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and description of a new species from Tobago represented by males
(Polydesmida: Leptodesmidea: Chelodesmidae:
Chelodesminae: Pandirodesmini)

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The enigmatic milliped genus *Pandirodesmus* Silvestri 1932 and description of a new species from Tobago represented by males (Polydesmida: Leptodesmidea: Chelodesmidae: Chelodesminae: Pandirodesmini)

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Abstract. *Pandirodesmus rutherfordi*, n. sp., represented by 18 individuals including eight adult males, occurs in secondary forests near Charlotteville and Speyside, Tobago, Trinidad and Tobago. Along with the type and second species, *P. disparipes* Silvestri, from Guyana and known only from females, the segmental legs of *P. rutherfordi* alternate between long (anterior pairs) and short (posterior ones), spiracular openings are on straw-like tubules, and ozopores are located on paramedian metatergal spines. These features appear to be adaptations for biotopes of loose sand, detritus, or frass, and 17 specimens, including the six juveniles, exhibit coatings of “sand grains” that are loosely cemented together and to the smooth, translucent, grayish-white exoskeleton. The tubules and spines elevate the spiracles and ozopores above the coating, thereby ensuring that they remain open and functional. The coating, which provides camouflage and lends strength and rigidity to the poorly sclerotized exoskeleton, is a subuniform “pavement” that covers the entire animal except the labrum/clypeus, tarsal and antennal apices, prozoniae, paraprocts, and the gonopods in males. Ramose/dendritic setae, particularly on narrowly rounded podo-/antennomeres, trap “sand grains,” and the ozopore secretions apparently constitute the “glue” that cements the coating, as evidenced circumstantially by layers of “sand” between the spines on the anterior metaterga, where they are physically closest. The alternating segmental leg lengths, in part due to differing ventrolateral and ventromedial origins, appear to be an adaptation for lateral/sideways motion in which the long (anterior) legs extend laterally and pull the body to the level of the short (posterior) ones, which continue the motion while the anterior legs extend to begin the next stroke. The opposing legs perform the complementary pushing motion a fraction after the long legs initiate the pulling stroke and hence are slightly and purposefully out of sync. An adult male paratype lacks the coating, probably because it had just molted and lacked time to amass it; the juvenile female paratype of *P. disparipes* also is “naked,” as was, according to Silvestri, the now lost adult female holotype. Until fresh material is collected, coatings cannot be confirmed for *P. disparipes* even though it shares the anatomical modifications that seem adaptations for such. The minute, triramous gonotelopodites of *P. rutherfordi* are unlike any known for a chelodesmid, so the current generic placement, in a monotypic tribe in the nominate chelodesmid subfamily, is retained. With species in both South America and the southern Antilles, *Pandirodesmus*/ini had to exist on both the “proto-Antillean” terrane and the adjoining part of Pangaeon Gondwana before the former rifted in the Cretaceous/Paleocene, ~66 million years ago, and *P. rutherfordi* is a remnant of the former population that became isolated on present-day Tobago when the terrane fragmented. Affinity between Guyanan and southern Antillean platyrhacid millipeds (Polydesmida: Leptodesmidea) suggest that *Pandirodesmus*/ini may occur sporadically as far north in the island chain as St. Lucia.

Key Words. adaptation, alternating leg lengths, Antilles, Guyana, metaterga/-zona, ozopores, “sand coating,” spiracles, Trinidad

Introduction

In 1932, Filippo Silvestri discovered two “extraordinary” polydesmidan millipeds among loaned AMNH material (acronyms below) from Kamakusa, Cuyuni-Mazaruni Region (Reg.), Guyana (then “British Guiana”). Two females, an adult and a juvenile, possessed bizarre somatic features that set them apart from all diplopods then known – stigmata on slender tubercles instead of flush with metazonal surfaces; ozopores on digitiform/spiniform metatergal projections rather than paranota; ventrolateral, rather than medial, origins of the anterior segmental legs; and disparate, rather than subequal, leg lengths, the anterior pair on each segment being substantially longer than the posterior one. Despite the absence of gonopods, Silvestri appropriately established *Pandirodesmus disparipes*, n. gen., n. sp., and Pandirodesminae, n. subfam., for this form and suggested affinity with *Trachelodesmus* Peters, which shares slender tarsal claws that are superseded in length and obscured by filiform setae. Hoffman (1975) and Adis and Golovatch (2000) expanded the association to Trachelodesmini (Chelodesmidae: Chelodesminae) in general, and Hoffman also noted their geographical concordance. Aspects of the gonopods and their general configurations are the key determinants of affinities among chelodesmids, so while relationships and the tribe’s position within Chelodesminae (*sensu* Hoffman 1978, 1980, 1982) are unknown, males of *Pandirodesmus* may illuminate this matter.

In June 2012, Michael G. Rutherford, Curator at the University of the West Indies Zoology Museum, St. Augustine, Trinidad, Trinidad and Tobago, encountered four small-bodied female millipeds with unequal legs (Fig. 1) on frass under bark of a decaying tree stump in northern Tobago (Fig. 2–3), and in 2013, he found eight males, six adults and two juveniles, on the same stump. All individuals except one adult male were covered with a coating of “sand” of subequal thickness. Despite the ~787 km (492 mi) distance between the Guyana and Tobago localities, 38% [~306 km (191 mi)] of which is open ocean, the somatic features match those characterized and illustrated for *P. disparipes* (Silvestri 1932, Adis and Golovatch 2000, Golovatch and Kime 2009) leaving no doubt about their congeneric status. With the substantial time separation indicated by the distance and occurrence on both a continent and island, specific-level divergence is likely, so we propose *P. rutherfordi*, n. sp., for the Tobagan form, characterize its gonopods, and generalize as to generic and tribal conditions 83 years after the taxa were established. We also discuss inferences RMS drew about the coating and anatomical modifications from examinations and observations of the type series and close with a hypothesis on the origin of the Tobagan population and a projected Antillean range. Repository acronyms are AMNH, American Museum of Natural History, New York, New York, United States (US/USA); FSCA, Florida State Collection of Arthropods, Gainesville, USA; NCSM, North Carolina State Museum of Natural Sciences, Raleigh, USA; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, DC; and UWIZ, University of the West Indies Zoology Museum, St. Augustine, Trinidad, Trinidad and Tobago.

