

Revision of fossil Metretopodidae (Insecta, Ephemeroptera) in Baltic amber – Part 4: Description of two new species of *Siphloplecton* Clemens, 1915, with notes on the new *S. jaegeri* species group and with key to fossil male adults of *Siphloplecton*

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Abstract

The *Siphloplecton jaegeri* species group is established here for three extinct species, namely for the earlier described *Siphloplecton jaegeri* Demoulin, 1968, and for two new species from Eocene Baltic amber, *Siphloplecton landolti* **sp. nov.** and *Siphloplecton studemannae* **sp. nov.** Based on the well-preserved specimens of these species, a diagnosis is provided for the newly established species group. Representatives of the *S. jaegeri* species group are characterized by the presence of large, medially contiguous eyes, stout pointed setae along the outer margin of the foretibia, three intercalaries in the cubital field of the forewing, and elongated penis lobes, which are apically triangular or rounded, medially contiguous, and with a V-shaped cleft apically. Further new specimens of the *S. jaegeri* species group are documented that cannot be attributed to species level due to their poor preservation. Finally, a key to male adults of fossil species of *Siphloplecton* is given.

Keywords

Fossil insects, mayflies, Siphonuroidea, new species, species group, Eocene

Introduction

Metretopodidae Traver, 1935 is a small, monophyletic mayfly family of Holarctic distribution, comprising 11 extant species in three genera (Berner 1978; Kluge 2004). While *Metretopus* Eaton, 1901 is distributed throughout the Holarctic, the extant distribution of *Siphloplecton* Clemens, 1915 is restricted to the Nearctic, and *Metreplecton* Kluge, 1996 is only found in the Palearctic. Recently, Staniczek and Godunko (2012, 2015, 2016) provided an overview of the taxonomic history of fossil Metretopodidae, which are only known from Eocene Baltic amber. They addressed the two fossil species of *Siphloplecton* Clemens, 1915 treated by Demoulin (1968): *S. jaegeri* Demoulin, 1968 was redescribed, whereas the lectotype of *S. macrops* (Pictet-Baraban & Hagen, 1856) was considered to be lost (Staniczek and Godunko 2012). Additionally, *S. barabani* Staniczek & Godunko, 2012; *S. picteti* Staniczek & Godunko, 2012; *S. hageni* Staniczek & Godunko, 2012; and *S. demoulini* Staniczek & Godunko, 2012 were described from historical material (Staniczek and Godunko 2012). The hitherto described fossil material of *Metretopus* (Demoulin, 1970) was also revised (Staniczek and Godunko 2015), and *M. dividus* Staniczek & Godunko, 2015 was described from new material. In a third part of the revision of fossil Metretopodidae, the rediscovery of the *S. macrops* lectotype was documented (Staniczek and Godunko 2016). Based on new material, complementary descriptions of *S. picteti* and *S. barabani* were given, and the *picteti* and *demoulini* species groups were established within *Siphloplecton*. Finally, two new species, *S. sartorii* Staniczek & Godunko, 2016 and *S. gattolliati* Staniczek & Godunko, 2016, were described from newly emerged material and attributed to these species groups, respectively (Staniczek and Godunko 2016).

In this fourth contribution to the knowledge of fossil Metretopodidae, we establish the *jaegeri* species group within *Siphloplecton* based on newly available material. Two recently discovered, well preserved male imagines from Baltic amber provide new data for a complementary description of the fossil species *Siphloplecton jaegeri*; two new species, *S. landolti* sp. nov. and *S. studemannae* sp. nov., are described and attributed to this species group; and finally, further two new specimens of the *S. jaegeri* group are documented that cannot be attributed to species level due to their poor conservation.

Material and methods

All specimens examined in this study are housed in the following collections (for details see under *Material examined* in the species descriptions):

- CCHH** collection of Christel and Hans Werner Hoffeins, Hamburg, Germany (later to be housed at Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI));
- MNB** Museum für Naturkunde, Berlin, Germany;
- MNHK** Museum of Natural History, Institute of Systematics and Evolution of Animals, PAS, Kraków, Poland;

MNHN Muséum national d'Histoire naturelle, Paris, France;

SMNS Staatliches Museum für Naturkunde Stuttgart, Germany.

Drawings were made with a camera lucida on an Olympus SZX7, a Leica S8 APO and a Leica M205 C stereo microscopes. Multiple photographs with different depth of field were taken through a Leica Z16 APO Macroscope using Leica Application Suite v. 3.1.8. Photo stacks were processed with Helicon Focus Pro 6.4.1 to obtain combined photographs with extended depth of field, and subsequently enhanced with Adobe Photoshop CS3.

Systematic palaeontology

Order Ephemeroptera Hyatt & Arms, 1890

Family Metretopodidae Traver, 1935

Genus *Siphloplecton* Clemens, 1915

Siphloplecton jaegeri species group

Diagnosis. Male imago: (1) eyes large, medially contiguous; (2) outer margin of foretibia with several stout, pointed setae; (3) cubital field with three long intercalary veins: one long intercalary vein connected with CuA by one or several crossveins; one pair of intercalary veins situated close to CuP and at least connected with CuA (or additionally with CuP) by a crossvein; (4) styliger plate angulate, mediocaudally only shallowly incised; incisions with relatively small pronounced triangular projections; with or without medial projection, if present, small and bluntly pointed apically; (5) forceps relatively long; basal segment conical, without apical hump on inner margin; (6) penis stem elongated; (7) penis significantly surmounting distal end of styliger plate, reaching 0.25–0.30× length of forceps segment 2; (8) penis lobes elongated, apically triangular or rounded, medially contiguous, with V-shaped cleft apically.

Species composition. *Siphloplecton jaegeri* Demoulin, 1968, *Siphloplecton landolti* sp. nov., *Siphloplecton studemannae* sp. nov., *Siphloplecton* sp. 5, *Siphloplecton* sp. 6.

Siphloplecton jaegeri Demoulin, 1968

Figures 1–4; Table 1

Siphloplecton jaegeri Demoulin, 1968 – *Deutsche Entomologische Zeitschrift*: 252, figs 18a, c (description, designation of holotype)

Siphloplecton jaegeri Demoulin, 1968 – Staniczek and Godunko 2012, *Paleodiversity*: 73, figs 10a, b, 11a–c (redescription of holotype). For complete list of synonymies see Staniczek and Godunko (2012: 73).

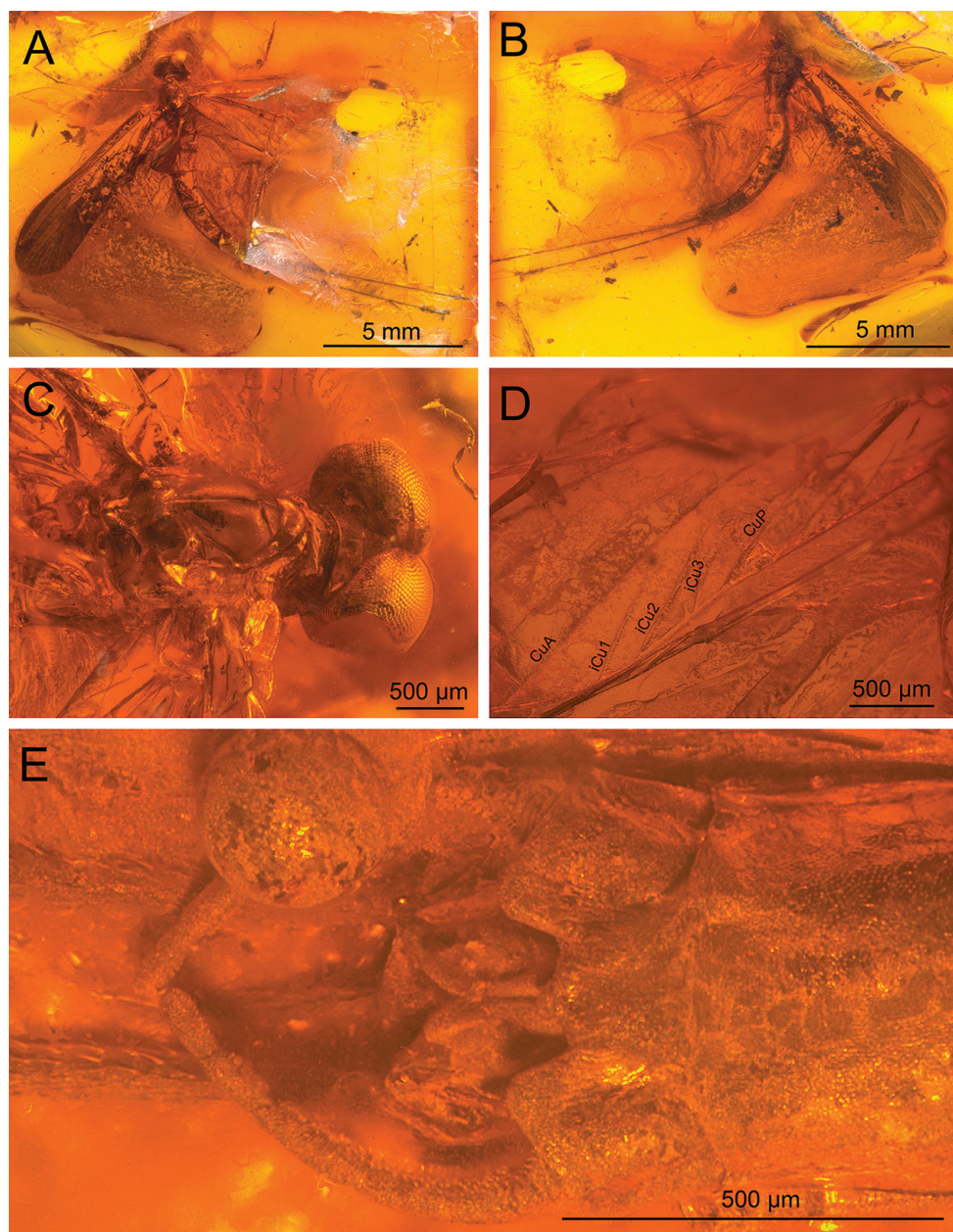


Figure 1. *Siphloplecton jaegeri* Demoulin, 1968, MNB, MB.I 7370, male imago (photographs) **A** general dorsal view **B** general ventral view **C** head and thorax in dorsal view **D** right forewings (details of cubital field in ventral view) **E** genitalia in ventral view.

Material examined. Male imago in Baltic amber (Eocene), MNB, MB.I 7370, specimen labelled as: “6. Pseudoneuroptera III Ephemeridae”; “Museum für Naturkunde Berlin”; “Paläontologisches Museum”; “Slg.: Künow Inv. Nr.: Nr. 268–294 nur noch



Figure 2. *Siphloplecton jaegeri* Demoulin, 1968, MNB, MB.I 7370, male imago (line drawing): general dorsal view.

9 Stück vorgefunden”; “Ephemeriden”; “*Siphloplecton* cf. *jaegeri* ♂ imago Nr.: 271” (Figs 1A–E, 2).

Well preserved specimen, visible in dorsoventral aspect. Wings completely preserved (Fig. 1A, B); posterior margin of left forewing and hind wings twisted. Ventral

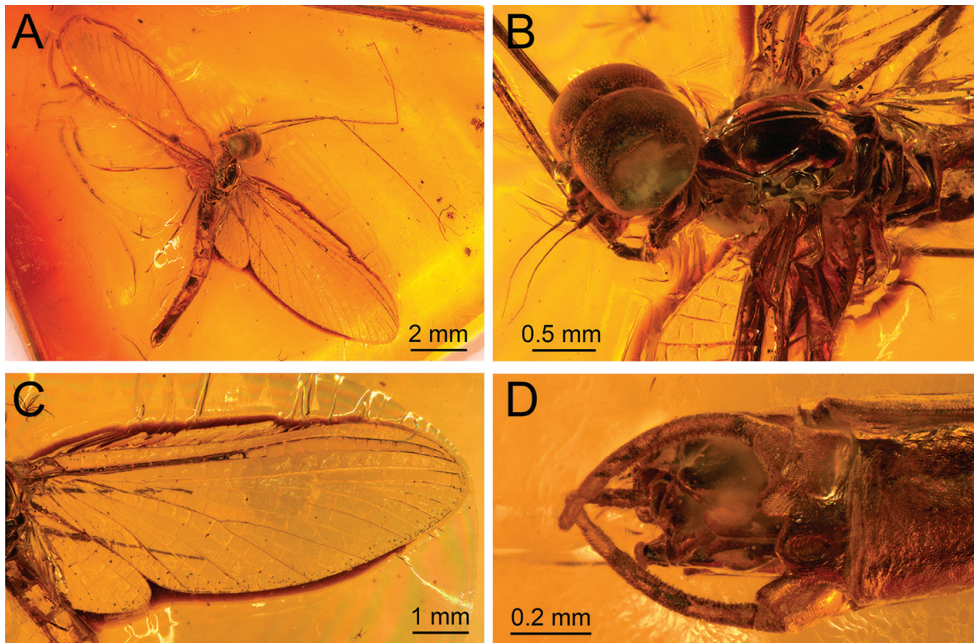


Figure 3. *Siphloplecton jaegeri* Demoulin, 1968, MNHN, 4655 BA, male imago (photographs) **A** general dorsal view (tip of abdomen twisted to ventral side) **B** head and thorax in dorsolateral view **C** right fore- and hind wing in dorsal view **D** genitalia in ventral view.

side of head and prosternum not visible, view obstructed by resin influx and cracks in stone. Foremargin and distal part of left forewing and entire left hind wing dirty brownish coloured; several dark spots on remaining part of left forewing. Such irregular pigmentation is a side effect of the specific conditions of fossilization, and must not be confused with the natural pigmentation of *Siphloplecton* wings (the right wings of the same specimen are colourless and translucent). Right fore- and left middle legs lost. Cerci partly damaged.

For measurements see Table 1.

Male imago in Baltic amber (Eocene), MNHN, 4655 BA (Figs 3–4).

The specimen is visible in dorsoventral and, partly, lateral aspect. Head and thorax ventrally with “Verlummung”. Right fore- and hind wings fully preserved; left pair of wings partly twisted; details of cubital field not discernible. Cerci lost.

Colour yellow to yellowish-brown with darker thorax, but generally paler than all other known specimens of *S. jaegeri*. Wings hyaline, translucent, without any pigmentation.

For measurements see Table 1.

Description of specimens. General colouration from pale (yellow to yellowish-brown), to dark brown (yellowish-brown to intensively brown); details of wing colouration are described above.

Head uniformly brown. Eyes large, well developed, medially contiguous (Figs 1C, 2, 3A, 4A), slightly flattened laterally (MNB specimen); ocelli of MNHN specimen

Table 1. Measurements of fossil representatives of the *Siphloplecton jaegeri* species group.

Adult characters	<i>Siphloplecton jaegeri</i> [MNB, MB.I 7370, male imago] (mm)	<i>Siphloplecton jaegeri</i> [MNH, 4655 BA, male imago] (mm)	<i>Siphloplecton landolti</i> sp. nov. [SMNS, BB-2377, holotype, male imago] (mm)	<i>Siphloplecton</i> <i>studenianae</i> sp. nov. [SMNS, BB-2626, holotype, female imago] (mm)	<i>Siphloplecton</i> <i>studenianae</i> sp. nov. [MNHK, MP/1626, paratype, female imago] (mm)	<i>Siphloplecton</i> sp. 5 [CCHH, BaB 1159/5, male imago] (mm)	<i>Siphloplecton</i> sp. 6 [MNB, MB.I 7372, male subimago] (mm)
Length of body	9.00	9.08	10.88	10.04	9.48	9.50	8.50
Length of right foreleg	–	9.64	–	–	–	–	5.11
Length of femur	–	1.80	–	–	–	–	1.77
Length of tibia	–	2.00	–	–	–	–	1.05
Length of tarsus	–	5.84	–	–	–	–	2.29
Tarsomere 1	–	1.40	–	–	–	–	0.48
Tarsomere 2	–	1.40	–	–	–	–	0.45
Tarsomere 3	–	1.44	–	–	–	–	0.48
Tarsomere 4	–	1.20	–	–	–	–	0.53
Tarsomere 5	–	0.40	–	–	–	–	0.35
Length of left foreleg	8.54	9.40	3.44*	4.04*	–	13.44	5.04
Length of femur	1.75	1.80	1.04*	2.02*	–	3.12	1.73
Length of tibia	1.95	1.88	2.40	1.52	–	2.72	1.10
Length of tarsus	4.84	5.72	4.64*	0.50*	–	7.60	2.21
Tarsomere 1	1.13	1.32	1.80	0.50	–	2.08	0.45
Tarsomere 2	1.13	1.32	2.00	–	–	1.88	0.45
Tarsomere 3	1.05	1.48	0.84*	–	–	1.64	0.50
Tarsomere 4	1.15	1.20	–	–	–	1.44	0.48
Tarsomere 5	0.38	0.40	–	–	–	0.56	0.33
Length of right middle leg	–	3.52	–	4.28	–	7.24	3.86
Length of femur	–	1.32	–	1.52	–	2.88	1.58
Length of tibia	–	0.40	–	1.20	–	1.60	0.85
Length of tarsus	–	1.80	–	1.56	–	2.76	1.43
Tarsomere 1	–	0.40	–	0.60	–	0.88	0.30
Tarsomere 2	–	0.44	–	0.32	–	0.68	0.40
Tarsomere 3	–	0.40	–	0.24	–	0.52	0.30
Tarsomere 4	–	0.40	–	0.22	–	0.32	0.23
Tarsomere 5	–	0.16	–	0.18	–	0.36	0.20
Length of left middle leg	2.11*	3.52	3.48*	4.31	4.09	7.28	3.84
Length of femur	–	1.32	1.80	1.52	1.63	2.92	1.55
Length of tibia	0.63*	0.40	1.04	1.21	1.00	1.64	0.85
Length of tarsus	1.48	1.80	0.64*	1.58	1.46	2.72	1.44
Tarsomere 1	0.35	0.40	0.64*	0.62	0.44	0.80	0.30
Tarsomere 2	0.50	0.40	–	0.34	0.45	0.72	0.40
Tarsomere 3	0.25	0.40	–	0.22	0.13	0.48	0.33
Tarsomere 4	0.20	0.40	–	0.20	0.21	0.36	0.20
Tarsomere 5	0.18	0.20	–	0.20	0.23	0.36	0.20
Length of right hind leg	3.52	3.10	–	4.52	2.68*	6.84	3.54
Length of femur	1.36	1.32	–	1.68	1.45	2.48	1.63
Length of tibia	0.78	0.40	–	1.10	0.90	1.64	0.70
Length of tarsus	1.38	1.38	–	1.74	0.33*	2.72	1.21
Tarsomere 1	0.35	0.44	–	0.46	0.33	0.88	0.30
Tarsomere 2	0.33	0.36	–	0.44	–	0.72	0.30
Tarsomere 3	0.25	0.22	–	0.38	–	0.48	0.20
Tarsomere 4	0.20	0.16	–	0.24	–	0.36	0.18
Tarsomere 5	0.25	0.20	–	0.22	–	0.28	0.23
Length of left hind leg	3.43	3.43	3.40*	4.42	3.01*	6.84	3.65
Length of femur	1.30	1.32	1.92	1.72	1.48	2.48	1.65

Adult characters	<i>Siphloplecton jaegeri</i> [MNB, MB.1 7370, male imago] (mm)	<i>Siphloplecton jaegeri</i> [MNHN, 4655 BA, male imago] (mm)	<i>Siphloplecton lundollii</i> sp. nov. [SMNS, BB-2377, holotype, male imago] (mm)	<i>Siphloplecton</i> <i>studentmannae</i> sp. nov. [SMNS, BB-2626, holotype, female imago] (mm)	<i>Siphloplecton</i> <i>studentmannae</i> sp. nov. [MNHK, MP/1626, paratype, female imago] (mm)	<i>Siphloplecton</i> sp. 5 [CCHI, BaB 1159/5, male imago] (mm)	<i>Siphloplecton</i> sp. 6 [MNB, MB.1 7372, male subimago] (mm)
Length of tibia	0.75	0.44	0.84	1.06	0.88	1.60	0.75
Length of tarsus	1.38	1.36	0.64*	1.64	0.65*	2.76	1.25
Tarsomere 1	0.35	0.40	0.64*	0.42	0.30	0.84	0.30
Tarsomere 2	0.35	0.40	–	0.42	0.35*	0.76	0.35
Tarsomere 3	0.25	0.20	–	0.38	–	0.52	0.25
Tarsomere 4	0.18	0.16	–	0.22	–	0.32	0.15
Tarsomere 5	0.25	0.20	–	0.20	–	0.32	0.20
Length of right forewing	8.13	8.20	11.60	8.80	9.95	9.84	8.75
Length of left forewing	8.25	8.08*	11.80	8.60	6.88*	9.86	8.55
Length of right hind wing	3.15	2.70	3.60	–	3.25	3.50	2.75
Length of left hind wing	3.20	–	3.25*	2.92	3.30	3.52	2.80
Hind/forewings length ratio	0.39	0.39	0.31	0.34	0.33	0.36	0.32
Length of right cercus	4.25*	–	2.84*	2.24*	3.03	–	4.25*
Length of left cercus	4.20*	–	3.16*	2.32*	4.50	8.80	4.00*

* – preserved part; “–” – not preserved.

with slightly paler apical part and darker basally; antennae light brown, longer than head (Fig. 3A); ocelli and antennae of MNB specimen not visible due to resin influxes (Fig. 1A–C).

Thorax brown with dirty maculation dorsally (MNB specimen), yellowish-brown with markedly darker sterna (MNHN specimen); mesonotal suture stretched backwards medially; lateroparapsidal suture elongated, without surrounding pigmentation; furcasternal protuberances of mesothorax fused.

Wings hyaline. Pterostigma with at least 6 anastomosed veins. Cubital field of right forewing with well-developed intercalary vein (iCu1) close to CuA and basally directly connected to it, followed by one pair of intercalaries (iCu2, iCu3) basally connected to each other and connected to CuA (in MNHN specimen also to CuP) by a short crossvein (Figs 1D, 2, 4A). Hind wings with triads RS, MA and MP (Fig. 4A); preserved part of hind wings 0.39× forewing length (MNB specimen). Hind wings of MNHN specimen with triads RS, MA and MP, poorly visible distally; preserved part of hind wings 0.35× forewing length. Costal process small.

Legs brownish; tibiae and tarsi darker than femora; structure and proportions of leg segments similar to those of holotype of *S. jaegeri*; outer margin of foretibia with pointed setae; measurements of leg segments in Table 1.

Abdominal segments well preserved, paler than thorax. Shape of styliger and penis lobes (Figs 1E, 3D, 4B) similar to those of *S. jaegeri* holotype (Demoulin 1968: 252, figs 18a, c, Staniczek and Godunko 2012: 74, fig. 11c). Styliger plate angulate, deeply incised with three prominent projections; medial projection markedly broad; basal segment of forceps basally (a) markedly narrower than adjoining apical part of styliger plate (b) (a/b = 0.57); forceps 4-segmented; segment 2 longest, segment 4 approximately 2.47 to 2.65 times as long as wide; length ratio of segment 3 to segment 4

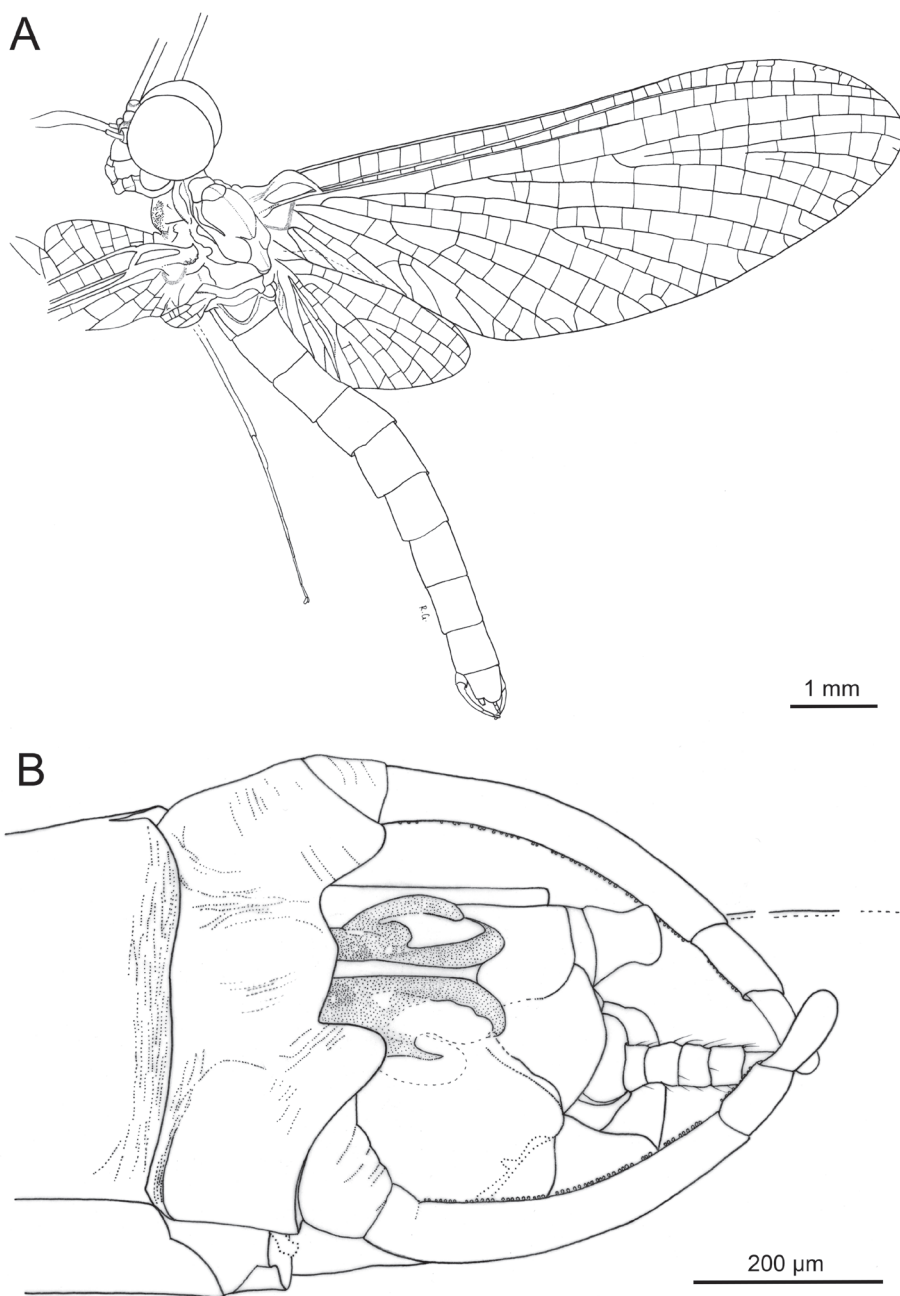


Figure 4. *Siphloplecton jaegeri* Demoulin, 1968, MNHN, 4655 BA, male imago (line drawings) **A** general dorsal view **B** genitalia in ventral view.

approximately 0.9:1. Penis lobes elongated, medially incised, triangular, with relatively inconspicuous incision between lateral and medial penis sclerites. Surface details of penis lobes not visible.

Paracercus vestigial, 5-segmented.

Comments. Some minor differences regarding the proportions of the fore/hind wings and forceps segments between the holotype of *S. jaegeri* and the specimens described above are present. However, we attribute these specimens to *S. jaegeri* due to the presence of 1+2 intercalaries in the cubital field, pointed setae along outer margin of foretibia, and the shape of styliger plate and penis lobes.

***Siphloplecton landolti* sp. nov.**

<http://zoobank.org/F5338779-9D55-48B5-9542-7357704A8A64>

Figures 5–7; Table 1

Material examined. Holotype. Male imago in Baltic amber (Eocene), SMNS BB–2377. Well preserved specimen in clear amber, well visible in dorsoventral aspect. Each of both forewings bent upwards approximately at half length (left forewing partly twisted); left hind wing twisted; genitalia visible in ventral and, partly, lateral view.

For measurements see Table 1.

Description. Colouration pale, dorsal side slightly darker than ventral side. Brownish diffuse maculation on thorax and abdomen preserved. Ocelli well preserved. Eyes large, medially contiguous; brownish maculation on eye surface partly preserved; antennae longer than head (Figs 5A–C, E, 6A–B).

Thorax with traces of brownish pigmentation on dorsal and ventral sides; “Verlummung” mainly on lateral sides near wing bases. Lateroparapsidal suture elongate, typical for *Siphloplecton*; no conspecific pigmentation around lateroparapsidal suture; mesonotal suture medially bulged (Fig. 6A); furcasternal protuberances of mesothorax contiguous (Fig. 6B); lateral aspect of thorax hardly visible.

Wings translucent, hyaline, not pigmented, venation well visible; pterostigma translucent, without pigmentation, with simple veins. Cubital field of forewing well visible on right wing only (twisted on left wing): one distinct pair of intercalary veins (iCu2 and iCu3) situated close to CuP and connected with CuP and CuA; one long intercalary vein (iCu1) connected with CuA and also with iCu2 by crossveins; additional short intercalaries present, ending at hind margin of wing (one of them between iCu1 and iCu2, basally joining both veins) (Fig. 5C). Hind wings with triads RS, MA and MP, 0.31× forewing length; costal process bluntly pointed (Fig. 5D).

Legs damaged; both right fore- and hind legs lost; tarsus of left foreleg only partly preserved (for details see Table 1). Tibia of left foreleg paler than femur and tarsus. Left foretibia with strong, sharply pointed setae along outer margin. Tibia of left middle and hind legs black; preserved part of first tarsomere of left middle leg black. Tibia of middle and hind legs with trace of tibiopatellar suture; first tarsomere of middle and hind legs fused with tibia. Tarsal claws lost (Fig. 5A–B).

Abdominal segments completely preserved, sterna visibly paler than terga; genitalia dark.

Styliger plate angulate, mediocaudally deeply incised; these incisions with pronounced, broad, triangular projections; medial projection not large, blunt apically

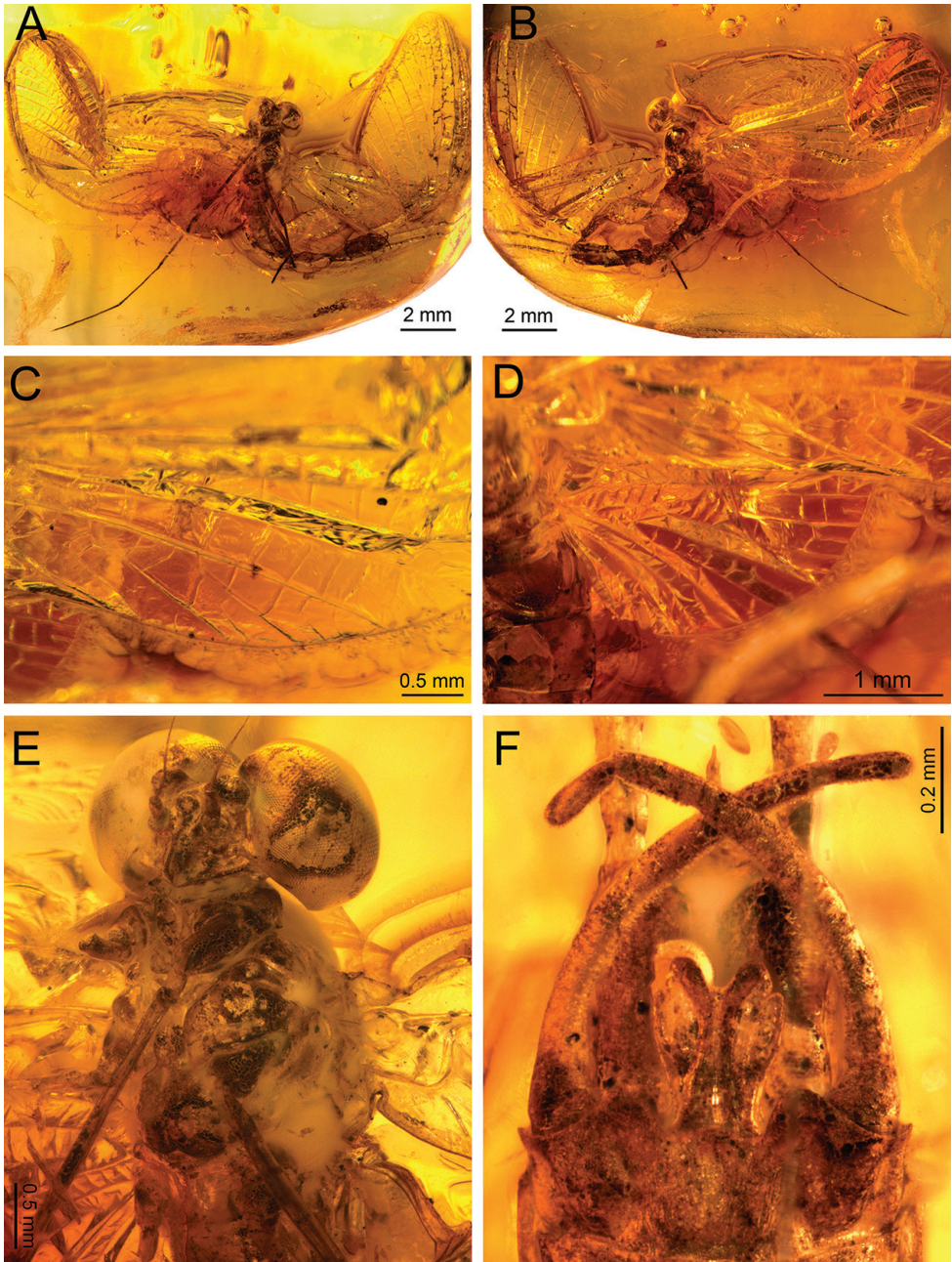


Figure 5. *Siphloplecton landolti* sp. nov., SMNS, BB-2377, holotype, male imago (photographs) **A** general dorsal view **B** general ventral view **C** cubital field of right forewing **D** right hind wing in dorsal view **E** head and thorax in ventral view **F** genitalia in ventral view.

(Figs 5F, 7). Basal segment of forceps basally relatively wide; forceps 4-segmented, segment 4 approximately 3.30 times longer than wide; length ratio of segment 3 to segment 4 approximately 1:1. Penis lobes distinctly elongated, well separated from each

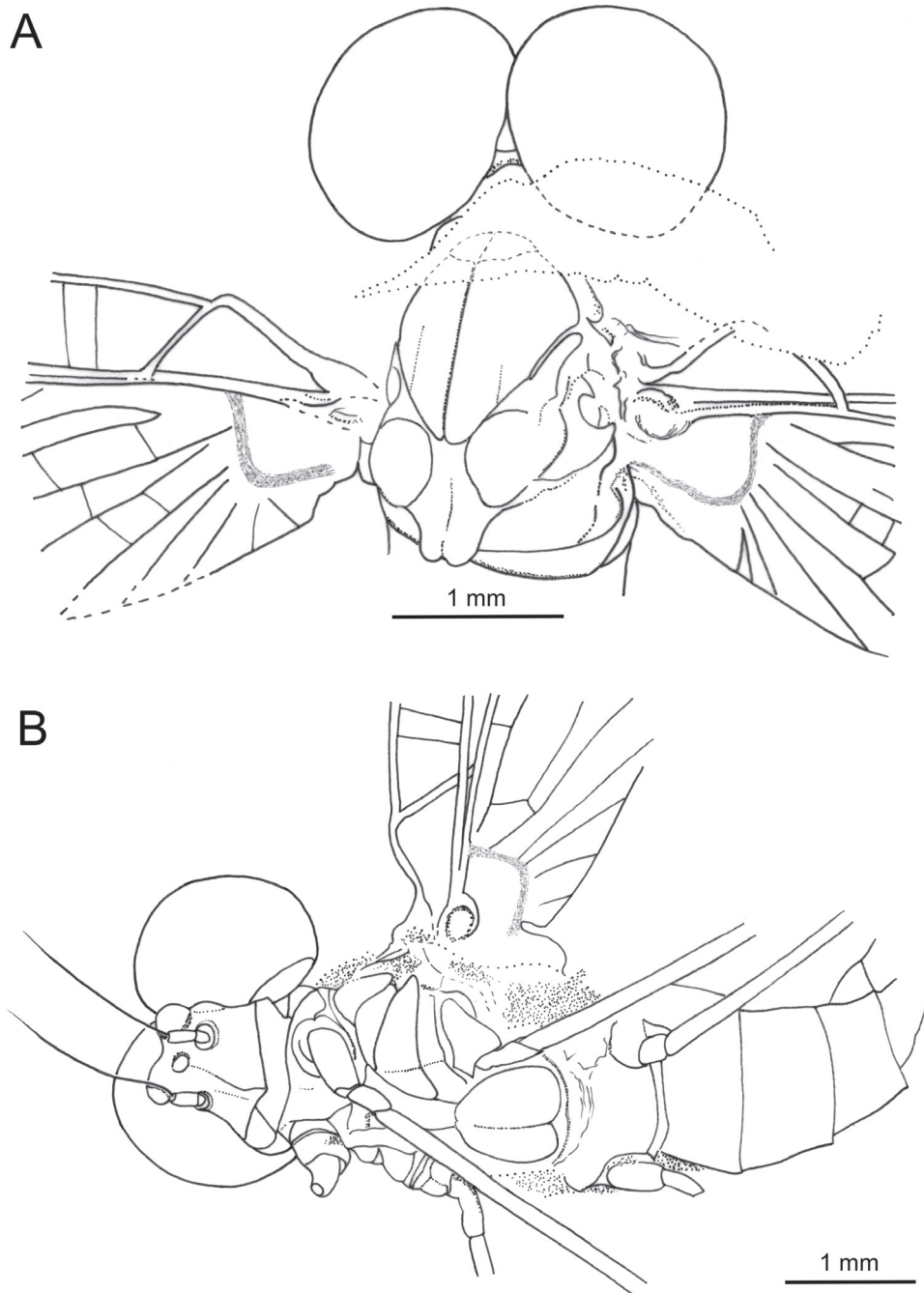


Figure 6. *Siphloplecton landolti* sp. nov., SMNS, BB–2377, holotype, male imago (line drawings) **A** head and thorax in dorsal view **B** head and thorax in ventral view.

