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Traditional and confocal descriptions of a new genus and two new species of deep water Cerviniinae Sars, 1903 from the Southern Atlantic and the Norwegian Sea: with a discussion on the use of digital media in taxonomy (Copepoda, Harpacticoida, Aegisthidae)

Paulo H. C. Corgosinho[1], Terue C. Kihara[2], Nikolaos V. Schizas[3], Alexandra Ostmann[2], Pedro Martínez Arbizu[2], Viatcheslav N. Ivanenko[4]

1 *Department of General Biology, State University of Montes Claros (UNIMONTES), Campus Universitário Professor Darcy Ribeiro, 39401-089 Montes Claros (MG), Brazil* **2** *Senckenberg am Meer, Department of German Center for Marine Biodiversity Research, Südstrand 44, 26382 Wilhelmshaven, Germany* **3** *Department of Marine Sciences, University of Puerto Rico at Mayagüez, Call Box 9000, Mayagüez, PR 00681, USA* **4** *Department of Invertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, 119899 Moscow, Russia*

Corresponding author: *Paulo H. C. Corgosinho* (pcorgo@gmail.com)

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Abstract

Aegisthidae is one of the most abundant and diverse families of harpacticoid copepods living in deep-sea benthos, and the phylogenetic relationships within the family are in state of flux. Females of two new deep-water species of harpacticoid copepods belonging to the *Hase* **gen. n.** (Aegisthidae: Cerviniinae) are described. The first taxonomic description of marine copepod species based on the combined use of interference and confocal microscopy for the study of the habitus and dissected appendages is presented here. CLSM (Confocal Laser Scanning Microscopy) is a non-destructive method, comparable in quality to SEM (scanning electron microscopy) at the same magnifications. To observe and reconstruct in detail the habitus and dissected appendages, whole specimens and dissected parts were stained with Congo Red, mounted on slides with glycerine for CLSM and scanned under three visible-light lasers. *Hase lagomorphicus* **gen. et sp. n.**

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and *Hase talpamorphicus* **gen. et sp. n.** were collected from the sediments of the Southern Atlantic and the Norwegian Sea, from 2270 m and 5468 m depths, respectively. *Hase* **gen. n.** is included within Cerviniinae based on the caudal rami which are relatively divergent. *Hase* **gen. n.** is the sister taxon of *Cerviniella* based on the following synapomorphies: sturdy body, exopodites 1–3 of pereopods 1–3 heavily built, transformed into digging limbs, with strong outer and distal spines/setae, two-segmented endopod on the pereopods 2 and 3, and a reduced pereopod 5. Compared to *Cerviniella, Hase* **gen. n.** exhibits a more developed armature on the pereopod 1, which has outer and distal elements transformed into strong and long spines vs. stiff setae on *Cerviniella. Hase* **gen. n.** has one or two strong and long spines on the inner margin of the exopodite 3 of pereopod 4 and pereopod 5 is fused to the somite, ornamented with three distal setae. The telson of *Hase* **gen. n.** is subquadratic, and the furca is among the shortest yet described for Aegisthidae. The new species differ in a number of diagnostic characters, three of which are: a) the somite bearing pereopods 3 and 4 with latero-distal spiniform processes in *H. talpamorphicus* **gen. et sp. n.** but smooth in *H. lagomorphicus* **gen. et sp. n.**, b) antenna is armed with three stout spines on the lateral inner margin of the exopod in *H. talpamorphicus* **gen. et sp. n.** and two proximal setae in *H. lagomorphicus* **gen. et sp. n.**, and c) pereopod 4 exopodite 3 has two long and strong spines on the inner margin in *H. lagomorphicus* **gen. et sp. n.** and one spine in *H. talpamorphicus* **gen. et sp. n.** The high quality of CLSM images should foster discussion about the use of high quality digital images as type or as part of the type series in zoological studies, especially when studying rare and small macrofaunal and meiofaunal taxa.

Keywords

Arctic biodiversity, *Cerviniella,* deep-sea biodiversity, digital taxonomy, meiofauna, *Paracerviniella*, Tropical Atlantic biodiversity

Introduction

Aegisthidae Giesbrecht, 1893 is one of the most abundant and diverse families of harpacticoid copepods living in deep-sea plankton and benthos (George et al. 2014). They are found in holoplankton, hyperbenthos, as well as hydrothermal vents and cold seeps (Giesbrecht 1891, Conroy-Dalton and Huys 1999, Lee and Huys 2000). According to Seifried and Schminke (2003) the Aegisthidae comprises three subfamilies: Aegisthinae with the genera *Aegisthus* Giesbrecht, 1891, *Andromastax* Conroy-Dalton & Huys, 1999, *Jamstecia* Lee & Huys, 2000, *Nudivorax* Lee & Huys, 2000, *Scabrantenna* Lee & Huys, 2000; Cerviniinae with the genera *Brodskaya* Huys, Møbjerg & Kristensen, 1997, *Cervinia* Norman, 1878, *Cerviniella* Smirnov, 1946, *Eucanuella* T. Scott, 1900, *Expansicervinia* Montagna, 1981, *Neocervinia* Huys, Møbjerg & Kristensen, 1997, *Paracerviniella* Brodskaya, 1963, *Pseudocervinia* Brodskaya, 1963; and Cerviniopseinae with the genera *Cerviniopsis* Sars, 1909, *Hemicervinia* Lang, 1935, *Herdmaniopsis* Brodskaya, 1963, *Pontostratiotes* Brady, 1883, *Stratiopontotes* Soyer, 1970, *Tonpostratiotes* Itô, 1982.

The phylogenetic relationships within the family Aegisthidae are in state of flux. According to Walter and Boxshall (2018), the family comprises 102 species in 18 genera and the four subfamilies Aegisthinae Giesbrecht, 1893, Cerviniinae Sars M., 1903, Cerviniopseinae Brotskaya, 1963, and Pontostratiotinae Scott, A., 1909. Seifried and Schminke (2003) suggested that the systematics of the group remains problematic, as species of Aegisthinae (formerly Aegisthidae) represent derived Cerviniopseinae. However, they decided to maintain the family division on Aegisthinae, Cerviniinae, and Cerviniopseinae until a more careful phylogenetic analysis is performed (Seifried and Schminke 2003, Kihara and Martínez Arbizu 2012). More recently, Huys (2009) reinstated the subfamily Pontostrationinae over Cerviniopseinae.

The paper describes two new species of copepod crustaceans designated to a new genus of the subfamily Cerviniinae (Harpacticoida: Aegisthidae) found in the deep waters of Southern Atlantic and Norwegian Sea. This is the first formal description of a marine copepod species based on combined use of interference and confocal microscopy in study of dissected appendages and the genital field. The methods for the acquisition of 3D rendered images are described by Corgosinho et al. (2017) and Kamanli et al. (2017). One of the most important advantages of using Confocal Laser Scanning Microscopy (CLSM) over Scanning Electron Microscopy (SEM) is that CLSM is a nondestructive imaging technique for the study of whole microscopic animals or small parts of them, such as millimetre or micrometre-long hydrated structures (see extensive discussion by Kamanli et al. 2017). In addition, the use of CLSM improves the presentation of appendages and structures in their natural 3-dimentional state, a property not easily transferable by the 2-dimentional inked drawings. High quality CLSM photos could substitute the need of taxonomists to acquire type specimens from Museums for comparisons, therefore lessening the burden of understaffed museums but also decrease the likelihood of a lost or damaged type material through the transfer of the specimens back and forth to the Museum. High quality CLSM photos depict structures as they appear in reality and potentially remove any shortcomings that an inexperienced taxonomist may have and will increase the quality of publications. The new species were sampled in the frame of the Census of Marine Life subproject CeDAMar (Census of the Diversity of Marine Abyssal Life, 2000–2010) and the IceAGE (Icelandic marine Animals: Genetics and Ecology, since 2011) project. The CeDAMar was a ten-year multinational project (from 2000 to 2010) devoted to map the world biodiversity in the abyssal plains between 4,000 to 5,000 meters deep. The aim of the IceAGE project was to combine classical taxonomic methods with modern biodiversity research, in particular phylogeography and ecological modelling in the climatically sensitive region around Iceland.

Material and methods

The copepods were extracted from sediment samples of three scientific cruises of the Research vessel (RV) "Meteor". Sediment samples (5127–5455 m depth) were collected by a multi corer (MUC) during the DIVA-1 expedition of the RV "Meteor" (Cruise No. M48/1) to southeast Atlantic Ocean in July–August 2000. During DIVA-2 Expedition of the RV "Meteor" (Cruise No. M63/2), samples were taken by a MUC in the equatorial east Atlantic at depths >5000 m. Additional samples were collected by a box corer (BC) during the Overflow, Circulation and Biodiversity Expedition of the

RV “Meteor” (Cruise No. M85/3) 307–2749 m deep (Fig. 1, Table 1), in the northernmost North Atlantic and the Arctic Ocean. Temperature and salinity were obtained by a CTD probe coupled to the MUC and BC.

For taxonomic studies, specimens were stained with Congo Red and mounted on slides for confocal laser scanning microscopy (CLSM) following Michels and Büntzow’s (2010) protocol. We used the following equipment and settings: Leica DCR 5000 SP5 (Leica, Wetzlar, Germany) equipped with a Leica DM 5000B microscope (Leica, Wetzlar, Germany) and three visible-light lasers (DPSS 10 mW 561 nm; HeNe 10 mW 633 nm; Ar 100 mW 458 nm, 476 nm, 488 nm and 514 nm), combined with the software LAS AF Lite, Leica Application Suite Advanced Fluorescence (Leica, Wetzlar, Germany). Series of stacked images were obtained, collecting overlapping optical sections throughout the whole preparation. Final images were obtained by maximum projection, and CLSM illustrations were composed and adjusted for contrast and brightness using the software Adobe Photoshop CS6 (Adobe Systems, San José, U.S.A.).

The habitus was drawn from whole specimens temporarily mounted in slides with glycerine, adhesive plastic discs were used to support the cover slip and prevent destruction of the specimen (Kihara and Falavigna da Rocha 2009). After CLSM microscopy, specimens were dissected under a Leica MZ12.5 (Leica, Wetzlar, Germany). Dissected parts were mounted on slides using glycerine as mounting medium, and preparations were sealed with transparent nail varnish. Drawings were made under a Leica DMR microscope equipped with Nomarsky interference contrast and a drawing tube at 400× and 1000× magnification (Leica, Wetzlar, Germany). Final illustrations were “digitally inked” using Adobe Illustrator CS6 (DIVA-1 and DIVA-2 species) or free hand inked (IceAGE species).

The terms ‘furca’ and ‘telson’ are used according to Schminke (1976). Terminology and homologisation of maxillary and maxillipedal structures follow Ferrari and Ivanenko (2008). Therefore, by the application of serial homology, the nomenclature of Huys and Boxshall (1991) for Mx2 (fig. 1.5.5, p. 26) is modified as follows: praecoxa of Mx2 is hereafter recognized as syncoxa (praecoxa and coxa), coxa is considered as the basis, and the basis is recognized as the first endopodal segment with claw. Other morphological terms are used according to Huys and Boxshall (1991).

The following abbreviations are used in the text:

A1	antennule;
Ae	aesthetasc;
A2	antenna;
enp	endopod;
enp-1 (2,3)	proximal (middle, distal) segment of endopod;
exp	exopod;
exp-1 (2,3)	proximal (middle, distal) segment of exopod;
Md	mandible;
Mx1	maxillule;
Mx2	maxilla;
Mxp	maxilliped;
P1–P6	first to sixth pereopods;
pl	plesiomorphy;
sy	synapomorphy.

Table 1. Sampling stations of the “Meteor” cruises. Abbreviations: BC – Box Corer, MUC – Multi Corer.

Species	Cruise	Station	Date	Gear	Latitude	Longitude	Depth [m]	Temperature [°C]	Salinity [‰]	No. of specimens
***Hase lagomorphicus* gen. et sp. n. (paratype CV and holotype)**	M48/1	330	17/07/2000	BC	19°06.986'S	003°52.017'E	5468	2.4941	34.7779	1 adult ♀, 1 subadult copepodite V
***Hase lagomorphicus* gen. et sp. n. (paratype)**	M63/2	105	24/03/2005	BC	00°37.266'N	006°28.119'W	5173	2.1087	34.5436	1 adult♀
***Hase talpamorphicus* gen. et sp. n. (paratype CV and adult)**	M85/3	1151	17/09/2011	MUC	69°05.60'N	009°56.01'W	2270	-0.7518	34.91	1 adult ♀, 1 subadult copepodite V
***Hase talpamorphicus* gen. et sp. n. (holotype)**	M85/3	1164	18/09/2011	MUC	67°35.28'N	006°57.48'W	2403	-0.82	34.91	adult ♀

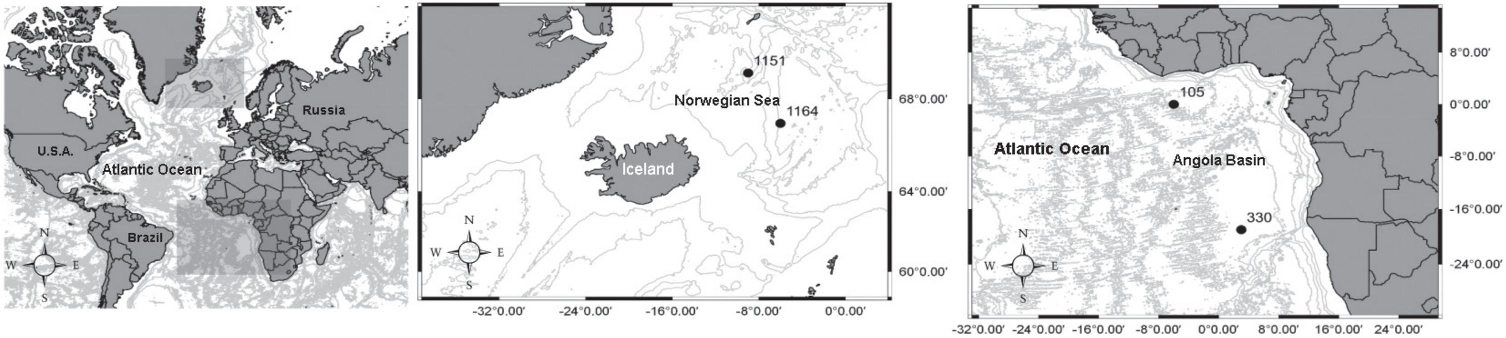

Figure 1. Sampling locations around Iceland (middle) and South Atlantic Ocean (right).

Hyphen (i.e., "-") between figure numbers, structures, number of spines and setae, etc. indicates all between and is inclusive (ex: P1-P5 = P1, P2, P3, P4, and P5; A-C = A, B and C; etc.)

The type material is deposited at the Forschungsinstitut und Naturmuseum Senckenberg (**SMF**) in Frankfurt, Germany.

Taxonomy

Order Harpacticoida Sars, 1903
Family Aegisthidae Giesbrecht, 1893
Subfamily Cerviniinae Sars M., 1903

Hase gen. n.

http://zoobank.org/158094D3-E3A5-427B-BFD7-1223015ABF72

Diagnosis. Female body sturdy with clear distinction between prosome and narrower urosome. Prosome 5-segmented, with cephalosome and four free pedigerous somites. Cephalosome with minute spinules covering surface and anastomosing reticulation towards rostrum and along margins; posterior margin slightly serrate. Pedigerous somites with reticulation along ventroposterior margins; lateral margins of third and fourth pedigerous somites smooth or expanded posteriorly forming hook-like projections laterally; posterior margins serrate. Urosome 5-segmented, comprising P5 bearing somite, genital double-somite, two free abdominal somites, and telson. Genital double-somite and two free abdominal somites with hook-like projections ventrolaterally. Genital double-somite original segmentation indicated by transverse, serrate surface ridge with reticulation and sensilla dorsal and laterally, completely fused ventrally; genital field with copulatory pore located in median depression; gonopores covered by operculum derived from sixth legs and by anteriorly directed flap arising from somite wall; P6 fused genital opercular plate armed with two setae. Telson with well-developed anal operculum; large anal opening with folded and reticulated cuticle; surface ornamentation consisting of pair of sensilla dorsally, minute spinules and pair of pores ventrally; ventral posterior margin with minute setules. Furca symmetrical; approximately 3.4× as long as maximum width; distinctly convergent. Each ramus with seven setae: setae I-III not inserted close to each other; seta I proximal, laterally inserted, spiniform and bipinnate; seta II median, dorsally inserted, spiniform, and bipinnate; seta III subdistal, laterally inserted, spiniform and bipinnate; setae IV and V distally inserted, bipinnate and fused basally; seta VI distally inserted, minute and naked; seta VII dorsally inserted, close to seta III, tri-articulate at base and pinnate.

Rostrum fused to cephalic shield; tip rounded, with tuft of spinules along distal margin or slightly bifid and smooth; with pair of sensilla near apex. A1 7-segmented, proximal segments 1–3 cylindrical or subcylindrical; distal segments flattened. Segment I the longest; segment III with aesthetasc fused basally to single seta and set on distinct pedestal; segment VII with aesthetasc fused basally to one seta. Armature formula: I-[1], II-[8-9 elements], III-[10-12 + (1 + Ae)], IV-[3], V-[2], VI-[2], VII-[6-7 + (one naked + Ae)]. A2 3-segmented, comprising cylindrical coxa and allobasis, and 1-segmented flattened enp. Coxa small. Basis and enp-1 fused, forming elongate allobasis and with abexopodal seta. Enp medial armature four elements, apical armature 3–4 spines, one seta, and three fused elements. Exp 4-segmented; armature formula: I-[2], II-[1], III-[1], IV-[2-3].

Md. Coxa with well-developed musculature, gnathobase curved inwards, bearing several multicuspid teeth and single seta on inner distal margin. Palp well developed, comprising basis, enp and exp. Basis with four setae. Enp 1-segmented with three lateral setae and 6–7 apical setae. Exp 4-segmented; armature formula: I-[2], II-[1], III-[1], IV-[2]. Mx1. Praecoxa with row of spinules; arthrite well developed and with 13–14 elements. Coxa endite cylindrical, bearing 5–6 setae distally; epipodite absent. Basis and enp fused; basis with eleven setae; enp incorporated into basis, represented by 2–3 naked setae. Exp 1-segmented, with 2–3 setae. Mx2 comprising syncoxa fused to allobasis, and 4-segmented enp. Syncoxa/allobasis with four endites; proximal coxal endite with five pinnate setae; distal coxal endite almost completely incorporated into syncoxa, with three setae; proximal basal endite with three setae; distal basal endite with two setae and one spine. Enp-1 endite forming strong claw; accessory armature consisting of two setae, one or two spines and zero or one tube pore; armature of fused enp-2 represented by three or four elements. Free enp 3-segmented; armature formula: I-[claw; 3–4 spines/setae; 0–1 tube pore], II-[3-4], III-[2], IV-[2-3], V-[3-4]. Mxp with elongated syncoxa, strong basis and 2-segmented enp; syncoxal endites represented proximal to distal by two elements, 3–4 elements, and 2–3 elements; basal endite represented by two elements. Enp with armature formula: I-[2], II-[four elements].

Pereopods biramous; exp and enp flattened, bent inwards, especially on P1 and P2. Praecoxa without ornamentation. Coxa without ornamentation (P1) or ornamented (P2-P4). Basis with (P1 and P2) or without (P3 and P4) one seta on outer proximal corner, with one seta on inner distal corner of P1. Exp 3-segmented. Enp 3-segmented (P1), 2-segmented (P2 and P3) and 1-segmented (P4). P5 1-segmented, pointing outwards, fused to supporting somite. Exp with three elements. P1-P4 spine and setal formulae as follows:

	Exp	**Enp**
P1	I, 1; I, 1; II, II+1, 1	0, 1; 0, 1; I, 2, 2
P2	I, 1; I, 1; II, II+1, 2	0, 1; I, 2, 1
P3	I, 1; I, 1; II, II+1, 2	0, 1; I, 2, 0
P4	I, 1; I, 1; II, II+1, I-II	0, 2, 0-I

Etymology. The generic name, *Hase*, from German, means “hare”, and refers to the very superficial resemblance of the new species to a hare or rabbit. Gender masculine.

Type species. *Hase lagomorphicus* sp. n., by present designation.

Hase lagomorphicus gen. et sp. n.

http://zoobank.org/582DC8A7-6041-44AE-85EC-AEB38ED60BBC
Figs 2–11

Type material. Holotype, adult female dissected on six slides (reg. no. SMF 37130/1-6), from DIVA-1 (M48/1, 330). Paratype, adult female (incomplete) dissected into three slides (reg. no. SMF 37131/1-3), from DIVA-2 (M63/2, 105). Paratype 2, subadult copepopid stage V (CV) dissected into five slides (reg. no. SMF 37132/1-5), from DIVA-1 (M48/1, 330).

Type locality. Angola Basin (DIVA-1 cruise M48/1, 330) (Fig. 1; Table 1), Atlantic Ocean.

Etymology. The specific epithet is built by combining the ancient Greek lexemes λαγός (lagós), meaning hare, and μοϱφώ (morphó), "the Shapely One".

Description. Female. Total body length 730 μm (paratype 1) and 735 μm (holotype) (*N* = 2; mean = 732.5 μm). Largest width measured at posterior margin of P2-bearing somite: 292 μm (paratype 1) and 295 μm (holotype) (*N* = 2; mean = 293.5 μm).

Body (Fig. 2A–C) with clear distinction between prosome and narrower urosome. Prosome (Fig. 2A–C) 5-segmented, with cephalosome and P1-P4 free pedigerous somites. Cephalosome with spinules covering surface and anastomosing reticulation towards rostrum and along margins; posterior margin slightly serrate. Pedigerous somites with reticulation along ventroposterior margins (Fig. 2B); lateral margins of third and fourth pedigerous somites smooth (Fig. 2A, B); posterior margins serrate.

Urosome (Figs 2A–C, 3A, B) 5-segmented, comprising P5-bearing somite, genital double-somite, two free abdominal somites and telson. Genital double-somite and two free abdominal somites with hook-like projections ventrolaterally, distalmost the largest.

Genital double-somite (Figs 2B, C, 3A–C, 4E) original segmentation indicated by transverse surface ridge with reticulation and sensilla dorsal and laterally, completely fused ventrally; genital field (Figs 3C, 4E) with copulatory pore slightly covered by a proximal flap, pointing posteriorly, located in a soft median depression; gonopores covered by operculum derived from sixth legs and anteriorly directed flap, medially depressed, arising from somite wall; P6 bearing two naked seta.

Telson (Figs 2A–C, 3A, B) with well-developed anal operculum; large anal opening with folded and reticulated cuticle; surface ornamentation consisting of pair of sensilla dorsally, minute spinules and pair of pores ventrally; ventral posterior margin with minute setules.

Furca (Figs 2A–C, 3A, B, 4F) symmetrical; approximately 3.4× as long as maximum width; distinctly convergent. Each ramus with seven setae: seta I, spiniform and bipinnate, inserted laterally, close to proximal margin; seta II, spiniform and bipinnate, dorsal and medially inserted; seta III laterally inserted, spiniform and bipinnate, located at outer subdistal corner; setae IV and V distally inserted, fused basally, seta IV bipinnate, seta V bipinnate and 4× longer than seta IV; seta VI distally inserted, minute and naked; seta VII dorsal, close to seta III, tri-articulate at base and pinnate.

Rostrum (Fig. 2A) fused to cephalic shield; tip rounded, with tuft of spinules along distal margin; with pair of sensilla near apex.

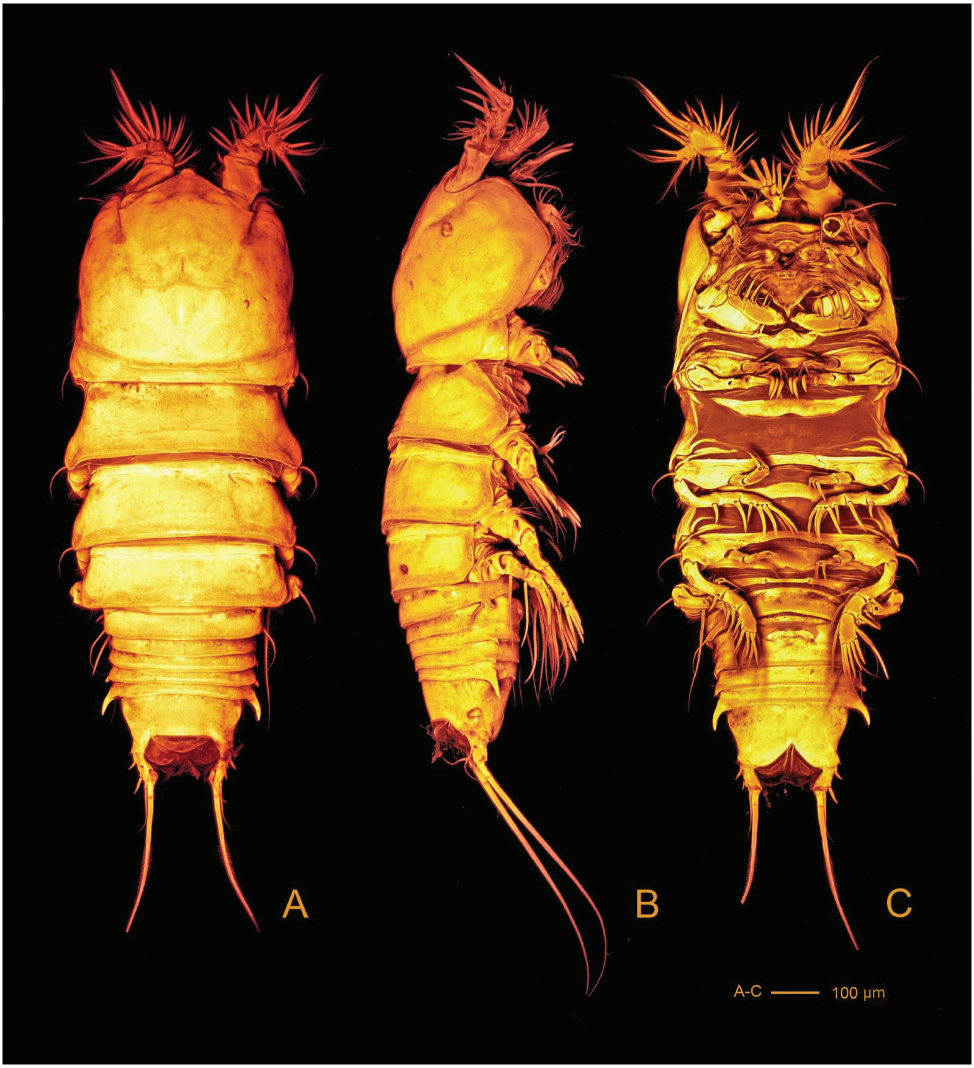

Figure 2. *Hase lagomorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M48/1, 330, DIVA-I): **A** habitus, dorsal **B** habitus, lateral **C** habitus, ventral.

A1 (Figs 4A, 5B, C) 7-segmented, proximal segments 1–3 cylindrical or subcylindrical; distal segments flattened. Segment I the longest, with rows of setules along outer and inner margins; segment III with aesthetasc fused basally to seta and set on distinct pedestal; segment VII with aesthetasc fused basally to one naked seta.

Armature formula: I-[one pinnate], II-[six naked + two unipinnate], III-[ten naked + (one naked + Ae)], IV-[one bipinnate + two naked], V-[two naked], VI-[one unipinnate + one naked], VII-[two naked, three bipinnate + one unipinnate + (one naked + Ae)].

A2 (Figs 4B, 7A) 3-segmented, comprising cylindrical coxa and allobasis, and 1-segmented and flattened enp. Coxa small, with spinules along inner margin. Basis

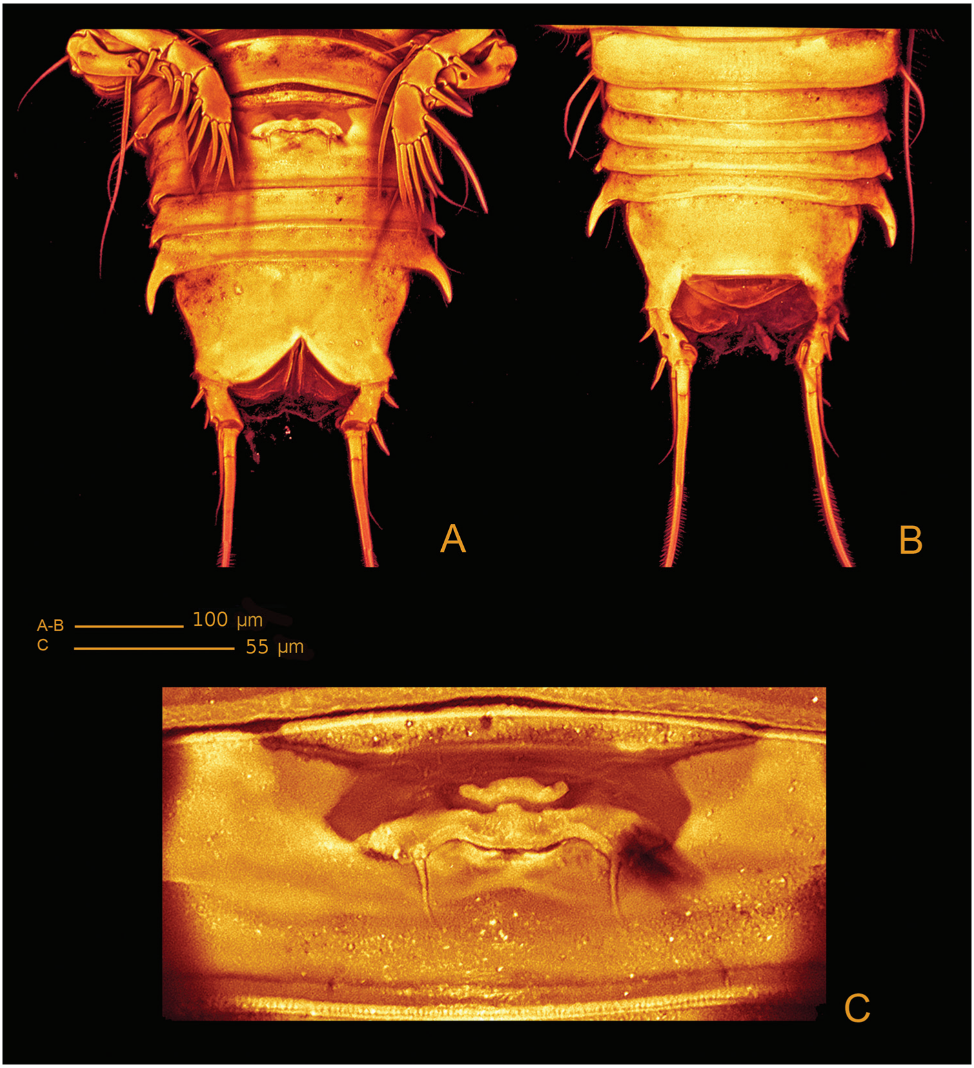

Figure 3. *Hase lagomorphicus* gen. et sp. n. Holotype (female) (M48/1, 330, DIVA-I): **A** urosome, ventral **B** urosome, dorsal **C** genital double somite, ventral.

and enp-1 fused, forming elongate allobasis, with patches of spinules as shown; abexopodal seta long and bipinnate. Medial armature of free enp consisting of two smooth setae, one seta medially unipinnate, one distally bipinnate spine and one seta medially unipinnate and distally bipinnate; apical armature consisting of three bipinnate spines, one naked seta and three elements fused basally (two long setae medially unipinnate, and one smooth). Exp 4-segmented; distal segment with row of spinules; armature formula: I-[two pinnate], II-[one pinnate], III-[one pinnate], IV-[two pinnate].

Md (Fig. 6A(a1, a2, a3), 7D, E). Coxa with well-developed musculature, gnathobase curved inwards, bearing several multicuspid teeth and one bipinnate seta on in-

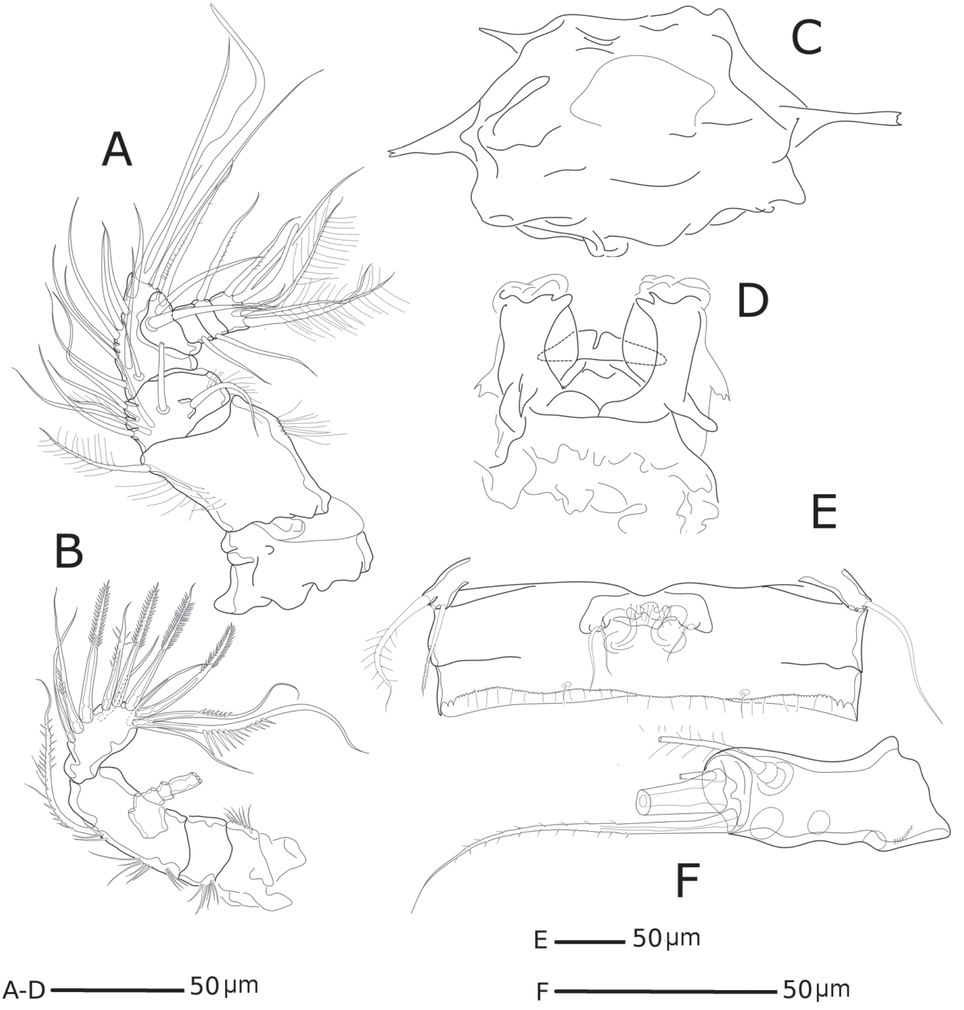

Figure 4. *Hase lagomorphicus* gen. et sp. n. Holotype (female) (M48/1, 330, DIVA-I): **A** A1 **B** A2 **C** labrum **D** labium **E** P5 and genital double somite **F** furca.

ner distal margin; two rows of spinules near insertion area of bipinnate seta. Palp well developed, comprising basis, enp and exp. Basis with four bipinnate setae and surface ornamentation as indicated in Fig. 6A (a1). Enp 1-segmented with three smooth lateral setae and six apical setae (four naked and two unipinnate). Exp 4-segmented, exp-1 as long as next three segments combined; armature formula: I-[one smooth and one bipinnate], II-[one bipinnate], III-[one bipinnate], IV-[two bipinnate].

Mx1 (Figs 6C(c1–c4), 8A, B). Praecoxa with row of spinules; arthrite well developed, with one pinnate and one smooth seta on anterior surface, four smooth spines, and three pinnate spines along distal margin (two ornate with two large spinules at

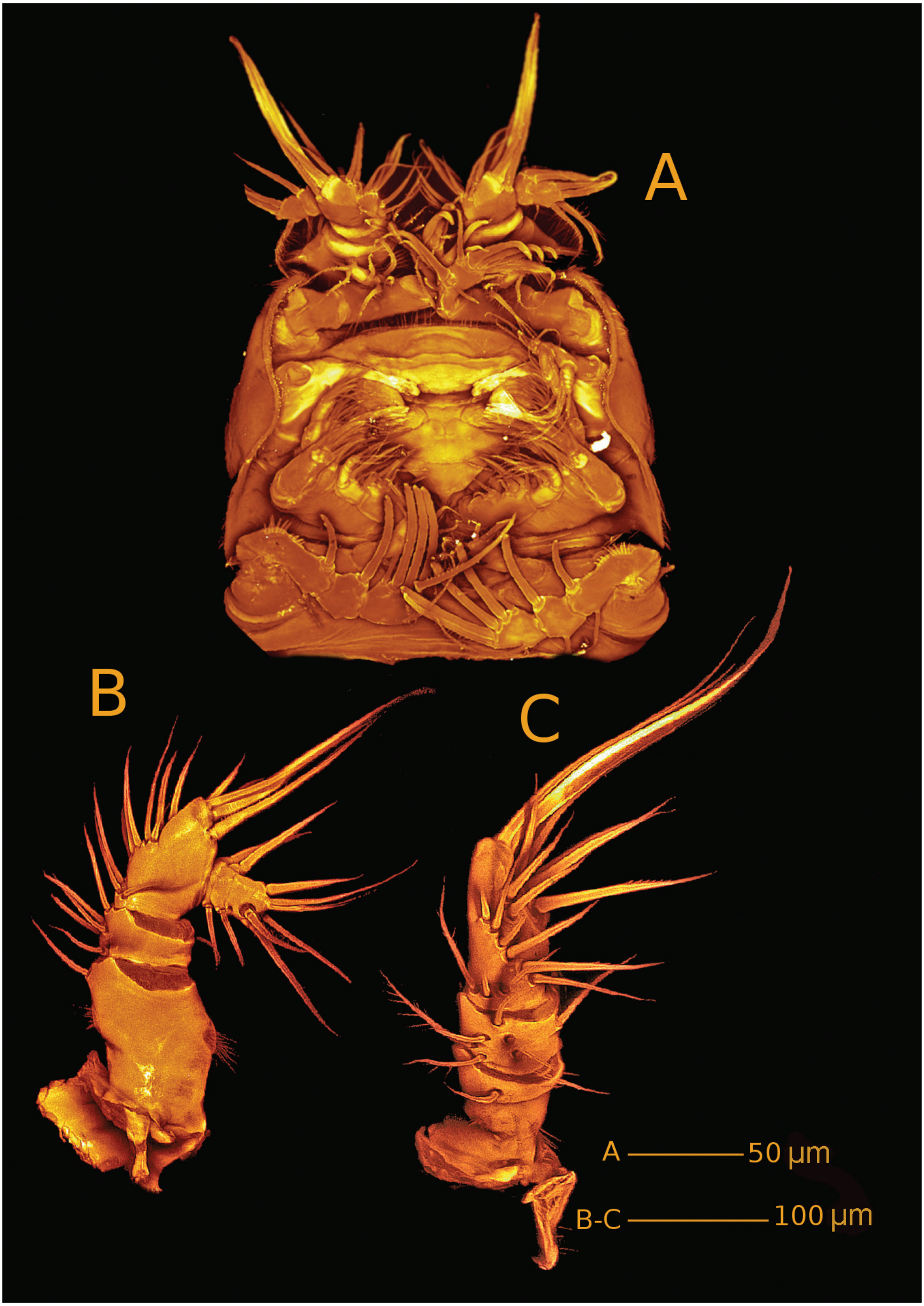

Figure 5. *Hase lagomorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M48/1, 330, DIVA-I): **A** cephalothorax and first pedigerous somite, ventral **B** A1, dorsal **C** A1, inner.

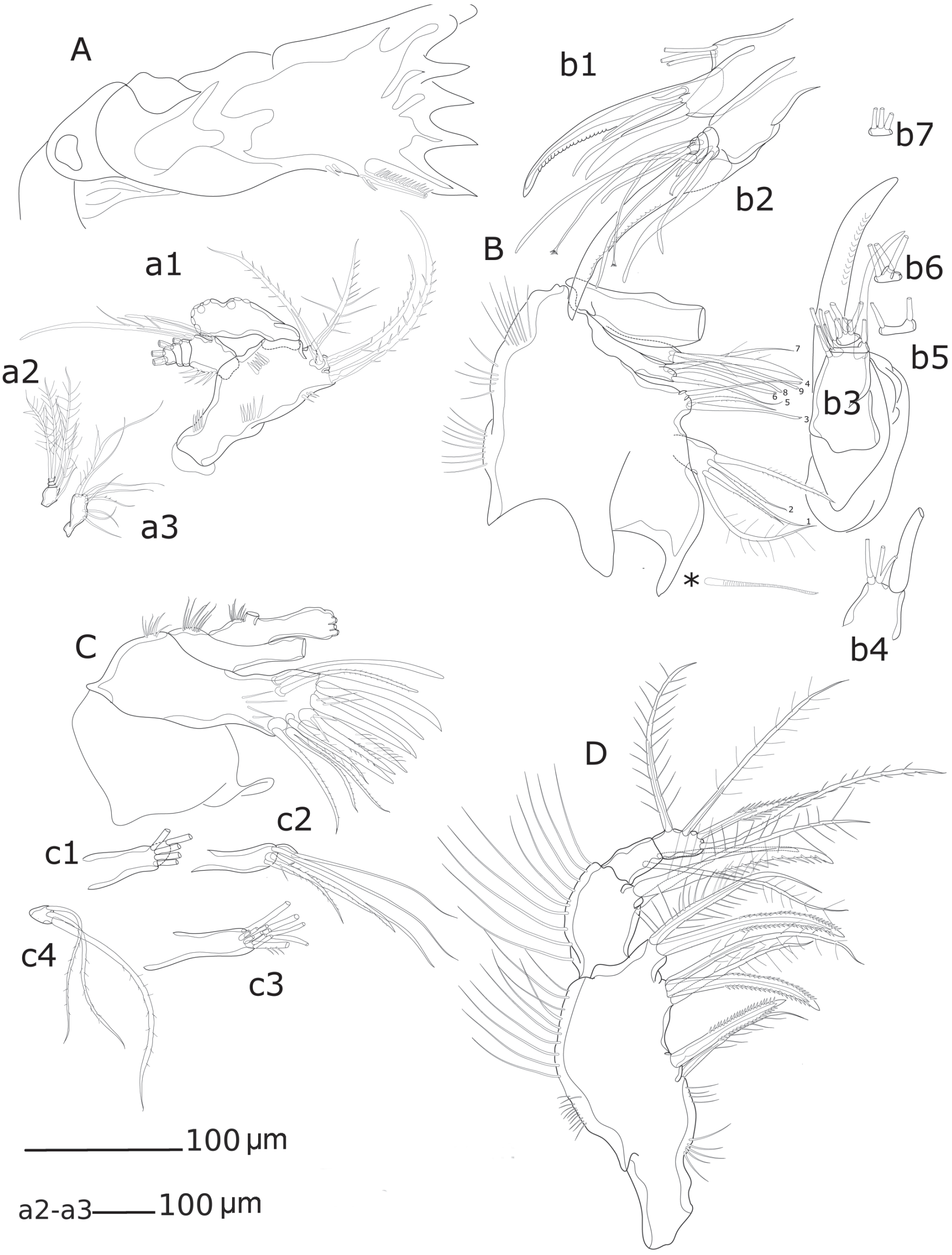

Figure 6. *Hase lagomorphicus* gen. et sp. n. Holotype (female) (M48/1, 330, DIVA-I): **A** Md gnathobasis; a1- mandibular palp with basis, exp and enp; a2- exp; a3- enp **B** Mx2 syncoxa, allobasis, and first enp without claw; b1 enp1 with claw and accessory spines, and 2nd enp (fused) in lateral view; b2 enp-1 with claw, and enp-2 to enp-5; b3 upper view of enp-1 to enp-5; b4 upper view of enp-2; b5-b7 upper view of enp-3 to enp-5 **C** Mx1 with unarmed coxa, basis, enp and exp; c1 and c2- coxa; c3 basis with incorporated enp; c4- exopod **D** Mxp.

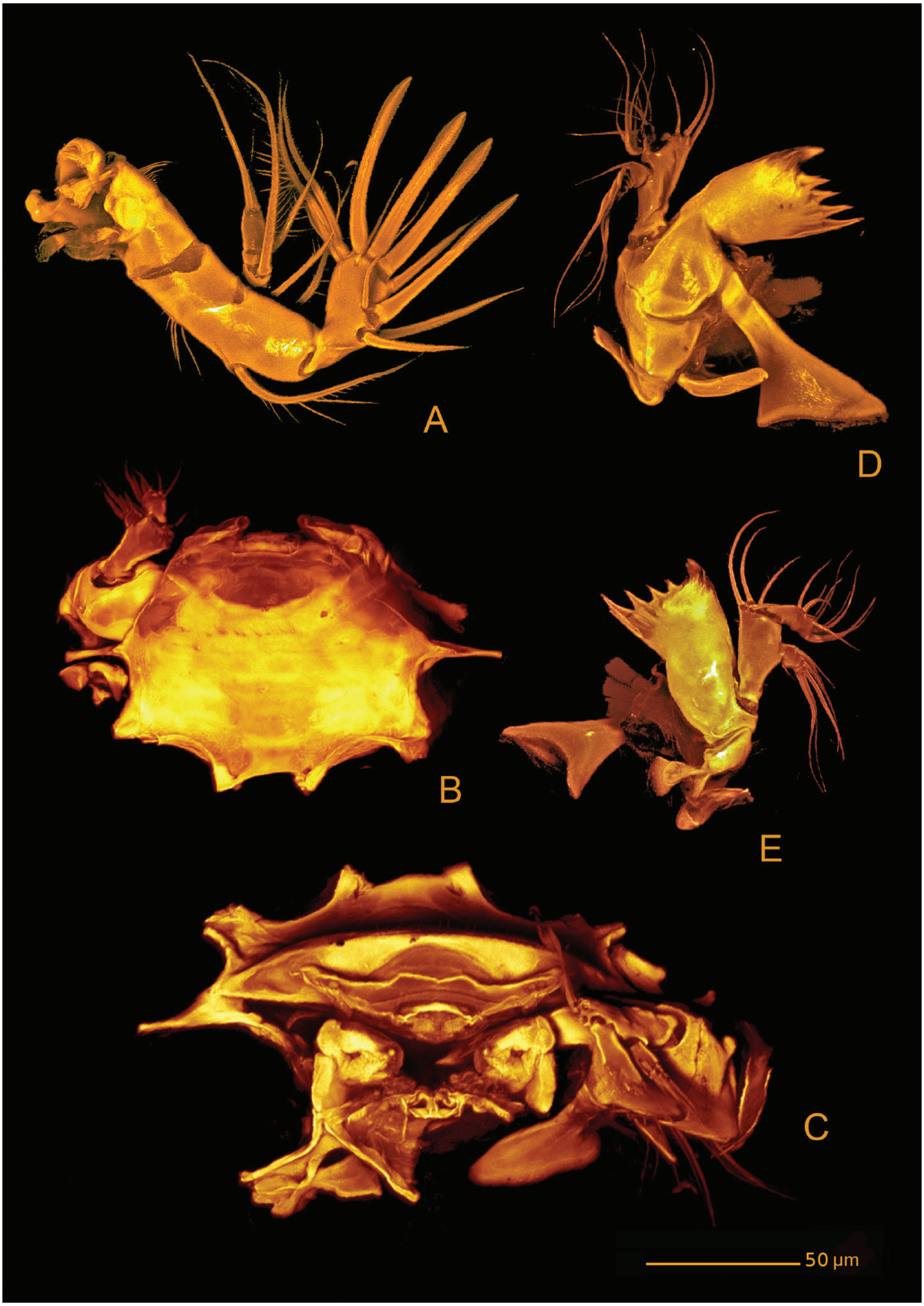

Figure 7. *Hase lagomorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M48/1, 330, DIVA-I): **A** A2 **B** labrum, anterior **C** labrum, labium and Md, ventral **D** Md, anterior **E** Md, posterior.

