°W, 1300 m: MHCH 2185–6 (JFB 21–2); PNVB: Bajo Mono: Sendero La Cascada: waterfall, 8.825°N, 82.5021°W, 1866 m: SMF 89716 (SL 400), 89717 (SL 401)$^{\text{16S}}$, 89718 (SL 402)$^{\text{16S, COI}}$; PNVB: Bajo Mono: Sendero La Cascada: waterfall, 8.825°N, 82.5021°W, 1876 m: MHCH 2191–2 (SL 462, 464); PNVB: Bajo Mono: Sendero La Cascada: camp, 8.8263°N, 82.4989°W, 1822 m: photo, MHCH 2188 (SL 398); PNVB: Bajo Mono: Sendero La Cascada: water-supply installation below Camp, 8.8273°N, 82.4964°W, 1778 m: photo, MHCH 2189 (SL 408), SMF 89719 (SL 409); Cerro Altrillería: Alto Jaramillo, 8.7769°N, 82.3889°W, 1991 m: SMF 90110 (JFB 63)$^{\text{16S, COI}}$, 90111 (JFB 70)$^{\text{16S, COI}}$; RFLF: Lost & Found Ecohostel, 8.6745°N, 82.2196°W, 1284 m: SMF 89464 (NH 30); RFLF near Lost&Found, 8.6746°N, 82.2196°W, 1250 m: photo by Konrad Mebert; RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: MHCH 2155 (SL 257), SMF 89462 (NH 10), 89705–6 (SL 349–50); RFLF: Lost & Found Ecohostel, 8.6745°N, 82.2193°W, 1283 m: MHCH 2153 (NH 37), SMF 89463 (NH 19); RFLF: near Lost & Found Ecohostel: trail to Río Hornito , 8.6739°N, 82.2185°W, 1320 m: photo; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2176°W, 1389 m: MHCH 2152 (NH 31); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, just below ridge, 8.6744°N, 82.2161°W, 1434 m: photo, MHCH 2158 (SL 588)$^{\text{16S, COI}}$, SMF 91458 (SL 590)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge, 8.674°N, 82.2154°W, 1455 m: photo; RFLF: near Lost & Found Ecohostel: "on/off-lake", 8.6751°N, 82.2143°W, 1340 m: photo; RFLF: near Lost & Found Ecohostel: "on/off-lake", 8.6751°N, 82.2143°W, 1377 m: photo, SMF 91457 (SL 589)$^{\text{16S, COI}}$; RFLF: W slope Cerro Pata de Macho: upper limit of bamboo ridge, 8.6755°N, 82.2057°W, 1419 m: MHCH 2156 (SL 264); RFLF: W slope Cerro Pata de Macho, 8.6745°N, 82.2049°W, 1423 m: SMF 89465 (NH 47); RFLF: W slope Cerro Pata de Macho, 8.6761°N, 82.2006°W, 1657 m: MHCH 2151 (JFB 08); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1752 m: MHCH 2154 (SL 190)$^{\text{16S, COI}}$, 2157 (SL 346), SMF 89466 (SL 198), 89707–8 (SL 347–8).

Norops lemurinus.— PANAMA: Bocas del Toro: HIISSPS: Río Negro: flooded forest on N bank, 9.5048°N, 82.5247°W, 8 m: SMF 90115 (SL 555); SMF 90114 (SL 552)$^{\text{COI}}$, MHCH 2197 (SL 553); Chiriquí grande, 8.951°N, 82.121°W, 3 m: photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: SMF 91486 (SL 736)$^{\text{COI}}$; Veraguas: Cerro Mariposa, 8.5146°N, 81.117°W, 855 m: MHCH 2196 (LSt 31); Cerro Mariposa, 8.5146°N, 81.1169°W, 846 m: SMF 89486 (LSt 25)$^{\text{COI}}$; PNSF: Cerro Narices, 8.5631°N, 81.0532°W, 700 m: SMF 89903 (AC 173); PNSF: Cerro Narices, 8.5598°N, 81.0457°W, 530 m: SMF 89904–5 (AC 179, 181); Minas de Cocuyo, Calovebora, Veragua, 8.75°N, 81°W, 195 m: MVUP 292.

Norops limifrons.— COSTA RICA: Limón: Cantón Talamanca, between Río Sixaola and Caribbean coast, near Panamanian border, 9.6476°N, 82.7818°W, 20 m: SMF xxxxx (JJK 025)$^{\text{16S}}$; Cantón Talamanca, between Río Sixaola and Caribbean coast, near Panamanian border, 9.5671°N, 82.703°W, 24 m: SMF xxxxx (JJK 037)$^{\text{16S}}$; Cantón Talamanca, between Río Sixaola and Caribbean coast, near Panamanian border, 9.6181°N, 82.6529°W, 23 m: SMF xxxxx (JJK 041)$^{\text{16S}}$; PANAMA: Bocas del Toro: HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: SMF 90119 (SL 550); HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: MHCH 2207 (SL 537), SMF 90117–8 (SL 535–6)$^{\text{both COI}}$; road from Chiriquí Grande to Almirante: km 13, 9.0011°N, 82.2592°W, 23 m: MHCH 2200–3 (SL 283, 284, 286, 287), SMF 89724 (SL 282)$^{\text{16S}}$, 89725 (SL 285); road from divide to caribbean coast, near Chiriquí Grande, 8.8998°N, 82.1837°W, 72 m: MHCH 2199 (SL 255), SMF 89723 (SL 256)$^{\text{16S}}$; Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: SMF 91487 (SL 587)$^{\text{COI}}$; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1050 m: MHCH 2206 (SL 499), SMF 90116 (SL 493); BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 730 m: SMF 91494 (SL 642)$^{\text{COI}}$; BPPS: Willie Mazú: camp, 8.7901°N, 82.1973°W, 643 m: MHCH 2210 (SL 705); Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1216 m: photo, MHCH 2211–2 (SL 720–1), SMF 91490–1 (SL 719, 722); Hacha trail: confluence of Río Marabí and Río Flor, 8.5224°N, 81.7783°W, 1197 m: obs.; Hacha trail: Río Flor: tree bridge, 8.5184°N, 81.7783°W, 1254 m: photo; Hacha trail: Hacha, 8.5362°N, 81.7739°W, 1125 m: obs.; Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: MHCH 2213 (SL 731)^{COI}, 2214 (SL 732), SMF 91492–3 (SL 733–4); above El Paredón: valley of Río Rasca: clearing with lookout, 8.4829°N, 81.178°W, 719 m: obs.; above El Paredón: valley of Río Rasca, 8.4851°N, 81.1727°W, 788 m: photo; above El Paredón: valley of Río Rasca, 8.4865°N, 81.1721°W, 776 m: MHCH 2208 (SL 631)^{COI}; above El Paredón: valley of Río Rasca, 8.4865°N, 81.1721°W, 779 m: SMF 91488–9 (SL 629–30); above El Paredón: valley of Río Rasca, 8.4878°N, 81.1712°W, 788 m: MHCH 2209 (SL 632); PNSF: Cerro Mariposa, 8.5256°N, 81.1321°W, 666 m: SMF 89488 (LSt 108); Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: photo; Cerro Mariposa, 8.5117°N, 81.1199°W, 996 m: SMF 89487 (LSt 13); Cerro Mariposa: Alto de Piedra, Restaurante, 8.5145°N, 81.1177°W, 850 m: MHCH 2205 (SL 485); Cerro Mariposa, 8.5134°N, 81.1166°W, 878 m: MHCH 2198 (LSt 47); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 690 m: SMF 89909–10 (AC 128, 183); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: photo, SMF 89489 (SL 230), 89490 (SL 231)^{COI}; PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 750 m: SMF 89908 (AC 86); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 800 m: SMF 89907 (AC 83); PNSF: Cerro Negro: ridge above camp: small clearing, 8.5756°N, 81.0976°W, 1083 m: MHCH 2204 (SL 378); PNSF: Cerro Negro: creek above camp, 8.5702°N, 81.0963°W, 774 m: SMF 89722 (SL 372);PNSF: Río Narices, 8.5628°N, 81.0628°W, 460 m: SMF 89911 (AC 185); PNSF: Cerro Narices, 8.5631°N, 81.0532°W, 700 m: SMF 89906 (AC 172); PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: photo, SMF 89491 (SL 167).

Norops lionotus.— PANAMA: Chiriquí: Reserva Forestal la Fortuna, Quebrada Arena, 8.7774°N, 82.2088°W, 1027 m: SMF 86387 (MHCH 505); Colón: Petaquilla, Distrito de Donoso, 8.8191°N, 80.658°W, 181 m: photo by Victor Martinez; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: SMF 91495 (SL 601)^{COI}; BPPS: Willie Mazú: creek, 8.7891°N, 82.1994°W, 724 m: SMF 91498 (SL 707); BPPS: Willie Mazú: camp, 8.7901°N, 82.1973°W, 643 m: MHCH 2219 (SL 648)^{COI}; Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 970 m: MHCH 2220 (SL 741); Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: SMF 91496 (SL 728)^{COI}; Hacha trail: Río Hacha: camp at creek, 8.5503°N, 81.7638°W, 986 m: SMF 91497 (SL 729)^{COI}; Veraguas: PNSF: Cerro Mariposa: I Brazo Mulaba, 8.5186°N, 81.1332°W, 662 m: SMF 89914–15 (AC 19, 22); PNSF: Cerro Mariposa: I Brazo Mulaba, 8.5269°N, 81.1305°W, 618 m: SMF 89913 (AC 17); Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: photo, MHCH 2221 (SL 767)^{COI}, SMF 89494 (SL 134); PNSF: Cerro Mariposa, 8.5124°N, 81.1216°W, 882 m: SMF 89493 (LSt 75); PNSF: Cerro Mariposa, 8.5133°N, 81.1215°W, 937 m: MHCH 2216 (LSt 72); PNSF: Cerro Mariposa, 8.5138°N, 81.1213°W, 935 m: SMF 89492 (LSt 21); Cerro Mariposa: creek above water supply, 8.5082°N, 81.121°W, 891 m: photo; Cerro Mariposa: creek above water supply, 8.5082°N, 81.121°W, 899 m: photo, MHCH 2222 (SL 768); Cerro Mariposa, 8.5142°N, 81.121°W, 900 m: MHCH 2215 (LSt 24); Alto de Piedra, 8.5161°N, 81.1185°W, 864 m: photo by Konrad Mebert; PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: MHCH 2218 (SL 376), SMF 89726 (SL 371)^{COI}, 89912 (AC 33), 90034 (AC 205); PNSF: Río Narices, 8.5628°N, 81.0628°W, 480 m: SMF 89916 (AC 195); PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: MHCH 2217 (SL 166), SMF 89495 (SL 171).

Norops magnaphallus.— PANAMA: Chiriquí: PNVB: Sendero Los Quetzales: Refugio Las Rocas, 8.848°N, 82.5196°W, 2366 m: SMF 89734 (SL 386)$^{16S, COI}$, 89735 (SL 387); PNVB: Sendero Los Quetzales: Refugio Las Rocas, 8.848°N, 82.5196°W, 2412 m: SMF 89736 (SL 388); PNVB: Sendero Los Quetzales: Quebrada El Silencio, 8.8491°N, 82.5162°W, 2114 m: SMF 90126 (JFB 32)^{16S}; PNVB: Sendero Los Quetzales: Quebrada El Silencio, Refugio, 8.8494°N, 82.5154°W, 2130 m: MHCH 2229–30 (SL 390–3), SMF 89731–2 (SL 391–2), 89733 (SL 394)^{16S}; PNVB: road to summit of Volcán Barú: area de acampar Mamecillos, 8.7909°N, 82.5142°W, 2580 m: SMF 90130 (JFB 50); PNVB: road to summit of Volcán Barú: area de acampar Mamecillos, 8.8015°N, 82.513°W, 2581 m: SMF 90131 (SL 508)^{16S}; PNVB: road to summit of Volcán Barú: just below "Las Zarzamora", 8.7972°N, 82.5068°W, 2326 m: SMF 90132 (SL 505)^{16S}; PNVB: Bajo Mono: Sendero La Cascada: waterfall, 8.825°N, 82.5021°W, 1866 m: SMF 89728 (SL 403); PNVB: Bajo Mono: Sendero La Cascada: waterfall, 8.825°N, 82.5021°W, 1876 m: obs., photo; PNVB: Bajo Mono: Sendero La Cascada, 8.8257°N, 82.5005°W, 1880 m: SMF 90128 (JFB 17)^{16S}; PNVB: Bajo Mono: Sendero La Cascada, 8.8257°N, 82.5001°W, 1840 m: MHCH 2224 (JFB 19)^{16S}, SMF 90127 (JFB 15); PNVB: Bajo Mono: Sendero La Cascada, 8.8262°N, 82.499°W, 1825 m: SMF 90129 (JFB 18); PNVB: Bajo Mono: Sendero La Cascada, 8.8262°N, 82.499°W, 1830 m: MHCH 2223 (JFB 16); PNVB: Bajo Mono: Sendero La Cascada, 8.8262°N, 82.499°W, 1831 m: MHCH 2225 (JFB 20); PNVB: Bajo Mono: Sendero La Cascada: camp, 8.8263°N, 82.4989°W, 1822 m: photo, MHCH 2231 (SL 396), SMF 89727 (SL 397)^{16S}; PNVB: Bajo Mono: Sendero La Cascada: water-supply installation below Camp, 8.8273°N, 82.4964°W, 1778 m: photo, MHCH 2233 (SL 406), SMF 89729–30 (SL 405, SL 407); PNVB: Bajo Mono: Sendero La Cascada: water-supply installation below Camp, 8.8273°N, 82.4964°W, 1804 m: MHCH 2232 (SL 404); Boquete, Volcancito, 8.7841°N, 82.4748°W, 1569 m: SMF 89262 (MHCH 416); Cerro Altrillería: Alto Jaramillo, 8.7755°N, 82.3903°W, 1930 m: MHCH 2228 (JFB 77); Cerro Altrillería: Alto Jaramillo, 8.7757°N, 82.3901°W, 1952 m: MHCH 2226–7 (JFB 75–6), SMF 90124 (JFB 74)^{16S}; Cerro Altrillería: Alto Jaramillo, 8.7766°N, 82.3901°W, 1966 m: SMF 90121–2 (JFB 71–2); Cerro Altrillería: Alto Jaramillo, 8.7761°N, 82.39°W, 1964 m: SMF 90123 (JFB 73)^{16S}; Cerro Altrillería: Alto Jaramillo, 8.7759°N, 82.3888°W, 2050 m: SMF 90125 (JFB 78)$^{16S, COI}$.