Taxonomy [from Shelley (2003) and Shear (2011)]

Order Polydesmida Pocock 1887

Suborder Leptodesmidea Brölemann 1916

Superfamily Chelodesmoidea Cook 1895

Family Chelodesmidae Cook 1895

Subfamily Chelodesminae Cook 1895

Tribe Pandirodesmini Silvestri 1932

Pandirodesminae Silvestri 1932: 11–12. Jeekel 1971: 366. Hoffman 1975 (text): 143; 1980: 153.

Pandirodesmidae: Attems 1940: 483. Jeekel 1963 (list): 5.

Pandirodesmini: Hoffman 1975 (text): 144; 1980: 153. Adis and Golovatch 2000 (text): 98.

Type- and only component genus. *Pandirodesmus* Silvestri 1932

Diagnosis. A tribe of small bodied Chelodesminae characterized by lightly sclerotized, smooth, grayish-white exoskeleton and alternating long and short legs, exposed parts usually covered with densely cemented but loosely attached sand grains imparting dark beige to black coloration and obliterating setae. Metaterga narrow, without sulci, with pair of moderately large, subconical/digitiform projections, ozopores opening subapically on latter. Paranota absent. Stigmata opening apically on slender, inconspicuous tubules narrowly segregated from, and slightly shorter than, adjacent coxae. Anterior (longer) segmental legs arising ventrolaterad, posterior (shorter) legs arising submediad, anterior halves of sterna thus broader than caudal halves; leg lengths alternating along most of length of body, posterior pair $\sim 2/3$ as long as anterior on segments 5–18; femora and tarsi substantially longer than remaining podomeres on all legs, postfemora short, swollen, and nodular, articulating extremities of tibiae and tarsi also swollen and nodular. Claws absent from legs 1–3, narrow and “pin-like” on remaining legs, surrounded and overhung by long, filiform setae, those on coxae to proximal end of tarsi apically ramose and dendritic. Gonopods minute; coxae without apophyses, joined by strong, distinct sternum; telopodite triramous, prefemoral process (medialmost) expanded, folded, and laminate, partly enveloping other branches, primary (lateralmost) long, curving broadly mediad and partly overhanging other branches, divided distad into medial solenomere and subequal tibiotarsus; secondary (inner) branch subupright, narrowing and expanding throughout length, tip bilobed. Prostatic groove opening apically on solenomere.

Distribution. Known only from west-central Guyana and the northern tip of Tobago, Trinidad and Tobago (Fig. 4).

Relationships. Based primarily on the shared minuteness of their tarsal claws that are overhung and partly concealed by apical setae, Silvestri (1932), Hoffman (1975), and Adis and Golovatch (2000) suggested affinity between Pandirodesmini and Trachelodesmini. As RMS has conducted two studies on Trachelodesmini (Shelley 1981, 1999) and has closely examined *P. rutherfordi*, we do not perceive such an affinity; among other differences, the exoskeleton of *P. rutherfordi* is as smooth as baby’s skin, not rough or tuberculate as in most trachelodesminines. To us, the partly volvated juvenile (Fig. 5) superficially resembles an oniscodesmid (Polydesmida: Polydesmidea), but we concur with the tribe’s present placement. Only three leptodesmidean families inhabit South America – Chelodesmidae, Platyrhacidae, and Aphelidesmidae – and with a triramous telopodite, Pandirodesmini is not assignable to the last two. From an anatomical standpoint, only two possibilities remain: assignment to Chelodesmidae, the only family with deeply bi- or tripartite telopodites, or placement in a monotypic taxon. Furthermore, rather than the apical tarsal trait, chelodesmid affinities are best revealed by gonopodal synapomorphies, but these appendages were not available to prior authors, and we do not find them helpful. Aside from the above works on trachelodesminines, we have no experience with chelodesmids and no thoughts as to Pandirodesmini’s affinities. As Chelodesmidae was a focus of the late R. L. Hoffman, we perused his papers and others in RMS’ library without finding any remotely similar gonopods; consequently, we leave Pandirodesmini in the nominate subfamily. Until another worker develops encyclopedic knowledge of Chelodesmidae, Pandirodesmini’s affinities will probably remain obscure, and our only present thought is that *Pandirodesmus/ini* may be the sole surviving remnant of an ancestral dichotomy that perhaps antedates development of the predominant diplosegment burrowing mechanisms. With two species and without obvious relatives remotely near its area, *Pandirodesmus/ini* are truly enigmatic taxa and similar in this regard to *Choctella* Chamberlin (Spirostreptida: Choctellidae) in the Cumberland Plateau of Tennessee and Alabama, United States (Hoffman 1969, Shelley and Floyd 2014).

Remarks. Silvestri (1932) originally assigned Pandirodesminae to Polydesmidae, and after Attems (1940) elevated the taxon to familial status, Hoffman (1980) reduced it to a tribe of the nominate chelodesmid subfamily.

Genus *Pandirodesmus* Silvestri 1932

Pandirodesmus Silvestri 1932: 1–3, 11. Attems, 1940: 483. Jeekel, 1971: 343. Hoffman, 1975 (text): 143; 1980: 153. Adis and Golovatch, 2000 (text): 98, 100, 105–106.

Type-species. *Pandirodesmus disparipes* Silvestri 1932, by original designation.

Diagnosis. With the characters of the tribe.

Distribution. Same as that of the tribe (Fig. 2).

***Pandirodesmus disparipes* Silvestri 1932**

Pandirodesmus disparipes Silvestri 1932: 11, fig. 1–5. Attems 1940: 484, fig. 682–683. Jeekel 1963 (list): 5. Adis and Golovatch 2000 (text): 97–105, fig. 1–18. Golovatch and Kime 2009 (text), fig. 3.

Type specimen. Juvenile F paratype (AMNH) collected by H. Lang on an unknown date prior to 1932 at Kamakusa, Cuyuni-Mazaruni Reg., Guyana. The adult F holotype, supposedly also at the AMNH, is lost. Thorough searches through their typical and non-typical holdings by RMS and entomology staff did not reveal it. Additionally, Dr. Maria Tavano checked the diplopod holdings at the Museo Civico di Storia Naturale “Giacomo Doria,” Genoa, Italy, which now houses Silvestri’s collection, and they too do not have this specimen.

