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**Research article**

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# A review of the previously monotypic tribe Dibolostethini (Chelodesmidae: Chelodesminae) with description of two new species and a summary of the Chelodesmidae of the Tropical Andes Biodiversity Hotspot

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**Abstract.** The chelodesmid genus *Dibolostethus* Hoffman, 2009, the sole member of the tribe Dibolostethini, is reviewed. The genus contains the type species *D. sicarius* Hoffman, 2009 known only from the Los Rios Province, Ecuador, and two new species from the Tropical Andes, *D. inopinatus* Means, Bouzan & Ivanov sp. nov. from the Morona-Santiago Province, Ecuador and *D. kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov. from the Valle del Cauca Department, Colombia. We redescribe *D. sicarius* and provide a revised diagnosis of the genus, images of diagnostic morphological

characters, and a key to the males of *Dibolostethus*. In addition, we provide a summary and a distribution map of the Chelodesmidae of the Tropical Andes Biodiversity Hotspot.

**Keywords.** Andes Mountains, Colombia, Diplopoda, Ecuador, endemism, Neotropics, Polydesmida.

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## Introduction

With more than 750 described species and 176 extant genera, Chelodesmidae Cook, 1895 is the second largest family (after Paradoxosomatidae Daday, 1889; Nguyen & Sierwald 2013) in the class Diplopoda Gervais, 1844. Hoffman (1980) proposed the division of Chelodesmidae into two geographical subfamilies: the New World Chelodesminae Cook, 1895 (139 genera) distributed across the Neotropical region, and the Old World Prepodesminae Cook, 1896 (37 genera) known from the Afrotropical and Palearctic regions. Currently, 21 tribes, 5 of which are monotypic, are recognized within the Chelodesmidae, the majority of which (19) are in the Chelodesminae. More than half of all Chelodesmidae genera (90+) and species (420+), however, have not yet been assigned to a tribe.

Hoffman (2009) described the monotypic genus *Dibolostethus* Hoffman, 2009 (type species, *D. sicarius* Hoffman, 2009) from two localities situated in the western and eastern foothills of the Andes Mountains of Ecuador. The unique combination of somatic characters displayed by *D. sicarius* (i.e., highly reduced paranota; metazona with distinct transverse sulcus; sternum of the 4$^{th}$ body ring prominent, with two slender acute projections; femora of 4$^{th}$ and 5$^{th}$ body rings modified) warranted the erection of the new tribe Dibolostethini Hoffman, 2009 (Hoffman 2009). Based on modifications of male anterior legs, Hoffman (2009) suggested affinities with the Andean Batodesmini Cook, 1896 (see Carl 1914: 910, figs 145–147; Kraus 1954: 29, 40–42, 35, figs 30–31; and Hoffman 1982: 636, figs 7–8) and Trichomorphini Hoffman, 1979 (see Carl 1914: 926, figs 181–182; Chamberlin 1923: 131, fig. 163; Loomis 1974: 172, fig. 5; and Jeekel 1986: 484, fig. 107b–c).

Recently, a previously unrecognized species of *Dibolostethus* was discovered among material housed at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. The species, herein described as *Dibolostethus kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov., represents the first record of the tribe Dibolostethini from Colombia and considerably expands its geographic distribution. During the course of this work, examination of *D. sicarius* type material, housed at the Virginia Museum of Natural History, revealed that the sole male paratype is not conspecific with the holotype and is herein described as *Dibolostethus inopinatus* Means, Bouzan & Ivanov sp. nov.

Part of the longest mountain range on Earth, the Tropical Andes are one of the most biodiverse areas in the world harboring over 35 000 plants and animals, nearly half of which are endemic (49%; Zador 2021). While plants and vertebrates are well documented throughout the region, the invertebrate communities, including Diplopoda, remain understudied and are poorly known. Chelodesmidae are known from throughout the Andes (Hoffman 1978, 1979, 1982, 1987, 2007; Barriga *et al.* 2019), however, they have received relatively little attention, especially when compared to other South American hotspots, such as the Cerrado (a tropical savanna ecoregion of Brazil) and the Atlantic Forest. Andean chelodesmids often display unique morphological characters which makes placement into established tribes difficult and indicates a rich taxonomic and evolutionary history (Hoffman 1975). At this point, however, there has

been no synthesis of the Andean representatives of the family, leaving us poorly equipped to disentangle hidden patterns of biodiversity and determine evolutionary relationships.

We provide a revised diagnosis of the genus and descriptions of *D. inopinatus* sp. nov. and *D. kattani* sp. nov. which help delineate the character set that defines the genus. We redescribe *D. sicarius* and include additional morphological details, measurements, and illustrations. In addition, we provide a key to the males of *Dibolostethus* and the first account of the chelodesmid diversity of the Tropical Andes Biodiversity Hotspot.

## Material and methods

The examined material is deposited in the following institutions (curators in parentheses): ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (E. Flórez); VMNH, Virginia Museum of Natural History, Virginia, USA (K. Ivanov).

Photographs used for illustrations were taken with a Canon 90D camera with a 65 mm Canon MP-E macro lens (Canon, Tokyo, Japan) mounted on a Stackshot vertical rail system (Cognisys, Michigan, USA) and focus-stacked in Helicon Focus Pro 7 (HeliconSoft, Kharkiv, Ukraine). Illustrations of relevant morphological features were made by tracing the focus-stacked images in Adobe Illustrator 2022 (Adobe Systems, California, USA, ver. 26.3.1). Scanning electron micrographs were taken using a FEI Quanta 250 SEM (FEI, Oregon, USA) with an attached SLR digital camera at Instituto Butantan, São Paulo, Brazil. Specimens selected for scanning electron imaging were cleaned two times (30 seconds each) ultrasonically, transferred to an ascending series of ethanol dilutions (70%, 80%, 90%, and 100%), bathed for 15 minutes at each step, and critical-point dried. The samples were mounted on aluminum stubs and coated with gold in a sputter coater for 240 seconds.

Relevant morphological features of *D. sicarius* and *D. inopinatus* sp. nov. were measured to the nearest 0.01 mm with an ocular micrometer mounted on an Olympus SZX16 dissecting microscope (Olympus, Pennsylvania, USA). Images of *D. kattani* sp. nov. were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereo microscope and measurements (to the nearest 0.01 mm) were performed with a Leica Application Suite ver. 2.5.0 (Leica Camera, Wetzler, Germany). Morphological terms follow Hoffman (2009) and Pena-Barbosa *et al.* (2013).

Locality data were obtained from examined material and published literature. Names of districts and provinces, altitude, and geographic coordinates, not presented on the specimen labels or in the published literature were obtained using Google Earth Pro ver. 7.3.4 (Alphabet, California, USA). The georeferenced localities were subsequently plotted in Google Earth Pro (X; Y, datum WGS84) using data from Hoffman *et al.* (2016; ver. 2016.1) to delineate the boundaries of the Tropical Andes Biodiversity Hotspot. Distribution maps were generated using the freeware DIVA-GIS ver. 7.5.0 (Hijmans *et al.* 2001).

Prior to submission, a few specimens possibly representing undescribed Dibolostethini taxa were discovered among material recently collected in the Cauca and Cundinamarca Departments, Colombia. Any additional taxa of Dibolostethini revealed through examination of these, and any other, specimens will be addressed in a follow-up publication.

**Abbreviations**

Cx = Coxae
Lb = Lobe before apex on the prefemoral process
Pf = Prefemur
PfP = Prefemoral process

S = Solenomere
Sh = Shelf on the prefemoral process

## Results

### *Taxonomy*

Class Diplopoda Gervais, 1844
Order Polydesmida Pocock, 1887
Suborder Leptodesmidea Brölemann, 1916
Family Chelodesmidae Cook, 1895
Subfamily Chelodesminae Cook, 1895
Tribe Dibolostethini Hoffman, 2009

Genus ***Dibolostethus*** Hoffman, 2009

*Dibolostethus* Hoffman, 2009: 151.

#### Type species

*Dibolostethus sicarius* Hoffman, 2009, by monotypy.