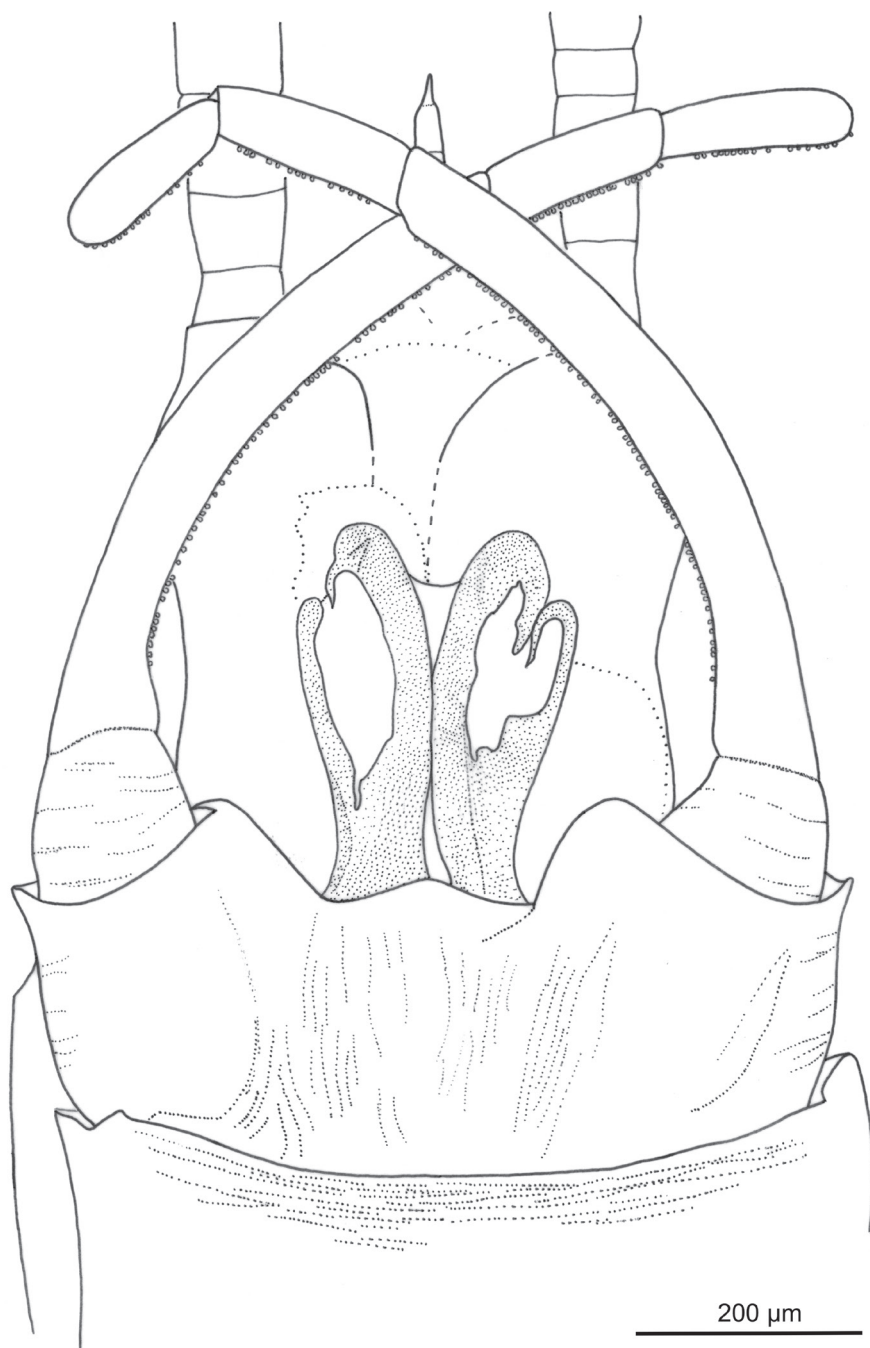


Figure 7. *Siphloplecton landolti* sp. nov., SMNS, BB-2377, holotype, male imago (line drawing): genitalia in ventral view.

other apically, ellipsoidal; medial sclerite rounded apically; lateral and medial sclerite markedly separated on outer side with inconspicuous incision between sclerites; features of ventral surface of penis lobes not visible (Figs 5F, 7).

Paracercus vestigial; cerci partly lost.

Comments. The new species can be placed within the *jaegeri* species group based on the characteristic shape of the penis lobes, the arrangement of cubital intercalaries of the forewing and the sharply pointed setae along the outer margin of the foretibia. *Siphloplecton landolti* sp. nov. can be separated from the closely related *S. jaegeri* by (1) shape of styliger with relatively small and apically rounded medial projection; (2) relatively wide base of basal forceps segment compared to adjoining apical part of styliger plate; (3) proportions of last forceps segments; (4) ellipsoidal shape of penis lobes with medial sclerite rounded at tip.

The body measurements of *S. landolti* sp. nov. are comparable to other representatives of the *S. jaegeri* species group, but the ratio of hind/forewing length is lower in comparison with *S. jaegeri* itself.

Etymology. Following our tradition of naming new fossil species of *Siphloplecton* after Swiss ephemeropterists, this species is named after Peter Landolt, Lausanne, to honour his contributions to the knowledge of Swiss mayflies.

***Siphloplecton studemannae* sp. nov.**

<http://zoobank.org/2D1C8631-DAFF-4B84-B10D-7D7FAB3E5334>

Figures 8–11; Table 1

Material examined. Holotype. Female imago in Baltic amber (Eocene), SMNS BB–2626. Well preserved specimen in clear amber, well visible in dorsoventral aspect. Right foreleg lost; hind wings (especially left wing) twisted. Head and thorax covered by “Verlummung”. Additionally, piece of amber with numerous cracks, thus details of thoracic terga invisible, and thorax only partly visible from ventral side. For measurements see Table 1.

Paratype. Female imago in Baltic amber (Eocene), MNHK, MP/1626. Partly damaged specimen, visible in ventral aspect. View on body hampered by resin influxes, numerous cracks, and considerable “Verlummung”, so thoracic sutures are hardly visible. Head lost. Pronotum damaged, its structure invisible. Distal part of mesonotum, metanotum and abdominal segments I–IV dorsally covered by plant tissue. Right forewing twisted along its length; left forewing lacks its basal part and distal end. Right foreleg, right middle leg, left middle tarsus, and both hind legs lost. Cerci only partly preserved. For measurements see Table 1.

Description of holotype. General colour of body pale, yellow to yellowish-brown. Ventral side of body slightly darker than dorsal side. Ocelli well preserved. Eyes medially separated, but approximated (Fig. 8A). Distance between eyes 0.22× of head width. Antennae complete, slightly longer than head, pale.

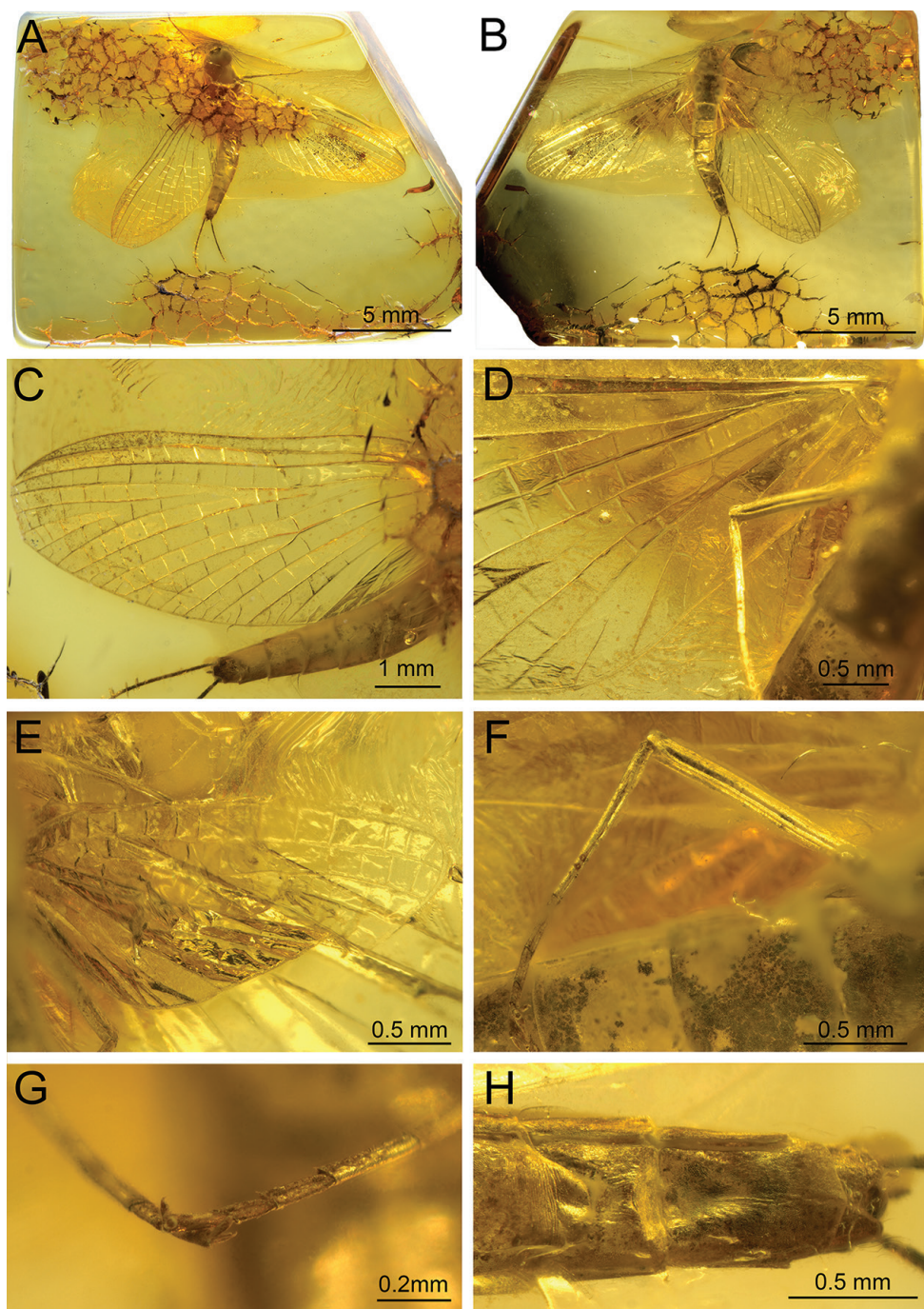


Figure 8. *Siphloplecton studemanna* sp. nov., SMNS, BB-2626, holotype, female imago (photographs) **A** general dorsal view **B** general ventral view **C** left forewing in dorsal view **D** wing base and cubital field of right forewing in ventral view **E** left hind wing in ventral view **F** right hind leg in medial view **G** claws of hind legs **H** abdominal segments VII–X in ventral view.

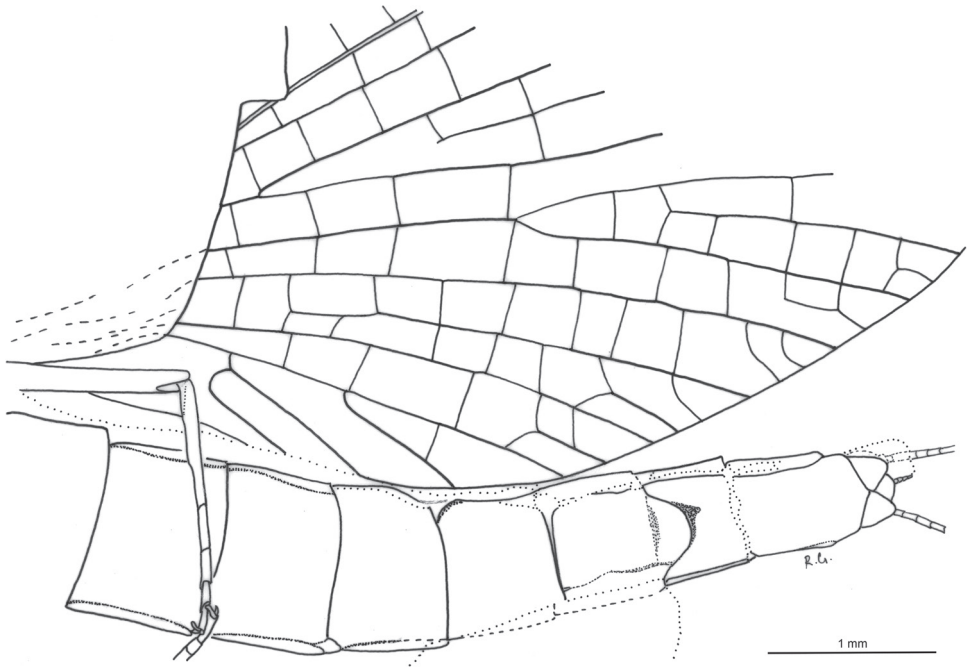


Figure 9. *Siphloplecton studemanna* sp. nov., SMNS, BB-2626, holotype, female imago (line drawing): abdomen and part of left forewing in ventral view.

Thorax ventrally yellowish coloured by “Verlummung”, mainly in posterior part. Furcasternal protuberances of mesothorax contiguous (Fig. 8B); lateral aspect of thorax not visible.

Wings translucent, hyaline, not pigmented. Wing venation well visible only from ventral side; basal part of wings covered by numerous cracks from dorsal side. Cubital field of both forewings with one pair of intercalary veins (iCu2, iCu3) towards CuP and one additional vein (iCu1) near CuA (Figs 8C–D, 9). Right hind wing hardly visible, twisted; left hind wing completely preserved with three pairs of triads, $0.34\times$ of right forewing length. Costal process bluntly pointed apically and small (Fig. 8E).

Legs relatively well preserved, except forelegs (right is lost; left incomplete). Measurements of leg segments in Table 1. Tibiae of middle and hind legs each with trace of tibiopatellar suture; first tarsomere of middle and hind legs fused with tibia (Fig. 8F). Tarsi with 5 tarsomeres; tarsal claws dissimilar: one hooked and one blunt (Fig. 8G).

Abdominal segments completely preserved, pale; terga VIII–X slightly darker than remaining terga. Abdominal sterna slightly covered by “Verlummung”. Subgenital plate relatively broad, $2.00\times$ as wide as long, convex and rounded apically. Subanal plate not elongated, narrow, with pointed tip (Figs 8H, 9). Paracercus poorly visible, vestigial, with at least 4 visible segments; cerci dark, partly preserved.

Description of paratype. Body colouration light, yellowish-brown to brown. Irregular brown, dirty brown to black maculation over body, especially on forewings and legs (Fig. 10A).

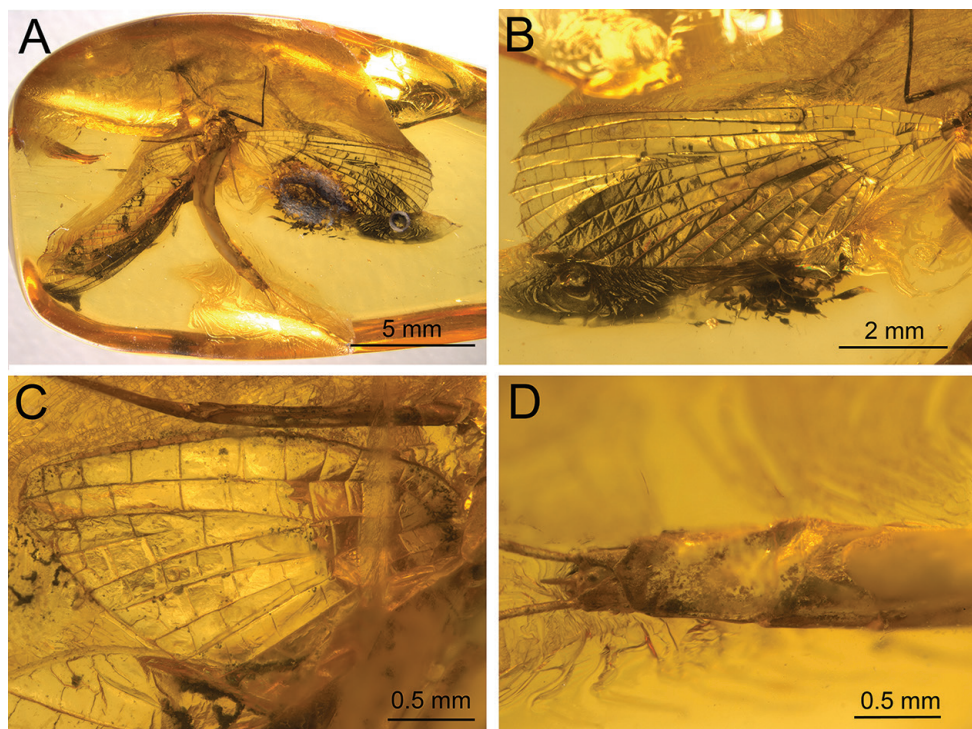


Figure 10. *Siphloplecton studemanna* sp. nov., MNHK, MP/1626, paratype, female imago (photographs) **A** general ventral view **B** left forewing in dorsal view **C** right hind wing in ventral view **D** abdominal segments VII–X in ventral view.

Details of mesonotum hardly visible; mesonotal suture typical for *Siphloplecton*, original lateroparapsidal suture colouration invisible due to resin influx. Furcasternal protuberances contiguous, distinctly brown; other parts of mesosternum paler.

Pterostigma with anastomosed crossveins. Cubital field of right forewing well preserved; iCu1 basally connected to CuA and iCu2 by crossveins, 2 additional CuA–iCu1 crossveins present. Pair of intercalaries iCu2 and iCu3 basally connected to each other; further crossveins connect to CuA and CuP (Figs 10B, 11A). Hind wings relatively long, approximately 0.40× of length of preserved right forewing; costal processes hardly visible. Hind wings with triads RS, MA and MP; costal process (visible only on right hind wing) small and blunt (Fig. 10C).

Left foreleg intensely brown to blackish distally; middle legs paler, yellow to yellowish-brown. Preserved foreclaw dissimilar (one claw hooked, one claw blunt).

Most of **abdominal** segments ventrally covered with “Verlummung”. Preserved sterna paler than terga. Subgenital plate not elongate, approximately 1.80× wide as long, widely rounded apically. Subanal plate not elongate, pointed at tip (Figs 10D, 11B). Paracercus 5-segmented.

Comments. We allocate *Siphloplecton studemanna* sp. nov. within the *S. jaegeri* species group based on the presence of three distinctive intercalaries (grouped in one pair and

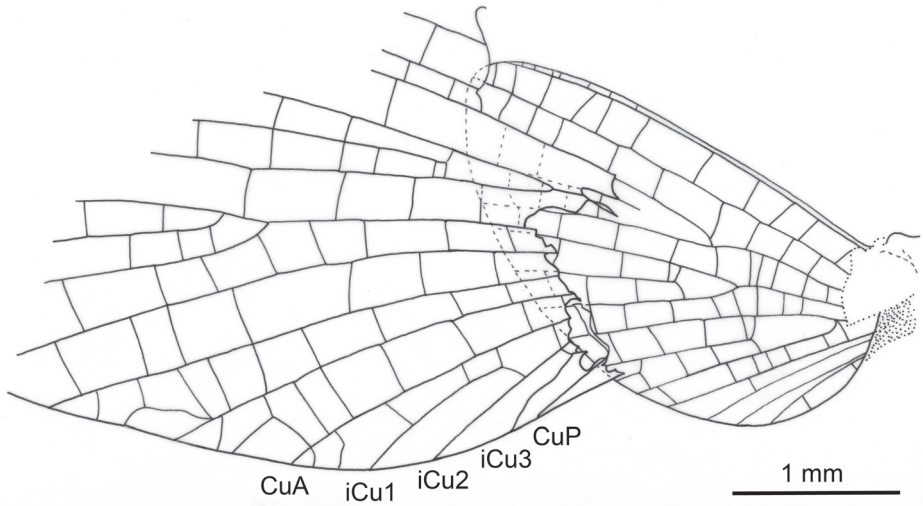
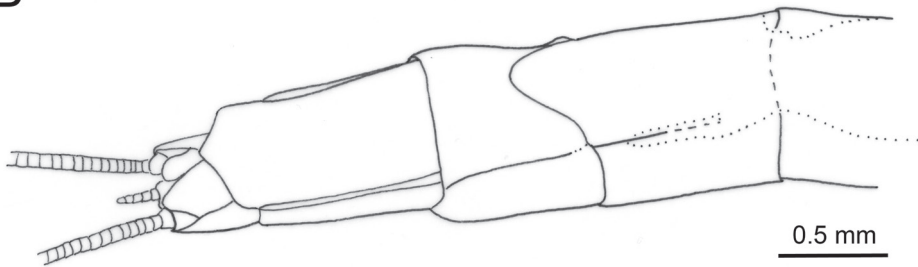
A**B**

Figure 11. *Siphloplecton studemanna* sp. nov., MNHK, MP/1626, paratype, female imago (line drawings) **A** fragments of left fore- and hind wings, dorsal view **B** abdominal segments VII–X in ventrolateral view.

one additional intercalary vein) in the cubital field of both forewings. The same arrangement of intercalary veins was described and figured for the holotype of *S. jaegeri* by Staniczek and Godunko (2012: 73, 74, fig. 10b). Other diagnostic characters of this species group, namely the presence of sharply pointed setae at the outer margin of the foretibia, cannot be observed in the type specimens of *S. studemanna* sp. nov. So it cannot be excluded that this character is present in the females of this fossil species, similarly to the different occurrence of this character in the two sexes of extant species (Berner 1978).

The new species can be characterized by the presence of the following characters: (1) eyes separated, but close-set; (2) cubital field of forewings with one pair of intercalaries and one intercalary vein connected with CuA; (3) subgenital plate relatively broad with width/length ratio 1.80–2.00. This combination of characters definitely separates the described females of *S. studemanna* sp. nov. from all other previously known Recent and fossil taxa.

Siphloplecton studemanna sp. nov. is currently the only species of the genus *Siphloplecton* described from female specimens that can also be attributed to a certain species group. This is only possible due to the unique arrangement of cubital intercalaries, which is characteristic for the *S. jaegeri* species group. The previously described *S. barabani* and *S. hageni*, also only known from female specimens, do not provide any clear distinguishing characters that would allow their placement in one of the other fossil species groups defined for *Siphloplecton*, which can only be grouped based on similarities in the male genitalia.

Etymology. Following our tradition of naming new fossil species of *Siphloplecton* after Swiss ephemeropterists, this species is named after Denise Studemann, Lausanne, to honour her contributions to the knowledge of Swiss mayflies.

Siphloplecton spp. (*jaegeri* species group)

Siphloplecton sp. 5

Figures 12–13; Table 1

Material examined. Male imago in Baltic amber (Eocene), CCHH, BaB Nr. 1159/5. A generally completely preserved specimen, well visible in dorsoventral aspect in translucent amber (Fig. 12A–B). Some resin influxes around specimen. Right foreleg and right cercus lost. Dorsal side of body only with several very small spots of “Verlummung”. Ventral side of head, thorax and, partly, abdominal sterna intensively covered with “Verlummung”. For this reason, some aspects of mesosternum and the shape of the genitalia are poorly visible. One female nonbiting midge (Diptera: Chironomidae) is embedded in the same stone.

Relatively pale specimen, yellowish to brown. Wings with artificial, irregular dark spots; distal portions of forewings and right hind wing with distinct concentration of such spots (Fig. 12E). Legs uniformly coloured. For measurements see Table 1.

Description. **Head** light brown. Eyes large, slightly flattened, pale, dirty yellowish. Several brownish spots on eye surface. Ocelli and antennae of same colouration as head, completely preserved; antennae slightly longer than head (Fig. 12C, E).

Thorax with traces of brownish pigmentation on dorsal and ventral sides, brown. Pronotum well preserved. Arrangement of thoracic sutures on dorsal and ventral sides of mesothorax typical for *Siphloplecton* (Figs 12C–D, 13). Most of head and thorax ventrally covered with “Verlummung”. Lateral aspect of thorax hardly visible.

Wings basally translucent, hyaline, with well visible longitudinal and transversal venation. Pterostigmatic area hyaline, opaque, with several anastomosed veins. Cubital field of forewings with well visible pair of intercalary veins connected with CuA, and one additional, well developed vein also directed toward CuA (Figs 12E–G, 13). Hind wings with triads RS, MA and MP, 0.36× forewing length; costal process bluntly pointed and small (Figs 12E, 13).

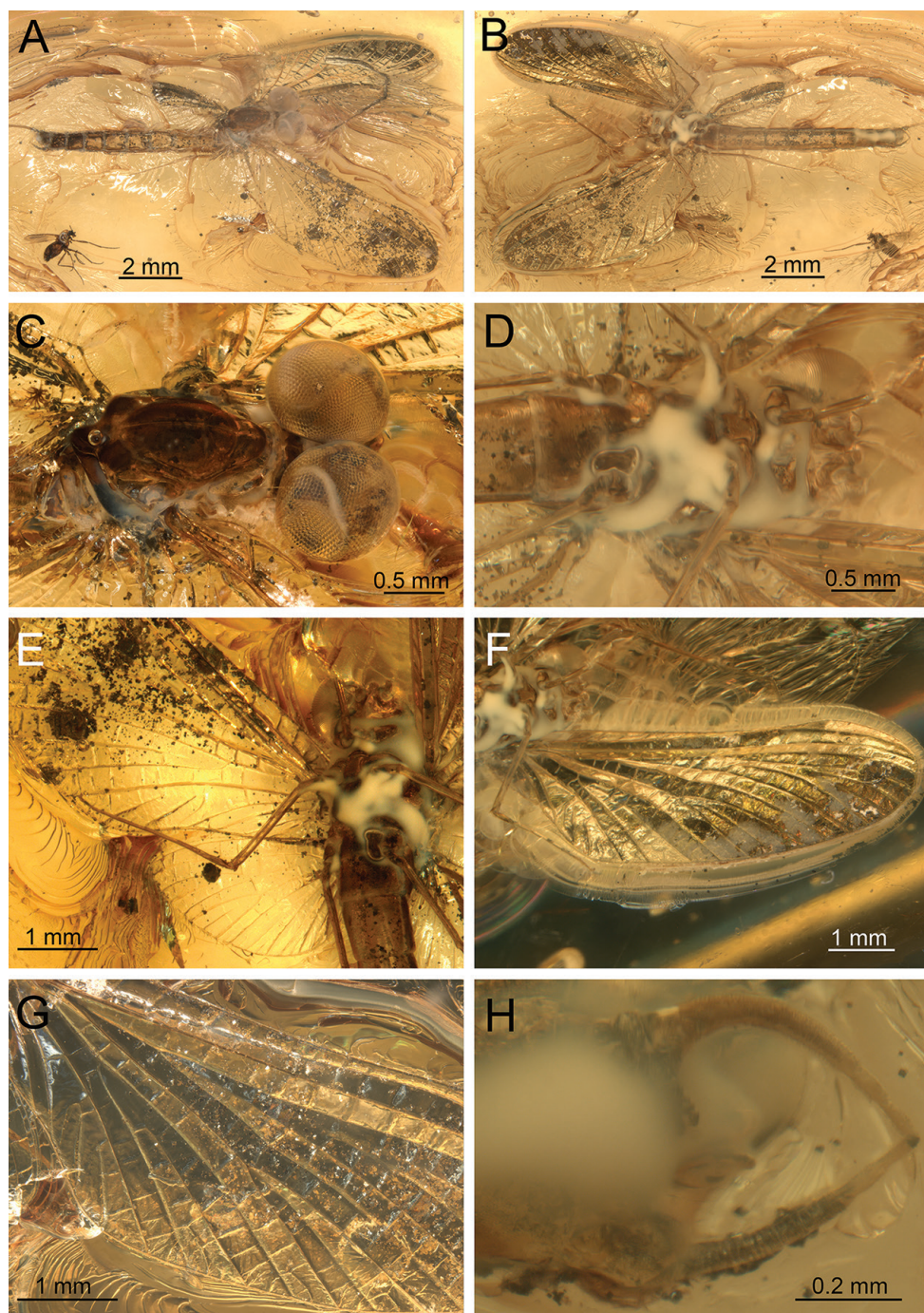


Figure 12. *Siphloplecton* sp. 5, CCHH, BaB 1159/5, male imago (photographs) **A** general dorsal view **B** general ventral view **C** head and thorax in dorsal view **D** head and thorax in ventral view **E** base of right forewing and hind wing in ventral view **F** left forewing in ventral view **G** cubital field of left forewing in ventral view **H** genitalia in ventral view.

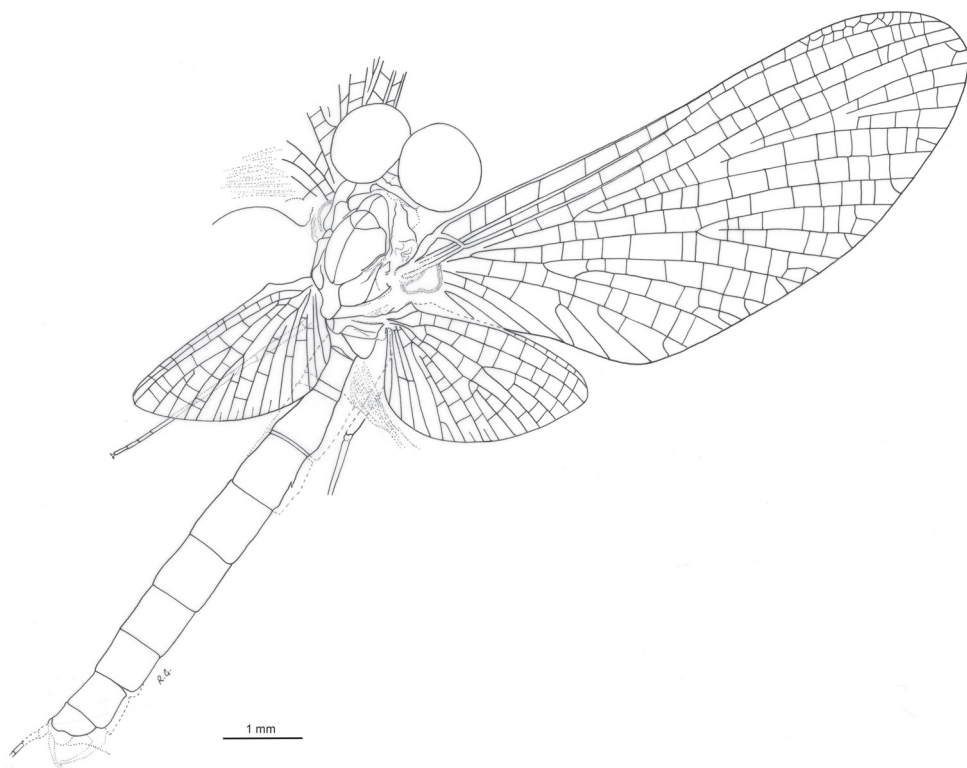


Figure 13. *Siphloplecton* sp. 5, CCHH, BaB 1159/5, male imago (line drawing): general dorsal view of body, right forewing, left and right hind wings.

Legs yellowish to light brown. Several pointed spines at outer margin of foretibia. Characteristics of legs similar to those of other representatives of *Siphloplecton*. Measurements of leg segments in Table 1.

Abdominal segments completely preserved; abdominal terga slightly paler than sterna.

Styliger plate only partly visible, most of styliger base covered with “Verlummung”. Thus, shape of styliger projections not clearly visible (Fig. 12H). Basal segment of forceps basally not widened, distinctly narrower than adjoining apical part of styliger plate (character well visible only in right clasper); forceps 4-segmented, segment 4 approximately 3.20 times longer than wide; length ratio of segment 3 to segment 4 approximately 1:1 (Fig. 12H).

Penis lobes covered with “Verlummung” (especially left lobe); penis lobes elongated, relatively narrow and separated from each other apically; medial sclerite rounded apically; lateral and medial sclerites probably separated on outer side (poorly visible) (Fig. 12H).

Paracercus vestigial, at least 3-segmented; left cercus slightly damaged; right cercus lost.

Comments. This species is closely related to *S. landolti* sp. nov. due to the similar proportions of the forceps segments and shape of the penis lobes, especially the apical portion of the medial sclerite, and the presence of 2+1 intercalary veins in the cubital field of the forewings. This last character also confirms the inclusion of *Siphloplecton* sp. 5 within the *S. jaegeri* species group. At the same time, we could not confirm its conspecificity with *Siphloplecton landolti* sp. nov. or other species, since the details of the male genitalia are poorly visible.

Siphloplecton sp. 6

Figure 14; Table 1

Material examined. Male subimago in Baltic amber (Eocene), MNB, MB.I 7372, specimen originally labeled as: “6. Pseudoneuroptera III Ephemeridae”; “Museum für Naturkunde Berlin”; “Paläontologisches Museum”; “Slg.: Künow Inv. Nr.: Nr. 268–294 nur noch 9 Stück vorgefunden”; “Ephemeriden”; “*Siphloplecton* cf. *jaegeri* subim. male Nr.: 272”.

Completely preserved specimen, well visible in lateral aspect. Details of head hardly visible due to resin influxes and small cracks in stone. Left forewing arcuated at half length; left hind wing twisted. Terga IX–X and, partly, genitalia covered by “Verlummung”. For measurements see Table 1.

Description. General colouration of body brown to dark brown. Head brown with paler antennae; eyes large, medially contiguous, uniformly brown coloured.

Thorax intensely brown; details of terga hardly visible; mesonotal suture typical for *Siphloplecton*; lateroparapsidal suture not visible. Thorax ventrally hardly visible, but furcasternal protuberances of mesothorax contiguous.

Wings opaque. Forewings with several irregular dark spots (probably an artefact of fossilisation). Pterostigmatic area with 7–8 anastomosed veins. In cubital field of forewing one pair of intercalaries close to CuP (connected with CuP and CuA); one additional intercalary vein close to CuA. Hind wings with triads RS, MA and MP, 0.32× forewing length; costal process bluntly pointed (Fig. 14).

Legs typical for the genus *Siphloplecton*.

Abdominal segments completely preserved; terga darker than sterna.

Shape of **styliger plate** poorly visible in ventral view, but generally close to the one of *S. landolti* (deeply incised mediocaudally, angulate, with relatively small medial projection). Shape of penis lobes hardly visible because of “Verlummung”. Visible part of penis lobes with apical sclerites rounded at tip.

Cerci partly damaged; paracercus vestigial.

Comments. Due to the general shape of the styliger and penis lobes, and proportions of the fore/hind wings, this specimen belongs with high probability to *S. landolti* sp. nov. Some of the observed differences might be related to differences between subimago and imago, or may be due to the bad preservation of the genitalia. However, in order to avoid any taxonomic confusion, we refrain from attributing *Siphloplecton* sp. 6 to a certain species within *Siphloplecton*.



Figure 14. *Siphloplecton* sp. 6, MNB, MB.I 7372, male subimago (photograph): general lateral view, left side.

Discussion

The first classification of extant representatives of the genus *Siphloplecton* into species groups was undertaken by Berner (1978) in his work dedicated to the taxonomy of Metretopodidae. That grouping was based on wing pigmentation, the shape of the setae along the outer margin of the foretibia, and penis shape (Berner 1978: 96; Staniczek and Godunko 2012: 59–61, figs 1–2). Staniczek and Godunko (2012), for the first time, added fossil *Siphloplecton* species from Eocene Baltic amber to Recent species groups. In this contribution, *S. picteti* and *S. demoulini* were attributed to the *S. basale* species group established by Berner (1978). At the same time, the remaining investigated taxa, *S. barabani* and *S. hageni*, were neither attributed to the *basale* species group nor to the *interlineatum* species group. This was due to these species having only been described from female imagines, and no traces of wing pigmentation were preserved. *Siphloplecton jaegeri* was also excluded from previously known species groups for peculiarities in the genitalia and for the presence of pointed setae along the outer margin of the foretibia (Staniczek and Godunko 2012). In fact, these characters pointed to a relatively isolated position of *S. jaegeri* within both fossil and recent species of *Siphloplecton*.

Based on the investigation of further male specimens, Staniczek and Godunko (2016) established another two *Siphloplecton* species groups for four fossil species:

S. picteti and *S. sartorii* were attributed to the *S. picteti* species group, and *S. demoulini* and *S. gattolliati* to the *S. demoulini* species group. At the same time, due to the poor preservation of the re-discovered lectotype of *S. macrops*, Staniczek and Godunko (2016) concluded that it is neither possible to define any distinguishing characters for this species nor to attribute it to any of the species groups proposed earlier. They also refrained from placing female specimens in the *S. sartorii* or *demoulini* species groups.

Representatives of the genus *Siphloplecton* are relatively abundant components of the mayfly fauna from Eocene Baltic amber. Judging from the museum and private collections investigated by us, this genus is not less abundant than *Paraleptophlebia* Lestage, 1917 (Leptophlebiidae), which is another commonly found mayfly genus in Baltic amber. Taxonomically, the genus *Siphloplecton*, with ten fossil and nine contemporary Nearctic species, is rather diverse.