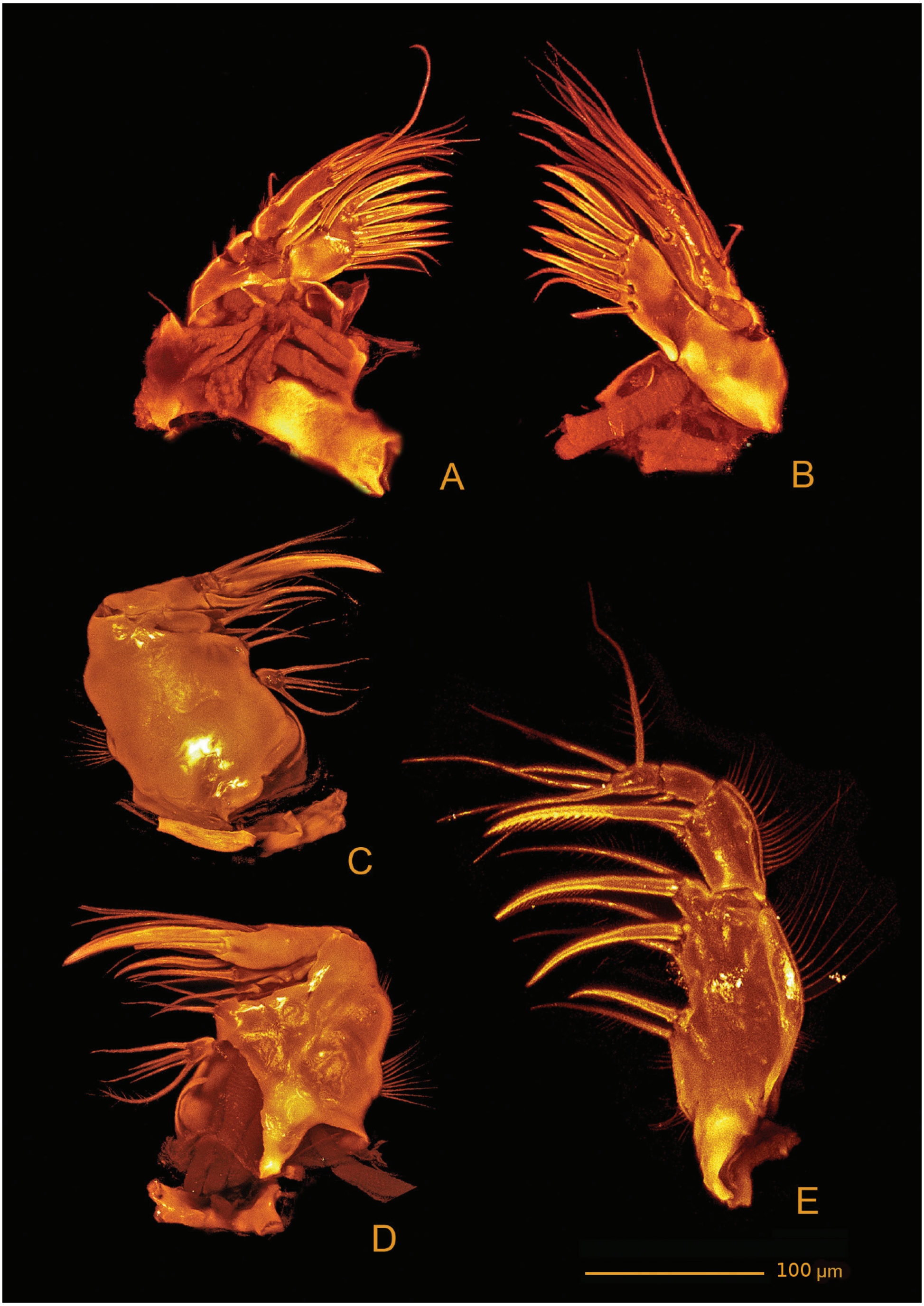

Figure 8. *Hase lagomorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M48/1, 330, DIVA-I): **A** Mx1, posterior **B** Mx1, anterior **C** Mx2, anterior **D** Mx2, posterior **E** Mp, anterior.

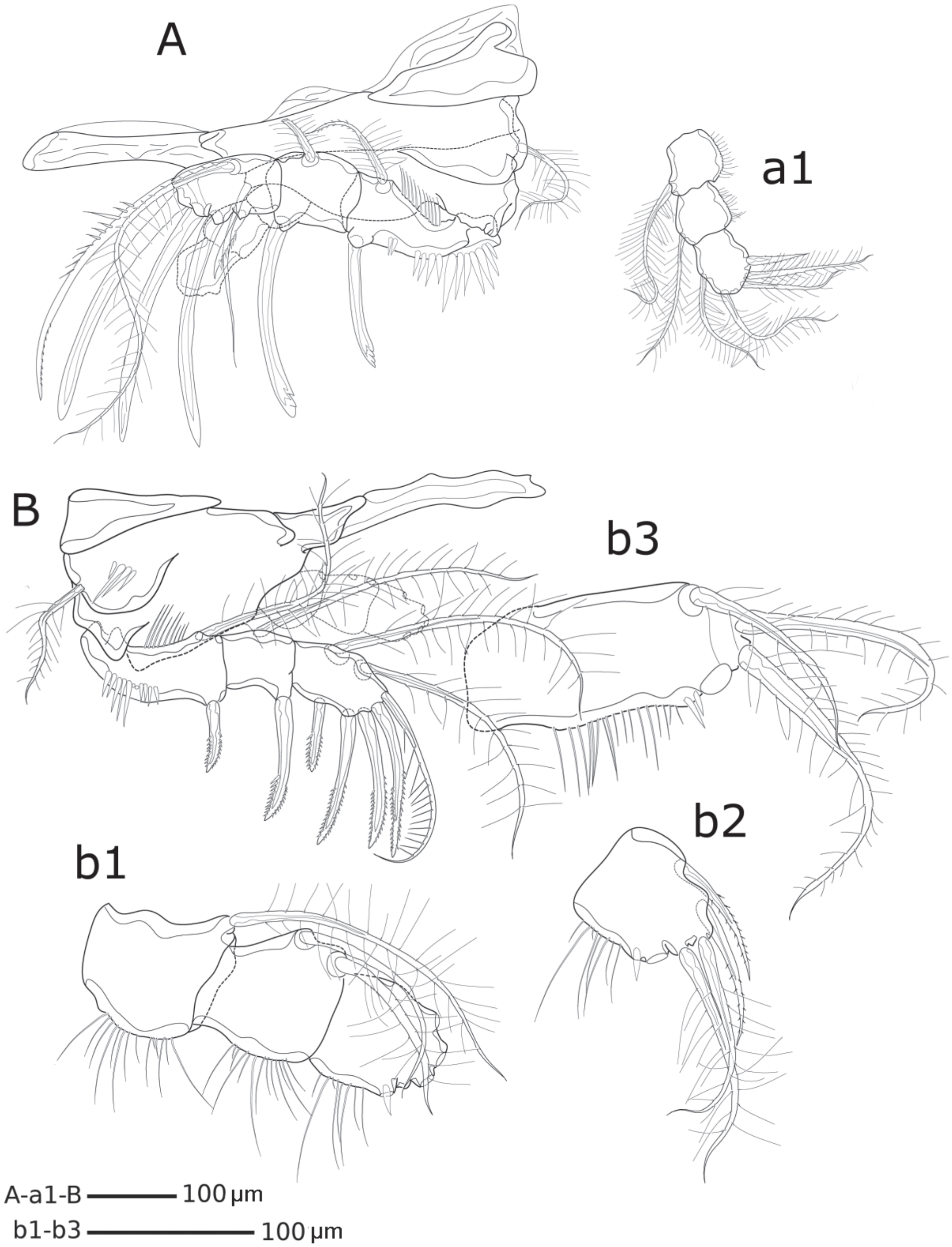

Figure 9. *Hase lagomorphicus* gen. et sp. n. Holotype (female) (M48/1, 330, DIVA-I): **A** P1; a1- P1 enp.; b3- P2 enp-2. Paratype (Copepodite V) (M48/1, 330, DIVA-I) **B** P2; b1- P2 enp; b2- P2 enp-3.

basis), four pinnate setae on aboral margin, two fused at basis. Coxa endite cylindrical, bearing five setae (four naked and one pinnate) distally; epipodite absent. Basis

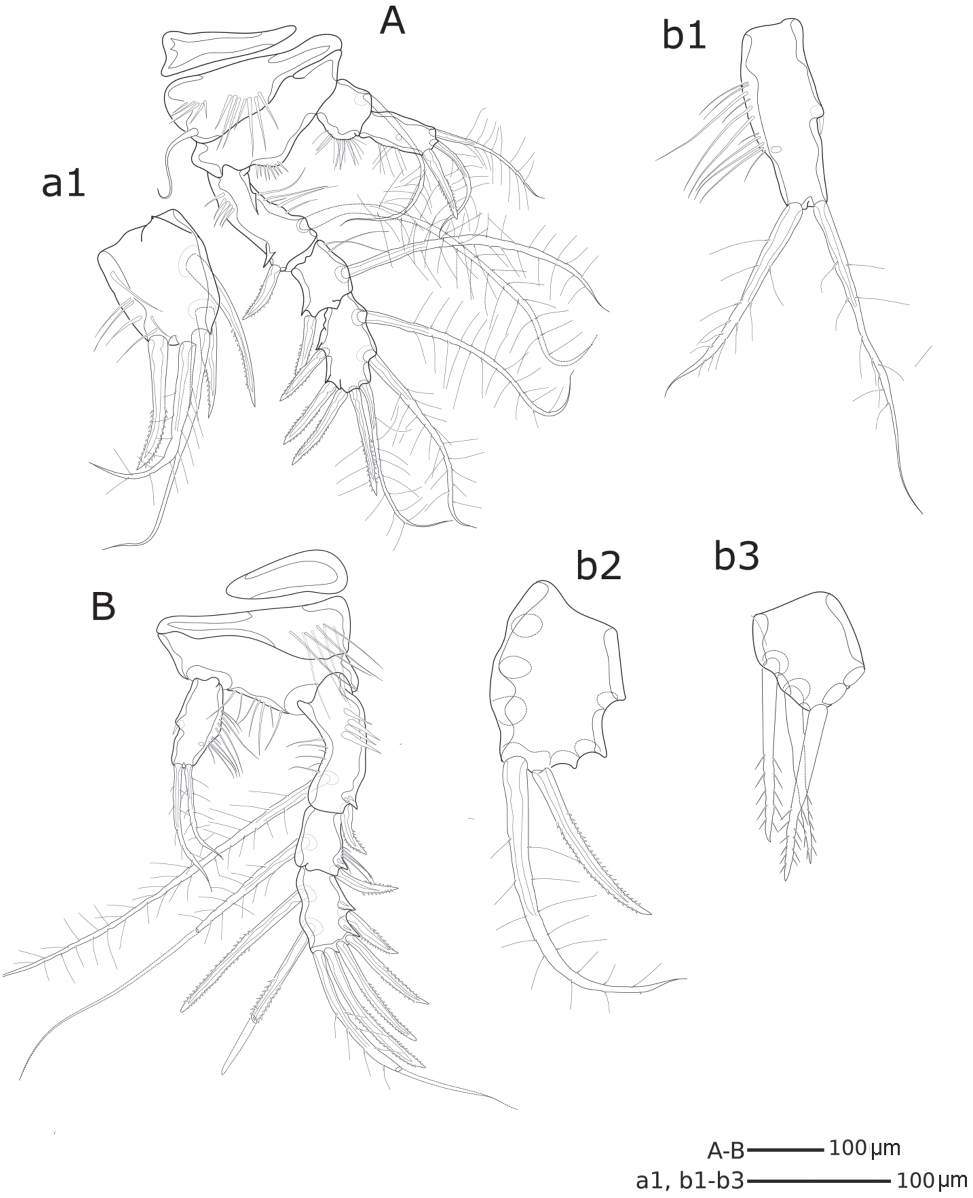

Figure 10. *Hase lagomorphicus* gen. et sp. n. Holotype (female) (M48/1, 330, DIVA-I): **A** P3 **B** P4; b1- P4 enp. Paratype (Copepodite V) (M48/1, 330, DIVA-I): a1- P3 enp-3; b2- P4 exp-3; b3- P4 enp-3.

and enp fused; basis with eleven setae; enp incorporated into basis, represented by two naked setae. Exp 1-segmented, with three bipinnate setae.

Mx2 (Figs 6B(b1–b7), 8C, D) comprising syncoxa fused to allobasis, and 5-segmented enp. Syncoxa/allobasis with four endites; proximal coxal endite with five pinnate

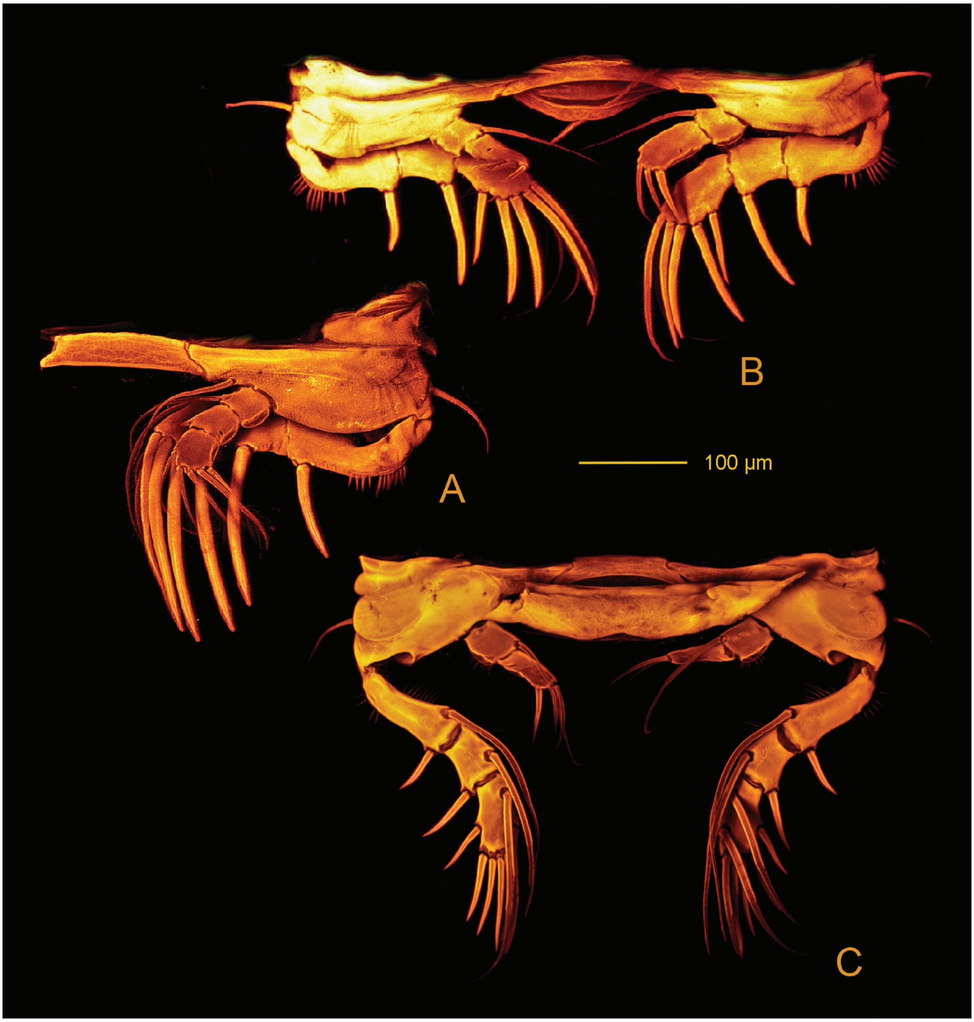

Figure 11. *Hase lagomorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M48/1, 330, DIVA-I): **A** P1 **C** P3. Paratype (female) (M63/2, 105, Diva II) **B** P2.

setae; distal coxal endite almost completely incorporated into syncoxa, with one pinnate setae, and two naked setae with bifid tip; proximal basal endite with three setae (two naked, one with bifid tip, and one weakly pinnate); distal basal endite with two naked setae with bifid tip, and one weakly pinnate spine. Enp-1 endite forming strong claw; accessory armature consisting of two naked setae (one long and flexible and one foliaceous), one spine and one claw-like spine; armature of fused enp-2 represented by three naked seta. Free enp 3-segmented; armature formula: I-[claw; 4], II-[3], III-[2], IV-[3], V-[3].

Mxp (Figs 6D, 8E) with elongated syncoxa, strong basis, and 2-segmented enp. Syncoxa with rows of spinules along inner and outer margins; syncoxa with three endites; first endite with one bipinnate seta and one bipinnate spine; second endite with two bipinnate setae and one bipinnate spine; third endite with one bipinnate seta and one bipinnate spine; basal endite with one bipinnate seta and one unipinnate spine. Enp with armature formula: I-[two setae; one bipinnate and one naked], II-[one unipinnate spine + three bipinnate setae].

Pereopods (Figs 5A, 9–11) biramous; exp and enp bent inwards, especially on P1 and P2. Praecoxa transversally elongate, without ornamentation. Coxa without ornamentation (P1) or ornamented (P2-P4), with position and strength of ornamentation differing from P2 to P4. Basis with (P1, P2) or without (P3, P4) bipinnate seta on outer proximal corner, with bipinnate seta on inner distal corner of P1. Exp 3-segmented; bent inwards against basis in P1 and P2, exp-1 with rows of setules along inner margin and spinules along outer margin, exp-2 without ornamentation on P1 and P2, with setules on inner margin of P3 and outer margin of P4. Enp 3-segmented on P1, 2-segmented on P2 and P3 but 1-segmented on P4; enp-1 with setules along outer margin of P1-P3; enp P4 with setules on outer margin. Setal formulae as follows:

	Exp	**Enp**
P1	I, 1; I, 1; II, II+1, 1	0, 1; 0, 1; I, 2, 2
P2	I, 1; I, 1; II, II+1, 2	0, 1; I (broken), 2, 1
P3	I, 1; I, 1; II, II+1, 2	0, 1; I, 2, 0
P4	I, 1; I, 1; II, II+1, II	0, 2, I

P5 (Fig. 4E) One-segmented, fused to supporting somite, pointing outwards. Exp with three elements (one lost during dissection), outer most a bipinnate seta, innermost a bipinnate spine.

Male unknown.

Occurrence. Angola and Guinea basins, Atlantic Ocean.

Remarks. In the subadult CV, enp is 3-segmented on P2-P4; exp-3 of P4 with 8 elements (Fig. 10 b2); enp-2 of P2-P4 with two inner setae (Fig. 9 B, b1), exp-3 of P2-P4 with 5 elements (Fig. 9 b3 and Fig. 10 (a1, b3)). Setal formulae as follows:

	Exp	**Enp**
P1	I, 1; I, 1; II, II+1, 1	0, 1; 0, 1; I, 2, 2
P2	I, 1; I, 1; II, II+1, 2	0, 1; 0, 2; 0, I+2 (?), II
P3	I, 1; I, 1; II, II+1, 2	0, 1; 0,2; 0, I+2, II
P4	I, 1; I, 1; II (?), II (?) +1, 3 elements (broken)	0, 1; 0, 2; 5 elements (two broken)

Hase talpamorphicus **gen. et sp. n.**

http://zoobank.org/E1475D7D-08B2-4E01-A1DE-3E849E71C2DB
Figs 12–20

Type material. Holotype female dissected on 21 slides (reg. no. SMF 37133/1-21) from station 1164, multi corer 9. Undissected paratypes: one female (reg. no. SMF 37134/1) from station 1151, MUC 12 and one subadult copepopid stage V (CV) (reg. no. SMF

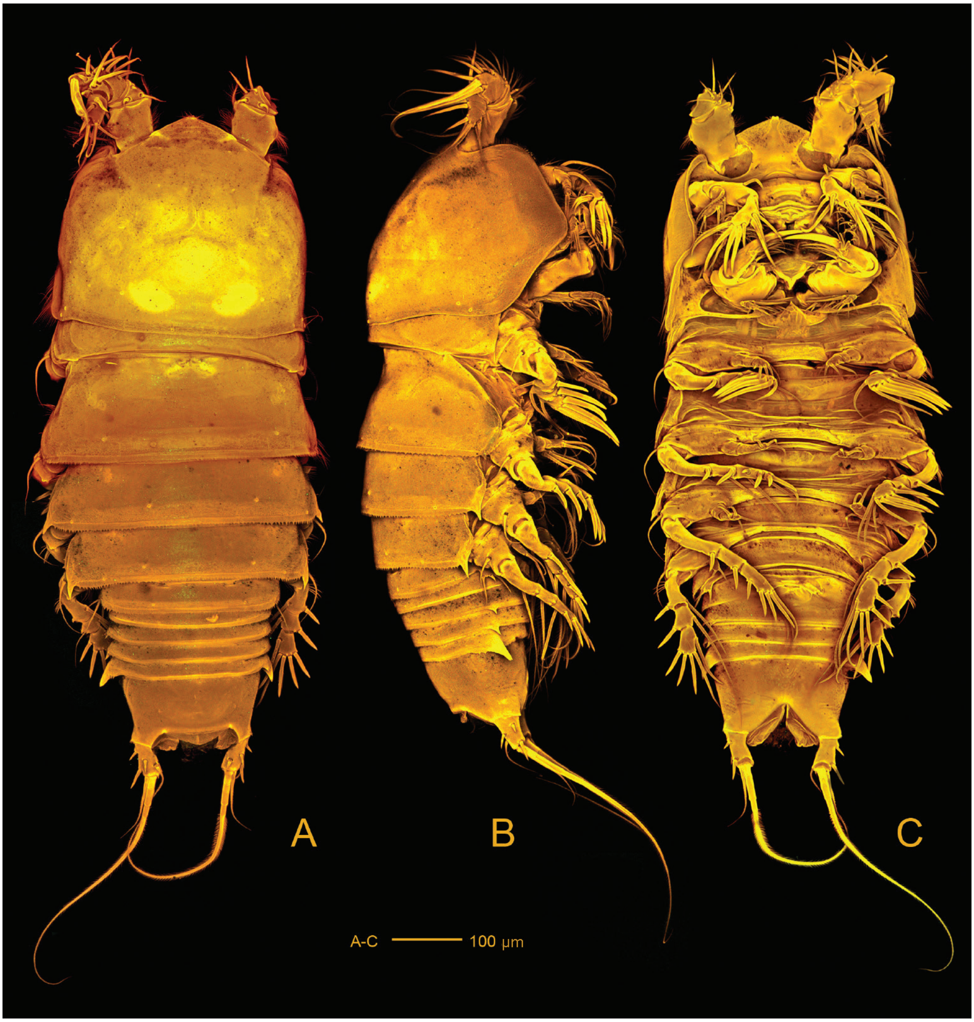

Figure 12. *Hase talpamorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M85/3, 1164): **A** habitus, dorsal **B** habitus, lateral **C** habitus, ventral.

37135/1) from station 1151, MUC 10. All specimens were collected during the Overflow, Circulation and Biodiversity Expedition of the RV "Meteor" (Cruise No. M85/3).

Type locality. Norwegian Sea (IceAGE cruise M85/3, 1164) (Fig. 1; Table 1).

Etymology. The specific epithet is built by combining the Latin *talpa*, meaning a mole, and the ancient Greek lexeme *μορφώ* (*morphó*), "the Shapely One".

Description. Female. Total body length 986.7 µm (holotype) and 1000.0 µm (paratype) (N = 2; mean = 993.4 µm). Largest width measured at posterior margin of P2-bearing somite: 400.0 µm (holotype) and 437.5 µm (paratype) (N = 2; mean = 418.7 µm).

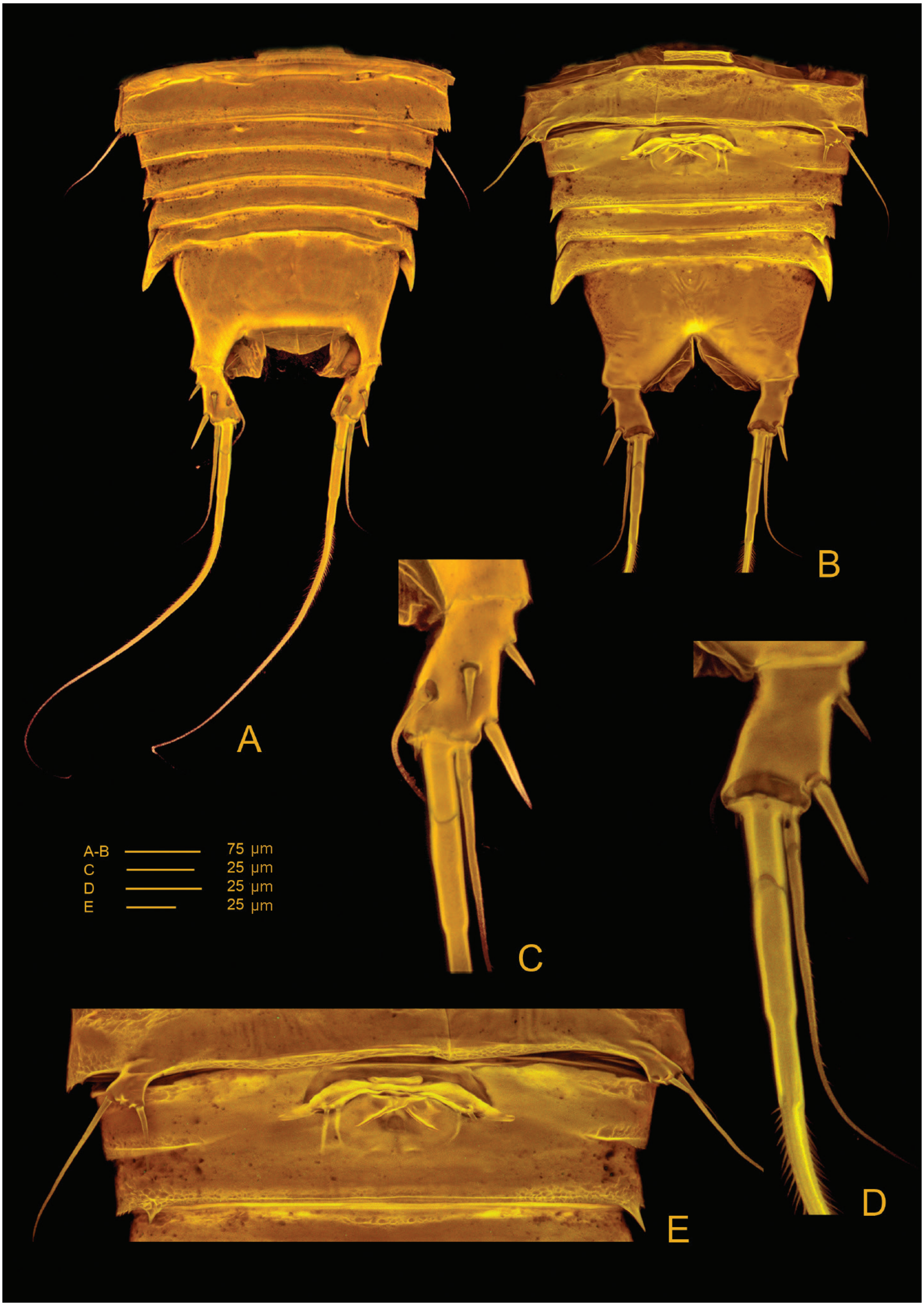

Figure 13. *Hase talpamorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M85/3, 1164): **A** urosome, dorsal **B** urosome, ventral **C** furca, dorsal **D** furca, ventral **E** P5 and double genital somite.

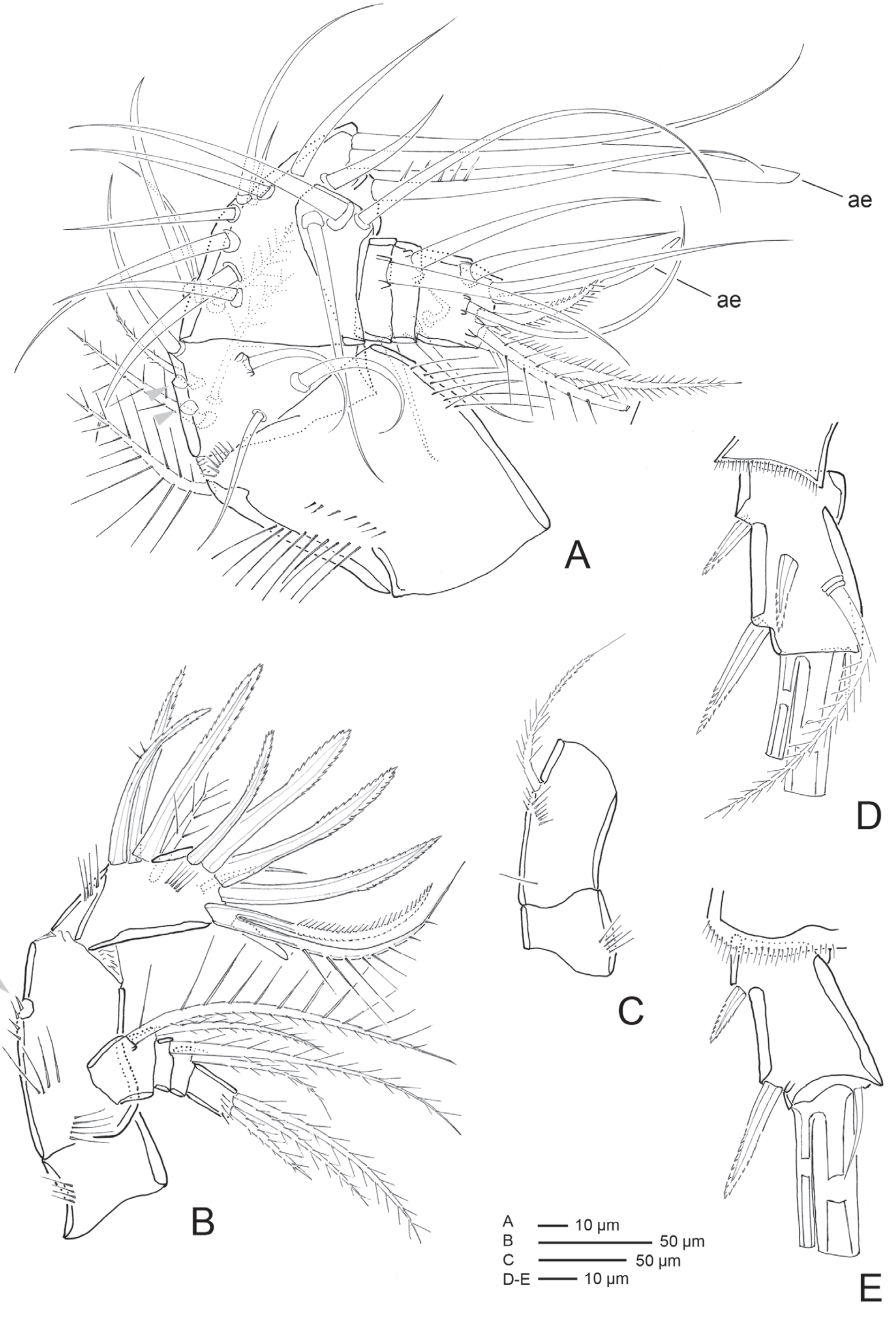

Figure 14. *Hase talpamorphicus* gen. et sp. n. Holotype (female) (M85/3, 1164): **A** antennule **B** A2 **C** A2 coxa and allobasis **D** furca, dorsal **E** furca, ventral.

Body (Fig. 12A–C) with clear distinction between prosome and narrower urosome. Prosome 5-segmented, with cephalosome and four free pedigerous somites. Cephalosome with minute spinules covering surface and anastomosing reticulation towards rostrum and along margins; additional ornamentation consisting of sensilla and pores; posterior margin slightly serrate. Pedigerous somites with reticulation along posterior margins and ornamentation consisting of sensilla; lateral margins of third and fourth pedigerous somites expanded posteriorly forming hook-like projections laterally; posterior margins serrate.

Urosome (Figs 12A–C, 13A, B) 5-segmented, comprising P5-bearing somite, genital double-somite, two free abdominal somites, and telson. Urosomites with surface ornamentation consisting of sensilla and minute spinules, spinules more conspicuous ventrally; posterior margin serrate and with reticulated surface, genital double-somite and two free abdominal somites with hook-like projections ventrolaterally, larger in somite anterior to telson.

Genital double-somite (Figs 12C, 13B, E, 19D) original segmentation indicated by transverse, serrate surface ridge with reticulation and sensilla dorsal and laterally, completely fused ventrally; genital field (Figs 12C, 13B, E, 19D) with copulatory pore completely visible, not covered by a proximal flap as observed for the previous species, located in a well-developed median depression; gonopores covered by operculum derived from sixth legs and by anteriorly directed and straight flap arising from somite wall; P6 bearing two naked setae.

Telson (Figs 12A–C, 13A, B) with well-developed anal operculum; large anal opening with folded and reticulated cuticle; surface ornamentation consisting of pair of sensilla dorsally, minute spinules and pair of pores ventrally; ventral posterior margin with minute setules.

Furca (Figs 12A–C, 13A–D, 14D, E) symmetrical; approximately 3.4× as long as maximum width; distinctly convergent. Each ramus with seven setae: seta I, spiniform and bipinnate, close to anterior margin; seta II, spiniform and bipinnate, located dorsally; seta III spiniform and bipinnate, located at outer distal corner; setae IV and V fused basally, seta IV bipinnate, seta V bipinnate and 4× longer than seta IV; seta VI minute and naked; seta VII tri-articulate at base and pinnate.

Rostrum (Fig. 12A, C) fused to cephalic shield; tip slightly bifid; with pair of sensilla and midventral tube-pore near apex.

A1 (Figs 14A, 15A, B) 7-segmented. Shape as in previous species. Segment I the longest, with rows of setules along outer and inner margins, with small spinules along outer distal corner; segment III with aesthetasc fused basally to seta and set on distinct pedestal; segment VII with aesthetasc fused basally to one naked seta.

Armature formula: I-[one pinnate], II-[four naked + three bipinnate + two missing elements], III-[eleven naked + one bipinnate + (one naked + ae)], IV-[three naked], V-[two naked], VI-[two naked], VII-[three naked, three pinnate + (one naked + ae)].

A2 (Figs 14B, C, 15C, D) 3-segmented, comprising cylindrical coxa and allobasis, and flattened 1-segmented enp. Coxa small, with spinules along inner margin.

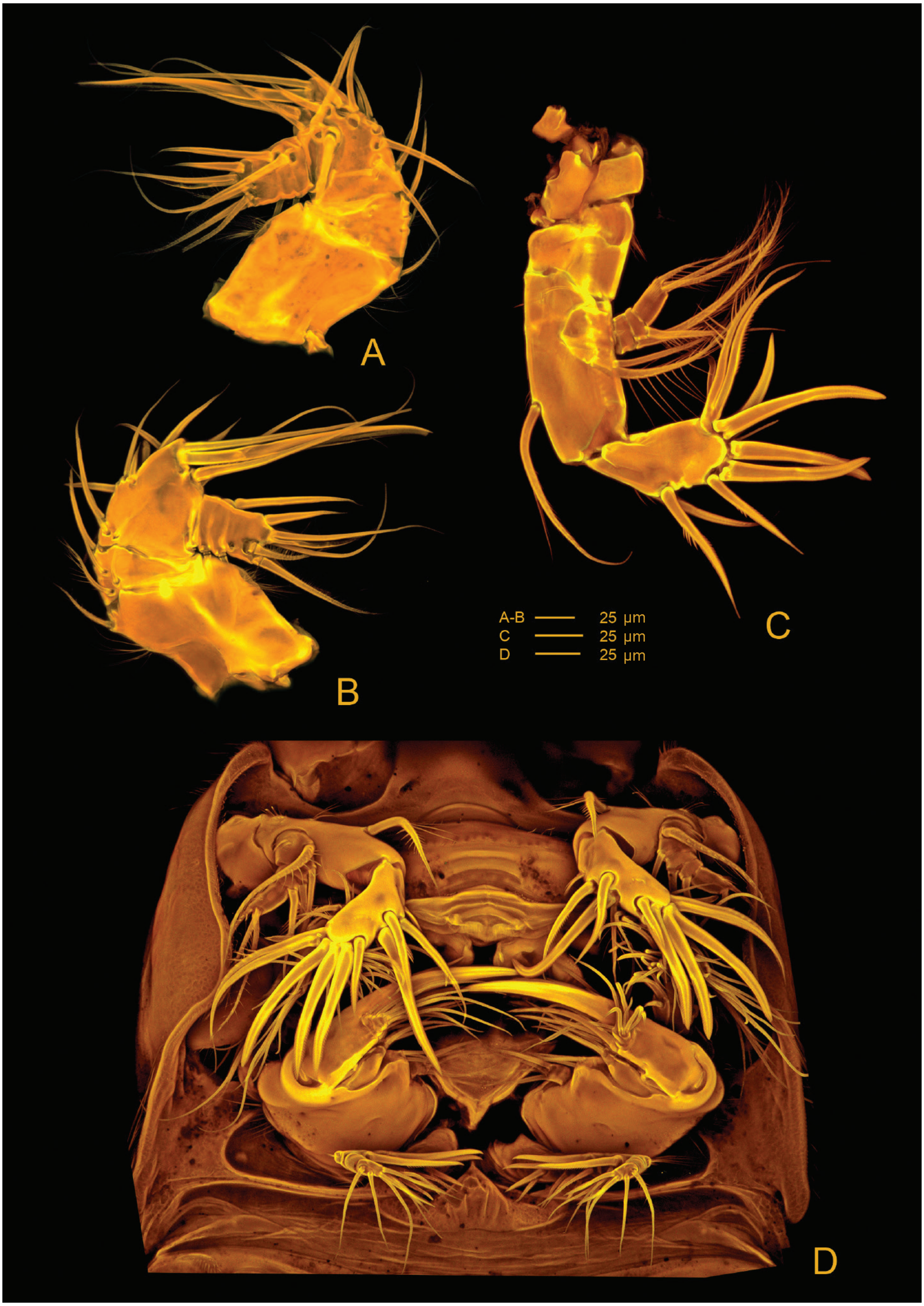

Figure 15. *Hase talpamorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M85/3, 1164): **A** A1, ventral **B** A1, dorsal **C** A2 **D** ventral cephalothorax showing A2 and mouthparts.

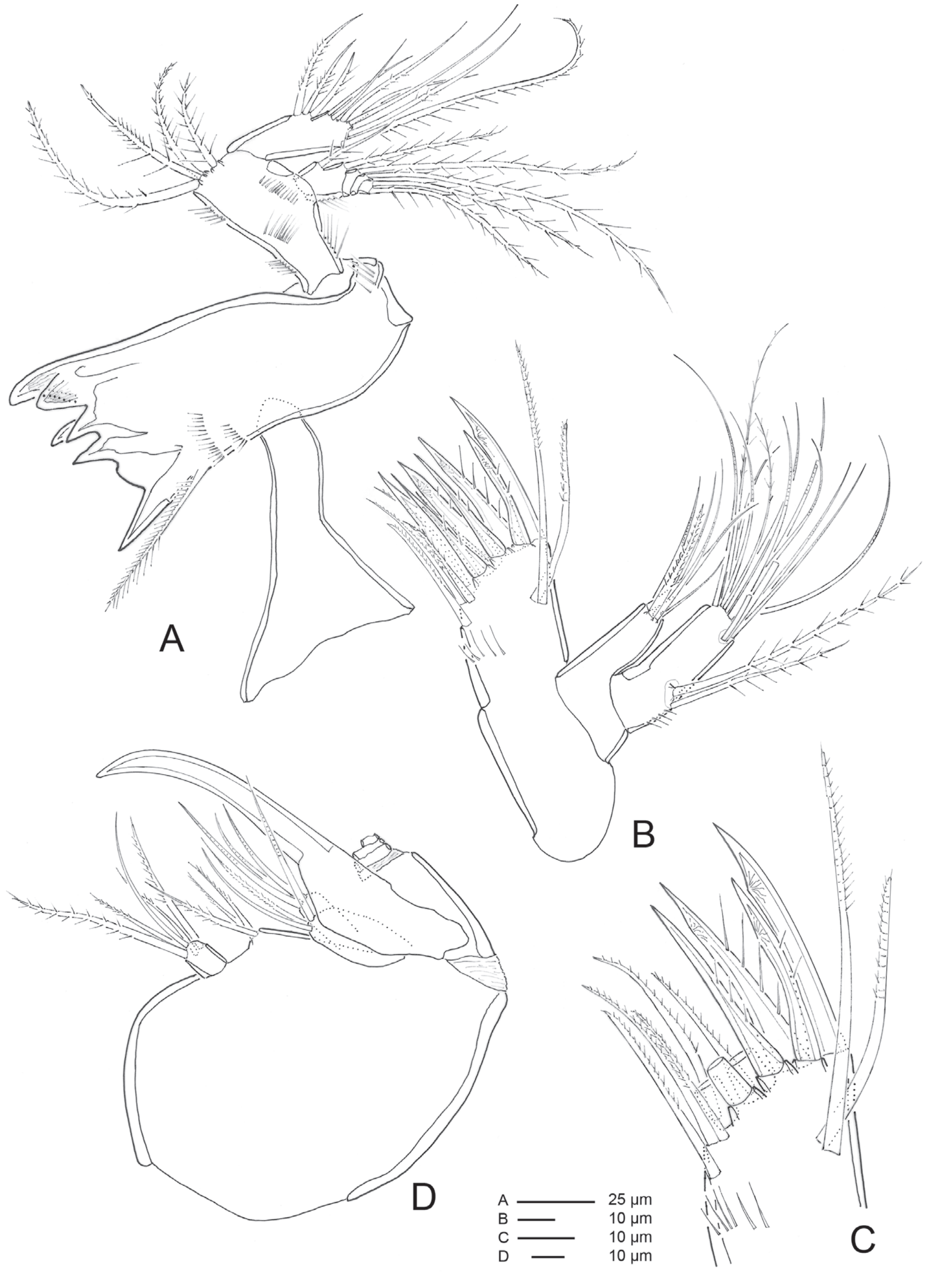

Figure 16. *Hase talpamorphicus* gen. et sp. n. Holotype (female) (M85/3, 1164): **A** mandible **B** Mx1 **C** Mx1 praecoxal arthrite **D** Mx2.

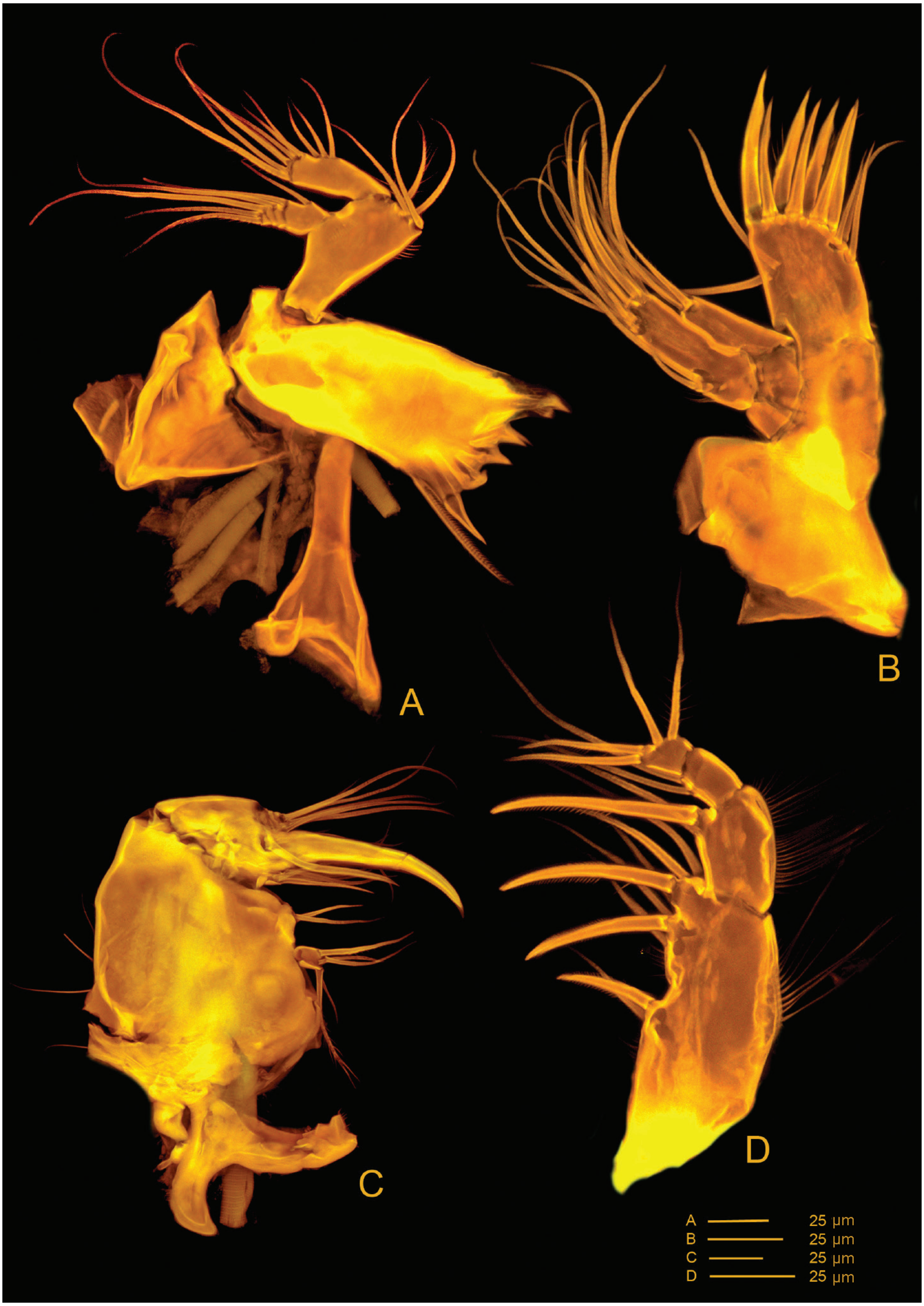

Figure 17. *Hase talpamorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M85/3, 1164): **A** Md, anterior **B** Mx1 **C** Mx2 **D** Mxp.

Basis and enp-1 fused, forming elongate allobasis, with denticles along abexopodal margin and patch of spinules; abexopodal seta bipinnate. Free enp ornamented with rows of spinules on anterior surface; medial armature consisting of three pectinate spines and one bipinnate seta; apical armature consisting of four pectinate spines, one naked seta and three elements fused basally (one bipinnate seta, one unipinnate seta and one small flattened seta). Exp 4-segmented; distal segment with row of spinules; armature formula: I-[two pinnate], II-[one pinnate], III-[one pinnate], IV-[three pinnate].

Md (Figs 16A, 17A). Coxa with well-developed musculature, gnathobase curved inwards, with several multicuspidate teeth and one bipinnate seta on inner distal margin; rows of spinules near insertion area of bipinnate seta. Palp well developed, with basis, enp and exp. Basis with four bipinnate setae and surface ornamentation as indicated in Figure 14A. Enp 1-segmented with three lateral setae (two bipinnate and one unipinnate) and seven apical setae (four naked, two bipinnate and one unipinnate). Exp 4-segmented, exp-1 as long as next three segments combined; armature formula: I-[two bipinnate], II-[one bipinnate], III-[one bipinnate], IV-[two bipinnate].

Mx1 (Figs 16B, C, 17B). Praecoxa with row of spinules as shown; arthrite well developed, with two pinnate setae on anterior surface, seven pinnate and striated spines and three bipinnate setae along distal margin, two bipinnate setae on posterior surface. Coxa endite cylindrical, bearing six setae (five naked and one pinnate) distally; epipodite absent. Basis and enp fused; basis with eleven setae (nine naked and two bipinnate); enp incorporated into basis, represented by three naked setae. Exp 1-segmented, with two bipinnate setae.

Mx2 (Figs 15D, 16D, 17C, 18A) with syncoxa fused to allobasis and 5-segmented enp. Syncoxa with four endites; proximal coxal endite with five setae (one naked and four pinnate); distal coxal endite almost completely incorporated into syncoxa, with three pinnate setae; proximal basal endite with three setae (two naked and one pinnate); distal basal endite with two naked setae and a pinnate spine. Enp-1 endite forming strong claw; accessory armature consisting of two naked setae, one spine and one tube pore; armature of fused enp-2 represented by three naked setae and one spine. Free enp 3-segmented with armature formula: I-[claw; 3 and tube pore], II-[4]; III-[2], IV-[2], V-[4].

Mxp (Figs 17D, 18B) with elongated protopod and 2-segmented enp. Protopod with rows of spinules along inner and outer margins; syncoxa with three endites; proximal endite with one bipinnate seta and one bipinnate spine; second endite with three bipinnate setae and one bipinnate spine; distal endite with two bipinnate setae and one bipinnate spine; basal endite represented by one naked seta and one unipinnate spine. Enp with armature formula: I-[2], II-[two unipinnate spines + one naked seta + one bipinnate seta].