Norops monteverde.— COSTA RICA: Guanacaste: road from Santa Elena to Reserva Santa Elena , 10.3414°N, 84.805°W, 1560 m: SMF 85541 (GK 1744)^{16S}; road from Santa Elena to Reserva Santa Elena , 10.3317°N, 84.7794°W, 1575 m: SMF 85540 (GK 1732)^{16S}.

Norops oxylophus.— PANAMA: Bocas del Toro: HIISSPS: Río Negro: flooded forest on N bank, 9.508°N, 82.5289°W, 13 m: SMF 90120 (SL 559)^{COI}.

Norops pachypus.— COSTA RICA: Puntarenas: Las Tablas, 8.9474°N, 82.7412°W, 1830 m: SMF 93577 (GK 2545)$^{16S, COI}$; San José: Road from San Isidro de El General to Cerro de la Muerte, 9.5057°N, 83.7085°W, 2320 m: SMF xxxxx (GK 2356)$^{16S, COI}$; PANAMA: Chiriquí: Nacimiento Quebrada Chevo, 8.8743°N, 82.7421°W, 1615 m: SMF 85443–4 (GK 1662–3); PILA: road to Jurutungo: pond and coffee plantation, 8.9021°N, 82.7378°W, 1782 m: photo; Cordillera de Talamanca, Cerro Jurutungo, 8.9008°N, 82.7374°W, 1890 m: SMF 85269–70 (GK 1312–3); PILA: road to Jurutungo: upper limit of large clearing, 8.9063°N, 82.7357°W, 1834 m: photo; PILA: road to Jurutungo: branch to the right, 8.9055°N, 82.7289°W, 1827 m: obs.; PILA: road to Jurutungo: branch to the right, towards building at WP 86, 8.9067°N, 82.7259°W, 1891 m: photo, MHCH 2252 (SL 524)^{16S}, 2253 (SL 525)$^{16S, COI}$, SMF 89504 (SL 212), 89739 (SL 423)^{16S}, 89740 (SL 427); PILA: Jurutungo: path to building at WP 86, 8.906°N, 82.7242°W, 1930 m: MHCH 2248 (SL 424); PILA: Jurutungo: S slope Cerro Pando, 8.9149°N, 82.7234°W, 2170 m: photo; PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: obs., photo; Jurutungo, 8.9106°N, 82.7231°W, 1950 m: SMF 85279–84 (GK 1356–8, 1360–3); PILA: Jurutungo: building under construction, 8.9069°N, 82.7229°W, 1954 m: MHCH 2249–50 (SL 425–6); Jurutungo, 8.9085°N, 82.7229°W, 1860 m: SMF 85285–6 (GK 1364–5); PILA: Jurutungo: ascent towards border trail on divide: shortly after sign "Limite del Parque", 8.9167°N, 82.7184°W, 2129 m: SMF 89741 (SL 436); PILA: Jurutungo: W slope Cerro without name, 8.912°N, 82.7182°W, 1977 m: MHCH 2251 (SL 439), SMF 89502 (SL 201)$^{16S, COI}$, 89743 (SL 440); Jurutungo, 8.9083°N, 82.7168°W, 2055 m: SMF 85278 (GK 1355); PILA: Jurutungo: W slope Cerro without name: entrance to ascent, 8.9111°N, 82.7159°W, 2018 m: MHCH 2247 (SL 205), SMF 89503 (SL 204), 89742 (SL 437); Jurutungo, 8.9108°N, 82.7147°W, 2060 m: SMF 85271 (GK 1319), 85274 (GK 1335); Cordillera (pueblo), 4 km SSE El Hato del Volcan, 8.7383°N, 82.6211°W, 1160 m: SMF 89363 (MHCH 1025); PILA: Las Nubes, 8.8986°N, 82.6195°W, 2351 m: SMF 90137 (JFB 51)^{16S}; PILA: Las Nubes, 8.8969°N, 82.6187°W, 2358 m: MHCH 2242 (JFB 52); PILA: Las Nubes, 8.8915°N, 82.6174°W, 2259 m: MHCH 2244 (JFB 56)$^{16S, COI}$; PILA: Las Nubes, 8.8961°N, 82.617°W, 2304 m: MHCH 2243 (JFB 54); PILA: Las Nubes, 8.8961°N, 82.617°W, 2305 m: SMF 90138 (JFB 53);

Cordillera de Talamanca, Parque Internacional La Amistad, Sendero Retoño, 8.8917°N, 82.6167°W, 2130 m: SMF 85262–3 (GK 1238–9); PILA: Las Nubes, 8.8926°N, 82.6163°W, 2252 m: SMF 90139 (JFB 57); PILA: Las Nubes, 8.8936°N, 82.6158°W, 2229 m: SMF 90140 (JFB 58); PILA: Las Nubes, 8.8942°N, 82.6149°W, 2117 m: MHCH 2245–6 (JFB 60–1), SMF 90141 (JFB 59)$^{16S, COI}$, 90142 (JFB 62); Cordillera de Talamanca, Cerro la Pelota, 8.8308°N, 82.6138°W, 1255 m: SMF 85294–5 (GK 1428–9); Cordillera de Talamanca, nahe Cerro Pelota, "WP sila", 8.8356°N, 82.6106°W, 1600 m: SMF 85288 (GK 1410), 85289–93 (GK 1411–2, 1423–5); PNVB, Aguacatal, 8.803°N, 82.5849°W, 2012 m: SMF 89269–73 (MHCH 378–9, 384, 398); PNVB, Aguacatal, 8.8017°N, 82.5844°W, 1971 m: SMF 89264–68 (MHCH 371–75); Cerro Punta, Finca ("Reserva Forestal") La Tatica, Senior Rios, 8.8778°N, 82.5835°W, 2000 m: SMF 89358–9 (MHCH 1005, 1004), 89361–2 (MHCH 1002–3), 89364–5 (MHCH 1007–8); Hotel Los Quetzales, Cerro Punta, 8.8667°N, 82.5833°W, 1880 m: SMF 89263 (MHCH 579); PNVB: Sendero Los Quetzales: Alto Respingo, 8.8411°N, 82.5346°W, 2553 m: MHCH 2241 (JFB 29), SMF 90143–4 (JFB 26–7)$^{both\ 16S, COI}$, 90145 (JFB 28)^{16S}; PNVB: Sendero Los Quetzales: Alto Respingo, 8.8416°N, 82.5345°W, 2552 m: SMF 90146 (JFB 30); PNVB: Sendero Los Quetzales: Alto Respingo, 8.8418°N, 82.5345°W, 2544 m: SMF 90147 (JFB 31)^{16S}; "westliches Panama": SMF 84950–1.

Norops pentaprion.— PANAMA: Bocas del Toro: HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: photo, SMF 90150–1 (SL 547–8); HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: MHCH 2254 (SL 564); Colón: Petaquilla, Distrito de Donoso, 8.8191°N, 80.658°W, 181 m: photo by Victor Martinez; Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Norops polylepis.— PANAMA: Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85204–10 (GK 1272, 1278–80, 1298–1300); Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1125 m: SMF 89749 (SL 416)$^{16S, COI}$; Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1160 m: MHCH 2262 (SL 413); Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1200 m: MHCH 2263–4 (SL 480–1); Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1209 m: MHCH 2266 (SL 617), SMF 91511 (SL 616); Quebrada Chevo, 8.8421°N, 82.7711°W, 1170 m: SMF 85441 (GK 1658); Hacienda Café de Eleta: creek, 8.8716°N, 82.771°W, 1380 m: MHCH 2257–9 (SL 150, 155); Hacienda Café de Eleta: creek, 8.8716°N, 82.771°W, 1380 m: SMF 89509–12 (SL 151–4); Hacienda Café de Eleta: citrus plantation between utility shed and Río Candela, 8.8829°N, 82.7595°W, 1464 m: obs., photo; Nacimiento Quebrada Chevo, 8.8743°N, 82.7421°W, 1615 m: SMF 85442 (GK 1664); Volante: camp, 8.587°N, 82.6683°W, 481 m: photo, MHCH 2259 (SL 225), SMF 89514 (SL 226); Cordillera (pueblo), 4 km SSE El Hato del Volcan, 8.7383°N, 82.6211°W, 1160 m: SMF xxxxx (MHCH 1022, 1024); Potrerillos Arriba: Finca Los Mameyes: pasture above Río Pedro, 8.7386°N, 82.514°W, 1350 m: obs., photo; Potrerillos Arriba: Finca Los Mameyes: pasture above Río Pedro, 8.7386°N, 82.514°W, 1362 m: SMF 90152 (SL 472); Potrerillos Arriba: Finca Los Mameyes: Río Pedro, 8.7376°N, 82.513°W, 1319 m: SMF 90153 (JFB 23)^{16S}; Potrerillos Arriba: Finca Los Mameyes: Río Pedro, 8.7376°N, 82.513°W, 1367 m: MHCH 2256 (JFB 24); Cabecera de Cochea: crossing Río Cochea, 8.7255°N, 82.4931°W, 1090 m: photo, MHCH 2261 (SL 274); Cabecera de Cochea: Rancho de Rodrigo, 8.7266°N, 82.4915°W, 1174 m: MHCH 2260 (SL 272), SMF 89747–8 (SL 273, 278); Boquete, Volcancito, 8.7841°N, 82.4748°W, 1569 m: SMF 86383 (MHCH 417); Los Algarrobos: near Río Majagua, 8.4846°N, 82.4342°W, 109 m: MHCH 2255 (JFB 14)^{COI}; Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: MHCH 2265 (SL 503), SMF 89513 (SL 173); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: obs.; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: photo by Meike Piepenbring, SMF 91510 (SL 586)$^{16S, COI}$; Los Algarrobos: old railway bridge over Río Majagua, 8.4809°N, 82.428°W, 88 m: photo; Sendero el Pianista, 8.8083°N, 82.4277°W, 1332 m: SMF 86384 (MHCH 485).

Norops pseudokemptoni.— PANAMA: Comarca Ngöbe-Buglé: SE slope Cerro Saguí: Alto Cedro: Quebrada Juglí above camp, 8.5576°N, 81.8262°W, 1708 m: MHCH 2268 (SL 661)^{16S}; SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge: elfin forest, 8.5642°N, 81.8221°W, 2013 m: SMF 91516 (SL 672)^{16S}; SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1925 m: MHCH 2269 (SL 674); SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1959 m: SMF 91515 (SL 673)$^{16S, COI}$; SE slope Cerro Saguí above Quebrada Juglí: clearing with grass, creek, 8.5613°N, 81.8214°W, 1874 m: photo; road to Cerro Colorado: Terminal de Hacha, 8.511°N, 81.7882°W, 1393 m: SMF 91519 (SL 748)$^{16S, COI}$; Hacha trail: Río Marabí, 8.5192°N, 81.7831°W, 1256 m: obs.; Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1216 m: MHCH 2270–1 (SL 715, 718), SMF 91517–8 (SL 716–7)$^{both\ 16S, COI}$; Hacha trail: Río Flor: camp at bridge, 8.5209°N, 81.7785°W, 1230 m: obs.; Hacha trail: confluence of Río Marabí and Río Flor, 8.5224°N, 81.7783°W, 1197 m: obs.; Hacha trail: Río Flor: tree bridge, 8.5184°N, 81.7783°W, 1254 m: photo; Hacha trail: Hacha, 8.5362°N, 81.7739°W, 1130 m: photo, MHCH 2272 (SL 743), SMF 91512–3 (SL 744–5), 91514 (SL 746)$^{16S, COI}$; La Nevera, 8.5°N, 81.7722°W, 1600 m: SMF 85420–1 (GK 1578, 1580); La Nevera, along dirt road, 8.5°N, 81.7722°W, 1630 m: SMF 85422 (GK 1606); W slope Cerro Santiago, La Nevera: small summit just above camp, 8.5009°N, 81.7685°W, 1644 m: MHCH 2267 (SL 513), SMF 89515 (SL 246)^{16S}, 90154 (SL 514)^{16S}; W slope Cerro Santiago, La Nevera: ascent creek, 8.4961°N, 81.7677°W, 1730 m: SMF 90156 (SL 519); W slope Cerro Santiago, La Nevera: elfin forest summit on continental divide, 8.4954°N, 81.7673°W, 1814 m: SMF 90155 (SL 518); E slope Cerro Santiago: secondary vegetation above Río Rey, 8.5064°N, 81.7186°W, 1564 m: MHCH 1335; E slope Cerro Santiago: continental divide above Río Rey, 8.5082°N, 81.7162°W, 1660 m: SMF 89750 (SL 367).