Key to males of *Siphloplecton* from Eocene Baltic amber

- 1 Four long intercalary veins grouped into two pairs in the cubital field of the forewings between CuA and CuP (Staniczek and Godunko 2012: 66, 76, figs 4C, 12C; Staniczek and Godunko 2016: 14, 19, 23, figs 7A, 11A, 13A) **2**
- Three long intercalary veins grouped into one pair and one separate intercalary vein in the cubital field of the forewings between CuA and CuP (Figs 1D, 2, 4A, 8D, 9, 10B, 11A, 12E, G, 13) [*S. jaegeri* species group] **5**
- 2 Outer margin of foretibia with two or more stout, pointed setae; penis relatively short, its tip barely reaching distal margin of basal forceps segment [*S. picteti* species group] **3**
- Outer margin of foretibia without stout, pointed setae; penis elongated, its tip significantly projecting beyond styliger plate, reaching one fourth of forceps segment 2 [*S. demoulini* species group] **4**
- 3 Basal segment of forceps nearly square; segment 4 of forceps moderately elongated (segment length/width ratio 2.58–2.72); forceps segments 3 and 4 of about same length; penis lobes contiguous almost along entire length, separated only by a shallow, broad, U-shaped cleavage apically; lateral sclerites of penis lobes relatively slender, only slightly expanding laterally (Staniczek and Godunko 2012: 64, fig. 3b; Staniczek and Godunko 2016: 12, 14–16, figs 6D, 7B, 8E, 9B) ***S. picteti***
- Basal segment of forceps slim and elongated; segment 4 of forceps clearly elongated (segment length/width ratio 3.38); forceps segment 3 slightly longer than segment 4; penis lobes well separated apically by a wide, V-shaped cleft; lateral sclerites of penis lobes distinctly broad and prominent laterally (Staniczek and Godunko 2016: 18, 19, figs 10H, 11B) ***S. sartorii***
- 4 Median projection of styliger plate slightly prominent, triangular (Staniczek and Godunko 2012: 76, 77, figs 12d, 13c) ***S. demoulini***
- Median projection of styliger plate absent (Staniczek and Godunko 2016: 22, 23, figs 12F, 13B) ***S. gattolliati***

- 5 Median projection of styliger plate well protruded, broad, triangular-shaped; basal segment of forceps basally markedly narrower than adjoining apical part of styliger plate; penis lobes distinctly elongated, nearly triangular-shaped apically (Figs 1E, 3D, 4B; Demoulin 1968: 253, fig. 18b; Staniczek and Godunko 2012: 74, fig. 11c) *S. jaegeri*
- Median projection of styliger plate relatively small, rounded apically; basal segment of forceps basally relatively wide in comparison to adjoining apical part of styliger plate; penis lobes distinctly elongated, smoothly rounded apically (Figs 5F, 7) *S. landolti*

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Review of the Arabian *Crematogaster* Lund (Hymenoptera, Formicidae), synoptic list, distribution, and description of two new species from Oman and Saudi Arabia

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Abstract

The genus *Crematogaster* is one of the most species-rich and widespread groups of ants. Despite their often-high local abundance and important ecological interactions, the taxonomy of the genus is fragmentary and in great need of modern revisionary studies. As a first step towards a revision for the Arabian fauna of *Crematogaster*, a review of all known species with synoptic species accounts is provided. Seventeen species are recognized and illustrated from the Arabian Peninsula, of which two new species are described: *C. jacindae* Sharaf & Hita Garcia, **sp. nov.** from the Dhofar Governorate, Oman, and *C. gryllsi* Sharaf & Hita Garcia, **sp. nov.** from the Kingdom of Saudi Arabia (KSA) based on the worker caste. *Crematogaster jacindae* **sp. nov.** is easily separated from the remainder of the Arabian *Crematogaster* fauna due to its complete lack of propodeal spines, slit-shaped propodeal spiracles, and its distinct bicoloration, whereas *C. gryllsi* **sp. nov.** is readily distinguished by its unlobed postpetiolar dorsum. Furthermore, new country records are presented: *C. acaciae* Forel for the KSA and Yemen, and *C. delagoensis* Forel and *C. jehovae* Forel for

the KSA *C. antaris* for Qatar, whereas *C. luctans* Forel is excluded from the Arabian fauna. In addition, on the basis of morphological examination of original type material, *C. affabilis* Forel is proposed as junior synonym of *C. chiarinii* Mayr, and *C. striaticeps* is elevated to species rank **stat. nov.** Furthermore, a new identification key for the Arabian species is provided, as well as distribution maps for all species.

Keywords

Arabian Peninsula, Asir Mountains, Dhofar Governorate, Middle East, new records, new species, new status, new synonymy, Qatar, taxonomy

Introduction

The myrmicine ant genus *Crematogaster* Lund, 1831 is one of the most species-rich genera of the family Formicidae with 500 described species, 269 valid subspecies and two fossil species (Blaimer 2012a; Bolton 2019). The genus is widely distributed worldwide throughout most of the tropical and subtropical regions (Hölldobler and Wilson 1990; Longino 2003). Most species are arboreal and build nests in dead branches, under bark or in carton nest structures, or, less commonly, nest directly in soil (Hölldobler and Wilson 1990; Madden and Young 1992; Palmer and Brody 2013). When natural history information is available, these ants are generalized foragers or omnivores with numerous species also tending homopterans and Hemipterans (e.g., Brown 2000; Campbell 1994; Gullan et al. 2018; Longino 2003) for honey dew.

Despite the remarkable diversity, ecological importance, and often high local abundance of the genus, it is one of the most taxonomically neglected hyper-diverse ant genera. Presently, the taxonomic situation is only moderate to satisfactory for a few regions, such as North America (Buren 1959; 1968), Costa Rica (Longino 2003), Madagascar (e.g., Blaimer 2010; 2012b; c), and parts of South East Asia (e.g., Hosoi-shi and Ogata 2008; 2009; 2015; 2017). However, apart from these, for most other regions, the taxonomy is in a very poor state, without modern revisionary treatments that cleared the taxonomic chaos from the 19th and early 20th century. As a consequence, the taxonomic validity of the majority of species and infraspecific taxa has not been comprehensively examined. We are certain that many nominally valid species and subspecies will have to be synonymized while at the same time there are numerous new species awaiting formal description. Therefore, species of *Crematogaster* are notoriously difficult to identify to species level in most parts of the world and the genus is in dire need of any modern, thorough revisionary study.

There are numerous, scattered, records of *Crematogaster* on the Arabian Peninsula. Prior to this study, the total number of species was 15 (plus one subspecies), recorded from the Kingdom of Saudi Arabia (KSA) (Collingwood 1985; Collingwood and Agosti 1996), the United Arab Emirates (UAE) (Collingwood and Agosti 1996; Collingwood et al. 2011), the Sultanate of Oman (Collingwood 1985; 1988; Collingwood and Agosti 1996; Sharaf et al. 2018), Yemen (Collingwood and van Harten 1994; 2001; 2005), and Kuwait (Collingwood and Agosti 1996). However, there are no records known from Bahrain, nor the Socotra Archipelago.

The taxonomy of Arabian *Crematogaster* is even more challenging than in other parts of the world due to the geographic location of the Arabian Peninsula, which connects sub-Saharan Africa or the Afrotropical region with the Mediterranean/Middle East or Palaearctic region (Kreft and Jetz 2010). As a consequence, the Arabian Peninsula shares biogeographical affinities with both, the Afrotropical and Palaearctic regions, however, no modern revisions of *Crematogaster* exist for these regions around the Arabian Peninsula. While there are some treatments covering particular countries or smaller areas in Europe or the northern Mediterranean, these either just describe new taxa or provide identification resources without revising the genus (Collingwood 1978, Agosti and Collingwood 1987, Cagniant 2005, Seifert 2007, Karaman 2008). In addition, many *Crematogaster* species have large female reproductives and good dispersal abilities leading to often vast distribution ranges. Thus, to be certain about the identity of any Arabian *Crematogaster* material it would require examining and comparing hundreds of Afrotropical and Palaearctic type specimens from numerous natural history collections. This enormous task is unfortunately outside the scope of our study; however, we believe this study can present a first important step towards understanding the species distributions of *Crematogaster* on the Arabian Peninsula.

We present a synoptic list, species accounts for all species that include detailed taxonomic histories, as well as data and maps showing the currently known distribution ranges. In addition, we also present a new identification key to the Arabian species of *Crematogaster* and describe two new species: *C. jacindae* sp. nov. from Oman and *C. gryllsi* sp. nov. from the Asir Mountains, KSA. Furthermore, we examine and propose some status changes for Arabian taxa and discuss doubts about identifications and species records for some species.

Materials and methods

Materials

Species names in this work follow the online catalogue of Bolton (2019) and in addition to published references (e.g., Collingwood 1985; Collingwood and Agosti 1996; Hita Garcia et al. 2013). The taxonomic histories of the treated taxa follow the online catalogue of ants of the world (Bolton 2019) and Antwiki (www.antwiki.org). Digital stacked color images were created using a Leica DFC450 digital camera with a Leica Z16 APO microscope and LAS (v3.8) software. These images are also available online on AntWeb (<https://www.antweb.org>) and are accessible through unique specimen identifiers attached (e.g., CASENT0872096). Distribution ranges were examined on Antmaps (<https://antmaps.org>; Guénard et al. 2017; Janicki et al. 2017) and general information of species on Antwiki. Distribution maps were made using DIVA-GIS (version 7.5.0.0).

Terminology and measurements

The terminology used to describe surface sculpture is based on (Harris 1979). Morphological terminology, measurements, and indices follow (Blaimer 2010, Longino 2003).

EL	Eye length; maximum diameter of compound eye in profile.
HL	Head length; maximum distance from the midpoint of anterior clypeal margin to midpoint of posterior margin of head, measured in full-face view.
HW	Head width: maximum width of head behind eyes in full-face view.
LHT	Length of metatibia, excluding the proximomedial condyle.
ML	Mesosomal length; diagonal length of mesosoma in profile from poster- oventral margin of propodeal lobe to anterior most point of pronotal slope, excluding neck.
PTH	Petiole height; measured from petiole sternum to apex in profile.
PPL	Postpetiole length: maximum length of postpetiole measured in dorsal view.
PPW	Postpetiole width: maximum width of postpetiole measured in dorsal view.
PRW	Pronotal width: maximum pronotal width in dorsal view.
PTL	Petiole length: measured in profile as distance from dorso-posterior margin of segment to anterior inflection point where petiole curves up to condyle.
PTW	Petiole width: maximum width of dorsal face of petiole node measured in dorsal view.
SL	Scape length; maximum scape length excluding basal condyle and neck.

Indices

OI	Ocular index: $EL / HW \times 100$
CI	Cephalic index: $HW / HL \times 100$
SI	Scape index: $SL / HW \times 100$
PTHI	Petiole height index: $PTH / PTL \times 100$
PTWI	Petiole width index: $PTW / PTL \times 100$
LBI	Leg-body index: $WL / LHT \times 100$
PPI	Postpetiole index: $PPW / PTW \times 100$

Throughout the text, ‘**w**’ stands for ‘worker’ or ‘workers’, ‘**q**’ for queen, ‘**m**’ for male, ‘**BS**’ for beating sheet, ‘**ML**’ for Malaise trap, and ‘**SF**’ sifting.

Institutions and museums

The abbreviations of natural history collections follow Evenhuis (2019) and Brandão (2000).

BMNH	The Natural History Museum, London, U.K.
CASC	California Academy of Sciences collection, California Academy of Sciences, San Francisco, California, USA.

- KSMA** King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia.
- MHNG** Muséum d'Histoire Naturelle, Geneva, Switzerland.
- OUMC** Oxford University Museum, Oxford, U.K.
- WMLC** World Museum Liverpool, Liverpool, U.K.

Results

Synoptic list of Arabian species of *Crematogaster*

- Crematogaster acaciae* Forel, 1892
Crematogaster aegyptiaca Mayr, 1862
Crematogaster antaris Forel, 1894b
Crematogaster auberti Emery, 1869a
Crematogaster chiarinii Emery, 1881
= *Crematogaster affabilis* Forel, 1907b syn. nov.
Crematogaster delagoensis Forel, 1894a
Crematogaster flaviventris Santschi, 1910
Crematogaster gryllsi Sharaf & Hita Garcia sp. nov.
Crematogaster inermis Mayr, 1862
Crematogaster jacindae Sharaf & Hita Garcia sp. nov.
Crematogaster jehovae Forel, 1907c
Crematogaster laestrygon Emery, 1869b
Crematogaster striaticeps Forel, 1909, stat. nov.
Crematogaster melanogaster Emery, 1895
Crematogaster mimosae Santschi, 1914a
Crematogaster oasisium Santschi, 1911
Crematogaster senegalensis Roger, 1863

Identification key to Arabian species of *Crematogaster*

- | | | |
|---|--|-----------------------------------|
| 1 | Postpetiole not bilobed dorsally (Figs 1A, 17A–C)..... | <i>C. gryllsi</i> sp. nov. |
| – | Postpetiole bilobed dorsally (Fig. 1B)..... | 2 |
| 2 | Propodeal spines completely absent (Fig. 1C) | 3 |
| – | Propodeal spines present, ranging from small denticles to long spines (Fig. 1D)..... | 4 |
| 3 | Unicolorous yellow-brown to brown species; cephalic surface including area in front of eyes unsculptured; eyes with ca. 14 ommatidia in longest row; | |

- posterior half of clypeus with fine appressed pubescence; mesonotum in profile with a small tubercle close to promesonotal suture (Fig. 1E); mesopleura and metapleura longitudinally striated (Fig. 1E); mesonotum without hairs; propodeal spiracles circular (Figs 1E, 20A–C) ***C. inermis* Mayr**
- Bicolored species, head black-brown or black, mesosoma, petiole and postpetiole dark brown, relatively lighter than head, gaster golden yellow; area in front of eyes finely longitudinally striated; cephalic surface feebly imbricate; eyes with ca. 11 ommatidia in longest row; posterior half of clypeus without hairs or pubescence; mesonotum in profile without tubercle (Fig. 1F); mesopleura and metapleura distinctly densely imbricate (Fig. 1F); mesonotum with a single pair of hairs; propodeal spiracles slit-shaped (Fig. 1F), gaster golden yellow (Fig. 21A–C) ***C. jacindae* sp. nov.**
- 4 Propodeal spines reduced to a small denticle (Fig. 14A–C) ***C. delagoensis* Forel**
- Propodeal spines well developed **5**
- 5 In full-face view, antennal scapes short, clearly not reaching posterior margin of head (Fig. 2A) **6**
- In full-face view, antennal scapes longer, clearly reaching or surpassing posterior margin of head (Fig. 2B) **9**
- 6 Propodeal spines short and blunt (Fig. 2C), approx. as long as their bases in profile; antennal fossae surrounded by curved striolae in full-face view (Figs 2A, 7A–C) ***C. aegyptiaca* Mayr**
- Propodeal spines long and acute, distinctly longer than their bases in profile (Fig. 2D); antennal fossae surrounded by longitudinal striolae in full-face view (Fig. 2E) **7**
- 7 Body distinctly opaque; cephalic surface completely densely longitudinally rugulose (Fig. 2F); head, mesosoma, petiole and postpetiole reddish (Fig. 27A–C) ***C. mimosae* Santschi**
- Body shining; only area in front of eyes faintly longitudinally rugulose; head, mesosoma, petiole and postpetiole uniform yellow or brown **8**
- 8 Body uniform yellow; head, in full-face view, with feebly-defined frontal triangle and without longitudinal carina; postpetiole in dorsal view broader posteriorly than anteriorly; propodeum dorsum seen from above longitudinally striated (Fig. 5A–C) ***C. acaciae* Forel**
- Head, petiole, postpetiole and gaster dark brown, mesosoma light brown; head, in full-face view, with well-defined frontal triangle and posterior longitudinal carina reaching posterior margin of eyes; propodeum dorsum seen from above transversally striated; postpetiole in dorsal view as broad as anteriorly and posteriorly (Fig. 12A–C) ***C. chiarinii* Emery**
- 9 Antennal scapes when laid back from their insertions just reach posterior margin of head in full-face view **10**
- Antennal scapes when laid back from their insertions clearly surpassing posterior margin of head in full-face view **11**

- 10 Unicolorous brown species; clypeus smooth; anterior half of head in full-face view longitudinally striated, ground surface between striae smooth (Fig. 3A); posterior half of head smooth, general appearance of head shining (Fig. 29A–C) ***C. senegalensis* Roger**
- Bicolored species, head, mesosoma, petiole, postpetiole and appendages brown or red-brown, gaster golden yellow; clypeus longitudinally striated; anterior half of head in full-face view finely longitudinally striated, ground surface between striae and posterior half of head finely densely punctate (Fig. 3B); general appearance of head dull (Fig. 15A–C) ***C. flaviventris* Santschi**
- 11 Mesonotum in profile without a small tubercle close to promesonotal suture **12**
- Mesonotum in profile with a small tubercle close to promesonotal suture **13**
- 12 Whole cephalic surface finely, densely longitudinally striated and dull; head in full-face view with antennal scapes surpassing posterior margin of head by approximate length of the three funicular segments together (Fig. 3C); propodeal spines long and acute, more than twice longer than bases (Fig. 3D); mesonotum in profile feebly convex (Fig. 3D); subpetiolar process well developed (Fig. 3D); mesosomal hairs numerous (Fig. 3D), five on promesonotum, two on pronotum, and a single pair on the propodeum (Fig. 26A–C) ***C. melanogaster* Emery**
- Anterior half of cephalic surface superficially striated, posterior half smooth and shining; head in full-face view with antennal scapes surpassing posterior margin of head by ca. thickness of the first funicular segment (Fig. 3E); propodeal spines shorter and blunt, ca. 1.5× longer than bases (Fig. 3F); mesonotum in profile strongly convex (Fig. 3F); subpetiolar process absent; mesosomal hairs restricted to a single pair on pronotum (Fig. 10A–C) ***C. auberti* Emery**
- 13 Cephalic surface and clypeus completely finely densely longitudinally striated (Fig. 30A–C) ***C. striaticeps* Forel**
- Anterior half of cephalic surface or at least area in front of eyes and clypeus longitudinally striated **14**
- 14 Promesonotum with at least four pairs of suberect hairs; petiole in dorsal view with pointed anterior corners; first gastral tergite with several pairs of hairs (ca. 7 pairs) (Fig. 28A–C) ***C. oasis* Santschi**
- Promesonotum with a single pair of hairs or without hairs; petiole in dorsal view with rounded anterior corners; hairs on first gastral tergites rare, restricted to few pairs on posterior margin of the tergite **15**
- 15 Petiole in dorsal view with concave anterior margin (Fig. 4A); promesonotum and mesonotum dorsum unsculptured (Fig. 8A–C) ***C. antarcticus* Forel**
- Petiole in dorsal view with a straight anterior margin (Fig. 4B); promesonotum and mesonotum dorsum distinctly longitudinally striated **16**
- 16 Postpetiole approx. twice broader than long in dorsal view (Fig. 4C); color black-brown or dark brown (Fig. 24A–C) ***C. laestrygon* Emery**
- Postpetiole little broader than long in dorsal view (Fig. 4D); color red-brown (Fig. 23A–C) ***C. jehovae* Forel**

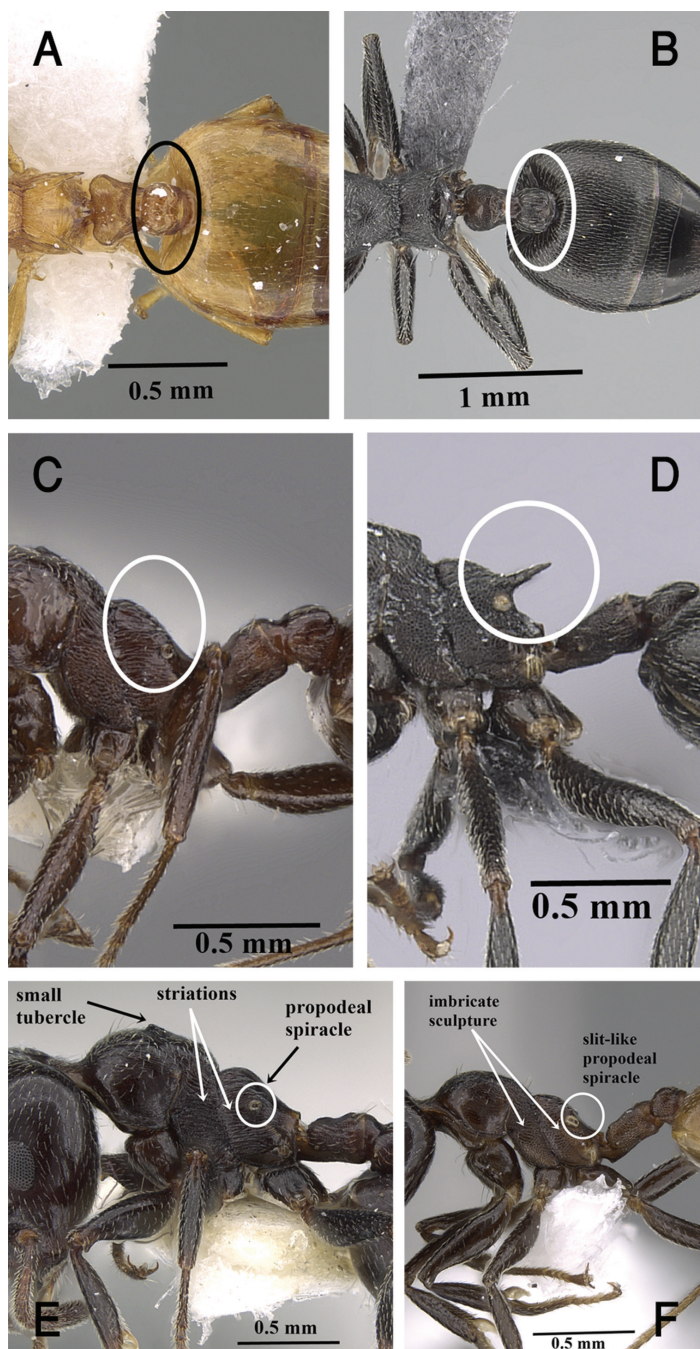


Figure 1. **A** Postpetiole of *C. gryllsi* sp. nov. in dorsal view, CASENT0919794 (Michele Esposito) **B** postpetiole of *C. chiarinii* in dorsal view, CASENT0263878 (Will Ericson) **C** propodeum of *C. inermis* in profile, CASENT0922679 (Wade Lee) **D** propodeal spines of *C. chiarinii* in profile, CASENT0263878 (Will Ericson) **E** mesosoma of *C. inermis* in profile, KG01956A (Michele Esposito) **F** mesosoma of *C. jacindae* in profile CASENT0922856 (Michele Esposito), www.AntWeb.org.

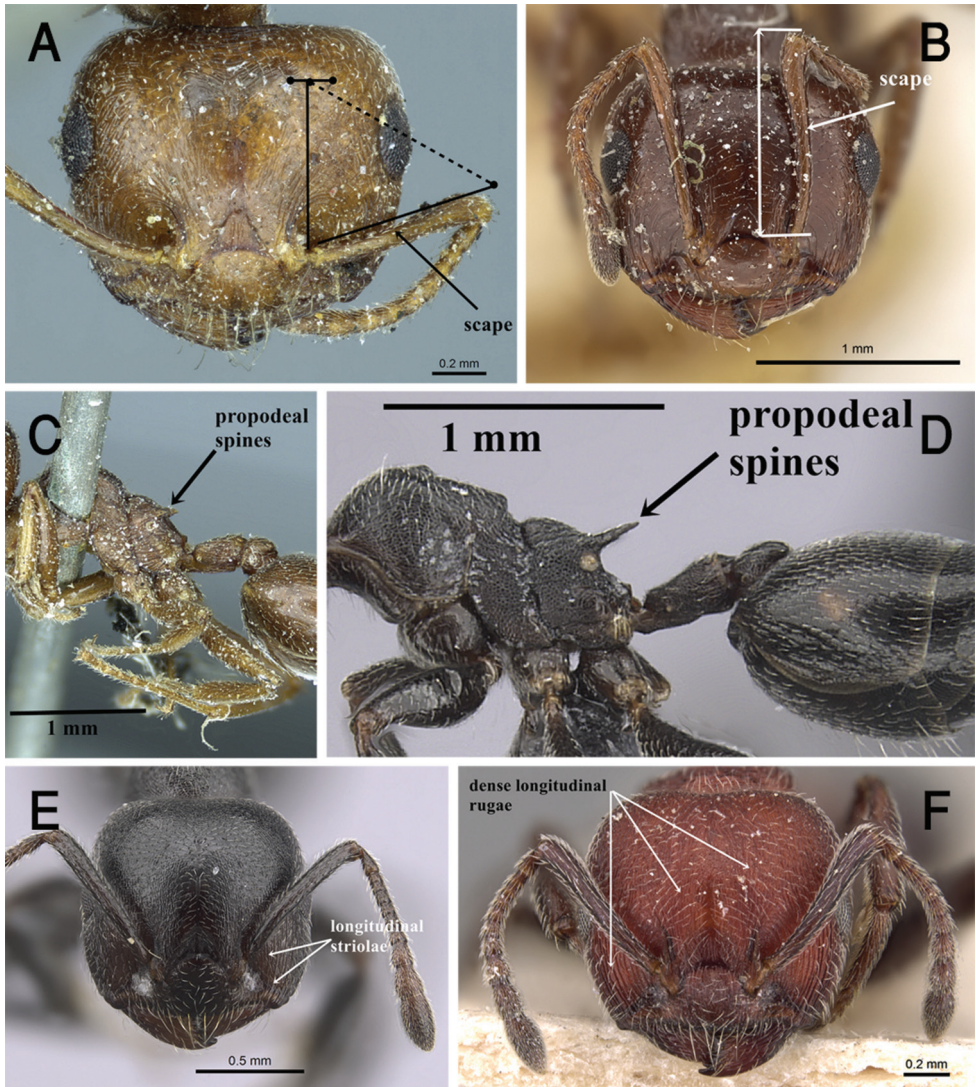


Figure 2. **A** Head of *C. aegyptiaca* in full-face view, CASENT0916082 (Anna Pal) **B** head of *C. oasium* in full-face view, CASENT0249821 (Ryan Perry) **C** mesosoma of *C. aegyptiaca* in profile, CASENT0916082 (Anna Pal) **D** propodeal spines of *C. chiarinii* in profile, CASENT0263878 (Will Ericson) **E** head of *C. chiarinii* in full-face view, CASENT0263878 (Will Ericson) **F** head of *C. mimosae* in full-face view, CASENT0904507 (Will Ericson), www.AntWeb.org.

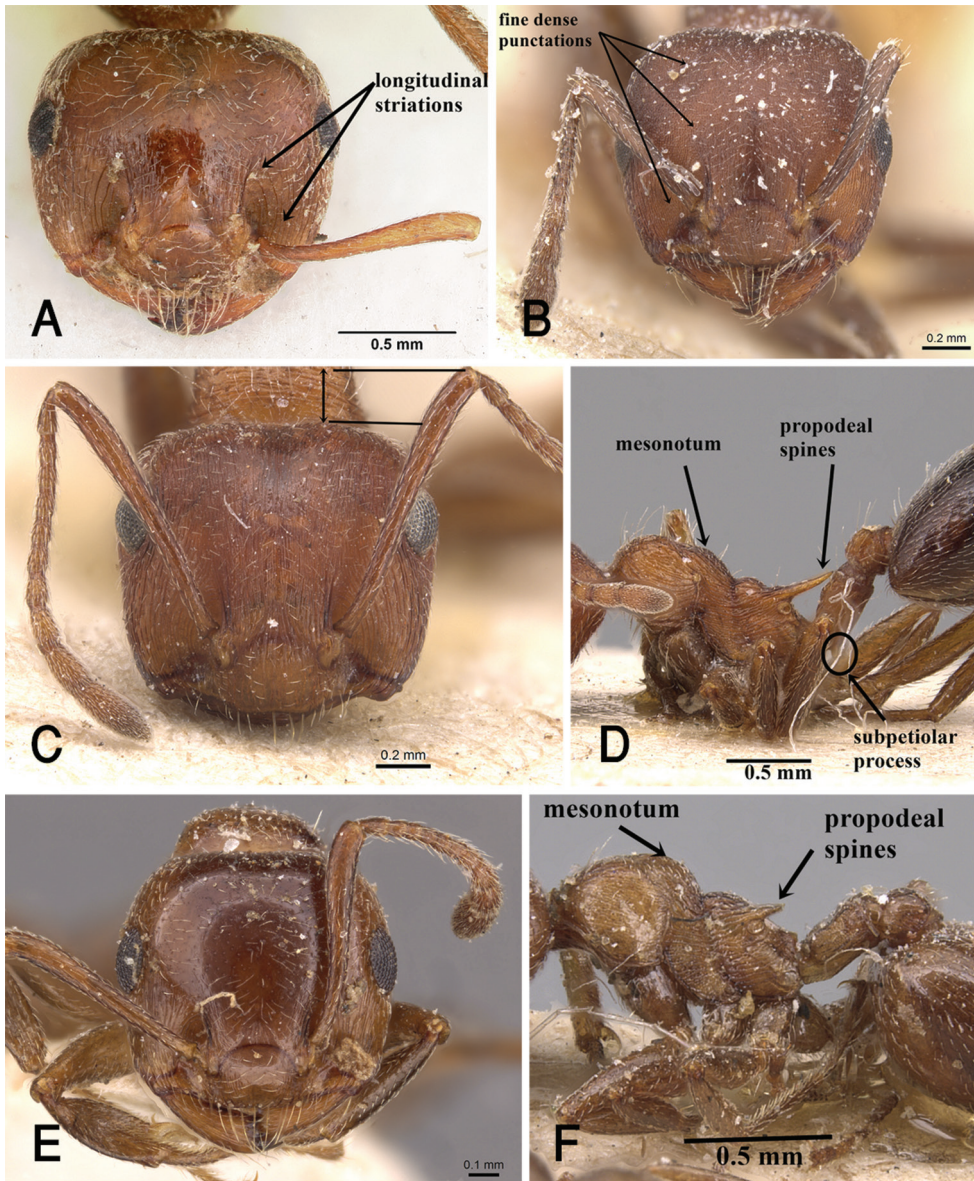


Figure 3. **A** Head of *C. senegalensis* in full-face view, CASENT0104592 (April Nobile) **B** head of *C. flaviventris* in full-face view, CASENT0912651 (Will Ericson) **C** head of *C. melanogaster* in full-face view, CASENT0904511 (Will Ericson) **D** mesosoma of *C. melanogaster* in profile, CASENT0904511 (Will Ericson) **E** head of *C. auberti* in full-face view, CASENT0908480 (Zach Lieberman) **F** mesosoma of *C. auberti* in profile, CASENT0904499 (Will Ericson), www.AntWeb.org.

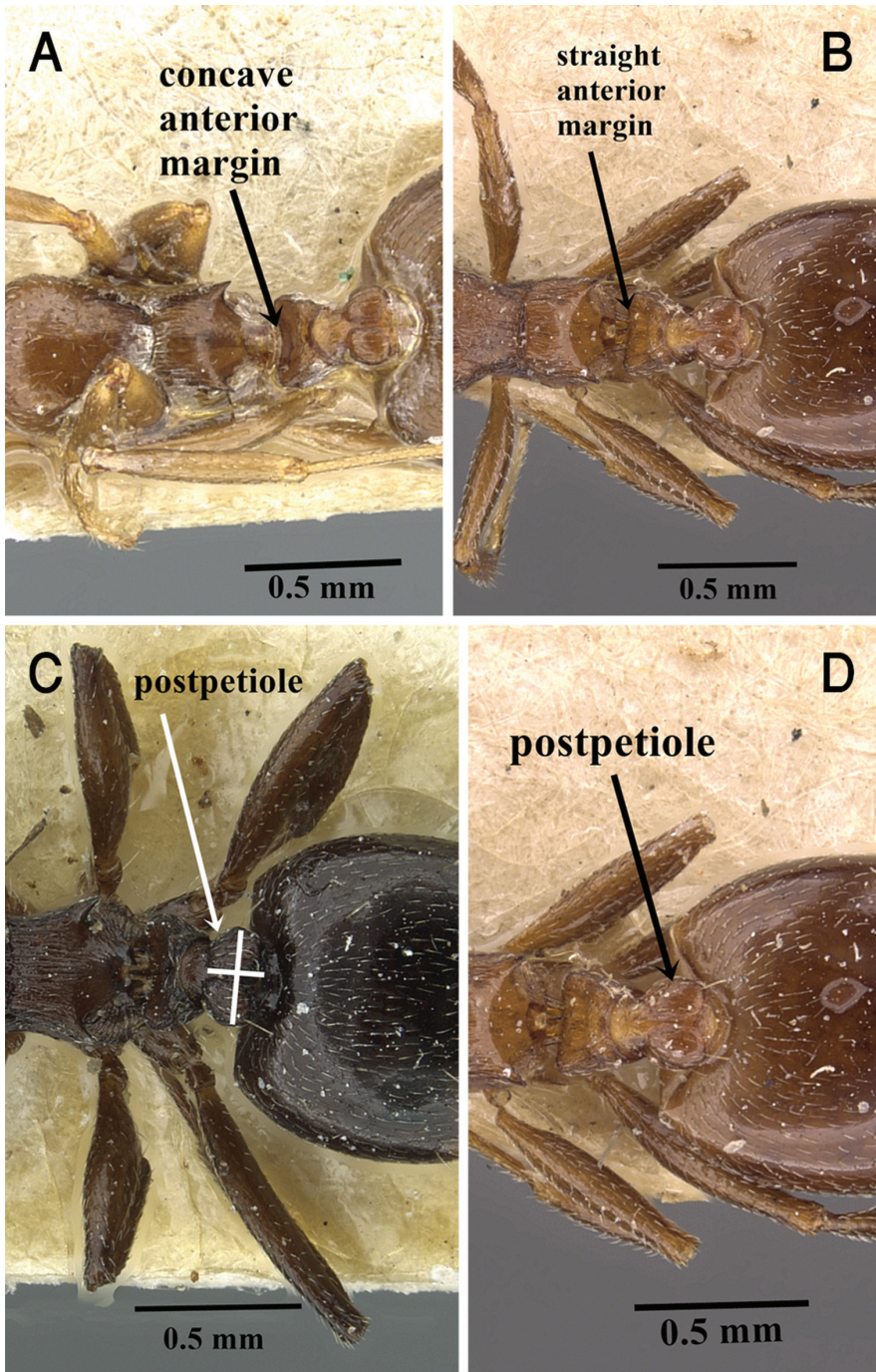


Figure 4. **A** Petiole of *C. antaris* in dorsal view, CASENT0903658 (Will Ericson) **B** petiole of *C. jehovae* in dorsal view, CASENT0908475 (Zach Lieberman) **C** postpetiole of *C. laestrygon* in dorsal view, CASENT0912691 (Zach Lieberman) **D** postpetiole of *C. jehovae* in dorsal view, CASENT0908475 (Zach Lieberman), www.AntWeb.org.

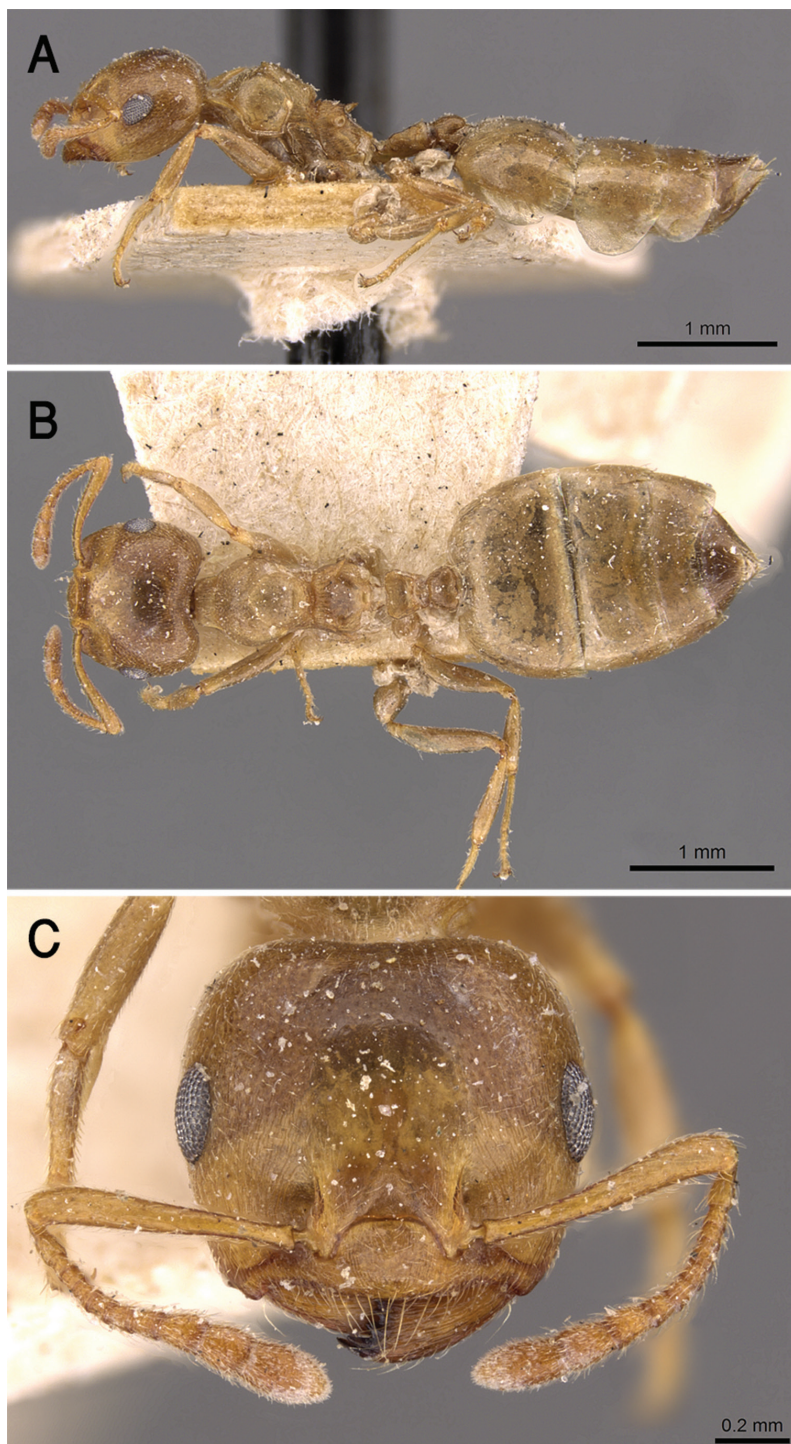


Figure 5. *C. acaciae* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0908494 (Zach Lieberman), www.AntWeb.org.

Review of Arabian species

Crematogaster acaciae Forel

Figure 5A–C

Taxonomic history.

Crematogaster acaciae Forel, 1892: 141 (w.) ETHIOPIA.

Combination in *Crematogaster (Acrocoelia)*: Emery 1922: 144; in *Crematogaster. (Crematogaster)*: Bolton 1995: 166.

Subspecies of *C. brunneipennis*: Wheeler 1922: 152.

Status as species: Emery 1922: 144; Collingwood 1985: 260.

Current subspecies: *C. acaciae generosa* Santschi, *C. acaciae gloriosa* Santschi, *C. acaciae victoriosa* Santschi.