Diagnosis. Metatergal spines digitiform to spiniform. Ambulatory postfemora subequal in length to prefemora, moderately swollen and appearing as normal podomere; apical tarsal setae distally curved. Gonopodal characters unknown.

Distribution. Known only from the type locality in west-central Guyana but may inhabit eastern Venezuela. Sampling is needed in these countries and poorly- and uninvestigated Suriname and French Guiana to recover males of *P. disparipes* and other leptodesmideans.

***Pandirodesmus rutherfordi* Shelley, new species**

Fig. 1, 5–14.

Type specimens. M holotype (FSCA) and 5M, 1F, and 2 juv. M paratypes (AMNH, FSCA, NCSM, NMNH) collected by M. G. Rutherford, 10 June 2013, under bark of a tree stump at 71 m elevation, 1 km (0.6 mi) N Charlotteville, Tobago, Trinidad and Tobago, in association with a tree stump along wooded/hilly Pirate’s Bay trail (11°19’52.9”N, 60°32’53.59”W); 4F paratypes (FSCA, NCSM, UWIZ) taken by same collector, 24 June 2012, at same locality on same stump; 1M, 2F paratypes (UWIZ) taken by same collector, 23 October 2014, along “Flagstaff Hill Trail” at the same general locality (11°19’34.82”N, 60°32’ 35.45”W).

Diagnosis. Metatergal spines entirely spiniform. Ambulatory postfemora short, strongly swollen and ring-like; apical tarsal setae sublinear. Gonopods as characterized generally for the tribe and genus, specific details in final descriptive paragraph.

Color in life. The entire body (head/face, segments, epi/para/hypoprocts, legs, gonopods, antennae) is poorly sclerotized and a translucent, grayish-white plastic color (Fig. 6), as in a pill-box for medications; some segments display a bluish tint. Most surfaces in most individuals are heavily encrusted with dark grains of “sand,” frass, and detritus that provide strength, rigidity, and camouflage, enabling the millipeds to blend with the substrate. The only parts of adult males that are not heavily encrusted are the prozonae, covered by the preceding metazonae in compressed individuals, the clypeus/labrum, paraprocts, and the gonopods, which need to be free for mating and reproduction. One adult male is “naked” (Fig. 6), entirely devoid of a coating, which enabled us to ascertain exoskeletal color, setal counts, and other features. It strongly resembles a troglobite with its alternately long legs and soft, poorly sclerotized body.

Description. Maximal length 9.3 mm, maximal width 1.4 mm, W/L ratio 15.2%. Body comprised of head and 20 segments including epiproct in both sexes; exoskeleton relatively soft, poorly sclerotized.

Head smooth, glabrous (Fig. 6). Epicranium with two dorsal knob-like structures; suture sharp, distinct, arising between knobs and terminating in supra-antennal region. Genal margins sublinear, extending at most only slightly beyond those of epicranium (Fig. 7). Facial setae fine, translucent, and difficult to discern against similarly translucent exoskeleton: epicranial 1–1; subantennal 1–1; frontal 2–2; genal 2–2; clypeal about 5–5; labral about 9–9, merging with clypeal series and continuing, and becoming progressively longer, for most of genal margins. Antennae short and stout (Fig. 7); reaching back to around midlength of 2nd tergite; antennomeres becoming broader distad, 1st antennomere subglobose, 2–5 clavate and with scattered moderately-long hairs on all surfaces, 6 short, broad, and ring-like, 7 truncate with four moderately-long apical cones; relative lengths of antennomeres 2>5>3=4>1>6>7.

Surfaces of pro- and metazonae smooth, glabrous (Fig. 5–6, 8). Collum short, narrow, and inconspicuous, with three narrow, tubular projections arising from anterior margin on either side of midline, two medialmost giving rise to long, slender, filiform setae. Metaterga 2–3 with two similarly tubular, aetose projections anteriolaterad, one per side; projections on 4–5 substantially longer and subdigitiform; projections continuing through segment 19, becoming basally broader and spiniform on 6–7 and positioned laterally at metatergal midlengths, becoming smaller on segments 13–14 and progressively more so caudad, reduced to short stubs on 18–19; ozopores opening subapically on all projections examined. Epiproct short, subtriangular, extending slightly beyond distal paraproctal margins (Fig. 6), with three small, marginal, subapical spinnerets per side giving rise to one hair each.

Sides of metazonae smooth, glossy, without noticeable grooves and impressions. Strictures strong, distinct. Spiracles located apically on thin, translucent, inconspicuous, straw-like tubules subequal in lengths to adjacent coxae, arising adjacent to coxal condyles. Pregonopodal sterna smooth, glossy, without noticeable modifications. Postgonopodal sterna smooth but slightly granular, with a few scattered hairs; anterior halves of sterna 5–18 (between anterior [longer] segmental leg pairs), substantially broader than caudal halves (between posterior [shorter] pairs) (Fig. 9). 1st legs short, crassate; 2nd legs longer, with tubular gonapophyses arising ventrally from coxae; 3rd–4th legs substantially longer; 5th legs short, around 2/3 as long as 4th; 6th legs long; 7th short; 8th long in females, replaced by gonopods in males; 9th legs short but longer than other short legs. Henceforth through segment 18, the last podous one, segmental legs alternating between long (anterior pair) and short (posterior pair) (Fig. 1, 9). Anterior legs arising ventrolaterad from ventral sternal surface (more lateral than in other chelodesmids) and progressively more laterally caudally (Fig. 9). Posterior legs about 3/4 as long as anterior legs but arising ventrad at about same position as in other chelodesmids (Fig. 9), lengths of coxae and 1/4th of that of prefemora offset by additional lengths of sterna between anterior leg coxae (Fig. 9), posterior legs thus extending laterad for only around 2/3 as far as adjacent anterior legs. Podomeres of legs 9–18 as follows (Fig. 8–9): coxae short, normal in appearance; prefemora and femora moderately long and slender; postfemora swollen and nodular; tibiae short but broad, ring-like but also appearing as small node; tarsi generally long and slender with slight to moderate, nodular swellings at 1/4 lengths, narrowing and tapering distad; relative lengths of podomeres as follows: tarsus > femur > prefemur > postfemur > coxa > tibia. Podomeres of legs 1–2 exhibiting same general pattern and arrangement but proportionally shorter; podomeres of legs 3–6 with dorsal postfemoral surfaces conspicuously swollen. Claws absent on legs 1–3, replaced by long, stiff setae, present on remaining legs but narrow, fine, and “pin-like”, surrounded by long filiform setae, only slightly larger and wider than claws, latter difficult to distinguish, slightly and gently curved, apically acuminate. Paraprocts (Fig. 9) subrectangular, margins not raised; hypoproct short and semilunar, with one subapical tubule per side giving rise to an apical seta.