#### Diagnosis

The genus differs from all other chelodesmid genera by the following combination of characters: body rings constricted between pro- and metazonites and paranota reduced, resulting in a moniliform body outline (Figs 1, 2A); spiracles reduced as compared to other members of the family, oval (Fig. 2B, red circle); gonopores located on subterminal convexity on the mesal side of 2nd coxae (Fig. 3A); in males, sternite of 4th body ring prominent, with a pair of acute projections curving anteriad (Figs 2B, 4); in males, femora of 4th pair of legs with large acute process (Fig. 3B); in males, femora of 5th pair of legs incrassate (Fig. 3C); gonopods large, straight; solenomere long, slender, and unbranched; prefemoral process widening at midpoint and terminating in several well-defined lobes (Figs 5–7).

#### Description

Body composed of 20 rings. Length of males between 25 mm (*D. sicarius*) and ~30 mm (*D. inopinatus* sp. nov.). Coloration (preserved in 70% isopropanol/ethanol): body rings yellowish (*D. inopinatus*) to dark reddish brown (nearly purple; *D. kattani* sp. nov., Fig. 1); antennae, head, legs, and paranota same color as the body (*D. inopinatus*) or light yellow, contrasting with the body; telson same color as the body (*D. inopinatus*) or reddish with posterior margin yellowish. Head: smooth, with epicranial setae 2–2, interantennal 1–1, and frontal 2–2; other facial setae sparse and irregular, becoming more dense closer to the mouthparts. Gnathochilarium without modifications, but narrower in relation to other members of Chelodesmidae, covered by few setae (Fig. 2C). Mandibular bases prominent. Incisura lateralis rounded, not completely closed. Antennae: sixth antennomere with an invagination possibly containing sensilla basiconica, obscured by debris in examined specimen; seventh antennomere having two well-demarcated invaginations and one slight invagination between the sensory cones; sensilla basiconica arranged into a small pocket, connected to the cones by a slit (Fig. 2D, red arrow). Body ring cuticle smooth, appearing slightly rugose at high magnification, with a median sulcus on the metazonites (Fig. 2A, red rectangle). Collum: small, more slender than the head; posterior margin concave, anterior margin convex; corners rounded. Paranota reduced, distantly separated, rounded, and without projections, not developed on 19th body ring, and body rings constricted between pro- and metazonites, all resulting in a moniliform appearance (Figs 1, 2A). Stigma oval (Fig. 2B, red circle). Sternites of males: 4th body ring with two slender acute projections (Figs 2B, 4); 5th body ring with two pairs of short, blunt projections (only in

**Fig. 1.** *Dibolostethus kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov., ♂ (ICN-MD-1367), habitus. Scale bar = 5 mm.

*D. kattani*; Fig. 3D, red oval); post-gonopodal sternites unmodified. Ozopores: posteriorly situated on paranota (Fig. 2A); peritremata indistinguishable; arrangement typical for Polydesmida (5, 7, 9, 10, 12, 13, 15–19); without a well-demarcated rim. Legs of males: femur of 4th pair produced into a large acute process (Fig. 3B); femur of 5th pair of legs incrassate and glandular; prefemur of 5th pair of legs with a small basal pore (Fig. 3C, E, red arrow); tibia of all legs with a ventro-apical translucent acute projection, reducing in size posteriorly (Fig. 3B–C, red arrows). Podosterna of 4th–6th body rings notably elevated (Figs 2B, 3D). Telson: subtriangular, with three pairs of macrosetae dorsolaterally and two pairs in the apical region. The apical pairs of macrosetae separate from and equidistant to the mesal lips of the paraproct, forming the four corners of a rectangle.

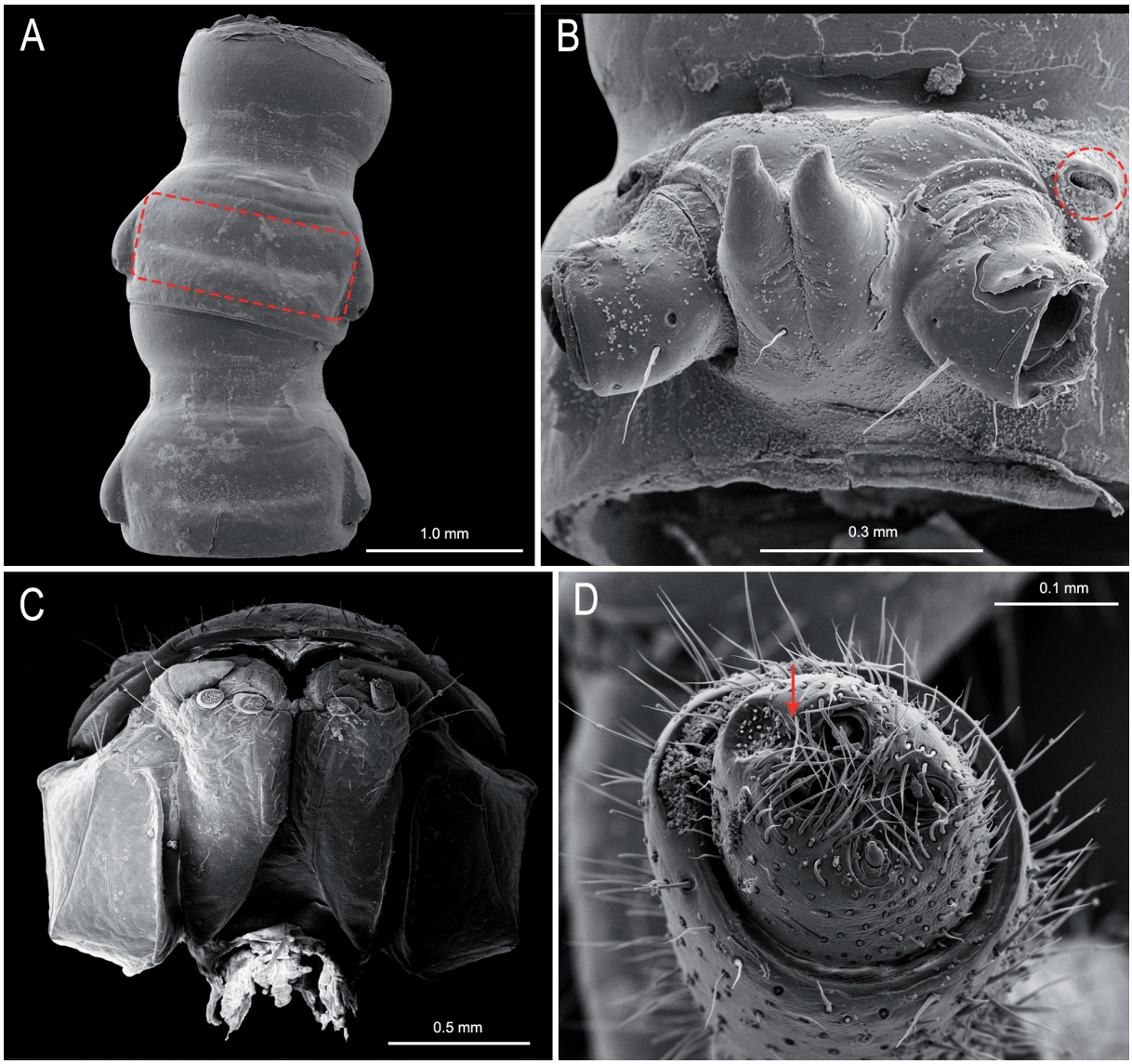


**Fig. 2.** Scanning electron microscope images of *Dibolostethus* Hoffman, 2009 showing somatic characters. *Dibolostethus kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov., paratype, ♂ (ICN-MD-1317B). **A**. Body rings 9th and 10th, red rectangle = median metazonal sulcus. **B**. Venter of 4th body ring, showing paired sternal projections, red oval = stigma. **C**. Venter of head, showing narrow gnathochilarium. **D**. Tip of seventh antennomere, red arrow = narrow slit connecting pocket containing sensilla basiconica and sensory cone area.