Material examined. **KSA:** Jebel Dhablah, 27.79175N, 41.34063E, 03.v.1985, 950 m (W. Buttiker) (1 w, WMLC); Alqatif, 26.51028N, 49.96889E, 14.iv.1983 (Collingwood CA) (1 w, WMLC); Alqatif, 26.51028N, 49.96889E, 15.iv.1983 (Collingwood CA) (48 w, WMLC); **Oman:** muqshen (mugshin), 19.55N, 54.883333E, 20.ix.1979 (R. W. Whitcomb) (1 w, WMLC); 67 km S. Mintirib, desert trade, 27.i.1986 (W. Buttiker) (9 w, eastern sand project, WMLC); W. of Muscat, 23.588N, 58.3829E, 26.ix.1982 (M. Gallagher) (2w, 6374, WMLC); **Yemen:** Al Kawd, 13.088622N, 45.364722E, x.1992 (1 q, WMLC); **Namibia:** Kuzikus Wildlife Reserve, Windhoek, 23.2306S, 18.401617E, 1340 m, 07.ix.2009 (H Campbell) (1 W, OUMC); **Sudan:** Khordonia, 11.85N, 34.25E, 24.x.2001 (J. Mathews) (2 W, OUMC); Khordonia, Damazine Plantation, Blue Nile, 11.85N, 34.25E, 25.x.2000 (J. Mathews) (2 W, OUMC); **Tanzania:** Mkomazi Igire Hill, 10.i.1996 (G. McGavin) (2 W, OUMC).

Geographic range. *Crematogaster acaciae* was originally described from Ethiopia but is also known from Democratic Republic of Congo, Somalia, South Africa, and Zambia (Guénard et al. 2017; Janicki et al. 2017). For the Arabian Peninsula, it was previously only known from Oman (Collingwood 1985; Collingwood and Agosti 1996; Borowiec 2014; Sharaf et al. 2018; Monks et al. 2019) (Fig. 6). In this study, we provide the first records for the KSA and Yemen.

Remarks. This species represents a typical problematic taxon within the genus. The known distribution of *C. acaciae* and its three subspecies in the Afrotropics is patchy and there are some notable morphological differences between the infraspecific taxa. At present, it is likely that the taxonomic status of the involved taxa will change within the frame of a comprehensive revision of the Afrotropical fauna.

Crematogaster aegyptiaca Mayr

Figure 7A–C

Taxonomic history.

Crematogaster aegyptiaca Mayr, 1862: 765 (w.) EGYPT.

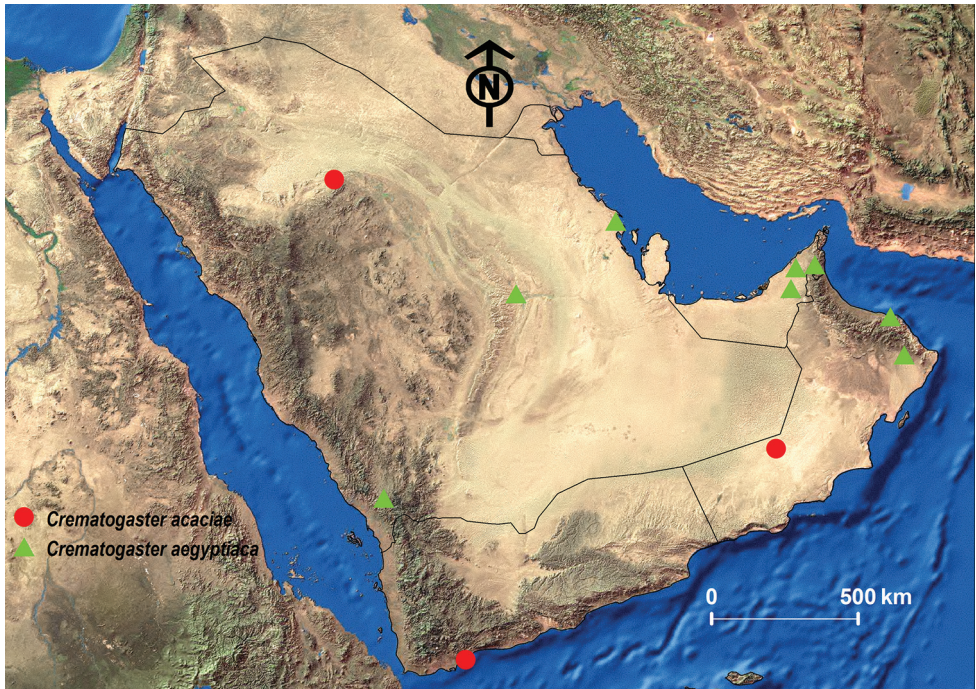


Figure 6. Distribution map of *C. acacia* and *C. aegyptiaca*.

Combination in *Crematogaster* (*Crematogaster*): Wheeler, 1922: 828; in *Crematogaster* (*Acrocoelia*): Emery, 1922: 144; in *Crematogaster* (*Crematogaster*): Bolton, 1995: 166. Current subspecies: *C. aegyptiaca pharaonis* Santschi, *C. aegyptiaca robusta* Emery, *C. aegyptiaca turkanensis* Santschi.

Material examined. **KSA:** Asir Province, Abha, Al Habala, 18.034167N, 42.858167E, 2397 m, 25.iv.2011 (Sharaf MR) (19 w, KSMA); Riyadh, Al Hay-er, 24.290833N, 46.9075E, 10.iii.2011 (Sharaf MR) (14 w, KSMA); **UAE:** Near Mahafiz, 25.09N, 55.48E, 24.iii-07.iv.2011 (M Hauser et al.), UAE13055 (1 w, CASENT0264387, 1 w, CASENT0264388, KSMA); Wadi Madaq, 25.18N, 56.07E, 15–31.x.2010 (M Hauser et al.), UAE12848 (1 w, CASENT0265207, KSMA); **Oman:** dunes near Mintirib, 22.4248N, 58.8032E, 17.xi.1984 (M. Gallagher) (1 w, WMLC).

Geographic range. This species was originally described from Egypt and can be found in most most countries of North Africa but also in Sudan and Kenya (Guénard et al. 2017; Janicki et al. 2017). For the Arabian Peninsula, it was recorded from the KSA, Oman, the UAE, and Yemen (Borowiec 2014; Collingwood 1985, Collingwood and Agosti 1996; Collingwood et al. 2011; Sharaf et al. 2018) (Fig. 6).

Remarks. As for *C. acacia* (and many other taxa), the taxonomic condition of this species is relatively unclear due to the absence of any revisions in the regions in question, and we cannot predict the taxonomic status of *C. aegyptiaca* and its subspecies after being revised. However, based on our experience with this species, it is readily identifiable and we are very confident of the Arabian material being genuine *C. aegyptiaca*.

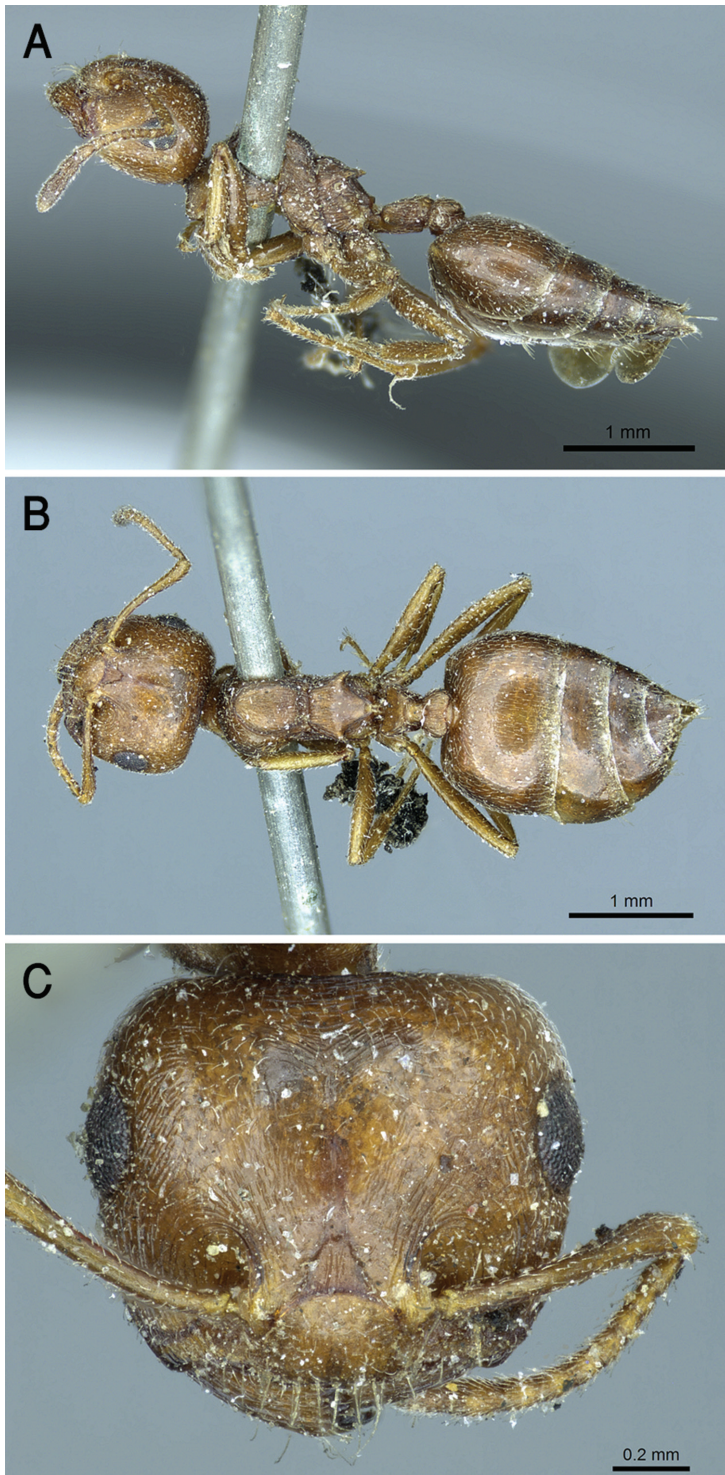


Figure 7. *C. aegyptiaca* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0916082 (Anna Pal), www.AntWeb.org.

***Crematogaster antaris* Forel**

Figure 8A–C

Taxonomic history.

Crematogaster (Acrocoelia) auberti r. *antaris* Forel, 1894b: 26 (w., q.) ALGERIA.

Combination in *Crematogaster (Acrocoelia)*: Emery 1922: 142; in *Crematogaster (Crematogaster)*: Bolton 1995: 166.

Subspecies of *C. inermis*: Emery 1926: 2; Menozzi 1927: 379; of *C. auberti*: Emery 1924: 8; Finzi 1930: 15; Santschi 1938: 38; Cagniant 1964: 103.

Status as species: Santschi 1921: 71; Collingwood 1985: 260.

Crematogaster auberti var. *sordida* Forel, 1909: 104 (w.) ALGERIA. [First available use of *Crematogaster auberti* r. *laestrygon* var. *sordida* Forel, 1894: 26; unavailable name]. Combination in *C. (Acrocoelia)*: Emery 1922: 142.

Subspecies of *C. antaris*: Santschi 1921: 71. Junior synonym of *C. antaris*: Cagniant 2005: 11.

Material examined. KSA: Riyadh, Al Mezahmyiah, 24.46633N, 46.25131E, 648 m, 29.xi.2014 (Salman S) (19 w, KSMA); Riyadh, Al Dawadmy, 24.55216N, 43.93170E, 873 m, 16.i.2015 (Salman S) (9 w, KSMA); Taif, Al Wesam district, 21.204722N, 40.345278E, 11.x.2010 (Al Dhafer et al.) (5 w, KSMA); Asir province, Ballasmer, A'l Azza, 18.60815N, 42.24628E, 2611 m, 27.iv.2019 (Sharaf MR) (2 w, KSMA); Asir province, Abha, Al Souda, 18.274167N, 42.364444E, 2982 m, 24.iv.2011 (Sharaf MR) (1 w, KSMA); Taif, Shafa of Shafa hwy, 21.139167N, 40.351389E, 12.x.2010 (Al Dhaffer et al.) (8 w, KSMA); Altawil, 18.016667N, 42.95E, 21–22.ix.1984 (W. Buttiker) (1 w, WMLC); W. Harith, 17.4863N, 44.0825E, 28.ix.1978 (W. Buttiker) (1 w, WMLC); El Shoiba, 20.680084N, 39.523233E, 28.xii.1978 (W. Buttiker) (1 w, WMLC); Jeddah, 21.4858N, 39.1925E, 26.ii.1934 (G. L. Bates, B.M. 1934–404) (6 w, BMNH). **Oman:** Mintrib, 22.4248N, 58.8032E (M. D. Gallagher) (7 w, WMLC); Qarhat Mu'ammur, 21.666667N, 59.316667E, 22.iv.1986 (M. D. Gallagher) (1 w, 7691, WMLC); khabura (Al Khaburah), 23.9628N, 57.0957E, 10.iii.1980 (R. W. Whitcomb) (1 w, WMLC); Musandan, 26.03333N, 56.3E (3 w, WMLC); Mu'ammur, 1986 (W. Buttiker) (1 q, WMLC); Um Qashab, 27.iv.1986 (M. D. Gallagher) (2 w, 7865, WMLC); 50–90 km E of Hayam, ii-iii.1993 (R.D. Schumann) (1 w, desert, in spirit tube, WMLC); Qarhat Mu'ammur, 21.666667N, 59.316667E, 135 m, 02.ii.1986 (W. Buttiker) (4 w in spirit tube, eastern sand project, dunes, WMLC); Khabura, 23.9628N, 57.0957E, 01.xii.1979 (R. W. Whitcomb) (6 w, BMNH); Rustaq, 23.387831782N, 57.421331648E, 07.v.1979 (R. W. Whitcomb) (11 w, BMNH); Khbura, 23.9628N, 57.0957E, 27.i.1980 (R. W. Whitcomb) (21 w, BMNH). **Qatar:** Umsaid Road, 09.iv.2005 (M. S. Abdel-Dayem) (10 w, KSMA); Al Kharara-Seleiy Road, 09.iv.2005 (M. S. Abdel-Dayem) (13 w, KSMA). **UAE:** Ras Ghanada, vi.1995 (B. Tigar) (15 w in spirit tube, WMLC); Public Hunting Ground, 12.viii.1994 (B. Tigar) (13 w in spirit tube, 2360, WMLC); Al Ain Zoo, 24.1792N, 55.7396E, iv-v.1995 (B. Tigar) (7 w in spirit tube, WMLC); Sweihan, 24.4582N, 55.3324E, 04.iii.1995 (Collingwood CA) (25 w in spirit tube, stony desert, WMLC); Khour Al Taafirah, 17.2N, 42.35E, 10.x.1984 (W. Buttiker) (14 w in spirit tube, WMLC); Dubai city, 25.2048N, 55.2708E, 2002 (K. Valsan) (4 w, BMNH).

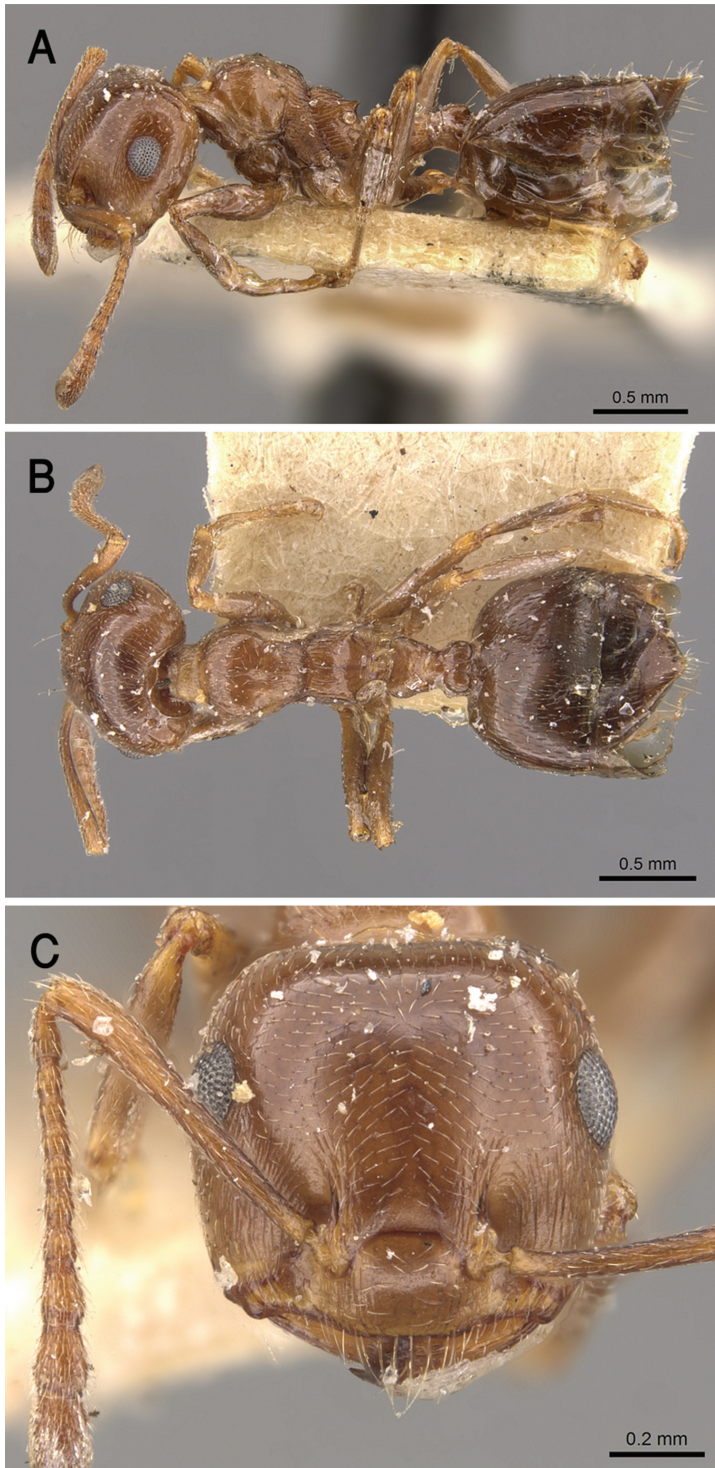


Figure 8. *C. antaris* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0908473 (Will Ericson), www.AntWeb.org.



Figure 9. Distribution map of *C. antaris*.

Yemen: W. Aden Port, Jebel Jihaf, 04.x.1937 (H. Scott & E. B. Britton. B.M.1933-246) (9 w, B. M. Expedition to S.W. Arabia, BMNH); Summit of Jebel Kohl, 15 miles N. of Sana'a, 01.ii.1938 (H. Scott & E. B. Britton. B.M.1933-246) (6 w, B.M. Expedition to S.W. Arabia, H. Scott & E. B. Britton, B.M.1933-246).

Geographic range. Originally described from Algeria, *C. antaris* is also found in Morocco, Tunisia, Egypt, and Iran (Sharaf 2006; Paknia et al. 2008; Vonshak and Ionescu-Hirsch 2009; Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). Its apparent absence in Libya is likely a sampling artifact. *Crematogaster antaris* is also broadly distributed in the Arabian Peninsula where it is known from Kuwait, Oman, the KSA, the UAE, and Yemen (Collingwood 1985; Tigar and Collingwood 1993; Collingwood and Agosti 1996; Collingwood et al. 2011; Borowiec 2014; Sharaf et al. 2018) (Fig. 9).

Remarks. This is a very widespread and common species, which appears to be one of the most arid-adapted species within the genus. Our collections represent a new record for Qatar.

Crematogaster auberti Emery

Figure 10A–C

Taxonomic history.

Crematogaster (Acrocoelia) auberti Emery, 1869a: 23 (footnote) (w.) FRANCE; André 1883: 395 (q.); Emery 1891: 14 (m.).

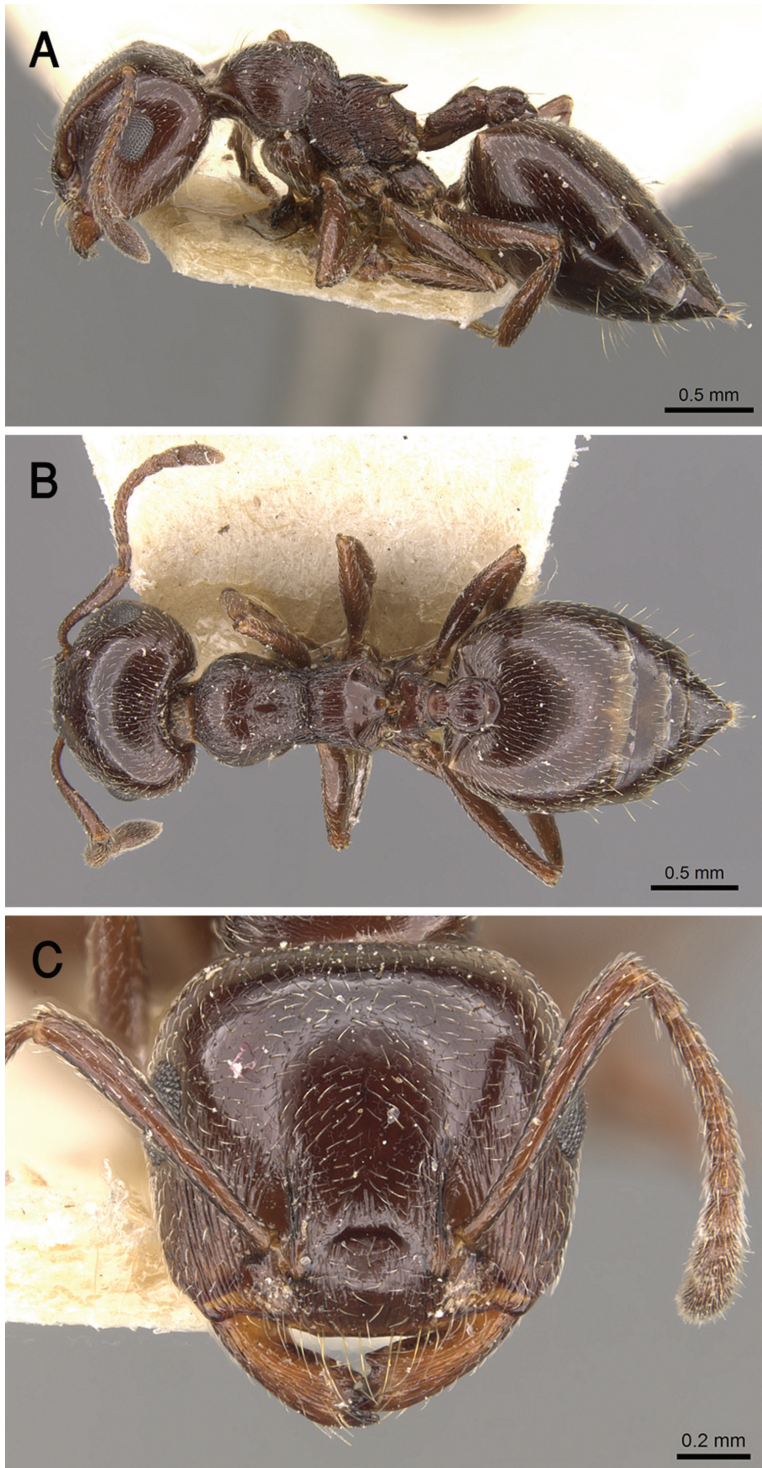


Figure 10. *C. auberti* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0908470 (Will Ericson), www.AntWeb.org.

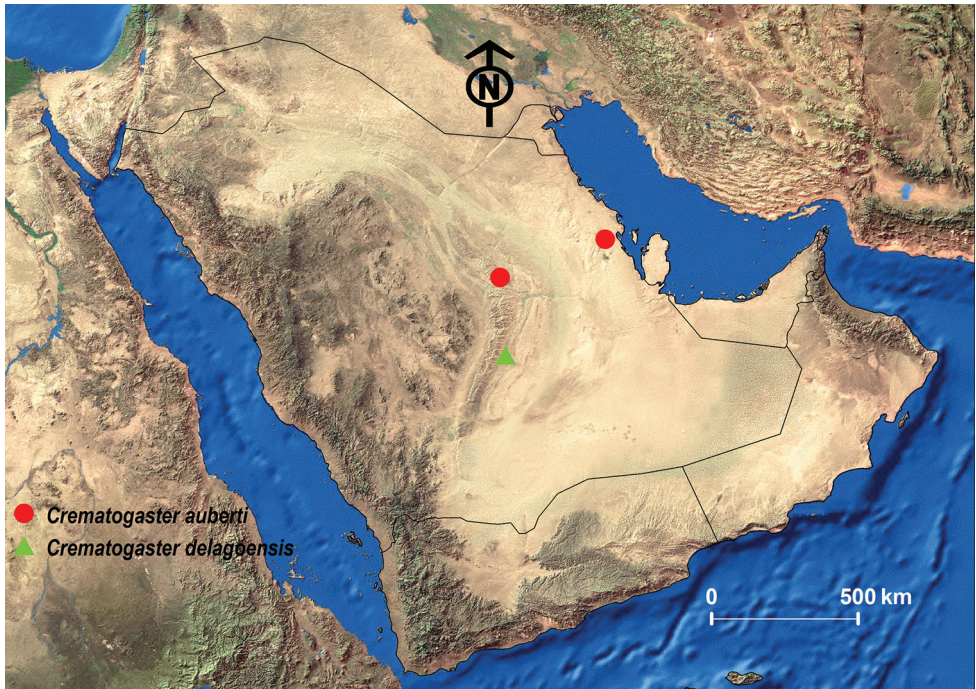


Figure 11. Distribution map of *C. auberti* and *C. delagoensis*.

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 142; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Subspecies of *C. scutellaris*: Emery and Forel 1879: 464; of *C. schmidtii*: Emery 1891: 14; of *C. inermis*: Emery 1926: 3.

Status as species: Forel 1894b: 24; Forel 1902: 152; Bondroit 1918: 115; Karavaiev 1927: 104; Finzi 1930: 15; Santschi 1937: 300.

Current subspecies: *C. auberti karawaewi* Ruzsky, *C. auberti levithorax* Forel, *C. auberti nigripes* Menozzi, *C. auberti regilla* Santschi, *C. auberti savinae* Zimmermann, *C. auberti vogti* Forel.

Senior synonym of *Crematogaster auberti* var. *iberica* Forel, 1909: 103 (w.) SPAIN.

Junior synonym of *C. auberti*: Collingwood 1978: 69.

Material examined. **KSA:** Riyadh, Al Ammaryia, 24.794167N, 46.423333E, 648 m, 21.i.2010 (Aldawood AS) (12 w, KSMA); Eastern province, Buqaiq, 25.962222N, 49.647139E, 95 m, 03.iii.2011 (Al Dhafer et al.) (2 w, KSMA); **Egypt:** Alexandria, 07.v.1899 (1w, BMNH); **Algeria:** Bona, 24.xi.1993 (2 w, BMNH); **Morocco:** Tamri N. de Agadir, 13–17.iii.1961 (Meinander) (3 w, BMNH).

Geographic range. This species was initially described from France and seems to have a broad distribution range from the south of France, the Iberian Peninsula, and the Canary Islands through all of North Africa to the Middle East, but is also found throughout the Balkans (Sharaf 2006; Borowiec and Salata 2012; Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). On the Arabian Peninsula it has been only

recorded from the KSA (Collingwood 1985; Collingwood and Agosti 1996; Borowiec and Salata 2012; Borowiec 2014) (Fig. 11).

Remarks. This is likely one of the most problematic species treated in this study. The taxonomic history provided above is complex with numerous status changes and infraspecific taxa. Borowiec (2014) states that all records from the eastern parts of the Mediterranean region are doubtful and likely misidentifications. If so, this would mean that the material from KSA is probably another species. However, at present and without a meaningful treatment of the European *Crematogaster* fauna, it is not possible for us to ascertain the genuine identity of this species. Thus, we maintain it as *C. auberti* for the moment and await further study of type material in European collections which might help elucidate its real identity.

Crematogaster chiarinii Emery

Figure 12A–C

Taxonomic history.

Crematogaster chiarinii Emery, 1881: 271, fig. (w.) ETHIOPIA: Forel 1892: 353 (q., m.). Combination in *Crematogaster* (*Crematogaster*): Wheeler 1922: 835; in *Crematogaster* (*Acrocoelia*): Emery 1922: 146; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166. Current subspecies: *C. chiarinii aethiops*, *C. chiarinii bayeri*, *C. chiarinii cincta*, *C. chiarinii nigra*, *C. chiarinii sellula*, *C. chiarinii subsulcata*, *C. chiarinii taediosa*, *C. chiarinii v-nigra*.

Crematogaster chiarinii var. *affabilis* Forel, 1907b: 142 (w.) SOMALIA. Syn. nov.

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 146; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Material examined. KSA: Al Baha Province: Elqamh park, Baljurshi, 19.913056N, 41.905E, 1931 m, 17.v.2010 (Sharaf MR) (12 w, KSMA); Al Mukhwah, Dhi Ayn village, 19.929417N, 41.441722E, 741 m, 18.v.2011 (Sharaf MR) (19 w, KSMA); Al Mukhwah, Dhi Ayn village, 19.929417N, 41.441722E, 741 m, 15.v.2011 (Sharaf MR) (4 w, KSMA); W. Elzaraeb (Kheir), 20.073417N, 41.38675E, 2123 m, 15.v.2010 (Sharaf MR) (3 w, KSMA); Amadan, Almandaq, 20.245278N, 41.468333E, 1881 m, 19.v.2010 (Sharaf MR) (3 w, KSMA); Al Baha city, 20.014533N, 41.4674E, 2172 m, 16.v.2010 (Sharaf MR) (3 w, KSMA); W. Jallah, 20.134472N, 41.342889E, 1912 m, 16.v.2011 (Sharaf MR) (15 w, 6 q, 6 m, KSMA); AlUrduya gov., W. Gonouna, 19.429361N, 41.605028E, 353 m, 12.v.2011 (Sharaf MR) (3 w, KSMA); W. Turabah, Almandaq, 20.211028N, 41.288222E, 1793 m, 10.v.2011 (Sharaf MR) (21 w, KSMA); W. Turabah, Almandaq, 20.241917N, 41.262833E, 1751 m, 19.ix.2011 (Sharaf MR) (1 w with broken waist and gaster, KSMA); Baljurshi forest, 19.80559N, 41.71198E, 1930 m, 21.ix.2011 (FA Esteve) (2 w, KSMA); AlTawla (Al Baha-Taif RD), W. Bawah, 20.7496N, 41.247433E, 1310 m, 08.xi.2012 (Sharaf MR) (10 w, KSMA); W. Dafa near Eiban, 17.37463N, 43.07539E, 888 m, 12.xi.2012 (Sharaf MR) (7 w, KSMA); Asir province: Khamis Mushayt, W. Bishah, 18.333639N, 42.703583E, 1990 m,

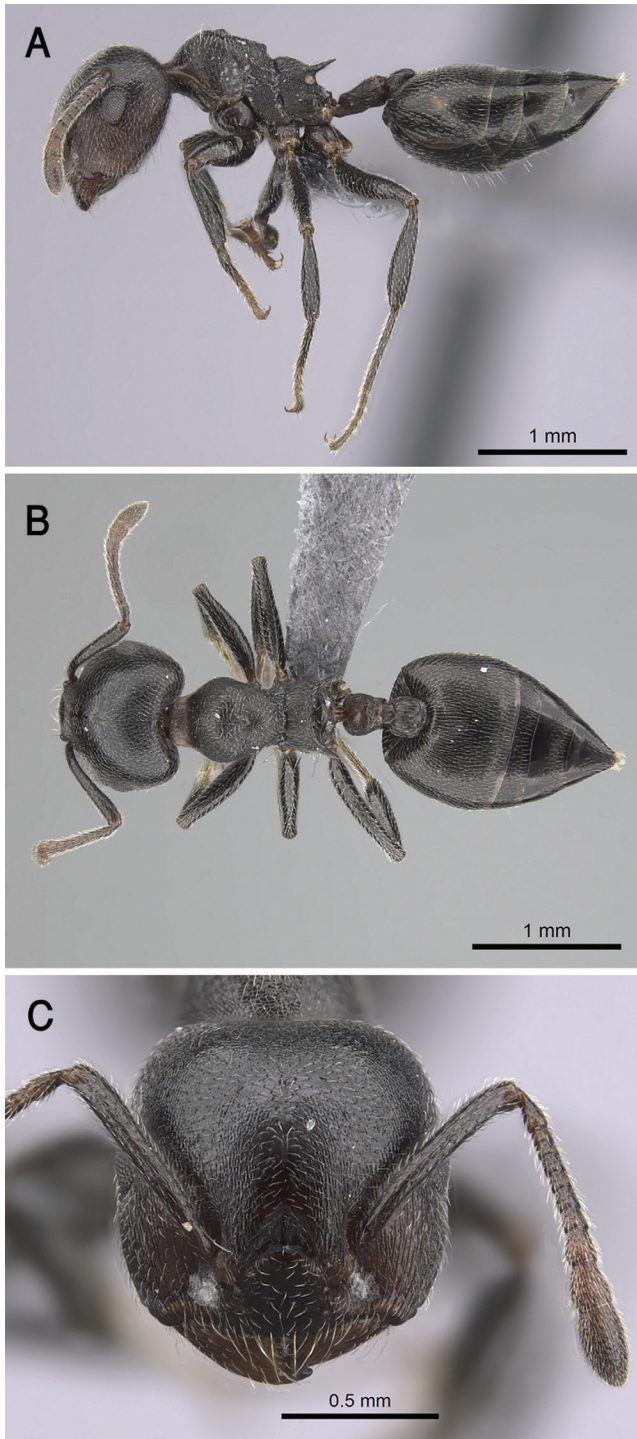


Figure 12. *C. chiarinii* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0263878 (Will Ericson), www.AntWeb.org.

27.iv.2011 (Sharaf MR) (4 w, KSMA); Abha, 18.2465N, 42.5117E, 25.iii.1983 (Collingwood CA) (9 w, WMLC); Ashaira, 21.7575N, 40.651944E, 1340 m, 14–15. ix.1980 (Collingwood CA) (1 w, WMLC); Ashaira, 21.7575N, 40.651944E, 1340m, 06–10.v.1936 (H. St. J. B. Philby, B.M.1936–405) (2 w, BMNH). Asir Province: Khamis Mushayt, W. Ben Hashbal, 18.594806N, 42.650361E, 26.iv.2011 (Sharaf MR) (18 w, KSMA); Khamis Mushayt, 18.3093N, 42.7662E, x.1997 (C. W. Mills) (2 w, WMLC); W. Saber, 20.18N, 41.1665E, 06.iii.2013 (Sharaf MR) (4 w, KSMA); Najran province: Najran city, 17.49590N, 44.12922E, 1323 m, 21.ii.2015 (S Salman) (3 w, KSMA); Najran, 17.5656N, 44.2289E, 25.iii.1983 (Collingwood CA) (2 w, WMLC); Fayfa, 17.29691N, 43.135E, iii.1983 (Collingwood CA) (25 w, WMLC). **Yemen:** Taiz (y529), 13.5776N, 44.0178E, x.1991 (A van Harten) (3 w, WMLC); W. Surdud, 15.266667N, 43.716667E, xii.1991 (A van Harten) (1 w, WMLC); Mabar, 14.7953N, 44.2905E, viii.1992 (A van Harten) (1 w, 1256, WMLC); W. Al Barahani, 13.3042N, 44.1003E, ii.1992 (M. Mahyoub) (1 w, 1001, WMLC); Khazam, 13.49N, 43.84E, 1950 m, ix.1979 (B. Lanza) (2 w, WMLC); Taiz, Maagala, 13.5776N, 44.0178E, ii.1993 (A van Harten) (15 w, 983, WMLC); Rehab, 14.23N, 44.19E, iii.1992 (A van Harten) (8 w, 1088, WMLC); Rehab, 14.23N, 44.19E, iv.1993 (M. Knapp) (18 w, 1999, WMLC); Suq Bani Mansur, 14.59646N, 43.594325E, iv.1991 (M. Knapp) (10 w, 191, WMLC); Taiz, 15.266667N, 43.716667E, ii.1992 (M. Knapp) (20 w, 1006, WMLC); Zingibar, 13.135N, 45.3886E, iii.1993 (20 w, in tube, WMLC); Sana'a, 15.3694N, 44.191E, 11–18.iii.1937 (Dr. Carl Rathien, B.M.1938–396) (1 w, BMNH); W. Aden Port, Al Huseini near Lahej, 13.0578N, 44.8833E, 29.xi.1937 (B.M. Expedition to S.W. Arabia, H. Scott & E. B. Britton. B.M.1933–246) (1 w, BMNH). **Oman:** W. Dhiyan, 19.7314N, 41.4219E, 13–14.ix.1983 (M. D. Gallagher) (1 w, WMLC); Dhofar, 17.0194N, 54.1108E, 04.ix.1985 (R. W. Whitcomb) (9 w, WMLC); Fasad (Dhofar), 18.4333N, 53.1333E, ii.1998 (M. D. Gallagher) (1 q, WMLC).

Geographic range. This species was originally described from Ethiopia and is widely distributed in the Afrotropical region. It seems to be a predominantly eastern African species but is also known from Central and South Africa (Guénard et al. 2017; Janicki et al. 2017). From the Arabian Peninsula, the species has been recorded from the southwestern mountains of the KSA and Oman (Wheeler 1922; Borowiec 2014; Collingwood 1985, Collingwood and Agosti 1996) (Fig. 13).