Gonopodal aperture ovoid and minute, located entirely in metazonum, compressing both stricture and prozonum, unmeasurable with accuracy using vernier calipers but roughly 0.6 mm wide and 0.2 mm long at midpoints, all margins – anterior, lateral and caudal – substantially elevated above level of metazonum, rims smooth, without lobes projecting into opening. Gonopods in situ (Fig. 10) lying parallel to each other with apices of telopodital branches protruding slightly from opening, not overhanging anterior margin or 6th sternum, except NMNH paratype (Fig. 10) with telopodites fully extruded, angling anteriorly, and overhanging anterior margin of aperture. Gonopod structure (Fig. 11–14) as follows: Coxae (black) small, closely appressed together, joined by sclerotized sternum, without lobes

or apophyses, with two distocaudal macrosetae. Prefemur inconspicuous, a small rounded, moderately hirsute podomere overhung and overshadowed by larger acropodite, sandwiched between latter and coxae. Acropodite comprising three large, curvilinear to broadly expanded, convoluted branches (Fig. 10–14), color-coded for clarity in Fig. 11–14: prefemoral process (light green), primary projection (light blue), and secondary projection (red). Prefemoral process largest and anteriormost, extending distad for $\sim 2/3$ of length of primary projection, expanding anteriorly into broad, transparent, barely perceptible, irregularly folded lamina, extending well beyond proximal margin of prefemur and overhanging half of coxa, basal corner prolonged into rounded lobe, medial margin irregularly scalloped and jagged, distal margin folding broadly dorsad and appearing “rib-like” in medial and lateral perspectives, extending medially beyond level of adjacent lamina and overhanging latter. Secondary/interior projection (red) extending ventrad for $\sim 3/4$ of length of primary branch (blue), generally upright but anterior and posterior margins smoothly folded, curved, indented, and expanded, posterior margin curving completely over anterior margin distad, extending short distance into broadly expanded, bilobed termination. Primary/caudalmost projection (blue) long, curvilinear, narrowing and curving broadly anteriorly basally with two acuminate basal spines (one or both invisible in certain perspectives) on inner surface, leaning, or curving anteriorly, overhanging prefemoral process and/or secondary branch, expanding slightly, narrowing, and dividing into short medial solenomere, curving dorsad, and subequal, spiniform, anteriorly directed tibiotarsus. Prostatic groove arising from small prefemoral fossa, extending along medial surface of primary projection, opening apically on solenomere.

Ecology. The holotype and the paratypes from Pirate’s Bay Trail were encountered beneath bark of a tree stump that was too decayed to identify to species. They were close together but not tightly clustered and slowly moving on the surface of wet frass under bark in the center of one side of the stump (Fig. 2–3, red circled areas). The surrounding habitat is young secondary forest with a mixture of *Heliconia* plants, bamboo, and various trees. The paratypes from Flagstaff Hill Trail were on the soil surface beneath a rotting log that also was too decayed to identify, and the individuals from near Speyside, also from secondary forest, were beneath stones in a dilapidated building. All individuals were active from 11:00 AM – 4:00 PM, and the substrate was not particularly sandy at any of these sites.

Distribution. Known from the type locality and the following site, which is approximately 3.5 km (2.2 mi) to the south-southeast; the dot in Fig. 4 covers all known sites. Mr. Rutherford revisited all known sites in July 2015 but did not find any individuals, perhaps a reflection of dry conditions then.

Trinidad and Tobago: *Tobago*, forest north of Speyside Waterwheel near Speyside (11°18′15.34″ N, 60°31′56.46″ W), M, F, 24 October 2014, M. G. Rutherford (UWIZ).

Remarks. Per Silvestri’s (1932) measurements, *P. rutherfordi* is smaller and shorter than *P. disparipes*, but both are less than 1 cm long and hence small leptodesmideans. The minuteness of its anatomical features exacerbates the difficulty of examining *P. rutherfordi*; structures that are readily visible under 50–100X magnification on other leptodesmideans are indistinct on *P. rutherfordi* and should be carefully dissected and mounted on slides for compound microscopic examinations, which Silvestri (1932) must have done as evidenced by his elegant illustrations. Scanning electron microscopy, unavailable to us, is really needed, as shown by Adis and Golovatch (2000), and while we suspect their presences, we could not detect distal microsensillae on the 5th and 6th antennomeres, which Silvestri (1932, fig. 2c) depicted for *P. disparipes*. Additionally, setal structure is only vaguely visible at 100X magnification, but the apical “fuzziness” that most have is consistent with the splayed, dendritic condition of *P. disparipes* (Adis and Golovatch (2000, fig. 3, 13, 15–18).

Discussion. The comments below are based on RMS’ observations while examining the millipeds, handling them with fingers and forceps, and manipulating them with a number “0” insect pin to try to infer the functions of its anatomical modifications, and how they enhance survival in its preferred biotope. Silvestri (1932) suggested occurrence in or near water, and Adis and Golovatch (2000) and Golovatch and Kime (2009) supported this theory. While we have not seen live individuals, RMS gained insight from closely examining external features and videos that Mr. Rutherford sent of adults attempting to walk on styrofoam, where they are floundering and cannot gain traction. Evidently, the slender tarsal

claws satisfactorily anchor *P. rutherfordi* in its regular environment but cannot penetrate the harder Styrofoam surface.