**Male characters**

Gonopores without modifications, located on the coxae of the 2nd leg-pair, with a subterminal pore. Gonopod aperture: on 7th body ring; oval; rim notably projecting above sternite, with a U-shaped concavity on posterior margin, posterior edge without folds. Gonopods: gonocoxae length variable relative to telopodite length; largely obscured by telopodite in ectal view; without a spiniform process (Figs 5–7). Cannula hook-shaped, without modifications (Figs 5C, 6C, 7A). Solenomere long, slender, unbranched, apex falciform (Figs 5–7). Prostatic groove visible along the entire length of the solenomere in mesal view, without a trace of torsion (Figs 5C, 6C, 7A, dashed lines). Prefemoral region (Figs 5–7): small, about ⅓ the length of the telopodite; a slight cingulum demarcates the transition zone between the prefemoral and solenomere regions (Figs 5–7, red ovals). Prefemoral process: long (similar in length to solenomere); apex broad, with a series of distinct lobes and lamellate flanges (Figs 5–7).

**Female characters**

Known only for *D. sicarius*. Vulvae: small, oval-shaped, unmodified (Fig. 8A); held against coxae of 2nd leg pair within deep emargination of 3rd segment, not protruding beyond U-shaped vulvar rim (Fig. 8B); composed of two subequal valves and a small operculum; setose (Fig. 8A, C).

**Remarks**

Although the structure of *Dibolostethus* gonopods (i.e., presence of a prefemoral process and a hook-shaped canula) shows definitive placement within the Chelodesmidae, all known Dibolostethini exhibit striking similarities with members of Paradoxosomatidae. These include the presence of a transverse metatergal sulcus, reduction of paranota and constriction between the pro- and metazonites giving the body a moniliform appearance (shared with several other groups of Chelodesmidae), elongated legs and antennae, and the positioning of the dorsal pair of the macrosetae in relation to the mesal lips of the paraproct (Fig. 2). In the Paradoxosomatidae, these macrosetae are positioned far away from the mesal lips of the paraproct, and located directly above the ventral pair of macrosetae, forming the four corners of a rectangle (Nguyen & Sierwald 2013: 1147). In the vast majority of the Chelodesmidae, the dorsal pair of macrosetae is located directly on the mesal lips of the paraproct, although this character is somewhat variable. For example, in the Lepturodesmini Hoffman, 1975, the dorsal pair of macrosetae is immediately adjacent to the mesal lips of the paraproct but not mounted on them. In species of *Dibolostethus*, the two pairs of macrosetae are positioned far away and equidistant from the mesal lips of the paraproct as in the Paradoxosomatidae. The elongated antennae and legs (similar to the chelodesmid Trichomorphini), and the presence of an adenostyle-like femoral process on leg pair 4 also resemble many species of Paradoxosomatidae.

**Distribution**

Known from the Andean regions of Colombia and Ecuador (Fig. 9).

**Composition**

*Dibolostethus sicarius* Hoffman, 2009, *D. inopinatus* sp. nov., and *D. kattani* sp. nov.

***Dibolostethus sicarius*** Hoffman, 2009
Figs 3A, E, 4A–B, 5, 8–9

*Dibolostethus sicarius* Hoffman, 2009: 151, figs 1–11.

**Diagnosis**

Adult males of *D. sicarius* differ from those of *D. kattani* sp. nov. based on the lack of short, blunt projections on the sternite of the 5th body ring, and from *D. inopinatus* sp. nov. and *D. kattani* sp. nov.

based on the following combination of gonopodal characteristics: solenomere relatively straight until gently curving dorsally at apex, tip sinuous (Fig. 5A); prefemoral process slightly wider basally, expanded at midpoint and recurved, forming a cup-shaped depression before apex; apex with three lamellate flanges, best seen in anterior view (Fig. 5B).

**Type material**

**Holotype**

ECUADOR • ♂; Los Rios Province [originally reported incorrectly as Pichinchi Province], Rio Palenque Science Center; [0.588° N, 79.362° W]; 21 Mar. 1977; J. Reiskind leg.; VMNH110810.

**Paratypes**

ECUADOR • 2 ♀♀; same collection data as for holotype; VMNH110811, VMNH110812.

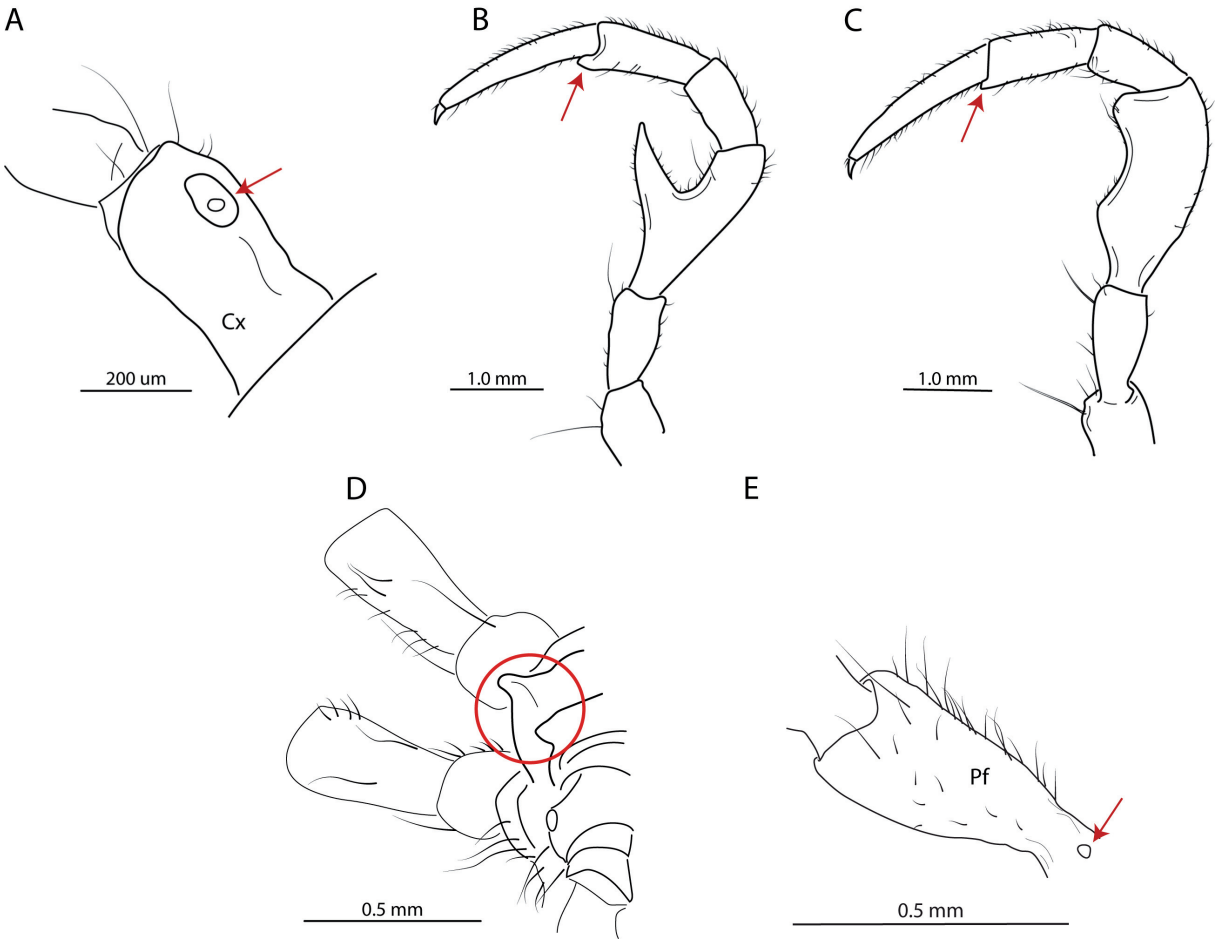


**Fig. 3.** *Dibolostethus* Hoffman, 2009 somatic characters continued. **A, E**. *Dibolostethus sicarius* Hoffman, 2009, holotype, ♂ (VMNH110810). **B–D**. *D. kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov., holotype, ♂ (ICN-MD-1317-1). **A**. Coxa 2, mesal view, red arrow = gonopore. **B**. Left leg 4, posterior view, red arrow = tibial ventro-apical projection. **C**. Left leg of 5th leg pair showing incrassate femur, red arrow = tibial ventro-apical projection. **D**. Body ring 5, lateral view, red circle = anterior pair of sternal projections. **E**. Prefemur 5, red arrow = basal pore. Abbreviations: Cx = coxa; Pf = prefemur.