Pereopods (Figs 18C, D, 19A–C, 20A–D) biramous and flattened; exp and enp bent inwards, especially on P1 and P2. Praecoxa without ornamentation. Coxa with

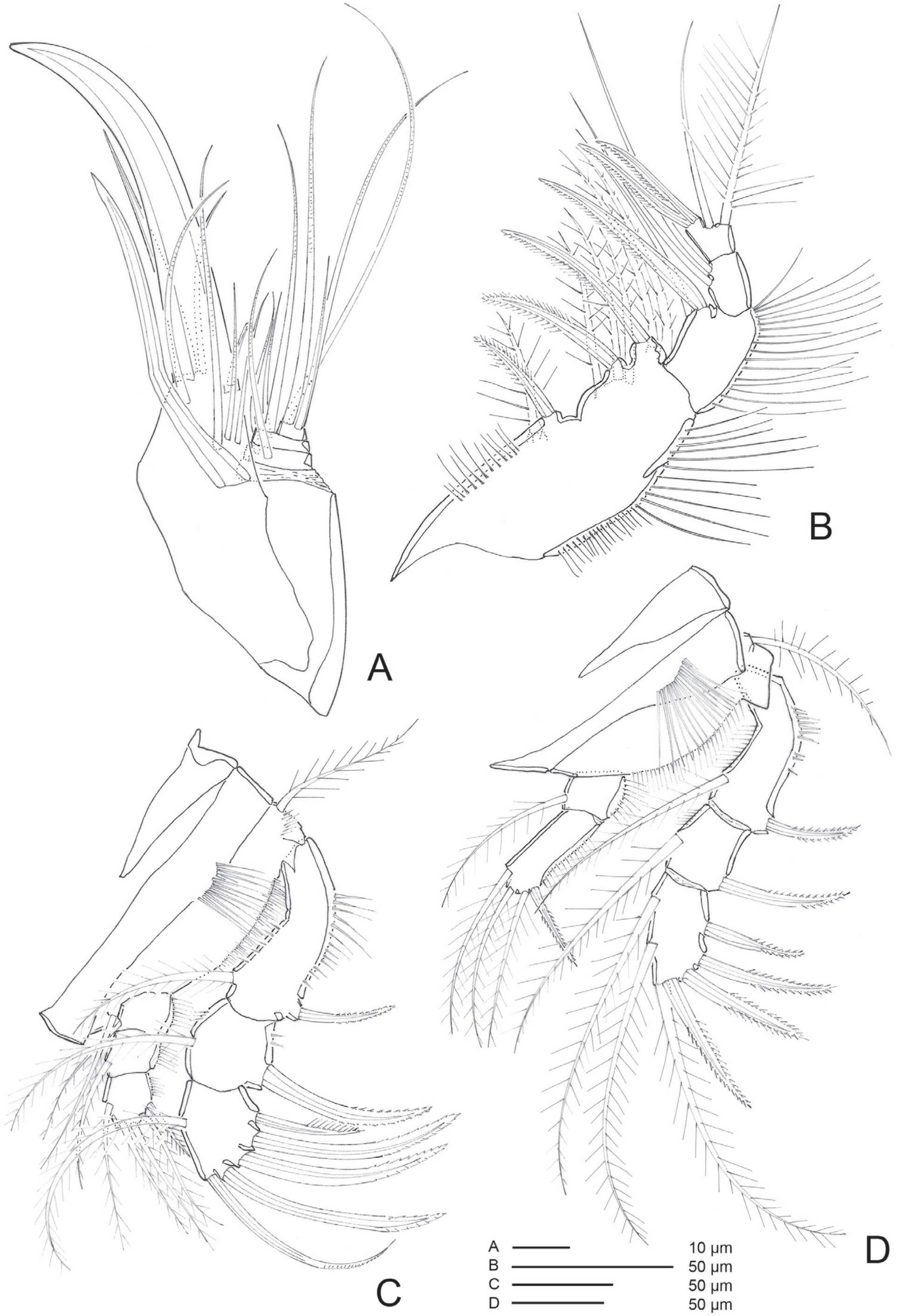

Figure 18. *Hase talpamorphicus* gen. et sp. n. Holotype (female) (M85/3, 1164): **A** Mx2 enp **B** Mxp **C** P1 **D** P2.

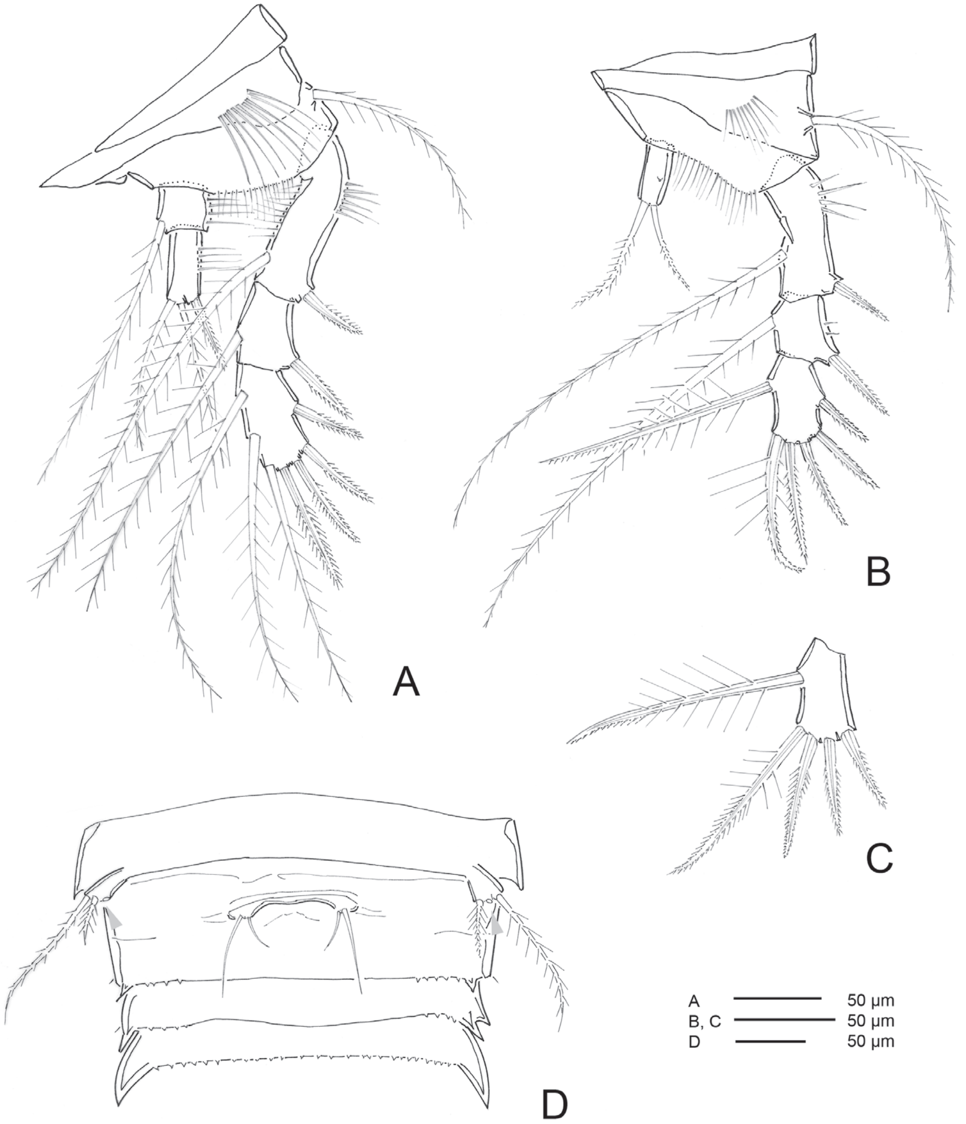

Figure 19. *Hase talpamorphicus* gen. et sp. n. Holotype (female) (M85/3, 1164): **A** P3 **B**P4 **C** variable P4 exp-3 found on the other side of the same specimen **D** P5, double genital somite and following urosomites.

row of spinules along distal margin (P1) or anterior surface (P2-P4). Basis with (P1) or without (P2-P4) bipinnate seta on outer proximal corner, with bipinnate seta on inner distal corner, ornamentation consisting of patches of setules along outer (P1) and distal margins. Exp 3-segmented; exp-1 with rows of setules along inner and outer margins, exp-2 with rows of setules along inner (P1, P2) and outer margins (P1, P4). Enp 3-seg-

Figure 20. *Hase talpamorphicus* gen. et sp. n. Confocal laser scanning images. Holotype (female) (M85/3, 1164): **A** P1 **B** P2 **C** P3 **D** P4.

mented (P1), 2-segmented (P2, P3) and 1-segmented (P4); enp- 1 with rows of setules along outer margin (P2, P3) or naked (P4). P1-P4 spine and setal formulae as follows:

	Exp	Enp
P1	I, 1; I, 1; II, II+1, 1	0, 1; 0, 1; I, 2, 2
P2	I, 1; I, 1; II, II+1, 2	0, 1; I, 2, 1
P3	I, 1; I, 1; II, II+1, 2	0, 1; I, 2, 0
P4	I, 1; I, 1; II, II+1, I	0, 2, 0

P5 (Figs 13E, 19D). Protopod fused to supporting somite, pointing outwards. Exp with three bipinnate setae.

Male unknown.

Remarks. P4 exp-3 bears two outer spines in the normal condition (formula [II, II+1, I], two females). However, in one female, P4 exp-3 displayed [II, II+1, I] on one side and [I, II+1, I] on other side (Fig. 19C)

In the juvenile CV, segmentation and armature of P1-P4 as in *Hase lagomorphicus* gen. et sp. n.

Discussion

Taxonomic discussion and phylogenetic position within the Aegisthidae

According to Seifried and Schminke (2003), the monophyly of Aegisthidae is supported by the following female autapomorphies: 1) anal somite elongated, tapering posteriorly; 2) caudal rami more than twice as long as wide; 3) antennule of female 8-segmented; fusion of Oligoarthra segments 3 and 4; 4) antenna with allobasis or incomplete basis; 5) enp-2 laterally with one spine (III) and two setae (2 + 4), spine I lacking; 6) endopod of mandible of one large segment and at least two times longer than wide; 7) proximal segment of exopod elongated, considerably longer than remaining segments and at least 3 times longer than wide; 8) epipodite of maxillule represented by two setae; 9) exopod of maxillule reduced in size with three setae; endopodal element 11 of allobasis of maxilla developed as large, strong spine inserted on posterior surface; 10) P5 without endopodal lobe.

Hase gen. n. can be included within Aegisthidae on account of the above mentioned apomorphies 5, 6, and 10. Species of Aegisthinae are derived Cerviniinae and Cerviniopseinae (Seifried and Schminke 2003). Cerviniinae and Cervinopseinae are paraphyletic and as such, are defined by plesiomorphies. Therefore, *Hase* gen. n. cannot be placed within any of the subfamilies on the account of synapomorphies and its taxonomic position must be typological and on account of the close proximity to one of the taxa composing a given subfamily.

Hase gen. n. has an antenna with four-segmented exp and could be included within both Cerviniinae and Cerviniopseinae. However, Cerviniinae and Cerviniopseinae are to date separated according to the degree of divergence of the caudal rami (see Boxshall and Halsey 2004). Within Cerviniopseinae the caudal rami are closely appressed along the entire length. *Hase* gen. n. is included within the Cerviniinae due to the presence of a more or less divergent caudal rami. Within this subfamily, *Hase* gen. n. is the adelphotaxon of *Cerviniella.* In *Cerviniella* the three segmented exp P1-P4 is absent and the limbs are much transformed as an adaptation to a burrowing life within the sediment. They share a sturdy body (sy), and the exp-1 to 3 of P1-P3 are heavily built, transformed into digging limbs (sy), with strong outer and distal spines/setae (sy). When in resting position, the exopodite bends against the basis on at least the P1 and P2 (sy). They also share a 2-segmented enp on the P2 and P3 (sy), and a reduced P5 (sy).

In *Cerviniella* the whole exopod or the exopodite-2 and 3 are fused on the P1-P3 (sy), keeping the inner and outer armature of the original segments, the endopodite of P1 is never 3-segmented (sy) and the P4 undergoes a further reduction both in segmentation and/or armature of the exopod and endopod (sy) (viz. Kihara and Martínez Arbizu 2012). The strongest armature occurs on P2 (sy) and P3 (sy), with the P2 somite showing a very large proximal region of weakly sclerotized cuticle. Within *Hase* gen. n. the armature is more developed on the P1 (sy). They are longer and stronger on P1 and P2; shorter yet stout on P3 and P4. The P1, although keeping the plesiomorphic 3-segmented exopodite and endopodite, have the outer and distal elements transformed into strong and long spines (sy), kept as stiff setae on *Cerviniella* (pl). *Hase* gen. n. has one or two strong and long spines on the inner margin of the exopodite-3 of P4 (sy). The P5, which is fused to the somite (sy), is stalked and with three distal setae (sy). Additionally, the anal somite of *Hase* gen.n. is subquadratic, slightly tapering posteriorly, wider than longer (sy) and the caudal rami is one of the shortest yet described for this family (sy), with spiniform setae I to III (sy).

Interestingly, the same morphology of the P5, telson and furca is depicted by Brotskaya (1963) in the deep-sea genus *Paracerviniella*. This author briefly described *Paracerviniella* based on a male specimen only, as follows: Body without outgrowths. The first thoracic somite not completely separated from the cephalothorax. Posterolateral corners of body somites, except for the first thoracic, drawn into pointed outgrowths. The posterior edge of all somites, except the anal, armed with a number of small teeth. Furcal rami 1.5 times shorter than the anal somite, width at the base one and a half times less than the length. The first antenna six-segmented, with two enlarged basal segments; the second, third and sixth segments of the male with sausage-like sensory cylinders, the fourth segment with a hooked spine, the fifth segment with two sensory cylinders of the usual structure. Both branches of P1-P4 triple-segmented. Endopodite of P1 and P2 with clawed spine at the distal part. P5 and P6 1-segmented with three apical bristles.

Most of these characters are not informative enough to allow the inclusion of *Paracerviniella* within any monophyletic clade within the Aegisthidae. With exception of the clawed spine present on the endopodites of P1 and P2, the P5 morphology and armature and maybe body ornamentation, the remaining characters are gender-linked or plesiomorphic within the family. In addition, the illustration of some characters that could be informative, such as the mouthparts, is insufficient. Considering this and on

Table 2. Distinctive characters of *Hase lagomorphicus* gen. et sp. n. and *Hase talpamorphicus* gen. et sp. n.

		***Hase lagomorphicus* gen. et sp. n.**	***Hase talpamorphicus* gen. et sp. n.**
Lateral margins of 3rd and 4th pedigerous somites		Smooth (Fig. 2A–B).	Expanded posteriorly forming hook-like projections laterally (Fig. 12A–B).
Rostrum	Tip	Rounded; with tuft of spinules along distal margin and with pair of sensilla near apex. (Fig. 2A).	Slightly bifid; with tuft of spinules along distal margin, with pair of sensilla and midventral tube-pore near apex (Fig. 12A and C).
A1	Segment II	8 setae (Fig. 4A).	7 setae + 2 missing elements (Fig. 14A).
	Segment III	10 setae + (1 seta+ ae) (Fig. 4A).	12 setae + (1 seta + ae)] (Fig. 14A).
A2	Enp medial armature	4 setae and 1 spine (Fig. 4B).	1 seta and 3 spines (Fig. 14B).
	Enp apical armature	3 spines, 1 seta and 3 elements fused basally (2 long setae medially unipinnate, and 1 smooth seta) (Fig. 4B).	4 spines, 1 seta and 3 elements fused basally (1 bipinnate seta, 1 unipinnate seta and 1 small flattened seta) (Fig. 14B).
	Exp-4	2 setae (Fig. 4B).	3 setae (Fig. 14B).
Md	Enp	3 lateral and 6 apical setae (Fig. 6A (a3)).	3 lateral and 7 apical setae (Fig. 16A).
Mx1	Arthrite	2 setae on anterior surface, 7 spines along distal margin, 4 setae on the aboral margin (Fig. 6C).	2 setae on anterior surface, 7 spines and 3 setae along distal margin, 2 setae on posterior surface. (Fig. 16B, C).
	Coxa endite distal armature	5 setae (Fig. 6C(c1 and c2)).	6 setae (Fig. 16B).
	Enp incorporated to basis	2 setae (Fig. 6C(c3)).	3 setae (Fig. 16B).
	Exp	3 setae (Fig. 6C(c4)).	2 setae (Fig. 16B).
Mx2	Enp-1 endite	2 setae, 1 spine and 1 claw-like spine (Fig. 6B(b5)).	2 setae, 1 spine and 1 tube pore (Fig. 18A).
	Enp-2	3 setae (Fig. 6B(b6)).	3 setae and 1 spine (Fig. 18A).
	Enp-5	3 setae (Fig. 6B(b7)).	4 setae (Fig. 18A).
Mxp	Syncoxal endites (proximal to distal)	1 seta and 1 spine, 2 setae and 1 spine, and 1 seta and 1 spine (Fig. 6D).	1 seta and 1 spine, 3 setae and 1 spine, and 2 setae and 1 spine (Fig. 17D).
	Enp-2	1 spine and 3 setae (Fig. 6D).	2 spines and 2 setae (Fig. 17D).
P4	Exp-3	II, II+1, II (Fig. 10B).	II, II+1, I (Fig. 19B).
	Enp	0, 2, I (Fig. 10B).	0, 2, 0 (Fig. 19B).
P5	Exp	1 seta, 1 spine and 1 missing element (Fig. 4E)	3 setae (Fig. 19D).
Genital Field	Copulatory pore	Slightly covered by a proximal flap, pointing posteriorly, located in a soft median depression (Fig. 3C).	Completely visible, not covered by a proximal flap as observed for the previous species, located in a well-developed median depression (Fig. 13E).
	Gonopores	Covered by medially depressed operculum (Fig. 3C).	Covered by a straight operculum (Fig. 13E).

the absence of females, we cannot address in what degree *Hase* gen. n. and *Cerviniella* are phylogenetically related to *Paracerviniella*.

The main differences in morphology of *H. lagomorphicus* gen. et sp. n. and *H. talpamorphicus* gen. et sp. n. are summarized on Table 2. The somite bearing P3 and P4 has latero-distal spiniform processes in *H. talpamorphicus* gen. et sp. n. and smooth in *H. lagomorphicus* gen. et sp. n.. The antenna is armed with three stout spines on the lateral inner margin in *H. talpamorphicus* gen. et sp. n. and two proximal setae in *H. lagomorphicus* gen. et sp. n.; the distal outer element is a spine in *H. talpamorphicus* gen. et sp. n. and a seta in *H. lagomorphicus* gen. et sp. n., the three outer endopodal elements fused at the basis are represented by three setae in *H. lagomorphicus* gen. et sp. n. and two setae and a short and blunt spine in *H. talpamorphicus*. P4 exp-3 has two long and strong spines on the inner margin in *H. lagomorphicus* gen. et sp. n. and one spine in *H. talpamorphicus* gen. et sp. n.

The shape of the gonopores and the position of the copulatory pore as they are depicted by the CLSM (Figs 3C, 13E) revealed to be important characters for the separation of the two species. The copulatory pore is completely visible in *H. talpamorphicus* gen. et sp. n., whereas it is covered by a proximal flap and pointing posteriorly in *H. lagomorphicus* gen. et sp. n. The depression in which the copulatory pore is inserted is less developed in *H. lagomorphicus* gen. et sp. n. than in *H. talpamorphicus* gen. et sp. n. Finally, the operculum covering the gonopores is medially depressed in *H. lagomorphicus* gen. et sp. n. and straight in *H. talpamorphicus* gen. et sp. n.

CLSM vs. SEM technology

There are some important differences among the scanning microscopy systems that produce high quality imaging, especially regarding to the subsequent fate of the specimens and the resolution limits. Some image systems (e.g., SEM) inevitably destroy type specimens; CLSM is highly desirable in this aspect as the studied specimen remains intact. According to Kamanli et al. (2017), the images obtained by CLSM are comparable in quality to SEM at the same magnifications, and the technique offers a 3D data set. In addition, the sample preparation routine for CLSM is simpler than that for SEM, it is practically a non-destructive method, and allows the study of hydrated material. It is difficult to establish a good SEM protocol for the study of miniaturized body parts of small macrofauna and meiofaunal specimens. Not infrequently they can be lost during manipulation, damaged before any observations are made (Michels 2007), or rendered unusable and in vain even during later processes such as coating in which the structure can become over-coated. CLSM also allows the appendages to be manipulated within the mounting medium to offer views of the specimen from multiple angles, which can be problematical to achieve using SEM since some viewpoints may be inaccessible due to the way that the specimen is mounted and the tilt limitations in SEM (Kamanli et al. 2017). After scanning, the material can be recovered intact and kept as a voucher. An example where CLSM is advantageous in the present species description is the dorsal (5B) and outer (5C) view of the same A1. In addition it offers a clear view of the natural 3-dimentional state of the antenna and the exact position of overlapping A1 setae, an arduous task during the traditional drawings of this structure. The continuous technological advancements in the field of microscopy are reducing the resolution gap among the different technologies. The resolution of SEM is approximately 10 nm whereas confocal microscopes have the potential to resolve microstructures in the 50 to 100 nm range (Schrader and Hell 1996). Practically, CLSM has reached a resolution comparable to SEM (Butler et al. 2010). In many situations, enhancing resolution beyond this range does not result in an increase in useful biological information about the specimen (St. Croix et al. 2005). Now, even for the smallest meiofaunal larvae, this level of resolution is more than sufficient to fully capture and catalogue the most minute external details such as pore morphology or individual setal ornamentation.

The importance of digital image acquisition in taxonomy

Recent papers have highlighted the importance of image acquisition in taxonomy (e.g., Michels 2007, Neusser et al. 2009, Neusser et al. 2011, Faulwetter et al. 2013, Akkari et al. 2015). Garraffoni and Freitas (2017) argued that the International Code of Zoological Nomenclature should be modified to allow, in some cases, as in the study of rare or soft-bodied meiofaunal organisms, the deposit of high quality photographs and videos as Type material. This proposal has met with strong opposition among some researchers (Dubois 2017, Rogers et al. 2017). The evolution of optical systems has led to the exponential increase in the use of high quality imaging systems in all fields of biology, including taxonomy. Our opinion in this debate is that the image quality obtained by scanning through either CLSM, SEM or Micro CT is so high, that we should consider how viable it is to designate a photomicrography as Type material. Although this may sound provocative, we must consider that a well-curated image lasts potentially forever, whereas the type specimen, especially when we take into account small macrofauna and meiofaunal groups, may deteriorate fast during study or even when mounted on "permanent" slides, those have a half-life of only few decades or centuries. Diminution of trained museum staff to maintain collections only exacerbates this problem and highlights the need to seek alternative solutions to record and study taxonomically the world's biodiversity (Decker et al. 2018). Hence, the use of CLSM and other high quality image acquiring systems should be considered not only as complimentary evidence to a taxonomical study. In some cases, the images generated should be also considered if not the type alone, at least part of the type series.

Conclusions

This contribution highlights the diversity of exquisite bauplans in deep-sea copepods and the broad distribution of a meiobenthic crustacean genus in the Atlantic Ocean basins. Additionally, it is a showcase on how confocal microscopy can assist in providing a better and more accurate description of small macrofaunal and meiofaunal organisms. We favour the inclusion of digital media at least as a component of the type series and we encourage the discussion for setting standards for such data. Additional studies and sampling effort must be continued to find the male of the genus *Hase* gen. n. to improve comparisons with *Paracerviniella* and *Cerviniella.*

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RESEARCH ARTICLE

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A new species of *Stenasellus* Dollfus, 1897 from Iran, with a key to the western Asian species (Crustacea, Isopoda, Stenasellidae)

Valiallah Khalaji-Pirbalouty[1], Yaser Fatemi[2],
Mohammad Javad Malek-Hosseini[3,4,5], Matjaž Kuntner[3,4]

1 *Department of Zoology, Faculty of Basic science, Shahrekord University, Shahrekord, Iran* **2** *Young Researchers and Elite Club, Bandar Abbas Branch, Islamic Azad University, Bandar Abbas, Iran* **3** *Evolutionary Zoology Laboratory, Department of Organisms and Ecosystems Research, National Institute of Biology, Ljubljana, Slovenia* **4** *Evolutionary Zoology Laboratory, Biological Institute ZRC SAZU, Ljubljana, Slovenia* **5** *Department of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia*

Corresponding author: *Valiallah Khalaji-Pirbalouty* (khalajiv@yahoo.com; vkhalaji@sku.ac.ir)

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Abstract

A new stenasellid isopod is described from Tashan Cave, Khuzestan Province, south-west Iran, belonging to the genus *Stenasellus* Dollfus, 1897. The first recorded species of Stenasellidae from Iran, *Stenasellus tashanicus* **sp. n.,** is diagnosed by the presence of antennae with a minute squama bearing paired, long, robust setae; a maxilliped endite with six coupling hooks; and slender appendix masculina with an acute apex. A revised generic diagnosis is provided with a key to the six known western Asian *Stenasellus* species.

Keywords

Iran, *Stenasellus*, Stenasellidae, Stygobitic, Tashan Cave

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Introduction

The genus *Stenasellus* Dollfus, 1897, with approximately 37 nominal species (Boyko et al. 2008), is the largest genus in the family Stenasellidae Dudich, 1924. This genus was established with the description of *Stenasellus virei* Dollfus, 1897 from the subterranean water of Padirac, France. According to Malard et al. (2014) and Magniez and Rahmadi (2006), members of the genus occur from southern Europe (France, Italy, Spain, Portugal) to east Africa, (Kenya, Somalia), the Arabian Peninsula (Oman), and east Asia (Thailand, Cambodia, Sumatra, Java). To date, five species of the genus *Stenasellus* have been described from western Asia: *S. asiaticus* Birstein & Starostin, 1949 from a thermal brook in southern Turkmenistan, in addition to four species (*S. henryi* Magniez & Stock, 2000; *S. grafi* Magniez & Stock, 2000; *S. messanai* Magniez & Stock, 2000 and *S. vermeuleni* Magniez & Stock, 2000) were described from Oman. Stygobitic Isopoda in Iran are poorly known, with a single described species *Microcharon raffaellae* Pesce, 1979 of the family Lepidocharontidae Galassi & Bruce, 2016. This species was found in the subterranean water of Shahrekord, Chaharmahal Va Bakhteyari Province (Pesce 1979).

As species of *Stenasellus* were reported from southeastern Turkmenistan to the south-eastern corner of the Arabian Peninsula and east Africa (Somalia, Kenya and Oman), it was also expected to document their presence in the intervening geographical regions, such as Iran and Yemen. As reported here, our finding of the new stygobiont isopod species from the Iranian underground environment narrows the gap between these broad geographical areas.

Materials and methods

Specimens for this study were collected from Tashan Cave, located inside a hill close to Sarjooshar Village, Tashan City, Behbahan County, Khuzestan Province, south-west Iran (Fig. 1A, B). The cave was visited seven times, but the isopods were only collected on the 13 and 27 August 2016. The specimens were preserved in 96% ethanol and deposited in the Zoological Museum, Shahrekord University, Iran. Appendages were drawn using an Olympus BX 51 compound microscope equipped with differential interference contrast and a camera lucida. Pencil drawings were scanned and electronically inked using Corel Draw X6 and were then processed using Adobe Photoshop CS5. Specimens were photographed with a Zeiss AxioCam ERc5s camera mounted on a Zeiss Stereomicroscope (Stemi 508). Appendages were dissected from specimens and stained by antibacterial glycerine-gelatine (Merck). The terminology of morphological characters follows Bruce and Buxton (2013).

Abbreviations: **ZMSU** – Zoological Museum, Shahrekord University, Iran; **RS** – robust seta/e; **SPS** – sensory palmate setae; **PMS** – plumose marginal setae.

Taxonomy

Aselloidea Latreille, 1802
Family Stenasellidae Dudich, 1924

Genus *Stenasellus* Dollfus, 1897

Stenasellus Dollfus, 1897:130; Racovitza 1924: 81; Birstein and Starostin 1949: 691; Magniez 1966: 177; Magniez 1968: 363; Magniez 1991: 99; Messana 1999: 1; Magniez and Stock 2000: 164.

Type species. *Stenasellus virei* Dollfus, 1897, by monotypy.

Diagnosis. Diagnoses to the genus can be found in Dollfus (1897) and Magniez (1966). The generic diagnosis presented here is more detailed than has been previously presented: Body lateral margins parallel and setose; pereonite VII longest; the antennal peduncle is 6-articulate, article VI longest, approximately 1.6 times the article V. Left mandible with incisor and lacinia mobilis bearing four cusps. Pereopod I with triangular carpus, dactylus elongated, an inferior margin with a row of contiguous scale-like flattened setae. Pereopods II-VII with an oval basis bearing some long distally plumose setae on the superior margin; dactylus shorter than elongated main unguis, bearing two secondary unguis. Pleopod I uniramous, protopod mesial margin with a simple RS or a single coupling hook, exopod elongated, mesial margin with a row distally plumose setae, distal margin fringed with a row of tiny simple short setae. Pleopod II exopod 2-articulate, article I short and without setae, article II longer than I, oval or round.

Remarks. The first restrictive diagnosis to the genus was given by Dollfus (1897) when describing *Stenasellus virei* from the subterranean waters of France. Later, Magniez (1966) wrote a more detailed diagnosis, when comparing stenasellids of Africa. Subsequently, Magniez (1999) divided species of the genus *Stenasellus* of the Iberian Peninsula in two species groups: (*S. breuili* group and *S.virei* group). The species of *S. breuili* group being recognized by protopod of the male pleopod I with a single simple seta; pleopod II appendix masculina with cylindroid and elongated distal article, little or no twisted, bearing short setae (spine) on apical margin; and pleopods IV and V with endopod smaller than exopod with round apical margin. The species and subspecies that compose *S. virei* group stand out by the protopod of the male pleopod I with a single coupling hook on mesial margin, pleopod II appendix masculina fusiform distal article, more or less twisted, without apical short setae (spine); the exopods of pleopod IV and V, initially lamellar and broad subequal to apically rounded endopods.

In this work, two other groups of the genus *Stenasellus* are proposed: the first group that has pleopod III–V with entirely bilobed endopod are from western and south-eastern Asia: *S. bedosae* Magniez, 1991 and *S. brignolii* Pesce & Argano, 1981 (Thailand); *S. chapmani* Magniez, 1982 (Malaysia); *S. covillae* Magniez, 1987, *S. stocki* Magniez, 2001 and *S. strinatii* Magniez, 1991 (Sumatra); *S. grafi* Magniez & Stock, 2000; *S. henryi* Magniez & Stock, 2000 and *S. messanai* Magniez & Stock, 2000 (Oman). The species of the second group have pleopod II appendix masculina with slender, elongated, and tapering to an acute apex distal article and pleopod III–V with distally bilobed endopod. Except *S. cambodianus* Boutin & Magniez, 1985 from Cambodia, the remaining species of the second group are distributed in eastern Africa and western Asia: *S. kenyensis* Magniez, 1975 (Kenya), *S. costai* Lanza, Chelazzi & Messana, 1970 and *S. migiurtinicus* Messana, Chelazzi & Lanza, 1974 (Solalia); *S. vermeuleni* Magniez & Stock, 2000 (Oman), *S. tashanicus* sp. n. (Iran).

Based on descriptions and illustrations of the nominal species, there are some variations between the included species. The main variation is the shape of the pleopods I–V. The exopod of pleopod 1 is elongated and the medial margin of its protopod has a single coupling hook in most species (e.g., *S. virei* Dollfus, 1897; *S. strinatii* Magniez, 1991; *S. vermeuleni* Magniez & Stock, 2000), while some species have a pleopod 1 with short exopod and without any coupling hook (e.g., *S. grafi* Magniez & Stock, 2000; *S. stocki* Magniez, 2001). The second article of the pleopod II is round and possesses less than five marginal setae in some species (e.g., *S. henryi* Magniez & Stock, 2000; *S. grafi* Magniez & Stock, 2000; *S. nuragicus* Argano, 1968), whereas some species have an oval and elongated second article with more than 10 marginal setae (e.g., *S. vermeuleni* Magniez & Stock, 2000; *S. buili* Remy, 1949; *S. kenyensis* Magniez, 1975). Moreover, the endopod of pleopods III–V has a rounded distal margin (e.g., *S. virei* Dollfus, 1897; *S. asiaticus* Birstein & Starostin, 1949; *S. buili* Remy, 1949), some species have distally bifurcated endopod (e.g., *S. ruffoi* Messana, 1993; *S. vermeuleni* Magniez & Stock, 2000; *S. kenyensis* Magniez, 1975) and in some species the endopod is deeply bilobed (e.g., *S. javanicus* Magniez & Rahmadi, 2006; *S. grafi* Magniez & Stock, 2000; *S. henryi* Magniez & Stock, 2000). In addition, the medial margin of their maxilliped endite differs in having a different number of coupling hooks (2–6).

Stenasellus tashanicus sp. n.

http://zoobank.org/F45E3E52-04AA-4238-8059-715858B80AD5
Figs 2–4

Material examined. All material from Iran with locality data as follows.

Holotype. ♂ (17.5 mm), Tashan Cave, Sarjooshar Village, Tashan City, Behbahan County, Khuzestan Province, Iran, 13 August 2016, 30°51'54"N, 50°10'29"E (altitude 559 m a.s.l.), coll. Fatemi, Y. (ZMSU 2010).

Paratypes. 3 ♂♂ (17.1, 12.5, 12 mm), 2 ♀♀ (20, 11mm); 2 juveniles (7.3, 8.5 mm), same data as holotype (ZMSU 2011). 1 ♂ (15 mm), 1 ♀ (18 mm); 1 juveniles (5.5 mm), Tashan Cave, Sarjooshar Village, Tashan City, Behbahan County, Khuzestan Province, Iran, 27 August 2016, 30°51'54"N, 50°10'29"E (altitude 559 m a.s.l.), coll. Fatemi, Y. and Malek-Hosseini, M.J. (ZMSU 2012).

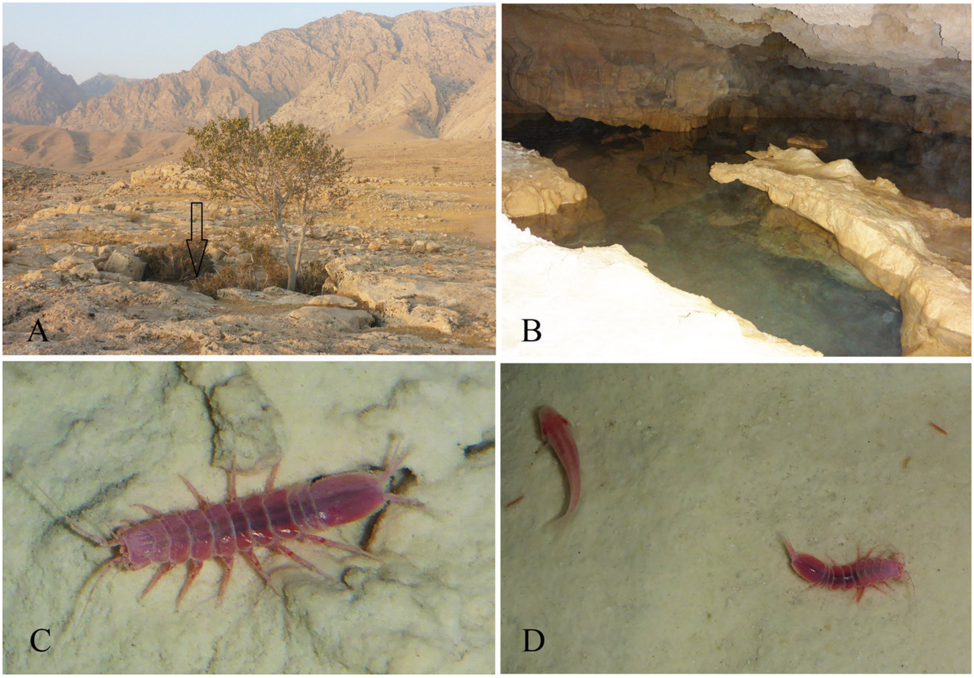

Figure 1. Tashan Cave. **A** Cave opening **B** a pool inside the cave **C** live specimen of *Stenasellus tashanicus* sp. n., in its habitat **D** *Stenasellus tashanicus* sp. n., and cave fish *Garra tashanensis* Mousavi-Sabet, Vatandoust, Fatemi & Eagderi, 2016.

Diagnosis. Body dorsal surface smooth, with scattered marginal setae. Antenna reaching to pereonite V posterior margin in male specimen, with a squama bearing three simple setae on the outer margin of the third article. Maxilla lateral and middle endites each bearing 11 curved pectinate RS; mesial margin of maxilliped endite with six coupling hooks. Appendix masculina slender, elongated, tapering to a curved acute apex; endopod of pleopods III–V distally bifurcated.

Description of male. *Body* completely coral pink in the live specimen (Fig. 1C, D), length 4.2 as greatest width, *head* trapezoidal, with slightly concave frontal margin, dorsal surface smooth. Pereonites II–IV subequal in length, with rounded lateral margins, pereonites V–VII with posterolateral margins projected posteriorly, pereonites VI and VII sub-equal, longest (Fig. 2A, D). Pleonites I–II subequal in length, with projected posterolateral corner.

Pleotelson elongated, 1.4 as long as broad, posterior margin with two slight excavations; with scattered marginal setae.

Antennula (Fig. 3A) short, reaching pereonite I posterior margin, slightly longer than the peduncle of antenna, flagellum with 18 articles, articles 8–18 each bearing a single aesthetasc.

Antenna (Fig. 3B) peduncle articles I and II reduced; the four others longer, increasing in length from the fourth to the sixth; article VI about 1.6 times as article V,

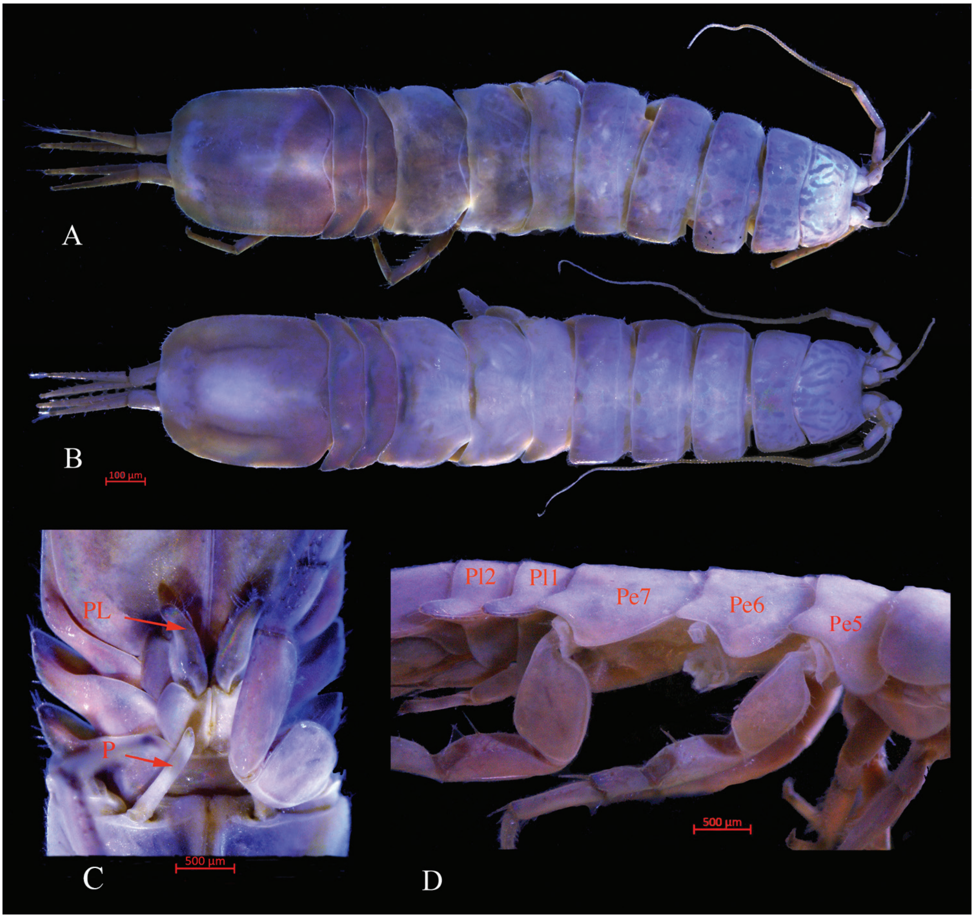

Figure 2. *Stenasellus tashanicus* sp. n., **A** holotype (ZMSU 2010) dorsal view **B** female dorsal view **C** holotype, ventral view (P: Penes, PL: Pleopod I) **D** lateral view (Pl1, Pl2: Pleonites I & II; Pe5, Pe6, Pe7: Pereonites V–VII).

with long simple setae distally; article III with minute squama bearing two long RS, flagellum reaching to pereonite V posterior margin, up to 86 articles.

Left mandible (Fig. 3D, E) incisor and lacinia mobilis with four cusps, spine row of 18 serrate spines, molar with a row of long, tiny, simple setae. Palp article II longer than I, articles III distolateral margins with approximately 15 pectinated setae.

Maxillula (Fig. 3F) lateral endite apical margin with 12 serrate RS and eight tiny serrated smaller setae; mesial endite with three long, robust, comb and two short simple setae.

Maxilla (Fig. 3G) lateral and middle endites each with 11 curved pectinate RS; mesial endite with several rarely plumose, long robust combs, and slender simple setae.

Maxilliped (Fig. 3H) endite mesial margin with six coupling hooks, distal margin with approximately 10 serrated and rarely plumose RS; palp article I with single RS on the inferior margin, palp articles II–V with several long simple setae on the inferior margin.

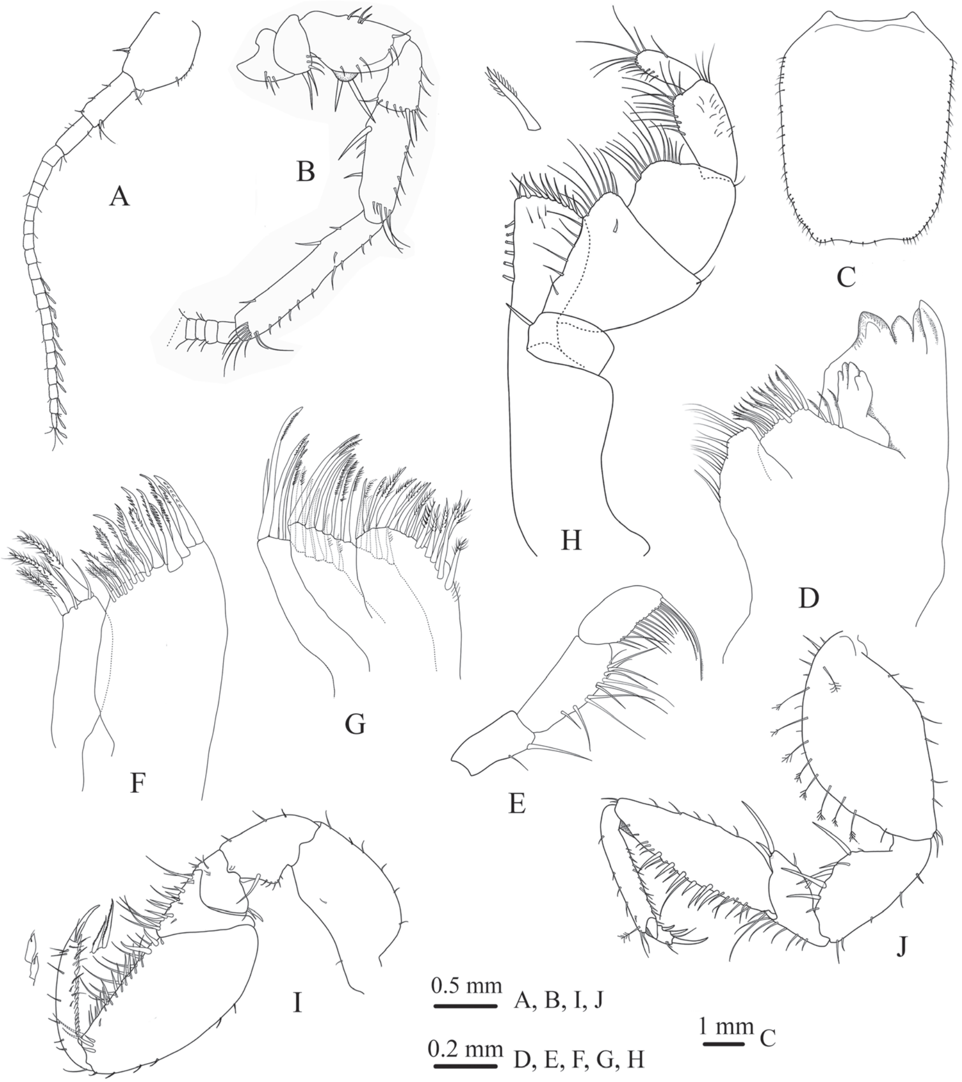

Figure 3. *Stenasellus tashanicus* sp. n., holotype (ZMSU 2010) **A** antennula **B** antenna **C** pleotelson **D** left mandible **E** palp of mandible **F** maxillula **G** maxilla **H** maxilliped **I** pereopod I **J** pereopod II.

Pereopod I (Fig. 3I) basis length 1.66 width, ischium superior margin with one RS on distal corner and five small RS on the medial projection; merus supradistal angle with three RS; carpus triangular, inferior margin covered with several long and short simple RS; propodus inferior margin covered with several long simple RS set in amongst some serrated RS; dactylus 9.2 times as long as basal width, inferior margin with a row of contiguous scale-like flattened setae with accessory setulae, main unguis elongate.

Pereopod II (Fig. 3J) basis about 1.8 times as long as the greatest width, superior margin with nine long distally plumose setae; ischium superior margin with five long

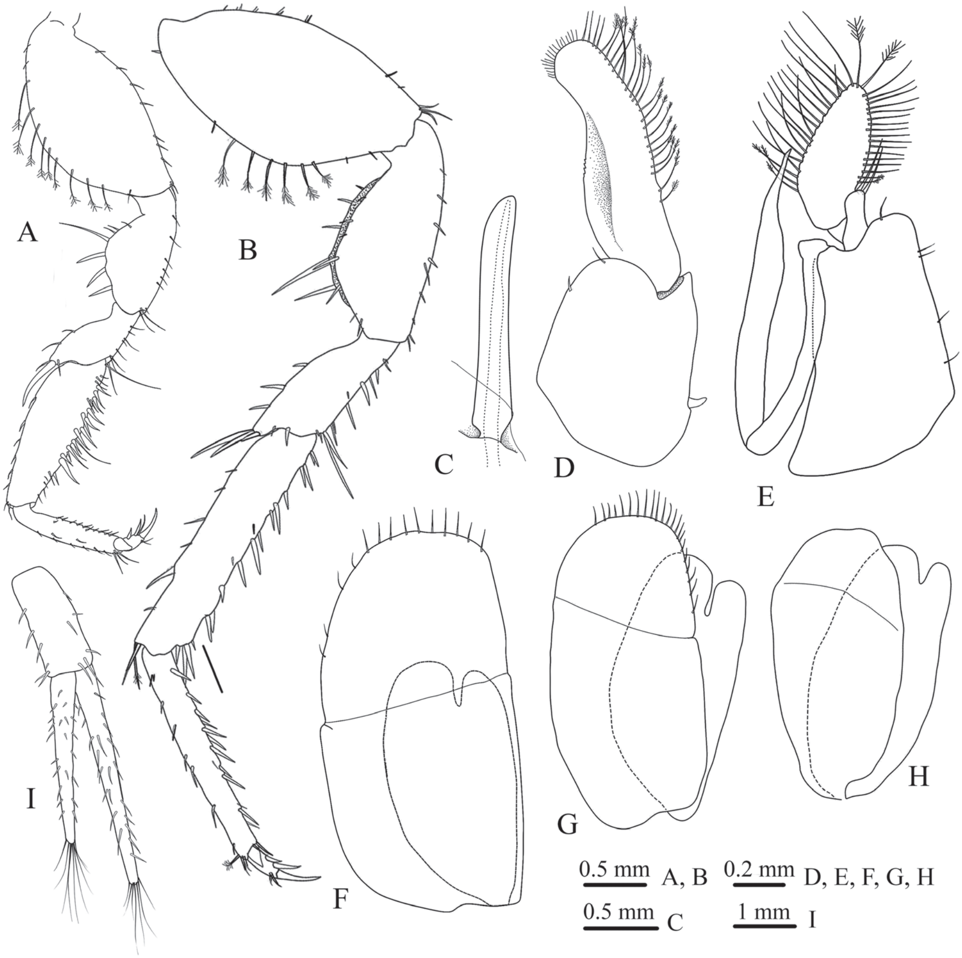

Figure 4. *Stenasellus tashanicus* sp. n., holotype (ZMSU 2010) **A** pereopod III **B** pereopod VII **C** Penial processes (left ramous) **D–H** pleopods I–V **I** Uropod.

RS; merus supradistal angle with two long RS, inferior margin with nine long simple setae; carpus superior margin with five simple setae, inferior margin covered with several long and short simple RS; propodus inferior margin covered with several short, simple, acute setae, supradistal angle with two long simple and single sensory palmate setae; dactylus shorter than main unguis, with two secondary unguis.

Pereopod III (Fig. 4A) is similar to pereopod II as illustrated.

Pereopod VII (Fig. 4B) basis about two times as long as the greatest width, superior margin with nine long distally plumose setae; *Ischium* length 2.2 width; merus supradistal angle with three long RS; carpus length 5.0 width, inferior margin covered with several long and short simple RS, supradistal angle with a long simple and a single sensory palmate setae; propodus length 7.3 width, inferior and superior margins covered with several short, simple, acute setae, supradistal angle with two long simple and a single sensory palmate setae; dactylus with elongated main unguis, bearing two secondary unguis.

Penial processes (Figs 2C, 4C) elongated, cylindrical, about 5.8 times as long as the greatest width.

Pleopod I (Fig. 4D) protopod length 1.2 width, mesial margin with a single coupling hook, exopod elongated, mesial margin with a row of 21 PMS and four simple setae, apical margin with row of ~18 simple fine setae, lateral margin concave.

Pleopod II (Fig. 4E) protopod elongated, length 1.7 width, exopod article I small, without seta, article II oval, with ~ 41 PMS; endopod small, with two apical, long, simple setae; *appendix masculina* length 1.4 article I length, 11.4 basal length, tapering to curve acute apex.

Pleopod III (Fig. 4F) exopod with transverse suture, apical margin with ten slender simple setae; endopod 0.6 as long as exopod, bifurcated distally.

Pleopod IV (Fig. 4G) exopod with transverse suture, distolateral margin with 22 slender simple setae; endopod 0.8 as long as exopod, bifurcated distally.

Pleopod V (Fig. 4H) exopod and endopod subequal in length, without marginal setae.

Uropods (Fig. 4I) protopod and rami covered with scattered acute simple setae; endopod longer than exopod, both rami with distal tuft of setae.

Female. (Fig. 2B) Typically, longer than the male, apart from sexual characteristics similar to male, pleotelson is broader and antenna is longer than male.

Etymology. The name of this species comes from the type locality, the Tashan Cave, Iran.