Gonopods. The gonopods, only a few hundred microns in each dimension, are the most minute of any polydesmidan RMS has attempted to examine, draw, and interpret. While tempted to draw them in situ, he thought that their true condition might not be evident without dissection, which is indeed the case. Telopodital branches are closely appressed and lie over/under each other requiring careful and repeated focusing to determine structural configurations and positions, and dissecting them from the aperture and separating them is tedious. They completely fill the aperture with only their apices protruding, leaving no space through which to insert a needle and extract them. Rather than removing the gonopods, it was easier to demolish segment 7 and tear the aperture away from the gonopods so that only the joined appendages remained. Separating them from each other is further difficult because of their being contiguous and connected by a strong sternum, perhaps the most sclerotized structure on the organism. After separation, the loose, colorless, and translucent gonopods are easily lost in a drop of alcohol or mounting medium; even in focus, one can look through them and miss them; they do not need clearing because they already are such. RMS removed and separated the gonopods from one male only to lose them in a small dish of alcohol; he then dissected a second male and noted the sectors of the drops where the gonopods were placed, because even at high power under a compound microscope, one can scan the drop and miss them, which happened with one gonopod. He found and drew the fourth gonopod (Fig. 11–14), but it was too flimsy to lift out of glycerine on a pin and so minute that the coxa could not be grasped with microforceps; our finest brush was required, but the gonopod immediately vanished into the bristles. Having lost four gonopods, we designate an undissected male as holotype; the two “gonopod-less” males are paratypes. The gonopods protrude from the aperture to the level of the coxa in the NMNH paratype, but RMS chose not to risk another dissection. In prior studies of millipeds with minute gonopods, like siphonophoridans (Shelley 1996a, b; Shelley and Hoffman 2004) and *Mitocybe auriportae* Cook and Loomis (Platydesmida: Andrognathidae) (Shelley 2010), losing gonopods was not an issue because they are solid, yellowish, opaque, and easy to find.

The gonopod drawings, done at magnifications $\geq 400\times$, are color coded to facilitate comprehension. Telopodital projections are complex and intertwined; dashed and solid lines are necessary along with color. The primary (blue) branch carries the prostatic groove and divides distad into a solenomere and tibiotarsus. The secondary (red) branch, which lacks the groove, curves around, over, and under both the primary projection and prefemoral process. Prefemoral elements include the prefemur itself, associated hairs (dark green), and the expansive, laminate prefemoral process (light green), the dominant branch which is replete with folds, curves, and marginal irregularities. Coxal elements – coxa, cannula, and coxal hairs – are black.

Exoskeleton and Coating. Soil encrusted polydesmidans and/or ones with ramose/palmate setae that help hold debris have been documented in the families Oniscodesmidae and Pyrgodesmidae, in the nominate suborder (Causey 1971; Shear 1973, 1977), and Campodesmidae (Schjötz 1966), in Leptodesmidea. However, the encrustation of *P. rutherfordi* is particularly intriguing because of its smooth exoskeleton, in contrast to the heavily tuberculate Campodesmidae, and that of *Campodesmus jugosus* (Cook) is characterized as “covered with a thin layer of earth particles” (Schjötz 1966). While possessing two spines per metatergum, *P. rutherfordi*'s exoskeleton is otherwise featureless, yet it is coated with a continuous, subuniform “pavement” in which the sand grains are lightly “cemented” together and to the underlying exoskeleton, the most poorly sclerotized we have seen on a polydesmidan aside from an obligate cavernicole. It also lacks pigmentation, being a translucent grayish-white plastic color, occasionally with a blueish tint, like a “pill box” for medications, thus contrasting with dark substrates and seemingly readily visible to predators. The milliped counters this vulnerability by coating itself with dark camouflage, grains of sand, frass, or debris, enabling it to blend with the substrate, and we term the coating “sand” for convenience, because of its granular texture. All the color one sees when viewing *P. rutherfordi* is the coating, not the organism itself (Fig. 1, 5–9). Excepting the gonopods, prozonae, clypeus/labrum, antennal/leg apices, and paraprocts, every skeletal surface is coated with sand, which also lends structural integrity to an organism that needs such. None of the 18 individuals was found near water, so the milliped's unique features seem adaptations for “sandy”

rather than aqueous environments. The respiratory spiracles open apically on short, straw-like tubules (Adis and Golovatch 2000, fig. 3–5), which elevate them above the coating and ensure that they remain open; were they on metazonal surfaces, they would become plugged and the milliped would suffocate. Likewise, elevating the ozopores on metatergal spines, instead of being flush with paranotal surfaces, enables them to remain open and functional instead of being clogged by sand. The spines also provide a modicum of structure to which the sand grains can adhere and accumulate, and this occurs to such a degree on the anteriormost segments of some individuals that the spines are joined by layers or ridges of “sand” (Fig. 8, arrow).

The coating is a coarse to fine, regular or irregular “pavement,” as on a roughly paved road that has not been smoothed by rollers. The grains are lightly “cemented” together and adhere loosely to each other and the underlying exoskeleton, such that only a few flake off with light handling. However, with rougher handling, as in grasping with forceps or attempting dissections with a pin, sizeable chunks break off cleanly exposing the exoskeleton beneath. An apt analogy is a “sticky note”; brushing it lightly will not detach it from a surface, but a firm pull will quickly do so. Similarly; a light touch of *P. rutherfordi* removes a few grains from the coating, but grasping the milliped firmly dislodges chunks of “pavement.”

What is the “glue/cement” and where does it derive? The only logical possibility is the ozopore secretions, and the occurrences of sand layers/ridges **only** on the anteriormost metaterga, where the spines/ozopores are physically closest (Fig. 8, arrow), constitutes circumstantial evidence that their secretions are indeed the “glue” that holds the grains to each other and the exoskeleton. The ability of juveniles to moderately volvate (Fig. 5) may explain the cemented coatings on the legs and venter, removed from the ozopores, because curling/volvating helps disperse secretions and induces flow over all surfaces. There is less sand on the tarsi, which directly contact the substrate and are the body part where the coating is most likely to be dislodged. The “naked” male suggests that juveniles somehow shed their thinner coatings before molting and reacquire them *de novo* each time, but they do not have to be shed after final molts to adult stages and can thus become thicker. Volvation would be difficult or impossible for adults, with thick, heavy, more firmly cemented coatings, but when freshly molted adults first acquire coats, there is no further need to replace them. The ramous/dendritic/palmate setae (Causey 1971; Shear 1973, fig. 23–25, 1977, fig. 44; Adis and Golovatch 2000, fig. 11, 13, 15–18) help hold the sand in place on the rounded surfaces of podo-/antennomeres, particularly the former where they are densely packed together. Sand grains lodge between the setal branches, and dense rows of dendritic setae hold continuous strands of sand that filiform setae cannot do. Three to four sand grains will submerge a seta, and in fully covered adults, the scattered, filiform body setae are obliterated by the coatings; sensory functions are difficult to envision because at most, only their invisible tips protrude above the sand. Presumably, the “naked” paratype molted shortly before collection and lacked time to amass the coating. Facial and body setae are visible and countable on this individual, whereas they are invisible on covered specimens.