**Description**

**Male** (holotype, VMNH110810)

With characteristics typical for the genus. Coloration (preserved in 70% isopropanol): body rings light brown to caramel; antennae and head light yellow; legs light yellow; telson reddish, with posterior margin (= spinnerets region) yellowish. Head: epicranial macrosetae 2+2, interantennal macrosetae 1+1, frontal macrosetae 2+2. Sternites: 4th body ring with two thin, blade-like acute projections, tips separated throughout, nearly translucent (Fig. 4A–B). Gonopod aperture on 7th body ring oval, rim notably projecting above sternite (0.35 mm), with a deep U-shaped concavity (0.2 mm) on posterior margin.

Gonopods (Fig. 5). Gonocoxae rounded, equivalent to about three quarters the length of the telopodite; dorsum of left and right gonocoxa with 2 and 3 (possible aberration) macrosetae, respectively. Solenomere long, slender, unbranched, apex falciform and partially enveloped by prefemoral process (Fig. 5, S). Prefemoral process: long (similar in length to solenomere), width subequal to solenomere, widening at halfway point with a medial knob before curving laterad into a cup-like structure; apex broad, with a series of lamellate flanges resembling a hammerhead shark in lateral view (Fig. 5, PfP).

Body measurements (mm). Total length 24.8, width of 10th body segment 1.98. Antennomere lengths (1–7): 0.38, 0.75, 0.85, 0.85, 0.85, 0.85, 0.25. Collum: length 0.5, width 1.4. Podomere lengths of 10th body ring (1–7): 0.28, 0.55, 0.9, 0.34, 0.53, 0.95, 0.09. Gonopod aperture: length 0.50, width 0.78. Gonopod: length 0.99, width 0.86. Gonocoxae: length 0.63, width 0.36. Telopodite: length 0.98, width 0.31. Telson length 0.78.

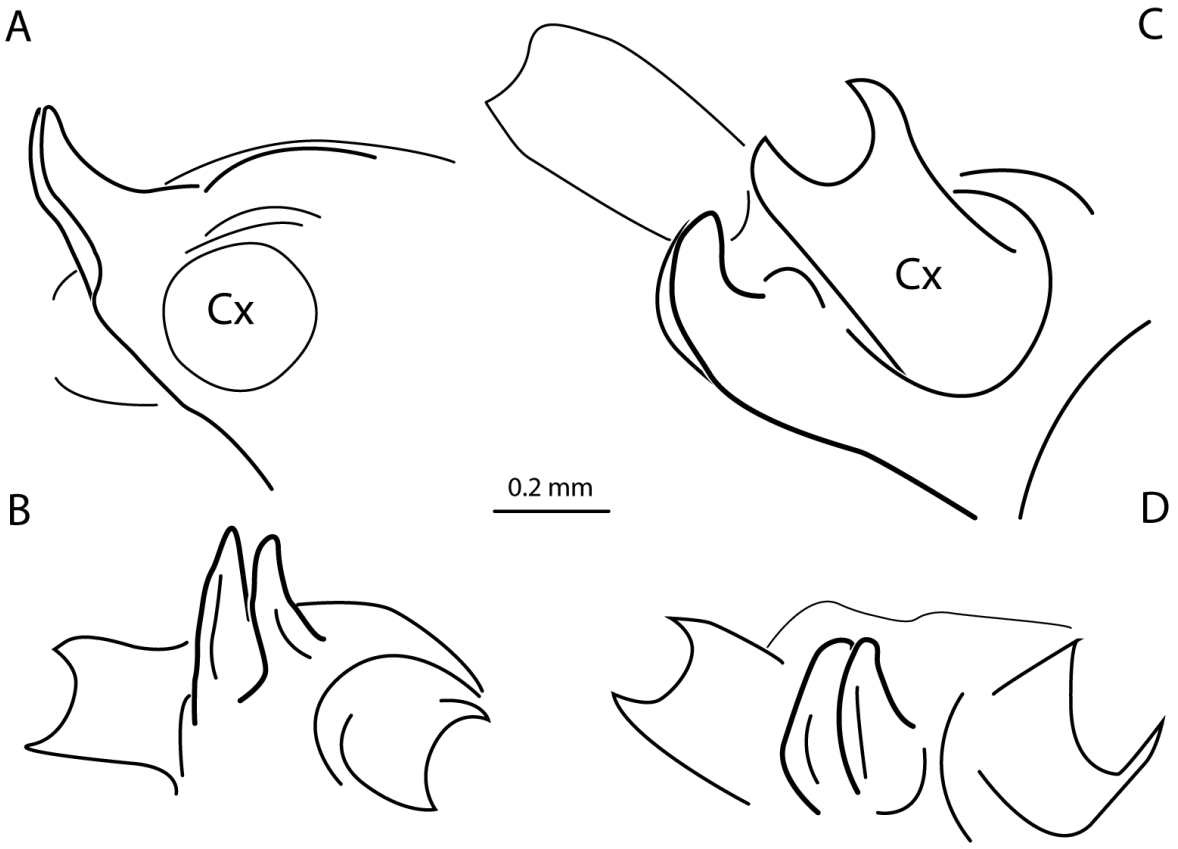


**Fig. 4.** Body ring 4, sternal projections. **A–B**. *Dibolostethus sicarius* Hoffman, 2009, holotype, ♂ (VMNH110810). **C–D**. *D. inopinatus* Means, Bouzan & Ivanov sp. nov., holotype, ♂ (VMNH110813). **A, C**. Lateral views. **B, D**. Posterolateral views. Abbreviation: Cx = coxae.

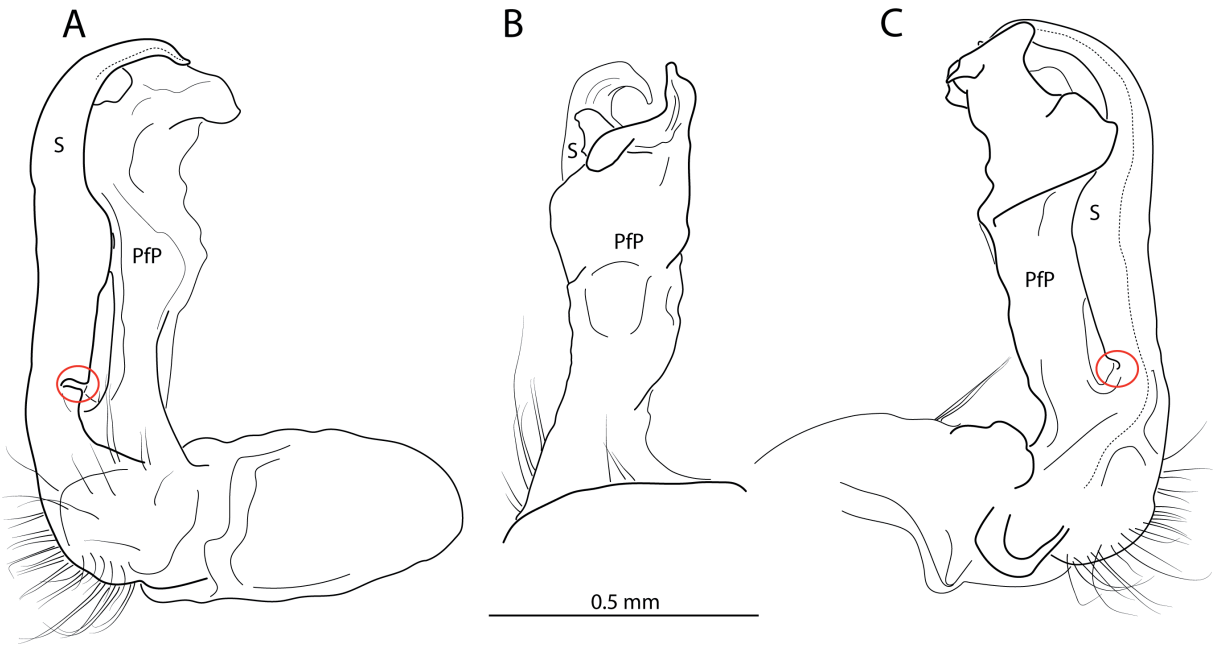


**Fig. 5.** *Dibolostethus sicarius* Hoffman, 2009, holotype, ♂ (VMNH110810), left gonopod. **A**. Lateral view. **B**. Anterior view. **C**. Mesal view. Red circles = cingulum. Dashed lines = prostatic groove. Abbreviations: PfP = prefemoral process; S = solenomere.