Habitat. The isopods were collected from two pools in the dark zone of the Tashan Cave (at 20 to 200 cm depths). They were observed in all life cycle stages. They were observed crawling on the floor and hiding inside the sediment and cavities of the pools, as well as swimming in the water column. Mousavi-Sabet et al. (2016) described a blind fish from this cave (see Fig. 1D).

Remarks. *Stenasellus tashanicus* sp. n. can be identified by a slender and distally acute appendix masculina, and a maxilliped endite with six coupling hooks on the mesial margin. The new species is the largest known *Stenasellus* member: length up to 18 mm in males and 20 mm in females. The new species is similar to *S. vermeuleni* Magniez & Stock, 2000 (known from Wadi Halban, Oman), in having an appendix masculinum with acute apex. The shape of pleopods III–V in both species is also similar. Based on the drawings and description of *S. vermeuleni*, the new species differs by having a uropodal exopod smaller than the endopod (rather than subequal in length), pleopod I apical margin with a row of 18 simple fine setae (rather than six), exopodal article II of pleopod II is narrower than pleopod II in *S. vermeuleni* and pleopod V exopod and endopod subequal in length (rather than a smaller exopod). Based on the description and drawings of *S. asiaticus* by Birstein and Starostin (1949) from Turkmenistan, this species is readily distinguished from the new species by setose body dorsal surface (rather than smooth body surface) and its flattened appendix masculina (rather than a narrow with an acute apex).

Key to the Western Asian species of *Stenasellus*

1 Body dorsal surface setose; pleopod endopod of pleopods III–V distally monolobate..***S. asiaticus*** (Turkmenistan)
– Body dorsal surface smooth; pleopod endopod of pleopods III–V distally bilobate..**2**
2 Pleopod II exopod article II small, with less than five marginal setae; Appendix masculina flat and swollen...**3**
– Pleopod II exopod article II large, with more than eight marginal setae; Appendix masculina elongate distally acute **4**
3 Pleopod II protopod heart shaped...................................... ***S. grafi*** (Oman)
– Pleopod II protopod trapezoid shaped ....***S. henryi*** (Oman)
4 Appendix masculine dislaolateral margin fringed with tiny setae.................. ....***S. messanai*** (Oman)
– Appendix masculine dislaolateral margin without setae..............................**5**
5 Antenna squama with three robust setae, exopod of pleopod I apical margin with a raw of ~6 simple fine setae; pleopod II exopod about 1.4 times as long as greatest width.. ***S. vermeuleni*** (Oman)
– Antenna squama with II robust setae, exopod of pleopod I apical margin with a raw of ~18 simple fine setae; pleopod II exopod about 2.4 times as long as greatest width ....***S. tashanicus* sp. n.**

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RESEARCH ARTICLE

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Morphological and molecular data reveal a new genus of the tribe Issini from Southern China (Hemiptera, Fulgoromorpha, Issidae)

Menglin Wang[1], Aimin Shi[1], Thierry Bourgoin[2]

1 *Key Laboratory of Southwest China Wildlife Resources Conservation of the Ministry of Education, China West Normal University, Nanchong, Sichuan Province, 637009, China* **2** *Institut de Systématique, Évolution, Biodiversité, ISYEB-UMR 7205 MNHN-CNRS-Sorbonne Université-EPHE, Muséum national d'Histoire naturelle, CP 50, 57 rue Cuvier, F-75005 Paris, France*

Corresponding author: *Menglin Wang* (wangmenglin123@126.com)

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Abstract

A new genus *Sinonissus* **gen. n.** of the tribe Issini (Issidae, Issinae) with a new species *Sinonissus brunetus* **sp. n.** from Chongqing municipality and Sichuan Province, China are described. Barcode of the species is provided. A molecular analysis combined with morphological characters confirms its placement into the Issini. Distribution of this new genus in the Oriental realm is briefly discussed in regard of other Issinae taxa in China.

Keywords

China, new species, *Sinonissus*, taxonomy

Introduction

In the family Issidae Spinola, 1839 (Hemiptera: Fulgoromorpha), Issini Spinola, 1839 (sec. Wang et al. 2016) is a small planthopper tribe, consisting of only two extant genera: *Issus* Fabricius, 1803 and *Latissus* Dlabola, 1974 with 39 species worldwide (Bourgoin 2018). A third monospecific fossil genus from Middle Eocene in Germany, *Issites glaber* Haupt, 1956 was recently reviewed and added to the tribe (Gnezdilov and Bourgoin 2016).

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The lineage was firstly separated as a subtribe Issina Spinola, 1839 by Gnezdilov (2002: 609), later abandoned (Gnezdilov 2016a: 343), but confirmed valid by different molecular analyses (Gnezdilov et al. 2015, Wang et al. 2016) and treated as a separate tribe of Issinae by Wang et al. (2016). In this last treatment, Issini is typically distributed in the Wallace Palaearctic (western area particularly) and Oriental regions, and more precisely into Holt's (2013) Oriental, Sino-Japanese, Palaearctic, and Saharo-Arabian zoogeographic realms (Gnezdilov et al. 2015, Bourgoin 2018). *Issus* and *Latissus* genera are natively distributed in the Mediterranean area of the Western Palaearctic region (Gnezdilov et al. 2014). They form the "*Issus* group" which is thought to have diverged early from the other Western Palaearctic taxa and was one of the first groups to colonise the proto-Mediterranean communities of the ancient Mediterranean in the Eocene (Gnezdilov 2016a, 2016b).

Issini are characterised by the presence of paired digitate processes on the inner side of the dorsolateral lobes of the periandrium (Gnezdilov 2016a), and not exclusive to the lineage, the veins run in parallel, and according to the schema "R2, M2, CuA2" until the tip of the tegmina (Gnezdilov 2003).

A new genus *Sinonissus* gen. n. is described from southwest China in the Oriental realm, represented by the new species *Sinonissus brunetus* sp. n. from Chongqing and Sichuan, for which both morphological data and molecular phylogeny place the taxon into the Issini sec. Wang et al. (2016).

Materials and methods

Type specimens are deposited in College of Life Science, China West Normal University, Nanchong, Sichuan Province, China. The abdomen of specimen was separated from the body, and then boiled in a 10% NaOH solution for 5 minutes until muscles were completely dissolved leaving tegumentary structures. After rinsing in distilled water for several times, the abdomen was subsequently transferred to glycerine for final dissection and observation. Terminalia were conserved under the specimen in genital vials. Photographs for external morphology and terminalia characters were taken using Leica DFC495 camera attached to Leica M205C stereomicroscope and further refined with LAS V3.8 and Helicon Focus v3.10 software. Morphological interpretations and subsequent terminologies for male genitalia follow Bourgoin (1987), for female genitalia Bourgoin (1993) and for wing venation Bourgoin et al. (2015).

The total genomic DNA was extracted from leg of holotype specimen (♂) using the TransGen EasyPure Genomic DNA Kit. COI gene was amplified using the same primers and amplification procedure as Wang et al. (2016). The DNA sequencing was conducted at Sangon Company (Shanghai, China). Software Seqman from package DNAstar v5.01 (www.dnastar.com) was used for checking sequence chromatograms and assembling contigs. Mega v7.0 (Kumar et al. 2016) was used for performing alignments. IQtree v1.4.1 (Nguyen et al. 2015) was used for maximum likelihood phylogenetic analysis using 10000 ultrafast bootstrap (Minh et al. 2013) with substitution model automatic selected. Figtree v1.1.2 (Rambaut 2016) was used to visual the tree. The COI sequence of *Sinonissus brunetus* sp. n. was registered in GenBank with accession number MG921598, the other COI sequences used in this study were obtained from Wang et al. (2016).

Taxonomy

Issidae Spinola, 1839
Issinae Spinola, 1839
Issini Spinola, 1839

Sinonissus gen. n.

http://zoobank.org/144A599D-DD5E-403A-AE46-95F43B9CAAC5

Type species. *Sinonissus brunetus* sp. n., here designated.

Diagnosis. This genus is similar to the genus *Latissus* Dlabola, 1974 (Gnezdilov et al. 2011, fig. 4; Gnezdilov et al. 2014, figs 13d–f) in general appearance, but differs by: 1) vertex without median carina but with carina in *Latissus*; 2) tubercles on frons very tiny and obscure but large and elevated in *Latissus*; 3) Pcu and A_1 fused at basal half of clavus but fused at apical 1/3 in *Latissus*.

Description. Head with compound eyes a little wider than pronotum, but nearly the same width as mesonotum (Fig. 1). Vertex rectangular, obviously broader than long, anterior margin elevated, slightly convex or nearly straight, lateral margins elevated, apical half nearly parallel and basal half broaden outward (Fig. 1) or parallel all the time, posterior margin anteriorly widely concave at middle, median carina absent on disc (Fig. 1). Frons obviously longer than wide, slightly broaden below level of compound eyes (Figs 3, 16); apical margin slightly concave almost straight, apical and lateral margins carinate and elevated, median carina elevated from apex extending to near base, but not reaching frontoclypeal sulcus (Figs 3, 16); frons with lateral area distributed with some faint tiny tubercles (Fig. 3). Frontoclypeal suture strongly convex (Fig. 3). Clypeus with median carina (Fig. 3). Rostrum slightly exceeding mesocoxae, apical segment shorter than subapical one. Gena in lateral view slightly protrude below frontoclypeal suture (Fig. 2). Antenna with scape short and cylindrical, pedicel rounded. Pronotum triangular, margins elevated, with several indistinct tubercles on disc, median carina absent (Fig. 1). Mesonotum with two carinae on the disc (Fig. 1). Forewings ovate, longitudinal veins obvious and elevated, costal margin and posterior margin subparallel (Figs 2, 15), with wide 'hypocostal plate' (Gnezdilov 2003) (Fig. 3), short common stem ScP+R separating in unforked ScP+RA and RP and reaching the outer margin of forewing; MP forking only once near the basal 1/3 into unforked MP_{1+2} and MP_{3+4}; CuA forking into CuA_1 and CuA_2 near middle (Figs 2, 15). Clavus closed, Pcu and A_1 fused at basal half of clavus (Figs 1, 15). Hindwing very rudimentary, almost absent. Metatibia with two lateral spines on apical half and approximately eight apically.

Male terminalia. Gonostyli subrectangular in profile, caudo-ventral angle rounded, dorsal margin without process (Figs 4, 7); capitulum broad, with auricular process (Fig. 7). Pygofer rectangular in lateral view, apparently longer than wide (Fig. 4). Periandrium symmetrical, tubular, apical part divided into dorsolateral lobe and ventral lobe (Figs 6, 17). Aedeagus with the pair of aedeagal processes emerging at 3/5 of periandrium length, hook-like, short (Figs 6, 17).

Female terminalia. Anal tube relatively short, in dorsal view a little longer than wide (Fig. 8). Two or three teeth at apex and three keeled teeth on outer lateral margin of anterior connective lamina of gonapophysis VIII (Fig. 14). Gonocoxa VIII quadrangular, connected to gonapophysis VIII with rectangular angle (Fig. 14). Gonapophysis IX in lateral view boat-shaped (Fig. 12). Gonoplacs rectangular in lateral view (Fig. 9), fused at middle near base, widest at basal 1/3 (Fig. 10). Hind margin of sternite VII concave medially (Fig. 13).

Distribution. China (Chongqing, Sichuan).

Etymology. This name is derived from the Latin prefix word "*sino*" freely associated with the generic name "*Issus*", referring to the special distribution of this genus representing the rarity of Issini in China. The gender is masculine.

Remarks. The new genus differs from *Issus* by the presence of a wide hypocostal plate, also present in *Latissus*, and from both genera by its rudimentary hindwings. It shows that this last character is not characteristic of the tribe, for which the diagnosis should be modified accordingly. Additionally, the Issina forking schema 'R2, M2, CuA2' indicating the number of main vein terminals in the tegmen appears to be modified in *Sinonissus* with two to four terminals in CuA: accordingly a 'R2, M2, CuA(2–4)' schema should be retained for Issini sec. Wang et al. (2016)'s diagnosis. In reverse, *Sinonissus* shares particularly with them the presence of paired digitate processes on the dorsolateral lobes of periandrium, two lateral and 5–9 apical metatibial spines. Molecular phylogeny analysis confirms also the placement of the taxon as sister to the two others, according to the schema (*Sinonissus* + (*Latissus* + *Issus*)) with node value of 90 (Fig. 19).

Sinonissus brunetus sp. n.

http://zoobank.org/710BAE8A-F0F7-4DDA-BA4F-30FBDAF30A42
Figs 1–18

Type materials. Holotype: ♂, China: Chongqing municipality, Jinyunshan, 6 vii 2017, coll. Menglin Wang. Paratypes: 1♂, Chongqing municipality, Jinyunshan, 5 vii 2011, coll. Ting Xu; 1♀, Sichuan Province, Emeishan, 5 vii 2010, coll. Meiyi Xia; 1♀, Sichuan Province, Emeishan, 5 vii 2010, coll. Yuling Zhang.

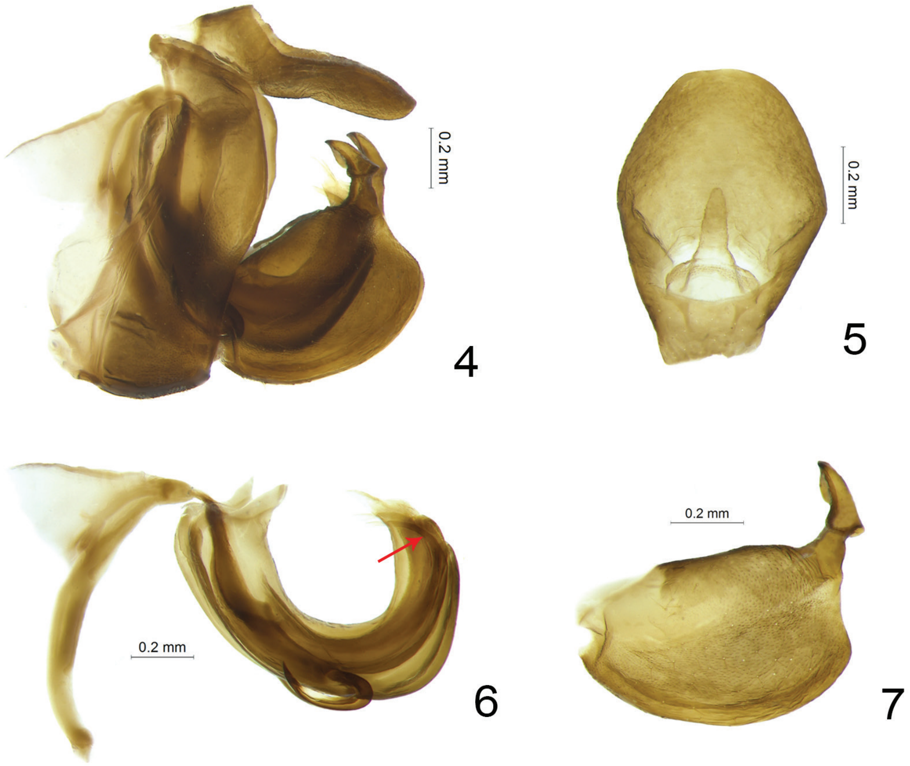
Diagnosis. This new species looks similar to *Latissus dilatatus* (Fourcroy, 1785), but differs by: frons much longer, 1.2 times longer in midline than broad at widest part (only 0.9 times in *L. dilatatus*); anal tube of male 1.4 times longer in midline than widest part (2.2 times in *L. dilatatus*); male genitalia less robust, the digitate processes near apex of periandrium slender and curved (broad and straight in *L. dilatatus*).

Figures 1–3. *Sinonissus brunetus* sp. n., holotype. **1** Adult, dorsal view **2** Adult, lateral view **3** Adult, ventral view.

Description. Length: male (including forewings) (N = 2): 4.2–4.3 mm; female (including forewings) (N = 2): 6.2–6.3 mm.

Coloration. Vertex brown, margins carinated and dark brown (Fig. 1). Compound eyes dark grey, supported by tawny callus (Fig. 1). Frons brown, apical and lateral margins carinated and dark brown, brown median carina extending from apex near to base, but not reaching the frontoclypeal sulcus (Figs 3, 16); lateral area of frons with some tawny inconspicuous tubercles on each side near the lateral margins (Figs 3, 16). Postclypeus brown, rostrum light brown (Fig. 3). Gena brown (Fig. 2). Antennae dark brown (Fig. 3). Pronotum brown, margins carinated and dark brown, lateral area with three unconspicuous light yellow tubercles on each side (Fig. 1). Mesonotum brown, lateral carinae dark yellow (Fig. 1). Forewings brown, longitudinal veins dark brown and transverse veins grey (Figs 1, 2). Legs brown (Figs 2, 3).

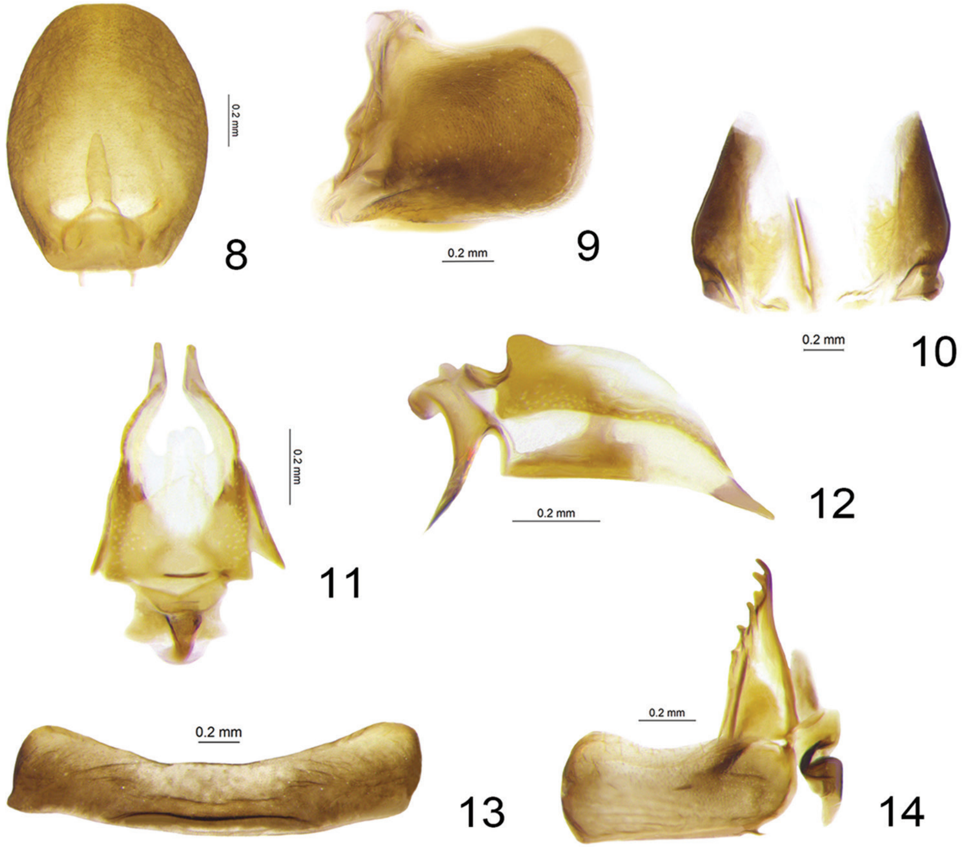
Head and thorax. Vertex 3.1 times wider at base than long in midline, lateral margins parallel in apical 1/2 and expanded outward at basal 1/2 (Fig. 1) or parallel all the time. Frons 1.2 times longer in midline than broad at widest part, 1.3 times broader at widest part than apical margin (Fig. 3). Pronotum 2.3 times wider at base than long in midline, anterior margin angularly convex, lateral margins straight (Fig. 1). Mesonotum with anterior margin 2.4 times wider than long in midline (Fig. 1). Forewings 1.9 times wider at longest part than widest part. Metatibiotarsal formula: 2–(7–8)/(6–8)/2.



Figures 4–7. *Sinonissus brunetus* sp. n., holotype. **4** Male terminalia, lateral view **5** Male anal tube, dorsal view **6** Phallic complex, lateral view **7** Gonostylus, lateral view. The red arrow indicates the paired digitate processes on the dorsolateral lobe of periandrium.

Male terminalia. Anal tube in dorsal view ovate, widest at apical 1/3; 1.4 times longer in midline than widest part, apical part rounded; epiproct long, around 1/3 length of anal tube, anal opening located at basal 1/3 (Fig. 5). Gonostylus subrectangular in lateral view, dorsal margin straight and sloping up posterior, posterior margin nearly straight, caudo-ventral angle rounded, and ventral margin rounded (Figs 4, 7). Capitulum of gonostylus relatively short and broad with an auriform process in the apical 2/3 (Figs 4, 7). Pygofer in lateral view much longer than broad, dorsal margin inclined downward, anterior and posterior margins sinuate (Fig. 4). Periandrium with dorsolateral lobe relatively triangular, weakly sclerotised, ventral lobe rounded apically in lateral view (Figs 6, 17); dorsolateral lobe longer than ventral lobe; pair of slender slightly sclerotised digitate processes originated from the dorsolateral lobe near the apex, curved upward and directed cephalad (Figs 6, 17). In ventral view apical part of dorsolateral lobe sharp, apical margin of ventral lobe rounded (Fig. 18). Paired aedeagal processes hooks-like, curved upward, originated from the basal 3/5 of phallic complex extending to the basal 2/5, tip of processes pointed and directed to dorso-anterior part (Figs 6, 17).

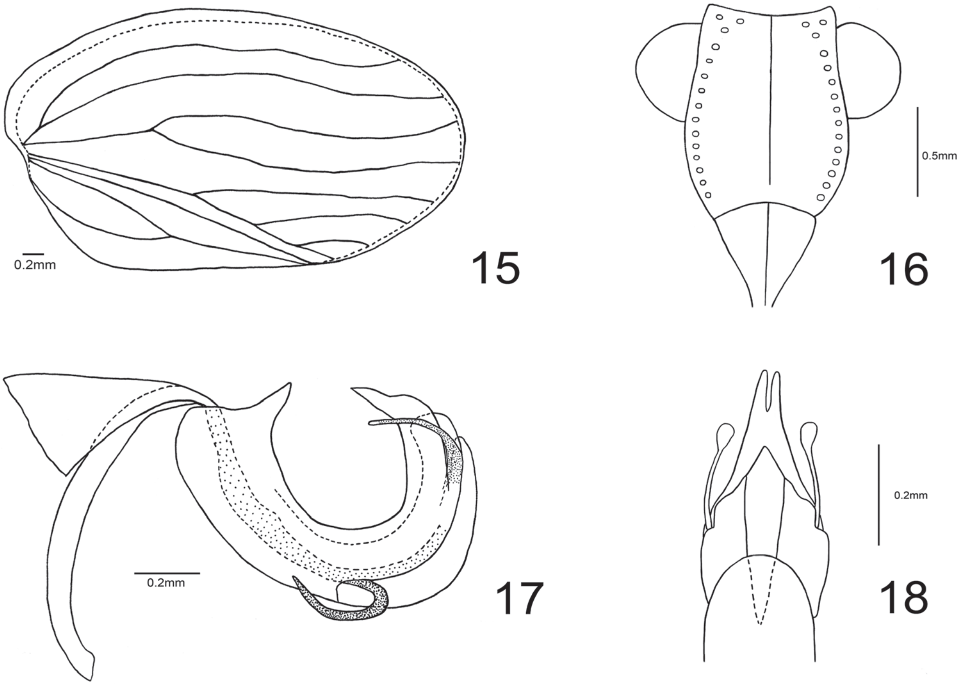
Female terminalia. Anal tube in dorsal view ovate, widest at middle, 1.2 times longer in midline than widest part, apical margin and lateral margins rounded;



Figures 8–14. *Sinonissus brunetus* sp. n., paratype. **8** Female anal tube, dorsal view **9** Gonoplacs, lateral view **10** Gonoplacs, dorsal view **11** Gonapophysis IX and gonaspiculum bridge, dorsal view **12** Gonapophysis IX and gonaspiculum bridge, lateral view **13** Sternite VII **14** Gonocoxa VIII and gonapophysis VIII, lateral view.

epiproct long, approximately 1/3 length of anal tube, anal opening situated at basal 1/4 (Fig. 8). Anterior connective lamina of gonapophysis VIII with two or three teeth at apex and three keeled teeth on the outer lateral margin, inner lateral margin without teeth (Fig. 14). Endogonocoxal process developed, slightly sclerotised in basal half and membranous in distal one (Fig. 14), apex of endogonocoxal process with two-digitate processes. Posterior connective lamina of gonapophysis IX in lateral view long and narrow, boat-shaped, tip pointed, dorsal margin roundly convex at base (Fig. 12); in dorsal view basal half broader than apical half, the apical half narrower to apex in outer lateral margins, bifurcate at apical 1/3 in inner part, basal half with outer margins nearly parallel, lateral area sclerotised (Fig. 11). Gonospiculum bridge small and short, in lateral view rectangular with needle-like ventrally (Fig. 12). Gonoplacs fused near base, outer lateral margins roundly convex (Fig. 10), in lateral view rectangular (Fig. 9).

Etymology. The Latin name *brunetus*, referring to the dark brown colour of the general appearance of this species.



Figures 15–18. *Sinonissus brunetus* sp. n. **15** Forewing **16** Frons **17** Phallic complex, lateral view **18** Apex of phallic complex, ventral view.

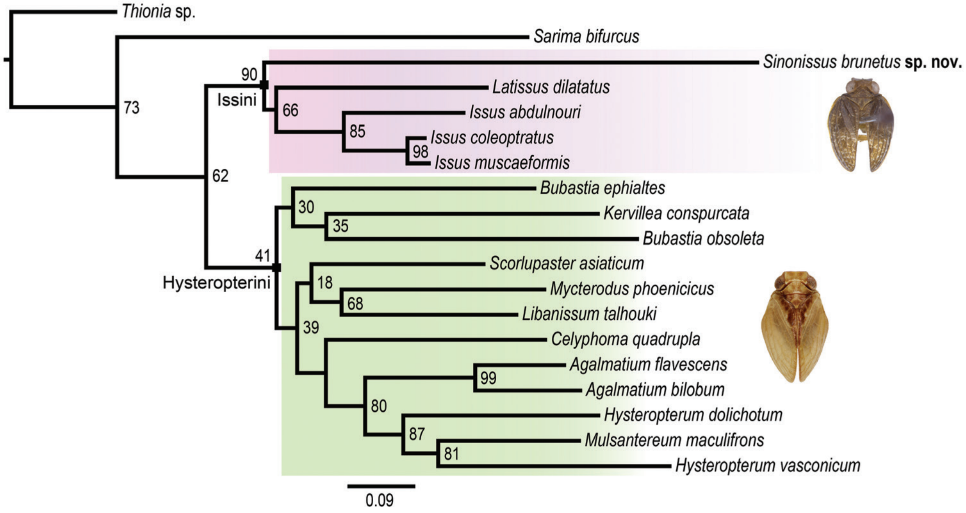


Figure 19. Maximum likelihood tree of Issinae based on COI sequence with *Thionia* sp. (Issidae Thioniinae) and *Sarima bifurcus* (Issidae, Hemisphaeriinae) as outgroup to test to position of *Sinonissus* gen. n. in the classification and phylogeny of Issidae. Node values denote ultrafast bootstrap support.

Distribution. China (Chongqing, Sichuan).

Remarks. The COI nucleotide composition of this species is A: T: G: C = 32.7: 32.7: 14.5: 20.0. It differs by 124 and 126 nucleotidic bases with *Issus coleoptratus* (Fabricius, 1781) (GenBank accession number: KX702932) and *Latissus dilatatus* (Fourcroy, 1785) (GenBank accession number: KX702947) respectively, along the complete length of 681 bp.

Discussion

The sub-family Issinae currently includes two tribes: Issini and Hysteropterini . They are characteristically distributed in Wallace's Palaearctic region (Bourgoin 2018), with exceptional distributions from Palaearctic Africa (= Saharo-Arabian Holt's 2013 realm) to Afrotropical or Oriental regions (= Sino-Japanese and Oriental Holt's 2013 realm). However, most true Issinae's non-Palaearctic occurrences need confirmation as these records are based on old observations, probably misidentified, or still not formally correctly assigned to the correct tribe (e.g., *Eupilis* Walker, 1857 in the Hysteropterini was shown to be close to *Tempsa* in the Sarimini by Gnezdilov 2016c).

In China, Issinae are rare but Hysteropterini were already reported from Xinjiang, Ningxia, Qinghai, Inner Mongolia and Gansu: *Celyphoma* Emeljanov, 1971 by Meng and Wang (2012), Chen et al. (2014) and Sichuan: *Hysteropterum boreale* = *Potaninum boreale* (Melichar, 1902) by Gnezdilov (2017). Issini have also been reported from Hong Kong (*Issus quadriguttatus* Walker, 1851 = *Issus coleoptratus* (Fabricius, 1781) by Gnezdilov et al. (2004). *Sinonissus* is therefore the second genus of the Issini to be reported from China. It appears to be a new genus of this rare group of taxa which has crossed Palaearctic and Sino-Japanese realm frontiers to evolve into the Oriental realm in the southwest areas of Chongqing and Sichuan in China.

Gnezdilov (2016a: 333 and fig. 43) supposed that the Issina lineage (sec. Gnezdilov, 2002 = Issini sec. Wang et al. 2016) had diverged early in the tree of the Western Palaearctic taxa as sister taxa to all other western Palaearctic genera, being one of the first groups to colonise the proto-Mediterranean communities of the ancient Mediterranean in the Eocene (Gnezdilov 2016b). The discovery of *Sinonissus* in the Issini lineage shows that radiation of Issinae in the Palaearctic is probably more complex than expected. Most Issinae genera still need to be molecularly tested to enable their possible placement in the phylogeny and is probably that other genera should join this tribe Issini to fill gaps in this paradoxical geographical distribution.

Acknowledgements

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RESEARCH ARTICLE

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Description of the larva of *Oecetis mizrain* Malicky & Graf, 2012 (Trichoptera, Leptoceridae) and *Lepidostoma scotti* (Ulmer, 1930) (Trichoptera, Lepidostomatidae) from Chilimo Forest, Central Ethiopia

Yonas Terefe[1,2], Simon Vitecek[3,4], Wolfram Graf[1]

1 *Institute of Hydrobiology and Aquatic Ecology Management, University of Natural Resources and Applied Life Sciences, Vienna, Austria* **2** *Department of Biology, College of Natural and Computational Sciences, Ambo University, Ambo, Ethiopia* **3** *Department for Limnology & Bio-Oceanography, University of Vienna, Vienna, Austria* **4** *Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany*

Corresponding author: *Yonas Terefe* (yonasterefe56@gmail.com)

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Abstract

The Ethiopian caddisfly fauna comprises 85 species, including 10 *Oecetis* species and three *Lepidostoma* species. In this context we provide the first species-level descriptions of Ethiopian caddisfly larvae. We describe and illustrate the larvae of *O. mizrain* and *L. scotti*, with additional notes on their habitats and distribution.

Keywords

caddisfly larvae, distribution, ecology, Afrotropical Region, diversity, ecological management

Introduction

Caddisflies are one of the most diverse aquatic insect groups, distributed all over the world. The order Trichoptera comprises approximately 15,000 species (including 685 fossils) in 616 genera and 49 families (Morse 2017). The Oriental region

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harbors the highest number of species (4865 species), followed by the Neotropical region (2562 species) (de Moor and Ivanov 2008; Holzenthal et al. 2015; Morse 2011). Species numbers in other biogeographic regions such as the Australasian (1439 species), the East Palearctic (1372 species), the Nearctic (1604 species) and the West Palearctic (1888 species) are lower in comparison (Morse 2011). The poorly explored Afrotropical region is currently represented by about 1200 species only, belonging to 28 families and 111 genera (Tobias and Tobias 2008). The Antarctic region is the only biogeographic area where no caddisflies have been recorded (Holzenthal et al. 2015; Morse 2011).

As in many Afrotropical countries, the Ethiopian caddisfly fauna is poorly studied. In a first effort to characterize the almost unknown African caddisfly fauna, Ulmer (1930) described and listed eight Ethiopian Trichoptera species. Three decades later, Kimmins (1963) reported 51 species, of which 17 were described as new. At present, the number has marginally increased to 85 species of 26 genera and nine families (Tobias and Tobias 2008; Morse 2017). Two families, Leptoceridae (35 species in 10 genera) and Hydropsychidae (22 species in six genera), represent over 60% of the currently known Ethiopian Trichoptera diversity.

Caddisflies of the widely distributed genera *Lepidostoma* Rambur, 1842 and *Oecetis* Mclachlan, 1877 comprise 453 and 539 extant species worldwide, respectively (Morse 2017). From Africa and its adjacent islands, 51 *Lepidostoma* and 103 *Oecetis* species are known (Tobias and Tobias 2008). The Checklist of East Africa (Johanson 1992) includes two *Lepidostoma* and 17 *Oecetis* species. Until now, three *Lepidostoma* and 10 *Oecetis* species have been recorded in Ethiopia (Table 1).

Within the genus *Lepidostoma*, the first species described from Ethiopia was *L. scotti* (Ulmer, 1930). Ulmer (1930) described the species based on the material obtained by Hugh Scott and Omur-Cooper during their expedition to the central highlands of Ethiopia. Since then, only two additional species have been described from Ethiopia, *L. missa* and *L. zepho* (Malicky & Graf, 2012). In the genus *Oecetis*, the species described first from Ethiopia was *O. montana* (Ulmer, 1930), based on specimens collected in the central highlands. Later, Kimmins (1963) described *O. tjonnelandi*, *O. ghibensis*, *O. brevis* and indicated the presence of *O. brunnescens* (Ulmer, 1923), *O. montana* (Ulmer, 1930), *O. pangana* Navás, 1930 and *O. setifera* (Ulmer, 1922) in Ethiopia. Most recently, Malicky and Graf (2012, 2015) described *O. armaros* Malicky & Graf, 2015, *O. mizrain* Malicky & Graf, 2012 and reported *O. portalensis* Mosely, 1939 from rivers in the Ethiopian highlands.

Caddisflies are frequently used along with other aquatic fauna as bioindicators in ecological assessment systems as they are sensitive to organic pollution and stream degradation (Barbour et al. 1999). In particular autecological characterization provides vital information for freshwater bioassessment by relating species to ecological conditions (Jones 2008). In this context, species-level identification of bioindicators is of great importance to fully reap the power of ecological analysis (Cranston 1990; Lenat and Resh 2001; Malicky et al. 2008). Species-level determination is achieved for Trichoptera and many other taxonomic groups in Central and Northern European

Table 1. Species of *Lepidostoma* and *Oecetis* occurring in Ethiopia following Kimmins (1963) and Malicky and Graf (2012, 2015); ecoregions according to Abell et al. (2008); distribution status from Tobias and Tobias (2008). AT, Afrotropical; EH, Ethiopian Highlands; LT, Lake Turkana; NER, Northern Eastern Rift; **, not reported outside of Ethiopia.

Taxa	Biogeographic region, Ecoregions (areas)	Distribution in Africa
Genus *Lepidostoma* Rambur, 1842		
L. missa Malicky & Graf, 2012	AT, EH (Semien Mts., Chenek pass)	**
L. scotti (Ulmer, 1930)	AT, EH (Leliso River, Small stream north of Addis Ababa), LT (Gughe Mt.)	**
L. zepho Malicky & Graf, 2012	AT, EH (Leliso River)	**
Genus *Oecetis* Mclachlan, 1877		
O. armaros Malicky & Graf, 2015	AT, EH (Small stream N from Addis Ababa)	**
O. brevis Kimmins, 1963	AT, LT (Gibe River)	Ghana
O. brunnescens (Ulmer, 1923)	AT, NER (Lake Awassa)	Sudan
O. ghibensis Kimmins, 1963	AT, LT (Gibe River), NER (Koka Dam, Sodere)	**
O. mizrain Malicky & Graf, 2012	AT, EH (Leliso River & Meribo River)	**
O. montana Ulmer, 1930	AT, EH (Central Highlands)	**
O. pangana Navás, 1930	AT, NER (Koka Dam, Gibe River)	Senegal, Ghana, D.R. Congo
O. portalensis Mosely, 1939	AT, EH (Leliso River, Meribo River)	Uganda
O. setifera Ulmer, 1922	AT, LT (Lake Awassa, Lake Abaya)	Sudan, D.R. Congo, Malawi, Namibia
O. tjonnelandi Kimmins, 1963	AT, LT (Gibe River)	Namibia

countries where this information is used for stream quality assessments (Hering et al. 2003; Schmidt-Kloiber et al. 2006). Most studies in tropical Africa including Ethiopia, however, are restricted to family-level identification due to the lack of taxonomic knowledge (Aschalew and Moog 2015). Therefore, to support efforts to maintain the general ecological health of fresh waters and thus ensure sustainable use of water resources in Ethiopia the compilation of taxonomic and autecological databases for all potential bioindicators is essential. Hence, in this contribution, we describe and illustrate the final instar larvae of *L. scotti* and *O. mizrain* from Ethiopia.

Material and methods

Larval and adult material was collected at small highland streams (9°4'N, 38°8'E) within Chilimo Forest, in the upper catchment of the Awash River. Association of larvae and adults was enabled by the exclusive occurrence of these *Lepidostoma* and *Oecetis* species at this site and the presence of mature pupae in the case of *O. mizrain*. Chilimo Forest is a dry afromontane forest, located about 97 km west of Addis Ababa and 7 km north of Ginchi town. It covers an area of more than 2500 hectares within an altitudinal range from 2170 m a.s.l. to 3054 m a.s.l. (Teshome and Ensermu 2013). The forest and its surrounding areas receive little precipitation from March to April, while precipitation is highest from June to September with a mean annual rainfall of >1000 mm (Aschalew 2015). The dominant trees species in this forest are *Juniperus procera*, *Podocarpus falcatus*, *Prunus africana*, and *Olea europaea* (Kassa et al. 2009; Teshome and Ensermu 2013).

The collected larval specimens were preserved in 70% ethyl alcohol. Morphological characteristics of specimens were examined and photographed using a Zeiss StereoLumar V.12 equipped with an AxioCamErc5s camera and the Zeiss-native image processing software ZEN. Image series at different focus levels were obtained and stacked via CombineZP (Hadley 2008; Brecko et al. 2014) to create single extended-depth-of-focus images. Larval morphological features and nomenclature of primary setae and setal areas follows Wiggins (1996) and Waringer and Graf (2011).

Results

Order Trichoptera
Family Leptoceridae

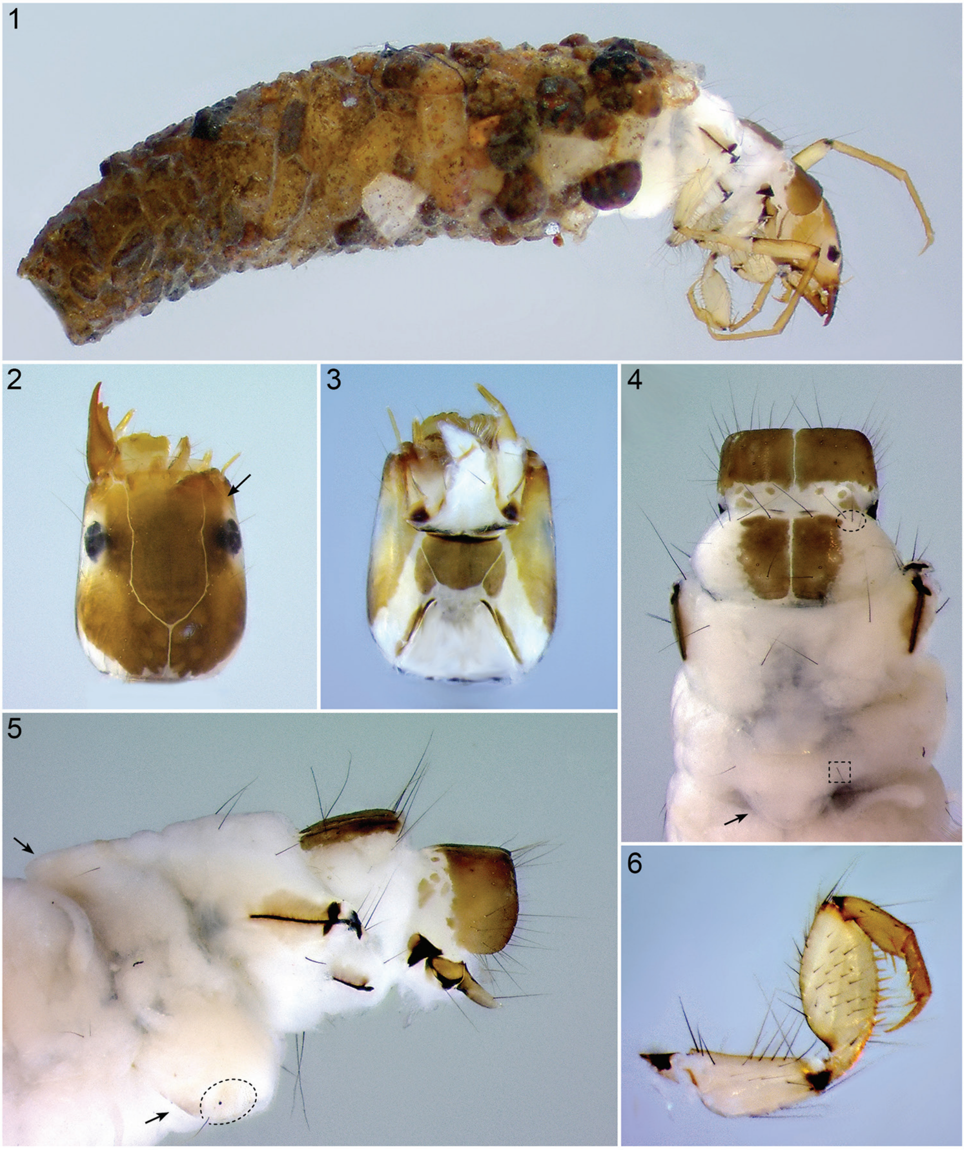
Oecetis mizrain Malicky & Graf, 2012

Figs 1–12

Material. 8 larvae: Ethiopia, Oromia Region, Chilimo forest N of Ginchi, 2451m a.s.l., 9.059719°N, 38.14332°E; 20.ii.2016; leg. & det. W. Graf; specimens deposited in the research collection of W. Graf at the University of Natural Resources and Applied Life Sciences Vienna [contact: wolfram.graf@boku.ac.at] and the Senckenberg Research Institute and Natural History Museum Trichoptera collection [collection number SMFTRI00018576; contact: Steffen U. Pauls – steffen.pauls@senckenberg.de].

Description of the 5th instar larva. *Biometry*. Larva eruciform, body length 4.5–5.0 mm, head width 0.69–0.78 mm (n=4).

Head. Head capsule hypognathous, elongated, with smooth surface; head capsule distally slightly narrower. As in all final instar larvae of Leptoceridae, subocular ecdysial line present on parietalia, running from foramen occipitale to lateral section of parietalia, ventrally to eyes, at anterior region of eyes bending dorsally, meeting frontoclypeal suture (Fig. 2, black arrow). General color of head capsule pale to golden brown (Figs 2, 3); posterodorsal margin whitish, ventral occipital margin whitish with pale-brown line; ventral apotome brown with white corners; lateroventral sclerites defined by subocular ecdysial suture dorsally brown; parietalia and frontoclypeus around dorsal ecdysial line with distinct, pale muscle attachment spots; white ring around eyes, slightly wider than eye diameter. Head capsule with complete set of primary setae, and additional linear groups of setae around setae #16 and 17. Frontoclypeus scutiform, without distinct medial constriction. Labrum light brown, with setal brush and all



Figures 1–6. *Oecetis mizrain*, 5th instar larva**. 1** Larva with the case, 14× **2** Head, dorsal view (arrow indicates subocular ecdysial line), 50× **3** Head, ventral view, 65× **4** Thorax (Pro-, Meso- and Metanotum) and abdominal segment I, dorsal view (dashed oval indicates mesonotal *sa*$_3$, dashed square indicates adominal segment I *sa*$_2$, arrow indicates abdominal segment I dorsal protuberance), 45× **5** Thorax and abdominal segment I, lateral view (arrows indicate abdominal segment I dorsal and lateral protuberances, dashed outline indicates abdominal segment I lateral sclerite), 45× **6** Left front leg, anterior face, 80×.

primary setae. Mandible slender, elongate, with single cutting edge and 3 teeth. Ventral apotome isosceles trapezoidal, rounded corners. Antennae near distal parietal border (Fig. 2), long (more than 6× longer than wide) and with single terminal seta (Fig. 2).

Figures 7–11. *Oecetis mizrain*, 5th instar larva. **7** Left middle leg, anterior face, 50× **8** Left hind leg, anterior face, 60× **9** Abdominal segment I–X, lateral view, 25× **10** Abdominal segment IX, dorsal view (dashed oval indicates abdominal segment IX tergite), 50× **11** Anal proleg, lateral view, 50× (arrow indicates section of anal proleg where prominent spines or tines may be present in other Leptoceridae).

Thorax. Prothorax fully covered by 2 large sclerites, light brown to brown; small fragments of sclerites present posterior to each pronotal half (Fig. 4). Including anterior setal rows, 25–28 setae of varying lengths distributed over each pronotal half (Figs 4, 5). Mesonotum with 2 large sclerites covering about 50% of its area while not reaching

	●	●	●					
	●	●	●					
I	II	III	IV	V	VI	VII	VIII	IX

Figure 12. *Oecetis mizrain*, 5th instar larva. Gill diagram indicating position of dorsal and ventral abdominal gills; lateral gills absent. Lateral line seemingly absent.

lateral margins, each with small anterior sclerite. Including anterior setal rows, 3–4 setae distributed over each mesonotal half; setae of setal area 3 (sa_3) on the unsclerotized part of each mesonotal half (Fig. 4; dashed oval). Metanotum completely unsclerotized; metanotal setal areas sa_2 and sa_3 each with single seta only; setal area sa_1 not developed (Fig. 4). Metasternum with transverse band of setae on either side, each comprising 2–3 setae (Fig. 5). Legs yellowish beige, with numerous setae (Figs 6–8); foreleg with numerous stout setae on anterior face of femur and with row of stout yellow setae along ventral edge of femur (Fig. 6); foretrochantin with single seta (Fig. 6); tarsal claw of mid leg curved (Fig. 7); hind leg much longer than mid leg, as typical for this genus (Fig. 8).

Abdomen. Abdomen white, cylindrical (Fig. 9). Abdominal segment I with 3 protuberances (Figs 4, 5; arrows); dorsal setal areas sa_1 and sa_3 not developed, dorsal setal area sa_2 with single seta on either side (Fig. 4, dashed square); lateral sclerite weakly sclerotized, mostly translucent, oval, with 1 seta (Fig. 5, dashed outline). Abdominal tergum IX with weakly sclerotized, mostly translucent sclerite, bearing 6 long setae in 2 groups concentrated laterally (Fig. 10, dashed oval). Anal proleg weakly sclerotized, each with large lateral sclerite and more strongly sclerotized anal claw and little accessory hook; each bearing several long setae; spines or tines on anal prolegs absent (Fig. 11, arrow). Lateral line not visible, a group of setae (2–3) present laterally on abdominal segment II (Fig. 9, dashed oval); dorsal gills only present at anterolateral position on segments II–IV, lateral gills absent, ventral gills only present at anterolateral position on segments II–IV (Fig. 12).

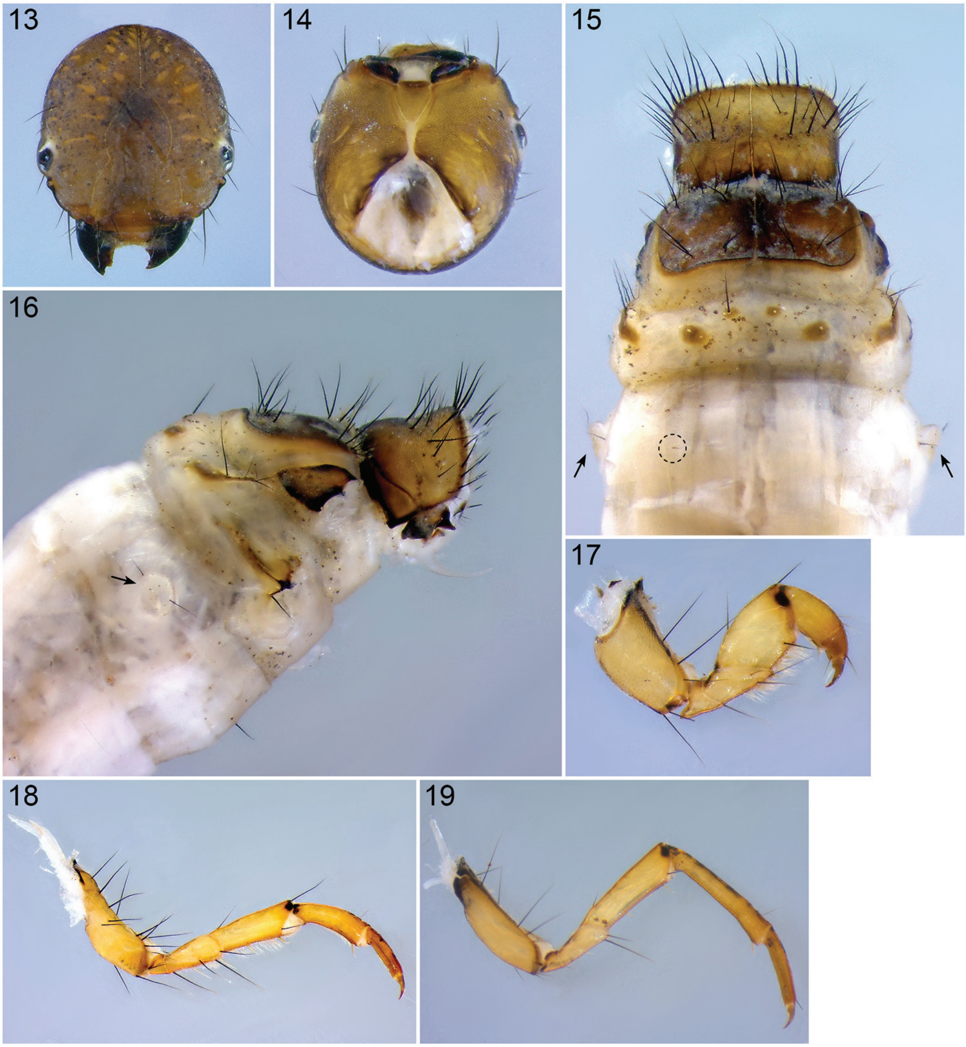
Case. Length 4.9–5.3 mm. Case of final instar larvae constructed of small sand grains, tusk-shaped; anterior opening with overhanging dorsal portion, posterior opening closed with silk (Fig. 1).