Norops pseudopachypus.— PANAMA: Chiriquí: RFLF: Cerro Guayabo, 8.7683°N, 82.2484°W, 1559 m: SMF 90161 (JFB 40)$^{16S, COI}$; RFLF: Cerro Guayabo, 8.7751°N, 82.2398°W, 1785 m: SMF 90159 (JFB 37), 90160 (JFB 38)$^{16S, COI}$; RFLF: W slope Cerro Pata de Macho, 8.6761°N, 82.2006°W, 1625 m: SMF 90166 (JFB 09); RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1652 m: photo; RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1657 m: MHCH 2280 (SL 269), SMF 89525 (SL 195); RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1700 m: obs.; RFLF: W slope Cerro Pata de Macho, 8.6776°N, 82.1981°W, 1732 m: MHCH 2275 (JFB 11); RFLF: W slope Cerro Pata de Macho, 8.6776°N, 82.1981°W, 1760 m: MHCH 2274 (JFB 10)$^{16S, COI}$; RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1750 m: SMF 89753 (SL 268); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1752 m: MHCH 2279 (SL 189), SMF 89524 (SL 191); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1732 m: photo; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1736 m: SMF 89523 (SL 186); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1739 m: MHCH 2285 (SL 571); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1740 m: photo; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1748 m: photo; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1750 m: photo; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1754 m: photo; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1764 m: MHCH 2284 (SL 570); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1776 m: MHCH 2273 (JFB 06)^{16S}; RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1800 m: SMF 89526 (SL 196), 89754 (SL 351); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1810 m: SMF 90165 (JFB 05); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1830 m: SMF 90164 (JFB 04); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1850 m: SMF 90163 (JFB 03); RFLF: W slope Cerro Pata de Macho, 8.6793°N, 82.193°W, 1860 m: SMF 90162 (JFB 02)$^{16S, COI}$; Comarca Ngöbe-Buglé: SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge: elfin forest, 8.5642°N, 81.8221°W, 2033 m: SMF 91522 (SL 670)$^{16S, COI}$; SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1925 m: photo, MHCH 2286 (SL 671); SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1942 m: SMF 91520 (SL 668)$^{16S, COI}$; SE slope Cerro Saguí above Quebrada Juglí: cloud forest ridge, 8.5636°N, 81.8217°W, 1981 m: SMF 91521 (SL 669); W slope Cerro Santiago, La Nevera: camp on road, 8.4997°N, 81.7724°W, 1699 m: MHCH 2276–8 (SL 117–9), SMF 89516 (SL 114)$^{16S, COI}$, 89517–8 (SL 115–6); "Cerro Nevera" = W slope Cerro Santiago, La Nevera, 8.5°N, 81.7722°W, 1600 m: SMF 85153–63 (GK 1579, 1583–4, 1586, 1612–8), 85296–7 (GK 1582, 1611); W slope Cerro Santiago, La Nevera: confluence of intermittent creeks, 8.4996°N, 81.77°W, 1638 m: photo; W slope Cerro Santiago, La Nevera: confluence of intermittent creeks, 8.4996°N, 81.77°W, 1650 m: obs.; W slope Cerro Santiago, La Nevera: camp, 8.5011°N, 81.7694°W, 1580 m: obs., photo; W slope Cerro Santiago, La Nevera: first confluence of creeks below camp, 8.5018°N, 81.7689°W, 1555 m: photo, SMF 89519–21 (SL 237–9); W slope Cerro Santiago, La Nevera: small summit just above camp, 8.5009°N, 81.7685°W, 1644 m: obs.; W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1583 m: MHCH 2282 (SL 510); W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1590 m: photo; W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1602 m: photo; W slope Cerro Santiago, La Nevera: ascent creek, 8.4989°N, 81.7682°W, 1607 m: MHCH 2283 (SL 511); W slope Cerro Santiago, La Nevera: second confluence of creeks below camp, 8.5032°N, 81.7675°W, 1533 m: photo; W slope Cerro Santiago, La Nevera: elfin forest summit on continental divide, 8.4954°N, 81.7673°W, 1814 m: SMF 89522 (SL 251), SMF 90157 (SL 520)$^{\text{16S, COI}}$, 90158 (SL 523); E slope Cerro Santiago: Quebrada Ardilla, 8.4968°N, 81.7221°W, 1577 m: MHCH 2281 (SL 364), SMF 89751 (SL 363)$^{\text{16S, COI}}$, 89752 (SL 365).

Norops salvini.— COSTA RICA: Puntarenas: Las Tablas, 8.9471°N, 82.739°W, 1860 m: SMF 92510 (GK 2546); PANAMA: Chiriquí: PILA: Jurutungo: path to building at WP 86, 8.906°N, 82.7242°W, 1903 m: SMF 89755 (SL 430); PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: photo, MHCH 2290–1 (SL 441–2), SMF 89757–8 (SL 432, 443); PILA: Jurutungo: building under construction, 8.9069°N, 82.7229°W, 1954 m: SMF 89756 (SL 431)$^{\text{16S}}$; Jurutungo, 8.9085°N, 82.7229°W, 1860 m: SMF 85451–2 (GK 1368–9); PILA: Jurutungo: W slope Cerro without name, 8.912°N, 82.7182°W, 1977 m: SMF 89527 (SL 208); Cerro Totuma, 8.8844°N, 82.6856°W, 1931 m: photo by Jeffrey Dietrich; Cordillera de Talamanca, Cerro Pelota, "WP pelota", 8.8308°N, 82.6139°W, 1580 m: SMF 85453–7 (GK 1405–9, 1645); Cerro Altrillería: Alto Jaramillo, 8.7769°N, 82.3889°W, 1991 m: MHCH 2287–9 (JFB 64, 67–8), SMF 90167–8 (JFB 65–6); Cerro Altrillería: Alto Jaramillo, 8.7759°N, 82.3888°W, 2050 m: SMF 90169 (JFB 69)$^{\text{16S}}$; Comarca Ngöbe-Buglé: SE slope Cerro Saguí: Alto Cedro: Quebrada Juglí above camp, 8.5576°N, 81.8262°W, 1708 m: MHCH 2293 (SL 662)$^{\text{COI}}$, SMF 91527–8 (SL 663–4); SE slope Cerro Saguí: Alto Cedro: camp at Quebrada Juglí, 8.5561°N, 81.8252°W, 1700 m: SMF 91526 (SL 657)$^{\text{16S, COI}}$; SE slope Cerro Saguí above Ratón: camp on pasture, 8.546°N, 81.8225°W, 1643 m: SMF 91525 (SL 656)$^{\text{16S}}$; SE slope Cerro Saguí above Ratón: corn plantation, 8.5466°N, 81.8216°W, 1680 m: photo, MHCH 2292 (SL 654), SMF 91523–4 (SL 653, 655).

Norops sp.— PANAMA: Chiriquí: PILA: Jurutungo: W slope Cerro without name: branch to first waterfall, 8.9116°N, 82.7105°W, 2150 m: photo; PILA: Jurutungo: W slope Cerro without name: ascent to summit, 8.9139°N, 82.7086°W, 2403 m: obs.

Norops tenorioensis.— COSTA RICA: Alajuela: Volcan Tenorio, 10.7052°N, 85.0307°W, 1160 m: SMF 91985 (GK 3324)$^{\text{16S}}$; 91987 (GK 3326)$^{\text{16S}}$.

Norops tropidogaster.— PANAMA: Darién: Caserete-Chepigana, 8.1186°N, 77.878°W, 34 m: MHCH 1634$^{\text{16S}}$.

Norops tropidolepis.— COSTA RICA: Alajuela: near Tapesco, 10.2328°N, 84.4263°W, 1460 m: SMF 93605–6 (GK 2219–20)$^{\text{both COI}}$; Road to Volcan Poas, 10.1638°N, 84.2268°W, 2370 m: SMF 93652 (GK 2442)$^{\text{16S}}$; Cartago: Southern slope of Volcan Irazu, 9.8969°N, 83.8795°W, 1875 m: SMF 93664 (GK 2523)$^{\text{COI}}$, 93667 (GK 2529)$^{\text{16S, COI}}$; Guanacaste: Monteverde, road from Santa Elena to Santa Elena Biological Reserva, 10.3317°N, 84.8128°W, 1557 m: SMF 85533 (GK 1734)$^{\text{16S, COI}}$; Heredia: Volcan Barva, Los Angeles de Paso Llano, 10.1077°N, 84.1033°W, 2260 m: SMF 93643 (GK 2425)$^{\text{COI}}$; Cerro Chompipe, 10.0978°N, 84.0729°W, 2613 m: SMF 93668 (GK 2612)$^{\text{COI}}$; San José: road (CR 226) from Santa Maria de Dota to Interamericana, 9.7206°N, 83.9603°W, 2300 m: SMF 93634 (GK 2400)$^{\text{16S, COI}}$; Road between Copey and Providencia, 9.6154°N, 83.908°W, 2370 m: SMF 93637 (GK 2410)$^{\text{COI}}$.

Norops vittigerus.— PANAMA: Veraguas: PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: SMF 89528 (SL 172).

Norops woodi.— PANAMA: Chiriquí: Nacimiento Quebrada Chevo, 8.8743°N, 82.7421°W, 1615 m: SMF 85433–5 (GK 1653–5); westlich von Volcán (Ort), 8.818°N, 82.6744°W, 1456 m: SMF 85398 (AJC 889).

Family Hoplocercidae

Enyalioides heterolepis.— PANAMA: Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Andreas Hertz, photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89558 (SL 232); Cerro Negro: camp, 8.569°N, 81.0989°W, 713 m: SMF 89955–6 (AC 32, 36).

Family Iguanidae

Ctenosaura similis.— PANAMA: Chiriquí: Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, 8.0732°N, 82.8857°W, 74 m: obs.; Peninsula de Burica: Puerto Limones, 8.1028°N, 82.8649°W, 2 m: obs.; private beach without name near Playa Hermosa, 8.2007°N, 82.1397°W, 2 m: obs., photo.

Iguana iguana.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: photo; Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, 8.0732°N, 82.8857°W, 74 m: obs., photo; Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: obs., photo; Los Algarrobos, 8.4959°N, 82.4327°W, 141 m: photo by Meike Piepenbring; Los Algarrobos: Bar El Corte, 8.4952°N, 82.4253°W, 154 m: photo; Dolega, 8.5747°N, 82.4201°W, 270 m: obs.; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: photo.

Family Phrynosomatidae

Sceloporus malachiticus.— PANAMA: Chiriquí: PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: photo, MHCH 2362 (SL 203)$^{\text{COI}}$, SMF 89595 (SL 213); PILA: Jurutungo: ascent towards border trail on divide: sign "Limite del Parque", 8.9148°N, 82.7182°W, 2014 m: obs.; Cerro Totuma, 8.8877°N, 82.6824°W, 1987 m: photo by Andreas Hertz, photo by Jeffrey Dietrich; PNVB: summit of Volcán Barú, 8.809°N, 82.5424°W, 3400 m: obs.; PNVB: Sendero Los Quetzales: Refugio Las Rocas, 8.848°N, 82.5196°W, 2393 m: obs.; PNVB: Bajo Mono: Sendero La Cascada: last clearing with hut before forest, 8.8281°N, 82.4893°W, 1679 m: SMF 89785 (SL 410); Sendero Los Quetzales: branch to Bajo Mono, 8.8418°N, 82.4812°W, 1688 m: obs.; Bajo Mono: bus stop at branching Alto Quiel/Alto Chiquero/Boquete/Sendero la Cascada, 8.8301°N, 82.4803°W, 1585 m: obs.

Family Polychrotidae

Polychrus gutturosus.— PANAMA: Chiriquí: Boqueron, Casa de Jesenka, 8.511°N, 82.573°W, 219 m: photo by Jesenka Espinosa; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Mabuyidae

Marisora unimarginata.— PANAMA: Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85445 (GK 1271); Hacienda Café de Eleta: citrus plantation between utility shed and Río Candela, 8.8829°N, 82.7595°W, 1464 m: MHCH 2349 (SL 157), SMF 89582 (SL 156); Comarca Ngöbe-Buglé: Guayabito: central soccer field, 8.5404°N, 81.4816°W, 1130 m: photo, SMF 91565 (SL 754).

Family Sphenomorphidae

Scincella cherriei.— PANAMA: Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85436 (GK 1277); Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1200 m: MHCH 2368 (SL 479), SMF 90210 (SL 478).

Family Xanthusiidae

Lepidophyma flavimaculatum.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Gymnophthalmidae

Anadia ocellata.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1209 m: SMF 90095 (SL 474); RFLF: road near Garganta del Diablo, 8.6917°N, 82.23°W, 1250 m: SMF 89443 (SL 253).

Bachia blairi.— PANAMA: Chiriquí: Río Chiriquí Viejo, Renacimiento, Chiriquí province, Panama, 8.7163°N, 82.8331°W, 515 m: photo by Marcos Ponce.

Echinosaura panamensis.— PANAMA: Comarca Ngöbe-Buglé: BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 730 m: SMF 91542 (SL 643); BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 739 m: MHCH 2313 (SL 644)^{COI}; Veraguas: PNSF: Cerro Mariposa: I Brazo Mulaba, 8.5186°N, 81.1332°W, 700 m: SMF 89954 (AC 14); PNSF: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: MHCH 2314 (SL 766)^{COI}, SMF 89557 (SL 135), 91541 (SL 759); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: SMF 89556 (SL 128), 91540 (SL 765)^{COI}; Cerro Mariposa, 8.504°N, 81.11°W, 885 m: MHCH 2312 (LSt 65); Cerro Mariposa, 8.5053°N, 81.1089°W, 825 m: SMF 89555 (LSt 104);

Gymnophthalmidae sp.— PANAMA: Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: obs.

Leposoma rugiceps.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: MHCH 2340 (SL 533)^{COI}, SMF 90192 (SL 534); HIISSPS: Río Negro: flooded forest on N bank, 9.508°N, 82.5289°W, 13 m: photo, MHCH 2341 (SL 557), SMF 90193 (SL 556); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Cerro Mariposa, 8.5095°N, 81.1173°W, 898 m: SMF 89577 (LSt 97); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 616 m: SMF 89964 (AC 103).

Potamites apodemus.— COSTA RICA: Puntarenas: Reserva Conte Burica, headwater of Río Coco, 8.31987°N, 83.08513°W, 110 m: JV 130, 131; PANAMA: Chiriquí: Chorogo, 8.31366°N, 82.99934°W, 380 m: SMF 92117–9 (GK 3386–7, 3414); Chorogo, 8.3095°N, 82.99437°W, 427 m: MHCH 1618 (GK 3417); Chorogo, 8.31022°N, 83.00030°W, 390 m: MHCH 1631 (GK 3422); Santa Clara: Finca Ecológica: junction of border creeks, 8.8306°N, 82.787°W, 1088 m: MHCH 2352 (SL 609)^{COI}; Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1120 m: SMF 89779 (SL 418); Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1125 m: SMF 91568 (SL 613)^{COI}; Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1149 m: SMF 91569 (SL 612)^{COI}.