**Female** (paratype, VMNH110811)
Coloration (preserved in 70% isopropanol) as in male. Body larger and more robust than male. Similar to male in general body outline and somatic characters, except sternite of 4th body ring without pair of acute projections, 4th, 5th, and 6th podosterna elevated to a lesser degree, 4th and 5th pair of legs not modified, and tibia lacking acute ventro-apical projections.

Body measurements (mm). Total length 30.95, width of 10th body segment 2.6. Antennomere lengths (1–7): 0.38, 0.9, 0.93, 0.88, 0.85, 0.83, 0.23. Collum: length 1.0, width 1.7. Podomere lengths of 10th body ring (1–7): 0.3, 0.53, 0.9, 0.38, 0.45, 0.98, 0.09. Vulvar aperture width 0.56. Posterior margin of vulvar rim: well sclerotized, U-shaped; width 0.13. Vulvae: small, unmodified, setose (Fig. 8); length 0.45, width 0.29. Valves symmetrical. External valve: lateral length 0.5, lateral height 0.44; dorsal length 0.39, dorsal width at midpoint 0.14. Operculum: length 0.06, width 0.21. Telson length 1.15.

**Distribution**

Herein restricted to the Los Rios Province, Ecuador (Fig. 9).

***Dibolostethus inopinatus*** Means, Bouzan & Ivanov sp. nov.
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Figs 4C–D, 6, 9

*D. sicarius* (in part) – Hoffman 2009: 151, misidentification.

**Diagnosis**

Adult males of *D. inopinatus* sp. nov. differ from those of *D. kattani* sp. nov. based on the lack of short, blunt projections on the sternite of the 5th body ring, and from *D. sicarius* and *D. kattani* based on

the following combination of gonopodal characteristics: solenomere sinuous before curving dorsally at nearly 90° at apex, outer edge with wide lateral flange just before apex, tip curving laterally (Fig. 6A, C); prefemoral process only slightly narrower than solenomere at base, with pronounced 45° angle on dorsal side, expanding at midpoint with lateral and medial edges becoming pronounced ridges widening into lamellate flanges on either side of prefemoral process; apex of prefemoral process acute, directed anteriad (Fig. 6B).

**Etymology**

The species epithet '*inopinatus*' is Latin for 'unexpected', 'unforeseen', reflecting its surprising discovery among the type series of *D. sicarius*. The species epithet is a masculine, singular adjective.

**Type material**

**Holotype**

ECUADOR • ♂; Cordillera del Cóndor, Morona-Santiago Province, Los Tayos [vicinity of Cueva de Los Tayos]; 3°04′ S, 78°15′ W [originally reported incorrectly in decimal degrees]; 22 Jul. 1976; collector unknown; on log; VMNH110813.

**Description**

**Male** (holotype, VMNH110813)

With characteristics typical for the genus. Coloration (preserved in 70% isopropanol): body rings, all appendages, and telson uniformly light yellow. Head: epicranial macrosetae 2–2, interantennal macrosetae 1–1, frontal macrosetae 2–2. Sternites: 4th body ring with two slender, conical, acute projections, appressed along entire length (Fig. 4C, D). Gonopod aperture on 7th body ring oval, rim notably projecting above sternite (0.48 mm), with a deep U-shaped concavity (0.2 mm) on posterior margin.

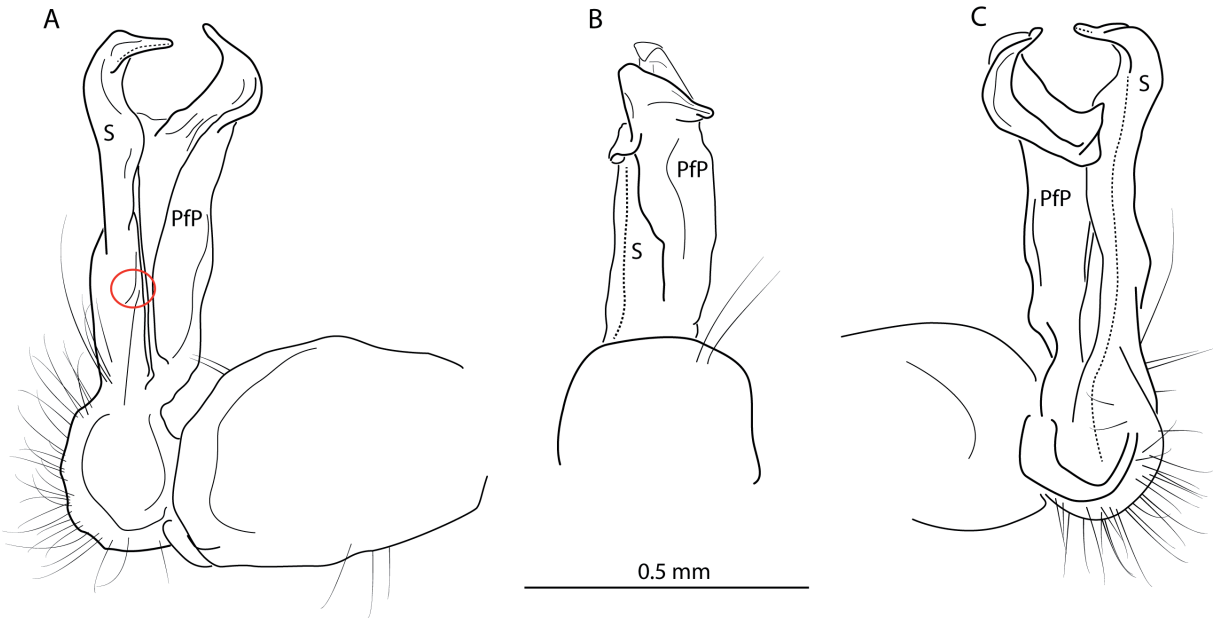


**Fig. 6.** *Dibolostethus inopinatus* Means, Bouzan & Ivanov sp. nov., holotype, ♂ (VMNH110813), left gonopod. **A**. Lateral view, red circle = cingulum. **B**. Anterior view. **C**. Mesal view. Dashed lines = prostatic groove. Abbreviations: PfP = prefemoral process; S = solenomere.

Gonopods (Fig. 6). Gonocoxae rounded, equivalent to about three quarters the length of the telopodite; with two macrosetae on the dorsum. Cannula appearing larger than in *D. sicarius*. Solenomere long, sinuous, unbranched, apex falciform and tip curving laterally (Fig. 6, S). Prefemoral process: long (similar in length to solenomere), narrow at base (width subequal to solenomere), widening at halfway point with lateral and medial flanges resembling a hooded cobra in lateral and medial views (Fig. 6A, C); medial flange with acute projection directed ventrally; prefemoral process and solenomere together resembling blacksmithing bolt tongs in lateral and medial views (Fig. 6A, C).