Silvestri (1932) did not mention encrustation on *P. disparipes* and surely would have if either specimen had been coated. It could occupy a different biotope, but we doubt this because the structural modifications seem adaptations for living amongst sand/detritus/frass. As with the “naked” paratype of *P. rutherfordi*, perhaps the lost holotype of *P. disparipes* had freshly molted and lacked time to acquire the coating before being preserved. We have seen the juvenile paratype, apparently an early instar, and it is indeed smooth, soft, and fragile, again suggesting recent molting. Fresh material, especially adult males, is needed to answer questions about *P. disparipes*, which we think occupies the same microhabitats as *P. rutherfordi*.

Legs. The anterior (long) segmental legs initiate the “side stroke motion,” and their sublateral origins enable greater reach to pull *P. rutherfordi* farther in this direction. If these legs arose at the same position as the posterior (shorter) ones, much of their lengths would be offset stretching across the sterna, and sideways movement would be hampered. Coupled with more lateral origins, their greater lengths enable greater stride, and the long femora and tarsi also appear to be adaptations for lateral/sideways motion. The thinner, weaker, posterior (short) legs, around $\frac{3}{4}$ as long as the anterior pair, extend only $\frac{2}{3}$ as far laterad because of their more medial origins; accordingly, the sterna are narrower between the posterior legs. When fully extended, the lengths of the posterior leg coxae and $\sim\frac{1}{4}$ of those of their prefemora are required just to reach the position of the anterior coxae, and when the

shorter legs assume the sideways pulling motion, the opposing legs have begun pushing; the anterior legs, however, initiate the motion without assistance from those on the opposite side of the body. The sideways motion is analogous to human side-stroke swimming, in which the arm on one side of the body extends beyond the head and pulls “downward” to the level of the other arm, which continues the motion until it is fully extended while the first arm reaches “upwards” to initiate the next stroke. As nearly as we could determine from the videos, the opposing legs perform the complementary pushing motion a fraction later than the pulling legs, so the two sides are slightly and purposefully out of sync.

In summary, the hypotheses that *Pandirodesmus* spp. are adapted for wet areas and that their alternating long/short legs function in swimming are not supported by the habitat, motion, and sandy coating of *P. rutherfordi*. However, it seems appropriate to characterize the millipeds as, effectively, “swimming in sand,” which, coincidentally, is a recommended technique for humans to escape quicksand.

Conclusion. The Antilles, of which Tobago is the southernmost, derive from a terrane that rifted from the northern coast of the “proto-South American” part of Pangaeon Gondwana in the Cretaceous/Paleocene, ~66 million years ago (mya); it subsequently drifted northward, rotated, and fragmented into today’s islands (Smith et al. 1994, Shelley and Golovatch 2011, Shelley and Martinez-Torres 2013). The southern islands, representing the eastern sector of the terrane, logically derive from northeastern “proto-South America,” and the gonopodal telopodite of *Nannorrhacus luciae* (Pocock) (Polydesmida: Platyrhacidae) on St. Lucia, ~296 km (185 mi) north of Tobago, shares more features with *Rhyphodesmus drurii* (Gray) in Guyana than with species in Colombia and Panama (Shelley and Martinez-Torres 2013). Consequently, indigenous Tobagan millipeds must be anatomically closer to ones in northeastern, rather than northwestern, South America, and discovery of the Guyanan genus *Pandirodesmus* on the closest Antillean island, rather than more distant ones, is logical. We cannot infer the origination date of *Pandirodesmus*/ini, but both had to exist 66 mya on both the “proto-Antillean” terrane and adjoining “proto-South America” when the former rifted, and *P. rutherfordi* is a remnant of the Antillean population that became isolated on present-day Tobago when the terrane fragmented. As *Nannorrhacus*, on St. Lucia, seems related to *Rhyphodesmus*, in Guyana, perhaps *Pandirodesmus*/ini also inhabits islands this far north, but being small and cryptic, we expect representatives to occur sporadically and be difficult to discover. In 83 years, field efforts on more northern islands along with Trinidad, ~437 km (273 mi) north-northwest of the Guyana site, have not yielded *Pandirodesmus*, and its discovery on Tobago was serendipitous. Mr. Rutherford could just as well have ignored the original stump, one of many near Charlotteville, and RMS sampled around Charlotteville in 1999 without finding this millipede. The discovery of *P. rutherfordi* proves that the genus and tribe survive today and enable us to project a potential Antillean range. Collectors sampling on St. Lucia and intervening islands – Grenada, St. Vincent, the Grenadines – should consciously peel bark off substantially decayed logs and stumps, ones that likely harbor more frass, and search for additional populations of this cryptic, sand-coated millipede genus.