Ptychoglossus plicatus.— PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, pasture above Río Clarito, 8.9982°N, 82.6677°W, 1538 m: SMF 91575 (SL 690); PILA: N slope Cerro Pando, upper limit of pasture above Río Clarito, 8.9921°N, 82.666°W, 1690 m: SMF 91576 (SL 691); Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: SMF xxxxx (MHCH 1039); Sendero el Pianista, 8.8818°N, 82.4058°W, 795 m: SMF 86382 (MHCH 444); Chiriquí: Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1125 m: SMF 89784 (SL 417); Fortuna, 8.7311°N, 82.2597°W, 1270 m: SMF 85389–91 (GK 1443–5); Fortuna, Trail from Finca to Dam site, 8.7318°N, 82.2567°W, 1075 m: SMF 85393–6 (GK 1527, 1529, 1530, 1532); RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 91573 (SL 605); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: MHCH 2360 (SL 446); Palo Seco, Sendero los tucanes, 8.7815°N, 82.2122°W, 1120 m: SMF 85392 (GK 1472); RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: MHCH 2359 (SL 160), 2361 (SL 639)^{COI}; RFLF: W slope Cerro Pata de Macho: lower limit of bamboo ridge, 8.6757°N, 82.2067°W, 1388 m: SMF 89783 (SL 259); RFLF: W slope Cerro Pata de Macho, 8.6752°N, 82.2056°W, 1436 m: SMF 89591 (NH 45); RFLF: W slope Cerro Pata de Macho, 8.6749°N, 82.205°W, 1419 m: SMF 89590 (NH 41); Comarca Ngöbe-Buglé: Hacha trail: Río Marabí, 8.5192°N, 81.7831°W, 1231 m: SMF 91574 (SL 747)^{16S}; Veraguas: Cerro Mariposa, 8.5122°N, 81.1202°W, 1000 m: MHCH 2358 (LSt 83); PNSF: Cerro Mariposa, 8.5003°N, 81.1174°W, 1261 m: SMF 89589 (LSt 124); PNSF: Cerro Mariposa, 8.5002°N, 81.1174°W, 1253 m: SMF 89588 (LSt 57); PNSF: Cerro Mariposa, 8.5°N, 81.1173°W, 1256 m: MHCH 2357 (LSt 52); Cerro Mariposa: northern summit, 8.4954°N, 81.1164°W, 1437 m: obs.

Family Teiidae

Ameiva praesignis.— PANAMA: Chiriquí: Los Algarrobos, 8.4959°N, 82.4327°W, 141 m: photo by Meike Piepenbring; Los Algarrobos, Prov. de Chiriquí, 8.4952°N, 82.4253°W, 154 m: MVUP 561.

Holcosus festivus.— PANAMA: Bocas del Toro: HIISSPS: beach east of Boca San San, 9.5212°N, 82.5035°W, 3 m: SMF 90093 (SL 540); Chiriquí Grande, 8.951°N, 82.121°W, 3 m: photo by Konrad Mebert; Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89894 (AC 87).

Holcosus quadrilineatus.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: SMF 90094 (SL 539); Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85447 (GK 1276); Santa Clara: Finca Ecológica: clearing with plaintain and coffe on descent to western border creek, 8.8322°N, 82.7844°W, 1179 m: SMF 91444 (SL 619); Veraguas: Cerro Mariposa, 8.5129°N, 81.1166°W, 853 m: SMF 89442 (LSt 41).

Family Colubridae

Chironius exoletus.— PANAMA: Chiriquí: RFLF: upper limit of Valle de la Mina on road, 8.6671°N, 82.2171°W, 1125 m: SMF 91535 (SL 599).

Chironius flavopictus.— PANAMA: Bocas del Toro: road from Chiriquí Grande to Almirante: km 35.5, bus stop, 9.1212°N, 82.2978°W, 35 m: SMF 89768 (SL 340); Río Sereno: next to border, 8.8182°N, 82.8616°W, 986 m: SMF 89541 (SL 234); Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: SMF 89540 (SL 178); Veraguas: Los Valles: creek above ANAM station, 8.4486°N, 81.2008°W, 404 m: SMF 91534 (SL 626)^{COI}.

Chironius grandisquamis.— PANAMA: Chiriquí: Cabecera de Cochea: Río Cochea above crossing, 8.7272°N, 82.4937°W, 1140 m: SMF 89766 (SL 280); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Alto de Piedra, 8.5161°N, 81.1185°W, 864 m: photo by Konrad Mebert.

Dendrophidion paucicarinatum.— PANAMA: Chiriquí: PNVB: Bajo Mono: Sendero La Cascada: camp, 8.825°N, 82.5021°W, 1837 m: SMF 90179 (SL 466); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: MHCH 2308 (SL 448), SMF 89544 (SL 147); Comarca Ngöbe-Buglé: road Cerro Colorado - Ratón, 8.5336°N, 81.8035°W, 1636 m: SMF 91538 (SL 652)^{COI}; Cerro Colorado, Bocas del Toro, 8.511°N, 81.792°W, 1413 m: MVUP 1120; W slope Cerro Santiago, La Nevera: first confluence of creeks below camp, 8.5018°N, 81.7689°W, 1555 m: SMF 89543 (SL 236)^{16S}.

Dendrophidion percarinatum.— PANAMA: Chiriquí: Santa Clara: road from Volcán to Río Sereno, 8.8344°N, 82.7741°W, 1157 m: SMF 89545 (SL 149).

Enuliophis sclateri.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Lampropeltis triangulum.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1209 m: SMF 90188 (SL 477); Hacienda Café de Eleta: camp next to workshop/utility shed, 8.8804°N, 82.76°W, 1437 m: SMF 89575 (SL 158); Jurutungo, road to (top of cerro), 8.8848°N, 82.7493°W, 1530 m: SMF 85298 (GK 1311); Río Colorado, 8.8751°N, 82.6882°W, 1733 m: photo by Jeffrey Dietrich; Río Colorado, 8.8824°N, 82.6772°W, 1874 m: photo by Jeffrey Dietrich; RFLF near Lost&Found, 8.6746°N, 82.2196°W, 1250 m: photo by Konrad Mebert.

Leptophis ahaetulla.— PANAMA: Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Fortuna Streetmargin, 8.6917°N, 82.23°W, 1250 m: photo by Ralph Mangelsdorff; road to La Fortuna, between Gualaca and Los Planes, 8.6088°N, 82.2251°W, 780 m: SMF xxxxx (AH 559); Veraguas: road Santiago - Santa Fé, halfway between Santiago and San Francisco, 8.1796°N, 80.9511°W, 76 m: SMF 89580 (SL 141).

Mastigodryas melanolomus.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: SMF 90197 (SL 538); Isla Colon - Caremero, 9.347°N, 82.233°W, 9 m: photo by Konrad Mebert; Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Los Algarrobos: old railway bridge over Río Majagua, 8.4809°N, 82.428°W, 88 m: photo; road Davíd-Boquete: Portachuelo, 8.4647°N, 82.4201°W, 67 m: MHCH 2350 (SL 384); RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 89777–8 (SL 271, 343); Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Santa Fé assumed, 8.5117°N, 81.0773°W, 441 m: SMF 90035 (AC 203); Finca La Providencia: creek, 7.8927°N, 80.9844°W, 41 m: SMF 91566 (SL 577).

Oxybelis aeneus.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: SMF 90204 (SL 543); Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: SMF xxxxx (MHCH 1040); road from Chiriquí Grande to Almirante: shortly after km 43, 9.1572°N, 82.3182°W, 53 m: MHCH 2353 (SL 303), SMF 89780 (SL 302); Chiriquí: Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: MHCH 2354 (SL 502); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Oxybelis brevirostris.— PANAMA: Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Andreas Hertz; Comarca Ngöbe-Buglé: above El Paredón: valley of Río Rasca, 8.4878°N, 81.1712°W, 800 m: SMF 91571 (SL 633)^{16S}; Veraguas: Cerro Mariposa, 8.5176°N, 81.1187°W, 852 m: MHCH 2355 (LSt 87); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: MHCH 2356 (SL 132); Cerro Mariposa: Alto de Piedra, Restaurante, 8.5145°N, 81.1177°W, 867 m: SMF 91570 (SL 755); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 750 m: SMF 89971 (AC 220); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 760 m: SMF 89970 (AC 81); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 805 m: SMF 89781 (SL 381).

Oxybelis fulgidus.— PANAMA: Chiriquí: Los Algarrobos: Bar El Corte, 8.4952°N, 82.4253°W, 154 m: SMF 90205 (SL 487); Veraguas: Cerro Mariposa, 8.5177°N, 81.1184°W, 854 m: SMF 89584 (LSt 81); PNSF: Cerro Tute, 8.4881°N, 81.1098°W, 900 m: SMF 89972 (AC 150).

Phrynonax poecilonotus.— PANAMA: Chiriquí: San Bartolo, 8.32°N, 82.92°W, 77 m: photo by Meike Piepenbring; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Rhinobothryum bovallii.— PANAMA: Comarca Ngöbe-Buglé: above El Paredón: Río Rasca, 8.491°N, 81.1694°W, 775 m: SMF 91577 (SL 635); Veraguas: PNSF: Cerro Tute, 8.4881°N, 81.1098°W, 1116 m: SMF 90022 (AC 92).

Spilotes pullatus.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: southern border creek, 8.8309°N, 82.7842°W, 1125 m: SMF 89788 (SL 412); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: photo; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: SMF 89600 (SL 179); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: PNSF: Cerro Negro: trail to camp, creek crossing, 8.5633°N, 81.0979°W, 675 m: photo.

Stenorrhina degenhardtii.— PANAMA: Chiriquí: RFLF: Lost & Found Ecohostel, 8.6747°N, 82.2197°W, 1260 m: SMF xxxxx (AH 563); San Felix - Chiriquí, 8.278°N, 81.872°W, 78 m: MVUP 304; Comarca Ngöbe-Buglé: Cerro Colorado, Chiriquí, 8.51°N, 81.8°W, 1136 m: MVUP 1119.

Tantilla alticola.— PANAMA: Chiriquí: RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 91582 (SL 596)^{COI}; RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: photo by Robert Maurer; Comarca Ngöbe-Buglé: road Cerro Colorado - Ratón, 8.5353°N, 81.8081°W, 1600 m: MHCH 2369 (SL 771)^{COI}, SMF 91583 (SL 772)^{COI}.

Family Dipsadidae

Amastridium veliferum.— PANAMA: Chiriquí: RFLF: near Lost & Found Ecohostel, 8.6744°N, 82.2161°W, 1434 m: SMF 90092 (JFB 01).

Clelia equatoriana.— PANAMA: Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 725 m: SMF 89923 (AC 202).

Coniophanes bipunctatus.— PANAMA: Bocas del Toro: HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: SMF 90178 (SL 541).

Dipsas articulata.— PANAMA: Veraguas: PNSF: Cerro Negro: ridge above camp, 8.5756°N, 81.0976°W, 1000 m: SMF 89952 (AC 85).

Dipsas temporalis.— PANAMA: Veraguas: PNSF: Cerro Mariposa, 8.5237°N, 81.1335°W, 717 m: SMF 89554 (LSt 111); PNSF: Cerro Mariposa, 8.5245°N, 81.1332°W, 697 m: SMF 89553 (LSt 110)^{16S}; PNSF: Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: MHCH 2311 (SL 770)^{COI}; Cerro Mariposa, 8.5107°N, 81.1207°W, 993 m: SMF 89552 (LSt 69); Cerro Mariposa, 8.515°N, 81.1196°W, 912 m: SMF 89551 (LSt 64); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89769 (SL 382)^{16S}, 90036 (AC 77); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 705 m: SMF 89953 (AC 40); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 900 m: photo.

Erythrolamprus bizona.— PANAMA: Chiriquí: Cerro Totuma, 8.8841°N, 82.6832°W, 1909 m: photo by Jeffrey Dietrich; Potrerillos - Chiriquí, 8.685°N, 82.491°W, 898 m: MVUP 562A, MVUP 562B.

Erythrolamprus epinephelus.— PANAMA: Chiriquí: PNVB: Bajo Mono: Sendero La Cascada: camp, 8.8263°N, 82.4989°W, 1822 m: SMF 90195 (SL 465); RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: MHCH 2347 (SL 595)^{COI}, SMF 89776 (SL 344), 91564

(SL 773); RFLF: near Lost & Found Ecohostel, 8.6743°N, 82.2157°W, 1400 m: MHCH 2346 (JFB 48); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: SMF 89581 (SL 148); RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: obs.

Geophis brachycephalus.— COSTA RICA: San José: Escazú, 9.917°N, 84.133°W, 1160 m: SMF xxxxx (GK 2636)$^{\text{16S}}$; PANAMA: Comarca Ngöbe-Buglé: Bosque Protector de Palo Seco, Chiriquí Grande, Bocas del Toro, 8.798°N, 82.229°W, 1020 m: MVUP 1749; Bosque Protector de Palo Seco, Chiriquí Grande, Bocas del Toro, 8.798°N, 82.229°W, 1050 m: MVUP 1750; BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1140 m: SMF 90181 (SL 491)$^{\text{16S}}$.

Geophis godmani.— COSTA RICA: Puntarenas: Las Tablas, 8.9478°N, 82.7404°W, 1850 m: SMF xxxxx (GK 2564)$^{\text{COI}}$; PANAMA: Chiriquí: PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1990 m: MHCH 2318 (SL 530)$^{\text{16S, COI}}$; PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: MHCH 2317 (SL 444), SMF 89565–6 (SL 200, 214); PNVB: Sendero Los Quetzales: Refugio Las Rocas, 8.848°N, 82.5196°W, 2354 m: SMF 89770 (SL 389)$^{\text{16S}}$.

Geophis hoffmanni.— COSTA RICA: Heredia: Volcan Barva, Paso Llano, 10.0933°N, 84.1065°W, 1700 m: SMF xxxxx (GK 2623); PANAMA: Chiriquí: Santa Clara: Finca Ecológica: clearing with plaintain and coffe on descent to western border creek, 8.8322°N, 82.7844°W, 1179 m: SMF 91549 (SL 610)$^{\text{16S, COI}}$, 91550 (SL 618)$^{\text{COI}}$; Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1209 m: MHCH 2319 (SL 611)$^{\text{16S, COI}}$, SMF 91548 (SL 620)$^{\text{COI}}$.