Body measurements (mm). Total length 29.7, width of 10th segment 1.95. Antennomere lengths (1–7): 0.48, 1.1, 1.1, 1.0, 1.05, 1.01, 0.28. Collum: length 0.8, width 1.55. Podomere lengths of 10th body ring (1–7): 0.33, 0.55, 1.0, 0.55, 0.65, 1.01, 0.11. Gonopod aperture: length 0.50, width 0.75. Gonopod: length 0.93, width 0.71. Gonocoxae: length 0.7, width 0.38. Telopodite: length 0.89, width 0.35. Telson length 0.95.

**Female**

Unknown.

**Distribution**

Known only from the Morona-Santiago Province, Ecuador (Fig. 9).

**Remarks**

Although no collector information is given on the specimen labels, review of material housed at VMNH revealed that *D. inopinatus* was collected during the "Los Tayos Expedition". The joint British-Ecuadorian expedition, which included over 100 researchers and supporting personnel, focused on exploring the archeology, geology, and biology of Cueva de Los Tayos, situated in the foothills of the Cordillera del Cóndor mountain range, and its vicinity between July 4th and August 5th, 1976.

***Dibolostethus kattani*** Means, Bouzan, Martínez-Torres & Ivanov sp. nov.
urn:lsid:zoobank.org:act:E4B3174C-2DC2-4584-B664-D0E4FB12D6B7
Figs 1–2, 3B–D, 7, 9

**Diagnosis**

Adults males of *D. kattani* sp. nov. differ from those of *D. sicarius* and *D. inopinatus* sp. nov. based on the presence of two pairs of short, blunt projections on the sternite of the 5th body ring (Fig. 3D), and the following combination of gonopodal characteristics: solenomere curving with distinct ridge at midway point, tip relatively straight (Fig. 7A, S); prefemoral process slightly thinner basally, with shelf under linear lobe just before apex (Figs 7A, C, PfP); apex with large, tongue-shaped lobe, best seen in anterior view (Fig. 7B).

**Etymology**

The species is named in honor of one of its first collectors, the late Dr Gustavo Kattan. Throughout his career, Dr Kattan collected myriapod specimens across Colombia and donated them to the Instituto de Ciencias Naturales. Noun in the genitive case.

**Type material**

**Holotype**

COLOMBIA • ♂; Valle del Cauca, Cali, 15 km vía Cali-Buenaventura; [3.496° N, 76.613° W]; 10 Dec. 1990; C. Murcia and G. Kattan leg.; under leaf litter in tropical forest; ICN-MD-1317A.

**Paratypes**

COLOMBIA • 2 ♂♂; same collection data as for holotype; ICN-MD-1317B.

**Other material**

COLOMBIA • 1 ♂; Valle del Cauca, Cali, 16 km vía Cali-Buenaventura; [3.493° N, 76.613° W]; 1800 m a.s.l.; 11 Oct. 1979; C. Murcia and G. Kattan leg.; under log in tropical forest; ICN-MD-1219 • 1 ♂; Valle del Cauca, Cali, 18 km vía Cali-Buenaventura; [3.517° N, 76.621° W]; 1900 m a.s.l.; 10 Nov. 2014; D. Martinez leg.; collected at night at the edge of a road; ICN-MD-1367.

**Description**

**Male** (holotype, ICN-MD-1317A)

With characteristics typical for the genus. Coloration (recently preserved in 70% ethanol): body rings dark, reddish brown (nearly purple); head light brown; legs yellowish ocher; telson reddish, with posterior margin (= spinnerets region) yellowish (Fig. 1). Antennae broken. Head: epicranial macrosetae 2–2, interantennal macrosetae 1–1, frontal macrosetae 2–2. Sternites: 4th body ring with two robust, conical, blunt projections, separated along entire length (Fig. 2B); 5th body ring with two pairs of short, blunt projections, the anterior pair more conspicuous (Fig. 3D). Gonopod aperture on 7th body ring oval, rim notably projecting above sternite (0.67 mm), with a deep U-shaped concavity (0.3 mm) on posterior margin.

Gonopods (Fig. 7). Gonocoxae rounded, equivalent to about half the length of the telopodite; not prominent in ectal view, with two macrosetae on dorsum. Cannula hook-shaped, broken in the holotype. Solenomere long, slender, unbranched, curving with distinct ridge at midway point, falciform at apex, tip straight (Fig. 7, S). Prefemoral process: thin at base, with shelf (Fig. 7A, Sh) under linear lobe just before apex (Fig. 7A, Lb); apex with large, tongue-shaped lobe, best seen in anterior view (Fig. 7B, PfP).

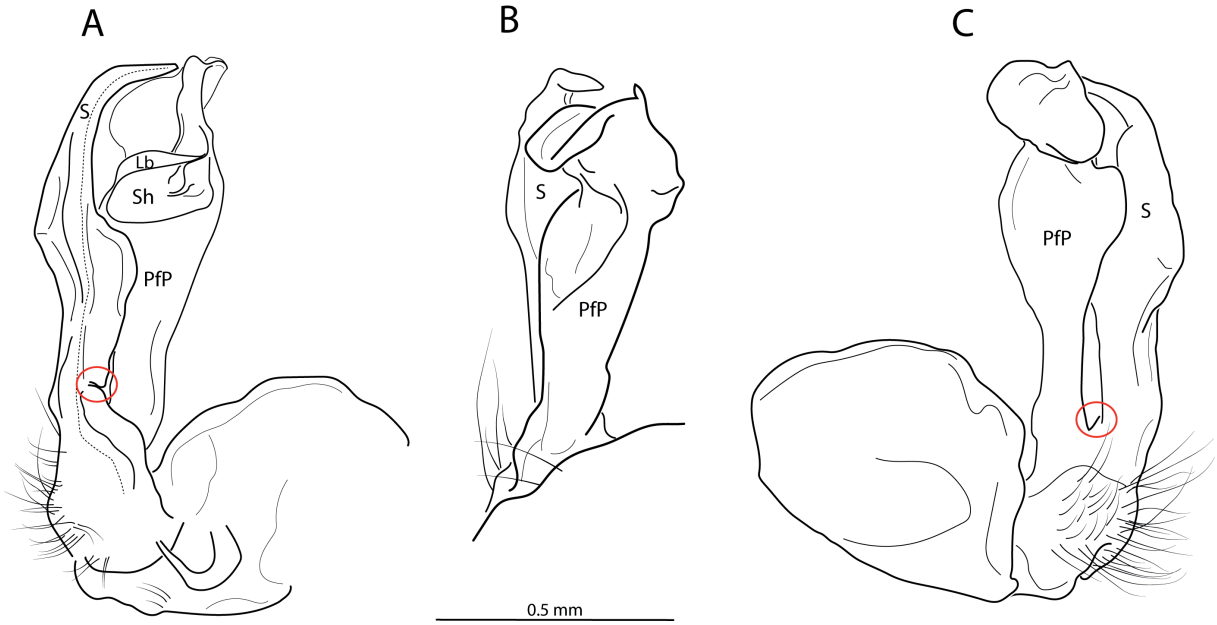


**Fig. 7.** *Dibolostethus kattani* Means, Bouzan, Martínez-Torres & Ivanov sp. nov., holotype, ♂ (ICN-MD-1317A), right gonopod. **A**. Mesal view. **B**. Anterior view. **C**. Lateral view. Red circles = cingulum. Dashed lines = prostatic groove. Abbreviations: Lb = lobe; PfP = prefemoral process; S = solenomere; Sh = shelf.

Body measurements (mm). Total length 29.33, total width 2.10. Collum: length 0.77, width 1.55. Podomere length of 10th body ring (1–7): 0.29, 0.56, 1.15, 0.52, 0.66, 1.05, 0.11. Gonopod aperture: length 0.50, width 0.86. Gonopod: length 1.21, width 0.96. Gonocoxae: length 0.54, width 0.59. Telopodite: length 1.19, width 0.42. Telson length 0.98.

**Female**

Unknown.

**Distribution**

Only known from the Valle del Cauca Department, Colombia (Fig. 9).