Family Lepidostomatidae

Lepidostoma scotti Ulmer, 1930

Figs 13–25

Material. 12 larvae: Ethiopia, Oromia Region, Chilimo forest N of Ginchi, 2451m a.s.l., 9.059719°N, 38.14332°E; 20.ii.2016; leg. & det. W. Graf; specimens deposited



Figures 13–19. *Lepidostoma scotti*, 5th instar larva**. 13** Head, dorsal view, 40× **14** Head, ventral view, 50× **15** Pro-, Meso- & Metanotum and abdominal segment I, dorsal view (arrows indicate abdominal segment I lateral protuberances, dashed circle indicate abdominal segment I sa_2), 25× **16** Thorax and abdominal segment I, lateral view (arrow indicates abdominal segment I lateral protuberance), 23× **17** Left front leg, anterior face, 50× **18** Left middle leg, anterior face, 40× **19** Left hind leg, anterior face, 40×.

in the research collection of W. Graf at the University of Natural Resources and Applied Life Sciences Vienna [contact: wolfram.graf@boku.ac.at] and the Senckenberg Research Institute and Natural History Museum Trichoptera collection [collection number SMFTRI00018577; contact: Steffen U. Pauls – steffen.pauls@senckenberg.de].

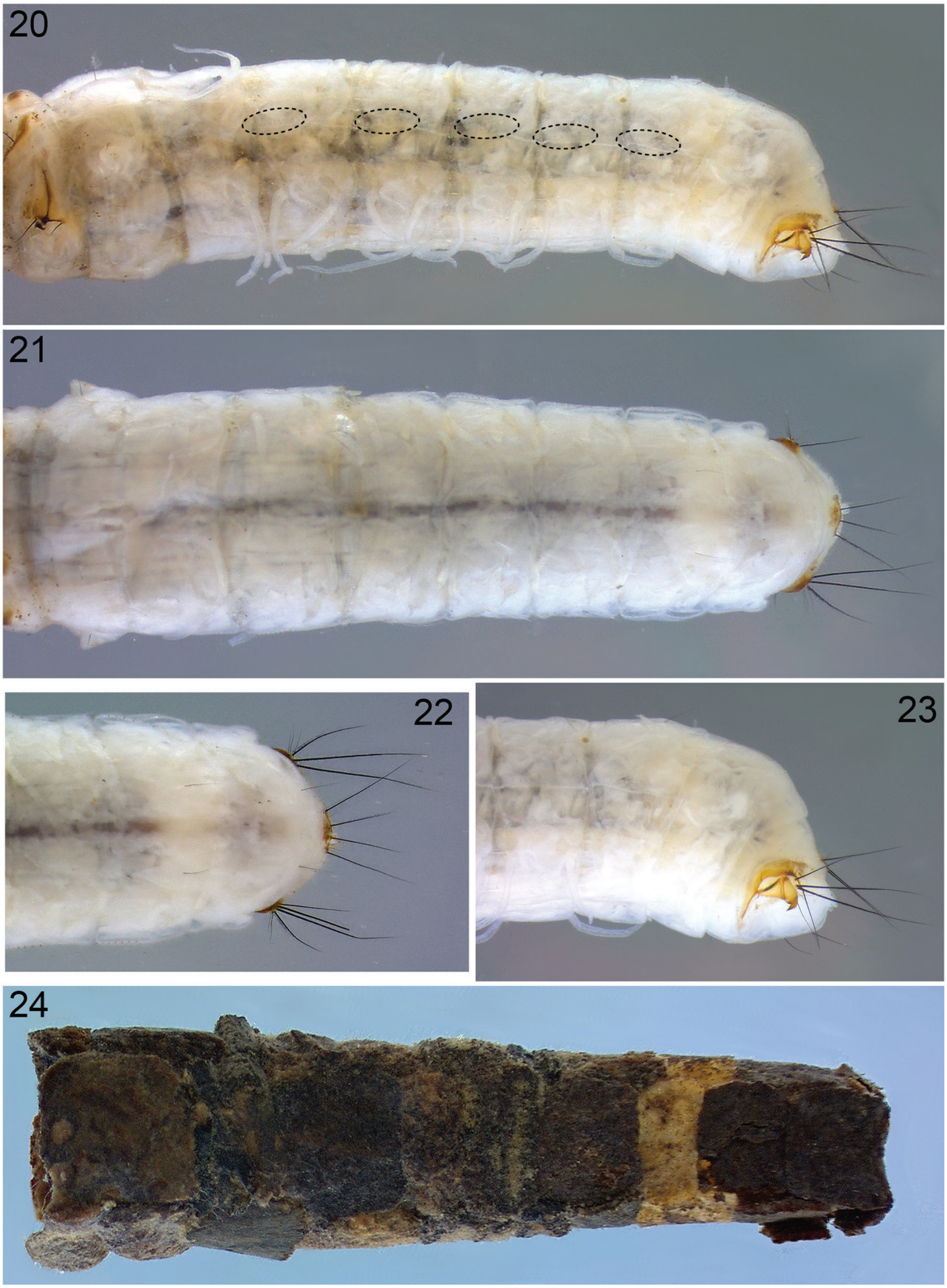
Description of 5th instar larva. *Biometry*. Larva eruciform, body length 8–9.5 mm, head width 0.87–0.94 mm (n=8).

Head. Head capsule hypognathous, round; surface granulated, covered in spicules. Color pale to dark brown, with scattered black markings (Fig. 13), area around occipital margin dark brown (Figs 13, 14). Muscle attachment spots pale brown, > 10 on each parietalia, slightly asymmetrical, lining in rows, absent on frontoclypeus. Complete set of 18 primary setae present; setae 4, 5, 13, 15 and 17 very lightly colored; short antenna situated near the anterior margin of each eye, positioned on discrete protuberance (Fig. 13). Whitish ring present around eyes. Frontoclypeus with central constriction; ventral apotome triangular, yellow-brown (Fig. 14). Labrum with 6 pairs of setae, labral brushes at anterior margin present. Mandible robust, black, with 3 teeth.

Thorax. Pronotum fully covered by 2 sclerites (Fig. 15), pale brown to brown, at posterior (with small lateral process) and posterolateral margins thickened and darkly lined (Fig. 15); each sclerite bears 20–25 long dark setae mostly concentrated in anterior half (including two rows of setae along anterior margin) (Figs 15, 16). Prosternal horn present, whitish, curved anteriorly (Fig. 16). Mesonotum fully covered by 2 sclerites, brown to dark brown (black near median suture), posterior margin with slightly sclerotized narrow dark line; mesonotal setal areas sa_1, sa_2 and sa_3 present; sa_1 bearing 3–4 setae; sa_2 bar-shaped, bearing 6–8 setae, stretching to posterior margin; sa_3 bearing 5–6 setae; sa_1 and sa_3 connected by regular bands of setae (Fig. 15). Metanotum with 6 distinct small sclerotized areas, corresponding to setal areas sa_1, sa_2 and sa_3; sa_1 and sa_2 rounded, each with 1 and 1–2 setae respectively (Fig. 15); sa_3 elongate, falcate shaped, bearing 4–6 setae (Figs 15, 16). Thoracic legs yellowish brown, with dark marking at femoro-tibial joint and with dense fringe of setae on ventral edge of coxa, trochanter and femur and long dark setae (Fig. 17); foreleg more robust, shorter than mid- and hind leg; mid leg bearing larger number of setae (majority at the coxa) than fore- and hind legs; tarsal claws similar in all legs, short, robust (Figs 17–19).

Abdomen. Color whitish (Figs 20, 21). Abdominal segment I with lateral humps bearing 2 setae (1 on anteroventral margin, 1 on dorsal margin) (Figs 15, 16, 20, 21; highlighted by arrows in Figs 15, 16); dorsal hump absent (Figs 15, 16, 20); dorsal setal areas sa_1 and sa_3 absent, sa_2 present, with a single seta (Fig. 15, dashed circles; Fig. 20); ventral setal areas sa_2 and sa_3 present, each with a single seta; sa_1 absent (Figs 16, 21). Tracheal gills simple, unbranched, as single filaments; dorsal gills on segment II (postsegmental position), segments III–VI (pre- & postsegmental position) and segment VII (postsegmental position); ventral gills on segment II (postsegmental position), segments III–VI (pre- & postsegmental position) and segment VII (postsegmental position); lateral gills absent; position of ventral gills shifted dorsad (Figs 20, 25). Lateral line from segment III–VIII; small bifurcated lamellae dorsal to lateral line present (Figs 20, 25; position of bifurcated lamellae highlighted in dashed ovals). Dorsal sclerite of segment IX semicircular, pale brown, with 4 pairs of setae (outermost lateral and medial setae very long, with interspersed shorter setae) (Fig. 22); anal proleg present, of limnephilid type (Fig. 23).

Case. Larval case 9.0–10.5 mm long, constructed from rectangular pieces of plant material; pieces subrectangular to quadratic, parts of barks or leaves; cross-section subrectangular to subquadrangular, tapering towards the posterior end (Fig. 24).



Figures 20–24. *Lepidostoma scotti*, 5th instar larva**. 20** Abdomen, segments I-X, lateral view (dashed ovals indicate position of forked lamellae), 13× **21** Abdomen, segment I-X, dorsal, 13× **22** Abdominal segment VII-X, dorsal, 25× **23** Abdomen, segment VII-X, lateral, 25×; **24** Larval case, left lateral view, 10×.

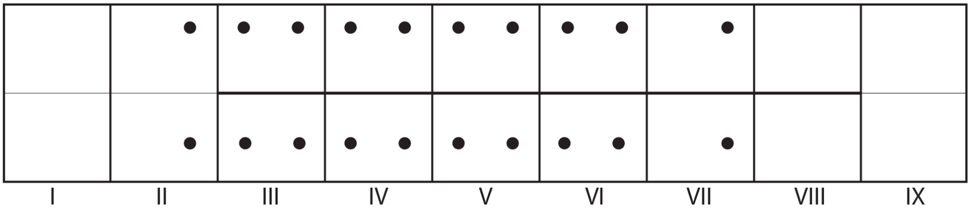


Figure 25. *Lepidostoma scotti*, 5th instar larva**.** Gill diagram indicating position of dorsal and ventral gills and extent of lateral line (bold line). Lateral gills absent.

Discussion

Historically, the most comprehensive faunistic African studies were done in South Africa, Madagascar and West Africa. These studies yielded hundreds of Trichoptera species to the Afrotropical region, of which 253 species are known from South Africa (de Moor and Day 2013), more than 500 species from Madagascar (Benstead et al. 2003), and 343 species were reported from the West Africa region (Tobias and Tobias 2008). However, other regions of the African continent are not as well represented in the available caddisfly literature. In Ethiopia, 85 species are known currently, and the discovery of several new species within the next decades is likely. Particularly, on-going projects on water resource management and capacity building will foster faunistic surveys and thus provide highly relevant baseline data for both taxonomy and ecosystem monitoring.

However, most of the data available on diversity of the African Trichoptera fauna were compiled based on adult specimens, and most species are not known in the larval stage. According to Scott (1986) only 105 of 747 Sub-Saharan species of African Trichoptera were known in the larval stage at that time. Thus, development of more precise biomonitoring tools is severely hampered. Moreover, description of these larval stages could foster development of taxonomic expertise as crucially needed for biomonitoring and sustainable development of freshwater resources in the Afrotropical region. Consequently, faunistic surveys and taxonomic treatment of yet undescribed larval stages are of great value for the development of knowledge and human resources as well as for the documentation of freshwater biodiversity.

In general, larvae of the genus *Lepidostoma* inhabit springs and cool streams that usually have slow water flow and substantial input of allochthonous organic material (Wiggins 2004). Indeed, it is evident from the mandibles of *L. scotti* larvae (Fig. 13) that this species is, like most *Lepidostoma*, a detritivorous shredder that feeds on leaf litter and decaying woody debris. Moreover, larvae of *Lepidostoma* are known to exploit even recalcitrant resources, including the leaves of coniferous plants (Grafius and Anderson 1980; Wiggins 2004). The riparian zone of Chilimo Forest streams is usually dominated by the coniferous plants *Juniperus procera* and *Podocarpus falcatus* (Kassa et al. 2009; Teshome and Ensermu 2013). The leaves of these species most likely represent the primary food source of *L. scotti* larvae in these habitats. Other studies in

Ethiopia indicated that *Lepidostoma* larvae exclusively live in forested streams instead of areas with intensified land use (Aschalew 2015; Ferengi 2016).

Larvae of the genus *Oecetis* are found in a wide range of freshwater habitats and are either carnivorous, or behave as detritivores or shredders (e.g., Waringer and Graf 2011). Larvae of carnivorous *Oecetis* species have elongated single-blade mandibles (Waringer and Graf 2011). Based on the elongated bladelike mandibles observed in *O. mizrain*, larvae of this species (Fig. 2) most likely have a predatory feeding behavior.

In addition to information on feeding ecology, stream zonation preference, sensitivity to organic pollution, or sediment load, knowledge on the flight periodicity of potential bioindicators is crucial to determine sampling seasons for biomonitoring approaches. According to Wright et al. (2013), caddisfly flight periodicity is likely controlled by a combination of innate behavior and environmental factors, most notably temperature. However, despite repeated sampling efforts in Ethiopia, the flight periods of single species could not yet be defined. Recent collections of adult *L. scotti* and *O. mizrain* revealed that these species were active in October and November (Malicky and Graf 2012, 2015), but their complete flight period remains unclear due to the lack of consistent faunistic surveys. In the eastern Afrotropical Region, these months are considered as the regeneration period for most macroinvertebrates following the heavy rainfall and high flooding season that extends from late June to mid-September (Aschalew 2015). However, flight periodicity of any Ethiopian caddisfly taxa has yet to be studied throughout the year, and further investigations on the annual flight period are currently under way.

Caddisfly larvae are widely used as indicator taxa in freshwater assessments as they exploit a wide range of ecological niches, often are found in abundance and cover a wide sensitivity range (Aschalew and Moog 2015; Barbour et al. 1999; Chakona et al. 2009; Hering et al. 2003). Ideally, assessment of the ecological condition of aquatic ecosystems is based on the identification of macroinvertebrates to species-level (Sharma et al. 2008). Jones (2007) also emphasizes the importance of species datasets for a better interpretation of bioassessment results, as well as testing ecological theories and evaluating threats of extinction to aquatic taxa. In particular, lack of species-level information leads to underestimating the actual differences in community structure (Benstead et al. 2003). Therefore, species-level resolution is fundamental for freshwater biomonitoring (Lenat and Resh 2001; Malicky et al. 2008; Corbi and Trivinho-Strixino 2006).

To achieve a better understanding of Ethiopian freshwater biodiversity and the biogeography of African freshwater fauna in general, description of species and preparation of species-level keys is imperative. Here we provide some data that might be useful for future studies to characterize the Ethiopian caddisfly fauna.

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Systematics of South American snail-eating snakes (Serpentes, Dipsadini), with the description of five new species from Ecuador and Peru

Alejandro Arteaga[1,2,3], David Salazar-Valenzuela[4], Konrad Mebert[5], Nicolás Peñafiel[4], Gabriela Aguiar[3], Juan C. Sánchez-Nivicela[6], R. Alexander Pyron[7,8], Timothy J. Colston[7,8], Diego F. Cisneros-Heredia[9,10,11], Mario H. Yánez-Muñoz[10], Pablo J. Venegas[12], Juan M. Guayasamin[4,13], Omar Torres-Carvajal[14]

1 Richard Gilder Graduate School, American Museum of Natural History, New York, USA **2** *Department of Herpetology, American Museum of Natural History, New York, USA* **3** *Tropical Herping, Quito, Ecuador* **4** *Centro de Investigación de la Biodiversidad y Cambio Climático (BioCamb), Facultad de Ciencias de Medio Ambiente, Ingeniería en Biodiversidad y Recursos Genéticos, Universidad Tecnológica Indoamérica, Quito, Ecuador* **5** *Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, Brazil* **6** *Laboratorio de Herpetología, Museo de Zoología de la Universidad del Azuay, Cuenca, Ecuador* **7** *Department of Biological Sciences, The George Washington University, Washington, D.C., USA* **8** *Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA* **9** *Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales, Instituto de Zoología Terrestre & Museo de Zoología, Quito, Ecuador* **10** *División de Herpetología, Instituto Nacional de Biodiversidad (INABIO), Quito, Ecuador* **11** *King's College London, Department of Geography, London, UK* **12** *División de Herpetología-Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru* **13** *Universidad San Francisco de Quito (USFQ), Colegio de Ciencias Biológicas y Ambientales, Laboratorio de Biología Evolutiva, campus Cumbayá, Quito, Ecuador* **14** *Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador*

Corresponding author: *Alejandro Arteaga* (aarteaga@amnh.org)

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Abstract

A molecular phylogeny of the Neotropical snail-eating snakes (tribe Dipsadini) is presented including 43 (24 for the first time) of the 77 species, sampled for both nuclear and mitochondrial genes. Morphological and phylogenetic support was found for four new species of *Dipsas* and one of *Sibon*, which are described here based on their unique combination of molecular, meristic, and color pattern characteristics. *Sibynomorphus* is designated as a junior subjective synonym of *Dipsas*. *Dipsas latifrontalis* and *D. palmeri* are resurrected from the synonymy of *D. peruana*. *Dipsas latifasciata* is transferred from the synonymy of *D. peruana* to the synonymy of *D. palmeri*. A new name, *D. jamespetersi*, is erected for the taxon currently known as *Sibynomorphus petersi*. Re-descriptions of *D. latifrontalis* and *D. peruana* are presented, as well as the first photographic voucher of an adult specimen of *D. latifrontalis*, along with photographs of all known Ecuadorian Dipsadini species. The first country record of *D. variegata* in Ecuador is provided and *D. oligozonata* removed from the list of Peruvian herpetofauna. With these changes, the number of Dipsadini reported in Ecuador increases to 22, 18 species of *Dipsas* and four of *Sibon*.

Keywords

Dipsadini, *Dipsas*, Ecuador, new species, Peru, phylogeny, *Sibon*, *Sibynomorphus*, snail-eating snakes, systematics

Introduction

With 70 currently recognized species (Table 1), the snail-eaters (tribe Dipsadini) are among the most diverse groups of arboreal snakes (Wallach et al. 2014; Uetz et al. 2016). Some authors have suggested that their tree-dwelling lifestyle and specialized diet resulted this large an adaptive radiation (e.g., MacCulloch and Lathrop 2004; Sheehy 2012). In the last decade, the limits of the tribe have been redefined to include five genera (*Dipsas*, *Plesiodipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*; Harvey et al. 2008), but recent studies suggest that not all of them are monophyletic (Sheehy 2012; Figueroa et al. 2016). Consequently, the limits between genera, species, and species groups appear to be poorly defined, and in need of revision for a robust and stable taxonomy.

One of the first modern attempts to clarify the taxonomy and summarize knowledge on the tribe Dipsadini was published by Peters (1960). Peters considered Dipsadini to include the genera *Dipsas*, *Sibon* and *Sibynomorphus*. Later, Zaher (1999) and Harvey et al. (2008) added *Tropidodipsas* and *Plesiodipsas* in the tribe. Peters also created seven species groups within *Dipsas*, three within *Sibon* (Table 1), and recognized *D. boettgeri*, *D. latifrontalis*, *D. latifasciata*, *D. polylepis*, and *D. peruana* as distinct species based on coloration and lepidosis. However, he considered *D. palmeri* and *D. praeornata* to be synonyms of *D. latifrontalis*.

After Peters, several authors continued to address the systematics of the group (Downs 1961, Hoge 1964, Peters and Orejas-Miranda 1970, Kofron 1982, Orcés and Almendáriz 1987, Porto and Fernandes 1996, Fernandes et al. 1998, Fernandes et al. 2002, Cadle and Myers 2003, Passos et al. 2004, Passos et al. 2005, Cadle 2005, Cadle 2007, Harvey 2008, Harvey and Embert 2008, Harvey et al. 2008). Of these, the works by Cadle and Myers (2003), Cadle (2007), Harvey (2008), and Harvey and

Table 1. Taxonomy of Dipsadini prior to this paper.

Genus	Group	Species	Authority	Reference
Dipsas	*D. articulata*	*D. articulata*	Cope, 1868	Harvey 2008
		D. bicolor	Günther, 1895	Peters 1960
		D. brevifacies	Cope, 1866	Harvey 2008
		D. gaigeae	Oliver, 1837	Harvey 2008
		D. gracilis	Boulenger, 1902	Harvey 2008
		D. maxillaris	Werner, 1910	Peters 1960
		D. tenuissima	Taylor, 1954	Harvey 2008
		D. viguieri	Bocourt, 1884	Harvey 2008
	D. catesbyi	*D. catesbyi*	Sentzen, 1796	Harvey 2008
		D. copei	Günther, 1872	Harvey 2008
		D. pavonina	Schlegel, 1837	Harvey 2008
	D. elegans	*D. elegans*	Boulenger, 1896	Harvey 2008
		D. ellipsifera	Boulenger, 1898	Harvey 2008
		D. oreas	Cope, 1868	Harvey 2008
	D. incerta	*D. alternans*	Fischer, 1885	Harvey 2008
		D. incerta	Jan, 1863	Harvey 2008
		D. praeornata	Werner, 1909	Harvey 2008
		D. sazimai	Fernandes et al., 2010	Fernandes et al. 2010
	D. indica	*D. bucephala*	Shaw, 1802	Harvey 2008
		D. cisticeps	Boettger, 1885	Harvey 2008
		D. indica	Laurenti, 1768	Harvey 2008
	D. pratti	*D. baliomelas*	Harvey, 2008	Harvey 2008
		D. chaparensis	Reynolds & Foster, 1992	Harvey 2008
		D. peruana	Boettger, 1898	Harvey 2008
		D. pratti	Boulenger, 1897	Harvey 2008
		D. sanctijoannis	Boulenger, 1911	Harvey 2008
		D. schunkii	Boulenger, 1908	Harvey 2008
	D. temporalis	*D. pakaraima*	MacCulloch & Lathrop, 2004	Harvey 2008
		D. temporalis	Werner, 1909	Harvey 2008
		D. vermiculata	Peters, 1960	Harvey 2008
	D. variegata	*D. albifrons*	Sauvage, 1884	Harvey 2008
		D. andiana	Boulenger, 1896	Harvey 2008
		D. nicholsi	Dunn, 1933	Harvey 2008
		D. trinitatis	Parker, 1926	Harvey 2008
		D. variegata	Duméril et al., 1854	Harvey 2008
Plesiodipsas	Unassigned	*P. perijanensis*	Aleman, 1953	–
Sibon	*S. annulatus*	*S. annulatus*	Günther, 1872	Savage 2002
		S. anthracops	Cope, 1868	Savage 2002
		S. dimidiatus	Günther, 1872	Savage 2002
		S. lamari	Solórzano, 2001	Solórzano 2001
		S. linearis	Pérez-Higareda et al., 2002	Pérez-Higareda et al. 2002
		S. manzanaresi	McCranie, 2007	McCranie 2007
		S. merendonensis	Rovito et al., 2012	Rovito et al. 2012
		S. miskitus	McCranie, 2006	McCranie 2006
		S. sanniolus	Cope, 1866	Savage 2002

Genus	Group	Species	Authority	Reference
Sibon	*S. argus*	*S. argus*	Cope, 1875	Savage 2002
		S. longifrenis	Stejneger, 1909	Savage 2002
	S. nebulatus	*S. carri*	Shreve, 1951	Peters 1960
		S. dunni	Peters, 1957	Savage 2002
		S. nebulatus	Linnaeus, 1758	Savage 2002
	Unassigned	*S. noalamina*	Lotzkat et al., 2012	–
		S. perissostichon	Köhler et al., 2010	–
Sibynomorphus	Unassigned	*S. lavillai*	Scrocchi et al., 1993	–
		S. mikanii	Schlegel, 1837	–
		S. neuwiedi	Ihering, 1911	–
		S. oligozonatus	Orcés & Almendáriz, 1989	–
		S. oneilli	Rossman & Thomas, 1979	–
		S. petersi	Orcés & Almendáriz, 1989	–
		S. turgidus	Cope, 1868	–
		S. vagrans	Dunn, 1923	–
		S. vagus	Jan, 1863	–
		S. ventrimaculatus	Boulenger, 1885	–
		S. williamsi	Carillo de Espinoza, 1974	–
Tropidodipsas	*T. fasciata*	*T. fasciata*	Günther, 1858	Kofron 1987
		T. philippii	Jan, 1863	Kofron 1987
	T. sartorii	*T. annulifera*	Boulenger, 1894	Kofron 1988
		T. sartorii	Cope, 1863	Kofron 1988
		T. zweifeli	Liner & Wilson, 1970	Kofron 1988
	Unassigned	*T. fischeri*	Boulenger, 1894	–
		T. repleta	Smith et al., 2005	–

Embert (2008) are worth addressing further because they focused on Ecuadorian species for which there is still taxonomic uncertainty. Cadle and Myers (2003) removed *D. variegata* from the herpetofauna of Ecuador, since previous records were based on museum misidentifications. Cadle (2007) reviewed the status of species of *Sibynomorphus* in Ecuador and Peru, and referred three additional specimens (AMNH 110587, BMNH 1935.11.3.108, and MUSM 2192) to *S. oligozonatus*, including the first country record for Peru. Cadle (2005) also reviewed three specimens of *D. gracilis* collected in Peru; however, Harvey (2008) concluded that only one of them corresponded to *D. gracilis*. In the same work, Harvey also redefined Peters' (1960) species groups (Table 1). Finally, Harvey and Embert (2008) transferred *D. boettgeri*, *D. latifrontalis*, and *D. polylepis* to the synonymy of *D. peruana*, based on both the difficulty of segregating these species using morphological characters and their "more or less continuous distribution along the eastern slopes of the Andes".

Here, we combine morphological analysis and molecular phylogenetics to revise generic and species limits within Dipsadini. We combine all available molecular sampling with new samples from Ecuador, Peru, Brazil and Costa Rica, and find support for five new species, as well as a number of changes to the geographic distribution of several Andean species.

Materials and methods

Ethics statement

This study was carried out in strict accordance with the guidelines for use of live amphibians and reptiles in field research (Beaupre et al. 2004) compiled by the American Society of Ichthyologists and Herpetologists (ASIH), the Herpetologists' League (HL) and the Society for the Study of Amphibians and Reptiles (SSAR). All procedures with animals (see below) were reviewed by the Ministerio de Ambiente del Ecuador (MAE) and specifically approved as part of obtaining the following field permits for research and collection: MAE-DNB-CM-2015-0017 (granted to Universidad Tecnológica Indoamérica), 018-IC-FAU-DNBAP/MA, 010-IC-FAU-DNBAPVS/MA, 004-IC-FAU/FLO-DPZCH-MA (granted to Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad) and 001-10 IC-FAU-DNB/MA, 001-11 IC-FAU-DNB/MA, 002-16 IC-FAU-DNB/MA, 003-15 IC-FAU-DNB/MA, 003-17 IC-FAU-DNB/MA, 005-14 IC-FAU-DNB/MA, 008-09 IC-FAU-DNB/MA, MAE-DNB-ARRGG-CM-2014-0002 (granted to Pontificia Universidad Católica del Ecuador). Specimens were euthanized with 20% benzocaine, fixed in 10% formalin or 70% ethanol, and stored in 70% ethanol. Museum vouchers were deposited at Museo de Zoología of the Universidad Tecnológica Indoamérica (MZUTI), Museo de Zoología (QCAZ) of Pontificia Universidad Católica del Ecuador, Museo de Zoología (ZSFQ) of Universidad San Francisco de Quito, División de Herpetología (DHMECN) of Instituto Nacional de Biodiversidad and Coleção Herpetológica da UnB (CHUNB).

Common names

Criteria for common name designation are as proposed by Caramaschi et al. (2006), as modified by Coloma and Guayasamin (2011–2017), and are as follows (in order of importance): (i) the etymological intention (implicit or explicit) that the authors used when naming the species (specific epithet); (ii) a common name that is already widely used in the scientific literature; (iii) a common name that has an important ancestral or cultural meaning; (iv) a common name based on any distinctive aspect of the species (distribution, morphology, behavior, etc.).

Sampling

Tissue samples from 85 individuals representing 28 species (including five new species described here) were sampled from Ecuador, Peru, Guatemala, Costa Rica, Nicaragua, Brazil, and Mexico. All specimens included in the genetic analyses were morphologically identified according to Arteaga et al. (2013), Cadle (2005), Cadle (2007), Cadle and Myers (2003), Duellman (1978), Harvey (2008), Harvey and Embert (2008), Peters (1957) and Savage (2002). We created photo vouchers (Figs 1, 2) for all Ecuadorian species of Dipsadini. We generated sequence data for samples marked with an asterisk under Appendix 1, which includes museum vouchers at MZUTI, QCAZ, Museo de Zoología de la Universidad del Azuay (MZUA), División de Herpetología del Instituto Nacional de Biodiversidad (DHMECN), Museum of Vertebrate Zoology at Berkeley (MVZ), Bioparque Amaru Cuenca (AMARU), Coleção Herpetológica da UnB (CHUNB), Museo de Zoología de la Universidad San Francisco de Quito (ZSFQ), and Centro de Ornitología y Biodiversidad (CORBIDI), along with individuals not accessioned in musem collections (CAMPO, JMG and TJC).

Laboratory techniques

Genomic DNA was extracted from 96% ethanol-preserved tissue samples (liver, muscle tissue or scales) using either a guanidinium isothiocyanate extraction protocol, or a modified salt precipitation method based on the Puregene DNA purification kit (Gentra Systems). We amplified the 16S gene using primer pairs 16Sar-L / 16Sbr-H-R from Palumbi et al. (1991) and 16sF.0 (Pellegrino et al. 2001) / 16sR.0 (Whiting et al. 2003). Additionally, the Cytb gene was obtained with primer pairs GLUDG-L (Palumbi et al. 1991) / ATRCB3 (Harvey et al. 2000) and LGL765 (Bickham et al. 1995) / CytbV (Torres-Carvajal et al. 2015), whereas the gene coding for the subunit 4 of the NADH dehydrogenase was amplified with the primers ND4 and Leu developed by Arévalo et al. (1994). The c-mos gene was retrieved with primers S77 and S78 developed by Lawson et al. (2005). PCR reactions contained 2 mM (Cytb and ND4) or 3 mM (16S and c-mos) $MgCl_2$, 200 µM dNTP mix, 0.2 µM (16S, Cytb and c-mos) or 0.8 µM (ND4) of each primer and 1.25 U (16S) or 0.625 U (ND4, Cytb and c-mos) Taq DNA Polymerase Recombinant (Thermo Fisher Scientific) in a 25 µL total volume. The nucleotide sequences of the primers and the PCR conditions applied to each primer pair are detailed in Appendix 2. PCR products were cleaned with either ExoSAP-IT (Affymetrix, Cleveland, OH), or Exonuclease I and Alkaline Phosphatase (Illustra ExoProStar by GE Healthcare) before they were sent to Macrogen Inc (Korea) for sequencing. All PCR products were sequenced in both forward and reverse directions with the same primers that were used for amplification. The edited sequences were deposited in GenBank (Appendix 1).

DNA sequence analyses

A total of 298 DNA sequences were used to build a phylogenetic tree of the tribe Dipsadini, of which 222 were generated during this work and 76 were downloaded from GenBank. Among the new sequences, 103 are 201–520 bp long fragments of the 16S gene, 91 are 586–1,090 bp long fragments of the Cytb gene, 45 are 443–583 bp long fragments of the c-mos gene, 31 are 242–473 bp long fragments of the 12S gene, and 28 are 593–699 bp long fragments of the ND4 gene. New sequences were edited and assembled using the program Geneious ProTM 5.4.7 (Drummond et al. 2010) and aligned with those downloaded from GenBank (Appendix 1) using MAFFT v.7 (Katoh and Standley 2013) under the default parameters in Geneious ProTM 5.4.7. Genes were combined into a single matrix with 11 partitions, one per non-coding gene and three per protein-coding gene corresponding to each codon position. The best partition strategies along with the best-fit models of evolution were obtained in PartitionFinder 2 (Lanfear et al. 2016) under the Bayesian information criterion.

Phylogenetic relationships were assessed under both a Bayesian inference (BI) and a maximum likelihood (ML) approach in MrBayes 3.2.0 (Ronquist and Huelsenbeck 2013) and RAxML v8.2.9 (Stamatakis 2006), respectively. For the ML analysis, nodal support was assessed using the rapid-bootstrapping algorithm with 1000 non-parametric bootstraps. All ML estimates and tests were run under the GTRCAT model, as models available for use in RAxML are limited to variations of the general time-reversible (GTR) model of nucleotide substitution. For the BI analysis, four independent analyses were performed to reduce the chance of converging on a local optimum. Each analysis consisted of 6,666,667 generations and four Markov chains with default heating settings. Trees were sampled every 1,000 generations and 25% of them were arbitrarily discarded as "burn-in." The resulting 5,000 saved trees per run were used to calculate posterior probabilities (PP) for each bipartition in a 50% majority-rule consensus tree. We used Tracer 1.6 (Rambaut et al. 2018) to assess convergence and effective sample sizes (ESS) for all parameters. Additionally, we verified that the average standard deviation of split frequencies between chains and the potential scale reduction factor (PSRF) of all the estimated parameters approached values of ≤0.01 and 1, respectively. Genetic distances between new species and their closest morphological relative were calculated using the uncorrected distance matrix in PAUP 4.0 (Swofford 2002). GenBank accession numbers are listed in Appendix 1.

Morphological data

Terminology for Dipsadini cephalic shields follows proposals by Peters (1960) and Harvey and Embert (2008). Diagnoses and descriptions generally follow Fernandes et al. (2010), and ventral and subcaudal counts follow Dowling (1951). When providing the standard deviation, we use the ± symbol. We examined comparative alcohol-preserved specimens from the herpetology collections at Museo de Zoología de la Universidad Tecnológica Indoamérica (MZUTI), Museum d'Histoire Naturelle de la Ville de Genève (MHNG), Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ), National Museum of Natural History (USNM), División de Herpetología del Instituto Nacional de Biodiversidad (DHMECN), Museo de Zoología de la Universidad del Azuay (MZUA), American Museum of Natural History (AMNH), Museo de Zoología de la Universidad San Francisco de Quito (ZSFQ), Museum of Natural Science of the Louisiana State University (LSUMZ), Museum of Comparative Zoology of Harvard University (MCZ), Natural History Museum and Biodiversity Research Center of University of Kansas (KU), British Museum of Natural History (BMNH), Museo de Historia Natural de la Escuela Politécnica Nacional (EPN), and Museo de la Universidad Nacional de San Marcos (MUSM) (Table 2). Morphological measurements were taken with measuring tapes to the nearest 1 mm, or with digital calipers to the nearest 0.1 mm. Abbreviations are as follows: snout-vent length (SVL); tail length (TL). Sex was determined by establishing the presence/absence of hemipenes through a subcaudal incision at the base of the tail unless hemipenes were everted.

Results

Molecular phylogeny and taxonomic consequences

We consider strong support to be bootstrap values of >70% and posterior probability values >95% following Felsenstein (2004). Overall, there is low support for the relationship between the genera *Dipsas*, *Sibon*, and *Tropidodipsas* (Fig. 3). The genus *Sibynomorphus* is not monophyletic and the included species are nested in four mutually exclusive clades within *Dipsas*. Two of the three included species of *Tropidodipsas*, *T. fischeri*, and *T. fasciata*, form a poorly supported clade, whereas *T. sartorii* is strongly supported as sister lineage to all other included samples of Dipsadini. The genus *Sibon* is monophyletic, and sister to *T. fischeri* and *T. fasciata* in the ML analysis, although this relationship is not strongly supported. In the BI analysis, *Sibon* is sister to *Dipsas*. We excluded *Sibon noalamina* (voucher SMF 91539) from the analyses as the short sequence available in GenBank (gene fragment 16S) represented a rogue taxon that assumed varying phylogenetic positions in the tree collection used to build the consensus tree.

Sibon longifrenis is recovered as the sister taxon to all other included species of *Sibon*. Deep intraspecific divergence is found between samples of *S. annulatus* from Central America (MVZ 269290, ADM 0007, ADM 242) and that from Ecuador (MZUTI 3034). The widespread species *S. nebulatus* is paraphyletic with respect to both *S. dunni* and a new species from Ecuador. Nonetheless, within *S. nebulatus*, the included subspecies *S. n. nebulatus* (Linnaeus, 1758) and *S. n. leucomelas* (Boulenger, 1896) are monophyletic, while the single Colombian specimen of *S. n. hartwegi* (Peters 1960) is sister to all other members of the Ecuadorian *S. nebulatus* group. However, posterior probabilites from our genetic data for the formation of monophyletic Ecuadorian clades *S. n. leucomelas*, *S. dunni*, and *Sibon*. sp. are variable, and as low as 48% PP for the node separating *Sibon* sp. from *S. nebulatus leucomelas* and *S. dunni*.

Table 2. Locality data for specimens examined in this study. Coordinates represent actual GPS readings taken at the locality of collection or georeferencing attempts from gazetteers under standard guidelines, though some variation from the exact collecting locality will be present. Similarly, elevations are taken from Google Earth, and may not exactly match the elevations as originally reported. Specimens listed here but not under Appendix 3 were examined indirectly (e.g., through photographs).

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. andiana	MZUA.RE.0230	Ecuador	Cañar	Ocaña	-2.48807	-79.18758	923
D. andiana	MHNG 2250.053	Ecuador	Cotopaxi	Las Pampas	-0.43021	-78.96663	1590
D. andiana	MZUTI 5413	Ecuador	El Oro	Reserva Buenaventura	-3.65477	-79.76830	497
D. andiana	MZUTI 3501	Ecuador	Pichincha	Mashpi lodge	0.16567	-78.88656	860
D. andiana	MZUTI 3505	Ecuador	Pichincha	Valle Hermoso–Los Bancos	-0.01371	-79.09462	571
D. andiana	ZSFQ D116	Ecuador	Pichincha	Tandayapa	0.00205	-78.67880	1734
D. andiana	ZSFQ D117	Ecuador	Pichincha	Hacienda La Joya	0.08291	-78.98311	763
D. andiana	ZSFQ D115	Ecuador	Manabí	5km W Puerto López	-1.59045	-80.84087	7
D. bobridgelyi	QCAZ 1706	Ecuador	Azuay	Ponce Enríquez	-3.06547	-79.74358	39
D. bobridgelyi	DHMECN 11527	Ecuador	El Oro	Remolino	-3.56551	-79.91948	229
D. bobridgelyi	MZUTI 3266	Ecuador	El Oro	Reserva Buenaventura	-3.65467	-79.76794	524
D. bobridgelyi	MZUTI 5414	Ecuador	El Oro	Reserva Buenaventura	-3.65310	-79.76336	572
D. bobridgelyi	MZUTI 5417	Ecuador	El Oro	Reserva Buenaventura	-3.65467	-79.76794	524
D. catesbyi	MHNG 2220.054	Ecuador	Morona Santiago	Macas	-2.31670	-78.11670	972
D. catesbyi	MHNG 2238.005	Ecuador	Morona Santiago	San Pablo de Kantesiya	-0.25001	-76.41849	250
D. catesbyi	USNM 283949	Ecuador	Morona Santiago	Sucúa	-2.45663	-78.16784	829
D. catesbyi	DHMECN 11555	Ecuador	Napo	El Reventador	-0.04669	-77.52898	1428
D. catesbyi	QCAZ 181	Ecuador	Napo	Hollín–Loreto	-0.74087	-77.51945	1020
D. catesbyi	MHNG 2220.052	Ecuador	Napo	San Rafael	-0.10354	-77.58337	1246
D. catesbyi	QCAZ 210	Ecuador	Napo	San Rafael	-0.09669	-77.58995	1464
D. catesbyi	MHNG 2206.086	Ecuador	Orellana	Hacienda Primavera	-0.48689	-76.63581	267
D. catesbyi	MHNG 2435.097	Ecuador	Pastaza	Puyo	-1.46678	-77.98335	953
D. catesbyi	QCAZ 5108	Ecuador	Pastaza	Villano B	-1.49961	-77.48234	341
D. catesbyi	MHNG 2249.001	Ecuador	Sucumbíos	El Reventador	-0.04480	-77.52858	1476
D. catesbyi	QCAZ 28	Ecuador	Sucumbíos	El Reventador	-0.04669	-77.52898	1428
D. catesbyi	MHNG 2238.014	Ecuador	–	–	–	–	–

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. catesbyi	MHNG 2307.091	Ecuador	–	–	–	–	–
D. catesbyi	MZUTI 4736	Ecuador	–	–	–	–	–
D. catesbyi	MZUTI 4999	Ecuador	–	–	–	–	–
D. elegans	MHNG 2435.084	Ecuador	Cotopaxi	Cutzualo	-0.54497	-78.91891	1952
D. elegans	MHNG 2440.098	Ecuador	Cotopaxi	Galápagos	-0.40583	-78.96667	1781
D. elegans	DHMECN 1693	Ecuador	Cotopaxi	Hacienda “La Mariela”	-1.14757	-79.09126	1256
D. elegans	MHNG 2457.078	Ecuador	Cotopaxi	Las Damas	-0.38402	-78.96741	1678
D. elegans	MHNG 2249.019	Ecuador	Cotopaxi	Las Pampas	-0.43021	-78.96663	1590
D. elegans	MHNG 2413.074	Ecuador	Cotopaxi	Palo Quemado	-0.61962	-78.99066	2402
D. elegans	USNM 285957	Ecuador	Pichincha	2.9 km SW of Tandayapa	0.00578	-78.67867	1844
D. elegans	MHNG 2399.072	Ecuador	Pichincha	Ilaló	-0.26166	-78.44444	2579
D. elegans	MZUTI 3695	Ecuador	Pichincha	Tambotanda	-0.02011	-78.65101	1875
D. elegans	MZUTI 3317	Ecuador	Pichincha	Tandapi	-0.42278	-78.79611	1550
D. elegans	MHNG 2457.079	Ecuador	Santo Domingo	Chiriboga	-0.22841	-78.76725	1813
D. elegans	MHNG 2308.002	Ecuador	Santo Domingo	Hacienda Las Palmeras	-0.24520	-78.84806	1876
D. elegans	MHNG 2220.093	Ecuador	–	–	–	–	–
D. elegans	MZUTI 3316	Ecuador	–	–	–	–	–
D. ellipsifera	MZUTI 4931	Ecuador	Carchi	Chilma Bajo	0.86274	-78.05080	2071
D. ellipsifera	QCAZ 14855	Ecuador	Carchi	Quebrada Golondrinas	0.83210	-78.12324	1737
D. ellipsifera	QCAZ 15225	Ecuador	Carchi	Río Pailón	0.95643	-78.23448	1669
D. ellipsifera	MHNG 2220.048	Ecuador	Imbabura	Cotacachi	0.29395	-78.26682	2446
D. gracilis	QCAZ 4137	Ecuador	Cañar	Manta Real	-2.55367	-79.36425	257
D. gracilis	QCAZ 3504	Ecuador	Esmeraldas	Angostura	1.02164	-78.86295	31
D. gracilis	QCAZ 10549	Ecuador	Esmeraldas	Caimito	0.69546	-80.08990	118
D. gracilis	QCAZ 14495	Ecuador	Esmeraldas	Estero Gasparito	0.91296	-78.84066	80
D. gracilis	QCAZ 2629	Ecuador	Esmeraldas	Fauna Granja Tropical	0.66152	-79.53875	29
D. gracilis	QCAZ 7321	Ecuador	Esmeraldas	La Mayronga	1.04361	-79.27786	14
D. gracilis	QCAZ 13738	Ecuador	Esmeraldas	Tundaloma	1.18166	-78.74945	74
D. gracilis	MZUA.RE.0280	Ecuador	Guayas	Naranjal	-2.72302	-79.63172	58
D. gracilis	MZUA.RE.0281	Ecuador	Guayas	Naranjal	-2.72302	-79.63172	58
D. gracilis	QCAZ 12478	Ecuador	Guayas	Río Patul	-2.55548	-79.37180	266

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. gracilis	QCAZ 8432	Ecuador	Los Ríos	Buena Fe	-0.89306	-79.48957	104
D. gracilis	MHNG 2309.038	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	QCAZ 10196	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	USNM 285477	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	USNM 285478	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	USNM 285479	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	USNM 285480	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
D. gracilis	DHMECN 2902	Ecuador	Manabí	El Aguacate	0.65348	-80.05190	43
D. gracilis	QCAZ 11427	Ecuador	Manabí	Jama Coaque	-0.11455	-80.12337	321
D. gracilis	QCAZ 4654	Ecuador	Manabí	Lalo Loor	-0.08337	-80.15004	75
D. gracilis	MHNG 1363.023	Ecuador	Manabí	Maicito	-0.27265	-79.57179	173
D. gracilis	MHNG 1363.024	Ecuador	Manabí	Maicito	-0.27265	-79.57179	173
D. gracilis	MHNG 1363.026	Ecuador	Manabí	Maicito	-0.27265	-79.57179	173
D. gracilis	MHNG 1363.027	Ecuador	Manabí	Maicito	-0.27265	-79.57179	173
D. gracilis	QCAZ 4649	Ecuador	Manabí	Reserva Jama Coaque	-0.11556	-80.12472	299
D. gracilis	MHNG 2453.019	Ecuador	Manabí	Zapallo Grande	0.78165	-78.98345	100
D. gracilis	QCAZ 14494	Ecuador	Pichincha	Cachaco–Lita	0.78886	-78.36794	1108
D. gracilis	MZUTI 1386	Ecuador	Pichincha	El Abrazo del Árbol	-0.00913	-78.81321	1064
D. gracilis	QCAZ 7532	Ecuador	Pichincha	El Monte	-0.06912	-78.76195	1316
D. gracilis	QCAZ 15718	Ecuador	Pichincha	Finca Ecológica Orongo	0.15304	-78.66737	1173
D. gracilis	MZUTI 3503	Ecuador	Pichincha	Mashpi lodge	0.16681	-78.88111	905
D. gracilis	QCAZ 15542	Ecuador	Pichincha	Rainforest Monterreal	0.01557	-78.88407	860
D. gracilis	QCAZ 7322	Ecuador	Pichincha	Road to Mindo	-0.03116	-78.75617	1638
D. gracilis	QCAZ 3693	Ecuador	Santo Domingo	8.5 km NW Santo Domingo	-0.17700	-79.21099	454
D. gracilis	QCAZ 3694	Ecuador	Santo Domingo	8.5 km NW Santo Domingo	-0.17700	-79.21099	454
D. gracilis	QCAZ 11238	Ecuador	Santo Domingo	Finca de Germán Cortez	-0.00027	-79.41194	194
D. gracilis	QCAZ 2040	Ecuador	Santo Domingo	La Perla	0.13417	-79.49432	132
D. gracilis	DHMECN 129	Ecuador	–	–	–	–	–
D. gracilis	MZUTI 4199	Ecuador	–	–	–	–	–
D. indica	MZUA.RE.0059	Ecuador	Morona Santiago	Rosa de Oro	–	–	–
D. indica	MHNG 2435.093	Ecuador	Orellana	Coca	-0.46167	-76.99310	253