Remarks. *Crematogaster affabilis* was originally described as a variety of *C. chitarianii* but subsequently elevated to species rank by Collingwood (1985) based on head width, length of the propodeal spines, and absence of the mesonotal tubercle. During the present study the type material of *C. chitarianii* and *C. affabilis* (MHNG) were examined and detailed morphological examinations of the type material shows that both are uniformly brown with the anterior half of the cephalic surface longitudinally striated; the frontal triangle is well-defined with a distinct posterior carina running back to the posterior level of the eyes; the propodeal spines long and acute, about $1.5 \times$ longer than their base, making an angle of about 45° with the longitudinal axis of the body in profile view; and, the mesonotum in profile descending abruptly to a deep metanotal groove. The type of *C. affabilis* is somewhat larger but not more than major workers in

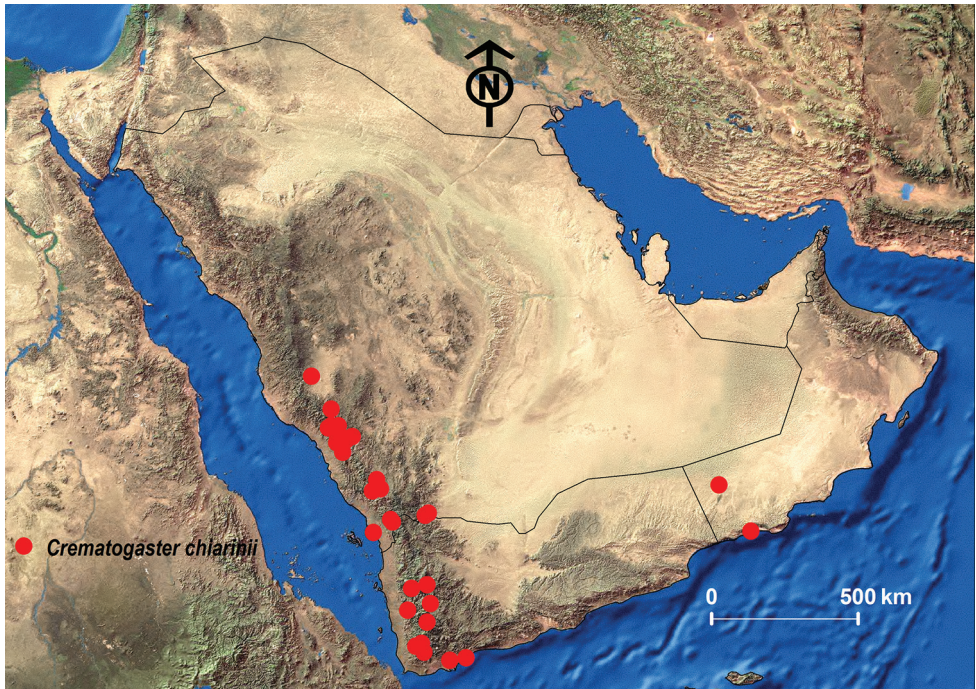


Figure 13. Distribution map of *C. chiarinii*.

both species are from minor workers. Consequently, even though both taxa are outside the focal region of Arabia, on the basis of any lack of significant phenotypical differences, we propose *C. chiarinii* as a senior synonym of *C. affabilis*.

Nevertheless, despite our synonymizing of both taxa, the taxonomic condition of *C. chiarinii* is still in need of a thorough revision. The taxonomic history above with all status changes, synonymic history, and numerous still valid infraspecific taxa shows clearly the complexity of this task. Based on superficial examination of material from the Afrotropical region, we are doubtful that the material from East Africa might remain conspecific with the one from Central and South Africa. Hopefully, a future revision of the Afrotropical fauna will resolve this situation.

***Crematogaster delagoensis* Forel**

Figure 14A–C

Taxonomic history.

Crematogaster inermis r. *delagoensis* Forel, 1894a: 99 (w.) MOZAMBIQUE.

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 146; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Status as species: Emery 1922: 146.

Current subspecies: *C. delagoensis acutidens* Arnold, *C. delagoensis merwei* Santschi, *C. delagoensis rhodesiana* Arnold.

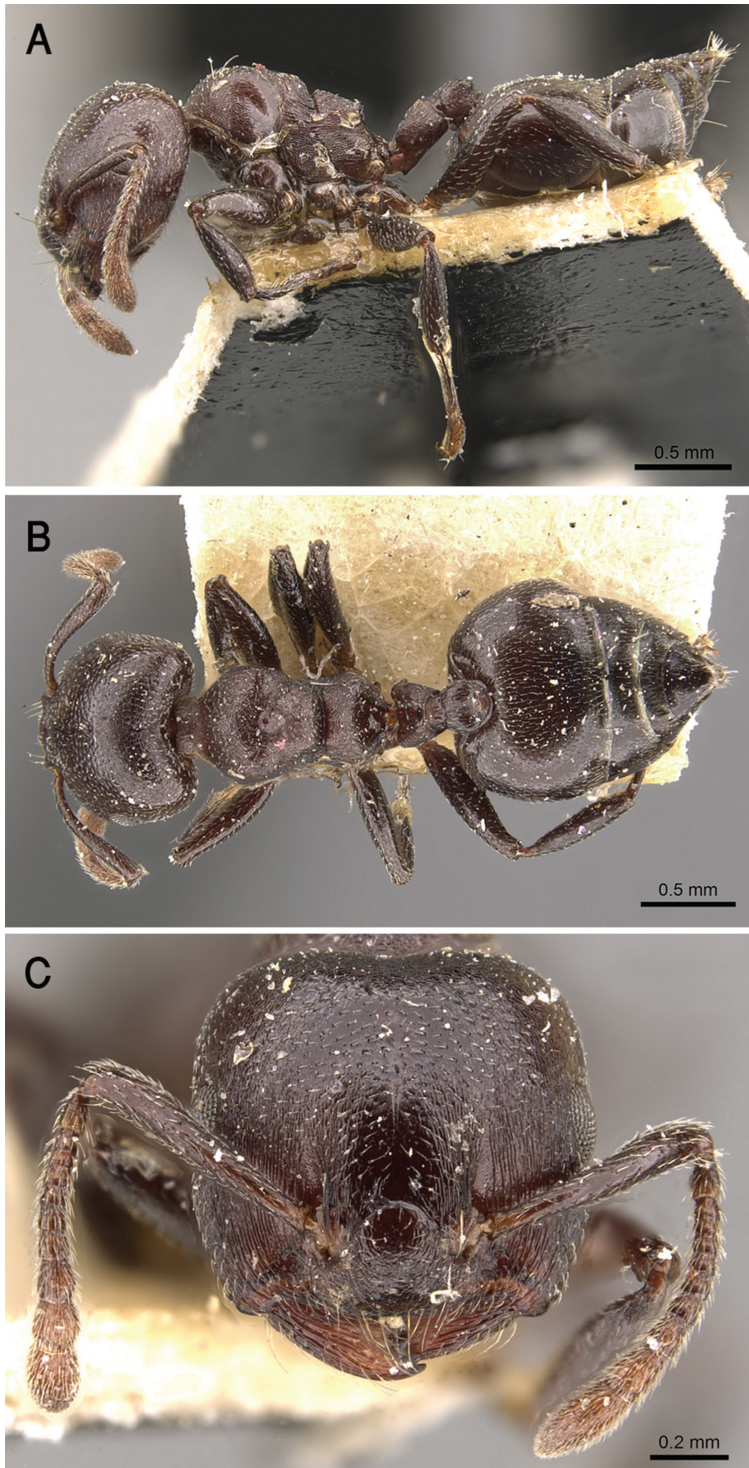


Figure 14. *C. delagoensis* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0908517 (Will Ericson), www.AntWeb.org.

Material examined. KSA: Alnaifiam Farshet Shaal, 22.41559N, 46.58806E, 602 m, 12.iv.2015 (Al Dhafer et al.) (1 w, KSMA).

Geographic range. This species was originally described from Mozambique and in the Afrotropical region seems to be restricted to Southern Africa (Guénard et al. 2017; Janicki et al. 2017). Our material represents the first record from the KSA since the species was previously only known from Yemen and Oman (Borowiec 2014; Collingwood and Agosti 1996; Sharaf et al. 2018) (Fig. 11).

Remarks. Again, the disjunctive distribution raises some doubts about the identity of our material. Even though it is conspecific the material previously identified from Oman and Yemen, it needs to be proven that it is indeed *C. delagoensis*. The lack of records from East Africa and the southwestern parts of KSA could be due to insufficient sampling, but it could also be that the Arabian material is not similar to the South African “genuine” *C. delagoensis*.

Crematogaster flaviventris Santschi

Figure 15A–C

Taxonomic history.

Crematogaster flaviventris Santschi, 1910: 370 (w, q, m) DEMOCRATIC REPUBLIC OF CONGO.

Subspecies of *C. inversa*: Santschi, 1914a: 86; of *C. castanea*: Santschi, 1935: 257.

Status as species: Collingwood and Agosti 1996: 330.

Geographic range. *Crematogaster flaviventris* was originally described from the Democratic Republic of Congo and is also found in Angola, Zambia, and southern Sudan (Guénard et al. 2017; Janicki et al. 2017). On the Arabian Peninsula, it seems to be restricted to Yemen (Collingwood and Agosti 1996; Blaimer 2012a; Borowiec 2014) (Fig. 16).

Remarks. This species record for Yemen is somewhat dubious. We have not examined the type material but preliminary examination of type images on AntWeb suggest that the material from Yemen is similar in color but there appear to be substantial differences in overall surface sculpture. This needs to be further investigated, ideally by comparing the Yemeni material with the type from Central Africa.

Crematogaster gryllsi Sharaf & Hita Garcia, sp. nov.

<http://zoobank.org/F3844A54-2467-4CBD-A04B-5BFB079077CB>

Figure 17A–C

Type material. Holotype: pinned worker, KSA: Fayfa, 17.29691N, 43.13500E, 837 m, 06.iv.2013 (Sharaf MR) (CASENT0872096, KSMA). **Paratypes:** 29 pinned workers, same data as the holotype (28 w, KSMA, 1 w, CASENT0919794, CASC); Asir Province, Abha, Raydah, 18.195817N, 42.389083E, 1614 m, 31.vii.2015 (Al Dhafer et al.) (8 w, KSMA; 1 w, WMLC); Abha, Raydah, 18.19465N, 42.39485E, 1851 m, 08.vi.2014 (Al Dhafer et al.) (1 w, KSMA).

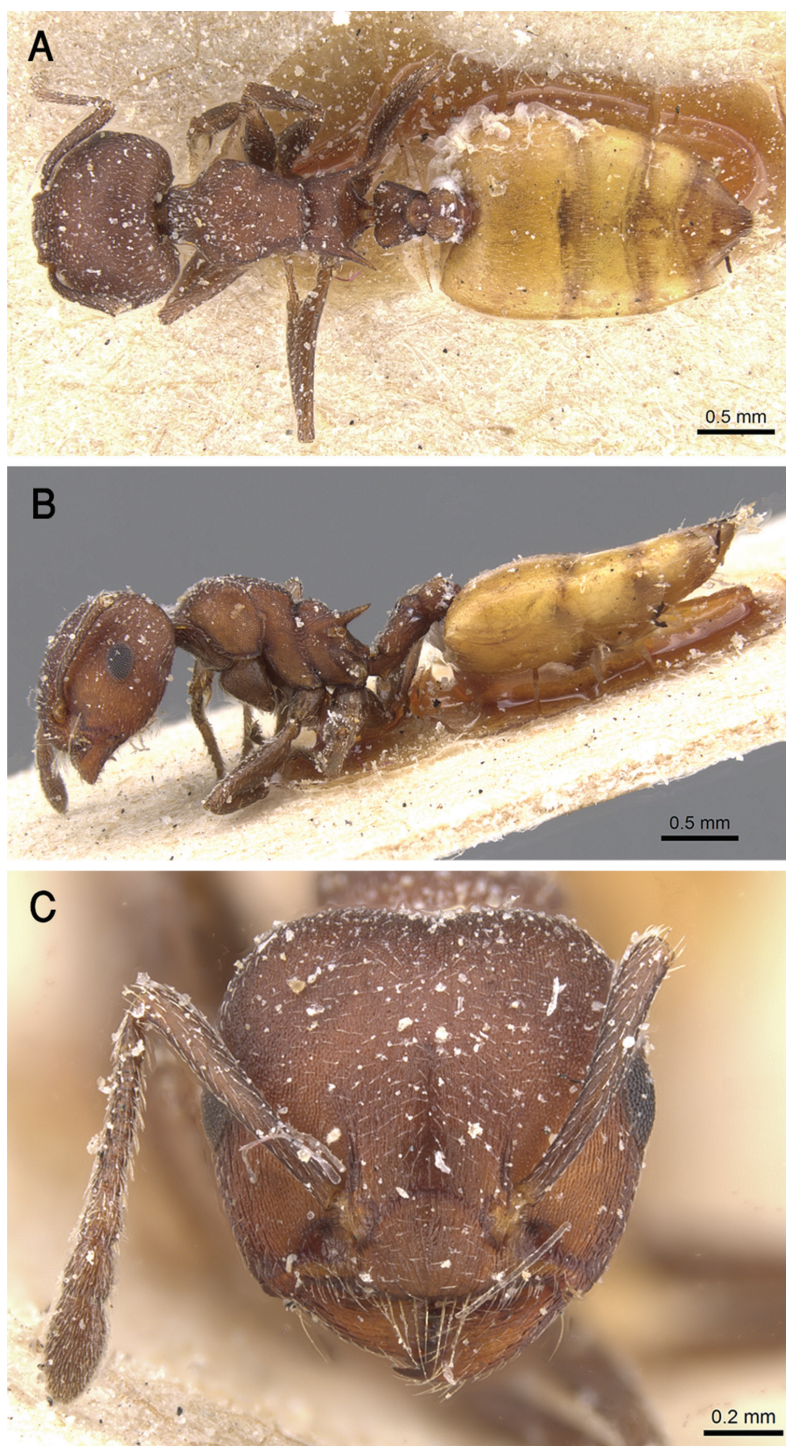


Figure 15. *C. flaviventris* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0912651 (Will Ericson), www.AntWeb.org.



Figure 16. Distribution map of *C. flaviventris* and *C. melanogaster*.

Diagnosis. *Crematogaster gryllsi* sp. nov. is distinguished from related congeners by the combination of the following characters: Mesonotum in profile without a tubercle on promesonotal suture; propodeal dorsum and propodeal spines forming a continuous concave curve in profile; postpetiolar node entire, not bilobed dorsally; mesopleura, petiole, and postpetiole distinctly densely punctate; color uniform yellow, second half of gaster brown-yellow.

Holotype worker. EL 0.22; HL 0.75; HW 0.80; LHT 0.57; PPL 0.12; PPW 0.20; PRW 0.45; PTH 0.17; PTL 0.22; PTW 0.32; SL 0.62; ML 0.90; Indices. CI 107; LBI 158; OI 28; PPI 63; PTHI 77; PTWI 145; SI 78.

Paratype workers. EL 0.15–0.25; HL 0.65–0.87; HW 0.67–0.87; LHT 0.45–0.57; PPL 0.12–0.18; PPW 0.17–0.25; PRW 0.40–0.55; PTH 0.12–0.25; PTL 0.12–0.25; PTW 0.27–0.42; SL 0.50–0.70; ML 0.75–1.0; Indices. CI 96–107; LBI 124–178; OI 22–31; PPI 59–81; PTHI 88–125; PTWI 145–267; SI 68–93 ($N = 15$).

Description. Worker. Workers of the new species showing marked size variation in the two nests.

Head. Head as long as or little broader than long with convex sides and feebly concave posterior margin; antennae 12-segmented; in full-face view antennal scapes when laid back from their insertions reach or surpass posterior margin of head by the length of the first funicular segment; eyes of moderate size (OI 22–31), located nearly at mid-length of head in full-face view and with about 12 ommatidia in the longest row; anterior clypeal margin broadly convex. **Mesosoma.** Mesonotum in profile without a small

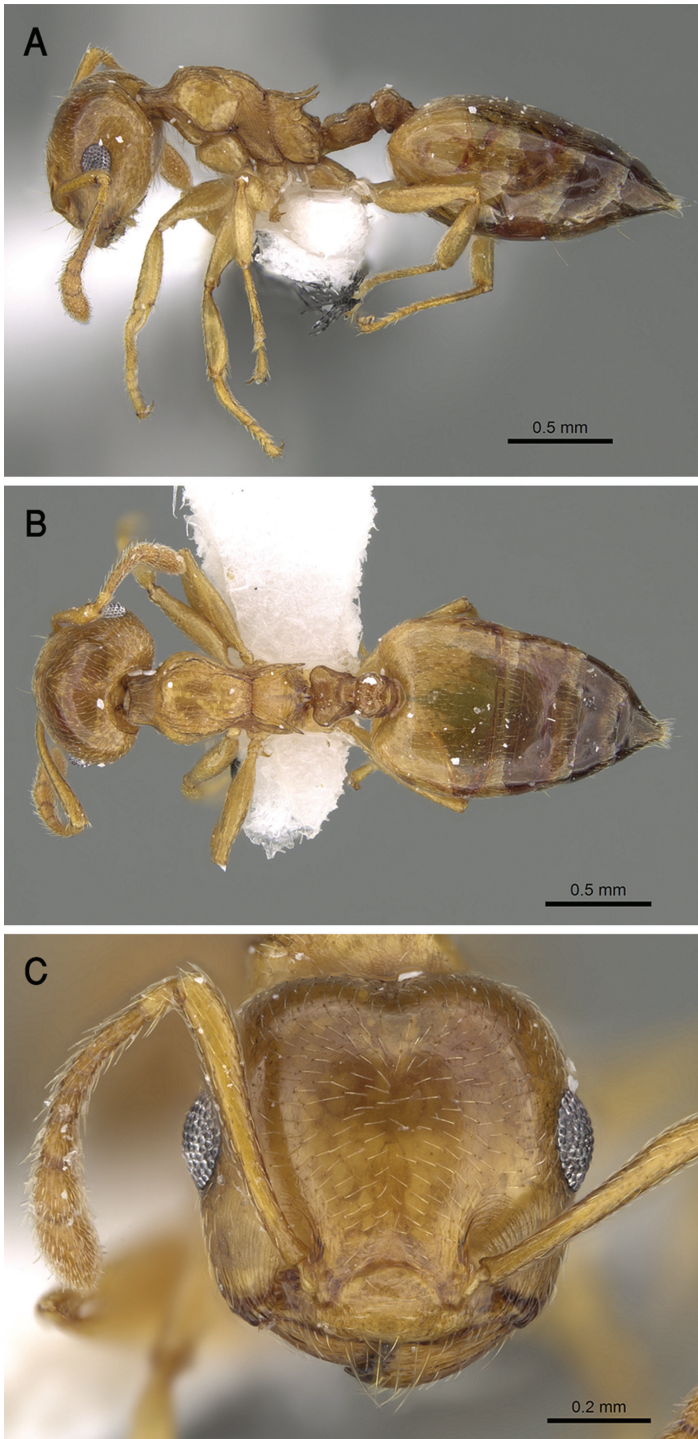


Figure 17. *C. gryllsi* sp. nov. **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0919794 (Michele Esposito), www.AntWeb.org.

tubercle on promesonotal suture; promesonotal suture feebly impressed; mesonotum convex in profile; median mesonotal carina absent; metanotal groove shallowly impressed but distinct; propodeal spines long, sharp and upward directed; propodeal spiracle circular, and located below the base of the propodeal spines; propodeal dorsum and propodeal spines forming a continuous concave curve in profile. *Petiole*. In profile petiole distinctly longer than high (PTHI 88–125; PTWI 145–267); approx. twice broader anteriorly than posteriorly in dorsal view; subpetiolar process well developed. *Postpetiole*. Postpetiolar node entire, not bilobed in dorsal view. *Pilosity*. Cephalic and clypeal surfaces with abundant scattered fine appressed pubescence; anterior clypeal margin and mandibles with abundant scattered long yellow hairs; antennae and legs with dense appressed pubescence; mesosoma without hairs; promesonotum and mesonotum dorsum with few appressed pubescence; petiole, postpetiole and the first three gastral tergites with appressed pubescence; few hairs on the terminal gastral segment. *Sculpture*. Mandibles longitudinally striated; clypeal surface smooth; area in front of eyes finely longitudinally striated; cephalic surface smooth; antennal fossae surrounded by fine and curved striolae; promesonotum side smooth; promesonotum dorsum faintly longitudinally rugulose; propodeal dorsum faintly longitudinally striated; mesopleura, petiole, and postpetiole distinctly densely punctate; metapleura faintly, irregularly striated; gastral tergites smooth. *Color*. Head, mesosoma, petiole, postpetiole, first gastral tergite, legs, and antennae uniform yellow, second half of gaster brown-yellow.

Etymology. The patronymic epithet has been selected in honor of Bear Grylls, the survival instructor in recognition of his remarkable efforts in spreading the culture of survival globally.

Ecological and biological notes. The microhabitat of *Crematogaster gryllsi* in the type locality (Fayfa Mountains) (Fig. 18) is the humid leaf litter under *Acacia* and *Calotropis procera* (Aiton) W. T. Aiton (Apocynaceae) trees. The specimens were collected by sifting leaf litter. The material from Raydah were collected by pitfall traps.

Geographic range. This new species is only known from the Asir Mountains, KSA (Fig. 19).

Remarks. This distinct new species immediately be separated from all Arabian *Crematogaster* species by the undivided postpetiolar node and the uniform yellow color. All other species have a divided postpetiolar node. *Crematogaster gryllsi* appears to be related directly to *C. luctans* Forel, 1907 from Kenya as it possesses an undivided postpetiolar dorsum as well. However, *C. gryllsi* can be separated by the following characters: metanotal groove shallowly impressed, propodeal dorsum and propodeal spines forming a continuous concave curve in profile; promesonotum side smooth; mesopleura distinctly densely punctate; whereas *C. luctans* has deeply impressed, U-shaped metanotal groove profile; convex propodeal dorsum in profile extending posteriorly to straight propodeal spines; mesosomal sides longitudinally striated.

Comments. The record of *C. luctans* given by Collingwood (1985) was based on material collected from Fayfa Mountains where the new species, *C. gryllsi* was collected. Considering that the shape of the postpetiole is uncommon in the Arabian fauna and the initial identification of *C. luctans* was probably based on this character, it is highly



Figure 18. Fayfa, type locality of *C. gryllsi* sp. nov. (M. Sharaf).



Figure 19. Distribution map of *C. gryllsi* sp. nov., *C. jacindae* sp. nov., and *C. jehovae*.

likely that the record of *C. luctans* by Collingwood (1985) represents a misidentification. This hypothesis is further supported by the complete lack of any material of *luctans* in the WMLC. Therefore, the species was omitted from the list of Arabic species.

***Crematogaster inermis* Mayr**

Figure 20A–C

Taxonomic history.

Crematogaster inermis Mayr, 1862: 766 (w.) EGYPT: André 1883: 395 (q.); Santschi 1937: 296 (q.); Santschi 1938: 38 (m.).

Combination in *Crematogaster* (*Crematogaster*): Wheeler 1922: 840; in *Crematogaster* (*Acrocoelia*): Emery 1922: 143; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166. Current subspecies: *C. inermis aphrodite* Santschi, *C. inermis armatula* Emery, *C. inermis lucida* Forel.

Material examined. Egypt: Elmenia, Abu Swelam, 30.75N, 28.1E, 29.vi.2003 (Sharaf MR) (1 w, OUMC).

Geographic range. *Crematogaster inermis* was originally described from Egypt and is widely distributed from the Iberian Peninsula through North Africa to the Middle East (Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). For the Arabian Peninsula, this species was only recorded from Yemen (Collingwood and van Harten 2001; Borowiec 20114).

Remarks. Knowing that the species is widespread in the Mediterranean and Middle East and the only record for the Arabian Peninsula is from Yemen, we think that it is likely that it is also present in the KSA. Further sampling is necessary to verify this.

***Crematogaster jacindae* Sharaf & Hita Garcia, sp. nov.**

<http://zoobank.org/15D56546-DEA0-4764-AA6C-D2BAD5A4621>

Figure 21A–C

Type material. Holotype: pinned worker, Oman: Dhofar, Ayn Sahlanoot, 17.14766N, 54.17878E, 151 m, 16.xi.2017 (Sharaf MR) (CASENT0872068, KSMA). **Paratype:** pinned workers, OMAN: DHOFAR: Ayn Hamran, 17.08631N, 54.28043E, 56 m, 22.xi.2017, BS (Sharaf MR) (11 w, KSMA, 1 w, CASENT0922856, CASC, 1 w, WMLC); Ayn Razat, 17.12443N, 54.23832E, 98 m, 20.xi.2017, ML (Sharaf MR) (8 w); Dhalkout, 16.72673N, 53.24942E, 623 m, 18.xi.2017, SF (Sharaf MR) (16 w); Dhalkout, 16.70703N, 53.25068E, 34 m, 19.xi.2017, BS (Sharaf MR) (7 w); Dhalkout, 16.69273N, 53.15621E, 628 m, 18.xi.2017, BS (Sharaf MR) (17 w); Ayn Sahlanot, 17.14766N, 54.17878E, 151 m, 16.xi.2017, BS (Sharaf MR) (4 w); Ayn Ashat, 16.99810N, 53.81954E, 202 m, 21.xi.2017, SF (Sharaf MR) (20 w); Dhalkout road, Aghbaroot village, 16.79818N, 53.55392E, 1034 m, 18.xi.2017, BS (Sharaf MR) (1 w) (KSMA).

Diagnosis. *Crematogaster jacindae* sp. nov. is distinguished from related congeners by the combination of the following characters: median mesonotal carina absent; propodeal spines absent; propodeal spiracle distinct in the form of a slit; area in front of eyes finely longitudinally striated; antennal fossae surrounded by fine and curved striolae; head black-brown or black, mesosoma, petiole and postpetiole dark brown, relatively lighter than head, gaster golden yellow.

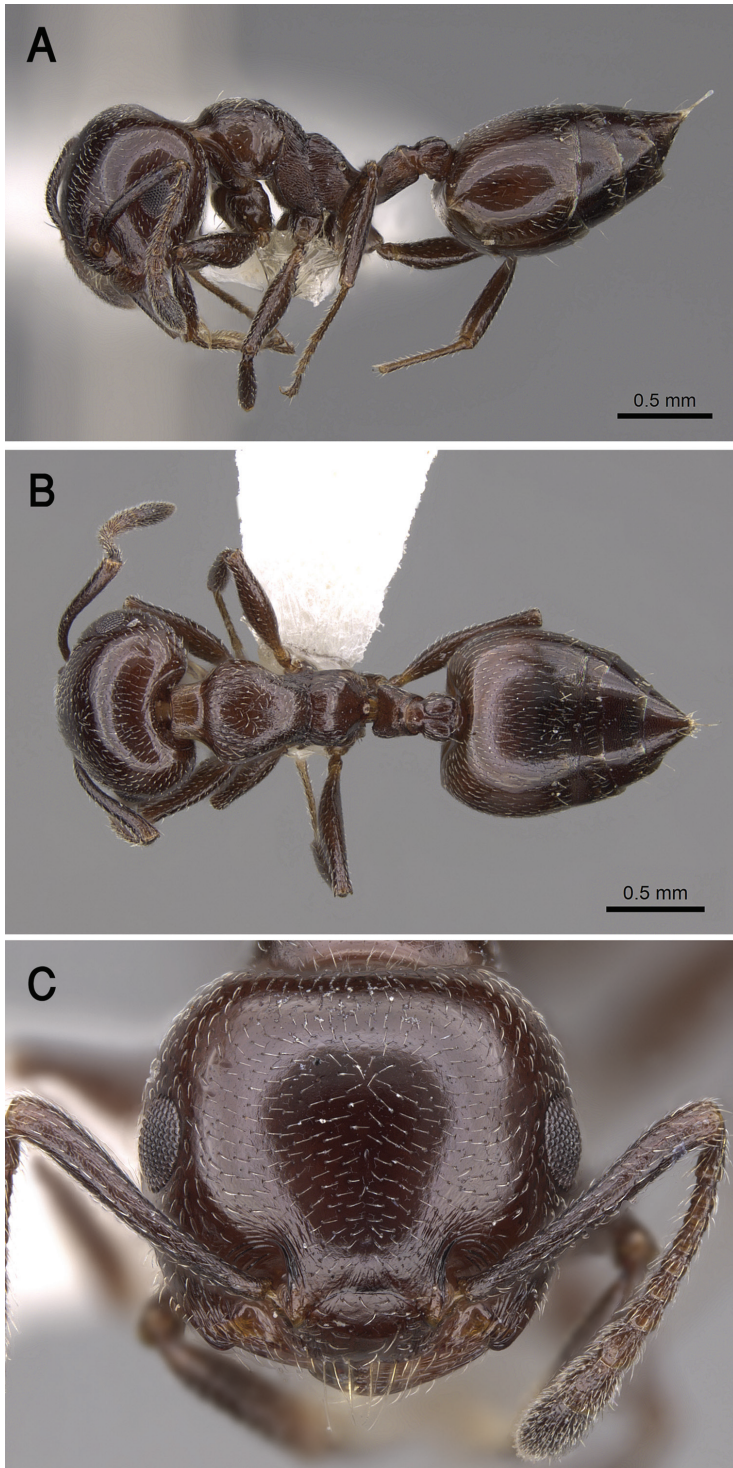


Figure 20. *C. inermis* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0922679 (Wade Lee), www.AntWeb.org.

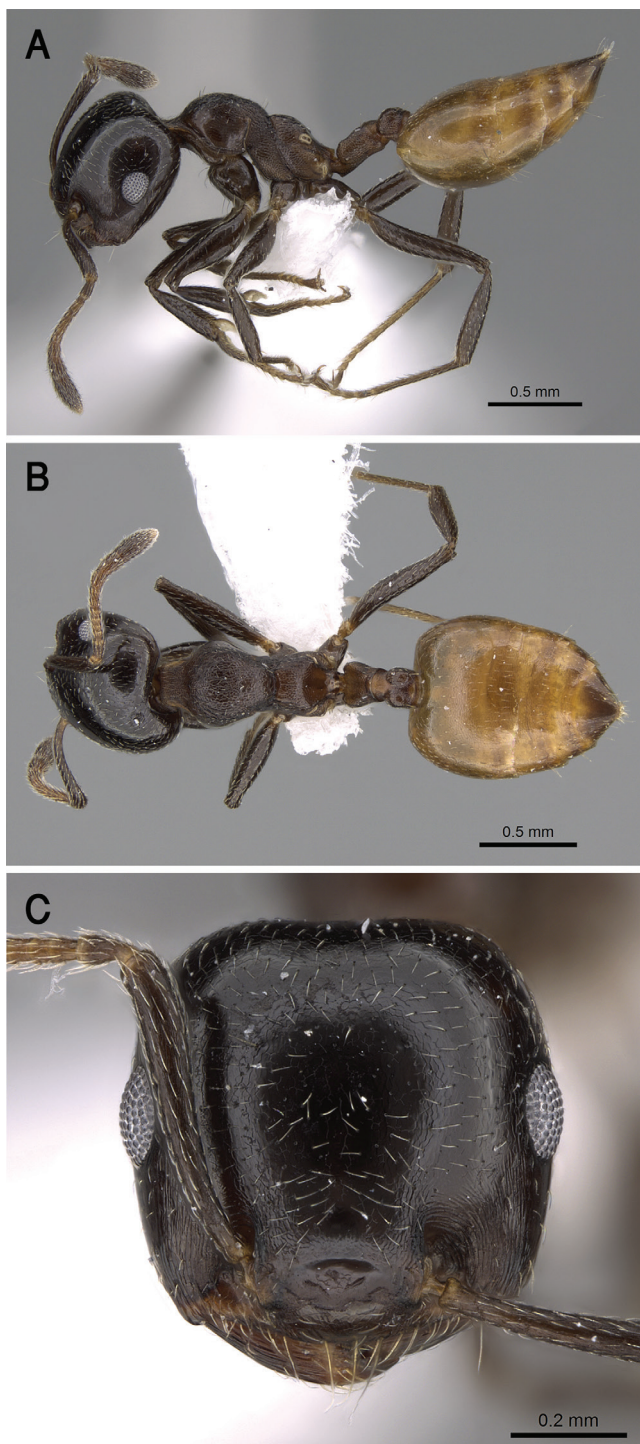


Figure 21. *C. jacindae* sp. nov., paratype worker **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0922856 (Michele Esposito), www.AntWeb.org.

Holotype worker. EL 0.20; HL 0.75; HW 0.82; LHT 0.55; PPL 0.12; PPW 0.20; PRW 0.42; PTH 0.12; PTL 0.25; PTW 0.22; SL 0.55; ML 0.87; Indices. CI 109; LBI 158; OI 24; PPI 167; PTHI 48; PTWI 88; SI 67.

Paratype workers. EL 0.17–0.22; HL 0.72–0.92; HW 0.75–1.0; LHT 0.52–0.75; PPL 0.12–0.17; PPW 0.15–0.25; PRW 0.32–0.50; PTH 0.12–0.17; PTL 0.20–0.32; PTW 0.20–0.30; SL 0.50–0.95; ML 0.77–1.02; Indices. CI 96–113; LBI 121–165; OI 16–27; PPI 125–208; PTHI 44–68; PTWI 78–125; SI 61–95 ($N = 20$)

Description. Worker. Head. Head as long as or little broader than long with convex sides and feebly concave posterior margin; antennae 12-segmented; in full-face view antennal scapes when laid back from their insertions fail to reach posterior margin of head; eyes of moderate size (OI 16–27), located nearly at mid-length of head in full-face view and with ca. eleven ommatidia in the longest row; anterior clypeal margin broadly convex. *Mesosoma.* Promesonotum and mesonotum forming continuous curve in profile; median mesonotal carina absent; metanotal groove well developed; propodeal dorsum short forming curve with longer propodeal declivity; propodeal spines absent; propodeal spiracle distinct and slit-shaped. *Petiole.* In profile petiole distinctly longer than high (PTHI 44–68; PTWI 78–125); broader anteriorly than posteriorly in dorsal view. *Postpetiole.* Postpetiolar node distinctly bilobed in dorsal view; nearly as high as petiole in profile. *Pilosity.* Cephalic surface with abundant scattered fine pale hairs; anterior clypeal margin and mandibles with several long yellow hairs; posterior half of clypeus without hairs or pubescence; antennae and legs with abundant appressed pubescence; promesonotum and mesonotum each with single pair of hairs; promesonotum and mesonotum dorsum with appressed pale pubescence; no hairs or pubescence on propodeum; petiole and postpetiole each with single pair of posteriorly directed hairs; gastral pilosity restricted to few pairs on posterior margins of gastral tergites; gastral tergites with scattered appressed pubescence. *Sculpture.* Mandibles longitudinally striated; clypeal surface smooth; area in front of eyes finely longitudinally striated; cephalic surface feebly imbricate; antennal fossae surrounded by fine and curved striolae; promesonotum lateral side faintly imbricate; promesonotum dorsum faintly reticulate rugulose; mesopleura, metapleura, petiole, and postpetiole distinctly densely imbricate; gastral tergites faintly imbricate. *Color.* Head black-brown or black, mesosoma, petiole and postpetiole dark brown, relatively lighter than head, gaster golden yellow and strongly contrasting with remainder of body.

Etymology. The patronymic epithet has been selected in honor of Ms. Jacinda Ardern, the Prime Minister of New Zealand in recognition of her humanitarian attitudes towards Muslim and minority communities in New Zealand.

Ecological and biological notes. The microhabitats where *C. jacindae* sp. nov. was encountered included leaf litter, soil, under stones, or on native vegetation, especially acacia trees (Fig. 22). The majority of specimens were collected foraging on plants using a beating sheet, but workers were also observed foraging on the ground and wild shrubs.

Geographic range. This new species is only known from Oman (Fig. 19).

Remarks. The distinctive golden yellow gaster and complete lack of propodeal armament of *C. jacindae* sp. nov. allows this Omani species to be immediately recognized



Figure 22. Ayn Sahlanoot, Dhofar, type locality of *C. jacindae* sp. nov. (photo: Annette Patzelt).

from all other Arabian species. The closest relative of the new species is *Crematogaster inermis* Mayr, 1862 from Egypt. Both species are similar in body size and the lack of propodeal spines, but *C. jacindae* sp. nov. can be readily separated by the following characters: area in front of eyes finely longitudinally striated; cephalic surface feebly imbricate; eyes with about 11 ommatidia in the longest row; posterior half of clypeus without hairs or pubescence; mesopleura and metapleura distinctly densely imbricate; mesonotum with a single pair of hairs and without anterior tubercles; propodeal spiracles distinct in the form of a slit; body bicolored with head black-brown or black, mesosoma, petiole and postpetiole dark brown, relatively lighter than head, gaster golden yellow. By contrast, *C. inermis* has an unsculptured cephalic surface including the area in front of the eyes, eyes with ca. 14 ommatidia in the longest row, the posterior half of clypeus with fine appressed pubescence, mesosoma with a small anterior tubercle close to the promesonotal suture seen in profile; mesopleura and metapleura longitudinally striated, mesonotum without hairs, propodeal spiracle circular, unicolorous black-brown body.

***Crematogaster jehovae* Forel**

Figure 23A–C

Taxonomic history.

Crematogaster (Acrocoelia) auberti subsp. *jehovae* Forel, 1907c: 207 (w.) ISRAEL: Menozzi 1933: 58 (q.).