### *Key to males of Dibolostethus Hoffman, 2009*

1. Sternite of 5th body ring with two pairs of short, blunt projections (Fig. 3D); apex of gonopodal prefemoral process with large, tongue-shaped lobe, best seen in anterior view (Fig. 7B); Colombia ..... ***D. kattani*** Means, Bouzan, Martínez-Torres & Ivanov sp. nov.
– Sternite of 5th body ring without modifications; apex of gonopodal prefemoral process not as above; Ecuador ..... 2

2. Projections on sternite of 4th body ring stout, conical, curving at tip between coxae, appressed along entire length (Fig. 4C–D); prefemoral process and solenomere together resembling blacksmithing bolt tongs in lateral and mesal views (Fig. 6A, C); body length approximately 30 mm; color of appendages and body uniform ..... ***D. inopinatus*** Means, Bouzan & Ivanov sp. nov.
– Projections on sternite of 4th body ring thin, blade-like, curving beyond coxae, separated along entire length (Fig. 4A–B); prefemoral process enveloping, and partially obscuring solenomere in mesal view (Fig. 5C); body length less than 25 mm; color of appendages lighter and contrasting with that of body ..... ***D. sicarius*** Hoffman, 2009

A total of 34 chelodesmid genera have been reported from the Tropical Andes Biodiversity Hotspot (Table 1). These include 24 genera from 9 nine tribes and 10 additional genera currently unassigned to a tribe. Of the 34 genera known from the Tropical Andes, 9 (25%) are monotypic. The most species rich genera in the region include *Trichomorpha* Silvestri, 1897 (26 spp.), *Leptodesmus* de Saussure, 1859 (13 spp.), *Chondrodesmus* Silvestri, 1897 (11 spp.), and *Biporodesmus* Attems, 1898, *Trachelodesmus*

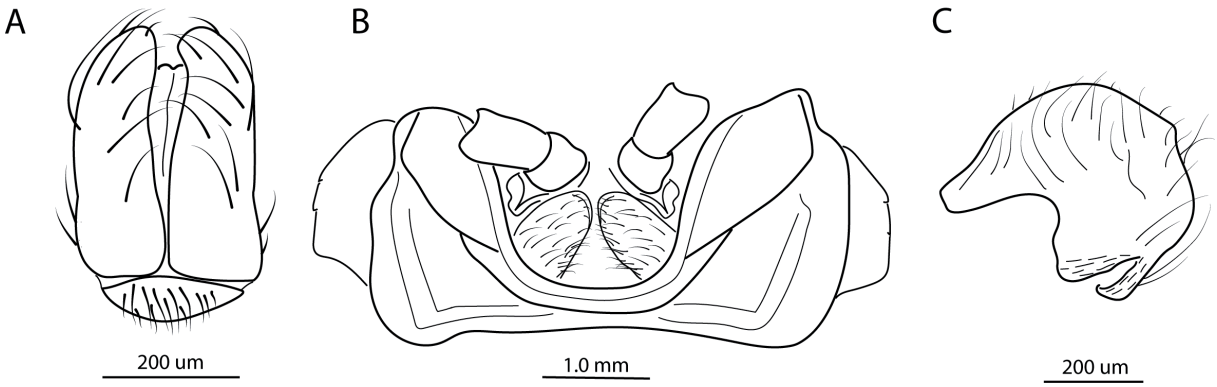


**Fig. 8.** *Dibolostethus sicarius* Hoffman, 2009, paratype, ♀ (VMNH110811), vulvae. **A**. Left vulva, lateroventral view, with operculum at base. **B**. Vulvae in situ, held appressed to 2nd leg pair coxae with valve openings facing each other. **C**. Left vulva, lateral view.

Peters, 1865, and *Leiodesmus* Silvestri, 1897 (5 spp. each). Conversely, 15 genera are represented in the region by a single species (Table 1).

Taxa have been reported from six of the seven (excluding Chile) countries falling within the boundaries of the Tropical Andes (Fig. 9). The most widespread genus in the region is *Leptodesmus*, stretching from

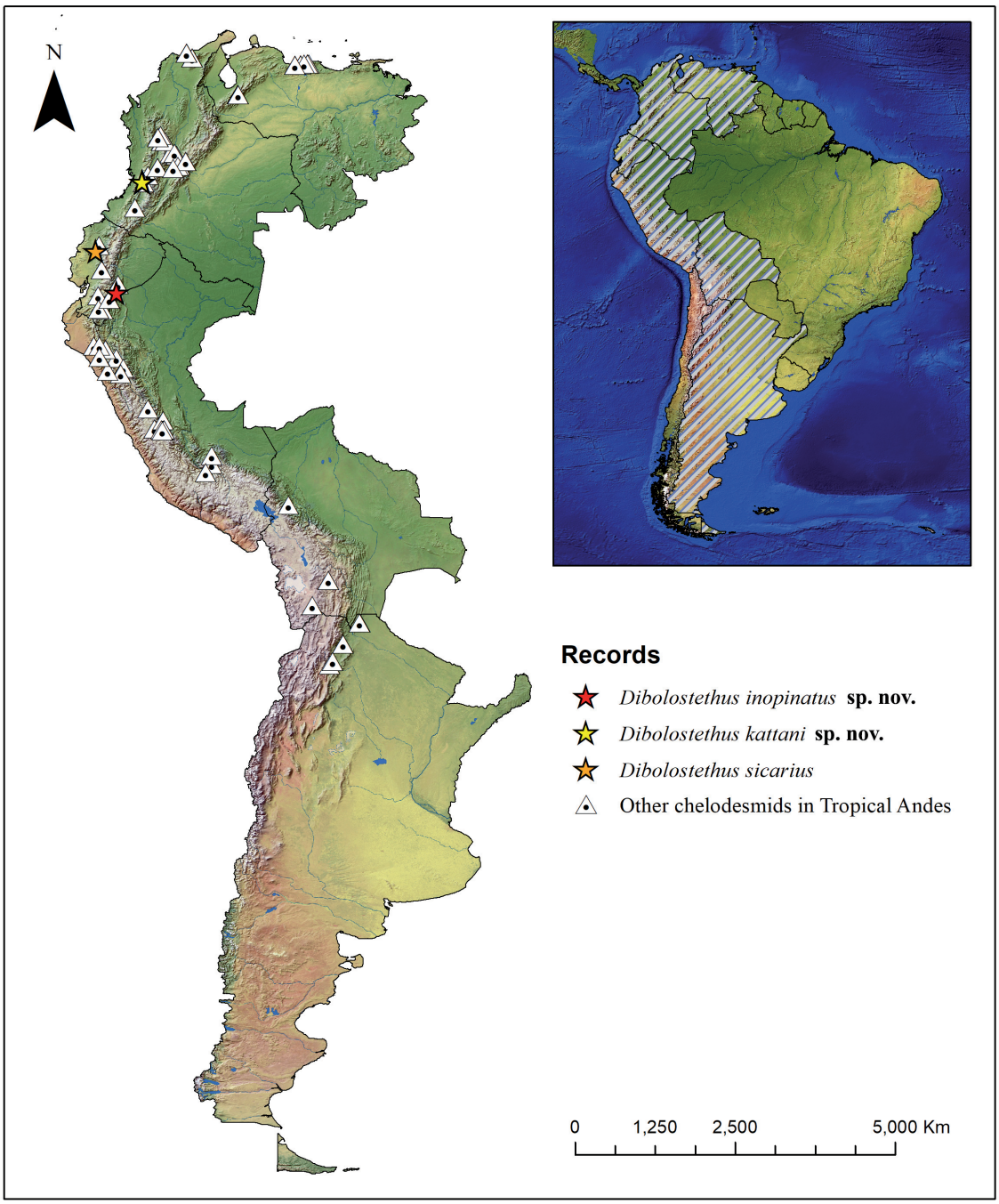


**Fig. 9.** Distribution of Chelodesmidae spp. in the Tropical Andes Biodiversity Hotspot, by country. Note: the type locality of *Dibolostethus sicarius* Hoffman, 2009 is included for completeness although it falls just outside of the boundaries of the Tropical Andes Biodiversity Hotspot. For information on these taxa see Supp. file 1.