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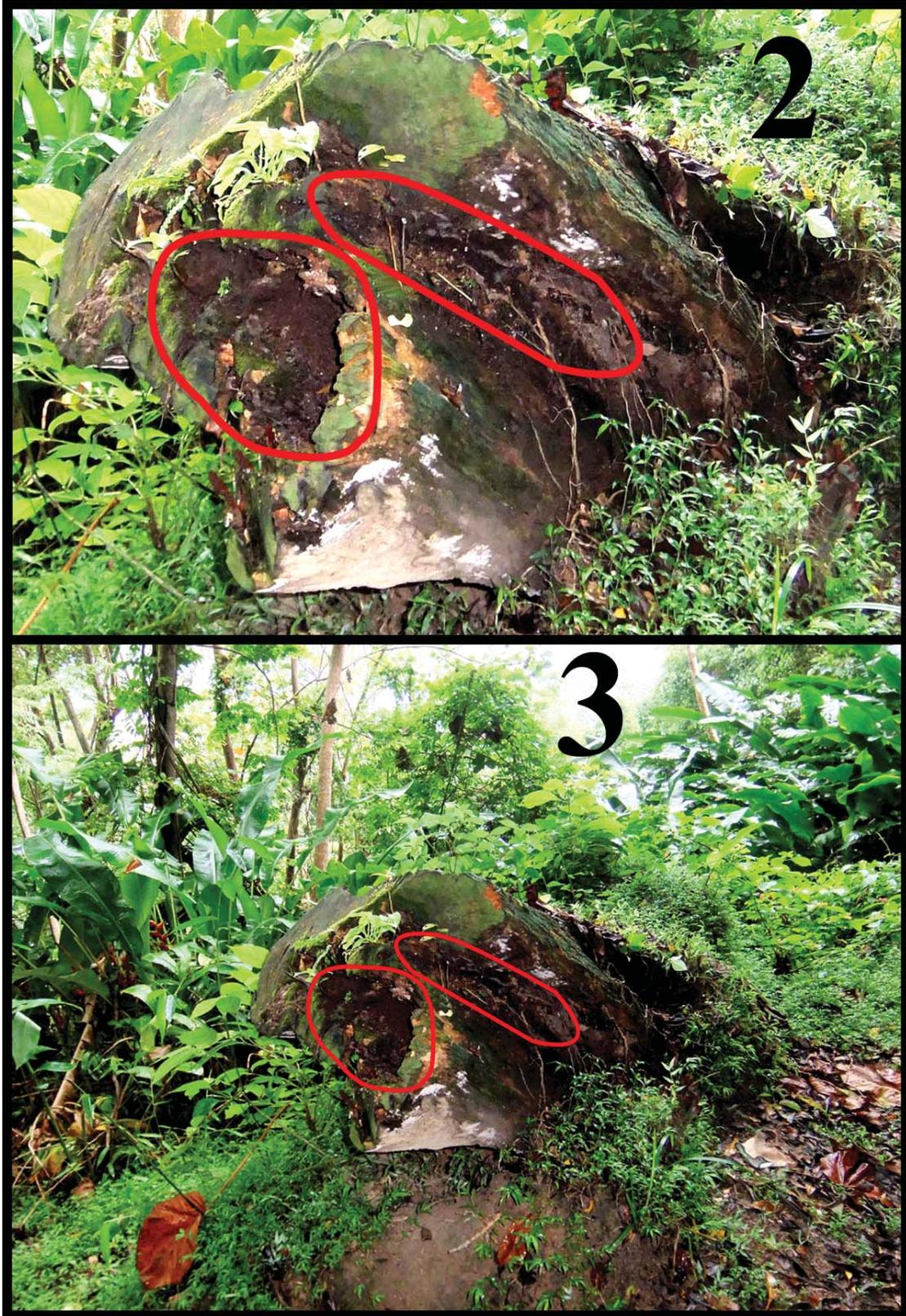
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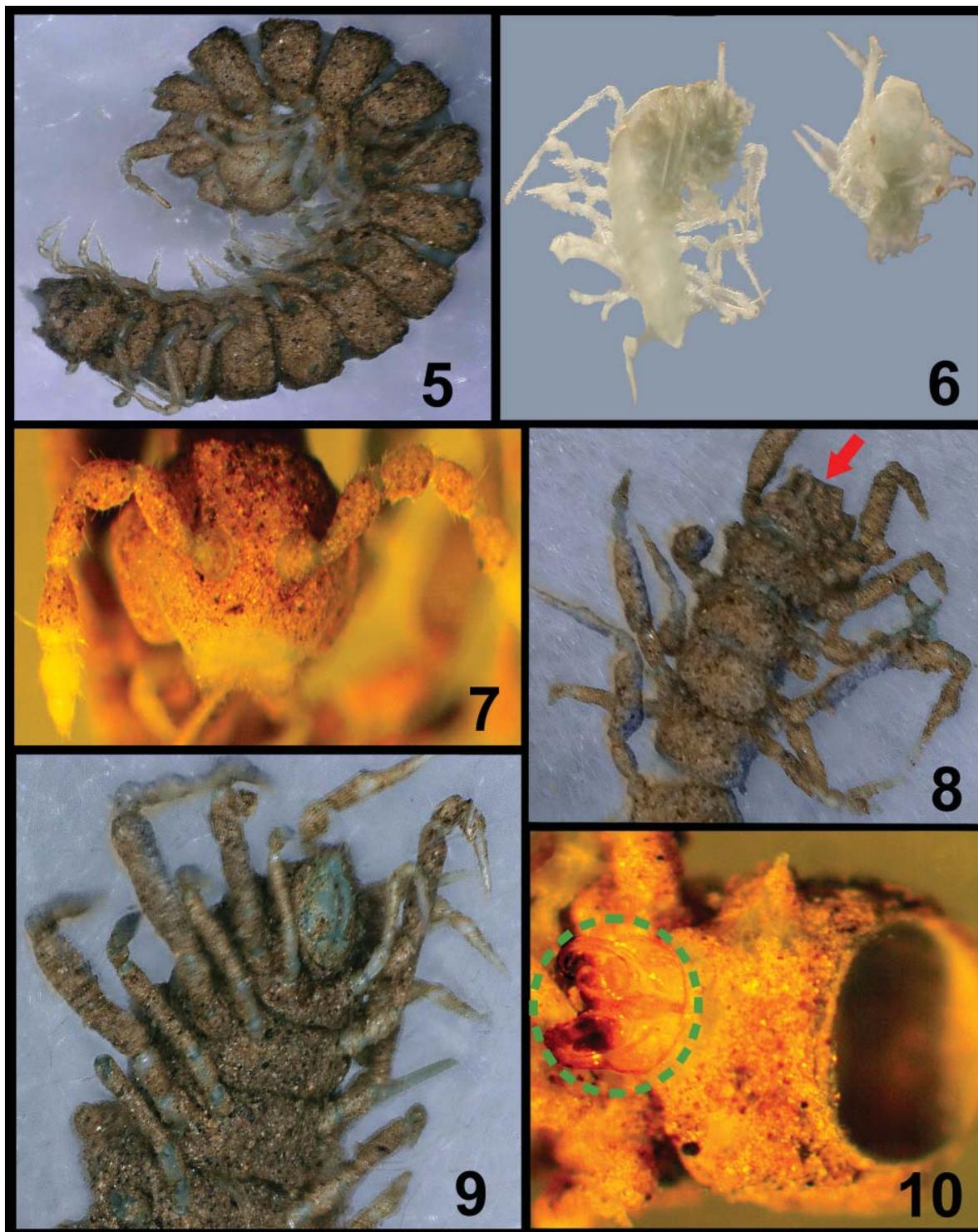
Figure 1. *Pandirodesmus rutherfordi* habitus. The arrow denotes a rounded accumulation of sand on the right anterior leg on segment 15.