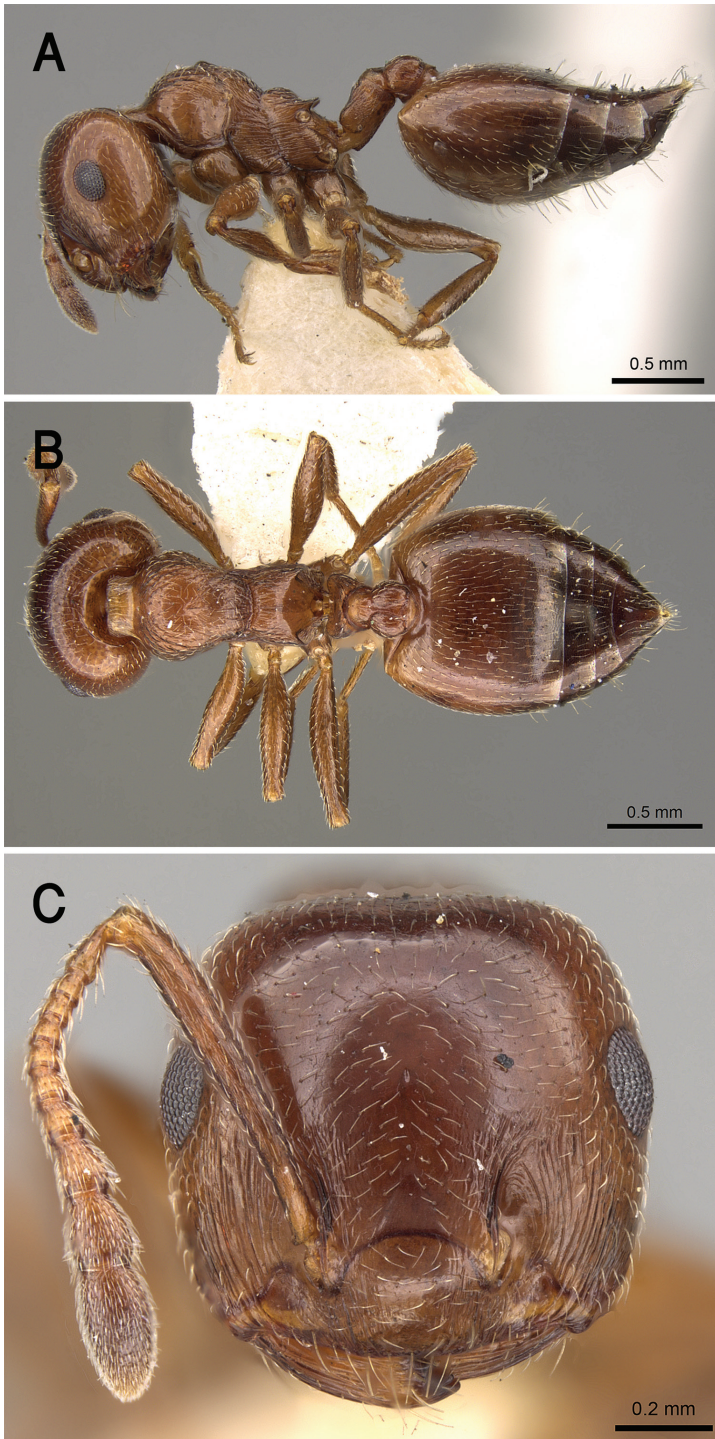


Figure 23. *C. jehovae* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0914150 (Zach Lieberman), www.AntWeb.org.

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 142; Santschi 1930: 266; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Status as species: Emery 1926: 3; Menozzi 1933: 58.

Current subspecies: *C. jehovae crawleyi* Emery.

Material examined. KSA: Asir province, Ballasmer, A'l Omer, 18.76008N, 42.26806E, 2455 m, 28.iv.2019 (Sharaf MR) (1 w, KSMA); Raydah: 18.204267N, 42.4124E, 2820 m, 21.ii.2014 (Al Dhafer et al.) (4 w, KSMA); Raydah: 18.20525N, 42.410117E, 2761 m, 21.ii.2014 (Al Dhafer et al.) (1 w, KSMA); Ballasmer, A'l Azza, 18.60815N, 42.24628E, 2611 m, 27.iv.2019 (Sharaf MR) (2 w, KSMA).

Geographic range. This species was originally described from Israel and is also known from the southeastern Europe and the Middle East (Borowiec and Salata 2012; Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). Our material represents the first record from the KSA since it was previously only known from UAE and Yemen (Borowiec and Salata 2012; Borowiec 2014) (Fig. 19).

Remarks. Considering that the species was known from most countries around the KSA, it is not surprising to now be discovered in this region. The taxonomy and identification of this species seems straightforward and we expect that this will remain this way.

Crematogaster laestrygon Emery

Figure 24A–C

Taxonomic history.

Crematogaster laestrygon Emery, 1869b: 135 (w.) ITALY: De Stefani 1889: 145 (q.); Baroni Urbani 1964: 43 (q.).

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 142; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Subspecies of *C. scutellaris*: Emery and Forel 1879: 464; André 1883: 393; of *C. schmidtii*: Emery 1891: 15; of *C. auberti*: Forel 1902: 154; Ruzsky 1902: 31; Stitz 1917: 341; Santschi 1921: 70; Emery 1922: 142; Santschi 1934: 167.

Status as species: Forel 1909: 104; Santschi 1915: 59; Emery 1926: 2; Wheeler 1927: 106; Santschi 1936: 201.

Current subspecies: *C. laestrygon airensis* Santschi, *C. laestrygon atlantis* Santschi, *C. laestrygon canariensis* Barquín, *C. laestrygon diminuta* Santschi, *C. laestrygon granulata* Santschi, *C. laestrygon maura* Forel, *C. laestrygon submaura* Lomnicki, *C. laestrygon theryi* Santschi, *C. laestrygon vivax* Santschi.

Crematogaster laestrygon subsp. *vaucheri* Emery, 1926: 2 (w.) MOROCCO.

[First available use of *Crematogaster auberti* st. *laestrygon* var. *vaucheri* Santschi, 1921: 71; unavailable name.] Junior synonym of *C. laestrygon*: Collingwood 1978: 69.

Material examined. Yemen: Hada, Sana'a, 15.3N, 44.166667E, 15.vii.1988 (P. Haney) (1 w, CASC).

Geographic range. This species is originally described from Italy and widespread in southern Europe, North Africa and the Middle East (Borowiec 2014; Guénard

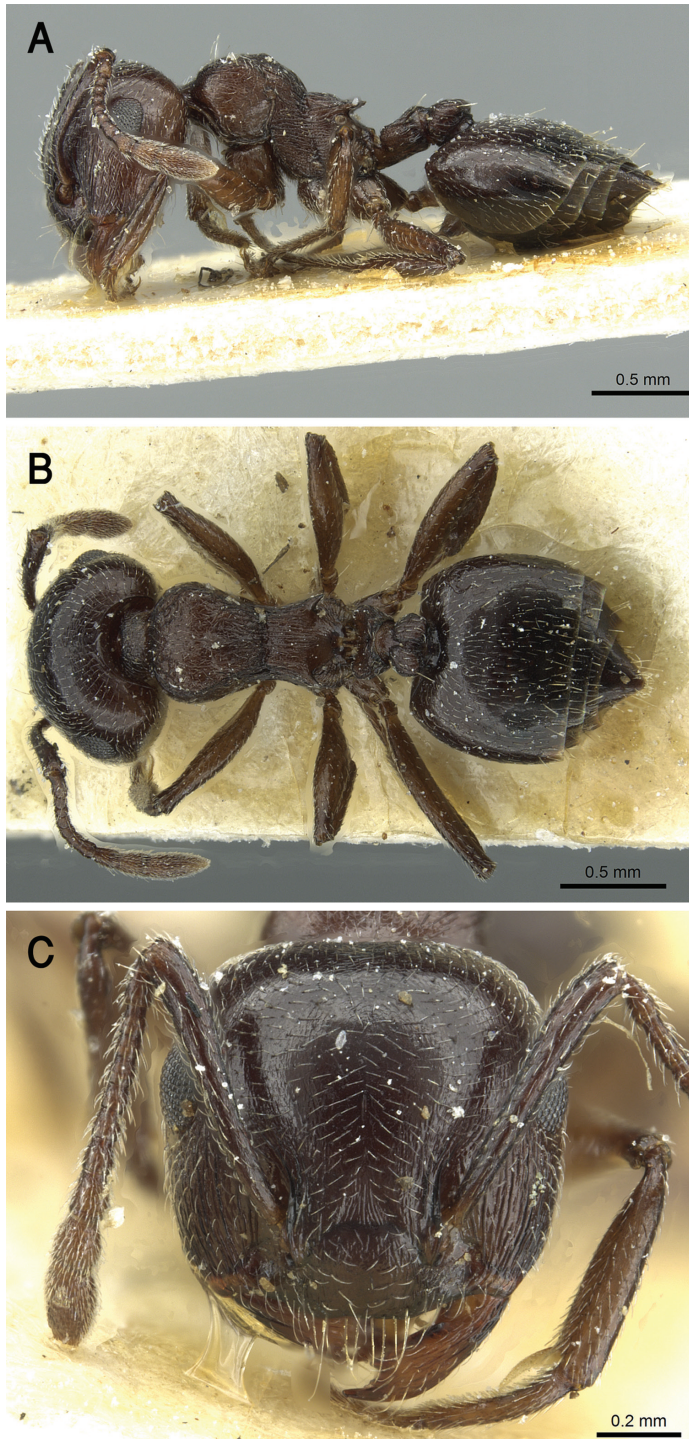


Figure 24. *C. laestrygon* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0912691 (Zach Lieberman), www.AntWeb.org.

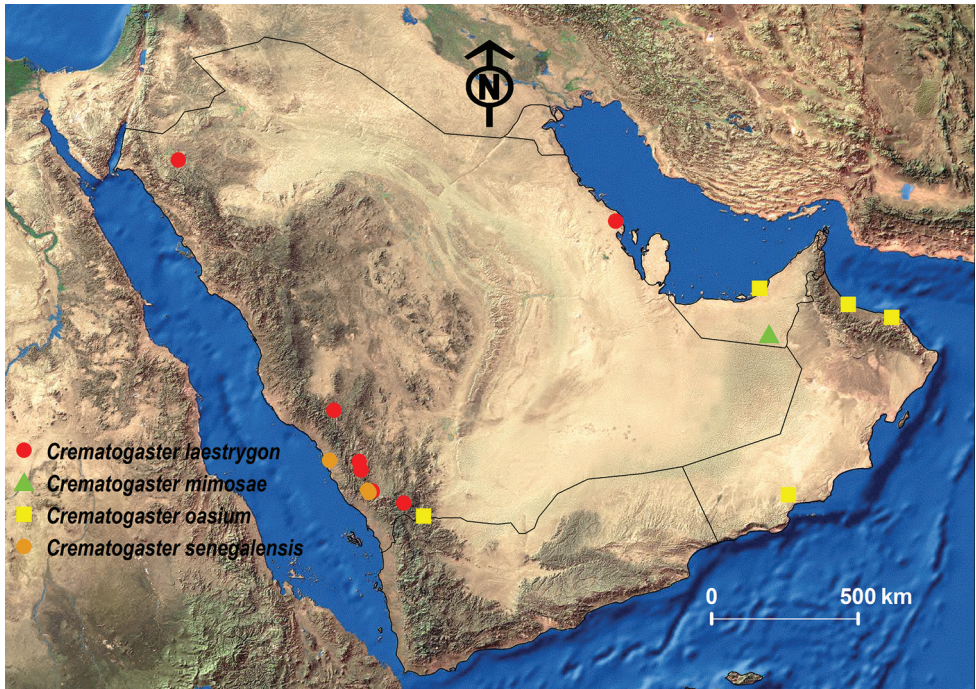


Figure 25. Distribution map of *C. laestrygon*, *C. mimosae*, *C. oasisum*, and *C. senegalensis*.

et al. 2017; Janicki et al. 2017). The Arabian records are from the KSA and Yemen (Borowiec 2014; Collingwood 1985, Collingwood and Agosti 1996) (Fig. 25).

Remarks. This is a good example of a *Crematogaster* species with a complex and uncertain taxonomic situation. It is relatively widespread in the Mediterranean and Middle East and currently has nine subspecies. It is doubtful that they are conspecific and it is possible that this is a species complex. As outlined below, we consider *C. laestrygon striaticeps* as sufficiently different to raise it to the rank of species.

Crematogaster melanogaster Emery

Figure 26A–C

Taxonomic history.

Crematogaster arborea subsp. *melanogaster* Emery, 1895: 29 (w., q.) SOUTH AFRICA.

Combination in *Crematogaster* (*Crematogaster*): Wheeler 1922: 840; in *Crematogaster*

(*Acrocoelia*): Emery 1922: 147; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Status as species: Wheeler 1922: 840.

Current subspecies: *C. melanogaster homonyma* Emery.

Geographic range. This species was described from South Africa for the Afrotropical region and it seems to be restricted to the southern African countries of Botswana,

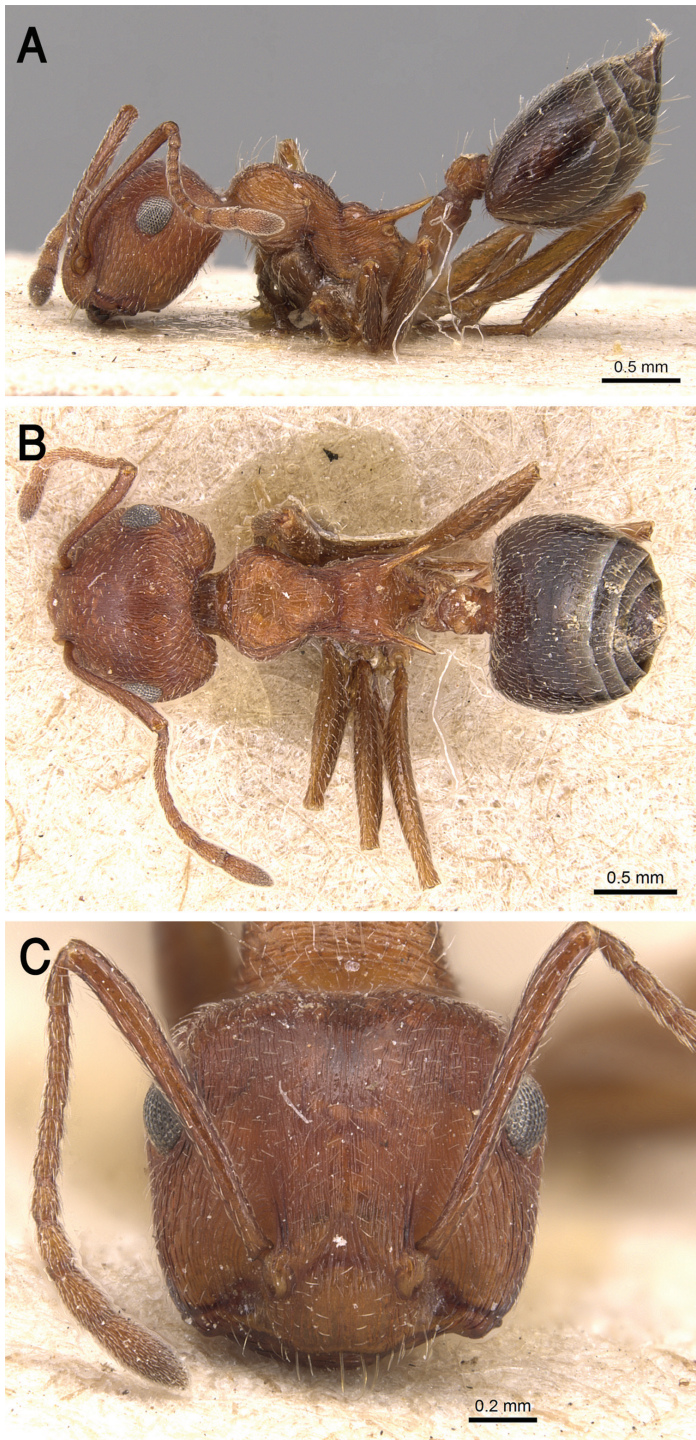


Figure 26. *C. melanogaster* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0904511 (Will Ericson), www.AntWeb.org.

Namibia, and South Africa (Guénard et al. 2017; Janicki et al. 2017). The only records for the Arabian Peninsula are from Oman (Collingwood and Agosti 1996; Borowiec 2014; Sharaf et al. 2018) (Fig. 16).

Remarks. The species record from Oman appears doubtful based on the strange distribution pattern noted above. However, since we were unable to examine any material of this species, we consider it prudent to list it as an Arabian species for the moment.

***Crematogaster mimosae* Santschi**

Figure 27A–C

Taxonomic history.

Crematogaster mimosae Santschi, 1914a: 87, fig. 11 (w.) KENYA: Menozzi 1939: 105 (q.).

Combination in *Crematogaster* (*Crematogaster*): Wheeler 1922: 841; in *Crematogaster* (*Acrocoelia*): Emery 1922: 148; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166. Current subspecies: *C. mimosae tenuipilis* Santschi.

Geographic range. Initially described from Kenya, in the Afrotropics this species is East African in its distribution found in Kenya, Uganda, Somalia, Sudan, and Tanzania (Guénard et al. 2017; Janicki et al. 2017). In the Arabian Peninsula, it was recorded from the KSA, Oman, the UAE and Yemen (Collingwood 1985, Collingwood and Agosti 1996; Borowiec 2014; Sharaf et al. 2018) (Fig. 25).

Remarks. *Crematogaster mimosae* is one of four species of obligate acacia ants, which have been well studied in East Africa, mostly Kenya (e.g., Young et al. 1997; Martins 2010). From a taxonomic perspective, this is one of the “easy” cases within the genus in Arabia, thus very straightforwardly identifiable.

***Crematogaster oasium* Santschi**

Figure 28A–C

Taxonomic history.

Crematogaster (*Acrocoelia*) *auberti* st. *oasium* Santschi, 1911: 84 (w.) TUNISIA; Santschi 1937: 303 (q.); Bernard 1953: 156 (m.).

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 142; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Subspecies of *C. antaris*: Santschi 1921: 71; of *C. auberti*: Santschi 1929: 99.

Status as species: Santschi 1937: 303; Collingwood 1985: 261.

Current subspecies: *C. oasium saharensis* Santschi.

Geographic range. *Crematogaster oasium* was described from Tunisia and can be found from Morocco east to Egypt (Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). In the Arabian Peninsula, it was recorded from Kuwait, KSA, Oman, and UAE (Collingwood 1985, Collingwood and Agosti 1996; Collingwood et al. 2011; Borowiec 2014; Sharaf et al. 2018) (Fig. 25).

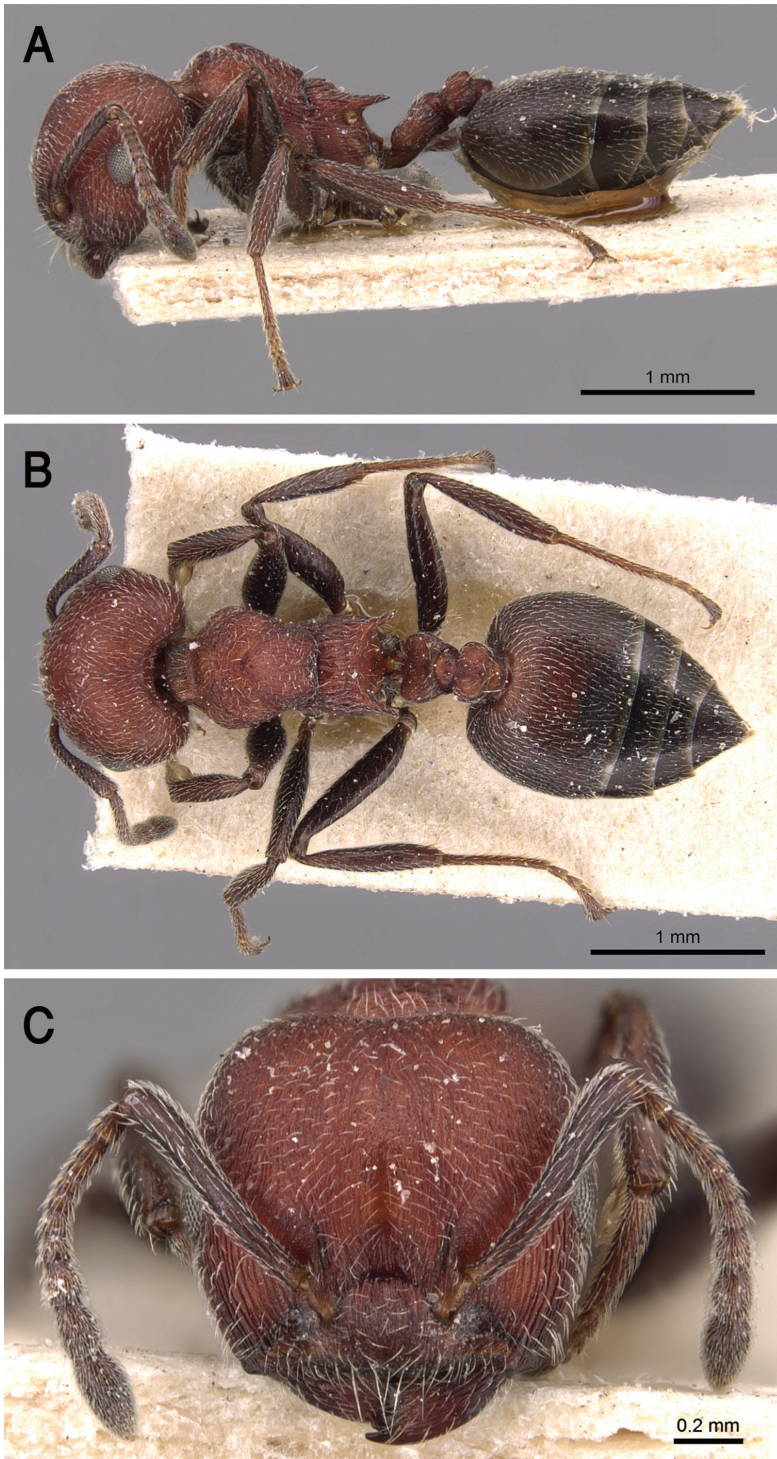


Figure 27. *C. mimosae* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0904507 (Will Ericson), www.AntWeb.org.

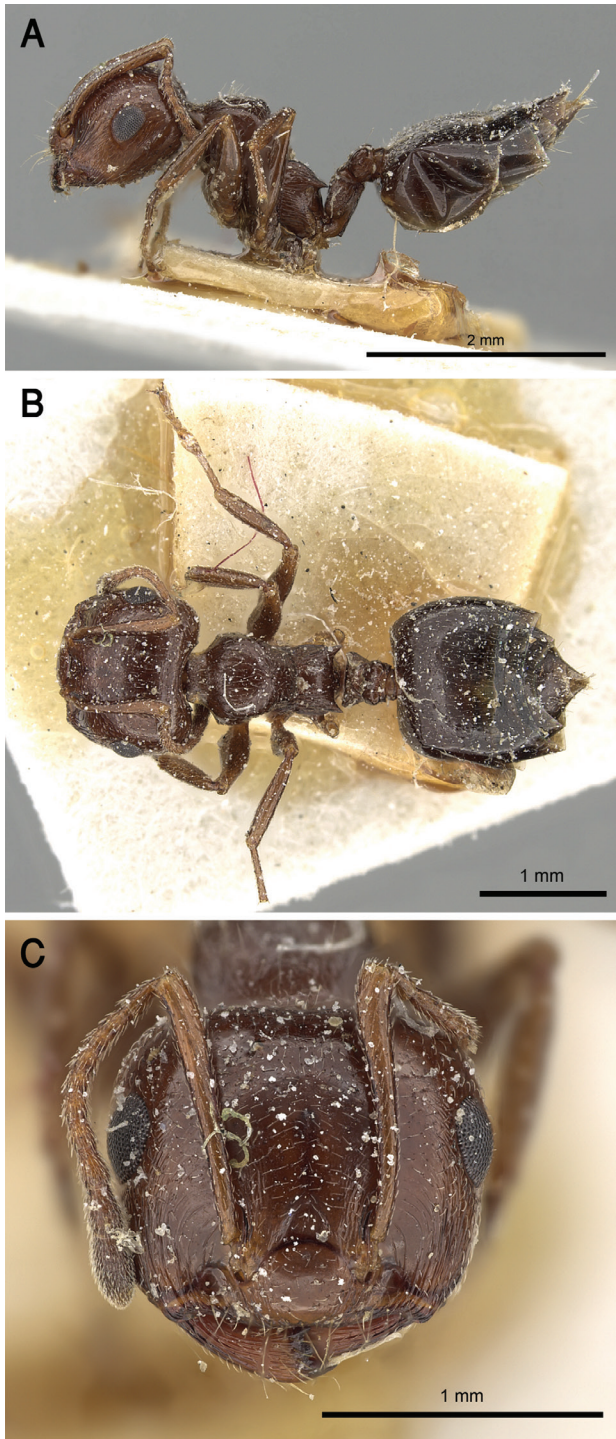


Figure 28. *C. oasium* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0249821 (Ryan Perry), www.AntWeb.org.

Remarks. This species seems to be common and widespread in northern Africa. Since we have not collected or examined any material from Arabia we list this provisionally as an Arabian species for the time being since it was listed by several authors (see above).

***Crematogaster senegalensis* Roger**

Figure 29A–C

Taxonomic history.

Crematogaster senegalensis Roger, 1863: 206 (w., q.) SENEGAL.

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 144; in *Crematogaster* (*Crematogaster*): Bolton 1995: 166.

Subspecies of *C. aegyptiaca*: Santschi 1914b: 344; Emery 1915: 10; Wheeler 1922: 828; Emery 1922: 144; Santschi 1929: 148.

Status as species: Forel 1922: 93; Bernard 1950: 288.

Current subspecies: *C. senegalensis goliathula* Forel.

Material examined. KSA: Asir province: Raydah: 18.204267N, 42.4124E, 2820 m, 21.ii.2014 (Al Dhafer et al.) (18 w, KSMA); Raydah: 18.221667N, 42.404167E, 2600 m, 13.iv.2011 (Sharaf MR) (21 w, 1 q, KSMA); Al Souda, 18.274167N, 42.364444E, 2982 m, 24.iv.2011 (Sharaf MR) (9 w, KSMA).

Geographic range. While this species was originally described from Senegal, it seems to have a fairly disjunctive distribution since it is known from eastern and northwestern Africa without being recorded from countries in-between (Guénard et al. 2017; Janicki et al. 2017). In the Arabian Peninsula, it was recorded from the KSA, Oman, and Yemen (Collingwood 1985; Collingwood and Agosti 1996; Collingwood et al. 2011; Borowiec 2014; Sharaf et al. 2018) (Fig. 25).

Remarks. The disjunct distribution of this species is a bit unusual and might require further attention in future studies of Afrotropical *Crematogaster*. It is likely that the odd distribution is just based on a sampling artifact or a preference of arid habitats, which are not as common in Central Africa. However, it could also be the case that this species, as currently defined, consists of several cryptic taxa. Without a thorough revision of the Afrotropical fauna it is impossible to be sure and we therefore list material examined as *C. senegalensis*.

***Crematogaster striaticeps* Forel, stat. nov.**

Figure 30A–C

Taxonomic history.

Crematogaster laestrygon striaticeps Forel, 1909: 104 (w.) ALGERIA; Santschi 1937: 308 (q., m.).

Combination in *Crematogaster* (*Acrocoelia*): Emery 1922: 142.

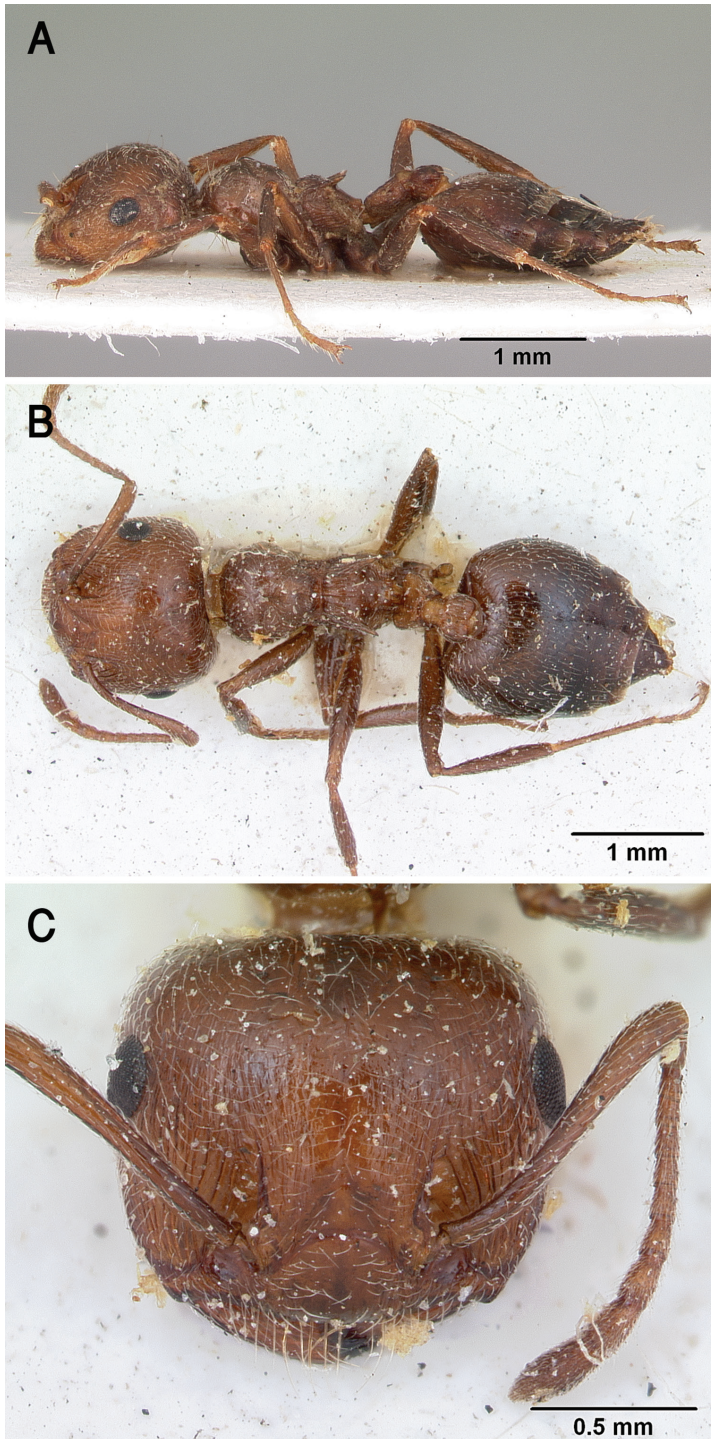


Figure 29. *C. senegalensis* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0104592 (April Nobile), www.AntWeb.org.

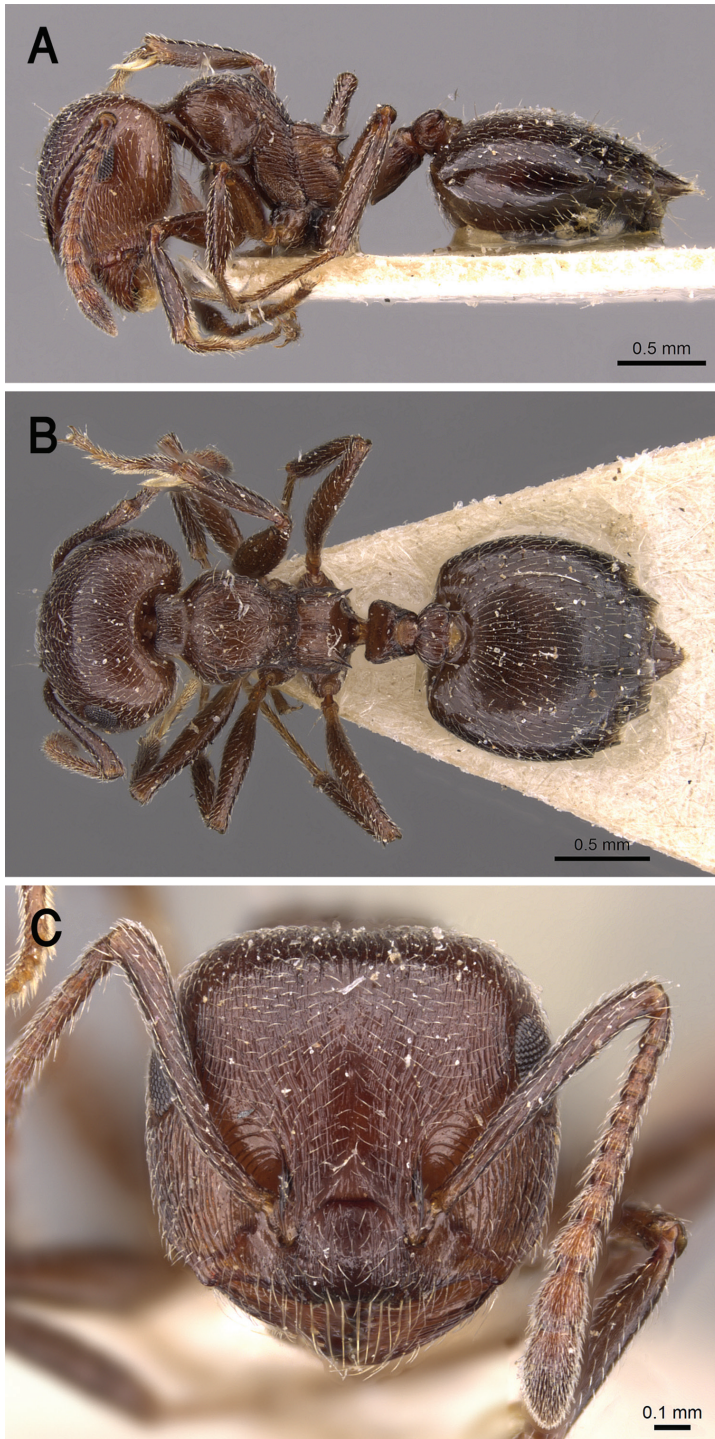


Figure 30. *C. striaticeps* **A** body in profile **B** body in dorsal view **C** head in full-face view, CASENT0908479 (Zach Lieberman), www.AntWeb.org.

Geographic range. This species was described from Algeria and is also found in the neighboring countries of Tunisia and Lybia (Borowiec 2014; Guénard et al. 2017; Janicki et al. 2017). In the Arabian Peninsula, it has been recorded from the KSA (Collingwood 1985).

Remarks. *Crematogaster striaticeps* was originally described as a subspecies of *C. laestrygon* but herein we treat this taxon as a good species. The main difference responsible for the decision to raise *striaticeps* to the specific rank is the presence of dense longitudinal striations on the entire cephalic surface whereas *laestrygon* has a smooth cephalic surface and longitudinal striations are feebly developed and restricted to the area in front of eyes.

We have been hesitant with this decision since both taxa are similar to other Afrotropical or Mediterranean *Crematogaster* taxa and it is not clear which taxonomic status they may assume after a thorough revision of the genus. However, since we established that *C. laestrygon* and *C. striaticeps* are not the same taxon, we propose to separate them by raising the latter to species rank to achieve clarity of their status for the Arabian region and future studies of its fauna.

Discussion

As can be seen from the species accounts presented above, the taxonomic histories of many species treated herein are complex and problematic. Many species have had numerous status changes and a changing number of infraspecific taxa. In some cases, it is likely that the species listed here will turn out to be senior or junior synonym of another taxon, and it is also very probable that some or many of the infraspecific taxa deserve to be treated as “good” species. As a consequence, except for the few species endemic to the Arabian Peninsula, for most others we suggest caution. Our review of species is based on literature records, material examined by the first author, and Arabian material examined in some European collections. We have pointed out which species we consider well identifiable and which ones are difficult. Overall, we consider previous identifications, as well as ours, as temporary. This study is meant as a first step stone towards a more comprehensive revision of the Arabian *Crematogaster* fauna. Since comprehensive taxonomic revisions of the genus are not to be expected from neither the Palaearctic nor the Afrotropical regions any time soon, the most sensible solution for the study of Arabian *Crematogaster* is to visit additional European collections and compare our material with as many types as possible in order to verify or improve the identifications of our material.

Notwithstanding the taxonomic problems lined out above, the treated fauna of *Crematogaster* exemplifies very well that the Arabian Peninsula shares substantial faunal elements with the Palaearctic (mostly Mediterranean species) and the Afrotropics, with a minority of species currently considered as Arabian endemics. At present, we recognize eight Afrotropical, seven Palaearctic, and two Arabian species, which we think fits fairly well with the biogeography of the Arabian Peninsula. However, this assessment might change with further studies and comparisons with types. We suspect that in some cases it might turn out that our material is not conspecific with any of the previ-

ously identified species and might represent another undescribed endemic, but this requires further taxonomic work.

The ant genus *Crematogaster* is one of the most abundant myrmicine genera in the Arabian Peninsula, especially in the Asir mountains, Yemen, and Oman, particularly in areas with open forests and woodlands of *Acacia* (Martius, 1829) (Fabaceae) and *Juniperus* L. (Cupressaceae) trees. The close ecological association between ants and *acacia* trees has been documented by several authors (e.g., Hölldobler and Wilson 1990; Isbell et al. 2013; Madden and Young 1992; Palmer and Brody 2013; Young et al. 1997). *Crematogaster mimosae* is known to have mutualistic relationships with other ants in East Africa (Boyle et al. 2017; Palmer and Brody 2013) and we anticipate similar associations to be found in the vast areas of *Acacia* forests of the southwestern part of the Arabian Peninsula.

Although at present only 17 species of *Crematogaster* are known from the Arabian Peninsula, further targeted collecting may yield both additional species records and more new species. For example, no *Crematogaster* have been collected from Bahrain but it is very unlikely that the genus is absent from the country. We are sure that the current absence of *Crematogaster* records from Bahrain is due to the lack of any national myrmecological studies. The identification key to the Arabian *Crematogaster* presented herein serves as a foundation for further faunistic studies and taxonomic revisions of the genus.

Acknowledgments

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Taxonomic revision of the genus *Machleida* Fåhraeus, 1870 (Tenebrionidae, Pimeliinae, Asidini)

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Abstract

The taxonomic concept of the genus *Machleida* Fåhraeus, 1870 is tested and revised based on newly identified material. The following new species are described: *Machleida banachi*, *M. flagstaffensis*, *M. tarskii*, and *M. zofiae* Kamiński. *Machleida capillosa* Wilke, 1925 is considered as a junior subjective synonym of *Asida devia* Péringuey, 1899. *Asida lecta* Péringuey, 1899 (= *Pseudomachla recurva* Wilke, 1925) (transferred to *Afrasida*), *Machleida nossibiana* Fairmaire, 1897 (transferred to *Scotinesthes*), and *Machleida tuberosa* Wilke, 1925 (interpreted as *incertae sedis* in Asidini) are excluded from *Machleida*. An identification key for the species of the newly revised *Machleida* is provided. The present paper brings the total number of species within the genus to six (*M. banachi* **sp. nov.**; *M. devia* (Péringuey, 1899); *M. flagstaffensis* **sp. nov.**; *M. nodulosa* Fåhraeus, 1870; *M. tarskii* **sp. nov.**; *M. zofiae* Kamiński **sp. nov.**). The morphology of female terminalia (ovipositor and genital tubes) is described for the genus for the first time.