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. indica	MHNG 2413.076	Ecuador	Orellana	Hacienda Primavera	-0.48689	-76.63581	267
D. indica	MZUTI 4735	Ecuador	Pastaza	Tzarentza	-1.35696	-78.05814	1355
D. jamespetersi	MZUA.RE.0147	Ecuador	Azuay	La Paz	-3.31481	-79.15166	3148
D. jamespetersi	MZUTI 5307	Ecuador	Azuay	Poetate	-3.41645	-79.26964	2269
D. jamespetersi	USNM 237040	Ecuador	Loja	0.5 km E of Loja	-3.99277	-79.18327	2263
D. jamespetersi	MHNG 2512.047	Ecuador	Loja	24 km S Loja	-4.22083	-79.24164	1562
D. jamespetersi	MHNG 2512.048	Ecuador	Loja	24 km S Loja	-4.22083	-79.24164	1562
D. jamespetersi	MHNG 2399.071	Ecuador	Loja	5 km E Loja	-3.98899	-79.16576	2610
D. jamespetersi	MHNG 2457.09	Ecuador	Loja	5 km E Loja	-3.98899	-79.16576	2610
D. jamespetersi	MHNG 2512.049	Ecuador	Loja	5 km E Loja	-3.98899	-79.16576	2610
D. jamespetersi	MHNG 2512.05	Ecuador	Loja	5 km E Loja	-3.98899	-79.16576	2610
D. jamespetersi	MHNG 2521.087	Ecuador	Loja	5 km E Loja	-3.98899	-79.16576	2610
D. jamespetersi	QCAZ 15100	Ecuador	Loja	Guachanamá	-4.04081	-79.88290	2787
D. jamespetersi	MHNG 2413.082	Ecuador	Loja	Loja	-4.00789	-79.21128	2166
D. latifrontalis	BMNH1946.1.20	Venezuela	Mérida	Aricagua	8.16162	-71.15776	1078
D. klebbai	QCAZ 1605	Ecuador	Napo	2 km E Borja	-0.41543	-77.83032	1608
D. klebbai	DHMECN 568	Ecuador	Napo	Borja	-0.42624	-77.84277	1698
D. klebbai	MHNG 2220.035	Ecuador	Napo	El Chaco	-0.33763	-77.80957	1595
D. klebbai	MHNG 2220.056	Ecuador	Napo	El Chaco	-0.33763	-77.80957	1595
D. klebbai	MHNG 2250.063	Ecuador	Napo	El Chaco	-0.33763	-77.80957	1595
D. klebbai	MHNG 2250.064	Ecuador	Napo	El Chaco	-0.33763	-77.80957	1595
D. klebbai	MZUTI 5412	Ecuador	Napo	Pacto Sumaco	-0.66377	-77.59895	1556
D. klebbai	MCZ 164674	Ecuador	Napo	Río Azuela	-0.14869	-77.65463	1402
D. klebbai	MCZ 164675	Ecuador	Napo	Río Azuela	-0.14869	-77.65463	1402
D. klebbai	USNM 286323	Ecuador	Napo	Río Azuela	-0.14869	-77.65463	1402
D. klebbai	MHNG 2220.038	Ecuador	Napo	San Rafael	-0.09669	-77.58995	1464
D. klebbai	MHNG 2220.039	Ecuador	Napo	San Rafael	-0.09669	-77.58995	1464
D. klebbai	MZUTI 63	Ecuador	Napo	Yanayacu	-0.60042	-77.89053	2110
D. klebbai	MHNG 2220.04	Ecuador	Sucumbíos	El Reventador	-0.04480	-77.52858	1476
D. klebbai	MHNG 2220.041	Ecuador	Sucumbíos	El Reventador	-0.04480	-77.52858	1476
D. klebbai	QCAZ 250	Ecuador	Sucumbíos	El Reventador	-0.04669	-77.52898	1428

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. klebbai	QCAZ 14281	Ecuador	Sucumbíos	La Bonita	0.47209	-77.54661	1953
D. klebbai	MHNG 2529.029	Ecuador	–	–	–	–	–
D. klebbai	ZSFQ D304	Ecuador	Napo	Cascada de San Rafael	-0.10007	-77.58034	1182
D. georgejetti	USNM 142595	Ecuador	Guayas	10 mi N of Guayaquil	-1.96418	-79.87988	5
D. georgejetti	QCAZ 9125	Ecuador	Guayas	Cerro Blanco	-2.17465	-80.02135	147
D. georgejetti	ENS 12817	Ecuador	Manabí	17 km NW Portoviejo	-1.00209	-80.31334	187
D. georgejetti	MZUTI 5411	Ecuador	Manabí	Cabuyal	-0.19698	-80.29059	15
D. georgejetti	QCAZ 10589	Ecuador	Manabí	El Aromo	-1.04665	-80.83276	295
D. georgejetti	DHMECN 11639	Ecuador	Manabí	Montecristi	-1.04694	-80.65766	136
D. georgejetti	MZUA.RE.0121	Ecuador	Manabí	El Aromo	-1.04665	-80.83276	295
D. georgejetti	MZUA.RE.0122	Ecuador	Manabí	El Aromo	-1.04665	-80.83276	295
D. georgejetti	DHMECN 11646	Ecuador	Manabí	Rocafuerte	-0.92371	-80.45212	19
D. georgejetti	ZSFQ D606	Ecuador	Manabí	Cerro La Mocora, foothill	-1.59817	-80.65431	308
D. oligozonata	MZUA.RE.0081	Ecuador	Azuay	Girón	-3.15891	-79.14755	2102
D. oligozonata	QCAZ 4472	Ecuador	Azuay	Granja Orgánica Susudel	-3.38885	-79.17847	2802
D. oligozonata	QCAZ 4492	Ecuador	Azuay	Susudel	-3.40543	-79.18378	2376
D. oligozonata	MZUA.RE.0240	Ecuador	Azuay	Via a Shaglli	-3.19178	-79.39623	2891
D. oligozonata	MZUA.RE.0020	Ecuador	–	–	–	–	–
D. oligozonata	MZUA.RE.0357	Ecuador	–	–	–	–	–
D. oreas	QCAZ 10140	Ecuador	Azuay	Luz María	-2.68548	-79.40992	1661
D. oreas	DHMECN 3478	Ecuador	Azuay	Naranjo Lanto	-2.92628	-79.39963	1847
D. oreas	DHMECN 7647	Ecuador	Azuay	Reserva Biológica Yunguilla	-3.22684	-79.27520	1748
D. oreas	DHMECN 7666	Ecuador	Azuay	Reserva Biológica Yunguilla	-3.22684	-79.27520	1748
D. oreas	MZUA.RE.0239	Ecuador	Azuay	San Rafael de Sharug	-3.27311	-79.54543	1593
D. oreas	MZUA.RE.0290	Ecuador	Azuay	San Rafael de Sharug	-3.27311	-79.54543	1593
D. oreas	QCAZ 9190	Ecuador	Azuay	Vía La Paz–Cuenca	-3.09021	-79.00800	2726
D. oreas	USNM 62797	Ecuador	Chimborazo	Pallatanga–Guayaquil	-2.07459	-78.98123	1404
D. oreas	USNM 62798	Ecuador	Chimborazo	Pallatanga–Guayaquil	-2.07459	-78.98123	1404
D. oreas	USNM 62800	Ecuador	Chimborazo	Pallatanga–Guayaquil	-2.07459	-78.98123	1404
D. oreas	DHMECN 10785	Ecuador	El Oro	Playa Limón	-3.50096	-79.74701	816
D. oreas	DHMECN 2572	Ecuador	El Oro	Reserva Buenaventura	-3.65467	-79.76794	524

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. oreas	MZUTI 3351	Ecuador	El Oro	Reserva Buenaventura	-3.64882	-79.75640	898
D. oreas	MZUTI 5415	Ecuador	El Oro	Reserva Buenaventura	-3.63432	-79.74985	1048
D. oreas	MZUTI 5418	Ecuador	El Oro	Reserva Buenaventura	-3.63370	-79.75040	1068
D. oreas	MHNG 2514.028	Ecuador	Loja	33 km E San Pedro	-3.97222	-79.25983	2493
D. oreas	MHNG 2521.084	Ecuador	Loja	6 km S Loja	-4.03770	-79.19975	2144
D. oreas	QCAZ 10068	Ecuador	Loja	Cazerío Balzones	-4.01502	-80.01635	1346
D. oreas	QCAZ 13875	Ecuador	Loja	Jimbura	-4.66668	-79.45322	2513
D. oreas	QCAZ 11290	Ecuador	Loja	Vía al Cerro Toledo	-4.38444	-79.15992	2214
D. oreas	QCAZ 678	Ecuador	Loja	Vilcabamba	-4.25792	-79.21962	1546
D. oreas	QCAZ 6020	Ecuador	Loja	Yangana–Vilcabamba	-4.32455	-79.20041	1742
D. palmeri	QCAZ 11411	Ecuador	Morona Santiago	9 de Octubre–Macas	-2.21820	-78.29920	1767
D. palmeri	QCAZ 5609	Ecuador	Morona Santiago	Chiguinda	-3.28125	-78.69829	2223
D. palmeri	DHMECN 11197	Ecuador	Morona Santiago	Concesión ECSA	-3.57524	-78.43609	1211
D. palmeri	QCAZ 13307	Ecuador	Morona Santiago	Laguna Chimerella	-2.07956	-78.20338	1795
D. palmeri	QCAZ 13304	Ecuador	Morona Santiago	Laguna Cormorán	-2.07153	-78.21590	1747
D. palmeri	QCAZ 13562	Ecuador	Pastaza	Tzarentza	-1.35696	-78.05814	1355
D. palmeri	QCAZ 4710	Ecuador	Tungurahua	3 km E Río Verde	-1.40249	-78.28369	1474
D. palmeri	AMNH 24126	Ecuador	Tungurahua	Abitagua	-1.41667	-78.16667	1353
D. palmeri	MZUTI 4804	Ecuador	Tungurahua	Agoyán	-1.39795	-78.38415	1661
D. palmeri	MZUA.RE.0044	Ecuador	Tungurahua	Baños	-1.39650	-78.42945	1847
D. palmeri	QCAZ 14071	Ecuador	Tungurahua	Baños	-1.39650	-78.42945	1847
D. palmeri	QCAZ 3288	Ecuador	Tungurahua	Baños	-1.39650	-78.42945	1847
D. palmeri	QCAZ 4710	Ecuador	Tungurahua	Caserío Machay	-1.40062	-78.28085	1531
D. palmeri	DHMECN 9229	Ecuador	Tungurahua	Chamanapamba	-1.40114	-78.39975	1808
D. palmeri	DHMECN 9230	Ecuador	Tungurahua	Chamanapamba	-1.40114	-78.39975	1808
D. palmeri	MZUTI 3956	Ecuador	Tungurahua	La Candelaria	-1.43051	-78.31246	1920
D. palmeri	AMNH 37939	Ecuador	Tungurahua	Palmera	-1.41613	-78.19663	1225
D. palmeri	DHMECN 9232	Ecuador	Tungurahua	Parque Juan Montalvo	-1.40005	-78.42070	1803
D. palmeri	QCAZ 13992	Ecuador	Tungurahua	Río Verde	-1.39406	-78.30405	1603
D. palmeri	QCAZ 4564	Ecuador	Tungurahua	Río Verde	-1.39406	-78.30405	1603

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. palmeri	DHMECN 12841	Ecuador	Tungurahua	Ulba	-1.39622	-78.39418	1702
D. palmeri	DHMECN 9219	Ecuador	Tungurahua	Vizcaya	-1.34789	-78.40518	2282
D. palmeri	QCAZ 6021	Ecuador	Zamora Chinchipe	18.2 km W Zamora	-3.97643	-79.02075	1609
D. palmeri	QCAZ 3001	Ecuador	Zamora Chinchipe	182 km Zamora–Loja	-3.95600	-79.02599	1665
D. palmeri	QCAZ 14338	Ecuador	Zamora Chinchipe	Estación San Francisco	-3.96128	-79.05556	1775
D. palmeri	QCAZ 12771	Ecuador	Zamora Chinchipe	Reserva Numbami	-4.17233	-78.95928	1615
D. palmeri	MZUTI 4971	Ecuador	Zamora Chinchipe	Reserva San Francisco	-3.97051	-79.07814	1850
D. palmeri	MZUTI 4975	Ecuador	Zamora Chinchipe	Reserva San Francisco	-3.97140	-79.07909	1730
D. palmeri	QCAZ 12772	Ecuador	Zamora Chinchipe	Reserva San Francisco	-3.97051	-79.07814	1850
D. palmeri	MZUTI 5419*	Ecuador	Zamora Chinchipe	Romerillos Alto	-4.23230	-78.94222	1547
D. palmeri	QCAZ 12510	Ecuador	Zamora Chinchipe	Zumba	-4.86517	-79.13384	1230
D. palmeri	MZUA.RE.0119	Ecuador	–	–	–	–	–
D. palmeri	BMNH 1946.1.2077	Peru	Cajamarca	Jaén	-5.72978	-78.84836	1438
D. palmeri	MCZ 17404	Peru	Cajamarca	Tabaconas	-5.31429	-79.29622	1892
D. pavonina	MZUA.RE.0198	Ecuador	Morona Santiago	Kushapuk	-3.04373	-78.03648	326
D. pavonina	QCAZ 5554	Ecuador	Morona Santiago	Tiink	-3.34389	-78.46805	730
D. pavonina	MHNG 2309.039	Ecuador	Napo	Archidona	-0.90856	-77.80814	571
D. pavonina	MHNG 2521.088	Ecuador	Napo	Tena	-0.98330	-77.81670	522
D. pavonina	MZUTI 4972	Ecuador	Zamora Chinchipe	Maycu	-4.38030	-78.74584	981
D. peruana	LSUMZ 27372	Peru	Amazonas	28 km SE Ingenio	-6.05753	-77.98919	2235
D. peruana	KU 212590	Peru	Amazonas	Pomacochas	-5.82155	-77.91692	2150
D. peruana	MCZ 178175	Peru	Cuzco	Amaibamba	-13.27703	-73.28636	1858
D. peruana	LSUMZ 27369–70	Peru	Cuzco	Bosque Aputinye	-12.92300	-72.67455	1502
D. peruana	KU 117109	Peru	Cuzco	Machu Picchu	-13.17104	-72.50585	2400
D. peruana	AMNH 147037	Peru	Cuzco	Paucartambo Mirador	-13.06972	-71.55527	1818
D. peruana	AMNH 147037	Peru	Cuzco	Paucartambo Mirador	-13.06972	-71.55527	1810
D. peruana	USNM 60718	Peru	Cuzco	Pucyura	-13.07450	-72.93437	2666
D. peruana	CORBIDI 11839	Peru	Cuzco	Rocotal	-13.10627	-71.57064	2004
D. peruana	SMF 20801	Peru	Cuzco	Santa Ana	-12.86755	-72.71670	1639
D. peruana	LSUMZ 45499	Peru	Huánuco	Playa Pampa	-9.95160	-75.69605	2091
D. peruana	BMNH 1946.1.2078	Peru	Pasco	Huancabamba	-10.42265	-75.51718	1775

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
D. peruana	USNM 299232	Peru	Puno	10 km NNE Ollachea	-13.78330	-70.46730	2598
D. peruana	USNM 299234	Peru	Puno	11 km NNE Ollachea	-13.78661	-70.47248	2601
D. peruana	USNM 299233	Peru	Puno	12 km NNE Ollachea	-13.78330	-70.46730	2598
D. peruana	AMNH 52444	Peru	San Martín	Cumbre Ushpayacu-Mishquiyacu	-6.99468	-76.03371	1279
D. temporalis	MZUTI 3331	Ecuador	Esmeraldas	Tundaloma Lodge	1.18317	-78.75245	74
D. temporalis	MHNG 2521.083	Ecuador	Imbabura	16 km W Lita	0.90235	-78.54504	799
D. vagrans	AMNH 63373	Peru	San Martín	Bellavista	-7.05346	-76.58928	316
D. vermiculata	MHNG 2521.085	Ecuador	Morona Santiago	69 km S Vilcabamba	-4.84920	-79.12731	1310
D. vermiculata	DHMECN 11197	Ecuador	Morona Santiago	Concesión ECSA	-3.57245	-78.46982	790
D. vermiculata	MHNG 2436.014	Ecuador	Napo	El Reventador	-0.04480	-77.52858	1476
D. vermiculata	MZUTI 5080	Ecuador	Pastaza	Kallana	-1.469629	-77.27838	325
D. vermiculata	QCAZ 13825	Ecuador	Pastaza	Sendero Higuerones	-4.11464	-78.96702	981
D. vermiculata	MZUTI 4738	Ecuador	Pastaza	Tzarentza	-1.35696	-78.05814	1355
D. vermiculata	MZUTI 3663	Ecuador	Zamora Chinchipe	Maycu	-4.20719	-78.63987	869
D. vermiculata	MZUA.RE.0261	Ecuador	Zamora Chinchipe	Nangaritza	-4.43169	-78.63869	1011
D. oswaldobaezi	QCAZ 14051	Ecuador	El Oro	Arenillas	-3.62110	-80.17513	41
D. oswaldobaezi	QCAZ 14060	Ecuador	El Oro	Guabillo	-3.60346	-80.18139	44
D. oswaldobaezi	MZUA.RE.0286	Ecuador	El Oro	Huaquillas	-3.54115	-80.08646	39
D. oswaldobaezi	QCAZ 10369	Ecuador	Loja	Quebrada El Faique	-4.17889	-80.04226	1004
D. oswaldobaezi	QCAZ 15108	Ecuador	Loja	Reserva La Ceiba-Pilares	-4.27502	-80.32805	534
D. oswaldobaezi	BMNH1935.11.3.108	Ecuador	Loja	Catamayo	-3.98064	-79.35928	1289
D. oswaldobaezi	MUSM 2192	Peru	Piura	Piura	-5.17882	-80.62231	32
S. annulatus	MZUTI 3034	Ecuador	Esmeraldas	Reserva Itapoa	0.51307	-79.13401	321
S. bevridgelyi	MZUA.RE.0424	Ecuador	Azuay	2 km N Palmales Nuevo	-3.65158	-80.09625	129
S. bevridgelyi	KU 152205	Ecuador	Azuay	30 KM E Pasaje	-3.31439	-79.57970	561
S. bevridgelyi	QCAZ 14446	Ecuador	Azuay	Ponce Enríquez–El Coca	-3.03197	-79.64615	1206
S. bevridgelyi	QCAZ 14444	Ecuador	Azuay	Proyecto Minas San Francisco	-3.30829	-79.47079	862
S. bevridgelyi	MZUA.RE.0142	Ecuador	Azuay	Sarayunga	-3.31431	-79.58069	552
S. bevridgelyi	MCZ R-17099	Ecuador	Chimborazo	Valle del Chanchán	-2.27383	-79.08735	697
S. bevridgelyi	DHMECN 11526	Ecuador	El Oro	Remolino	-3.56551	-79.91948	229
S. bevridgelyi	DHMECN 9483	Ecuador	El Oro	Reserva Buenaventura	-3.65467	-79.76794	524

Species	Voucher	Country	Province	Locality	Latitude	Longitude	Elev. (m)
S. bevridgelyi	MZUTI 3269	Ecuador	El Oro	Reserva Buenaventura	-3.65343	-79.76722	473
S. bevridgelyi	MZUTI 5416	Ecuador	El Oro	Reserva Buenaventura	-3.65467	-79.76794	524
S. bevridgelyi	AMNH 22092	Ecuador	Guayas	Reserva Ayampe	-1.65417	-80.81833	43
S. bevridgelyi	MCZ R-3564	Ecuador	Guayas	Río Daule	-1.87009	-80.00539	5
S. bevridgelyi	MZUA.RE.0328	Ecuador	Los Ríos	Jauneche	-1.33333	-79.58333	41
S. bevridgelyi	DHMECN 8976	Ecuador	Manabí	San Sebastián	-1.60002	-80.69974	602
S. bevridgelyi	DHMECN 10061	Ecuador	Manabí	Puerto López	-1.55598	-80.81200	3
S. bevridgelyi	ZSFQ D503	Ecuador	Manabí	Cerro La Mocora, tophill	-1.60379	-80.70191	818
S. bevridgelyi	CORBIDI 3791	Peru	Tumbes	El Caucho	-3.81438	-80.27101	379
S. bevridgelyi	CORBIDI 3792	Peru	Tumbes	El Caucho	-3.81438	-80.27101	379
S. bevridgelyi	CORBIDI 7894	Peru	Tumbes	El Caucho	-3.81844	-80.26856	478
S. bevridgelyi	CORBIDI 7994	Peru	Tumbes	El Caucho	-3.81244	-80.26716	481
S. nebulatus	MZUTI 4810	Ecuador	Cotopaxi	El Jardín de los Sueños	-0.83142	-79.21337	349
S. nebulatus	DHMECN 9585	Ecuador	Esmeraldas	Canandé	0.52580	-79.20880	310
S. nebulatus	DHMECN 5645	Ecuador	Esmeraldas	Lita–San Lorenzo	1.18236	-78.79528	42
S. nebulatus	MZUTI 3911	Ecuador	Esmeraldas	Reserva Itapoa	0.51307	-79.13401	321
S. nebulatus	DHMECN 5647	Ecuador	Esmeraldas	Tundaloma	1.18236	-78.75250	74
S. nebulatus	DHMECN 10312	Ecuador	Imbabura	Selva Alegre	0.26667	-78.58333	1299
S. nebulatus	USNM 285501	Ecuador	Los Ríos	Hacienda Cerro Chico	-0.62444	-79.42940	170
S. nebulatus	MZUA.RE.0174	Ecuador	Los Ríos	Macul	-1.12980	-79.65730	65
S. nebulatus	USNM 285498	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
S. nebulatus	USNM 285499	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
S. nebulatus	USNM 285500	Ecuador	Los Ríos	Río Palenque	-0.58333	-79.36667	173
S. nebulatus	DHMECN 2882	Ecuador	Manabí	Aguacate	0.65348	-80.05190	43
S. nebulatus	MZUTI 5342	Ecuador	Manabí	Jama Coaque	-0.11556	-80.12472	299
S. nebulatus	DHMECN 1704	Ecuador	Pichincha	Curipogio	0.13112	-78.67632	1171
S. nebulatus	USNM 283534	Ecuador	Santo Domingo	Rancho Santa Teresita	-0.25277	-79.37946	288

Eight *Sibynomorphus* species were included in the molecular analyses. These are *S. mikanii*, *S. neuwiedi*, *S. oligozonatus*, *S. petersi*, *S. turgidus*, *S. vagus*, *S. ventrimaculatus*, and *S. williamsi*. In the ML analysis, all of them are nested within different *Dipsas* subclades, whereas in the BI analysis, the clade containing *S. mikanii* and *S. turgidus* is not nested within *Dipsas*. Crucially, *Dipsas mikanii* Schlegel, 1837 is the type species of *Sibynomorphus* (Fitzinger, 1843). Thus, we synonymize *Sibynomorphus* with *Dipsas* primarily based on the ML analysis, which mirrors the results of Sheehy (2012).

Based on our transfer of the genus *Sibynomorphus* Fitzinger to the synonymy of *Dipsas*, we propose the following binomial nomenclature for the eleven species traditionally included in the genus *Sibynomorphus*: *Dipsas lavillai* comb. n., *D. mikanii*, *D. neuwiedi* comb. n., *D. oligozonata* comb. nov., *D. oneilli* comb. n., *D. turgida* comb. nov., *D. vagrans* comb. n., *D. vaga* comb. n., *D. ventrimaculata* comb. n., and *D. williamsi* comb. n. However, we refrain from applying *D.* "*petersi*" for *Sibynomorphus petersi* here, because the name *Dipsas* "*indica*" *petersi* (Hoge & Romano, 1975), another taxon and putative species from southeastern Brazil, is often already named as *Dipsas petersi* (e.g., Centeno et al. 2008, Wallach et al. 2014), and this name predates *Sibynomorphus petersi* (Orces & Almendáriz, 1989). Therefore, the latter is now a secondary junior homonym in conflict upon transfer to *Dipsas* Laurenti, and thus requires a replacement name. We therefore erect the name *Dipsas jamespetersi*, which still honors James A. Peters, for the taxon *Sibynomorphus petersi* Orces & Almendariz, 1989.

There are several clades within *Dipsas peruana* sensu lato. One is *D. peruana*, the other is a new species from northern Ecuador, which we describe below, and the third is the lineage corresponding to the population distributed along the Amazonian slopes of the Andes between central Ecuador and northern Peru. Below, we resurrect the name *D. palmeri* (Boulenger, 1912) for this lineage, as the type locality of *D. palmeri* (El Topo, province of Tungurahua, Ecuador) is located within the geographic range of the included samples (Fig. 4) and the holotype agrees in coloration and lepidosis with other specimens (Appendix 3) in the same region that were included in the genetic analyses.

Dipsas oligozonata is the strongly supported sister lineage of a clade that includes three species: *D. williamsi* and two new species from western Ecuador and northern Peru, which we describe below. *Dipsas indica* is paraphyletic with respect to *D. bucephala*. *Dipsas jamespetersi* is paraphyletic with respect to a sample of *D. vaga* (KU 219121).

Based on the species included in the phylogenetic analysis, the *Dipsas articulata* and *D. indica* groups, sensu Harvey 2008 (Table 1), are recovered as monophyletic. The other groups included in the phylogenetic analysis (i.e., *catesbyi*, *oreas*, *pratti*, *temporalis* and *variegata*) are not monophyletic. The two included members of the *D. catesbyi* group (i.e., *D. catesbyi* and *D. pavonina*) are not sister taxa. The included members of the *Dipsas oreas* group form a paraphyletic unit, because besides including *D. elegans*, *D. ellipsifera*, and *D. oreas*, this group also includes *D. andiana*, a species that was considered a member of the *D. variegata* group (Harvey 2008, and Table 1). Accordingly, we transfer *D. andiana* to the *D. oreas* group. The two included members of the *D. pratti* group (i.e., *D. peruana* and *D. pratti*) are placed in different branches of the phylogeny. The same is true for the included members of the *D. temporalis* group (i.e., *D temporalis* and *D. vermiculata*), whereby *D. vermiculata* clusters with *D. variegata*, and accordingly we move it into that group. We refrain from merging the *Dipsas temporalis* and *D. pratti* groups because we did not examine the specimens of *D. pratti* included in the analysis (MHUA 14278). We also refrain from assigning further species groups until a more complete taxon sampling is made available.

New records for Ecuador

One individual (Fig. 1v) of *Dipsas variegata* photographed (not collected) at Gareno Lodge, province of Napo (S1.03559, W77.39864; 336 m), represents the first record of this species in Ecuador (Fig. 4). This individual agrees in coloration with the description of the species provided by Cadle and Myers (2003) and Mebert et al. (submitted), including dorso-lateral blotches/saddles resembling vertically stretched rhomboids or bars, often with a light center or spots, border of blotches being zig-zag shaped and following the outline of adjacent dorsal scales, variably numbered and shaped spots in the interspaces, cephalic blotches lacking yellow borders, and a light-colored eye. It shows also the typical truncated head (see Peters 1960 for description of head truncation) of *D. variegata*, in particular the short, but high preorbital region including an upturned chin, a convex supraocular, narrow and vertically elongated anterior labials (here 2nd–6th supralabials), and 15 dorsal scale rows. This *D. variegata* expands the known distribution 1,186 km SW from the nearest localities along the Venezuelan Andes (Natera-Mumaw et al. 2015) and 1,343 km NW from the nearest locality in southeastern Peru (Catenazzi et al. 2013).

Systematic accounts

We seek here to name or provide re-descriptions only for species that are monophyletic in our molecular phylogeny and share diagnostic features of their coloration pattern and lepidosis. Based on these species delimitation criteria, which follow the general species concept of de Queiroz (2007), we describe four new *Dipsas*, one new *Sibon* and revalidate *D. palmeri* and *D. latifrontalis*.

***Sibon bevridgelyi* sp. n.**

http://zoobank.org/E98CD0B9-A101-4693-9529-0AC2134DFECE
Figs 2b, 6, 7

Proposed standard English name. Bev Ridgely's Snail-Eater

Proposed standard Spanish name. Caracolera de Bev Ridgely

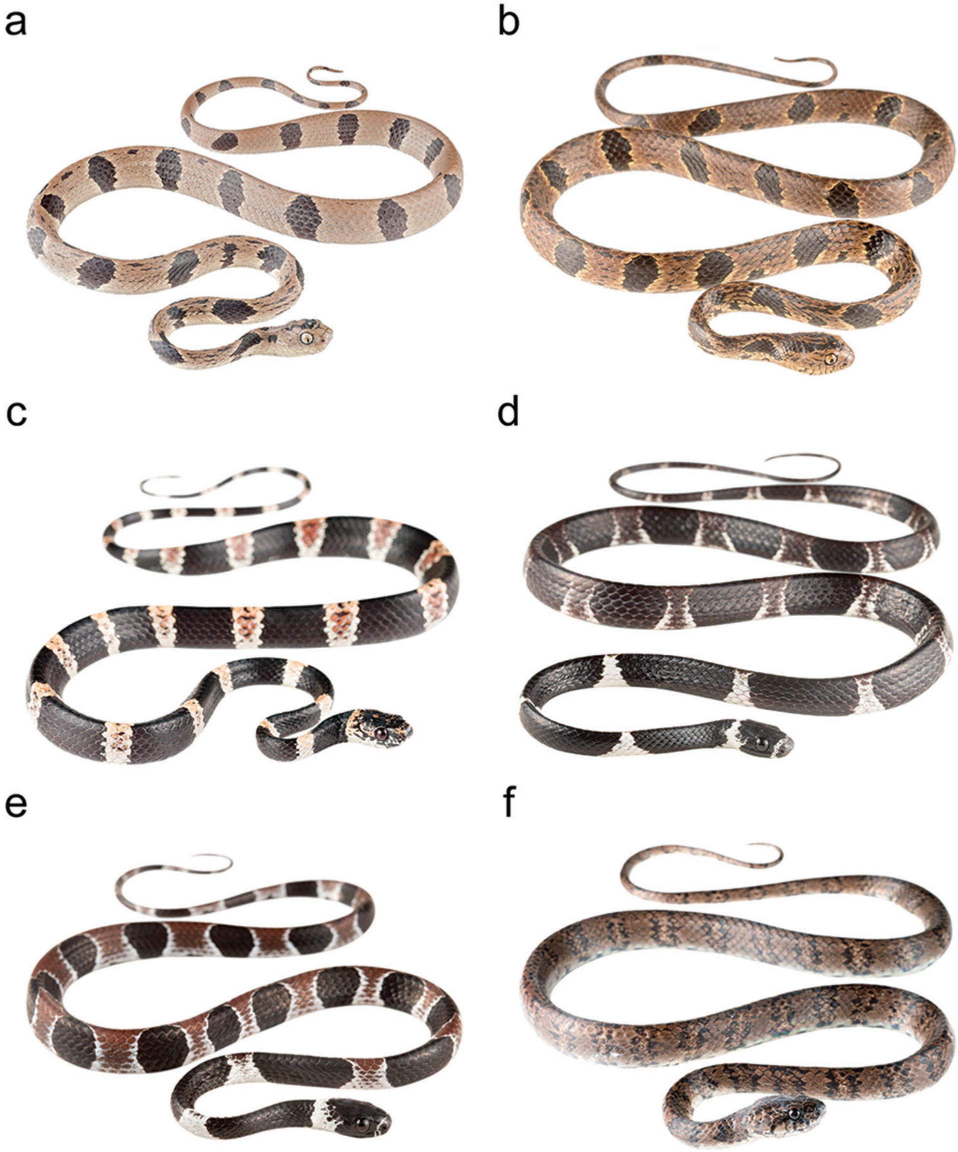

Figure 1. Photographs of some species of *Dipsas* in life: **a** *D. andiana* MZUTI 5413 from Bilsa, province of Esmeraldas, Ecuador **b** *D. andiana* from Mindo, province of Pichincha, Ecuador **c** *D. bobridgelyi* MZUTI 5414 from Buenaventura, Province of El Oro, Ecuador **d** *D. catesbyi* from Gareno, province of Napo, Ecuador **e** *D. catesbyi* from Gareno, province of Napo, Ecuador **f** *D. elegans* from Calacalí–Mindo, province of Pichincha, Ecuador.

Holotype. MZUTI 5416 (Figs 6, 7), adult male collected by Matthijs Hollanders on August 01, 2017 at Reserva Buenaventura, province of El Oro, Ecuador (S3.65467, W79.76794; 524 m).

Figure 1. Continued: **g** *D. ellipsifera* from Pimampiro, province of Imbabura, Ecuador **h** *D. gracilis* from Canandé, province of Esmeraldas, Ecuador **i** *D. gracilis* from Mashpi, province of Pichincha, Ecuador **j** *D. indica* from Gareno, province of Napo, Ecuador **k** *D. jamespetersi* AMARU 1123 from province of Azuay, Ecuador **l** *D. klebbai* from El Chaco, province of Napo, Ecuador.

Paratypes. AMNH 22092, adult male collected by George H. Tate on December 01, 1921 at Bucay, province of Guayas, Ecuador (S2.19788, W79.12909; 433 m). CORBIDI 3791, adult male collected by Pablo Venegas and Caroll Landauro on May 07, 2009 at El Caucho, department of Tumbes, Peru (S3.81438, W80.27101; 379 m). CORBIDI

Figure 1. Continued: **m** *D. klebbai* from El Chaco, province of Napo, Ecuador **n** *D. latifrontalis* from San Isidro, state of Mérida, Venezuela **o** *D. oligozonata* from Poetate, province of Azuay, Ecuador **p** *D. oreas* MZUTI 5414 from Buenaventura, province of El Oro, Ecuador **q** *D. oreas* from Poetate–Corraleja, province of Azuay, Ecuador **r** *D. palmeri* from Agoyán, province of Tungurahua, Ecuador.

3792, adult female collected by Pablo Venegas and Caroll Landauro on May 07, 2009 at El Caucho, department of Tumbes, Peru (S3.81438, W80.27101, 379 m). CORBIDI 7894, adult female collected by Vilma Durán and Germán Chávez on October 21, 2010 at El Caucho, department of Tumbes, Peru (S3.81844, W80.26856; 478 m). CORBIDI

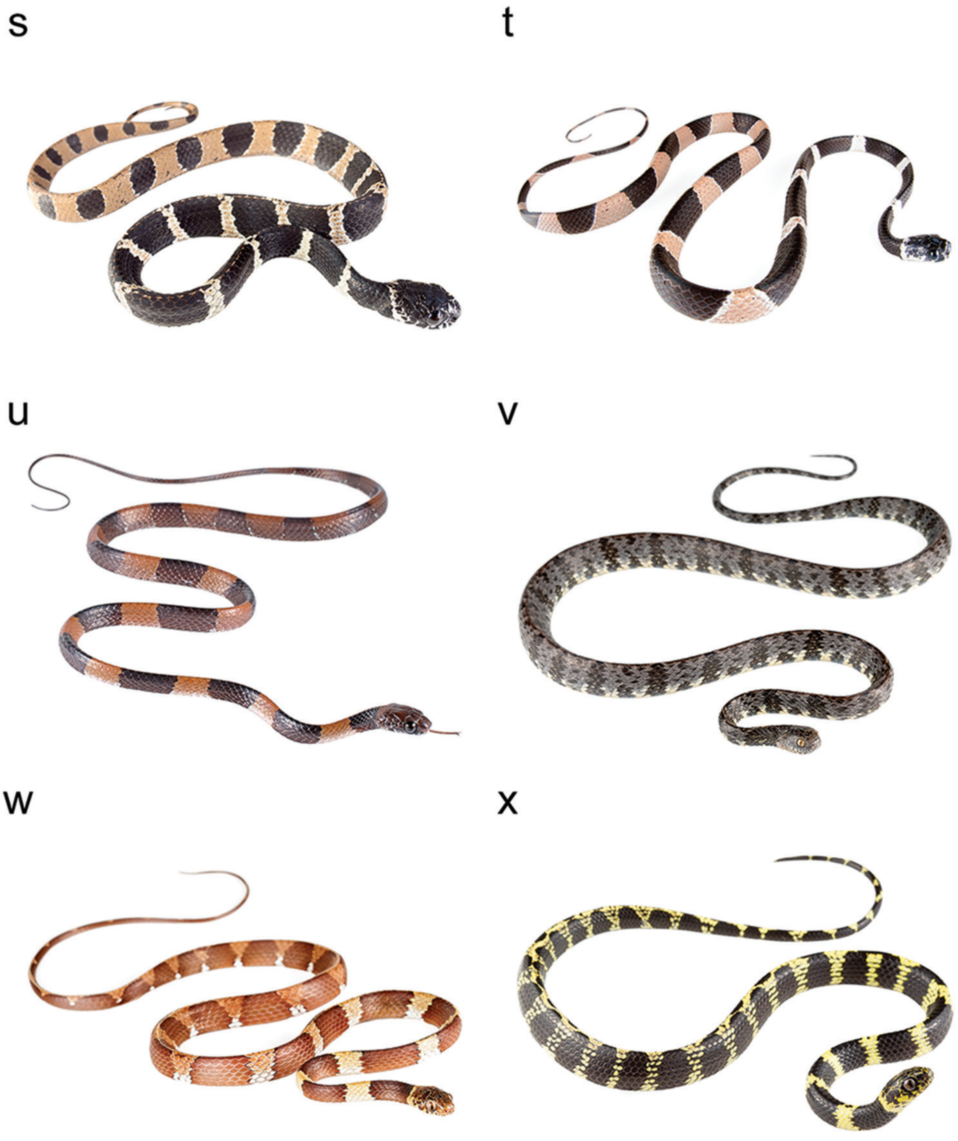

Figure 1. Continued: **s** *D. palmeri* MZUTI 4975 from Reserva San Francisco, province of Zamora, Ecuador **t** *D. pavonina* from Maycu, province of Zamora, Ecuador **u** *D. temporalis* from Colombia **v** *D. variegata* from Gareno, province of Napo, Ecuador **w** *D. vermiculata* from Miazi, province of Zamora, Ecuador, and **x** *D. vermiculata* from Narupa, province of Napo, Ecuador.

7994, adult female collected by Pablo Venegas on September 24, 2010 at El Caucho, department of Tumbes, Peru (S3.81244, W80.26716; 481 m). DHMECN 8976, juvenile collected by Michael Harvey and Luis A. Oyagata at Cerro San Sebastián, Parque Na-

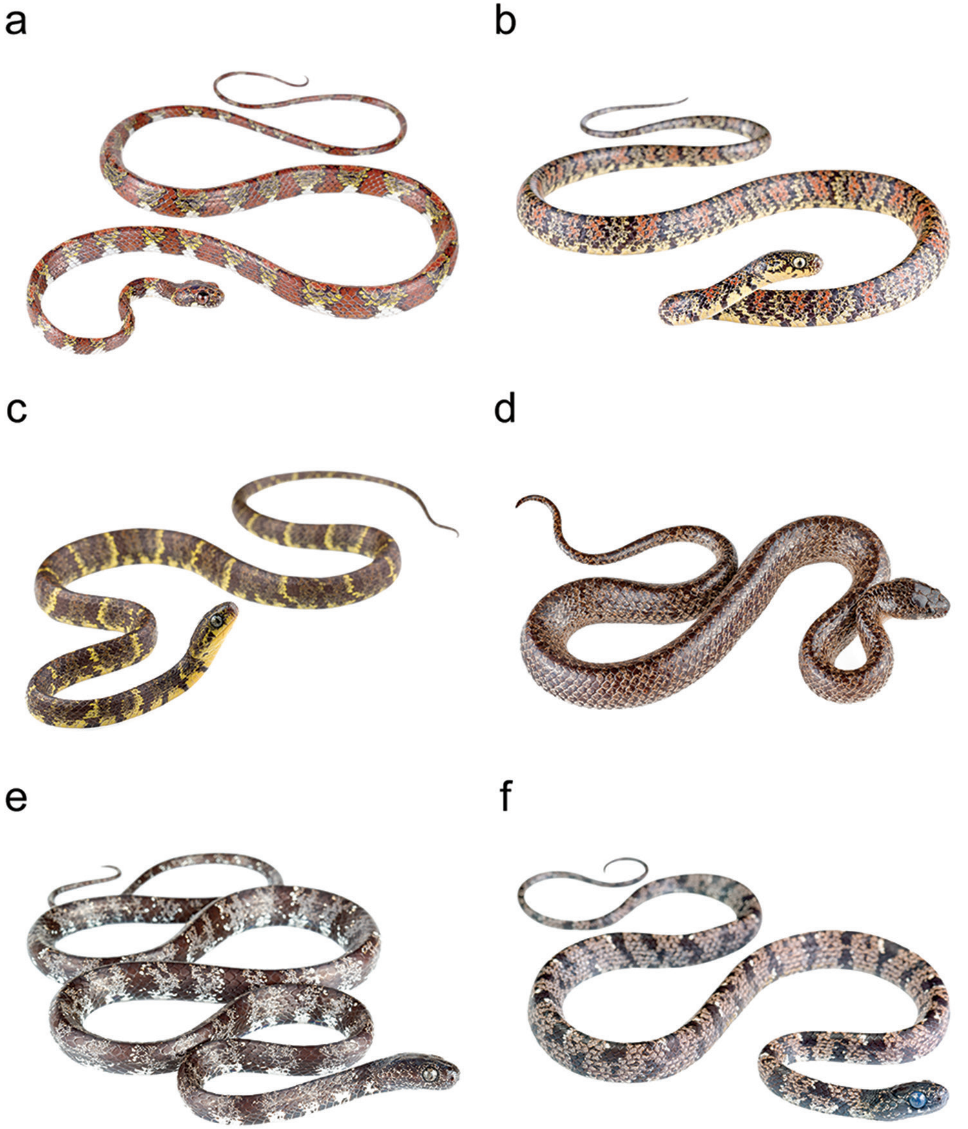

Figure 2. Photographs of some species of *Sibon* in life: **a** *S. annulatus* from Verdecanandé, province of Esmeraldas, Ecuador **b** *Sibon bevridgelyi* MZUA.RE.0424 from Palmales Nuevo, province of El Oro, Ecuador **c** *S. bevridgelyi* MZUTI 3269 from Buenaventura, province of El Oro, Ecuador **d** *S. dunni* CAMPO 533 from Pimampiro, province of Imbabura, Ecuador **e** *S. nebulatus* from Milpe, province of Pichincha, Ecuador, and **f** *S. nebulatus* from Canandé, province of Esmeraldas, Ecuador.

cional Machalilla, province of Manabí, Ecuador (S1.60002, W80.69974, 602 m). DHMECN 9483, adult male collected by Mario Yánez-Muñoz, María Pérez, Miguel Alcoser, Marco Reyes-Puig and Gabriela Bautista in 2012 at the type locality. DHMECN 10061, adult male collected by Manuel Morales, María Perez Lara and Karem López at Reserva Biológica Ayampe, province of Manabí, Ecuador (S1.65417, W80.81333; 43 m). DH-

Figure 3. Phylogenetic relationships within Dipsadini derived from analysis of 3,375 bp of DNA (gene fragments 12S, 16S, Cytb, ND4 and c-mos). Support values on intraspecic branches are not shown for clarity. Voucher numbers for sequences are indicated for each terminal when available. **a** Maximum likelihood analysis. Black dots indicate clades with bootstrap values from 90–100%. Grey dots indicate values from 70–89%. White dots indicate values from 50–69% (values <50% not shown).

MECN 11526, adult of undetermined sex collected by Juan Carlos Sánchez-Nivicela, Karem López, Verónica Urgilés, Bruno Timbe, Elvis Celi and Valentina Posse at Remolino, province of El Oro, Ecuador (S3.56551, W79.91948; 229 m). KU 152205, adult of undetermined sex collected at 30 km E Pasaje, province of Azuay, Ecuador (S3.31439, W79.57970; 561 m). MCZ R-17099, a juvenile of undetermined sex collected at Valle del Chanchán, province of Chimborazo, Ecuador (S2.27383, W79.08735; 697 m). MCZ R-3564, a juvenile of undetermined sex collected by Samuel Walton Garman on January 1, 1875 at Daule River, province of Guayas, Ecuador (S1.87009, W80.00530; 5

Figure 3. Continued. **b** Bayesian inference analysis. Black dots indicate clades with posterior probability values from 95–100%. Grey dots indicate values from 70–94%. White dots indicate values from 50–69% (values <50% not shown).

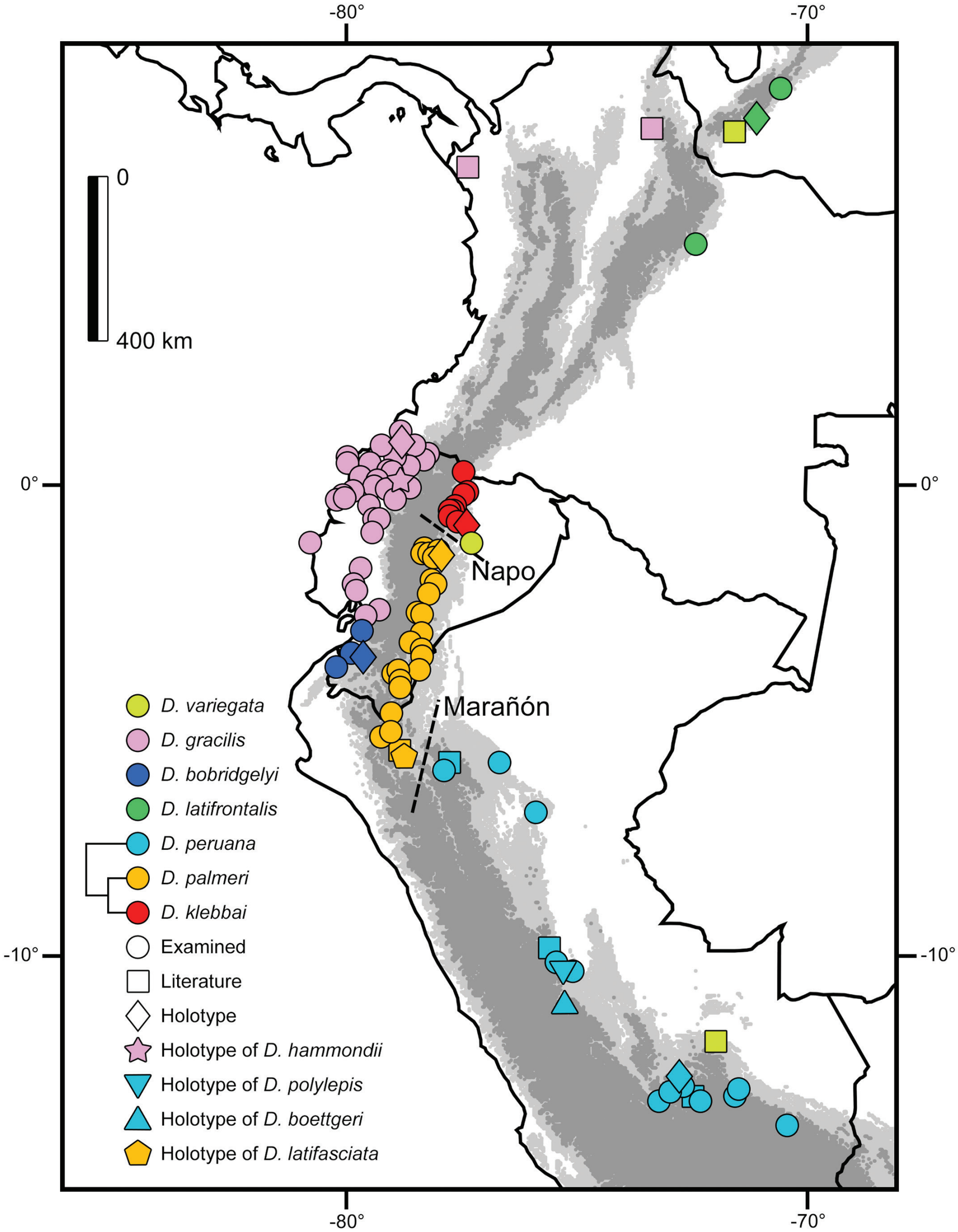

Figure 4. Distribution of various species of *Dipsas*, and potential geographical barriers between taxa.

m). MZUA.RE.0142, adult female collected by Jose Manuel Falcón at Sarayunga, province of Azuay, Ecuador (S3.31431, W79.58069; 552 m). MZUA.RE.0328, adult male collected by Keyko Cruz on April 04, 2016 at Jauneche, province of Los Ríos, Ecuador (S1.33333, W79.58333; 41 m). MZUA.RE.0424, adult male collected by Fausto Siavichay, Valentina Posse and Xavier Clavijo on June 29, 2017 at 2 km N Palmales Nuevo, province of El Oro, Ecuador (S3.65158, W80.09625; 129 m). MZUTI 3269, adult male collected by Lucas Bustamante on November 07, 2013 at the type locality. QCAZ 14444, adult male collected by Fernando Ayala, Steven Poe and Chris Anderson on January 10, 2016 at Proyecto Minas San Francisco, province of Azuay, Ecuador (S3.30829, W79.47079; 862 m). QCAZ 14446, adult male collected by Fernando Ayala, Steven Poe and Chris Anderson on January 10, 2016 at Ponce Enríquez–El Coca, province of Azuay, Ecuador (S3.03197, W79.64615; 1206 m). ZSFQ D503, adult male collected by Diego Cisneros-Heredia on June 07, 2000 at Cerro La Mocora, Parque Nacional Machalilla, province of Manabí, Ecuador (S1.60379, W80.70191; 818 m).

Diagnosis. *Sibon bevridgelyi* is placed in the genus *Sibon* based on phylogenetic evidence (Fig. 3) and on having the labial beneath primary temporal conspicuosly higher than other labials. The species differs from all described species of *Sibon* based on the following combination of characters: (1) 15/15/15 smooth dorsals with enlarged vertebral row (1.3–1.7 times as wide as adjacent rows); (2) seven supralabials with 4th and 5th contacting orbit or eight supralabials with 5th and 6th contacting orbit; (3) one pair of infralabials in contact behind symphysial; (4) postmental absent; (5) 175–193 ventrals in males, 193 in the single female; (6) 80–94 divided subcaudals in males, 98 in the single female; (7) dorsal and ventral ground color pale yellow with or without irregular black bands, and with a black stippled disruptive pattern of irregular rusty to reddish brown blotches that are separated from each other by light interspaces (Figs 6, 2b, c); bands incomplete and stippling not prominent or absent on ventral surfaces; head heavily speckled or blotched with black or rusty pigment; eyes light slate blue to pale goldenrod with black speckles and reticulations; (8) 349–732 mm SVL in males, 786 mm in the single female; (9) 124–268 mm TL in males, 204 mm in the single female.