Geophis sp.— PANAMA: Chiriquí: RFLF near Lost&Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: photo by Konrad Mebert; RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 89771 (SL 258), 91543–4 (SL 566, 650)$^{\text{both 16S, COI}}$, 91546 (SL 594)$^{\text{16S, COI}}$; RFLF: Lost & Found Ecohostel, 8.6742°N, 82.2195°W, 1277 m: SMF 89562 (NH 40)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito , 8.6739°N, 82.2185°W, 1320 m: SMF 89563 (SL 143)$^{\text{16S}}$; 184°W, 1310 m: SMF 89559 (NH 1)$^{\text{16S}}$; RFLF: near Lost & Found Ecohostel, 8.6746°N, 82.2184°W, 1335 m: SMF 89561 (NH 14)$^{\text{16S}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, just below ridge, 8.6744°N, 82.2161°W, 1434 m: MHCH 2316 (SL 651)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel, 8.6743°N, 82.2157°W, 1400 m: MHCH 2315 (JFB 47)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge, 8.674°N, 82.2154°W, 1455 m: photo, SMF 89560 (NH 4)$^{\text{16S, COI}}$, 91545 (SL 593)$^{\text{16S, COI}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: photo, SMF 90183 (SL 447)$^{\text{16S}}$; RFLF: Río Hornito: "Tuna's cave", 8.6736°N, 82.2078°W, 1317 m: SMF 91547 (SL 565)$^{\text{16S, COI}}$; RFLF: W slope Cerro Pata de Macho: traps, 8.674°N, 82.2022°W, 1521 m: SMF 89564 (SL 194)$^{\text{16S}}$; Comarca Ngöbe-Bugle: road Cerro Colorado - Ratón, 8.5353°N, 81.8081°W, 1600 m: SMF xxxxx (AH 567); road Cerro Colorado - Ratón, 8.5303°N, 81.7987°W, 1660 m: SMF xxxxx (AH 576); road Cerro Colorado - Ratón, 8.5341°N, 81.8071°W, 1627 m: SMF xxxxx (AH 568); road Cerro Colorado - Ratón, 8.5303°N, 81.7987°W, 1660 m: SMF xxxxx (AH 577).

Geophis talamancae.— PANAMA: Chiriquí: PILA: road to Jurutungo: upper limit of large clearing, 8.9063°N, 82.7357°W, 1834 m: SMF 89567 (SL 218)$^{\text{16S}}$; PILA: Las Nubes, 8.8942°N, 82.6149°W, 2117 m: SMF 90182 (JFB 55); Bajo Mono - Boquete, Chiriquí, 8.8418°N, 82.4812°W, 1688 m: MVUP 963.

Geophis cf. *talamancae.*— PANAMA: Chiriquí: Cerro Totuma, 8.8803°N, 82.6872°W, 1880 m: photo by Jeffrey Dietrich.

Geophis tectus.— PANAMA: Bocas del Toro: Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: SMF xxxxx (MHCH 1043)$^{\text{16S}}$; Sendero el Pianista, 8.8793°N, 82.4084°W, 825 m: SMF 86410 (MHCH 470); Comarca Ngöbe-Buglé: La Loma (= Buena Vista), 8.833°N, 82.217°W, 300 m: MCZ 19325, MCZ 19326; BPPS: Willie Mazú: trail above camp, branch, 8.7902°N, 82.2011°W, 716 m: SMF 91551 (SL 641)$^{\text{16S, COI}}$.

Imantodes cenchoa.— PANAMA: Bocas del Toro: HIISSPS: Boca San San, Centro AAMVECONA, 9.5259°N, 82.5099°W, 1 m: obs., photo; HIISSPS: beach east of Boca San San, 9.5212°N, 82.5035°W, 3 m: SMF 90187 (SL 546); Sendero el Pianista, Casa de Ancon, 8.8714°N, 82.4159°W, 1005 m: SMF 86409 (MHCH 419), xxxxx (MHCH 1063); road from Chiriquí Grande to Almirante: shortly after km 43, 9.1572°N, 82.3182°W, 53 m: SMF 89774 (SL 305); Isla Colon - Caremero, 9.347°N, 82.233°W, 9 m: photo by Konrad Mebert; Chiriquí: Cordillera (pueblo), 4 km SSE El Hato del Volcan, 8.7383°N, 82.6211°W, 1160 m: SMF xxxxx (MHCH 1030); Chiriquí: Potrerillos Arriba: Finca Los Mameyes: Río Pedro below bridge, 8.7386°N, 82.5107°W, 1301 m: MHCH 2331 (SL 471); Cabecera de Cochea: crossing Río Cochea, 8.7255°N, 82.4931°W, 1090 m: MHCH 2328 (SL 276), SMF 89772 (SL 275); Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo, MHCH 2327 (SL 229), 2334 (SL 504); Fortuna, Laguna, 8.7264°N, 82.2614°W, 1000 m: SMF 85082 (GK 1575); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, ridge, 8.674°N, 82.2154°W, 1455 m: MHCH 2325 (NH 11); RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6772°N, 82.2104°W, 1291 m: SMF 89572 (NH 29); RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: obs.; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: MHCH 2333 (SL 495), SMF 91554 (SL 604); BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1060 m: SMF 90186 (SL 490); BPPS: Willie Mazú: trail above camp, 8.7885°N, 82.2016°W, 739 m: SMF 91557 (SL 647); BPPS: Willie Mazú: trail above camp, branch, 8.7902°N, 82.2011°W, 730 m: photo; BPPS: Willie Mazú: trail above camp, 8.7903°N, 82.2003°W, 718 m: MHCH 2335 (SL 640); BPPS: Willie Mazú: trail above camp, 8.7903°N, 82.1989°W, 681 m: photo; BPPS: Willie Mazú: camp, 8.7901°N, 82.1973°W, 643 m: photo; road Cerro Colorado - Ratón: camp on road, 8.5303°N, 81.7987°W, 1662 m: SMF 89573 (SL 113); Hacha trail: Río Hacha: stairs, 8.5522°N, 81.7645°W, 953 m: SMF 91556 (SL 740)$^{\text{COI}}$; Hacha trail: Río Hacha: stairs, 8.5522°N, 81.7645°W, 960 m: MHCH 2336 (SL 739)$^{\text{COI}}$; E slope Cerro Santiago: Quebrada Ardilla, 8.4968°N, 81.7216°W, 1570 m: SMF 89773 (SL 362); above El Paredón: valley of Río Rasca, 8.4878°N, 81.1712°W, 805 m: SMF 91555 (SL 634); Veraguas: PNSF: Cerro Mariposa: I Brazo Mulaba, 8.5186°N, 81.1332°W, 700 m: SMF 89961 (AC 16); PNSF: Cerro Mariposa, 8.5139°N, 81.1222°W, 863 m: SMF 89570 (SL 138); PNSF: Cerro Mariposa, 8.5137°N, 81.1219°W, 879 m: SMF 89569 (LSt 77); Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 855 m: photo; Cerro Mariposa: trail meets creek at water supply, 8.5117°N, 81.1216°W, 900 m: photo; Cerro Mariposa, 8.5163°N, 81.1187°W, 865 m: MHCH 2324 (LSt 68); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 1010 m: MHCH 2332 (SL 483); Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 883 m: photo, MHCH 2326 (SL 130); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: MHCH 2330 (SL 375); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 750 m: SMF 89960 (AC 76); PNSF: Cerro Negro: ridge above camp, 8.577°N, 81.0971°W, 1085 m: SMF 89571 (SL 233); PNSF: Cerro Negro: creek above camp, 8.5702°N, 81.0963°W, 778 m: MHCH 2329 (SL 374).

Imantodes sp.— PANAMA: Veraguas: PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: obs.

Leptodeira annulata.— PANAMA: Chiriquí: Playa La Barqueta: road to Davíd, 8.3128°N, 82.5782°W, 18 m: MHCH 2342 (SL 180); Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: photo; Los Algarrobos, 8.4959°N, 82.4327°W, 141 m: photo by Meike Piepenbring; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: SMF 89578 (SL 235); Los Algarrobos: Casa de Mair, 8.4928°N, 82.4263°W, 147 m: MHCH 2343 (SL 422); Los Algarrobos: Bar El Corte, 8.4952°N, 82.4253°W, 154 m: MHCH 2344 (SL 501); Dam "Represa de Caldera", 8.6151°N, 82.3529°W, 257 m: SMF 89579 (SL 163); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: Guayabito: central soccer field, 8.5404°N, 81.4816°W, 1147 m: SMF 91561 (SL 752)$^{\text{COI}}$; Veraguas: Finca La Providencia: houses, 7.8973°N, 80.9865°W, 53 m: photo, SMF 91560 (SL 578)$^{\text{COI}}$.

Leptodeira septentrionalis.— PANAMA: Chiriquí: Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, 8.0732°N, 82.8857°W, 74 m: SMF 91562 (SL 583), 91563 (SL 584)$^{\text{COI}}$; Peninsula de Burica: road to Puerto Limones, 8.1519°N, 82.8782°W, 20 m: MHCH 2345 (SL 579); Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek, 8.0858°N, 82.8743°W, 62 m: obs.; RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 90194 (SL 456).

Leptodeira cf. *septentrionalis.*— PANAMA: Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 800 m: photo.

Ninia maculata.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: Abarrotería La Sorpresa, 8.8331°N, 82.7824°W, 1209 m: SMF 90203 (SL 476); Potrerillos: Finca Los Mameyes, 8.74°N, 82.5142°W, 1422 m: photo by Juan Castillo; Veraguas: Cerro Mariposa, 8.5132°N, 81.1166°W, 864 m: SMF 89583 (LSt 60).

Oxyrhopus petolarius.— PANAMA: Chiriquí: Los Algarrobos: trail enters Río Majagua, 8.4846°N, 82.4342°W, 109 m: photo; Los Algarrobos: Casa de Mair, 8.4928°N, 82.4263°W, 147 m: SMF 89782 (SL 281); Veraguas: PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 716 m: SMF 89973 (AC 38); PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: SMF 89585 (SL 169).

Pliocercus euryzonus.— PANAMA: Bocas del Toro: HIISSPS: Río Negro: flooded forest on N bank, 9.508°N, 82.5289°W, 13 m: SMF 90206 (SL 560); Veraguas: Cerro Mariposa, 8.507°N, 81.1144°W, 866 m: SMF 89586 (LSt 92); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 850 m: SMF 89974 (AC 215); PNSF: Río Chilagres: camp and rancho above confluence with Río Santa María, 8.5872°N, 81.0363°W, 476 m: SMF 89587 (SL 170).

Pseudoboa neuwiedii.— PANAMA: Chiriquí: Las Lajas, 8.1703°N, 81.865°W, 34 m: photo by Andreas Hertz; specimen donated to La Mica Biological station; Peninsula de Burica: road to Puerto Limones, 8.1275°N, 82.8736°W, 26 m: SMF 91572 (SL 580).

Rhadinaea calligaster.— PANAMA: Chiriquí: PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: SMF 89593 (SL 216); PILA: Jurutungo: ascent towards border trail on divide: shortly after sign "Limite del Parque", 8.9167°N, 82.7184°W, 2099 m: SMF 89592 (SL 215); PILA: Jurutungo: ascent towards border trail on divide: sign "Limite del Parque", 8.9148°N, 82.7183°W, 2014 m: photo; Cerro Totuma, 8.893°N, 82.6779°W, 2419 m: photo by Jeffrey Dietrich.

Rhadinaea decorata.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Rhadinella godmani.— PANAMA: Chiriquí: PILA: road to Jurutungo, 8.9063°N, 82.7318°W, 1840 m: SMF 89594 (SL 217); Volcán Barú, Straße nach Alto Chiquero, 8.8489°N, 82.4864°W, 1610 m: SMF 85091 (GK 1381).

Sibon annulatus.— PANAMA: Bocas del Toro: PILA: N slope Cerro Pando, Río Changena: "middle" camp 2, 8.9785°N, 82.6901°W, 1641 m: SMF 91578 (SL 700)$^{\text{16S}}$; Sendero el Pianista, Casa de Ancon, 8.8714°N, 82.4159°W, 1005 m: SMF 86411 (MHCH 420), 88713–4 (MHCH 1066, 1068); RFLF: Cerro Guayabo, 8.7553°N, 82.2543°W, 1247 m: SMF 90208 (JFB 35)$^{\text{COI}}$; RFLF: near Lost & Found Ecohostel: trail to Río Hornito , 8.6739°N, 82.2185°W, 1320 m: SMF 88715 (SL 144)$^{\text{16S, COI}}$; RFLF: near Río Hornito, 8.6773°N, 82.2111°W, 1325 m: SMF xxxxx (AH 560); Palo Seco, 8.7776°N, 82.2092°W, 1030 m: SMF 85077–8 (GK 1478, 1576); RFLF: W slope Cerro Pata de Macho, 8.6761°N, 82.2062°W, 1408 m: SMF xxxxx (AH 565); Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: MHCH 2364 (SL 603), SMF 90207 (SL 496)$^{\text{16S}}$, 91579 (SL 602); BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1080 m: MHCH 2363 (SL 497); above Guayabito: forest, 8.5494°N, 81.4847°W, 1510 m: SMF 91580 (SL 625)$^{\text{16S, COI}}$; Veraguas: PNSF: Cerro Mariposa, 8.5249°N, 81.1328°W, 679 m: SMF 89596 (LSt 109); PNSF: Cerro Mariposa: creek above water supply, 8.5082°N, 81.121°W, 899 m: MHCH 2365 (SL 769)$^{\text{16S}}$; Cerro Mariposa, 8.5146°N, 81.1193°W, 1003 m: SMF 89597 (LSt 119); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 680 m: SMF 90023 (AC 29); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 900 m: SMF 89786 (SL 379)$^{\text{16S}}$; PNSF: Cerro Negro: ridge above camp, 8.577°N, 81.0971°W, 1085 m: SMF 90024 (AC 78).

Sibon longifrenis.— COSTA RICA: Guanacaste: Volcán Miravalles, 10.7478°N, 85.1095°W, 1030 m: SMF 94598; PANAMA: Veraguas: Cerro Mariposa: water supply hut near Alto de Piedra, 8.5161°N, 81.1185°W, 895 m: SMF 91581 (SL 756)$^{\text{16S, COI}}$.