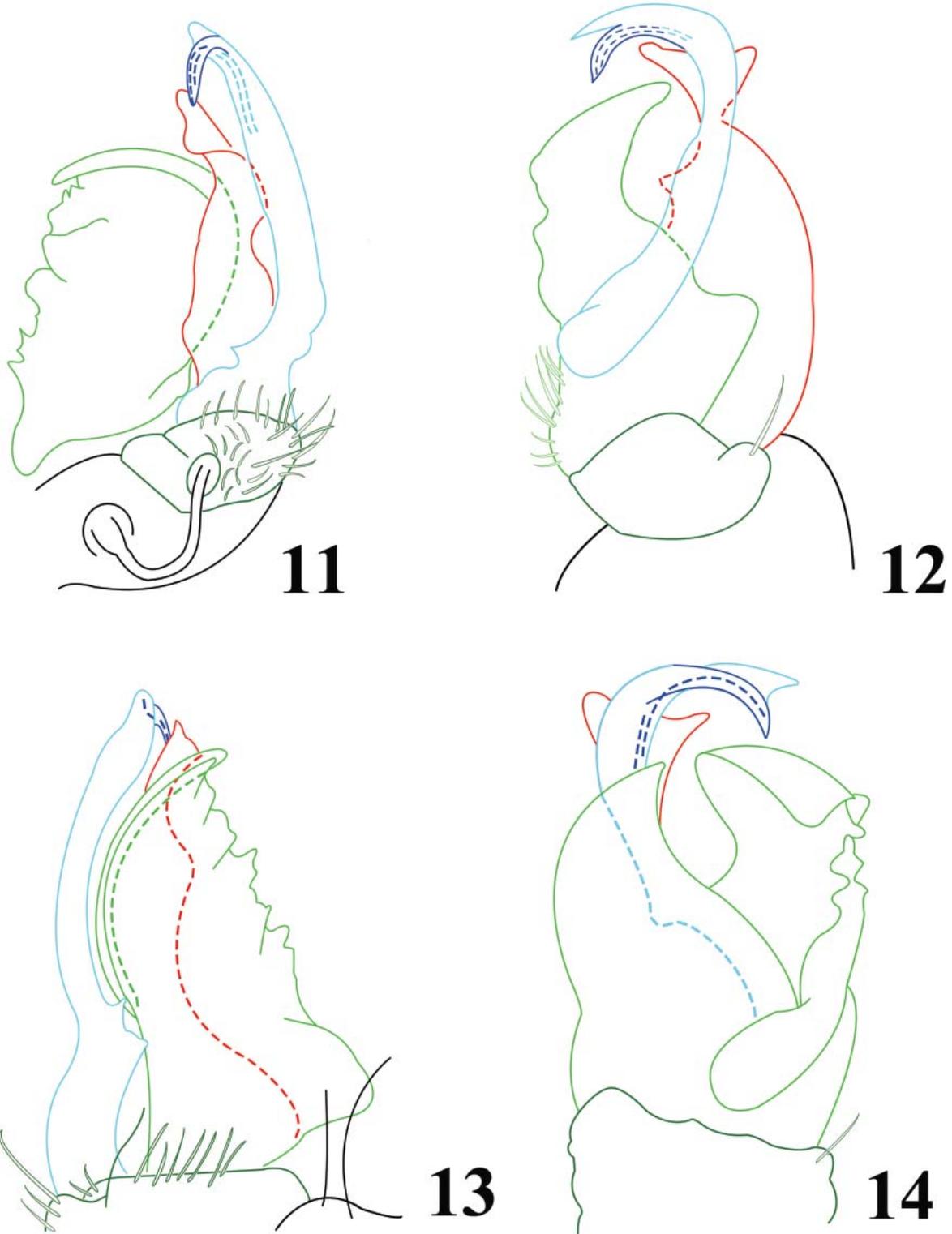
Figures 2–3. 2) Stump where the first two series of *P. rutherfordi* were discovered. 3) Setting of the stump in secondary forest along Pirate’s Bay Trail near Charlotteville, Tobago. The red circles in both figures enclose the surface areas, originally beneath bark, where *P. rutherfordi* was found.



Figure 4. Distributions of *Pandirodesmus* and Pandirodesmini. Red dot, *P. rutherfordi*. Red star, *P. disparipes*.



Figures 5–10. Male paratypes of *P. rutherfordi*. **5)** Partly volvated juvenile showing the uniformity of the thinner coating. **6)** “Naked,” fragmented, and probably freshly molted adult showing the natural exoskeletal color. **7)** Anterior view of the head showing the clear, uncoated frons/clypeus/labrum and distal antennomeres. **8)** Dorsal view of anterior tergites showing a ridge of accumulated sand (arrow) between the physically closer spines/ozopores on that metatergum. **9)** Ventral view of the caudal end showing sand coatings on the sterna and legs (excepting tarsi), the alternating leg lengths, the more lateral origins of the anterior segmental legs, and the wider sterna between them. **10)** Segment 7 of NMNH paratype showing protruded gonopods, encircled by dashed green line, in situ.



Figures 11–14. Left gonopod. **11)** Submedial view. **12)** Subanterior view. **13)** Sublateral view. **14)** Subcaudal view. Coxa (black), prefemur (dark green), prefemoral process (light green), secondary branch (red), primary branch (light blue), solenomere (dark blue).