**Table 1** (continued on next page). Summary of the taxa of Chelodesmidae Cook, 1895 reported from the Tropical Andes Biodiversity Hotspot. Taxa are arranged alphabetically by tribe and genus. The number of species reported from each country is provided parenthetically. See Supp. file 1 for a list of species.

| **Tribe** | **Genera** | **Tropical Andes Distribution** |
|---|---|---|
| Batodesmini | *Alocodesmus* | Colombia (1), Venezuela (2) |
| | *Batodesmus* | Colombia (2) |
| | *Biporodesmus* | Colombia (2), Ecuador (1), Peru (1) |
| | *Colombodesmus* | Colombia (2) |
| | *Cordilleronomus* | Ecuador (2) |
| | *Cormodesmus* | Colombia (1) |
| | *Heteropeltis* | Colombia (1) |
| | *Plusioporodesmus* | Colombia (1) |
| | *Tunochilus* | Venezuela (2) |
| Chondrodesmini | *Alyssa* | Ecuador (1) |
| | *Chondrodesmus* | Colombia (9), Ecuador (1), Venezuela (1) |
| Dibolostethini | *Dibolostethus* | Colombia (1), Ecuador (1) |
| Leptodesmini | *Leptodesmus* | Argentina (1), Colombia (2), Ecuador (3), Peru (5), Venezuela (2) |
| Lepturodesmini | *Camptomorpha* | Ecuador (2), Peru (1) |
| | *Eressea* | Venezuela (1) |
| | *Lepturodesmus* | Venezuela (4) |
| Macrocoxodesmini | *Eucampesmella* | Peru (1) |
| Platinodesmini | *Platinodesmus* | Argentina (1) |
| Trachelodesmini | *Alassodesmus* | Colombia (1) |
| | *Diarcuaria* | Colombia (1) |
| | *Hypodesmus* | Colombia (1), Venezuela (1) |
| | *Phlyzakium* | Venezuela (2) |
| | *Trachelodesmus* | Colombia (2), Venezuela (3) |
| Trichomorphini | *Trichomorpha* | Colombia (22), Ecuador (1), Venezuela (3) |

**Table 1** (continued).

| Tribe | Genera | Tropical Andes Distribution |
|---|---|---|
| Not assigned to a tribe | *Arthromachus* | Peru (1) |
| | *Chondrodesmoides* | Peru (1) |
| | *Desmoleptus* | Peru (3) |
| | *Guayapeltis* | Ecuador (1) |
| | *Incodesmus* | Peru (1) |
| | *Inconus* | Peru (1) |
| | *Leiodesmus* | Argentina (2), Bolivia (4), Peru (1) |
| | *Odontopeltis* | Argentina (1) |
| | *Perudesmus* | Peru (1) |
| | *Peruprion* | Peru (2) |

northwestern Venezuela to northwestern Argentina (>3800 km). It is important to note that Hoffman (1971) restricted the genus to only 21 species endemic to Brazil, with the remaining taxa considered incertae sedis, and without assignment at the generic level (Bouzan *et al.* 2021).

The number of species and records (in parentheses) from each country are as follows: Colombia – 49 species (61 records); Venezuela – 21 (26); Peru – 19 (27); Ecuador – 13 (13); Argentina – 5 (6); and Bolívia – 4 (4); for a total of 110 species and 137 records (Supp. file 1). A .kmz file of the Chelodesmidae of the Tropical Andes is provided as Supp. file 2.

## Discussion

The previously monotypic Andean genus *Dibolostethus* is reviewed and expanded to include two previously unrecognized species, *D. inopinatus* sp. nov. (Ecuador) and *D. kattani* sp. nov. (Colombia). The recognition of these taxa helps delineate the character set that defines the genus, including the presence of a pair of acute sternal projections on the 4$^{th}$ body ring, modified femora of the 4$^{th}$ and 5$^{th}$ pairs of legs, tibia of all legs in males with a ventro-apical translucent acute projection, and gonopodal prefemoral processes widening at midpoint and terminating in several well-defined lobes. Although modifications of the front legs of *Dibolostethus* males suggest affinities with the Andean Batodesmini and/or Trichomorphini, a more rigorous approach utilizing molecular techniques is needed to elucidate relationships with other chelodesmid groups, which is beyond the scope of the present work.

In overall appearance, Dibolostethini exhibit a striking similarity to members of Paradoxosomatidae including the presence of a transverse metatergal sulcus, reduction of paranota giving the body a moniliform appearance, elongated legs and antennae, and the positioning of the dorsal pair of macrosetae on the paraproct. As a result, Dibolostethini field identifications and identifications based on popular online platforms, such as iNaturalist, may erroneously place them within the Paradoxosomatidae. In addition, it is easy to envision that unknown material of Dibolostethini exists among museum collections of Paradoxosomatidae. Careful examination of male reproductive structures is critical for the proper identification of this group.

The finding of *Dibolostethus* in Colombia considerably expands its known range (~550 km to the northeast) and suggests that this previously monotypic genus is likely more widely distributed across the

Tropical Andes. Review of associated documentation revealed that the herein described *D. inopinatus* sp. nov. from the vicinity of the Cueva de Los Tayos, Ecuador was collected during the 1976 "Los Tayos Expedition", one of the biggest cave explorations ever undertaken. A look at the published literature reveals that at least one bromeliad (*Aechmea tayoensis* Gilmartin (Gilmartin 1981)), one bat species (*Lonchophylla handleyi* Hill, 1980), one frog species (*Hyloxalus nexipus* Frost, 1986), one scorpion genus and three species (*Tityus demangei* Lourenço, 1981, *Ananteris ashmolei* Lourenço, 1981, and *Troglotayosicus vachoni* Lourenço, 1981, which is still only known from the single female holotype), one shorttailed whipscorpion (*Tayos ashmolei* (Reddell & Cokendolpher, 1984)), one opilionid (*Metagovea philipi* Goodnight & Goodnight, 1980), one spider genus and three species (*Specloctenizа ashmolei* Gertsch, 1982; *Alpaida tayos* Levi, 1988; *Scaphidysderina tayos* Platnick & Dupérré, 2011), one termite genus and species (*Caetetermes taquarussu* Fontes, 1981), and one ant species (*Alfaria vriesi* Brandão & Lattke, 1990) were described based on material collected during the expedition, a testament to the incredible diversity of the Tropical Andes.

In total, 110 species of Chelodesmidae are known from the Tropical Andes, 98 (89%) of which are endemic to the region. This is a markedly higher rate of endemism than in other groups, such as vascular plants (50% endemic to the region), fish (74%), amphibians (71%), reptiles (40%), birds (30%), and mammals (13%; Zador 2021). These results indicate that millipedes may represent one of the most endemic groups within the Tropical Andes, which is unsurprising given their evolutionary age and low rate of dispersal.

As with the majority of natural areas across the globe, the Tropical Andes are under a variety of serious threats that negatively impact biodiversity. The 2021 Critical Ecosystem Partnership Fund report on the Tropical Andes Biodiversity Hotspot (found at https://www.cepf.net) lists mining, climate change, deforestation, and agricultural encroachment among the top threats facing the region (Zador 2021). The continued destruction of habitat critical to the survival of innumerable plant and animal species contributes to the decline of the world's biodiversity, and seriously reduces our ability to document and understand the natural world. While the prevalence of endemic species of Chelodesmidae is remarkably high in the Tropical Andes (89%), it is by no means an exception for biodiverse areas around the world, and makes the study of threatened natural ecosystems, flora, and fauna more necessary than ever before.

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## Supplementary Material

**Supp. file 1.** List of the species of Chelodesmidae Cook, 1895 reported from the Tropical Andes Biodiversity Hotspot. Species are arranged alphabetically by tribe and genus. The number of records reported from each country is provided parenthetically by species. See Table 1 for a summary of taxa of Chelodesmidae reported from the hotspot. https://doi.org/10.5852/ejt.2023.885.2189.9393

**Supp. file 2.** .kmz file of the Chelodesmidae Cook, 1895 of the Tropical Andes.
https://doi.org/10.5852/ejt.2023.885.2189.9395