Sibon nebulatus.— PANAMA: Bocas del Toro: Sendero El Pianista, Casa de Calixto, 8.881°N, 82.41°W, 870 m: SMF 88717 (MHCH 1044); road from Chiriquí Grande to Almirante: shortly after km 53, 9.2061°N, 82.3616°W, 50 m: MHCH 2367 (SL 311); road from Chiriquí Grande to Almirante: shortly after km 43, 9.1572°N, 82.3182°W, 53 m: SMF 89787 (SL 304); Chiriquí: Volante: camp, 8.587°N, 82.6683°W, 481 m: SMF 89599 (SL 227)$^{\text{16S, COI}}$; Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: MHCH 2366 (SL 165); RFLF: Lost & Found Ecohostel, 8.6746°N, 82.2196°W, 1250 m: SMF 90209 (SL 455); Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Andreas Hertz; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: PNSF: Cerro Mariposa, 8.5122°N, 81.1214°W, 933 m: SMF 89598 (LSt 55)$^{\text{16S}}$.

Sibon noalamina.— PANAMA: Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: SMF 90180 (SL 494)$^{\text{16S, COI}}$, 91539 (SL 775)$^{\text{16S, COI}}$; Veraguas: Cerro Mariposa: trail towards summit, 8.5001°N, 81.117°W, 1255 m: SMF 89550 (LSt 15)$^{\text{16S, COI}}$.

Sibon perissostichon.— PANAMA: Chiriquí: RFLF: near Lost & Found Ecohostel: trail to Río Hornito, just below ridge, 8.6744°N, 82.2161°W, 1434 m: SMF 88716 (SL 145)$^{\text{16S}}$.

Sibon sp.— PANAMA: Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Wouter Beukemer.

Trimetopon pliolepis.— PANAMA: Chiriquí: Distr. Renacimiento, 8 km NE Río Sereno, Finca C.A.S.A., 8.8714°N, 82.7954°W, 1210 m: SMF 85388 (GK 1283).

Trimetopon slevini.— PANAMA: Chiriquí: RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6741°N, 82.2178°W, 1389 m: SMF 89602 (NH 48); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1740 m: SMF 90211 (SL 450).

Urotheca decipiens.— PANAMA: Chiriquí: RFLF: Lost & Found Ecohostel, 8.6745°N, 82.2193°W, 1283 m: SMF 89604 (NH 12)$^{\text{16S, COI}}$; Comarca Ngöbe-Buglé: Bosque Protector de Palo Seco, Chiriquí Grande, Bocas del Toro, 8.798°N, 82.229°W, 1020 m: MVUP 1753; W slope Cerro Santiago, La Nevera: camp, 8.5011°N, 81.7694°W, 1580 m: SMF 90212 (SL 522)$^{\text{16S, COI}}$.

Urotheca guentheri.— PANAMA: Bocas del Toro: road from Chiriquí Grande to Almirante: km 35.5, bus stop, 9.1212°N, 82.2978°W, 35 m: SMF 89789 (SL 341); Veraguas: PNSF: Cerro Mariposa, 8.5002°N, 81.1175°W, 1248 m: SMF 89603 (LSt 51).

Xenodon rabdocephalus.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Elapidae

Micrurus alleni.— PANAMA: Bocas del Toro: HIISSPS: Río Negro: flooded forest on N bank, 9.508°N, 82.5289°W, 13 m: SMF 90200 (SL 561).

Micrurus clarki.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Micrurus mosquitensis.— PANAMA: Bocas del Toro: Las Tablas, 9.545°N, 82.7401°W, 23 m: SMF xxxxx (MHCH 561).

Micrurus multifasciatus.— PANAMA: Chiriquí: RFLF: Cerro Guayabo, 8.7547°N, 82.2534°W, 1230 m: SMF 90202 (JFB 34); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Micrurus nigrocinctus.— PANAMA: Chiriquí: Río Sereno: Casa de Porfirio Yangüez, 8.8257°N, 82.8525°W, 945 m: SMF 90201 (SL 527), 91567 (SL 704); Cochea, 8.7255°N, 82.4931°W, 1090 m: photo by Meike Piepenbring; Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: MHCH 2351 (SL 488).

Micrurus stewarti.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Viperidae

Atropoides mexicanus.— PANAMA: Veraguas: PNSF: Cerro Mariposa, 8.5166°N, 81.1285°W, 841 m: SMF 89529 (LSt 61); PNSF: Cerro Negro, 8.5664°N, 81.0989°W, 650 m: SMF 89918 (AC 37).

Atropoides picadoi.— PANAMA: Chiriquí: RFLF: near Lost & Found Ecohostel, 8.6755°N, 82.2128°W, 1337 m: SMF 90170 (JFB 46)^{COI}; RFLF: Río Hornito, 8.678°N, 82.2102°W, 1274 m: photo; RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1650 m: SMF 89759 (SL 265).

Bothriechis lateralis.— PANAMA: Chiriquí: Nacimiento Quebrada Chevo, 8.8743°N, 82.7421°W, 1615 m: SMF 85432 (GK 1665); Bajo Mono, 8.8301°N, 82.4803°W, 1585 m: photo by Meike Piepenbring; RFLF: near Lost & Found Ecohostel: trail to Río Hornito, 8.6745°N, 82.2139°W, 1400 m: SMF 89762 (SL 254); RFLF: W slope Cerro Pata de Macho, 8.6746°N, 82.2054°W, 1431 m: SMF 89537 (NH 46); RFLF: W slope Cerro Pata de Macho: "fallen log in bamboo thicket", 8.6761°N, 82.2006°W, 1657 m: photo; RFLF: W slope Cerro Pata de Macho: camp at "Río Perdido", 8.6719°N, 82.1997°W, 1421 m: MHCH 2298 (SL 185); RFLF: W slope Cerro Pata de Macho: elfin forest ridge, 8.6776°N, 82.1981°W, 1752 m: photo; Comarca Ngöbe-Buglé: W slope Cerro Santiago, La Nevera: camp on road, 8.4997°N, 81.7724°W, 1699 m: SMF 89533 (SL 249); W slope Cerro Santiago, La Nevera: slope with secondary growth, 8.5004°N, 81.77°W, 1644 m: SMF 89532 (SL 123).

Bothriechis nigroviridis.— PANAMA: Chiriquí: PILA: Jurutungo: Finca of Porfirio Yangüez, 8.9106°N, 82.7231°W, 1996 m: MHCH 2299 (SL 526); Jurutungo, 8.9074°N, 82.7137°W, 2115 m: SMF 85071 (GK 1351); Cerro Totuma, 8.8877°N, 82.6824°W, 1987 m: photo by Jeffrey Dietrich; PNVB: Sendero Los Quetzales: Alto Respingo, 8.8428°N, 82.5342°W, 2538 m: SMF 90173 (JFB 25); Bajo Mono, 8.8263°N, 82.4989°W, 1822 m: photo by Ralph Mangelsdorff; PNVB: Bajo Mono: Sendero La Cascada: camp, 8.8263°N, 82.4989°W, 1822 m: SMF 90174 (SL 463); Comarca Ngöbe-Buglé: W slope Cerro Santiago, La Nevera: confluence of intermittent creeks, 8.4996°N, 81.77°W, 1652 m: SMF 89534 (SL 122).

Bothriechis schlegelii.— PANAMA: Bocas del Toro: HIISSPS: beach east of Boca San San, 9.5212°N, 82.5035°W, 3 m: MHCH 2300 (SL 544), SMF 90175 (SL 545); Chiriquí: Horconcito, Chiriquí, 8.315°N, 82.153°W, 53 m: MVUP 390; Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Andreas Hertz, photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: PNSF: Cerro Mariposa, 8.5157°N, 81.1197°W, 863 m: SMF 89535 (SL 137); PNSF: Cerro Negro: camp, 8.569°N, 81.0989°W, 700 m: SMF 89922 (AC 52).

Bothriechis supraciliaris.— PANAMA: Chiriquí: Santa Clara: Finca Ecológica: junction of border creeks, 8.8306°N, 82.787°W, 1088 m: SMF 89764 (SL 419); Santa Clara: Finca Ecológica: clearing with plaintain and coffe on descent to western border creek, 8.8322°N, 82.7844°W, 1130 m: MHCH 2301 (SL 606)^{COI}; Cabecera de Cochea: crossing Río Cochea, 8.7255°N, 82.4931°W, 1090 m: SMF 89763 (SL 277).

Bothrops asper.— PANAMA: Bocas del Toro: Cerro Tebata, 9.5659°N, 82.8475°W, 491 m: SMF xxxxx (MHCH 577); HIISSPS: finca GTZ, vivero on N bank Río San San, 9.5017°N, 82.5243°W, 11 m: SMF 90176 (SL 542); Chiriquí: Los Algarrobos: Casa Culebra, 8.4953°N, 82.4294°W, 134 m: SMF 89536 (SL 199); Los Algarrobos: Casa de Mair, 8.4928°N, 82.4263°W, 147 m: MHCH 2302 (SL 370); Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: BPPS: headwaters of Río Chiriquí Malí, 8.7891°N, 82.2155°W, 1054 m: SMF 91532 (SL 774)^{COI}; Hato Chamí, 8.4479°N, 81.771°W, 1007 m: SMF 91533 (SL 675)^{COI}.

Cerrophidion sasai.— PANAMA: Chiriquí: PILA: Jurutungo: path to building at WP 86, 8.906°N, 82.7242°W, 1900 m: SMF 89765 (SL 429); PILA: Jurutungo: path to building at WP 86, 8.906°N, 82.7242°W, 1930 m: SMF 89538 (SL 220); PILA: Jurutungo: building under construction, 8.9069°N, 82.7229°W, 1954 m: MHCH 2303–4 (SL 221–2), SMF 89539 (SL 223); PNVB, Aguacatal, 8.803°N, 82.5849°W, 2012 m: SMF 86412 (MHCH 399).

Lachesis stenophrys.— PANAMA: Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Comarca Ngöbe-Buglé: pipeline road, 8.787°N, 82.214°W, 1182 m: photo by Robert Maurer.

Porthidium nasutum.— PANAMA: Bocas del Toro: Cerro Tebata, 9.5659°N, 82.8475°W, 491 m: SMF xxxxx (MHCH 582); Veraguas: PNSF: Cerro Negro: ridge above camp, 8.5756°N, 81.0976°W, 1000 m: SMF 89975 (AC 108).

Family Boidae

Boa constrictor.— PANAMA: Bocas del Toro: Isla Colon - Caremero, 9.347°N, 82.233°W, 9 m: photo by Konrad Mebert; Chiriquí: Los Algarrobos: trail to Río Majagua, 8.4893°N, 82.4333°W, 128 m: photo; road to La Fortuna, between Los Planes and Valle de la Mina, 8.6358°N, 82.2121°W, 997 m: SMF 89531 (SL 142); Coclé: PNGDOTH, 8.6667°N, 80.6167°W, 800 m: photo by Konrad Mebert; Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo; Veraguas: Finca La Providencia: houses, 7.8973°N, 80.9865°W, 53 m: photo.

Corallus ruschenbergerii.— PANAMA: Chiriquí: Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek, 8.0677°N, 82.8867°W, 61 m: MHCH 2305 (SL 582); Peninsula de Burica: dirt road from Puerto Limones to Bella Vista, creek, 8.0858°N, 82.8743°W, 62 m: SMF 91536 (SL 581)^{COI}.

Epicrates maurus.— PANAMA: Chiriquí: Las Lomas, 8.4398°N, 82.3935°W, 80 m: SMF xxxxx; near Chiriquí, 8.398°N, 82.3279°W, 54 m: SMF xxxxx (GK 3210); Colón: Distrito de Donoso: Botija, Brazo, Petaquilla, Río del Medio, 8.8423°N, 80.6564°W, 162 m: photo by Michael Castillo.

Family Anomalepididae

Liotyphlops albirostris.— PANAMA: Chiriquí: Los Algarrobos: Casa de la Alemana, 8.4959°N, 82.4327°W, 141 m: MHCH 2348 (SL 776); Los Algarrobos: Bar El Corte, 8.4952°N, 82.4253°W, 154 m: SMF 90196 (SL 457).

Appendix 3: Own contributions to publications incorporated in this work

Below, I outline the specific the input I contributed to the published articles on LCA reptiles which are incorporated in the present work. I have modified most passages adopted from these publications, and in doing so paid special attention to replace the "we" commonly used therein by the more specific "I" whenever referring to analyses and workflows which were exclusively performed by myself. I proofread each manuscript listed below several times.

Bienentreu et al. (2013): I collected about half of the examined specimens together with AH, took about half of the photographs, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, and created the map.

Köhler et al. (2010a): I collected the holotype together with AH, provided coloration and environmental data, and produced the head drawings.

Köhler et al. (2012b): I collected three of the examined *Norops gaigei* and several *N. polylepis* together with AH, provided coloration and environmental data, generated the 16S barcodes together with JFB and performed the molecular analyses, provided coloration and environmental data, assembled the georeferenced dataset, and produced the maps as well as the phylogenetic tree.

Lotzkat & Hertz (2011): I collected almost all examined specimens together with AH, took about half of the photographs, examined all specimens, performed literature research and GIS analyses, wrote much of the manuscript, and created the Figure and Table 2.

Lotzkat et al. (2010a): I collected all newly reported specimens together with AH, took all photographs, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, wrote the manuscript except for the hemipenis description, and created the color plate.

Lotzkat et al. (2010b): I collected most newly reported specimens together with AH, took most photographs, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, wrote the manuscript except for one color description, and created the color plate as well as the map.

Lotzkat et al. (2010c): I collected about half of the reported specimens together with AH, examined all specimens recording morphological data, performed all literature research as well as GIS analyses, wrote the manuscript, and created the map.

Lotzkat et al. (2011): I collected most Panamanian examined specimens together with AH, took most photographs, examined most specimens (morphological data recorded by JFB), performed all literature research as well as univariate morphological comparisons and GIS analyses, wrote most of the manuscript, created the table, color plates, and diagrams, and layouted the line drawings.

Lotzkat et al. (2012a): I collected almost half of the newly reported specimens together with AH, took most photographs, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, wrote the manuscript except for one color description, and created the color plates as well as the map.