Comparisons. *Sibon bevridgelyi* is most similar to *S. nebulatus*, from which it differs on the basis of its distinctive coloration (Figs 6, 2b, c). In *S. nebulatus* (Figs 2e, f), the dorsal and ventral color is a combination of mainly black to dark-brown blotches or bands on a gray to grayish brown background (interblotch) color; the dorso-lateral blotches can partly be bordered by white to rosy scales or edges. In some regions, the blackish pattern and gray ground color is often replaced by dark and light brown tones (e.g., in Venezuela, adjacent regions in Colombia, and Trinidad and Tobago); the spaces between the blotches are heavily invaded by blotch color and strongly stippled, spotted and mottled with white and black pigment. Although *S. bevridgelyi* also has a disruptive pattern, the diagnostic white and gray pigment of *S. nebulatus* from Central America and northern South America is lacking in *S. bevridgelyi*. Instead of white pigment, there is golden yellow; instead of gray, the dominant ground color is bright rusty brown to maroon. Additionally, the infralabials and the whitish throat in *S. nebulatus* from Central America and northern South America are heavily stippled or at least partly interrupted with black pigment, whereas in *S. bevridgelyi* the infralabials and the throat are immaculate or have few scattered blotches (Fig. 7b). Finally, the black blotches and stippling diagnostic of *S. nebulatus* are lacking in the majority of the specimens of *S. bevridgelyi*. Specimens of *S. nebulatus* with rosy gray or reddish brown ground color have white (instead of yellowish) blotches and stippling. Genetic divergence in a 521 bp long fragment of the mitochondrial Cytb gene between *S. bevridgelyi* and *S. nebulatus leucomelas* is 1.9–2.5%, whereas intraspecific distances are less than 0.4% in both species.

Description of holotype. Adult male, SVL 602 mm, tail length 186 mm (31% SVL); head length 20.9 mm (3% SVL) from tip of snout to commissure of mouth; head width 12.4 mm (59% head length) taken at broadest point; snout-orbit distance 21 mm; head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral 3.5 mm wide, broader than high; internasals 1.9 mm wide, broader than long; prefrontals 4.4 mm wide, longer than broad, entering orbit; supraocular 4.4 mm long, longer than broad; frontal 4.1 mm long, pentagonal and rounded, in contact with prefrontals, supraoculars, and parietals; parietals 7.7 mm long, longer than broad; nasal weakly divided, in contact with first three supralabials, loreal, prefrontal, internasal, and rostral; loreal 3.7 mm long, longer than high, entering the orbit; eye diameter 3.9 mm; pupil semi-elliptical; no preocular; two postoculars; temporals 1+3 on the right side, 2+3 on the left side; eight supralabials with 5th and 6th contacting orbit on the right side, seven supralabials with 4th and 5th contacting orbit on the left side; symphysial separated from chinshields by the first pair of infralabials; nine infralabials, 1–7 contacting chinshields; anterior pair of chinshields broader than long, posterior pair longer than broad; dorsal scales in 15/15/15 rows, smooth, without apical pits; 184 ventrals; 80 divided subcaudals; cloacal plate single.

Natural history. Specimens of *Sibon bevridgelyi* have been found active at night (20h56–03h56) on arboreal vegetation 30–500 cm above the ground in secondary and primary semideciduous foothill forest, pastures, and cacao plantations, usually close to streams. QCAZ 14444 was found feeding on a snail. In captivity, MZUA.RE.0142 fed on slugs and snails. By daytime, one individual (not collected) was found hidden under tree bark, and another (ZSFQ D503) was found coiled on the center of a palm tree about 2 m above the ground. DHMECN 9483 was collected in sympatry with *Dipsas andiana* and *D. bobridgelyi* at Reserva Biológica Buenaventura.

Distribution. Northwestern Peru in the department of Piura, and southwestern Ecuador in the provinces of Azuay, Chimborazo, El Oro, Guayas, Los Ríos and Manabí at elevations between 5 and 1206 m (Fig. 8).

Etymology. The specific epithet honors the late Prof. Beverly S. Ridgely, life-long birder and conservationist, and father of Robert S. Ridgely, well known in Ecuadorian ornithological circles and co-author of *The Birds of Ecuador*. Though he never got to visit Buenaventura, from afar Bev continued to delight in the conservation successes of Fundación Jocotoco, which now owns and manages one of the few protected areas where the Vulnerable *Sibon bevridgelyi* is known to occur.

Conservation status. We consider *Sibon bevridgelyi* to be Vulnerable following B2a,b(i,iii) IUCN criteria (IUCN 2001) because its area of occupancy is estimated to be less than 2,000 km^2, it is known only from 15 patches of forest lacking connectivity between them, and its habitat is severely fragmented and declining in extent and quality due to deforestation. Furthermore, only three of the localities (Parque Nacional Machalilla, Reserva Buenaventura, and Reserva Ayampe) where *S. bevridgelyi* occurs are currently protected.

Dipsas bobridgelyi sp. n.

http://zoobank.org/6B9E1F98-77A9-41F7-8CF1-F56404F8CBD0
Figs 1c, 9, 10

Proposed standard English name. Bob Ridgely's Snail-Eater

Proposed standard Spanish name. Caracolera de Bob Ridgely

Holotype. MZUTI 5417 (Figs 9, 10), adult male collected by Matthijs Hollanders on August 01, 2017 at Reserva Buenaventura, province of El Oro, Ecuador (S3.65467, W79.76794; 524 m).

Paratypes. DHMECN 11527, adult female collected by Juan Carlos Sánchez-Nivicela, Karem López, Verónica Urgilés, Bruno Timbe, Elvis Celi and Valentina Posse at Remolino, province of El Oro, Ecuador (S3.56551, W79.91948; 229 m). MZUTI 3266, adult female collected by Lucas Bustamante on October 06, 2013. MZUTI 5414, adult male collected by Matthijs Hollanders and Paulina Romero on June 08, 2017. QCAZ 1706, adult male collected by Fernando Ayala, Steven Poe, and Chris Anderson on March 03, 1994 at Ponce Enríquez, province of Azuay, Ecuador (S3.06547, W79.74358; 39 m).

Diagnosis. *Dipsas bobridgelyi* is placed in the genus *Dipsas* based on phylogenetic evidence (Fig. 3), and the absence of a labial that is noticeably higher than other labials and in contact with the postocular, primary, and secondary temporals. The species differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with enlarged vertebral row (2.1–2.2 times as wide as adjacent rows); (2) loreal and prefrontal in contact with orbit; (3) 9 supralabials with 4th and 5th contacting orbit; (4) one pair of infralabials in contact behind symphysial; (5) 180–201 ventrals in males, 178–184 in females; (6) 95–117 divided subcaudals in males, 96–98 in females; (7) dorsal and ventral color made up of 30–35 bold black body rings (up to 7–12 vertebral scales long) separated from each other by narrow (up to 3–4 vertebral scales long) dingy white interspaces; dorsal aspect of interspaces heavily speckled with rusty and black pigment; ventral surfaces lacking speckling; ground color of head dingy white with various degrees of scattered black pigment that coalesce on the top of the head, and various degrees of rusty speckling concentrated on the snout, nape and sides of the head; iris rich dark brown; (8) 372–478 mm SVL in males, 286–404 mm in females; (9) 158–212 mm TL in males, 117–158 mm in females.

Comparisons. *Dipsas bobridgelyi* is most similar to *D. gracilis*, from which it differs in coloration. In *D. gracilis* (Figs 1h, i), the black rings are up to 10–16 vertebral scales long and the interspaces are up to 5–7 scales long, whereas in *D. bobridgelyi* the black rings and interspaces are shorter, up to 8–9 and 3–4 vertebral scales long, respectively. In *D. gracilis*, the head plates are either completely black or black scattered with reddish brown, whereas in *D. bobridgelyi* the head plates are heavily stippled with white and tan pigment, especially on the prefrontals and internasals. In all known specimens of *D. bobridgelyi*, the ground color of the interspaces is white with contrasting reddish-tan pigment in the center, whereas in *D. gracilis* the ground color of the light interspaces on body and tail is either completely light brown or light reddish white, gradually becoming reddish brown towards the center. Finally, the nape and temporal region of the head in *D. gracilis* are either immaculate light reddish brown or marked with bold black speckles, whereas in *D. bobridgelyi* they are an irregular mix of fine speckling of white, rusty, and black pigments. Genetic divergence in a 689 bp long fragment of the mitochondrial Cytb gene between *D. bobridgelyi* and *D. gracilis* is 8.7–9.0%, whereas intraspecific distances are less than 0.3% in both species.

Description of holotype. Adult male, SVL 372 mm, tail length 158 mm (43% SVL); head length 15.1 mm (4% SVL) from tip of snout to commissure of mouth; head width 8.1 mm (54% head length) taken at broadest point; snout-orbit distance 4.3 mm; head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral 2.4 mm wide, broader than high; internasals 2.3 mm wide, broader than long; prefrontals 2.5 mm wide, longer than broad and contacting orbit; supraocular 3.2 mm long, longer than broad; frontal 3.9 mm long, hexagonal, in contact with prefrontals, supraoculars, and parietals; parietals 4.7 mm long, longer than broad; nasal divided, in contact with first three supralabials, loreal, prefrontal, internasal, and rostral; loreal 1.8 mm long, slightly higher than long, entering the orbit; eye diameter 2.7 mm; pupil semi-elliptical; no preocular; two postoculars; temporals 2+3; nine supralabials, 4th and 5th contacting orbit; symphysial separated from chinshields by the first pair of infralabials; 13 infralabials, 1–7 contacting chinshields; anterior pair of chinshields longer than broad, posterior pair broader than long; dorsal scales in 15/15/15 rows, smooth, without apical pits; 182 ventrals; 101 divided subcaudals; cloacal plate single.

Natural history. Individuals of *Dipsas bobridgelyi* have been found active at night (19h00–23h26) on arboreal vegetation 100–250 cm above the ground in secondary semi-deciduous foothill forest. MZUTI 5414 was found feeding on a snail.

Distribution. Foothills of the southwestern Ecuadorian Andes in the provinces of Azuay and El Oro, and northwestern Peruvian Andes in the department of Tumbes, at elevations between 39 and 572 m (Fig. 4).

Etymology. This species is named in honor of Dr. Robert "Bob" S. Ridgely, a leading ornithologist and distinguished conservationist who has dedicated almost 50 years of his life to the study and conservation of birds and biodiversity across Latin America. Bob is the President of Rainforest Trust and for the past twenty years has been a major driver of conservation in Ecuador through Fundación Jocotoco, which he helped establish twenty years ago. In 1980, Bob visited the type locality of *Dipsas bobridgelyi* (Buenaventura, meaning "good fortune"), now known to be a key area for the conservation of biodiversity. Bob embarked on conservation and worked diligently to raise funds through Rainforest Trust for the past 18 years to purchase private properties and establish what is now the Reserva Buenaventura of Fundación Jocotoco.

Conservation status. We consider *Dipsas bobridgelyi* to be Endangered following the IUCN criteria B1a,b(i,iii) (IUCN 2001) because its extent of occurrence is estimated to be less than 5,000 km^2, it is known only from 4 patches of forest lacking connectivity between them, and its habitat is severely fragmented and declining in extent and quality due to deforestation. Furthermore, only two of the localities (Buenaventura reserve and Reserva Nacional de Tumbes) where *D. bobridgelyi* occurs are currently protected.

Remarks. Cadle (2005) and Harvey (2008) examined MUSM 17589 from Tumbes department, Peru, and concluded that it was *Dipsas gracilis*. Although we did not examine this specimen, we believe that it corresponds to *D. bobridgelyi* based on Cadle's (2005) color description (i.e., head white with many irregular black markings on the top and sides).

Dipsas georgejetti sp. n.

http://zoobank.org/AAE7F2F6-8082-4FEA-AE59-BC0901FE9211
Figs 11, 12

Proposed standard English name. George Jett's Snail-Eater

Proposed standard Spanish name. Caracolera de George Jett

Holotype. MZUTI 5411 (Figs 11, 12), adult male collected by Melissa Costales on August 31, 2017 at Cabuyal, province of Manabí, Ecuador (S0.19698, W80.29059; 15 m).

Paratypes. DHMECN 11639, adult male collected by Jacinto Bravo in 2014 at Montecristi, province of Manabí, Ecuador (S1.04694, W80.65766; 136 m). DHMECN 11646, adult male collected by Félix Almeida in 2014 at Rocafuerte, province of Manabí, Ecuador (S0.92371, W80.45212; 19 m). MZUA.RE.0121 and MZUA.RE.0122, adult female and adult male, respectively, collected by Juan Carlos Sánchez-Nivicela at El Aromo, province of Manabí, Ecuador (S1.04665, W80.83227; 295 m). QCAZ 10589, adult male collected at El Aromo, province of Manabí, Ecuador (S1.04665, W80.83227; 295 m). QCAZ 9125, adult male collected at Cerro Blanco, province of Guayas, Ecuador (S2.17465, W80.02135; 147 m). USNM 142595, juvenile of undetermined sex collected on December 1959 at 10 mi N of Guayaquil, province of Guayas (S1.96418, W79.87988; 5 m). ZSFQ D606, juvenile male collected by Diego F. Cisneros-Heredia at the foothills of Cerro La Mocora, Parque Nacional Machalilla, province of Manabí, Ecuador (S1.59817, W80.75431; 308 m).

Diagnosis. *Dipsas georgejetti* is placed in the genus *Dipsas* based on phylogenetic evidence (Fig. 3) and the absence of a labial that is noticeably higher than other labials and in contact with the postocular, primary and secondary temporals. The species differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with a slightly enlarged vertebral row (1–1.4 times as wide as adjacent rows); (2) loreal and prefrontal in contact with orbit; (3) 7 supralabials with 4th and 5th (3th–5th in DHMECN 11646) contacting orbit; (4) no infralabials in contact behind symphysial; (5) 172–180 ventrals in males, 177 in one female; (6) 69–86 divided subcaudals in males, 58 in one female; (7) dorsal ground color light sandy brown with a pattern of 53–61 drab to brown black-edged middorsal blotches that are wider (6–7 vertebral scales long) and solid down to the edges of the ventrals on the first one third of the body, but becoming narrower (1–3 vertebral scales long) and broken up laterally towards the tail; interspaces finely speckled with brown pigment; ground color of the head light sandy brown with bold dark brown to black irregular blotches scattered on head plates and edging supralabials; ventral surfaces sandy brown with fine black speckling; iris sandy brown with dense dark brown speckling; (8) 270–711 mm SVL in males, 856 mm in one female; (9) 87–170 mm TL in males, 150 mm in one female.

Comparisons. *Dipsas georgejetti* is most similar to *D. oswaldobaezi*, *D. williamsi*, *D. oligozonata*, and *D. vagrans*, in that order, all of which were previously included in the genus *Sibynomorphus*. From *D. oswaldobaezi* (Figs 13, 14) and *D. williamsi*, it differs in having 7 supralabials with 4th and 5th bordering the eye (instead of 6 with 3rd and 4th bordering the eye). It further differs from *D. williamsi* in having the first supralabial not in contact with prefrontal (vs. in broad contact in *D. williamsi*). From *D. oligozonata* (Fig. 1o) and *D. vagrans*, it differs in having more than 160 ventrals. *Dipsas georgejetti* further differs from *D. oligozonata* in having distinct bold crossbands at least middorsally along the whole length of the body, instead of being present only on the anterior half of the body. Genetic divergence in a 529 bp long fragment of the mitochondrial Cytb gene between *D. georgejetti* and *D. oswaldobaezi* is 8.3%, whereas intraspecific distances are less than 0.4% in *D. georgejetti*. For the same fragment, the distance between *D. georgejetti* and *D. williamsi* is 7.8–7.9%.

Description of holotype. Adult male, SVL 315 mm, TL 87 mm (28% SVL); head length 13.6 mm (4% SVL) from tip of snout to commissure of mouth; head width 8.4 mm (62% head length) taken at broadest point; snout-orbit distance 3.5 mm; head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral 2.0 mm wide, broader than high; internasals 1.7 mm wide, broader than long; prefrontals 2.5 mm wide, longer than broad and contacting orbit; supraocular 3.4 mm long, longer than broad; frontal 3.3 mm long, pentagonal, in contact with prefrontals, supraoculars, and parietals; parietals 5.5 mm long, longer than broad; nasal divided, in contact with first two supralabials, loreal, prefrontal, internasal, and rostral; loreal 1.7 mm long, slightly higher than long, entering orbit; eye diameter 2.8 mm; pupil semielliptical; no preocular; two postoculars; temporals 2+2; seven supralabials, 4th and 5th contacting orbit; symphysial in contact with first pair of chinshields; nine infralabials, 1–6 contacting chinshields; anterior pair of chinshields longer than broad, posterior pair broader than long; dorsal scales in 15/15/15 rows, smooth, without apical pits; 178 ventrals; 69 divided subcaudals; cloacal plate single.

Natural history. The holotype was active during a dry night after a sunny day. It was perched on tangled vegetation 130 cm above the ground in dry shrubland besides recently cleared pasture. MZUA.RE0121 and MZUA.RE0122 were found actively moving at night between the branches 80–200 cm above the ground. ZSFQ D606 was found active during daytime after bulldozers opened a track in old-growth forest.

Distribution. Deciduous and semideciduous forests along the central Pacific coast in Ecuador in the provinces of Manabí and Guayas, at elevations between 5 and 317 m (Fig. 5).

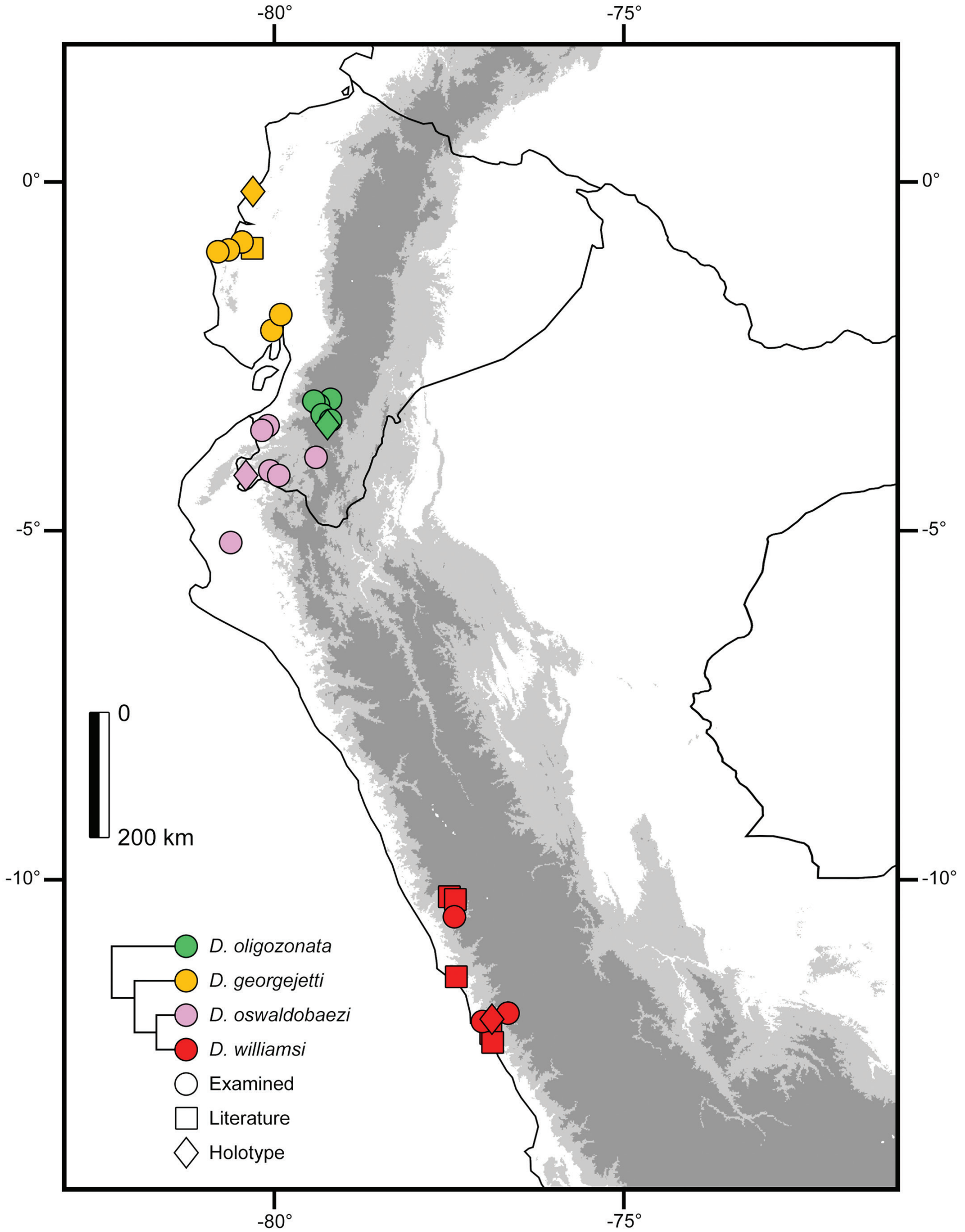

Figure 5. Distribution of *Dipsas georgejetti*, *D. oligozonata*, *D. oswaldobaezi*, and *D. williamsi* in Ecuador and Peru. Figures represent known localities.

Figure 6. Adult male holotype of *Sibon bevridgelyi*. MZUTI 5416.

Figure 7. Adult male holotype of *Sibon bevridgelyi* MZUTI 5416 in (a) dorsal and (b) ventral view. Scale bar: 1 cm.

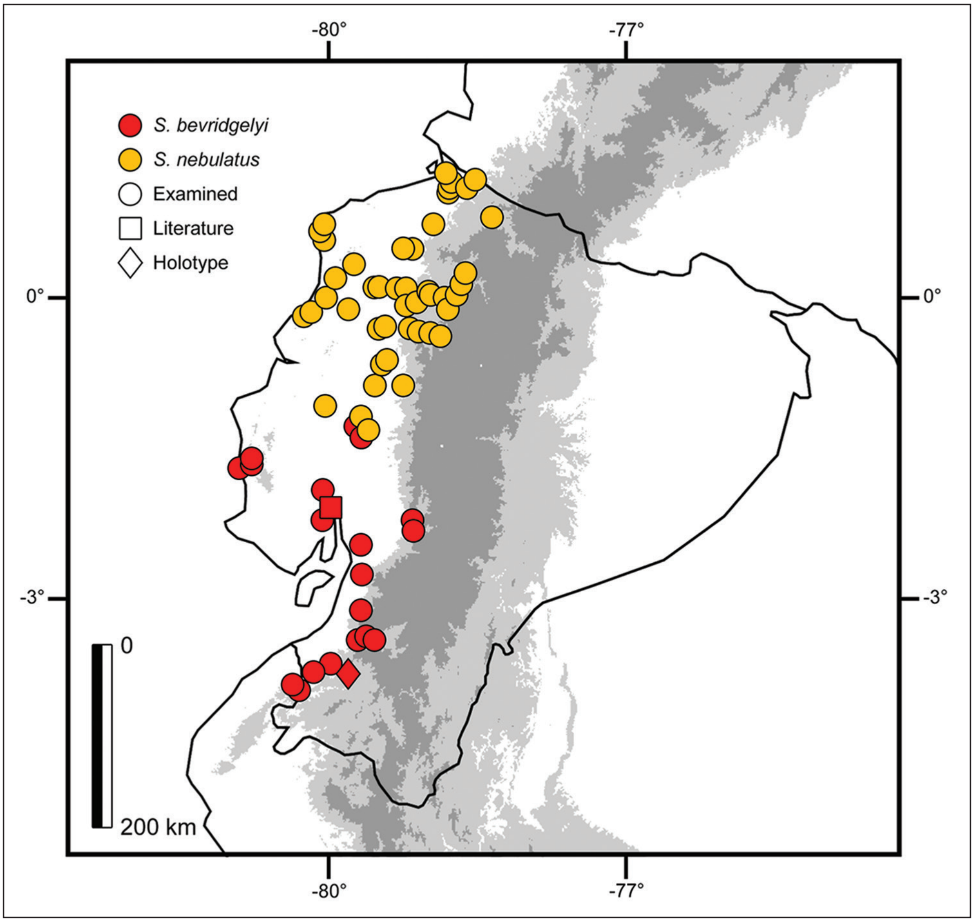

Figure 8. Distribution of *Sibon nebulatus* and *S. bevridgelyi* in Ecuador. Figures represent known localities.

Etymology. The specific name *georgejetti* honors George Jett, who has been a long-time donor to Rainforest Trust and has supported the reserves of Fundación Jocotoco in Ecuador. He is an international traveler with a passion for reptiles, amphibians, and birds.

Conservation status. We consider *Dipsas georgejetti* to be Vulnerable following the IUCN criteria A1c,B1a,b(iii, iv) (IUCN 2001) because its extent of occurrence is estimated to be 10,193 km^2, it is known only from 9 localities effectively corresponding to 4 patches of forest lacking connectivity between them, and its habitat is severely fragmented and declining in extent and quality due to deforestation. At the type locality, *D. georgejetti* was found in a patch of deciduous forest of 13 km^2 that was being cleared to accommodate cattle pastures. One of the localities, 15 km N of Guayaquil, where *D. georgejetti* was collected in 1959, is now completely deforested, which suggests that this arboreal species is no longer present there.

Figure 9. Adult male holotype of *Dipsas bobridgelyi*. MZUTI 5417.

Figure 10. Adult male holotype of *Dipsas bobridgelyi*. MZUTI 5417. Scale bar: 1 cm.

Figure 11. Adult male holotype of *Dipsas georgejetti*. MZUTI 5411.

Figure 12. Adult male holotype of *Dipsas georgejetti*. MZUTI 5411. Scale bar: 1 cm.

Dipsas oswaldobaezi sp. n.

http://zoobank.org/EA450E16-23F3-4A84-B067-00614621FFD1
Figs 13, 14

Sibynomorphus oligozonatus Cadle, 2007: 195 (part).

Proposed standard English name. Oswaldo Báez' Snail-Eater

Proposed standard Spanish name. Caracolera de Oswaldo Báez

Holotype. QCAZ 10369 (Fig. 13), adult female collected by Silvia Aldás and Gabriel Zapata on March 03, 2010 at Quebrada El Faique, province of Loja, Ecuador (S4.17889, W80.04226; 1004 m).

Paratypes. BMNH1935.11.3.108, adult female collected by Clodoveo Carrión in the valley of Catamayo, province of Loja, Ecuador (S3.98064, W79.35928; 1289 m). MUSM 2192, adult male collected by Otavio Ruíz in Piura (department or city not specified), Peru. MZUA.RE.0286, adult of undetermined sex collected by Valentina Posse on December 2015 at Huaquillas, province of El Oro, Ecuador (S3.54115, W80.08646; 39 m). QCAZ 14051, adult of undetermined sex collected by Paul Székely and Diana Székely on March 18, 2015 at Reserva Ecológica Arenillas, province of El Oro, Ecuador (S3.62110, W80.17513; 41 m). QCAZ 14060, adult of undetermined sex collected by Paul Székely and Diana Székely on June 16, 2015 at Guabillo, province of El Oro, Ecuador (S3.60346, W80.18139; 44 m). QCAZ 15108, adult female collected by Diego Almeida, Darwin Núñez, Eloy Nusirquia, Santiago Guamán and Guadalupe Calle on November 12, 2016 at Reserva La Ceiba-Pilares, province of Loja, Ecuador (S4.27502, W80.32805; 534 m) (Fig. 14).

Diagnosis. *Dipsas oswaldobaezi* is placed in the genus *Dipsas* based on phylogenetic evidence (Fig. 3) and the absence of a labial that is noticeably higher than other labials and in contact with the postocular, primary and secondary temporals. The species differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with a slightly enlarged vertebral row (1–1.2 times as wide as adjacent rows); (2) loreal and prefrontal in contact with orbit; (3) six supralabials with 3rd and 4th contacting orbit; (4) no infralabials in contact behind symphysial; (5) 163–179 ventrals in males, 177–179 in females; (6) 68–70 divided subcaudals in males, 65–66 in females; (7) dorsal ground color light sandy brown with a pattern of 55–63 drab to brown black-edged middorsal blotches that are wider (7–9 vertebral scale rows) and solid down to the edges of the ventrals on the first one third of the body, but becoming narrower (1–3 vertebral scales long) and broken up laterally towards the tail; interspaces finely speckled with brown pigment; ground color of the head light sandy brown with a thin light cream nuchal collar and bold dark brown to black irregular blotches scattered on head plates and edging supralabials; ventral surfaces sandy brown with fine black speckling (Fig. 13b); iris sandy brown with dense dark brown speckling; (8) 277–348 mm SVL in males, 407–428 mm in females; (9) 85–114 mm TL in males, 110–122 mm in females.

Comparisons. *Dipsas oswaldobaezi* is most similar to *D. williamsi*, *D. georgejetti*, *D. oligozonata*, and *D. vagrans*, in that order, all of which were previously included in

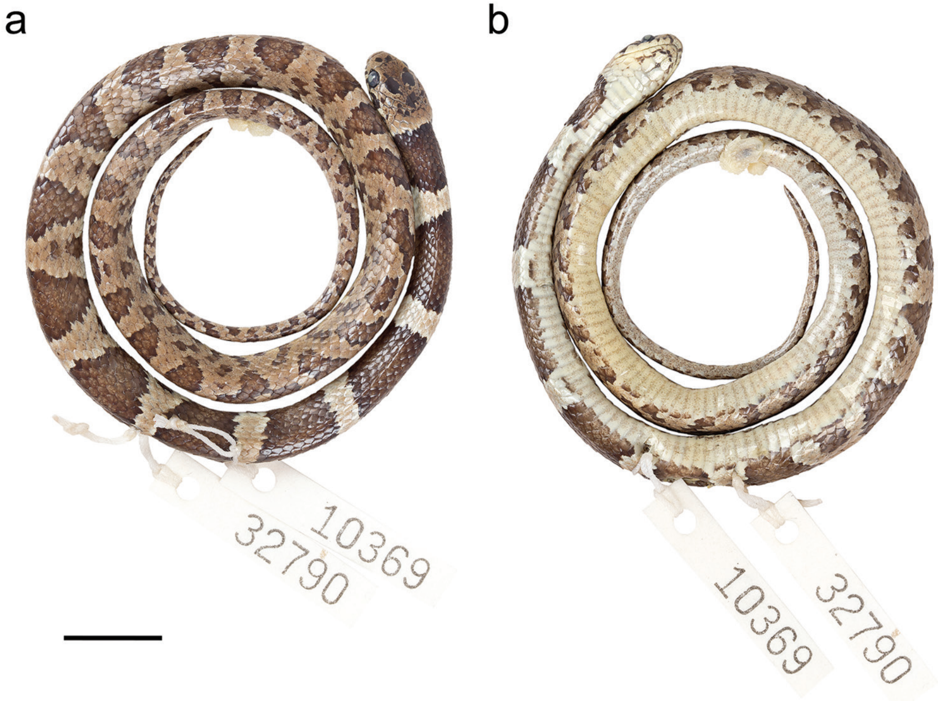

Figure 13. Adult female holotype of *Dipsas oswaldobaezi* QCAZ 10369 in **a** dorsal and **b** ventral view. Scale bar: 1 cm.

the genus *Sibynomorphus*. From *D. williamsi*, it differs in having 7–9 infralabials (vs. 10 in *D. williamsi*), first supralabial not in contact with prefrontal (vs. in broad contact in *D. williamsi*), and dorsal blotches that are lighter in the middle (vs. dark solid blotches). From *D. georgejetti* (Figs 11, 12), it differs in having 6 supralabials with 3rd and 4th bordering the eye (vs. 7 supralabials with 4th and 5th bordering the eye in *D. georgejetti*). From *D. oligozonata* (Fig. 1o) and *D. vagrans*, it differs in having more than 160 ventrals. *Dipsas oswaldobaezi* further differs from *D. oligozonata* in having distinct bold crossbands at least middorsally along the whole length of the body, instead of being present only on the anterior half of the body. Genetic divergence in a 529 bp long fragment of the mitochondrial Cytb gene between *D. oswaldobaezi* and *D. williamsi* is 4.0–4.2%, whereas intraspecific distances are less than 0.2% in *D. williamsi*. For the same fragment, the distance between *D. oswaldobaezi* and *D. georgejetti* is 8.3%.

Description of holotype. Adult female, SVL 277 mm, tail length 85 mm (31% SVL); head length 9.5 mm (3.4% SVL) from tip of snout to commissure of mouth; head width 7.3 mm (76% head length) taken at broadest point; snout-orbit distance 3.3 mm; head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral 2.1 mm wide, broader than high; internasals 1.2 mm wide, broader than long; prefrontals 2.2 mm wide, slightly broader than long and contacting orbit; supraocular 2.6 mm long, longer than broad; frontal 2.9 mm long, pentagonal, in contact with

Figure 14. Adult female paratype of *Dipsas oswaldobaezi*. QCAZ 15108.

prefrontals, supraoculars, and parietals; parietals 4.2 mm long, longer than broad; nasal not divided, in contact with first supralabial, loreal, prefrontal, internasal, and rostral; loreal 1.3 mm long, longer than high, entering orbit; eye diameter 2.2 mm; pupil semi-elliptical; no preocular; two postoculars; temporals 2+2; 6 supralabials, 3rd and 4th contacting orbit; symphysial separated from chinshields by the first pair of infralabials; 9/8 (right/left) infralabials, 1–6/1–5 contacting chinshields; both pairs of chinshields longer than broad; dorsal scales in 15/15/15 rows, smooth, without apical pits; 179 ventrals; 70 divided subcaudals; cloacal plate single.

Natural history. Individuals of *Dipsas oswaldobaezi* have been found active by night on vegetation or at ground level in forested environments, pastures, or rural gardens. One individual (QCAZ 15108) was found hidden under leaf litter during daytime. Two individuals (MZUA.RE.0286 and QCAZ 14060) were found dead on roads.

Distribution. Deciduous and semideciduous lowland to lower montane forests and dry lowland shrublands in southwestern Ecuador (provinces of Loja and El Oro) and northwestern Peru (department of Tumbes), at elevation between 39 and 1289 m (Fig. 5).

Etymology. The specific name *oswaldobaezi* honors Dr. Oswaldo Báez, a renowned Ecuadorian biologist and researcher who has dedicated his life to the teaching of science, scientific thinking, and the conservation of nature. Oswaldo Báez has played a major role in science education in Ecuador through many popular science articles and books.

Conservation status. We consider *Dipsas oswaldobaezi* to be Vulnerable following the IUCN criteria B1a,b(iii, iv) (IUCN 2001) because its extent of occurrence is estimated to be 8,605 km^2; it is known only from eight localities effectively corresponding to four patches of forest lacking connectivity between them, and its habitat is severely fragmented and declining in extent and quality due to deforestation.

Remarks. In his revision of *Dipsas oligozonata*, Cadle (2007) allocated three additional specimens (AMNH 110587, BMNH 1935.11.3.108 and MUSM 2192) to a species known only from the holotype (EPN 3612), collected at Zhila, province of Azuay (S3.50280, W79.18808; 2795 m) (Fig. 5). AMNH 110587 was collected ca. 34 km airline distance from the type locality at an elevation of 2204 m, and it resembles the holotype in both color and lepidosis. However, BMNH 1935.11.3.108 and MUSM 2192 have more than 160 ventral scales and have broad dark brown crossbars that are at least twice as long as those present in both the holotype, AMNH 110587 and in the other four specimens of *D. oligozonata* examined by us (Table 2; Fig. 1o), all of which have fewer than 160 ventral scales and come from elevations between 2102 and 2891 m in the watershed of the Río Jubones (Fig. 5). The coloration and ventral scale counts in BMNH 1935.11.3.108 and MUSM 2192 are more similar to *D. oswaldobaezi*, and we designated them as paratypes of this species.

Systematics of the *Dipsas peruana* complex.

Based on differences in coloration and the topology of the molecular phylogeny obtained here (Fig. 3), we partition *Dipsas peruana* sensu Harvey and Embert (2008) into four allopatric species. This includes restriction of *D. peruana* to Peruvian-Bolivian populations, the resurrection of *D. palmeri* for populations ranging from northern Peru to central Ecuador, the description of a new species for northern Ecuador, and the resurrection of *D. latifrontalis* for populations in Colombia and Venezuela (Fig. 4).

Dipsas klebbai **sp. n.**

http://zoobank.org/83EDA906-74F7-4D2F-8E6A-59B23964897C
Figs 1l, m, 15, 16

Dipsas peruana Harvey & Embert, 2008: 79 (part).

Proposed standard English name. Klebba's Snail-Eater

Proposed standard Spanish name. Caracolera de Klebba

Holotype. MZUTI 5412 (Figs 15, 16), adult male collected by Phillip Torres on April 28, 2016 at Pacto Sumaco, province of Napo, Ecuador (S0.66377, W77.59895; 1556 m).

Paratypes. DHMECN 568, adult female collected by Thomas Begher on 1980 at Borja, province of Napo, Ecuador (S0.42054, W77.84104; 1717 m). MCZ 164674–75, two adults of undetermined sex collected by Giovani Onore on June 01, 1983 at Río Azuela, province of Napo, Ecuador (S0.148693, W77.65463; 1402 m). MHNG 2220.035, 2220.056, 2250.063, 2250.064, one juvenile female and three adult males, respectively, collected by Giovani Onore on 1984 at El Chaco, province of Napo, Ecuador (S0.33763, W77.80957; 1595 m). MHNG 2220.038–039, adult female and adult male, respectively, collected by Giovani Onore on November 1984 at San Rafael, province of Napo, Ecuador (S0.09669, W77.58995; 1464 m). MHNG 2220.04,

Figure 15. Adult male holotype of *Dipsas klebbai*. MZUTI 5412.

2220.041, adult females collected by Giovani Onore on May 1984 at El Reventador, province of Napo, Ecuador (S0.04480, W77.52858; 1476 m). MZUTI 63, adult male collected by Alejandro Arteaga on August 08, 2011 at Yanayacu, province of Napo, Ecuador (S0.60042, W77.89053; 2110 m). MNHG 2529.029, adult female collected by Eugen Kramer on February 22, 1992 at Napo province, Ecuador. QCAZ 12488, collected by Pablo Medrano on March 02, 2015 at Río Quijos, province of Napo, Ecuador (S0.45224, W77.94249; 1929 m). QCAZ 12600, collected by Pablo Medrano on March 27, 2014 at Santa Rosa, province of Napo, Ecuador (S0.39630, W77.82343; 1113 m). QCAZ 13124, collected by Fabián Vallejo on November 21, 2014 at Las Palmas, province of Napo, Ecuador (S0.54691, W77.87762; 1903 m). QCAZ 14281, adult male collected by Andrea Narváez on December 02, 2016 at La Bonita, province of Sucumbíos, Ecuador (N0.47209, W77.54661; 1953 m). QCAZ 1496, collected on October 18, 1992 at Sardinas, province of Napo, Ecuador (S0.38484, W77.83782; 1641 m). QCAZ 1605, adult male collected by Victor Utreras on February 04, 1992 at 2 km E Borja, province of Napo, Ecuador (S0.41543, W77.83032; 1608 m). QCAZ 250, adult male collected at El Reventador, province of Napo, Ecuador (S0.04480, W77.52858; 1476 m). QCAZ 358–59, collected on January 10, 1984 at Cascada de San Rafael, province of Napo, Ecuador (S0.10354, W77.58337; 1246 m). QCAZ 4500, collected by Estefanía Boada on August 01, 2011 at Hostería Cumandá, province of Napo, Ecuador (S0.45249, W77.88071; 1856 m). QCAZ 9696, collected by Steven Poe on August 04, 2009 at 2.3 km N of turnoff to Baeza, province of Napo, Ecuador (N0.45236, W77.88212; 1840 m). USNM 386323, adult female col-

Figure 16. Adult male holotype of *Dipsas klebbai*. MZUTI 5412. Scale bar: 1 cm.

lected on February 24, 1979 at Río Azuela, province of Napo, Ecuador (S0.148693, W77.65463; 1402 m). ZSFQ D304, female collected by Jean-Marc Touzet and Diego F. Cisneros-Heredia at Cascada de San Rafael, province of Napo, Ecuador (S0.10007, W77.58034; 1182 m).

Diagnosis. *Dipsas klebbai* is placed in the genus *Dipsas* based on phylogenetic evidence (Fig. 3), and the absence of a labial that is noticeably higher than other labials and in contact with the postocular, primary and secondary temporals. The species differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with enlarged vertebral row (1.5–1.8 times as wide as adjacent rows); (2) one loreal and one preocular in contact with orbit; (3) 9–11 supralabials with (usually) 4th to 6th contacting orbit; (4) one pair of infralabials in contact behind symphysial; (5) 181–201 ventrals in males, 187–194 in females; (6) 99–123 divided subcaudals in males, 98–106 in females; (7) dorsal and ventral ground color light brown with various degrees of fine black speckling and 27–36 dark brown to black, cream-edged oblong blotches that are longer that interspaces and become smaller towards the tail (Fig. 2m, n); on first half of body, the dark bands meet ventrally to form full body rings; on second half they fail to meet ventrally; head black with different degrees of whitish edging on the labial scales, and a thin (1–2 scales long) cream to light brown irregular nuchal collar; dorsal blotches usually incomplete ventrally, extending far onto ventrals and occasionally fusing midventrally; cream edges of neighboring blotches fused in first 6–9 blotches; (8) 401–749 mm SVL in males, 525–630 mm in females; (9) 169–330 mm TL in males, 209–240 mm in females.

Comparisons. *Dipsas klebbai* is compared to species previously subsumed under *D. peruana*: *D. latifrontalis*, *D. palmeri*, and *D. peruana*. From *D. latifrontalis* (Fig. 1n) and *D. palmeri* (Figs 1r, s), it differs in having longer oblong to rectangular body blotches up to 7–13 vertebral scales long (vs. fewer than 8 vertebral scales long in *D. latifrontalis* and *D. palmeri*) that are also longer than the interspaces (Fig. 1l, m). Specimens of *D. klebbai* can be separated from specimens of *D. peruana*, with the exception of BMNH 1946.1.2078, based on the presence of the following characteristics (condition of *D. peruana* in parentheses): posterior body blotches twice to four times as long as interspaces (vs. posterior body blotches ca. equal in length or marginally longer than interspaces); interspaces never completely obscured by black pigment (vs. completely melanized in some specimens); dorsal surface of head black (vs. dark brown with dingy cream reticulations); dorsal body blotches fused ventrally on the first half of the body (vs. rarely fused); longest body blotch at least 7 vertebral scales long (vs. longest body blotch 4–7 vertebral scales long). Genetic divergence in a 684 bp long fragment of the mitochondrial Cytb gene between *D. klebbai* and *D. palmeri* is 8.2–9.2%, whereas intraspecific distances are less than 1.1% in both species. For the same fragment, the distance between *D. klebbai* and *D. peruana* is 10.7–11.0%.

Description of holotype. Adult male, SVL 608 mm, tail length 262 mm (43% SVL); head length 20.3 mm (3% SVL) from tip of snout to commissure of mouth; head width 12.7 mm (62% head length) taken at broadest point; snout-orbit distance 5.4 mm; head distinct from neck; snout short, blunt in dorsal and lateral outline; rostral 4.0 mm wide, broader than high; internasals 2.6 mm wide, as broad as long; prefrontals 3.9 mm wide, broader than long, excluded from entering orbit by preocular; supraocular 4.3 mm long, broader than long; frontal 4.5 mm long, hexagonal, in contact with prefrontals, supraoculars, and parietals; parietals 6.6 mm long, longer than broad; nasal divided, in contact with first two supralabials, loreal, prefrontal, internasal, and rostral; loreal 2.6 mm long, slightly longer than high, entering orbit; eye diameter 4.5 mm; pupil semi-elliptical; one preocular; two postoculars; temporals 2+2; ten supralabials, 5th and 6th contacting orbit; symphysial separated from chinshields by the first pair of infralabials; 14 infralabials, 2–7 contacting chinshields; anterior pair of chinshields longer than broad, posterior pair broader than long; dorsal scales in 15/15/15 rows, smooth, without apical pits; 188 ventrals; 116 divided subcaudals; cloacal plate single.

Natural history. At night (21h53–02h13), specimens of *Dipsas klebbai* have been found active during or after light rain on arboreal vegetation 50–500 cm above the ground in a variety of environments ranging from primary montane cloud forests and evergreen montane forests to silvopastures and forest borders, occasionally close to rivers. By day, individuals have been found hidden underground in pastures or among shrubs in rural gardens, or coiled on leaves at 300 cm above the ground. At dusk, after warm days, individuals of *Dipsas klebbai* have been seen crossing roads. QCAZ 13124 laid six eggs on December 2014. Five eggs were found inside a rotten trunk at El Chaco, province of Napo Ecuador.

Distribution. Endemic to the eastern slopes of the Ecuadorian Andes in the provinces of Napo and Sucumbíos at elevations between 1246 and 2120 m (Fig. 4).

Etymology. Named after Casey Klebba, in recognition of his appreciation of and passion for Andean wildlife, and his invaluable support of AA's field expeditions to remote areas of Ecuador. After a visit to Peru in 2011, Casey became an active supporter of conservation and scientific projects in Ecuador.

Conservation status. All known localities of occurrence for *Dipsas klebbai* fall within the limits or within the buffer zone of the following protected areas: Parque Nacional Cayambe Coca, Parque Nacional Sumaco Napo Galeras, Reserva Ecológica Antisana, and Reserva Ecológica Cofán Bermejo. Furthermore, the species is common in degraded environments, which suggests a degree of tolerance for habitat modification. For these reasons, and because it does not meet the criteria (IUCN 2001) for qualifying in a threatened category, we here list it as Least Concern following IUCN guidelines.

Remarks. In their revision of *Dipsas peruana*, Harvey and Embert (2008) included specimens of *D. klebbai*. However, they found no characters that could diagnose these specimens from the rest of Ecuadorian and Peruvian specimens of *D.* "*peruana*" in order to establish species boundaries. They also grouped the then valid *D. boettgeri*, *D. latifrontalis*, and *D. polylepis* under *D. peruana*. The authors were right to point out that the different populations cannot be separated based on characters of lepidosis. However, they did not include molecular data in their analyses, and also failed to notice the geographically structured differences in the length of the body blotches and their relationship to the length of the interspaces.

Dipsas palmeri (Boulenger, 1912)

Fig. 1r, s

Leptognathus palmeri Boulenger, 1912: 422. Holotype BMNH, a male from El Topo, province of Tungurahua, Ecuador.

Leptognathus latifasciatus Boulenger, 1913: 72. Holotype BMNH 1946.1.2007, a juvenile male from Upper Marañón, department of Cajamarca, Peru.

Dipsas peruana Harvey & Embert, 2008: 79 (part).

Proposed standard English name. Palmer's Snail-Eater

Proposed standard Spanish name. Caracolera de Palmer

Diagnosis. *Dipsas palmeri* differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with enlarged vertebral row; (2) one loreal and one preocular in contact with orbit; (3) 8–10 supralabials with (usually) 4th to 6th contacting orbit; (4) one pair of infralabials in contact behind symphysial; (5) 172–202 ventrals in males, 181–200 in females; (6) 91–118 divided subcaudals in males, 86–102 in females; (7) dorsal and ventral ground color light brown with various degrees of fine black speckling and with 32–41 brown to blackish, white-edged circular blotches that are longer than interspaces in the first half of the body, but shorter in the second half (Figs 1r, s); adult head gray with different degrees of whitish edging on the labial scales, and a thin (1–2 scales long) white to light grayish brown irregular parietal collar; dorsal blotches incomplete ventrally, extending marginally onto ventrals but not fusing midventrally; (8) 215–907 mm SVL in males, 642–1187 mm in females; (9) 78–390 mm TL in males, 246–298 mm in females.

Comparisons. *Dipsas palmeri* is compared to species previously subsumed under *D. peruana*: *D. latifrontalis*, *D. klebbai* (Fig. 1l, m), and *D. peruana*. From *D. latifrontalis* (Fig. 1n), it differs in having the first 19–35 dorsal blotches edged with white or cream, vs. the first 9–10 in *D. latifrontalis*. The only known adult of *D. latifrontalis* photographed in life has bronze interspaces (Fig. 1n), a coloration not seen in any adult of *D. palmeri*. From *D. klebbai*, it differs in having shorter blotches (longest blotch up to 3–7 vertebral scales long) that are circular (instead of oblong) and that are only longer than the interspaces on the first half of the body. From *D. peruana*, it differs in having dorsal blotches that are shorter than interspaces on posterior half of the body, and in lacking melanized interspaces in adult individuals.

Distribution. Eastern slopes of the Ecuadorian and Peruvian Andes south of the Jatunyacu–Napo river valley in Ecuador and north of the Huancabamba depression at elevations between 1211 and 2282 m (Fig. 4).

Conservation status. An estimated 31 out of the 42 known localities of occurrence for *Dipsas palmeri* are located within the limits or the buffer area of the following protected areas: Bosque Protector del Alto Nangaritza, Parque Nacional Llanganates, Parque Nacional Podocarpus and Parque Nacional Sangay. Furthermore, the presence of the species in degraded environments suggests a degree of tolerance for habitat modification. For these reasons, and because it does not meet the criteria for qualifying in a threatened category, we here list it as Least Concern following IUCN guidelines.