Keywords

Afrasida, darkling beetles, female terminalia, new species, *Scotinesthes*, synonyms, South Africa

Introduction

Darkling beetles (Coleoptera, Tenebrionidae) are a morphologically diverse group of over 20,000 described species (Ślipiński et al. 2011), with many still being discovered every year (e.g., Aloquio et al. 2019; Ando 2019; Giraldo-Mendoza and Flores 2019; Merkl 2019; Masumoto et al. 2019; Nabozhenko and Purchart 2019; Schawaller and Bouchard 2019; Silvestro 2019; Smith and Rincon 2019; Soldati et al. 2019; Zúñiga-Reinoso et al. 2019). This publication focuses on the representatives of the subfamily Pimeliinae Latreille, 1802, specifically on *Machleida* Fåhraeus, 1870, which is one of the seven southern African genera representing Asidini Fleming, 1821 (Koch 1962).

Prior to this publication the genus *Machleida* included the following five species (Koch 1962): *M. capillosa* Wilke, 1925, *M. devia* (Péringuey, 1899), *M. lecta* Péringuey, 1899, *M. nodulosa* Fåhraeus, 1870 (type species), and *M. nossibiana* Fairmaire, 1897. All of them, except the Malgascan *M. nossibiana*, were exclusively known from single localities in the Eastern Cape Province of South Africa (Fåhraeus 1870; Péringuey 1899; Wilke 1925).

According to the most recent hypothesis, this genus can be distinguished from the other Asidini by the following combination of characters (Koch 1962): pronotum strongly cordiform, often with subangular sides; pronotal base as broad as the elytral base (except for *M. nossibiana* with narrowed pronotal base); pronotal disc with large primary sculpturing consisting at least of two median carinae on the basal half of the middle section; hypomeron with shallow, posteriorly-abbreviated antennal sulcus; elytra with large tubercles; sides of the elytral surface limited by the apically abbreviate costa; epipleuron ventral in position (not visible from above); underside of the basal segment of the protarsi simple, non-tomentose; basal segment of posterior tarsi not elongated; and outer margin of anterior tibiae inermous.

As a result of the recent efforts aimed at revising South African Asidini many previously unstudied specimens of *Machleida* were gathered. This, together with an examination of existing type material, enabled a detailed revaluation of the taxonomic status of this genus and its species components.

Material and methods

This study was based on material from the Museum für Naturkunde der Humboldt Universität, Berlin, Germany (referred as Berlin Mus.); Natural History Museum, London, United Kingdom (British Mus.); Muséum national d'Histoire naturelle, Paris, France (Paris Mus.); Hungarian Natural History Museum, Budapest, Hungary (Budapest Mus.); and Ditsong National Museum of Natural History, Pretoria, South Africa (Transvaal Mus.). The original label data for the specimens is given in quotation marks and separated by a comma. Each line of the original label data is separated by a forward slash.

Morphological terminology mostly follows that of Doyen (1994) and Smith (2013), with additional specialized terms used for the male and female terminalia

(Tschinkel and Doyen 1980; Pérez Vera 2014; Giraldo-Mendoza and Flores 2019). Terminalia were investigated using standard methodologies (see Iwan and Kamiński 2016). Morphological measurements were recorded with a filar micrometer. Length was measured along the midline from the anterior margin of the clypeus to the apex of the elytra. Width was measured across the widest points.

The phylogenetic species concept of Wheeler and Platnick (2000) is employed, as in several recent taxonomic works (Smith et al. 2011; Smith 2013; Smith and Wirth 2016). This species concept is appropriate due to its emphasis on character transformations between species and the lack of available data beyond adult morphology and distribution for any of the species in the genus.

Images were taken using a Canon 1000D body with accordion bellows and a Canon EF 100 mm macro lens. Drawings were prepared in Photoshop CS5 using photographs as templates. The distribution of species was illustrated using Quantum GIS (QGIS) v. 2.4, while the vector layers were downloaded from the Natural Earth web-page (<http://www.natureearthdata.com>). The division of the Afrotropical Realm into ecoregions follows Olson et al. (2001). The list of all investigated localities is presented in Appendix 1.

Taxonomy

Genus *Machleida* Fähræus, 1870

Machleida Fähræus, 1870: 256

= *Machloida* Rye, 1873: 286. Type species: *Machleida nodulosa* Fähræus, 1870, by monotypy. Note. Unjustified emendation of *Machleida* Fähræus, 1870, not in prevailing usage.

Type species. *Machleida nodulosa* Fähræus, 1870; by monotypy.

Revised diagnosis. Exclusion of *Asida lecta* Peringuey, 1899, *Machleida nossibiana* Fairmaire, 1897, and *Machleida tuberosa* Wilke, 1925 (see below) from *Machleida* increased the morphological consistency of the genus. As a result, some of the previously listed diagnostic characters needed to be revised (e.g., sculpture of pronotum). Additionally, the present investigation reveals that some of the characters proposed by Koch (1962) are too variable within Afrotropical Asidini to be sustained as diagnostic for *Machleida*. A revised diagnosis is presented below.

The representatives of this genus can be distinguished from other Afrotropical Asidini by the following combination of characters: antenna appearing as 10-segmented, with antennomeres 10 and 11 of equal in width (Fig. 1D); mentum reduced basally, not fully filling buccal cavity (Fig. 1C); pronotal disc with large primary sculpturing consisting of two median carinae merged in the middle (Fig. 1B), carinae not merging in *M. zofiae* Kamiński sp. nov. (Fig. 1A); hypomeron with shallow, posteriorly abbreviated antennal sulcus; elytra with large tubercles (Fig. 2); and expanded epipleura (sometimes fully

fused with the neighbouring part of elytra) (Fig. 3A, B). Moreover, all *Machleida* species shares a peculiar structure of mesoprescutum, i.e. base deeply emarginate (Fig. 3C).

Species composition (6). *M. banachi* sp. nov.; *devia* (Péringuey, 1899); *flagstaffensis* sp. nov.; *nodulosa* Fähræus, 1870; *tarskii* sp. nov.; *zofiae* Kamiński sp. nov.

Excluded species (lecta, nossibiana, tuberosa). These species are hereby excluded from *Machleida* based on differences in the structure of the mentum (fully filling buccal cavity), prosternal process (base straight in lateral view, process not convex), and pronotum (disc only basally with median carinae, lateral tubercles absent). *Asida lecta* Péringuey, 1899 does not fall within the newly formulated concept of *Machleida*. The aforementioned pronotal structure place this species within the subgenus *Archasida* Wilke 1922 of *Afrasida* Wilke, 1925 (Koch 1962). As a result, the following new combination is proposed: *Afrasida (Archasida) lecta* (Péringuey, 1899) comb. nov. A habitus photo of this species is presented in Appendix 2: Fig. S1A.

Because of its Malagasy distribution, the taxonomic placement of *M. nossibiana* Fairmaire, 1897 within the South African *Machleida* was previously questioned by several authors (Chatanay 1914; Wilke 1925; Gebien 1937). However, based on a single non-typical specimen, Koch (1962) tried to provide some morphological support for this taxonomic hypothesis. According to his view *M. nossibiana* generally resembles species of *Machleida* and can be separated from other Malagasy Asidini by the non-soleate underside of the tarsi. In his diagnosis he compared this species to *M. nodulosa* and highlighted two main morphological differences: antennae robust in *M. nossibiana*, slender in *M. nodulosa*; and prosternal process broad in *M. nossibiana*, narrow in *M. nodulosa*. The current reinvestigation of the type material of *M. nossibiana* (Appendix 2: Fig. S1B) revealed a high morphological resemblance of this species to representatives of the genus *Scotinesthes* Fairmaire, 1895 (Koch 1962). Namely, the aforementioned characters used by Koch to separate *M. nossibiana* from *M. nodulosa* are characteristic for *Scotinesthes*. Moreover, *M. nossibiana* shares a common structure of the mentum (fully filling buccal cavity; reduced basally in *Machleida*) with the other species representing that Malagasy genus. As a result, *nossibiana* is transferred from *Machleida* and the following new combination is introduced: *Scotinesthes nossibianus* (Fairmaire, 1897) comb. nov.

Reinvestigation of the type material revealed that *Machleida tuberosa* Wilke, 1925 has a peculiar pronotal sculpturing, i.e., disc without carinae but densely covered with small setose tubercles (Appendix 2: Fig. S1C). The second character seems to be unique for this species among the other southern African Asidini. Because of the aforementioned features, *M. tuberosa* does not fit the newly proposed taxonomic concept of *Machleida* and is hereby excluded from this genus. The exact placement of this species (possibly a new genus) requires further investigation in a wider taxonomic context. At the moment *tuberosa* is treated as *incertae sedis* Asidini.

Distribution. Representatives of this genus have been collected in the following ecoregions of South Africa (Fig. 5): Drakensberg Montane Woodlands and Grasslands, KwaZulu-Cape coastal forest mosaic, Maputaland-Pondoland bushland, and thickets, Southern Africa mangroves.

Key to the species of the genus *Machleida*

- 1 Pronotal disc with two median carinae merging in middle of pronotum (Fig. 1B); lateral tubercles situated above half pronotal length (in some cases tubercles merged with median carinae) (Fig. 1B)..... **2**
- Pronotal disc with median carinae not merging in of middle of pronotum (Fig. 1A); lateral tubercles situated below half pronotal length (Fig. 1A) ***Machleida zofiae* Kamiński sp. nov.**
- 2 Body size = 13.0–15.0 mm **3**
- Body size = 7.0–9.5 mm **4**
- 3 Lateral sides of pronotum sinuate (Fig. 2B). Elytral disc rugose and densely covered with microtubercles (Fig. 3D) ***Machleida devia***
- Lateral sides of pronotum rounded. Elytral disc sparsely covered with tubercles; surface between them glabrous ***Machleida flagstaffensis* sp. nov.**
- 4 Elytral tubercles distributed evenly, not forming ridges (Fig. 2D). Elytra densely covered with noticeable punctures (Fig. 3E) ***Machleida nodulosa***
- Elytral tubercles absent or sparse in middle of disc, laterally forming at least two lateral ridges (Fig. 2E). Elytra impunctate or with extremely sparse punctures... **5**
- 5 Elytral disc only basally with pair of oblong tubercles (middle part of elytra without tubercles). Elytral humerus dentate, protruding laterad (Fig. 2A). Elytral slope gradually falling towards apex of elytra (Fig. 3B)..... ***Machleida banachi* sp. nov.**
- Median part of elytral disc covered with tubercles. Elytral humerus obtuse, not protruding laterad (Fig. 2E). Elytral slope extremely steep (Fig. 3A) ***Machleida tarskii* sp. nov.**

Redescriptions***Machleida devia* (Péringuey, 1899)**

Figs 1E, 2B, 3D, 4C, 5

Asida devia Péringuey, 1899: 258 [transferred to *Machleida* by Wilke (1925: 536)]
= *Machleida capillosa* Wilke, 1925: 536 [syn. nov.]

Material studied. *Syntype* of *Machleida capillosa* (Berlin Mus.): “Natal Mus., / Maritzburg. / 1913-330”, “capillosa / sp. n.”. Two specimens (Transvaal Mus.): Tugela River / nr Kranskop / Lawrence & / Haacke; single specimen (Transvaal Mus.): “S. Afr.: Zululand / Hluhluwe Game Res. / 28.05S–32.04E”, “20.111992: E-Y: 2840 / fung. Trunk & litter / leg. Endrody – Younga”.

Notes. During the preparation phase for this study the holotype of *Asida devia* was not found in any of the queried collections, i.e. Iziko Museum of South Africa in Cape Town and the institutions listed in the Material and methods section. However,

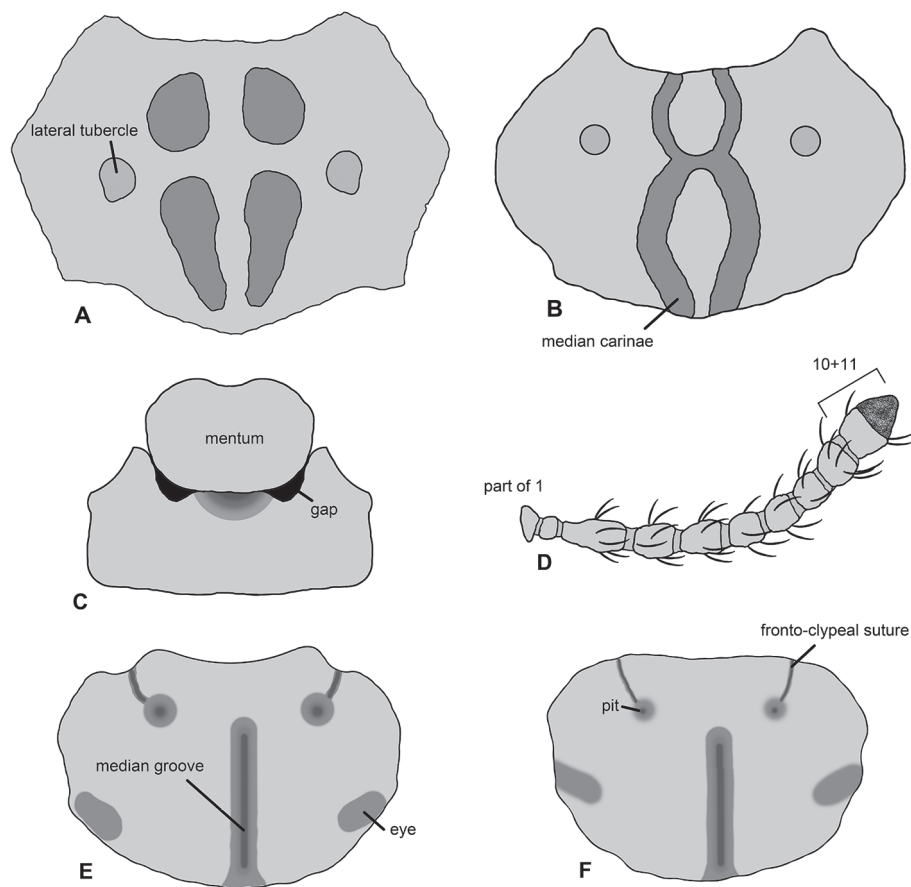


Figure 1. Selected diagnostic characters proposed for *Machleida* and its species. **A, B** Pronotal disc with specific surface modifications **C** ventral aspect of postoral regions **D** antenna **E, F** dorsal aspect of head. Illustrated species: **A, D** *Machleida zofiae* **B** *M. nodulosa* **C** *M. tarskii* **E** *M. devia* **F** *M. flagstaffensis*.

the original description indicates several unique morphological features of this species (i.e. large body size, presence of densely distributed microtubercles on the elytral disc), which were used to differentiate it from other congeners.

Redescription. Length 13.0–14.0 mm, width of elytra 8.5–9.5 mm. Integument black, often densely coated with debris. **Head:** frons with longitudinal median depression, densely punctate (~0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; frontoclypeal suture medially indistinguishable, weakly indented at margins, with pair of lateral depressions; apical clypeal margin broadly and shallowly emarginate; clypeus projected toward front of body (Fig. 1E); apical margin of labrum strongly and sharply emarginate, densely punctate (~0.2 diameters apart), each puncture with short yellowish acuminate seta. Eye elongate oval, length approximately 8× width, weakly emarginate around epistomal base. Mentum with rounded

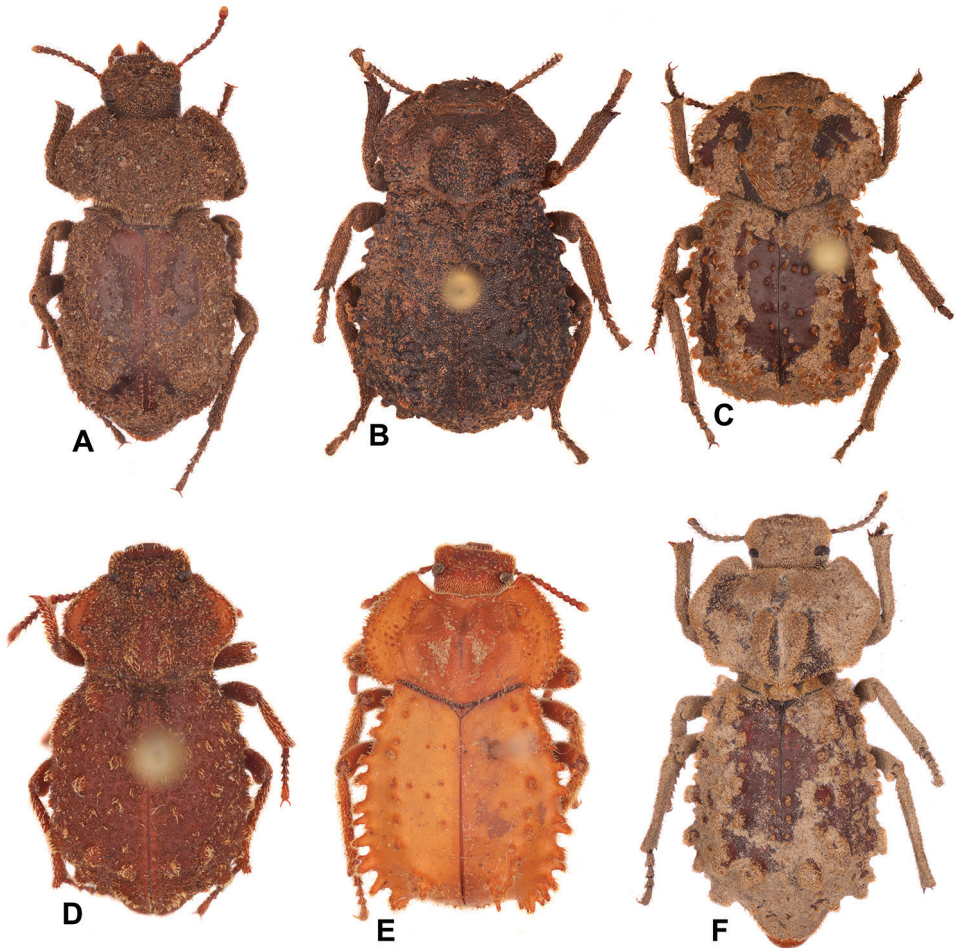


Figure 2. Habitus images of the studied species. **A** *Machleida banachi* **B** *M. devia* **C** *M. flagstaffensis* **D** *M. nodulosa* **E** *M. tarskii* **F** *M. zofiae*.

base, not fully filling buccal cavity; anterior margin weakly medially emarginate; densely punctate, each puncture with single rectangular flattened scale-like seta. Submentum semicircular, concave medially, densely punctate. Antenna moderately clothed in erect acuminate yellowish setae; length of antennomeres 10+11 equal to 0.8 of antennomere 3 length; length of antenna equal to 0.75 of pronotal length. **Prothorax:** pronotal lateral margin sinuate, slightly raised. Pronotum widest below middle. Disc with two median carinae merging in middle; lateral tubercles confluent with median carinae, forming convexities situated above half pronotal length; surface densely punctate (~ 0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; anterior margin strongly emarginate, anterior apices strongly produced; base bisinuate. Hypomeron with shallow antennal sulcus, densely punctate (~ 0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta. Prosternal process

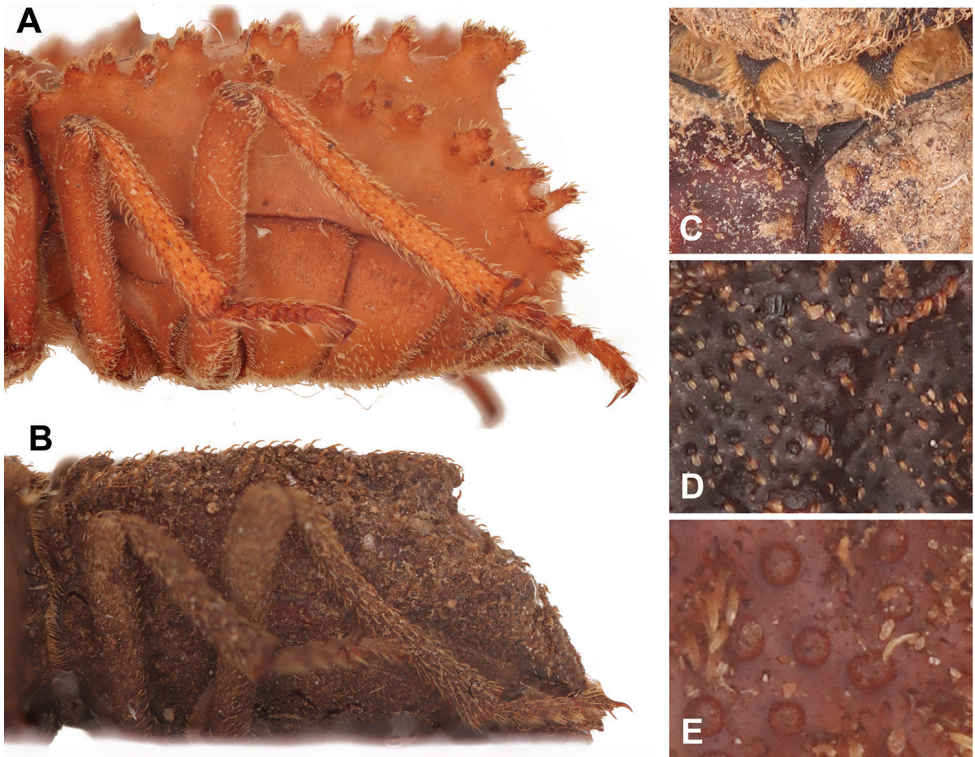


Figure 3. Morphological details of selected *Machleida* species. **A, B** Lateral aspect of elytron **C** scutellum and **D, E** elytral disc. Illustrated species: **A** *Machleida tarskii* **B** *M. banachi* **C** *M. zofiae* **D** *M. devia* **E** *M. nodulosa*.

strongly convex, without median sulcus (ventral view). **Pterothorax:** scutellum without median groove. Elytra widest behind middle, clothed with extremely short yellowish rectangular, flattened scale-like setae and microtubercles (Fig. 3D); marginal costae present, tuberculate, apex of each tubercle densely covered with acuminate setae, divided near humera, with marginal branch extending to approximately middle of 4th abdominal ventrite, dorsal branch extending to base of 3rd abdominal ventrite, terminal tubercles transverse; disc rugose, without any trace of intervals and rows, covered with microtubercles; ventral portion of elytra basally impunctate. Elytral slope steep (falling at angle of 75°). Epipleura clearly distinguishable. Mesanepisternum, mesepimeron, and metepimeron impunctate or sparsely punctate. Meso- and metaventrite densely punctate and covered with acuminate setae. Lateral regions of metaventrite (between coxae) extremely short. **Legs:** apex of profemora with small denticle on outer margin. Femora and tibia densely punctate and setose. Tarsi cylindrical, not flattened. **Abdomen:** ventrites 1–3 moderately punctate and weakly rugulose; ventrites 4 and 5 densely punctate and setose; ventrite 5 without submarginal sulcus. **Terminalia:** aedeagus bipartite, with apical part slightly shorter than basal portion (Fig. 4C). Female specimens were not dissected due to scarcity of available materials.

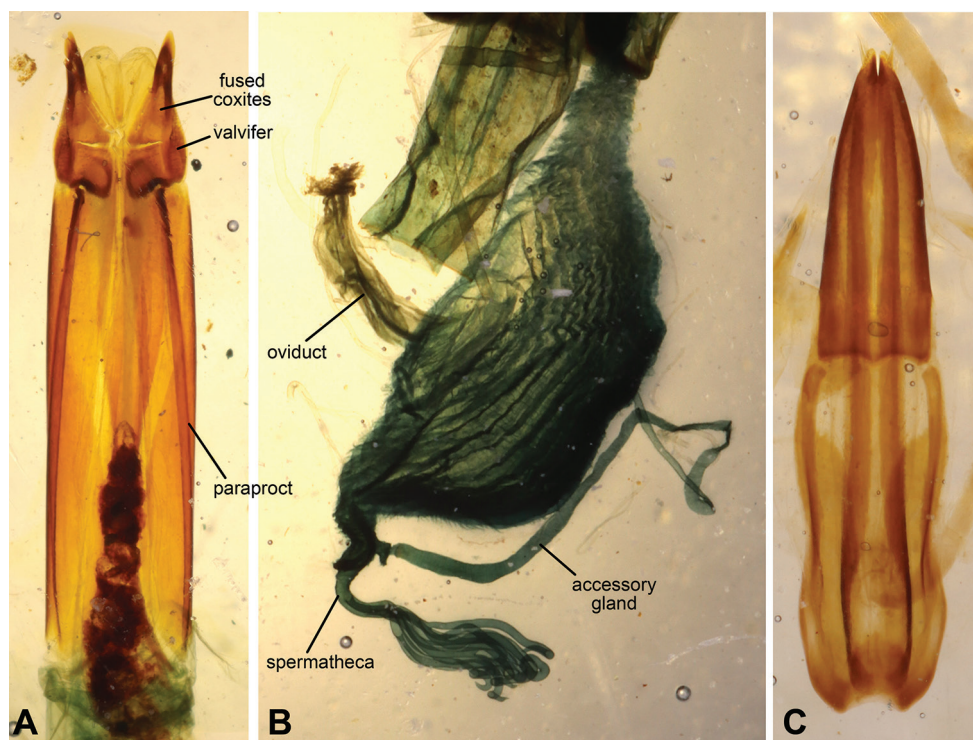


Figure 4. Female and male terminalia of *Machleida*. **A, B** Ovipositor and genital tubes of *Machleida flagstaffensis* **C** aedeagus of *M. devia*.

Notes on synonymy. Type investigation of *Machleida capillosa* did not reveal any characters to support its taxonomic distinctiveness from *Asida devia* (e.g. both share a unique structure of elytral disc – surface densely covered with microtubercles) (Péringuey 1899). Furthermore, both species have the same *locus typicus* (“Maritzburg”, South Africa). As a result, *M. capillosa* is considered here as a junior subjective synonym of *Asida devia*.

Distribution. Representatives of this species have been collected in the following ecoregions of South Africa (Fig. 5): Drakensberg Montane Woodlands and Grasslands, Maputaland-Pondoland bushland and thickets.

Machleida nodulosa Fähræus, 1870

Figs 1B, 2D, 5

Machleida nodulosa Fähræus, 1870: 256

= *Asida legitima* Péringuey, 1899: 266 [syn. by Péringuey (1904: 296)]

Material studied. Single specimen (Transvaal Mus.): “Umkomaas / III.1951 / A.L. Capener”; single specimen (Berlin Mus.): “Natal / Durban”; single specimen (Transvaal Mus.):

“Malvern / Natal”; single specimen (Budapest Mus.): “Natal / P. Reineck”, “Machleida / nodulosa / Fahr”; single specimen (Transvaal Mus.): “Lower / mKomas N. / 9/97”, “Durban Museum”; single specimen (Transvaal Mus.): “Tongaat / V.1953 / Mrs. R. Koch”.

Notes. The last researcher to study the types of *Machleida nodulosa* and *Asida legitima* was Péringuey (1904). This fact indicates that those specimens should be preserved in the Iziko Museum of South Africa (Cape Town). However, the types of those both synonymous species were not found in any of the queried collections, i.e. Iziko Museum of South Africa in Cape Town and the institutions listed in the Material and methods section.

Descriptions of *M. nodulosa* and *A. legitima* indicate several specific morphological features (i.e. relatively small body size; presence of dense punctures on elytra; elytral tubercles distributed evenly, not forming ridges), which were used to differentiate them from other congeners.

Redescription. Length 8.5–9.0 mm, width of elytra 4.5–5.0 mm. Integument brownish, often densely coated with debris. **Head:** frons with shallow longitudinal median depression, densely punctate (~0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; frontoclypeal suture medially indistinguishable, weakly indented at margins, with pair of lateral depressions; apical clypeal margin broadly shallowly emarginate; clypeus slightly projected toward front of body; apical margin of labrum sharply emarginate medially, densely punctate in apical half (~0.2 diameters apart), each puncture with short yellowish setae. Eye elongate oval, length approximately 4× width, weakly emarginate around epistomal base. Mentum with rounded base, not fully filling buccal cavity, anterior margin weakly medially emarginate; densely punctate, each point with single acuminate seta. Submentum semicircular, slightly concave medially, densely punctate. Antenna moderately clothed in erect acuminate yellowish setae; length of antennomeres 10+11 equal to 0.8 of antennomere 3 length; length of antenna equal to 0.7 of pronotal length. **Prothorax:** pronotal lateral margin strongly sinuate, slightly raised. Pronotum widest in middle. Disc with two median carinae merging in middle, lateral tubercles situated above half pronotal length; surface densely punctate (~0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; anterior margin strongly emarginate, anterior apices strongly produced; base v-shaped. Hypomerion with shallow antennal sulcus, sparsely punctate to impunctate, each puncture, if present, with short yellowish acuminate seta. Prosternal process strongly convex, longitudinally depressed in middle (ventral view). **Pterothorax:** scutellum without median groove. Elytra widest behind middle, densely punctured and evenly covered with tubercles (tubercles sometimes merging), each tubercle clothed with short yellowish rectangular, flattened scale-like setae; ventral portion of elytra, except epipleuron, similarly structured as dorsal side. Elytral slope gradually falling towards elytral apex (at angle of 50°). Epipleuron clearly distinguishable. Mesanepisternum, mesepimeron, and metepimeron sparsely punctate. Meso- and metaventrite densely punctate and covered with acuminate setae. Lateral regions of metaventrite (between coxae) extremely short. **Legs:** apex of profemora with small denticle on outer margin. Femora and tibia densely punctate and setose. Tarsi cy-



Distribution. Representatives of this species have been collected in the following ecoregion of South Africa (Fig. 5): Southern Africa mangroves.

Figs 2A, 5

Type material. *Holotype* (Transvaal Mus.): “26.11.1988; E-Y:2582 / forest floor litter / leg. Endrody-Younga”, “S. Afr., Transkei / Ntsubane forest / 31.27S–29.44E”. *Paratypes* (Transvaal Mus.): single specimen: same data as holotype; single specimen: same data, except “1.12.1988; E-Y:2593 / forest floor litter / leg. Endrody-Younga”; single specimen:

same data, except “25.11.1988; E-Y:2579 / forest floor litter / leg. Endrody-Younga”; two specimens: same data, except: 25.11.1988; E-Y:2580 / groundtraps, 14 days / leg. Endrody-Younga”, “groundtrap with / banana bait”; two specimens: same data, except “25.11.1988; E-Y:2537 / fungi & for. litter / leg. Endrody-Younga”; single specimen: “Z.A.82 / Port St. John D. / Ingogo Forest”, “Humus / XII-1961”, “N. Leleup leg.”.

Diagnosis. This species can be distinguished from all its congeners by the unique structure of elytra: disc medially lacking tubercles and dentate humerus (strongly protruding laterad) (Fig. 2A). This species most closely resembles *Machleida tarski* (see identification key above).

Description. Length 8.0–9.5 mm, width of elytra 4.0–7.0 mm. Integument brownish, often densely coated with debris. **Head:** frons with longitudinal median depression, densely punctate (~0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; frontoclypeal suture medially indistinguishable, weakly indented at margins, with pair of lateral depressions; apical clypeal margin broadly shallowly emarginate; clypeus slightly projected toward front of body; apical margin of labrum sharply emarginate medially, densely punctate in apical half (~0.2 diameters apart), each puncture with short yellowish acinate setae. Eye elongate oval, length approximately 5× width, weakly emarginate around epistomal base. Mentum with rounded base, not fully filling buccal cavity; anterior margin weakly medially emarginate; densely punctate, each with single acuminate seta. Submentum semicircular, concave medially, densely punctate. Antenna moderately clothed in erect acuminate yellowish setae; length of antennomeres 10+11 equal to 0.8 of antennomere 3 length; length of antenna equal to 0.75 of pronotal length. **Prothorax:** pronotal lateral margin rounded, strongly raised. Pronotum widest below middle. Disc with two median carinae merging in middle; lateral tubercles confluent with median carinae, forming convexities situated above half pronotal length; surface densely punctate (~0.2 diameters apart), each puncture with short yellowish rectangular, flattened scale-like seta; anterior margin strongly emarginate, anterior apices strongly produced; base bisinuate. Hypomeron with shallow antennal sulcus, sparsely punctate to impunctate, each puncture, if present, with short yellowish acuminate seta. Prosternal process strongly convex, longitudinally depressed in middle (ventral view). **Pterothorax:** scutellum without median groove. Elytra widest behind middle, clothed with short yellowish rectangular, flattened scale-like setae; marginal costae present, tuberculate, apex of each tubercle densely covered with setae, marginal branch extending to approximately apex of 4th abdominal ventrite, dorsal branch extending to apex of 3rd abdominal ventrite, terminal tubercles transverse; disc smooth, without any trace of intervals, sparsely covered with flattened setae, with elongated tubercles near base (Fig. 3B); ventral portion of elytra basally impunctate, apically with sparse punctures. Elytral slope gradually falling towards elytral apex (at angle of 50°). Epipleura indistinguishable from neighbouring portion of elytra. Mesanepisternum, mesepimeron, and metepimeron impunctate or sparsely punctate. Meso- and metaventrite densely punctate and covered with setae. Lateral regions of metaventrite (between coxae) extremely short. **Legs:** Apex of pro-femora with small denticle on outer margin. Femora and tibia densely punctate and

setose. Tarsi cylindrical, not flattened. **Abdomen:** ventrites 1–3 moderately punctate and weakly rugulose; ventrites 4 and 5 densely punctate and setose; ventrite 5 without submarginal sulcus. **Terminalia:** aedeagus as in *M. devia* (Fig. 4C). Female specimens were not dissected due to scarcity of available materials.

Etymology. This newly introduced name honours Stefan Banach (30 March 1892–31 August 1945), prominent Polish mathematician and founder of modern functional analysis. He was educated at the Technical University of Lwów and was a founder of the Lwów School of Mathematics.

Distribution. Representatives of this species have been collected in the following ecoregions of South Africa (Fig. 5): KwaZulu-Cape coastal forest mosaic, Maputaland-Pondoland bushland and thickets.

***Machleida flagstaffensis* sp. nov.**

<http://zoobank.org/1D55CB36-328A-4CA7-BA51-27434AEF42EF>

Figs 1F, 2C, 4A, B, 5

Type material. Holotype (Transvaal Mus.): “1.12.1988; E-Y:2593 / forest floor litter / leg. Endrody-Younga”, “S. Afr., Transkei / Ntsubane forest / 31.27S–29.44E”.

Paratypes: single specimen (Transvaal Mus.): same data as holotype; single specimen (Transvaal Mus.): “24.11.1987; E-Y:2533 / indig. Forest litter / leg. Endrody-Younga”, “S. Afr., Transkei / Silaka For. Reserve / 31.33S–29.30E”

Diagnosis. On account of a large body size this species is similar to *Machleida devia*. Both species can be separated by the characters listed in the identification key provided above.

Description. Length 13.0–15.0 mm, width of elytra 7.0–7.5 mm. Integument brownish, often densely coated with debris. **Head:** frons with longitudinal median depression, densely punctate (~0.2 diameters apart), each puncture with short yellowish acuminate seta; frontoclypeal suture medially indistinguishable, weakly indented at margins, with pair of lateral depressions; apical clypeal margin broadly shallowly emarginate; clypeus projected toward front of body (Fig. 1F); apical margin of labrum sharply emarginate, densely punctate (~0.2 diameters apart), each puncture with short yellowish seta. Eye elongate oval, length approximately 6× width, weakly emarginate around epistomal base. Mentum with rounded base, not fully filling buccal cavity, anterior margin weakly medially emarginate; densely punctate, punctures moderately sized, each with single slender setae. Submentum triangular, concave, densely punctate. Antenna moderately clothed in erect acuminate clear to yellowish setae; length of antennomeres 10+11 equal to 0.9 of antennomere 3 length; antennomeres 10+11 noticeably widened; length of antenna equal to 0.75 of pronotal length. **Prothorax:** pronotal lateral margin rounded, slightly elevated. Pronotum widest in middle base. Disc with two median carinae merging in middle, and lateral tubercles situated above half pronotal length; surface sparsely punctate, covered with noticeable microsculpture and extremely short, brownish setae. Median carinae and

remaining tubercles apically covered with elongated scale-like setae and short elongated setae; anterior margin emarginate, densely setose; base bisinuate. Hypomeron with relatively deep antennal sulcus, impunctate. Prosternal process strongly convex, rounded at apex. **Pterothorax:** scutellum with median longitudinal groove. Elytra widest behind middle; surface between tubercles glabrous, covered with microsculpture; marginal costae present, tuberculate, apex of each tubercle densely covered with numerous short acuminate setae and large single scale-like seta apically, divided near humera, marginal branch extending to approximately middle of 4th abdominal ventrite, dorsal branch extending to base of 3rd abdominal ventrite, terminal tubercles transverse; disc without any trace of intervals or rows, sparsely covered with tubercles; ventral portion of elytra basally impunctate. Elytral slope steep (falling at angle of 75°). Epipleuron indistinguishable from neighbouring portion of elytra. Mesanepisternum, mesepimeron, and metepimeron sparsely punctate. Meso- and metaventrite sparsely punctate and covered with setae. Lateral regions of metaventrite (between coxae) extremely short. **Legs:** apex of profemora with small denticle on outer margin. Femora and tibia densely punctate and setose. Tarsi cylindrical, not flattened. **Abdomen:** ventrites 1–3 sparsely punctate and setose; ventrites 4 and 5 moderately punctate and setose; ventrite 5 without submarginal sulcus. **Terminalia:** ovipositor with paraproct much longer than coxites, plates 2–4 fused (Fig. 4A). Genital tubes similarly structured to other Asidini (Fig. 4B). Male specimens were not dissected due to scarcity of available materials.

Etymology. The species epithet refers to Flagstaff (Eastern Cape, South Africa), a town near the collecting localities of this new species.

Distribution. Representatives of this species have been collected in the following ecoregions of South Africa (Fig. 5): KwaZulu-Cape coastal forest mosaic, Maputaland-Pondoland bushland and thickets.

***Machleida tarskii* sp. nov.**

<http://zoobank.org/52AF9427-4126-49E2-BF5C-DC6BEEEA7ED2>

Figs 1C, 2E, 5

Type material. **Holotype** (Transvaal Mus.): “Z.A. 86 / Pirie Forest / King Williams Town”, “Humus / XII.1961”, “N. Leleup leg.”. **Paratype:** single specimen same data as holotype.