Lotzkat et al. (2012b): I collected all of the newly reported specimens together with AH, took most photographs, examined all specimens recording morphological data, performed all literature research as well as morphological comparisons and GIS analyses, wrote the manuscript, and created the figures as well as the map.

Lotzkat et al. (2012c): I collected most of the newly reported specimens together with AH, took all photographs except those of the type locality, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, wrote the manuscript, and created the figures, map, and table.

Lotzkat et al. (2012d): I collected the type series and many examined specimens together with AH, took all photographs, examined all Panamanian specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, produced the line drawings, wrote the manuscript, and created the figures (except the map) as well as the tables.

Lotzkat et al. (2013): I collected the type series and most examined specimens together with AH, took most of the photographs that are not hemipenis close-ups, examined all specimens recording morphological data, generated the 16S barcodes together with JFB and carried out all molecular analyses, performed all literature research as well as morphological and GIS analyses, wrote the manuscript, and created the figures, maps, and tables.

Lotzkat et al. (2014): I collected all of the newly reported specimens together with AH, took all photographs, examined all specimens recording morphological data, performed all literature research as well as morphological and GIS analyses, wrote the manuscript, and created the figures, map, and table.

Affidavit

I herewith declare in lieu of an oath that I have produced the present dissertation

"Diversity, taxonomy, and biogeography of the reptiles inhabiting the highlands of the Cordillera Central (Serranía de Talamanca and Serranía de Tabasará) in western Panama"

autonomously and in doing so did not avail myself of resources which are not specified therein. In particular, all borrowings taken from other writings are marked with references to the respective writings.

I assure that I have adhered to the principles of good scientific practice and did not make use of the services of any commercial doctorate agencies or consultants.

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorgelegte Dissertation

"Diversity, taxonomy, and biogeography of the reptiles inhabiting the highlands of the Cordillera Central (Serranía de Talamanca and Serranía de Tabasará) in western Panama"

selbständig angefertigt und mich anderer Hilfsmittel als der in ihr angegebenen nicht bedient habe, insbesondere, dass alle Entlehnungen aus anderen Schriften mit Angabe der betreffenden Schrift gekennzeichnet sind.

Ich versichere, die Grundsätze der guten wissenschaftlichen Praxis beachtet, und nicht die Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen zu haben.

Frankfurt am Main, den ....

Sebastian Lotzkat

Curriculum vitae

Dipl.-Biol. Sebastian Lotzkat

Contact:

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Senckenberganlage 25
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slotzkat@senckenberg.de
lotzkat@yahoo.com

Personal Information:

Born: 4th September 1981 in Friedberg (Hesse), Germany
Nationality: German
Marital status: engaged

Education

04/2008–03/2011	PhD scholarship holder of the Studienstiftung des deutschen Volkes
since 10/2007	Doctoral studies at the Faculty of Biosciences at Goethe-Universität Frankfurt, in cooperation with the Herpetology Section at Senckenberg Research Institute Frankfurt Thesis: "Diversity, taxonomy, and biogeography of the reptiles inhabiting the highlands of the Cordillera Central (Serranía de Talamanca and Serranía de Tabasará) in western Panama." Supervisors: Prof. Dr. Bruno Streit (Goethe-University), Dr. Gunther Köhler (Senckenberg Research Institute)
05/2007	Diploma in Biology (specialization biodiversity) with the grade point average "very good" (1.0) and the rating "passed with distinction". Diploma thesis: "Taxonomie und Zoogeographie der Herpetofauna des Nirgua-Massivs, Venezuela." Supervisors: Prof. Dr. Bruno Streit, Dr. Gunther Köhler Diploma examinations in ecology and evolution of animals (Prof. Dr. Bruno Streit), ecology and evolution of plants and fungi (Prof. Dr. Georg Zizka), and plant physiology (Prof. Dr. Wolfgang Brüggemann)
10/2001–05/2007	Diploma course of studies in Biology at Goethe-Universität Frankfurt major subjects: physiology and biochemistry of plants and fungi (Prof. Dr. C. Büchel, Prof. Dr. W. Brüggemann, Prof. Dr. G. Sandmann), ecology and evolution of plants and fungi (Prof. Dr. M. Piepenbring, Prof. Dr. W. Brüggemann, Prof. Dr. R. Wittig, Prof. Dr. G. Zizka), ecology and evolution of animals (Prof. Dr. J. Oehlmann, Prof. Dr. F. Schrenk, Prof. Dr. B. Streit)
2000–2001	Civilian service at Jugendcafé Oberursel, a municipial youth center
1991–2000	secondary school: Kaiserin-Friedrich-Gymnasium (KFG) Bad Homburg
1988–1991	primary school in Bad Homburg

Language skills

English	fluent in spoken and written
Spanish	fluent in spoken and written
Portuguese	very good basic knowledge in spoken and written
Russian	basic knowledge in spoken and written

Practical experience (selection)

10–11/2013	herpetological field work on Isla del Coco, Costa Rica, on invitation by the country's environmental authorities (4 weeks)
since 12/2008	maintainance of the homepage of the Herpetology Department at Senckenberg Research Institute Frankfurt; publication of subpages on the own research project
06/2008	lecture and practical course "Introducción a la taxonomía y sistemática de anfíbios y reptiles" at the Universidad Autónoma de Chiriquí, Panama
since 05/2008	tutelage and supervision of German as well as international Bachelor, Master, Diploma, and PhD students in Germany and Panama
05/2008–08/2010	planning, realization, and direction of herpetological field work in Panama (4 research trips amounting to more than 12 months)
since 10/2007	referee in the peer-review process of scientific journals, e.g., Check List, Herpetological Review, Herpetologica, and Zootaxa
since 08/2007	involvement in the collection management at the Herpetological Department of Senckenberg Research Institute Frankfurt
since 07/2007	freelancer for the garden educational service ("Grüne Schule") at Palmengarten Frankfurt and the museum educational service ("Museumspädagogik") at Senckenberg Naturmuseum Frankfurt: realization of the regular offer of guided tours and events; conceptual design and realization of own guided tours, courses, and events as well as special offers behind the scenes and/or outside of opening hours
since 07/2007	contribution of own photographs to herpetological books and The Reptile Database
05/2007–04/2008	assistant at Zentrum für Lehrerbildung, Schul- und Unterrichtsforschung: videography of lectures, processing of videos, publication on streaming servers and e-learning platforms
05–11/2006	herpetological field work in Nicaragua and Venezuela (5.5 months)
04–05/2006	student assistant at Herbarium Senckenbergianum: digital cataloging of voucher specimens with the collection database tool SESAM
2005–2007	student assistant in practical courses for 1st and 2nd semester students of biology
2004–2006	teaching lessons at two private coaching institutes in Bad Homburg ("Sprach- und Schülerzentrum" and "Schülerhilfe")

Affiliations and voluntary service (selection)

09/2009–06/2012	elected speaker of the Young Scientists @ Senckenberg Gesellschaft für Naturforschung: interface to Board of Directors, internal & external communication, retreats, homepage
since 2012	member of the scientific advisory board of the Reptile Database
since 2012	member of Physikalischer Verein Frankfurt a.M.
since 2010	member of Gesellschaft für Tropenökologie (gtö)
since 2006	member of Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT)
08–09/2003	volunteer work at the rain forest sanctuary Jatun Sacha, Ecuador
2002	organization of a fundraising tour of Alfred Welker SJ through Germany on behalf of the Jesuit Mission Germany
10–11/2001	volunteer work at the mission station of the Jesuit Alfred Welker SJ in Cali, Colombia
since 1993	member of Frankfurter Fischereiverein von 1875
since 1992	member of Naturschutzbund Deutschland (NABU)

Further training (selection; if not otherwise stated, courses at Goethe Graduate Academy Frankfurt)

2012	Media training for scientists (scientific editorial offices of the southwest-German broadcasting corporation SWR, Baden-Baden) Management and curation of zoological collections Species distribution modelling with R and Maxent
2011	Introduction to ArcGIS I+II Writing for the media PR for scientists

2010	Analysis and interpretation of multivariate data in ecology
	Conflict Management
	Leadership for young scientists
	Preparing a conference poster
	Project coordination
2009	Oral scientific presentation
	Scientific English writing skills
	Statistics: Theory & R basics

Scientific talks and posters (selection)

2014	Two names are too few names: a revision of Central American *Lepidoblepharis* (Deutscher Herpetologentag, 02.–03.10.2014 in Bonn, Germany)
	Two species are too few species: the herpetofauna of Isla del Coco, Costa Rica (Deutscher Herpetologentag, 02.–03.10.2014 in Bonn, Germany)
2013	Reptile diversity in the highlands of western Panama (Deutscher Herpetologentag, 26.–27.09.2013 in Bonn, Germany)
2012	Reptile diversity and distribution in the highlands of western Panama (7th World Congress of Herpetology, 08.–14.08.2012 in Vancouver, Canada)
2011	Deciphering reptile diversity in western Panama (16th European Congress of Herpetology, 25.–29.09.2011 in Luxemburg)
2010	Biodiversidad de la Herpetofauna (del oeste) de Panamá – Avanzes del proyecto (Universidad Autónoma de Chiriquí, Panama)
	Reptilien in Westpanama – neue Erkenntnisse in Taxonomie und Zoogeografie (Deutscher Herpetologentag, 02.–05.09.2010 in Frankfurt, Germany)
	Known vertical distributions: a matter of fact or just of altitudes studied? (Poster at Deutscher Herpetologentag, 02.–05.09.2010 in Frankfurt, Germany)
2009	Diversidad y ecología de los anfibios y reptiles de Panamá (Universidad de Panamá, Facultad de Ciencias Agropecuarias, Dirección de Extensión, Chiriquí, Panamá)
	On noteworthy records of amphibians and reptiles from western Panama (Deutscher Herpetologentag, 02.–06.09.2009 in Karlsruhe, Germany; presented by Andreas Hertz)
2007	Taxonomie und Zoogeographie der Herpetofauna des Nirgua-Massivs, Venezuela (joint annual meeting of the DGHT and ÖGH, 3.–7.10.2007 in Hallein, Austria)
	Die Herpetofauna des Nirgua-Massivs, Venezuela (Poster at joint annual meeting of the DGHT and ÖGH, 3.–7.10.2007 in Hallein, Austria)

Popular scientific talks, guided tours, and workshops (selection)

2014	Was kriecht denn da... verborgener Vielfalt auf der Spur (presentation on reptile diversity research for kids and teenagers at "Tschira Explore Science 2014", 4 talks á 30–50 min)
since 2013	Kaltblütige Nachbarn (yearly interactive workshop on German herpetofauna for 7th grade students of Elisabethenschule Hofheim, including field excursion, 2 x 3 days á 4 h)
	Was kriecht denn da? (herpetological excursions at day- and nighttime on behalf of the Senckenberg Naturmuseum Frankfurt, 4 events á 8–9 h)
since 2012	Science Slam: "Wer bin ich – und wenn ja, wie viele?" (on reptile diversity research, á 10 min, held in presentation contests with audience jury, winner in 29 of 36 competitions)
2011	Climate change and human health (public guided tours at Senckenberg Naturmuseum Frankfurt, 3 tours á 60 min)
since 2009	Collections and research at the Herpetology Department of the Senckenberg Research Institute (tours "behind the scenes" for selected groups, á 30–120 min)
08/2008	Serpientes venenosas del oeste de Panamá (presentation for the medical staff of the Hospital de San Félix, Panama, 60 min)
since 2008	Public Weekend Guided Tours at the Palmengarten Frankfurt (diverse topics, á 90 min)
	interactive hands-on stations at the Senckenberg Naturmuseum Frankfurt (herpetological and general biodiversity topics, during special events)
since 2007	Public Wednesday Night Guided Tours at the Senckenberg Naturmuseum Frankfurt (more than 25 topics, á 60 min)
	Science after Work at the Senckenberg Naturmuseum Frankfurt (interactive evening workshops on 7 different topics, á 90 min)

Publications

Scientific publications (peer-reviewed)

2014 Batista, A., A. Hertz, K. Mebert, G. Köhler, **S. Lotzkat, M.** Ponce & M. Vesely: Two new fringe-limbed frogs of the genus *Ecnomiohyla* (Anura: Hylidae) from Panama. Zootaxa 3826 (3): 449–474.

Lotzkat, S., A. Batista, M. Ponce & A. Hertz: Distribution extension for *Anolis pseudokemptoni* Köhler, Ponce, Sunyer and Batista, 2007 (Reptilia: Squamata: Dactyloidae), a microendemic to the Serranía de Tabasará in the Comarca Ngöbe-Buglé of western Panama. Check List 10 (1): 189–192.

2013 Bienentreu, J.-F., A. Hertz,. G. Köhler & **S. Lotzkat**: Distribution extension for *Anolis salvini* Boulenger, 1885 (Reptilia: Squamata: Dactyloidae), in western Panama. Check List 9 (1): 169–174.

Hertz, A., **S. Lotzkat,** & G. Köhler: New distribution records and variation of the two common lowland salamanders *Bolitoglossa colonnea* (Dunn, 1924) and *B. lignicolor* (Peters, 1873) in Panama (Amphibia: Caudata: Plethodontidae). Check List 9 (1): 83–91.

Hertz, A., **S. Lotzkat,** & G. Köhler: A new species of *Bolitoglossa* (Caudata, Plethodontidae) from the continental divide of western Panama. Zootaxa 3636 (3): 463–475.

Lotzkat, S., A. Hertz, J-F. Bienentreu & G. Köhler: Distribution and variation of the giant alpha anoles (Squamata: Dactyloidae) of the genus *Dactyloa* in the highlands of western Panama, with the description of a new species formerly referred to as *D. microtus*. Zootaxa 3626 (1): 1–55.

2012 Hertz, A., F. Hauenschild, **S. Lotzkat** & G. Köhler: A new golden frog species of the genus *Diasporus* (Amphibia, Eleutherodactylidae) from the Cordillera Central, western Panama. ZooKeys 196: 23–46.

Hertz, A. & **S. Lotzkat**: A new range extension record of the canopy-dwelling frog *Isthmohyla picadoi* (Dunn, 1937) (Amphibia: Hylidae) from the Serranía de Tabasará, Panamá. Herpetology Notes 5: 37–39.