Remarks. Neither Peters (1960) nor Harvey and Embert (2008) recognized the geographic morphological distinctiveness of *Dipsas palmeri* from Ecuador and Peru. Certainly, *D. palmeri* is most similar in coloration and lepidosis to *D. latifrontalis* (Fig. 1n) from Venezuela, and that is why Peters considered them synonyms. However neither Peters (1960) nor Harvey and Embert (2008) saw live specimens of *D. latifrontalis* in order to recognize the differences in life color pattern between the two species.

Two other junior synonyms of *Dipsas peruana* are *D. latifasciata* and *D. polylepis*, both of which occur in Peru (Fig. 4). Of these, only the latter must remain a synonym of *D. peruana*; the former should be transferred to the synonymy of *D. palmeri*, as defined here. Examination of photographs of the specimen of *D. latifasciata* (BMNH 1946.1.2077) reveals this species has dorsal blotches shorter than interspaces on posterior half of the body, a character seen in *D. palmeri* but not in *D. peruana*. The holotype was collected by A. E. Pratt in "Upper Marañón", with no further specific locality mentioned. However, the type locality can be restricted to the immediate environs of the town of Jaén, as the "Upper Marañón" is considered the segment of the Marañón river that goes from the town of Jaén until the river meets the Santiago River. Additionally, in a letter to his wife in 1913, the explorer explains how he crossed the Ecuadorian Andes and arrived at the town of Jaén in northern Peru, where he stayed and collected specimens for the BMNH before proceeding to Iquitos along the Marañón river, with no mention of visiting any locality east of the river at elevations where *D. palmeri* and *D. peruana* are known to occur. Harvey and Embert (2008) pointed out that the Huancabamba depression could be a geographic barrier separating species within the *D. peruana* complex, but they did not find evidence to support this view. Our results suggest that the Huancabamba depression is a major geographic barrier separating *D. palmeri* (north) from *D. peruana* (south).

***Dipsas peruana* (Boettger, 1898)**

Leptognathus peruana Boettger, 1898: 128. Holotype SMF 20801, a female from Santa Ana, department of Cuzco, Peru.
Leptognathus boettgeri Werner, 1901: 11. Holotype MTKD D 1671 M, a female from Chanchamayo, department of Junín, Peru.
Leptognathus boliviana Werner, 1909: 240. Holotype ZMH, a female from department of Beni, Bolivia.
Leptognathus polylepis Boulenger, 1912: 422. Holotype BMNH 1946.1.2078, a female from Huancabamba, department of Pasco, Peru.

Proposed standard English name. Peruvian Snail-Eater

Proposed standard Spanish name. Caracolera Peruana

Diagnosis. *Dipsas peruana* differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with moderately enlarged vertebral row; (2) one loreal and one preocular in contact with orbit; (3) 8–9 supralabials with 4–6 or 3–5 contacting orbit; (4) one pair of infralabials in contact behind symphysial; (5) 177–200 ventrals in males, 180–203 in females; (6) 75–127 divided subcaudals in males, 79–105 in females; (7) dorsal and ventral ground color brown to dark brown (light brown in juveniles) with 33–43 blackish brown to complete black, white to cream edged circular to vertically elliptical blotches that are longer than interspaces; head dark brown with dingy cream reticulations and different degrees of whitish edging on the labial scales, and a thin (1–3 scales long) white to light grayish brown irregular nuchal collar; dorsal blotches extending marginally onto ventrals and rarely fusing midventrally; (8) 199 mm SVL in males, 610–725 mm in females; (9) 85 mm TL in males, 155–241 mm in females.

Comparisons. *Dipsas peruana sensu stricto* is compared to species previously subsumed under *D. peruana sensu lato*: *D. latifrontalis*, *D. palmeri*, and *D. klebbai*. From *D. latifrontalis* and *D. palmeri*, it differs in having dorsal blotches along the entire body similar in length or longer than interspaces (shorter than interspaces in *D. latifrontalis* and *D. palmeri*), and in having melanized interspaces in some adult individuals. With the exception of BMNH 1946.1.2078, specimens of *D. peruana* can be separated from specimens of *D. klebbai* by possessing at least one of the following characteristics: posterior body blotches similar in length or marginally longer than interspaces (twice to four times as long in *D. klebbai*); short circular to vertically elliptical body blotches usually only up to 4–7 vertebral scales long; melanized interspaces; dorsal surface of the head not completely black; and dorsal body blotches rarely fused ventrally.

Distribution. Eastern slopes of the Peruvian and Bolivian Andes south of the Huancabamba depression at elevations between 1279 and 2671 m (Fig. 4).

Dipsas latifrontalis (Boulenger, 1905)

Leptognathus latifrontalis Boulenger, 1905: 561. Holotype BMNH 1946.1.20.98, a female from Aricagua, state of Mérida, Venezuela.

Dipsas peruana Harvey & Embert, 2008: 79 (part).

Proposed standard English name. Broad-fronted Snail-Eater

Proposed standard Spanish name. Caracolera frentona

Diagnosis. *Dipsas latifrontalis* differs from all described species of *Dipsas* based on the following combination of characters: (1) 15/15/15 smooth dorsals with moderately enlarged vertebral row; (2) one loreal and one preocular in contact with orbit; (3) 8–10 supralabials with 3rd to 6th contacting orbit; (4) one pair of infralabials in contact behind symphysial; (5) 192 ventrals in one male (CVULA 7883), 194 in the female holotype; (6) 109 divided subcaudals in the single male, 95 in the female holotype; (7) dorsal and ventral ground color bronze (light brown in juveniles) with 32–36 dark reddish brown to black, circular to vertically elliptical blotches that are longer than interspaces and white to cream edged on first half of body; head grayish brown to black with different degrees of whitish edging on the labial scales, and with or without a thin (1–2 scales long) dingy white irregular nuchal collar; dorsal blotches extending marginally onto ventrals and occasionally fusing on the anterior part of the body; (8) 800 mm SVL in the holotype female; (9) 220 mm TL in the holotype female.

Comparisons. *Dipsas latifrontalis* is compared to species previously subsumed under *D. peruana*: *D. palmeri*, *D. peruana*, and the herein described *D. klebbai*. From *D. palmeri*, it differs in having the first 9–10 dorsal blotches edged with white or cream, vs. the first 19–35 in *D. palmeri*. The only known adult of *D. latifrontalis* photographed in life has bronze interspaces (Fig. 1n), a coloration not seen in any adult of *D. palmeri* (see also Remarks below). From *D. klebbai*, it differs in having shorter blotches (longest blotch up to 6–8 vertebral scales long) that are circular (instead of oblong) and that are only longer than the interspaces on the first half of the body. From *D. peruana*, it differs in having dorsal blotches in posterior half of the body shorter than interspaces, and in lacking melanized interspaces in adult individuals.

Distribution. Known only from two localities in the Venezuelan Andes and one in the Northern Colombian Andes at elevations between 1000 and 1400 m (Fig. 4).

Remarks. Neither Peters (1960) nor Harvey and Embert (2008) examined the holotype of *Dipsas latifrontalis*, and they used Boulenger (1905) description to assign specimens of *D. palmeri* and *D. peruana*, respectively, to *D. latifrontalis*. We examined pictures of the holotype of *D. latifrontalis* from the BMNH, provided to us by César L. Barrio-Amorós. In coloration, the holotype is nearly identical to the uncollected adult presented in Figure 1n (San Isidro, Barinas province, Venezuela), with faint cream edging restricted to blotches 1–9, and indistinct blotches on the posterior part of the body. The previously only known photograph of a *D. latifrontalis* is of a juvenile from the same location as the specimen in Figure 1n (Rivas et al. 2012).

All *Dipsas latifrontalis* depicted in Lotzkat et al. (2008) and Natera-Mumaw et al. (2015) refer to a different species related to the *D. incerta* group, except for the holotype of *D. latifrontalis* BMNH 1946.1.20.98 (formerly 1905.5.31.76).

Discussion

Higher-level relationships within Dipsadini are still far from being resolved. The monotypic *Plesiodipsas perijanensis* was not included in our analysis or other recent molecular phylogenies. The species of *Dipsas*+*Sibynomorphus* and *Sibon* included here form monophyletic groups, but this is not the case for the genus *Tropidodipsas*, for which *T. sartorii* and *T. fasciata* + *T. fischeri* are the successive sister lineages of *Dipsas*+*Sibynomorphus* and *Sibon* (Fig. 3). This arrangement mirrors the results of Sheehy's (2012) unpublished PhD thesis, which presented evidence that groups consisting of *T. sartorii*, *T. annulifera*, *T. fischeri*, *T. philippii*, and *T. fasciatus*, as well as several new species of *Tropidodipsas* were not each other's closest relatives, and some merited recognition as distinct genera. Sheehy (2012) also presented phylogenetic evidence that *Sibon sanniolus* and *Dipsas gaigeae* do not belong to their nominal genera. Instead, each is more closely related to *Tropidodipsas sensu stricto* (*D. gaigeae*) or "*T.*" *sartorii* + *Geophis* + "*T.*" *annulifera* (*S. sanniolus*) than any species of *Dipsas* or *Sibon*.

Decades ago, Parker (1926) and Smith and Taylor (1945) suggested that *Sibynomorphus* and *Dipsas* were synonyms. More recently, Zaher et al. (2009), Grazziotin et al. (2012), and Sheehy (2012) recognized that *Dipsas* is paraphyletic with respect to *Sibynomorphus*, a conclusion we corroborate based on the results of our ML molecular phylogeny. In fact, members of former *Sibynomorphus* fall into four different clades across the phylogeny of *Dipsas*. In general, we suggest that the former *Sibynomorphus* species represent cases of convergent evolution; apparently from within several independent *Dipsas* clades or they represent an ancient morphotype successfully persisting through today.

Additionally, many traditional infrageneric groups are either non-monophyletic, or poorly supported and weakly placed. We recognize that this may reflect inadequate sampling of taxa (only 43 of 77 species are included) or characters (only four mtDNA and one nuclear locus were used). From the eight *Dipsas* species groups recognized by Harvey (2008) (Table 1), we only found phylogenetic support for the *D. articulata* and *D. indica* species groups. Two groups of species that are monophyletic in our molecular phylogeny and are similar in coloration and lepidosis are: 1) *D. georgejetti* + *D. oligozonata* + *D. oswaldobaezi* + *D. williamsi*, and 2) *D. klebbai* + *D. palmeri* + *D. peruana*. The sampled members of the *D. oreas* group are monophyletic if *D. andiana* is placed in this group, as it is the strongly supported (in both BI and ML analyses) sister taxon of *D. oreas*. We therefore place *D. andiana* in the *D. oreas* group and propose that the same be done for the morphologically similar *D. nicholsi* from Panama.

Dipsas bobridgelyi is most similar in coloration to *D. gracilis* (Fig. 1h, i). These species are recovered as sister taxa in our phylogenetic analyses (Fig. 3) and have non-overlapping, but adjacent distribution ranges in western Ecuador (Fig. 4). This scenario suggests a parapatric speciation event, as the distribution of *D. gracilis* is congruent with Chocoan evergreen forest in northwestern Ecuador whereas the distribution of *D. bobridgelyi* is congruent with Tumbesian semi-deciduous forests in southwestern Ecuador.

Although we did not examine MUSM 17589 from Tumbes department, Peru, the description of the coloration and head scales of this specimen provided by Cadle (2005) and Harvey (2008) suggests that it is a *Dipsas bobridgelyi*, rather than a *D. gracilis*, as was originally suggested by both authors before the description of *D. bobridgelyi* herein. There is no other voucher of *D. gracilis* from Peru and it is unlikely that two morphologically and phylogenetically, and likely also ecologically very close species, occur in sympatry. Hence, from a biogeographic perspective, we suggest *D. gracilis* does not occur in Peru and that all specimens from south of the southern limit of *D. gracilis* in southwestern Ecuador and adjacent northwestern Peru represent *D. bobridgelyi*.

Peters (1960) recognized a geographic morphological structure within the widely distributed *Sibon nebulatus* when he defined the subspecies *nebulatus*, *leucomelas*, *hartwegi*, and *popayanensis*. Here, our genetic results corroborate that *S. nebulatus leucomelas* from Ecuador and *S. nebulatus hartwegi* are distinct from the two Central American samples from Belize and northeastern Costa Rica, a divergence already put forward by Sheehy (2012). Yet, *S. nebulatus* is paraphyletic with respect to both *S. dunni* and *S. bevridgelyi*, which group with *S. nebulatus leucomelas* from Ecuador. Elevation of the two subspecies *S. nebulatus leucomelas* and *S. nebulatus hartwegi* to full species status would resolve this paraphyly. However, we refrain from taking this step because our sample size for *S. nebulatus hartwegi* is small, even though plenty of photographic data from references (e.g., Natera-Mumaw et al. 2015) and online sources confirm that long nuchal bands and often brownish color pattern are typical of *S. nebulatus hartwegi* occurring from Medellin, Colombia, east into Venezuela. In addition, the supposedly diagnostic darker ground color of *S. nebulatus leucomelas* with copious blackish stippling of the interspaces and head (Peters 1960) is not exclusive of this subspecies. There is ample evidence (photographic vouchers, preserved specimens, online photo sources) that this color pattern is rather consistent in *S. n. nebulatus* from Nicaragua through Panama, and can even be observed in single specimens as far as the northern limit of the species in Mexico. Furthermore, we have no genetic data of *S. nebulatus* from southern Costa Rica, Panama, and Colombia, which could confirm a clear split between two species, rather than a gradient of two intergrading subspecies.

Sibon bevridgelyi and *S. nebulatus leucomelas* were not recovered as sister taxa in our phylogenetic analyses (Fig. 3), despite being similar in coloration and lepidosis, and having adjacent marginally overlapping distribution ranges in western Ecuador (Fig. 8), a pattern that would suggest an allopatric speciation event. Our phylogeny suggests a more complex scenario that includes *S. dunni* from the dry valley of the Mira River in northwestern Ecuador. In any case, the three species are segregated geographically in western Ecuador, with *S. n. leucomelas* occupying the evergreen lowland and forest of northwestern Chocoan Ecuador, *S. bevridgelyi* the semi-deciduous forest in southwestern Ecuador, and *S. dunni* dry montane shrublands. Whether the current low genetic divergence between these three taxa constitutes a scenario of recent or ongoing gene flow between them is worth addressing further using nuclear markers. Strong local selection may have affected traits other than the mitochondrial genes.

Unlike the previous examples, the pattern of cladogenesis recovered in our phylogeny for the species of the *Dipsas peruana* complex (Fig. 3) suggest that a series of allopatric speciation events could be responsible for the current observed pattern of geographic genetic divergence between *D. peruana* and *D. palmeri* + *D. klebbai*. Two geographic barriers (i.e., Napo and Marañón rivers; Fig. 4) are located between the geographic ranges of the aforementioned species, and these features of the Andean geography have previously been recognized as important barriers to gene flow (Hackett 1993, Funk et al. 2007, Lynch Alfaro et al. 2015).

A different scenario of speciation can be interpreted from the current distribution (Fig. 5) of the clade comprised by *Dipsas georgejetti*, *D. oligozonata*, *D. oswaldobaezi*, and *D. williamsi*. All of these species are adapted to dry shrublands, and the distribution of this vegetation type in northern Peru and south-central Ecuador is not continuous. We hypothesize that the discontinuity of dry shrubland west of the Andes in Ecuador and Peru is what explains best the observed pattern of geographic genetic divergence in this group of snakes.

We suspect that there are numerous additional species to be described across all genera of Dipsadini. Our results and the results of other recent researchers such as Sheehy (2012) indicate that additional taxonomic changes are also needed at the species-group and genus level to create a robust, stable taxonomy that agrees with the molecular phylogeny. Other morphological data such as visceral topology (e.g., Wallach 1995) suggest that morphological synapomorphies may exist for these clades, but are complex and difficult to identify accurately. Hence, in order to clarify species richness and higher-level to detailed relationships in Dipsadini, a systematically intensive revision that includes genetic, biogeographic, and morphological data from the greatest number of species representing the known genera is needed.

Author contributions

Conceived and designed the work: AA JMG DSV OTC. Performed the analyses: AA RAP NP. Gathered morphological data: AA KM GA JCSN TJC RAP DSV DFCH PJV MYM OTC. Contributed reagents/materials/analysis tools: RAP JMG DSV NP GRC PJV TJC DFCH. Wrote the paper: AA DSV KM NP GA JCSN RAP DFCH PJV MYM JMG OTC.

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Appendix I

GenBank accession numbers for loci and terminals of taxa and outgroups sampled in this study. Novel sequence data produced in this study are marked with an asterisk (*).

Species	Voucher	Country	12S	16S	CYTB	ND4	c-mos
A. iridescens	MZUTI 4178	Ecuador	-	KT944040	KY610080	-	KT944066
D. albifrons	MZUSP 13993	Brazil	JQ598803	JQ598866	JQ598925	-	-
D. andiana	MZUTI 3501	Ecuador	-	MH341009*	MH375032*	-	-
D. andiana	MZUTI 3505	Ecuador	-	MH341010*	MH374974*	-	-
D. andiana	MZUTI 5413	Ecuador	-	MH341011*	MH374978*	-	-
D. andiana	QCAZ 10756	Ecuador	-	MH341014*	MH375012*	-	-
D. andiana	QCAZ 13538	Ecuador	-	MH341015*	MH375018*	-	-
D. andiana	QCAZ 5731	Ecuador	-	MH341012*	MH375005*	-	-
D. andiana	QCAZ 8452	Ecuador	-	MH341013*	MH375011*	-	-
D. articulata	USNM 348490	Panama	JQ598804	JQ598867	-	-	-
D. bobridgelyi	MZUTI 5414	Ecuador	-	MH341016*	MH374984*	-	-
D. bobridgelyi	MZUTI 5417	Ecuador	-	MH341017*	MH374985*	-	-
D. bucephala	GRCOLLI 25659	Brazil	MH341087*	MH341018*	MH375026*	MH375052*	MH374932*
D. bucephala	IBSP72899	Brazil	GQ457789	GQ457730	-	-	GQ457850
D. catesbyi	KU 214851	Peru	-	-	EF078537	EF078585	-
D. catesbyi	LSUMNS 13989	Brazil	-	KX660267	KX660536	-	-
D. catesbyi	MZUSP 14664	Brazil	JQ598805	KX694637	KX694856	-	JQ598977
D. catesbyi	QCAZ 13558	Ecuador	MH341088*	MH341019*	MH374975*	MH375042*	MH374933*
D. elegans	DHMECN 10311	Ecuador	-	MH341020*	MH374979*	-	-
D. elegans	MZUTI 3317	Ecuador	-	MH341021*	MH375033*	-	-
D. elegans	MZUTI 3695	Ecuador	-	MH341022*	MH375031*	-	-
D. elegans	ZSFQ 10	Ecuador	-	-	MH374994*	-	-
D. elegans	ZSFQ 151	Ecuador	-	MH341023*	MH374992*	-	-
D. ellipsifera	MZUTI 4931	Ecuador	-	MH341024*	MH375030*	-	MH374934*
D. ellipsifera	TH	Ecuador	-	-	MH374966*	-	MH374935*

Species	Voucher	Country	12S	16S	CYTB	ND4	c-mos
D. georgejetti	MZUA.RE.121	Ecuador	-	MH341025*	MH375024*	-	MH374936*
D. georgejetti	MZUA.RE.122	Ecuador	-	MH341026*	MH375025*	-	MH374937*
D. georgejetti	QCAZ 10589	Ecuador	-	MH341027*	-	-	-
D. gracilis	JMG 070	Ecuador	-	MH341028*	MH374980*	-	MH374938*
D. gracilis	MZUTI 1386	Ecuador	-	MH341029*	MH374970*	-	-
D. gracilis	MZUTI 3331	Ecuador	-	MH341030*	MH374995*	-	-
D. gracilis	MZUTI 3503	Ecuador	-	MH341031*	MH375023*	-	-
D. gracilis	QCAZ 10196	Ecuador	-	MH341033*	MH375000*	-	-
D. gracilis	QCAZ 11238	Ecuador	-	MH341034*	MH375001*	-	-
D. gracilis	QCAZ 12478	Ecuador	-	MH341035*	MH375002*	-	-
D. gracilis	QCAZ 15717	Ecuador	-	MH341036*	MH375013*	-	-
D. gracilis	QCAZ 5265	Ecuador	-	-	MH374998*	-	-
D. gracilis	QCAZ 5886	Ecuador	-	MH341032*	MH374999*	-	-
D. indica	-	French Guiana	NN	AF158488	-	-	-
D. indica ecuadoriensis	QCAZ 13305	Ecuador	MH341089*	MH341037*	MH375006*	MH375043*	MH374939*
D. indica ecuadoriensis	QCAZ 13306	Ecuador	MH341090*	MH341038*	MH375007*	MH375044*	MH374940*
D. indica ecuadoriensis	QCAZ 13561	Ecuador	MH341091*	MH341039*	MH375008*	MH375045*	MH374941*
D. jamespetersi	AMARU 1123	Ecuador	-	MH341040*	-	-	MH374943*
D. jamespetersi	AMARU 383	Ecuador	-	-	-	-	MH374942*
D. jamespetersi	CAMPO 488	Ecuador	-	MH341041*	MH375028*	-	MH374944*
D. jamespetersi	QCAZ 9190	Ecuador	-	MH341042*	MH375014*	-	-
D. klebbai	JMG 050	Ecuador	-	MH341043*	MH375022*	-	MH374945*
D. klebbai	MZUTI 5412	Ecuador	-	MH341045*	MH374977*	-	-
D. klebbai	MZUTI 63	Ecuador	-	MH341044*	MH374986*	-	-
D. klebbai	QCAZ 12717	Ecuador	-	MH341046*	MH375019*	-	-
D. klebbai	QCAZ 12799	Ecuador	-	MH341047*	MH374996*	-	-
D. klebbai	QCAZ 14280	Ecuador	-	MH341048*	-	-	-
D. klebbai	QCAZ 14281	Ecuador	-	MH341049*	-	-	-
D. mikanii	MZUSP 14658	Brazil	GQ457832	GQ457771	KX694855	-	GQ457892
D. neuwiedi	MCP13291	Brazil	GQ457831	GQ457770	-	-	GQ457891

Species	Voucher	Country	12S	16S	CYTB	ND4	c-mos
D. neuwiedi	MZUSP 13972	Brazil	JQ598838	JQ598898	-	-	-
D. oligozonata	MZUA.RE.081	Ecuador	-	MH341050*	MH375029*	-	-
D. oreas	DHMECN 7647	Ecuador	-	MH341051*	MH374971*	-	-
D. oreas	DHMECN 7648	Ecuador	-	MH341052*	MH374967*	-	-
D. oreas	MZUA.RE.239	Ecuador	-	MH341053*	MH374987*	-	-
D. oreas	MZUTI 3351	Ecuador	-	MH341054*	-	MH375038*	-
D. oreas	MZUTI 5415	Ecuador	-	MH341055*	-	-	-
D. oreas	MZUTI 5418	Ecuador	-	MH341056*	MH374981*	-	-
D. oreas	QCAZ 10068	Ecuador	-	MH341057*	MH375015*	-	-
D. oreas	QCAZ 11290	Ecuador	-	MH341058*	MH375016*	-	-
D. oreas	QCAZ 13875	Ecuador	-	MH341059*	MH375017*	-	-
D. oswaldobaezi	QCAZ 10369	Ecuador	-	MH341060*	MH374997*	-	-
D. palmeri	JMG 069	Ecuador	-	MH341061*	MH374976*	-	MH374946*
D. palmeri	MZUTI 4804	Ecuador	-	MH341062*	MH374982*	-	MH374947*
D. palmeri	MZUTI 4975	Ecuador	-	MH341063*	-	-	-
D. palmeri	MZUTI 5419	Ecuador	-	MH341064*	MH374988*	-	MH374948*
D. palmeri	QCAZ 13304	Ecuador	MH341092*	MH341065*	MH375009*	MH375046*	MH374949*
D. palmeri	QCAZ 13307	Ecuador	MH341093*	MH341066*	MH375004*	MH375047*	MH374950*
D. palmeri	QCAZ 13562	Ecuador	MH341094*	MH341067*	MH375010*	MH375048*	MH374951*
D. pavonina	LSUMNS 14372	Brazil	-	KX660268	KX660537	-	-
D. pavonina	MZUTI 4972	Ecuador	-	MH341068*	MH374983*	-	MH374952*
D. peruana	LSUMNS 1532	Peru	-	-	KX660538	-	KX660406
D. pratti	MHUA 14278	Colombia	-	-	GQ334482	GQ334583	-
D. temporalis	QCAZ 5050	Ecuador	-	MH341069*	MH375003*	-	-
D. turgida	FML 14969	Argentina	JQ598839	JQ598899	KX660547	-	-
D. turgida	LSUMNS 6459	-	-	KX660279	-	KX660659	KX660418
D. vaga	KU 219121	Peru	-	KX660252	-	-	KX660393
D. variegata	MZUSP 14665	Brazil	-	GQ457731	-	-	GQ457851
D. variegata	-	-	AF158406	AF158476	-	-	-
D. ventrimaculata	MCP4870	Brazil	JQ598840	JQ598900	-	-	JQ598997

Species	**Voucher**	**Country**	**12S**	**16S**	**CYTB**	**ND4**	**c-mos**
D. vermiculata	MZUTI 3663	Ecuador	-	MH341070*	MH374989*	-	-
D. vermiculata	QCAZ 13563	Ecuador	MH341095*	MH341071*	MH374972*	MH375049*	MH374953*
D. vermiculata	QCAZ 13582	Ecuador	MH341096*	MH341072*	-	MH375040*	MH374954*
D. vermiculata	QCAZ 13825	Ecuador	-	MH341073*	MH374973*	MH375050*	MH374955*
D. vermiculata	SBI 171139	Peru	Z46459	Z46496	-	-	-
D. williamsi	CORBIDI 12695	Peru	-	-	MH374968*	MH375041*	-
D. williamsi	CORBIDI 12919	Peru	-	-	MH374969*	MH375039*	-
G. godmani	-	-	JQ598814	JQ598877	JQ598932	-	-
S. annulatus	ADM 0007	Costa Rica	-	KX660170	KX660444	KX660573	KX660309
S. annulatus	ADM 242	Costa Rica	-	KX660169	KX660443	KX660572	KX660308
S. annulatus	MVZ 269290	Nicaragua	MH341097*	MH341074*	MH375034*	MH375053*	MH374956*
S. annulatus	MZUTI 3034	Ecuador	-	MH341075*	MH375021*	-	-
S. anthracops	MVZ 215680	Costa Rica	MH341098*	MH341076*	MH375035*	MH375054*	MH374957*
S. bevridgelyi	MZUA.RE.424	Ecuador	-	-	MH374990*	-	-
S. bevridgelyi	MZUTI 3269	Ecuador	-	MH341077*	MH374962*	-	-
S. bevridgelyi	MZUTI 5416	Ecuador	-	MH341078*	MH374963*	-	-
S. dimidiatus	LSUMNS 6689	-	-	KX660278	-	-	KX660417
S. dunni	CAMPO 533	Ecuador	-	MH341079*	MH374991*	-	-
S. longifrenis	MVZ 215681	Costa Rica	MH341099*	MH341080*	MH375036*	MH375055*	MH374958*
S. merendonensis	MVZ 263880	Guatemala	MH341100*	MH341081*	MH375037*	MH375056*	MH374959*
S. nebulatus hartwegi	MHUA14511	Colombia	-	-	GQ334556	GQ334662	-
S. nebulatus leucomelas	DHMECN 9585	Ecuador	-	MH341082*	-	-	-
S. nebulatus leucomelas	MZUTI 3911	Ecuador	-	MH341083*	MH374964*	-	-
S. nebulatus leucomelas	MZUTI 4810	Ecuador	-	MH341084*	MH374965*	-	MH374960*
S. nebulatus nebulatus	Belize	Belize	AF544777	AF544806	-	-	AF544736
S. nebulatus nebulatus	MVZ 233298	Costa Rica	EU728583	EU728583	EU728583	EU728583	-
T. fasciata	TJC 666	Mexico	MH341101*	MH341085*	MH375027*	MH375057*	MH374961*
T. fischeri	MVZ 143527	Guatemala	MH341102*	MH341086*	MH374993*	MH375051*	-
T. sartorii	KU 289806	El Salvador	-	-	EF078540	EF078588	-

Appendix 2

List of PCR and sequencing primers and their respective PCR conditions (denaturation, annealing, extension and number of corresponding cycles) used in this study. All PCR protocols included an initial 3-min step at 94 °C and a final extension of 10 min at 72 °C.

Locus	Primer name	Sequence (5'-3')	Reference	PCR profile:
16S	16Sar-L	CGCCTGTTTATCAAAAACAT	Palumbi et al. (1991)	30 cycles of 94 °C (45 sec), 53 °C (45 sec), 72 °C (1 min)
	16Sbr-H-R	CCGGTCTGAACTCAGATCACGT		
Cytb	GLUDG-L	TGACTTGAARAACCAYCGTTG	Palumbi et al. (1991)	35–42 cycles of 95°C (30 sec), 50 or 56 °C (45 sec), 72 °C (45 sec)
	ATRCB3	TGAGAAGTTTTCYGGGTCRTT	Harvey et al. (2000)	
ND4	ND4	CACCTATGACTACCAAAAGCTCATGTAGAAGC	Arévalo et al. (1994)	94 °C (25 sec), 56 or 60 °C (1 min), 72 °C (2 min) [x25–30]
	Leu	CATTACTTTTACTTGGATTTGCACCA		
c-mos	S77	CATGGACTGGGATCAGTTATG	Lawson et al. (2005)	1 cycle of 94 °C (3 min), 56 °C (45 sec), 72 °C (1 min), followed by 34 cycles of 94 °C (45 sec), 56 °C (45 sec), 72 °C (1 min)
	S78	CCTTGGGTGTGATTTTCTCACCT		

Appendix 3

Morphological data and sex for specimens of Dipsadini species examined. Codes: V = ventrals; SC = subcaudals; D1–3 = dorsal scale rows at neck, midbody, and vent; PO = postoculars; SL = supralabials; IL = infralabials; SVL = snout-vent length (mm); TL = tail length (mm); M = Male, F = Female.

Species	Voucher	V	SC	D1	D2	D3	PO	SL	IL	SVL	TL	Sex
D. andiana	MZUA.RE.0230	187	96	15	15	15	3	9	11	744	196	M
D. andiana	MHNG 2250.053	194	85	15	15	15	2	9	12	292	71	F
D. andiana	MZUTI 5413	190	101	14	15	15	2	10	11	471	165	M
D. andiana	MZUTI 3501	187	98	15	15	15	2	9	12	398	137	M
D. andiana	MZUTI 3505	192	–	15	15	15	2	8	10	674	167	F
D. andiana	ZSFQ D115	189	84	15	15	15	2	10	10	680	150	F
D. andiana	ZSFQ D116	186	90	15	15	15	2	10	10	453	149	M
D. andiana	ZSFQ D117	189	101	15	15	15	2	9	9	405	139	M
D. bobridgelyi	QCAZ 1706	201	117	15	15	15	2	9	12	445	212	M
D. bobridgelyi	DHMECN 11527	178	98	15	15	15	2	9	12	404	158	F
D. bobridgelyi	MZUTI 3266	184	96	15	15	15	2	9	11	286	117	F
D. bobridgelyi	MZUTI 5414	180	95	15	15	15	2	9	13	478	195	M
D. bobridgelyi	MZUTI 5417	182	101	15	15	15	2	9	13	372	158	M
D. catesbyi	MHNG 2220.054	180	98	13	13	13	1	8	9	366	147	F

Species	Voucher	V	SC	D1	D2	D3	PO	SL	IL	SVL	TL	Sex
D. catesbyi	MHNG 2238.005	176	94	13	13	13	2	9	10	420	155	F
D. catesbyi	USNM 283949	168	81	13	13	13	1	7	8	276	98	F
D. catesbyi	DHMECN 11555	164	97	–	–	–	2	7	–	222	80	–
D. catesbyi	QCAZ 181	172	93	13	13	13	2	9	10	470	169	F
D. catesbyi	MHNG 2220.052	175	83	13	13	13	1	8	10	505	180	F
D. catesbyi	QCAZ 210	199	97	13	13	13	2	8	9	441	165	F
D. catesbyi	MHNG 2206.086	183	108	13	13	13	1	8	9	480	202	M
D. catesbyi	MHNG 2435.097	184	98	13	13	13	1	8	10	308	117	F
D. catesbyi	QCAZ 5108	197	105	13	13	13	2	7	8	583	223	M
D. catesbyi	MHNG 2249.001	178	93	13	13	13	2	8	9	311	112	F
D. catesbyi	QCAZ 28	181	101	13	14	13	2	8	10	591	232	F
D. catesbyi	MHNG 2238.014	175	93	13	13	13	2	8	9	429	158	F
D. catesbyi	MHNG 2307.091	181	92	13	13	13	2	7	9	431	155	F
D. catesbyi	MZUTI 4736	187	103	13	13	13	2	8	10	454	186	M
D. catesbyi	MZUTI 4999	177	93	13	13	13	2	9	9	397	160	M
D. elegans	MHNG 2435.084	178	102	15	15	15	2	6	10	305	111	M
D. elegans	MHNG 2440.098	180	98	15	15	15	2	7	11	178	65	F
D. elegans	DHMECN 1693	181	97	15	15	15	2	7	9	119	71	M
D. elegans	MHNG 2457.078	182	94	15	15	15	1	7	10	183	65	F
D. elegans	MHNG 2249.019	179	95	15	15	15	2	6	11	505	195	M
D. elegans	MHNG 2413.074	178	93	15	15	15	1	7	11	607	211	F
D. elegans	USNM 285957	183	100	15	15	13	2	7	11	152	60	–
D. elegans	MHNG 2399.072	180	82	15	15	15	1	7	9	555	161	F
D. elegans	MZUTI 3695	182	102	15	15	15	2	7	11	296	102	M
D. elegans	MZUTI 3317	186	108	15	15	15	2	7	11	409	175	M
D. elegans	MHNG 2457.079	177	90	15	15	15	2	7	9	687	246	F
D. elegans	MHNG 2308.002	180	90	15	15	13	2	7	10	605	212	F
D. elegans	MHNG 2220.093	181	109	15	15	15	1	8	10	591	251	M
D. elegans	MZUTI 3316	182	86	15	15	15	1	8	11	657	220	F
D. ellipsifera	MZUTI 4931	164	86	15	15	15	2	7	10	229	79	M
D. ellipsifera	QCAZ 14855	175	93	15	15	15	2	8	7	580	230	M
D. ellipsifera	QCAZ 15225	183	101	15	15	15	2	6	8	488	234	M
D. ellipsifera	MHNG 2220.048	163	62	15	15	15	2	7	8	406	114	F
D. gracilis	QCAZ 4137	185	94	15	15	15	2	8	9	289	128	M
D. gracilis	QCAZ 14495	179	99	15	15	15	2	10	11	530	235	F
D. gracilis	QCAZ 7321	189	98	15	15	15	2	11	10	361	150	M
D. gracilis	MZUA.RE.0280	189	101	13	13	13	3	10	12	590	172	F
D. gracilis	MZUA.RE.0281	184	110	15	15	15	2	10	12	343	100	–
D. gracilis	QCAZ 12478	193	102	15	15	15	2	11	10	425	161	M
D. gracilis	MHNG 2309.038	190	–	15	15	15	2	8	11	291	92	M
D. gracilis	QCAZ 10196	180	89	15	15	15	2	10	12	283	110	M
D. gracilis	USNM 285477	203	118	15	15	15	3	9	13	356	166	M
D. gracilis	USNM 285478	197	118	15	15	15	3	9	12	416	189	–
D. gracilis	USNM 285479	203	131	15	15	15	3	9	12	418	199	M
D. gracilis	USNM 285480	193	107	15	15	15	2	10	11	181	74	–
D. gracilis	DHMECN 2902	205	121	15	15	15	2	7	11	554	265	M
D. gracilis	QCAZ 11427	196	–	15	15	15	2	9	11	365	150	M
D. gracilis	MHNG 1363.023	206	120	15	15	15	3	11	11	395	187	M

Species	Voucher	V	SC	D1	D2	D3	PO	SL	IL	SVL	TL	Sex
D. gracilis	MHNG 1363.024	210	122	15	15	14	3	10	12	458	210	M
D. gracilis	MHNG 1363.026	201	113	15	15	15	2	9	12	464	203	F
D. gracilis	MHNG 1363.027	209	118	15	15	15	2	10	11	426	193	M
D. gracilis	MHNG 2453.019	203	113	15	15	15	2	9	11	332	142	F
D. gracilis	QCAZ 14494	203	109	15	15	15	2	7	8	473	220	M
D. gracilis	MZUTI 1386	194	110	15	15	15	2	9	12	451	187	F
D. gracilis	MZUTI 3503	197	113	15	15	15	2	9	10	468	199	F
D. gracilis	DHMECN 129	192	101	15	15	15	2	9	11	425	191	M
D. gracilis	MZUTI 4199	205	109	15	15	15	2	10	11	402	166	F
D. indica	MZUA.RE.0059	180	97	13	13	13	2	9	15	1153	293	F
D. indica	MHNG 2435.093	196	95	13	13	11	2	9	14	537	172	F
D. indica	MHNG 2413.076	197	109	13	13	11	2	9	14	327	121	M
D. indica	MZUTI 4735	199	112	13	13	13	2	9	14	672	230	M
D. jamespetersi	MZUA.RE.0147	178	71	15	15	15	2	8	13	663	156	M
D. jamespetersi	MZUTI 5307	178	75	15	15	15	2	7	11	560	156	H
D. jamespetersi	USNM 237040	183	84	15	15	15	2	8	11	150	61	–
D. jamespetersi	MHNG 2512.047	171	81	15	15	15	2	8	9	424	152	M
D. jamespetersi	MHNG 2512.048	186	76	15	15	15	2	8	12	511	157	F
D. jamespetersi	MHNG 2399.071	178	73	15	15	15	2	8	10	469	136	F
D. jamespetersi	MHNG 2457.09	179	69	15	15	15	2	8	11	–	–	F
D. jamespetersi	MHNG 2512.049	169	83	15	15	15	3	8	10	421	154	M
D. jamespetersi	MHNG 2512.05	190	–	15	15	15	2	8	9	466	125	F
D. jamespetersi	MHNG 2521.087	178	81	15	15	15	3	8	9	378	133	M
D. jamespetersi	QCAZ 15100	185	98	15	15	15	2	8	7	412	133	M
D. jamespetersi	MHNG 2413.082	185	73	15	15	15	2	8	11	505	143	F
D. klebbai	QCAZ 1605	181	97	15	15	15	2	9	10	569	251	M
D. klebbai	DHMECN 568	–	104	15	15	15	2	10	13	630	240	F
D. klebbai	MHNG 2220.035	194	115	15	15	15	2	11	14	286	118	F
D. klebbai	MHNG 2220.056	185	106	13	13	13	2	8	8	505	209	M
D. klebbai	MHNG 2250.063	197	104	15	15	15	2	9	12	489	199	M
D. klebbai	MHNG 2250.064	196	109	15	15	15	2	10	12	401	169	M
D. klebbai	MZUTI 5412	188	116	15	15	15	2	10	14	608	262	M
D. klebbai	USNM 286323	198	117	15	15	15	2	8	11	263	105	F
D. klebbai	MHNG 2220.038	193	106	15	15	15	2	9	11	570	219	F
D. klebbai	MHNG 2220.039	190	109	15	15	15	2	11	12	500	204	M
D. klebbai	MZUTI 63	199	112	15	15	15	2	10	12	701	297	M
D. klebbai	MHNG 2220.04	191	102	15	15	15	2	9	13	525	210	F
D. klebbai	MHNG 2220.041	187	101	15	15	15	2	9	13	604	229	F
D. klebbai	QCAZ 250	184	99	15	15	15	2	9	12	495	205	M
D. klebbai	QCAZ 14281	201	123	15	15	15	2	9	11	749	330	M
D. klebbai	MHNG 2529.029	188	98	15	15	15	2	9	12	534	209	F
D. klebbai	ZSFQ D304	189	101	15	15	15	2	9	11	303	121	F
D. georgejetti	USNM 142595	182	59	15	15	15	2	7	11	131	30	M
D. georgejetti	MZUTI 5411	178	69	15	16	15	2	7	9	315	87	M
D. georgejetti	DHMECN 11639	172	86	15	15	15	2	7	10	270	90	M
D. georgejetti	MZUA.RE.0121	177	58	15	15	15	2	7	10	856	150	F
D. georgejetti	MZUA.RE.0122	175	79	15	15	15	2	7	9	711	170	M
D. georgejetti	DHMECN 11646	180	72	15	15	15	2	7	9	382	140	M

Species	Voucher	V	SC	D1	D2	D3	PO	SL	IL	SVL	TL	Sex
D. georgejetti	ZSFQ D606	182	63	15	15	15	2	7	10	163	51	M
D. oligozonata	MZUA.RE.0081	144	62	15	15	15	2	8	10	446	127	M
D. oligozonata	MZUA.RE.0240	150	53	15	15	15	2	7	12	772	154	F
D. oligozonata	MZUA.RE.0020	149	60	15	15	15	2	8	10	632	134	M
D. oligozonata	MZUA.RE.0357	138	63	15	15	15	2	8	11	538	139	M
D. oreas	DHMECN 7647	168	77	15	15	15	2	7	11	270	106	M
D. oreas	DHMECN 7666	170	79	15	15	15	2	8	12	532	107	M
D. oreas	MZUA.RE.0239	171	84	15	15	15	2	7	11	785	214	M
D. oreas	MZUA.RE.0290	182	95	15	15	15	2	7	13	561	138	–
D. oreas	QCAZ 9190	181	93	15	15	15	2	7	10	495	191	F
D. oreas	USNM 62797	180	77	15	15	15	2	8	11	377	124	F
D. oreas	USNM 62798	178	75	–	15	15	–	–	11	367	120	M
D. oreas	USNM 62800	180	84	15	15	15	2	8	12	144	46	M
D. oreas	DHMECN 10785	198	97	15	15	15	2	7	11	222	76	M
D. oreas	DHMECN 2572	178	89	15	15	15	2	7	11	417	141	M
D. oreas	MZUTI 3351	177	87	14	15	15	2	7	10	473	181	M
D. oreas	MZUTI 5415	178	75	15	15	15	2	7	11	487	156	M
D. oreas	MZUTI 5418	183	86	15	15	15	2	7	10	252	81	M
D. oreas	MHNG 2514.028	176	–	15	15	15	2	7	11	384	128	M
D. oreas	MHNG 2521.084	171	79	15	15	15	2	9	12	571	184	F
D. oreas	QCAZ 10068	157	84	15	15	15	2	8	11	181	60	M
D. oreas	QCAZ 13875	175	63	15	15	15	2	7	10	499	151	M
D. oreas	QCAZ 11290	176	102	14	14	14	2	9	12	334	131	M
D. oreas	QCAZ 6020	167	59	15	15	15	2	7	–	586	149	M
D. palmeri	QCAZ 11411	192	107	15	15	15	2	9	12	470	193	M
D. palmeri	QCAZ 5609	193	–	15	15	15	2	9	13	753	271	M
D. palmeri	QCAZ 13307	186	118	15	15	15	2	8	11	660	278	M
D. palmeri	QCAZ 13562	189	91	15	15	15	2	9	11	215	78	M
D. palmeri	QCAZ 4710	182	97	15	15	15	2	9	12	472	200	M
D. palmeri	AMNH 24126	196	116	15	15	15	2	9	13	234	91	M
D. palmeri	MZUTI 4804	190	101	15	15	15	3	8	10	602	269	M
D. palmeri	MZUA.RE.0044	181	86	15	15	15	2	9	10	893	225	F
D. palmeri	QCAZ 14071	187	101	15	15	15	2	9	11	642	246	F
D. palmeri	QCAZ 3288	185	103	15	15	15	2	9	11	615	274	M
D. palmeri	MZUTI 3956	202	116	15	15	15	2	10	12	656	239	M
D. palmeri	AMNH 37939	190	–	15	15	15	2	9	13	694	188	M
D. palmeri	QCAZ 13992	192	97	15	15	15	2	9	11	–	–	M
D. palmeri	QCAZ 4564	185	109	15	15	15	2	9	11	248	93	M
D. palmeri	QCAZ 6021	196	103	15	15	15	2	9	12	791	290	M
D. palmeri	QCAZ 14338	172	110	15	15	15	2	9	12	907	390	M
D. palmeri	QCAZ 12771	197	104	15	15	15	2	9	12	273	98	M
D. palmeri	MZUTI 4971	196	106	15	15	15	2	8	12	332	121	M
D. palmeri	MZUTI 4975	191	114	15	15	15	2	8	11	631	299	M
D. palmeri	QCAZ 12772	182	101	15	15	15	2	9	12	403	146	M
D. palmeri	MZUTI 5419	189	117	15	15	15	2	9	13	658	286	M
D. palmeri	QCAZ 12510	182	93	15	15	15	2	9	12	740	252	F
D. palmeri	MZUA.RE.0119	200	102	15	15	15	2	9	12	1187	298	F
D. pavonina	MZUA.RE.0198	211	119	13	13	13	3	11	13	745	241	M

Species	Voucher	V	SC	D1	D2	D3	PO	SL	IL	SVL	TL	Sex
D. pavonina	QCAZ 5554	187	95	13	13	13	2	10	12	493	256	M
D. pavonina	MHNG 2309.039	204	–	13	13	13	2	9	11	341	90	M
D. pavonina	MHNG 2521.088	198	117	13	13	13	2	10	12	413	196	M
D. pavonina	MZUTI 4972	196	115	13	13	13	2	9	10	441	207	M
D. peruana	AMNH 147037	187	111	15	15	15	2	9	13	199	85	M
D. peruana	USNM 60718	177	75	15	15	15	3	9	12	258	79	M
D. peruana	USNM 299232	188	92	15	15	15	2	9	13	467	198	M
D. peruana	USNM 299233	200	127	15	15	15	2	9	12	235	99	M
D. oswaldobaezi	MZUA.RE.0286	185	61	15	15	15	2	6	9	395	70	–
D. oswaldobaezi	QCAZ 10369	179	70	15	15	15	2	6	9	277	85	M
D. oswaldobaezi	QCAZ 14051	175	66	15	15	15	2	6	7	287	86	–
D. oswaldobaezi	QCAZ 14060	180	64	15	15	15	2	6	8	500	132	–
D. oswaldobaezi	QCAZ 15108	179	65	15	15	15	2	6	9	407	110	F
D. temporalis	MZUTI 3331	202	113	15	15	15	2	9	11	226	92	F
D. temporalis	MHNG 2521.083	175	116	15	15	15	1	7	9	234	111	F
D. vagrans	AMNH 63373	153	82	15	15	15	2	9	11	302	129	M
D. vermiculata	MHNG 2521.085	181	93	15	15	15	–	–	–	215	81	F
D. vermiculata	DHMECN 11197	181	116	13	13	13	2	8	9	109	84	M
D. vermiculata	MHNG 2436.014	182	103	13	13	13	2	9	8	270	104	M
D. vermiculata	MZUTI 5080	183	113	13	13	13	2	7	9	515	220	M
D. vermiculata	QCAZ 13825	191	116	15	15	15	2	8	9	588	279	M
D. vermiculata	MZUTI 4738	183	105	13	13	13	2	7	9	234	90	M
D. vermiculata	MZUTI 3663	181	98	13	13	13	2	8	9	542	195	M
D. vermiculata	MZUA.RE.0261	183	107	13	13	13	1	8	9	689	190	M
S. annulatus	MZUTI 3034	197	–	15	15	14	2	7	8	464	70	M
S. bevridgelyi	AMNH 22092	185	88	15	15	15	2	7	10	572	268	M
S. bevridgelyi	MZUA.RE.0424	181	82	15	15	15	2	7	8	515	126	M
S. bevridgelyi	QCAZ 14446	181	94	15	15	15	2	8	7	545	220	M
S. bevridgelyi	QCAZ 14444	179	80	15	15	15	2	7	8	487	156	M
S. bevridgelyi	MZUA.RE.0142	193	98	15	15	15	2	7	7	786	204	F
S. bevridgelyi	DHMECN 9483	182	91	15	15	15	2	7	11	436	158	M
S. bevridgelyi	MZUTI 3269	175	88	15	15	15	2	7	9	349	124	M
S. bevridgelyi	MZUTI 5416	184	80	15	16	15	2	7	9	602	186	M
S. bevridgelyi	ZSFQ D503	182	87	15	15	15	2	7	9	405	122	M
S. nebulatus	MZUTI 4810	187	–	15	15	15	2	7	7	480	110	F
S. nebulatus	MZUTI 3911	186	67	15	15	15	2	7	9	280	90	M
S. nebulatus	USNM 285501	184	95	15	15	15	2	7	8	363	127	M
S. nebulatus	MZUA.RE.0328	183	95	15	15	15	2	8	10	732	190	M
S. nebulatus	MZUA.RE.0174	178	78	15	15	15	2	7	9	714	170	F
S. nebulatus	USNM 285498	184	80	15	15	15	2	8	10	235	79	–
S. nebulatus	USNM 285499	189	90	15	15	15	2	7	9	267	101	M
S. nebulatus	USNM 285500	183	95	15	15	15	2	7	9	316	124	–
S. nebulatus	MZUTI 5342	185	103	15	15	15	2	7	7	324	104	M
S. nebulatus	DHMECN 10061	198	89	15	15	15	2	7	11	447	143	M
S. nebulatus	USNM 283534	183	94	15	15	15	2	7	9	501	185	–