Hertz, A., **S. Lotzkat,** A. Carrizo, M. Ponce, G. Köhler & B. Streit: Field notes on findings of threatened amphibian species in the central mountain range of western Panama. Amphibian and Reptile Conservation 6 (2): 9–30.

Köhler, G., A. Batista, M. Vesely, M. Ponce, A. Carrizo & **S. Lotzkat**: Evidence for the recognition of two species of *Anolis* formerly referred to as *A. tropidogaster* (Squamata: Dactyloidae). Zootaxa 3348: 1–23.

Lotzkat, S., A. Batista, J. Vargas, A. Hertz & G. Köhler: Reptilia, Squamata, Gymnophthalmidae, *Potamites apodemus* (Uzzell, 1966): Distribution extension and first records from Panama. Check List 8 (2): 302–306.

Lotzkat, S., A. Hertz, R. De Leon & G. Köhler: Distribution extension for *Leposoma rugiceps* (Cope, 1869) (Squamata: Gymnophthalmidae) in Panama, with first record from Bocas del Toro Province. Check List 8 (3): 520–524.

Lotzkat, S., A. Hertz & G. Köhler: A new species of *Sibon* (Squamata: Colubroidea: Dipsadidae) from the Cordillera Central of western Panama, with comments on other species of the genus in this area. Zootaxa 3485: 26–40.

Lotzkat, S., L. Stadler, A. Batista, A. Hertz, M. Ponce, N. Hamad & G. Köhler: Distribution extension for *Anolis gruuo* Köhler, Ponce, Sunyer and Batista, 2007 (Reptilia: Squamata: Dactyloidae), in the Comarca Ngöbe-Buglé of western Panama, and first records from Veraguas province. Check List 8 (4): 620–625.

2011 Hertz, A., **S. Lotzkat,** L. Stadler, N. Hamad, A. Carrizo & G. Köhler: Noteworthy records of Amphibians from Western Panamá. Herpetological Review 42 (2): 245–250.

Lotzkat, S., J.-F. Bienentreu, A. Hertz & G. Köhler: A new species of *Anolis* (Squamata: Iguania: Dactyloidae) formerly referred to as *A. pachypus* from the Cordillera de Talamanca of western Panama and adjacent Costa Rica. Zootaxa 3125: 1–21.

Lotzkat, S. & A. Hertz (2011 "2010"): La herpetofauna (Amphibia: Anura, Caudata; Reptilia: Crocodylia, Squamata, Testunides) de Los Algarrobos, Chiriquí, occidente de Panamá. Puente Biológico 3: 89–99.

2010 Hertz, A. & **S. Lotzkat**: Notes on vocalisation and natural history of *Hylomantis medinae* (Funkhouser, 1962) (Anura, Hylidae) from northern Venezuela. Salamandra 46 (2): 121–124.

Hertz, A. & **S. Lotzkat**: *Cochranella albomaculata.* Predation. Herpetological Review 41 (2): 194.

Köhler, G., **S. Lotzkat** & A. Hertz: A new species of *Sibon* (Squamata: Colubridae) from western Panama. Herpetologica 66 (1): 80–85.

Lotzkat, S., A. Hertz, L. Stadler, N. Hamad, A. Carrizo & Köhler, G. (2010): Noteworthy

Distribution Records of Reptiles from Western Panamá. Herpetological Review 41 (4): 520–523.

LOTZKAT, S., J.J. KÖHLER, A. HERTZ & G. KÖHLER: Morphology and colouration of male *Anolis datzorum* (Squamata: Polychrotidae). Salamandra 46 (1): 48–52.

LOTZKAT, S., L. STADLER, A. CARRIZO, A. HERTZ & G. KÖHLER: Notes on the easternmost population of *Diploglossus bilobatus* (Squamata: Anguidae) in Veraguas, Panama. Salamandra 46 (1): 59–62.

2009 HERTZ, A., M. NATERA, **S. LOTZKAT,** J. SUNYER & D. MORA: Life History: *Bothrops asper*. Prey. Herpetological Review 40 (2): 230.

2008 **LOTZKAT, S.**, M. NATERA-MUMAW, A. HERTZ, J. SUNYER & D. MORA: New state records of *Dipsas variegata* (Duméril, Bibron and Duméril 1854) (Serpentes: Colubridae) from northern Venezuela, with comments on natural history. Herpetotropicos 4 (1): 25–29.

SUNYER, J., **S. LOTZKAT,** A. HERTZ, D.B. WAKE, B.M. ALEMAN, S.J. ROBLETO & G. KÖHLER: Two new species of salamanders (genus *Bolitoglossa*) from southern Nicaragua (Amphibia, Caudata, Plethodontidae). Senckenbergiana biologica 88 (2): 319–328.

2007 **LOTZKAT, S.**, A. HERTZ & J. VALERA-LEAL: Amphibia, Anura, Hylidae, *Hylomantis medinai*: distribution extension by discovery of a third population. Check List 3 (3): 200–203.

Other publications (selection)

2014 **LOTZKAT, S.** & J. VARGAS (2013–2014): Isla del Coco Expeditions-Blog. 13 illustrated blog entries. Accessible at: http://www.senckenberg.de/root/index.php?page_id=5201&id=28.

2013 **LOTZKAT, S.** (2013): Slammer des Monats: Eine Suche der anderen Art. GEO 03/2013: 140. Accessible at: http://www.geo.de/GEO/heftreihen/geo_magazin.

LOTZKAT, S. (2013): Book Review: The Amphibians and Reptiles of Cyprus**.** Herpetological Review 44 (1): 162–164.

LOTZKAT, S. & A. HERTZ (2008–2013): Biodiversität, Ökologie und Zoogeographie der Herpetofauna der Zentralkordillere im westlichen Panama. Project website. Accessible at: http://www.senckenberg.de/root/index.php?page_id=5815.

2012 HERTZ, A. & **S. LOTZKAT** (2012): Die Frösche pfeifen auf Kupfer – Amphibienforschung in der Serranía de Tabasará. Senckenberg – Natur · Forschung · Museum 142 (7/8): 270–273.

LOTZKAT, S. (2012): Neue Schneckennatter setzt Zeichen gegen Raubbau. Terraria/elaphe 39: 54–55.

LOTZKAT, S. (2012): YS@S – Wissenschaftlicher Nachwuchs bei Senckenberg. Pp. 104–107 in: Mosbrugger, V. (Eds.) 2012: Forschung für die Zukunft – Senckenberg Jahresbericht 2009–2010.

2011 KÖHLER, G., KÖHLER, J., SCHULZE, A., VARGAS, J., **LOTZKAT, S.** & E. THIEL (2011): Frösche, Schlangen, Salamander – Biodiversitäts-Monitoring in Costa Rica. Senckenberg – Natur · Forschung · Museum 141 (7/8): 246–253.

LOTZKAT, S.· (2011): Buchbesprechung: Grundkurs Amphibien- und Reptilienbestimmung. Senckenberg – Natur · Forschung · Museum 141 (7/8): 274.

LOTZKAT, S. (2011): Book Review: The Snakes of Honduras — Systematics, Distribution, and Conservation**.** Herpetological Review 42 (4): 627–628.

LOTZKAT, S. & V. KÖCKE (2011): Networken mit Spaß dabei! Viertes Jahrestreffen der Young Scientists @ Senckenberg. Senckenberg – Natur · Forschung · Museum 141 (5/6): 192.

2010 **LOTZKAT, S.** & A. HERTZ, A. (2010): Panama Expeditions-Blog. 16 illustrated blog entries. Accessible at: http://www.senckenberg.de/root/index.php?page_id=8019&id=9.

2009 HERTZ, A. & **S. LOTZKAT** (2009): Herpetologische Forschung in Mittelamerika. Terraria 20: 79–82.

LOTZKAT, S., A. HERTZ & G. KÖHLER (2009): Auf herpetologischer Expedition in den Bergwäldern Panamas. Natur und Museum 139 (7/8): 228–235.

LOTZKAT, S. & G. KÖHLER (2009): Book Review: The Amphibians and Reptiles of Cusuco National Park, Honduras / Los Anfibios y Reptiles del Parque Nacional Cusuco, Honduras**.** Herpetological Review 40 (4): 472–473.

2008 HERTZ, A., **S. LOTZKAT** & G. KÖHLER (2008): Ein Gebirge, zwei Gesichter – eine herpetologische Forschungsreise nach Venezuela. Natur und Museum 138 (1/2): 1–13.

2007 **LOTZKAT, S.** (2007): Taxonomie und Zoogeographie der Herpetofauna des Nirgua-Massivs, Venezuela. Diploma thesis, Johann Wolfgang Goethe-Universität Frankfurt am Main, 160 pp.

LOTZKAT, S. (2007): Taxonomía y zoogeografía de la herpetofauna del Macizo de Nirgua, Venezuela. Spanish translation of diploma thesis, 160 pp.

2006 HERTZ, A. & **S. LOTZKAT** (2006): Terrestrische Fauna der Umgebung von Rovinj. Pp. 89–100 in: Türkay, M. & C. Winter [Eds.]: Bericht über die meeresbiologische Exkursion des Zoologischen Institutes der Universität Frankfurt nach Rovinj/Kroatien 21.VIII–3.IX 2005.

Books containing own photographs of amphibians and reptiles

2014 McConnell, G. (2014): A field guide to the snakes of Costa Rica. Edition Chimaira, Frankfurt. 233 pp. **73 photos.**

Steinmann, F. & C. van der Lingen (2014): *Oophaga pumilio* – das Kompendium. Edition Chimaira, Frankfurt. 220 pp. **7 photos.**

2013 Ray, J.M. & J.L. Knight (2013): Venomous snakes and their mimics of Panama and Costa Rica. CreateSpace. 282 pp. **9 photos.**

2012 Bellosa, H. & H. Bisplinghof (2012): Regenbogenboas — das Kompendium. Edition Chimaira, Frankfurt. 223 pp. **2 photos.**

Eisenberg, T. & J. Kaesling (2012): Rotaugenlaubfrösche. Die Gattungen *Agalychnis* und *Cruziohyla*. Natur und Tier Verlag, Münster. 191 pp. **4 photos.**

2011 Köhler, G. (2011): Amphibians of Central America. Herpeton Verlag, Offenbach. 378 pp. **1 photo.**

2009 Fläschendräger, A. & L. Wijffels (2009): *Anolis*. Natur und Tier Verlag, Münster. 319 pp. **24 photos.**

2008 Köhler, G. (2008): Reptiles of Central America. Second updated and revised edition. Herpeton Verlag, Offenbach. 400 pp. **18 photos.**

2007 Lötters, S., Jungfer, K.-H., Henkel, F. W. & W. Schmidt (2007): Poison Frogs. Edition Chimaira, Frankfurt. 668 pp. **3 photos.**

Addenda & Corrigenda

The present PhD thesis has been submitted in this original version to the Faculty of Biosciences of Goethe University Frankfurt on 20. November 2014. Until its final publication in July 2015, I have noticed several text passages requiring corrections or additions. In the following, I list these Addenda and Corrigenda in the order of their appearance in the text:

Addenda:

page 872, second paragraph, last line: the institutions they represent are missing for Julia Offe (scienceslam.de) and Nina Schaller (Klaus Tschira Stiftung gGmbH)

page 873, second paragraph: my colleagues Lisa Schulte, Ross McCulloch, Robert W. Murphy, Dennis Rödder, and When-zi Wang should be included

page 872, second paragraph, last lines: Andreas Hertz and Joe-Felix Bienentreu should be included in the line drawing acknowledgements

page 882: between DeJesus (2007) and Doan & Castoe (2005), the following reference repeatedly cited in the species accounts for the three members of *Chironius* on pp. 538–542 should be inserted:

Dixon, J.R., J.A. Wiest & J.M. Cei (1993): Revision of the neotropical snake genus *Chironius* Fitzinger (Serpentes, Colubridae). Museo Regionale di Scienze Naturali Torino Monografie, 13: 1–280.

Corrigenda:

page 8, second paragraph, line 3: "*Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013" should read "*Dactyloa ginaelisae* Lotzkat, Hertz, Bienentreu & Köhler 2013"

page 14, line 3: "*Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013" should read "*Dactyloa ginaelisae* Lotzkat, Hertz, Bienentreu & Köhler 2013"

page 20, second paragraph, line 3: "*Dactyloa ginaelisae* Lotzkat, Bienentreu, Hertz & Köhler 2013" should read "*Dactyloa ginaelisae* Lotzkat, Hertz, Bienentreu & Köhler 2013"

page 23, line 3: "gut über 1000 m liegenden Höhen" should read "gut über 1000 m liegende Höhen"

page 23, penultimate line: "La Amistad, und" should read "La Amistad und"

page 82, line 9: "ascents" should read "ascends"

page 121, second paragraph, line 16f: "after assessing verifying" should read "after verifying"

page 222, second paragraph, line 13: "scales.Contrary" should read "scales. Contrary"

page 223, line 1: "to our knowledge" should read "to my knowledge"

page 334, Tab.4.26, right column, rows 1 and 2: the *Corallus* species names should be indented the same way as the following ones

page 364, penultimate line: "tree next close to our camp" should read "tree close to our camp"

page 388, second paragraph, line 2: "2.4H;2.5A" should read "2.4H; 2.5A"

page 848, second paragraph, line 28: "information on its color) have tought" should read "information on its color), have tought"

page 891, Lotzkat et al. (2013), last line: "1–55" should read "1–54"

page 903: "on enclosed DVD-ROM" should read "on enclosed CD-ROM"

page 928, Lotzkat et al. (2013), last line: "1–55" should read "1–54"

page 929, second Lotzkat (2012), line 2: "Mosbrugger, V. (Eds.)" should read "Mosbrugger, V. (Ed.)"

Moreover, for the final publication in July 2015, I included this sheet of Addenda & Corrigenda after the last page and inserted the third referee as well as the date of my thesis defense on p. 3 of the present thesis, and included a revised version of the digital Appendix 9 with corrected species names for *Trachemys grayi* and *Phrynonax poecilonotus* as well as some minor layout adjustments.