Diagnosis. This species most closely resembles *Machleida banachi*, as both share a similar body size, structure of pronotal disc (median carinae merging) and elytra (tubercles forming two lateral ridges). They can be separated by different formation of the elytral slope (extremely steep in *tarskii*; gradually falling in *banachi*) (Fig. 3A, B). For other characters separating those both species see the identification key.

Description. Length 9.0–9.2 mm, width of elytra 5.0–5.2 mm. Integument dark brown (yellowish in holotype), often densely coated with debris. **Head:** frons with lon-

gitudinal median depression, sparsely punctate (3.0–4.0 diameters apart), each puncture with short yellowish acuminate setae; frontoclypeal suture medially indistinguishable, indented at margins, with pair of lateral depressions; apical clypeal margin broadly shallowly emarginate; clypeus slightly projected toward front of body; apical margin of labrum strongly emarginate, densely punctate apically (~0.2 diameters apart), each puncture with short yellowish setae. Eye elongate oval, length approximately 4× width, weakly emarginate around epistomal base. Mentum with rounded base, not fully filling buccal cavity, anterior margin medially emarginate; sparsely punctate, each puncture with single seta. Submentum semicircular, concave, impunctate. Antenna moderately clothed in erect acuminate clear to yellowish setae; length of antennomeres 10+11 equal that of antennomere 3; length of antenna equal to 0.75 of pronotal length. **Prothorax:** pronotal lateral margin rounded, strongly raised, densely covered with tubercles, each tubercle densely covered with patch of short setae and medially with few scale-like longer setae. Pronotum widest below base. Disc with two median carinae merging in middle; lateral tubercles confluent with median carinae, forming convexities situated above half pronotal length; surface moderately punctate (1.0–2.0 diameters apart), punctures without setae; anterior margin strongly emarginate, anterior apices strongly produced; base bisinuate. Hypomerion with shallow antennal sulcus, impunctate. Prosternal process strongly convex, densely covered with short scale-like setae, longitudinally depressed in middle (ventral view). **Pterothorax:** scutellum with median longitudinal groove. Elytra widest behind middle, impunctate; two marginal rows of tubercles present, apex of each tubercle densely covered with setae; marginal branch extending to approximately middle of 5th abdominal ventrite, dorsal branch extending to base of 5th abdominal ventrite, terminal tubercles transverse; disc without any trace of intervals, between tubercles glabrous, tubercles distributed sparsely, each apically with dense patch of setae; ventral portion of elytra, mesanepisternum, mesepimeron, and metepimeron impunctate, and sparsely covered with short, brownish setae. Elytral slope extremely steep (falling at angle of 80°). Epipleura indistinguishable from neighbouring portion of elytra. Meso- and metaventrite moderately punctate and covered with yellowish setae. Lateral regions of metaventrite (between coxae) extremely short. **Legs:** apex of profemora with small denticle on outer margin. Femora and tibia densely punctate and setose. Tarsi cylindrical, not flattened. **Abdomen:** ventrites 1–4 sparsely covered with brownish short setae; ventrite 5 moderately punctate and setose, (yellowish setae) without submarginal sulcus. **Terminalia:** specimens were not dissected due to scarcity of available materials.

Etymology. The species epithet is in honor of Alfred Tarski (14 January 1901–26 October 1983), Polish-American logician and mathematician. Educated at the University of Warsaw and a member of the Lwów–Warsaw school of logic, he immigrated in 1939 to the USA, where he became a citizen in 1945. Alfred Tarski carried out research in mathematics at the University of California, Berkeley, from 1942 until his death in 1983.

Distribution. Representatives of this species have been collected in the following ecoregion of South Africa (Fig. 5): Drakensberg Montane Woodlands and Grasslands.

***Machleida zofiae* Kamiński, sp. nov.**

<http://zoobank.org/721AF25A-EC87-4DD1-B138-F020C37759D1>

Figs 1AD, 2F, 3C, 5

Type material. *Holotype* (Transvaal Mus.): “Transkei: coast / Dwesa for. Res. / 32.17S–28.50E”, “26.2.1985; E-Y: 2165 / groundtraps, 7 days / leg. Endrody-Younga”, “groundtrap with / banana bait”.

Diagnosis. Easily distinguishable from other congeners by the specific structure of pronotum: disc with median carinae interrupted in the middle of pronotal disc (Fig. 1A); lateral tubercles situated below the half pronotal length (Fig. 1A). This is also the only *Machleida* species with relatively large tuberculate horns on frons. Superficially this species can be confused with *M. flagstaffensis*. However, besides the characters listed above those two species can be distinguished by different structure of elytral slope, i.e. steep in *flagstaffensis* (falling at angle of 75°) versus gradually falling in *zofiae* (at angle of 50°).

Description. Length 11.5 mm, width of elytra 5.5 mm. Integument brownish, densely coated with debris. **Head:** frons with pair of tuberculate horns, densely punctate (~0.2 diameters apart), each puncture with short yellowish acuminate seta; frontoclypeal suture medially indistinguishable, indented at margins, with pair of lateral depressions; apical clypeal margin broadly and shallowly emarginate; clypeus slightly projected toward front of body; apical margin of labrum strongly emarginate, densely punctate apically (~0.2 diameters apart), each puncture with short, yellowish seta. Eye elongate oval, length approximately 4× width, weakly emarginate around epistomal base. Mentum with rounded base, not fully filling buccal cavity, anterior margin medially emarginate; sparsely punctate, each puncture with single seta. Submentum semi-circular, concave, impunctate. Antenna moderately clothed in erect acuminate clear to yellowish setae; length of antennomeres 10+11 equal that of antennomere 3 (Fig. 1D); length of antenna equal to 0.85 of pronotal length. **Prothorax:** pronotal lateral margin sinuate, strongly raised, densely covered with setae. Pronotum widest in middle. Disc with median carinae not merging in middle (Fig. 1A); lateral tubercles located below half pronotal length; surface moderately to densely punctate (0.2–2.0 diameters apart), punctures with flattened setae; anterior margin strongly emarginate, anterior apices strongly produced; base bisinuate. Hypomerion with shallow antennal sulcus, sparsely punctate or impunctate. Prosternal process strongly convex, densely covered with short scale-like setae, longitudinally depressed in middle (ventral view). **Pterothorax:** scutellum with median longitudinal grove (Fig. 3C). Elytra widest behind middle, impunctate; two marginal rows of tubercles present, apex of each tubercle densely covered with acuminate setae, marginal branch extending to approximately base of 4th abdominal ventrite, dorsal branch extending to middle of 3th abdominal ventrite; terminal tubercles of both rows enlarged; disc without any trace of intervals, covered with tubercles distributed in two rows near suture, each tubercle apically with dense patch of setae, surface of disc glabrous between tubercles; ventral portion of elytra, mesane-pisternum, mesepimeron, and metepimeron impunctate, sparsely covered with short brownish setae. Elytral slope gradually falling towards elytral apex. Epipleuron clearly

distinguishable. Meso- and metaventrite moderately punctate and covered with yellowish setae. Lateral regions of metaventrite extremely short. **Legs:** apex of profemora with small denticle on outer margin. Femora and tibia densely punctate and setose. Tarsi cylindrical, not flattened. **Abdomen:** ventrites 1–4 sparsely covered with short, brownish setae; ventrite 5 moderately punctate and setose, (yellowish setae) without submarginal sulcus. **Terminalia:** single holotype was not dissected.

Etymology. *Machleida zofiae* is named in honour of the first author's daughter, Zofia Irena Kamińska, born on November 3, 2018 (Flagstaff, USA).

Distribution. The holotype of this species was collected in the following ecoregion of South Africa (Fig. 5): KwaZulu-Cape coastal forest mosaic.

Acknowledgements

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Appendix I

Analysed distributional data in CSV format

Genus, Species, Locality, Latitude, Longitude

Machleida, *banachi*, St John, -31.6288, 29.5369
Machleida, *banachi*, Ntsubane forest, -31.276506, 29.439460
Machleida, *devia*, Maritzburg, -29.61679, 30.39278
Machleida, *devia*, Hluhluwe, -28.308716, 31.877668
Machleida, *devia*, Kranskop, -28.967373, 30.86351
Machleida, *flagstaffensis*, Ntsubane forest, -31.276506, 29.439460
Machleida, *flagstaffensis*, Silaka Reserve, -31.652780, 29.508211
Machleida, *nodulosa*, Durban, -29.883333, 31.05
Machleida, *nodulosa*, Umkomaas, -30.2, 30.8
Machleida, *nodulosa*, Malwern, -29.884374, 30.919393
Machleida, *tarskii*, King Williams Town, -32.883333, 27.4
Machleida, *zofiae*, Dwesa, -32.302013, 28.821885

Appendix 2

Habitus photographs of the species hereby excluded from *Machleida*

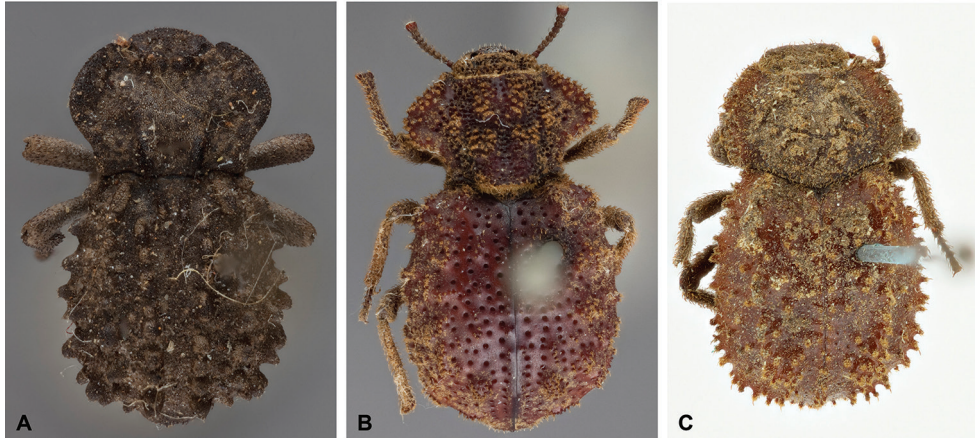


Figure S1. Habitus photographs of the species hereby excluded from *Machleida*. **A** Syntype of *Pseudomachla recurva* Wilke, 1925 synonym of *Afrasida (Archasida) lecta* (Peringuey, 1899) comb. nov. **B** holotype of *Scotinesthes nossibianus* (Fairmaire, 1897) comb. nov. **C** holotype of *tuberosa* Wilke, 1925 (*incertae sedis*).

Label data for analysed specimens:

Afrasida (Archasida) lecta (Peringuey, 1899) comb. nov.

Asida lecta Peringuey, 1899 (= *Pseudomachla recurva* Wilke, 1925)

Material studied. Three specimens (Transvaal Mus.): “Algoa bay / CApland / Dr. Brauns / 9.2.96”; single specimen (Transvaal Mus.): “Resolution / Albany Distr. 21–22.II.1925 / A. Walton”.

Scotinesthes nossibianus (Fairmaire, 1897) comb. nov.

Machleida nossibiana Fairmaire, 1897

Material studied. Holotype (Paris Mus.): “Type”, “Nossibe”, “Machla / nossibiana / Fairm Madaga / D. unreadable”

tuberosa Wilke, 1925 (*incertae sedis* Asidini)

Machleida tuberosa Wilke, 1925

Material studied. Holotype (British Mus.): “F. Steph”, “Type”, “tuberosa / sp. nov. det. S. Wilke”, “1913:466”, “NHMUK 013903124”.

A new species of stygobitic snail in the genus *Antrorbis* Hershler & Thompson, 1990 (Gastropoda, Cochliopidae) from the Appalachian Valley and Ridge of eastern Tennessee, USA

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Abstract

A new species of cave snail (Littorinimorpha: Cochliopidae) in the genus *Antrorbis* is described from the dark zone of two caves in the Appalachian Valley and Ridge province in eastern Tennessee, United States. The Tennessee Cavesnail, *Antrorbis tennesseensis* Perez, Shoobs, Gladstone, & Niemiller, **sp. nov.** is distinguished from its only known congener, *Antrorbis breweri*, by the absence of raised tubercles on its finely spirally striate protoconch, and its unique radular formula. Moreover, *A. tennesseensis* is genetically distinct from *A. breweri* based on substantial divergence at the mitochondrial CO1 locus. This is the first cavesnail to be described from the Appalachian Valley and Ridge (AVR) physiographic province in the state of Tennessee, which previously represented a substantial gap in the distribution of stygobitic (i.e., aquatic, subterranean-obligate) gastropods.

Keywords

Antrorbis, cavesnail, Cochliopidae, stygofauna, systematics

Introduction

Among the hydrobioid snails (i.e., Hydrobiidae s.l.; Davis 1979) are a morphologically diverse group of minute gastropods living in freshwater subterranean habitats in karstic regions of North America (Hershler and Holsinger 1990; Niemiller et al. 2019). These stygobitic (i.e., aquatic, subterranean-obligate) gastropods are characterized by reduced shell thickness, soft body depigmentation, nearly complete eye reduction, and miniaturization (Hershler and Holsinger 1990; Grego et al. 2019; Prié 2019).

Of the North American stygobitic snails, the Lithoglyphidae initially contained the highest species diversity and has been traditionally divided into several groups on the basis of morphology and geographic distribution: 1) *Phreatodrobia*, *Phreatoceras*, *Balconorbis*, *Stygopyrgus*, and *Texapyrgus*, endemic to the Edwards-Trinity Aquifer System in south and central Texas; 2) *Antrorbis* and *Holsingeria*, found in the Appalachians karst region of the eastern United States; and 3) *Pterides* from northeastern Mexico (Hershler and Longley 1986; Hershler 1989; Hershler and Holsinger 1990; Hershler and Thompson 1990). However, the classification of related groups of minute snails has been recently revised (Wilke et al. 2013). Several genera of stygobitic snails from North America that were members of Lithoglyphidae (*Phreatodrobia*, *Phreatoceras*, *Balconorbis*, *Stygopyrgus*, and *Texapyrgus*) were reassigned to Cochliopidae (Clark 2019a). *Antrorbis*, *Holsingeria*, and *Pterides* were retained in Lithoglyphidae (Clark 2019b), despite no new evidence for these designations. More recent studies of both stygobitic and spring-dwelling gastropods emphasize the need to incorporate molecular evidence in taxonomy and classification due to morphological convergence among snails adapted to these habitats (Delicado 2018; Delicado et al. 2019).

The Appalachians karst region occurs within the Appalachian Valley and Ridge (AVR) physiographic province that extends from southeastern New York to eastern Tennessee, northwestern Georgia, and northeastern Alabama in the eastern United States. The province is situated between the Blue Ridge Mountains to the east and the Appalachian Plateau (specifically the Cumberland Plateau) to the west. Karst terrain in the AVR has developed in valleys of folded and faulted shale and carbonate rocks between parallel ridges of sandstone strata. The Appalachians karst region harbors the highest stygobitic diversity in North America (Niemiller et al. 2019), including five species of hydrobioid snails: three species in the genus *Fontigens* found throughout the Greenbrier Valley of West Virginia and into southwestern Virginia (Holsinger et al. 1976; Holsinger and Culver 1988), one species in the genus *Holsingeria* found in several caves within the Clinch-Powell watershed in Lee County, Virginia, and one species in the genus *Antrorbis* endemic to a single cave system within the Coosa River watershed in DeKalb County, Alabama. No stygobitic snails have been described from the Appalachians karst region of eastern Tennessee to date; however, this region has not received the attention of cave biologists relative to other areas in the state (Niemiller and Zigler 2013) and within the Appalachians karst region of other states (e.g., Culver et al. 2003).

During ongoing cave biological inventory efforts to address the previously identified sampling gaps in the AVR of eastern Tennessee, we discovered three distinct populations of an undescribed stygobitic snail within the Tennessee River watershed of Roane and Knox counties, Tennessee. These snails resembled the Manitou Cavesnail, *Antrorbis breweri* Hershler and Thompson 1990 described from Fort Payne, Alabama, and would represent a ca. 250 km extension in the distribution of the genus (Hershler and Thompson 1990) and a second species in this monotypic genus. After assessment of shell morphology, reproductive anatomy, and molecular barcoding analyses, we describe two of these new populations (Cave Creek Cave and Eblen Cave) as the first stygobitic snail in eastern Tennessee, *Antrorbis tennesseensis* sp. nov. In addition, we tentatively classify a third population (Pedigo Cave) as *Antrorbis* cf. *tennesseensis*, reflecting the uncertainty in phylogenetic analyses despite similar morphology. Lastly, we generate a phylogeny to test the position of *Antrorbis* among other stygobitic and non-stygobitic Cochliopidae.

Materials and methods

Survey protocol and site descriptions

Since 2012, the authors have conducted more than 200 biological inventories in caves throughout the AVR in Tennessee and neighboring states (Engel et al. 2016; Niemiller et al. 2016a, b, 2017; Gladstone et al. 2018; Zigler et al. in press) to address previously identified sampling gaps (Niemiller and Zigler 2013). Biological inventories involve systematic visual encounter surveys (VES) for cave life by traversing the cave from entrance to the farthest extent of the explorable passage. Search effort includes lifting rocks and other cover, as well as searching through cobbles, detritus, and organic matter. Typically, each VES consists of 2–7 surveyors, with search effort ranging from 2–5 person-hours per cave visit and depending on the length and extent of the system. General water physiochemistry was assessed in each cave at the time of snail observation and collection using standard, handheld electrode methods for pH and conductivity (Fisher Scientific Accumet AP115 and AP75, respectively), each with temperature. Cave descriptions and location details are maintained by the Tennessee Cave Survey (TCS, <http://www.subworks.com/tcs/>) and we report only the TCS cave inventory number with the cave name. General cave locations are indicated on Fig. 1 in relation to major and minor watersheds, and summaries of the cave sites are in Table 1.

Morphological analyses

Snails to be dissected for examination of the internal anatomy were collected, relaxed using dissolved menthol in the field, then preserved in 70% ethanol. Shells were partially dissolved in 1:1 water to hydrochloric acid, with remaining shell removed by hand. Following shell removal, tissues were immersed in Bouin's solution as a staining fluid to enhance contrast of the tissues.

Table 1. Detailed site descriptions of Tennessee caves sampled in this study.

Cave name	TCS no.	County	Visitation dates	Personnel	Lithology	Cave description	Water depth	Benthic habitat	Watershed
Cave Creek Cave	TRN5	Roane	28 June 2014; 3 May 2018, 3 June 2018, 3 July 2018, 15 December 2018	1 st trip: MLN, ASE, ETC, CDR Stephen, S Engel, A Paterson, and J Carter; Later trips: NSG and EBP	Ordovician Mascot Dolomite	Ca. 135 m traversable passage with stream, discharging as a spring entrance	5 cm to 3 m at normal flow	Primarily silt and sand with interspersed gravel and cobbles	The cave stream flows into Cave Creek, which empties directly into Warts Bar Lake on the Tennessee River.
Pedigo Cave	TKN103	Knox	14 July 2018; 27 July 2018; 15 December 2018	1 st & 3 rd trip: NSG and EBP; 2 nd trip: MLN and NSG	Cambrian Maynardville Limestone	Ca. 35 m of traversable passage, with stream flow in small room near cave terminus	2-meter deep pool	Fine silt, sand, and gravel mixed with larger cobble and smooth-faced rocks	The cave is within the Melton Hill Lake watershed of the Clinch River, which flows into Warts Bar Lake and the Tennessee River.
Eblen Cave	TRN6	Roane	24 March 2019	ETC, NSG, and EBP	Copper Ridge Dolomite	1,020 m of traversable passage, with 200 m of cave stream	<0.3 m deep	Larger rocks at first ~25 m, with cobble/fine silt/sand throughout passage	The cave stream flows into Mill Creek on the surface, which is in the Clinch River watershed of the Tennessee River.

Table 2. Shell measurements of *A. tennesseensis* sp. nov. and *Antrorbis* cf. *tennesseensis*.

Specimen	Diameter	Height	Minimum Diameter	Whorls
ANSP 476793 (holotype)	1.75	0.77	1.40	3.15
ANSP A477042 (paratopotype)	1.35	0.58	1.12	3.2
ANSP A477042 (paratopotype)	1.17	0.63	0.93	2.75
ANSP A476794 (Pedigo Cave)	1.00	x	0.80	2.85
ANSP A476794 (Pedigo Cave)	1.18	x	0.97	3.2
ANSP A476794 (Pedigo Cave)	1.27	x	1.01	3.25

Shells and other hard parts were prepared, examined, and imaged at ANSP by NFS. Measurements in Table 2 were taken from the images of the specimens and cross checked using a calibrated ocular micrometer in a Zeiss Stemi 2000-C stereomicroscope. Following the dissection of individual holotype and paratype specimens, the shells, radulae, and opercula were prepared for mounting on SEM stubs by immersion in full strength bleach, followed by immersion in distilled water and finally 80% ethanol. Specimens were then mounted on SEM stubs, allowed to dry for 2 days, and sputter coated with gold using a Denton Desk II.

Specimen photographs for Figs 2A–E, 3 were taken by NFS using a Nikon DSLR at ANSP. The camera was controlled using HeliconRemote to take focus stacks of 3–15 images which were then combined in HeliconFocus. Brightness, color, contrast, and highlights were adjusted using the “Auto Levels” function in Lightroom Classic CC 2018 before cropping in Photoshop CC 2018. Scanning electron micrographs of shells, radulae, and opercula were taken using the Phenom G2 Pro desktop scanning electron microscope (SEM) at the Academy of Natural Sciences of Philadelphia, Drexel University. Photo- and micrographs were cropped and arranged into plates by NFS using Adobe Photoshop CC 2018.

Molecular analyses

Genomic DNA was isolated from three specimens from two populations (Cave Creek and Pedigo) each using the Qiagen DNeasy Blood and Tissue Kit following the manufacturer’s protocol. We amplified a 658-bp fragment of the mitochondrial cytochrome oxidase subunit 1 (CO1) locus using primers LC01490 and HC02198 (Folmer et al. 1994). PCR products were purified using ExoSAP-IT (Affymetrix) and sequenced in both directions using BigDye chemistry at Eurofins MWG Operon (Louisville, KY, USA). Forward and reverse sequences were quality trimmed at the ends and assembled into contigs in DNA Baser v4.36 (Heracle BioSoft) and aligned using MUSCLE (Edgar 2004). Sequences were not generated for specimens collected from Eblen Cave due to low sample size and were thereby not included in the phylogenetic analysis. However, given geographic proximity, geological similarity, and morphological similarity, we diagnose this population as a second population of *A. tennesseensis*. CO1 sequences generated in this study were accessioned into GenBank (MN366030–MN366035).

GenBank accession numbers for all other, previously published snail sequences used in this study are listed in Suppl. material 1: Table S1.

We generated a CO1 phylogeny using a maximum likelihood (ML) method in W-IQ-TREE (Trifinopoulos et al. 2016) and used its model-testing function to infer the best-fit substitution model for each codon partition under the corrected Akaike's Information Criterion (AICc). We implemented a general time-reversible model with corrections for a discrete gamma distribution (GTR+ Γ) for the first and second codon positions, and the same model with a proportion of invariant sites (GTR+ Γ +I) for the third codon position. Branch support was assessed with 10,000 ultrafast bootstrap replicates (Hoang et al. 2017). Prior to the generation of the phylogeny, tests for nucleotide saturation were performed in the software package DAMBE 7.2.1 using the I_{ss} index of saturation (Xia et al. 2003; Xia and Lemey 2009). These tests revealed no saturation among first and second codon positions ($I_{ss} = 0.5966$, $I_{ss,c} = 0.7385$) or third position ($I_{ss} = 0.6283$, $I_{ss,c} = 0.6343$). Lastly, due to the maximum likelihood topology showing ambiguous relationships among *Antrorbis* spp., we performed a Kishino–Hasegawa (KH) test (Kishino and Hasegawa 1989) and Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa 1999) to assess the alternative *a priori* phylogenetic hypothesis that the Cave Creek Cave and Pedigo Cave are monophyletic within *Antrorbis*. These tests were implemented in PAUP* (Swofford 2002). Alternative topology was generated as a customized Newick tree file.

Conservation assessment

We conducted IUCN Red List and NatureServe conservation assessments for *Antrorbis tennesseensis* (IUCN 2001; Master et al. 2009). We additionally include the Pedigo Cave population in these assessments, despite the ambiguous affinity of this population. Both assessments rank species into one of seven unique categories on a continuum of increasing extinction risk. Risk categories were calculated using the RAMAS Red List 3.0 (Akçakaya et al. 2007) and the NatureServe Rank Calculator v3.186 (Faber-Langendoen et al. 2012) for the IUCN Red List and NatureServe assessments, respectively. Geographic range size was calculated using two different measures for the extent of occurrence (EOO) and area of occupancy (AOO). Abundance data from all surveys were incorporated into each assessment. Additionally, we utilized the threat classification scheme proposed by Salafsky et al. (2008) to calculate an overall threat impact to this species.

Systematic account

***Antrorbis tennesseensis* Perez, Shoobs, Gladstone, & Niemiller, sp. nov.**

<http://zoobank.org/8DBE2C9C-7378-48B1-AAF8-7AD7095DEE43>

Figs 1A–F, 2A–J

Holotype. ANSP 476793 (one dry shell in vial, radula, and operculum on SEM stub), stream in Cave Creek Cave (TCS no. TRN5), Roane County, Tennessee, U.S.A.

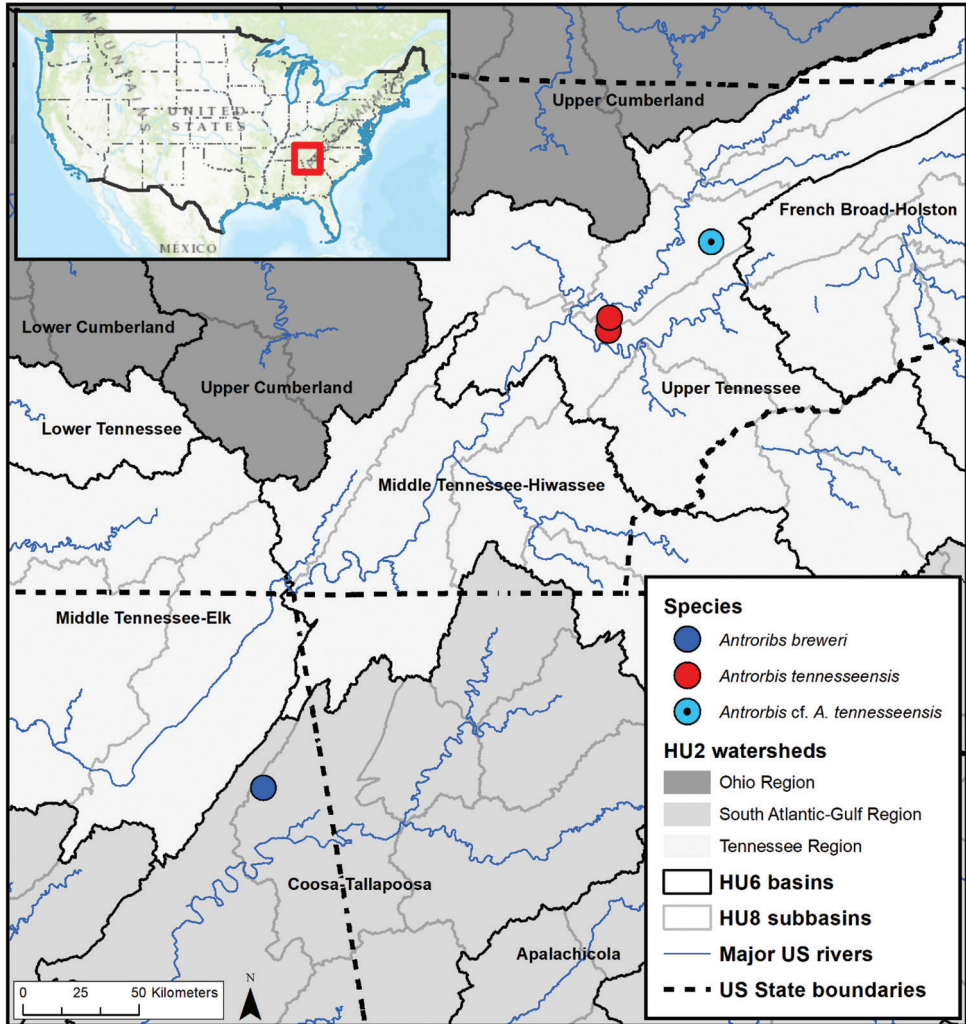


Figure 1. Distribution of *Antrorbis* spp. in relation to USGS hydrologic units: regions (HU2, shaded areas), basins (HU6, solid black lines), and subbasins (HU8, solid grey lines; unlabeled in map). *Antrorbis breweri* occurs within the Upper Coosa subbasin of the South Atlantic-Gulf region, whereas *A. tennesseensis* and *Antrorbis cf. A. tennesseensis* occurs in the Watts Bar Lake and Lower Clinch subbasins within the Upper Tennessee basin (Tennessee region), respectively.

Paratypes. ANSP A477042 (same lot as holotype, two whole wet specimens, two dissected wet specimens, one operculum on SEM stub). Three specimens (one dry shell on SEM stub, two whole wet specimens) from Eblen Cave (TCS no. TRN6), Roane County, Tennessee, U.S.A. Specimens are currently housed at the University of Alabama in Huntsville.

Other examined material. ANSP A476794 (three whole wet specimens), stream in Pedigo Cave (TCS no. TKN103), Knox County, Tennessee, U.S.A. Tentatively classified as *Antrorbis cf. tennesseensis*.

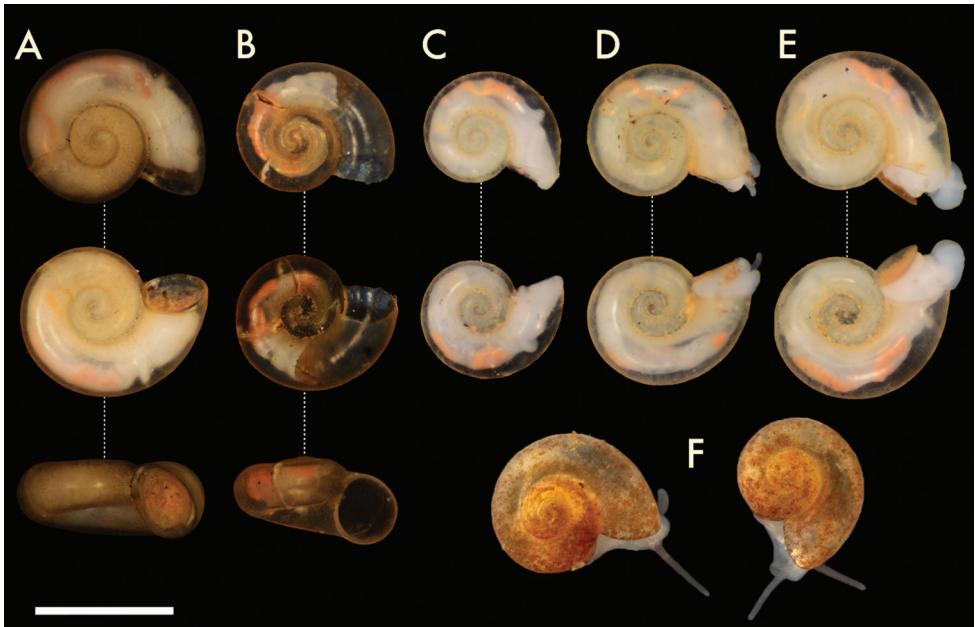


Figure 2. Paratype specimens of *Antrorbis tennesseensis* sp. nov. **A, B** Paratypes ANSP A477042 **C–E** *Antrorbis* cf. *tennesseensis*; ANSP A476794 **F** live specimens of *Antrorbis* cf. *tennesseensis* from Pedigo Cave. Scale bar: 1 mm. Photograph credits: **A–E** NFS; **F** MLN.

Morphological diagnosis. A minute, planispiral *Antrorbis*, which can be readily distinguished from its sole known congener by the absence of raised tubercles on its finely spirally striate protoconch and its unique radular formula.

Molecular diagnosis. Average uncorrected pairwise genetic distance at the mitochondrial CO1 locus between *A. tennesseensis* and *A. breweri* is 11.7%, with 74.5 ± 2.14 mutations separating the two species. Additionally, average uncorrected pairwise genetic distance at CO1 between the holotype *A. tennesseensis* and the Pedigo Cave population (*Antrorbis* cf. *tennesseensis*) is 9.8%.

Description. Shell (Figs 2A–F; 3A–C) planispiral, 1.0–1.75 mm in diameter; 0.58–0.78 mm in height, with 2.75 to 3.25 rounded and variably descending whorls marked by deeply impressed sutures. Aperture nearly circular, almost as wide as high (0.55×0.56 mm in the holotype), with an internally thickened and slightly reflected peristome. Umbilicus wide, rapidly expanding. Color pale translucent yellow, with a thick, mottled yellow-orange periostracum. Protoconch (Fig. 3C) 1.8 whorls, finely spirally striate, with the innermost striae occasionally and variably punctuated or sub-tuberculate. Spiral striae continuing into the teleoconch weakly, intersecting with similarly weak axial growth lines.

Operculum (Fig. 3D, E) paucispiral with 4.5 whorls, ovate, thin, round, externally concave and sub-conical in profile, with a fragile, tapered periphery. Inner side smooth, with retractor muscle scar variably and roughly thickened but with no peg. Outer side covered with a noticeably thick periostracum.

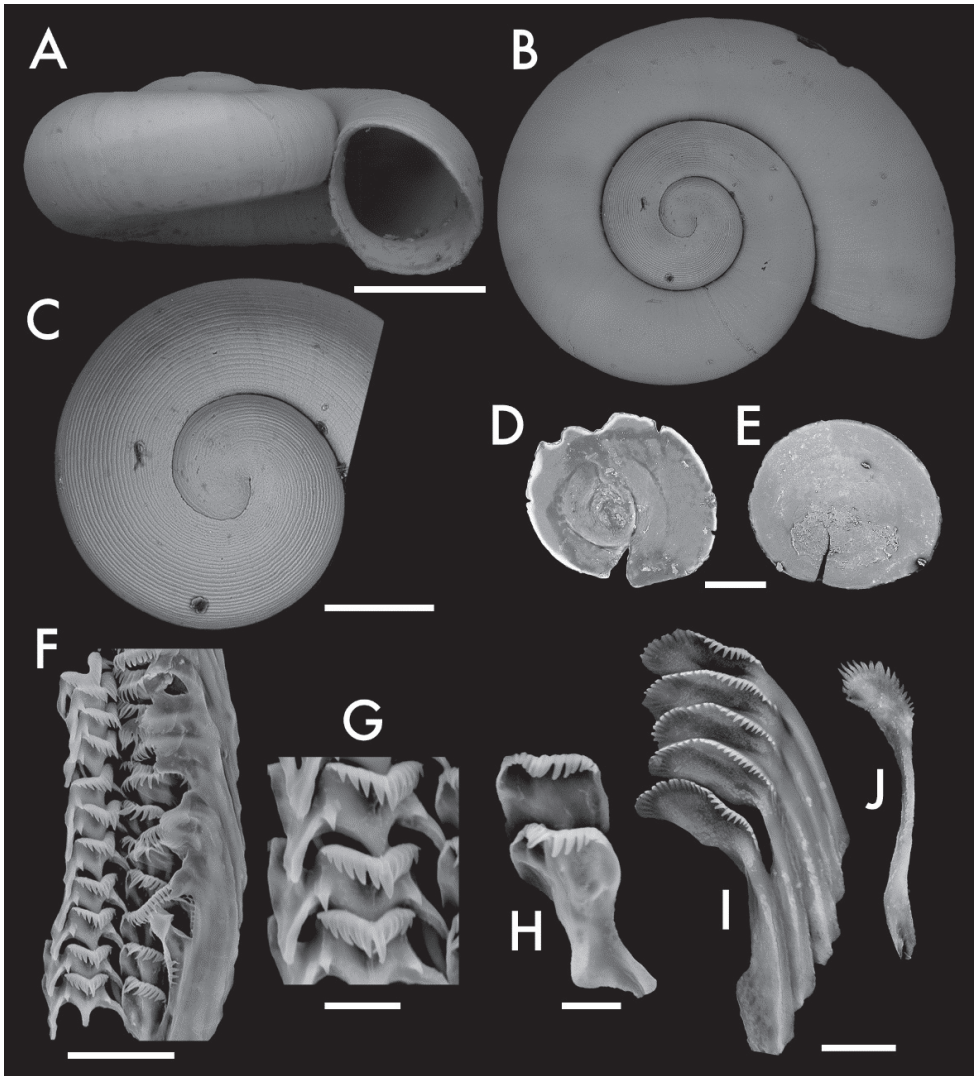


Figure 3. Shell, opercula, and radula of *Antrorbis tennesseensis* sp. nov. **A,B** Holotype, ANSP 476793 **C** protoconch of *Antrorbis* cf. *tennesseensis*, ANSP 476793 **D** operculum, outer side, ANSP A477042 **E** operculum, inner side, ANSP 476793 **F** radula of ANSP 476793 **G** central teeth, ANSP 476793 **H** lateral teeth, ANSP 476793 **I** inner marginal teeth, ANSP 476793 **J** outer marginal teeth, ANSP 476793 Scale bars: 0.5 mm (**A**, **B**); 200 μ m (**C**); 200 μ m (**D**, **E**); 20 μ m (**F**); 5 μ m (**G**); 5 μ m (**H**); 10 μ m (**I**, **J**). Photograph credits: NFS.

Radula (Fig. 3F–J) as in its congener *A. breweri*, but differing slightly in the number of cusps on each tooth: central teeth with 11–13 cusps (5-6+1+5-6) and two basal cusps, laterals with 6–8 cusps on the outer side and 5–6 on the inner side, inner marginals with 26–30 cusps, outer marginals with 19–21 cusps. Data from ANSP 476793, the holotype.

Animal soft body is absent of pigment except for scattered clumps of black granules on stomach and digestive gland; intestine with orange, oval fecal pellets extends

from terminal end of animal through body whorl. Digestive system anatomy similar to that described for *A. breweri*, including intestinal coil in anterior pallial roof exhibiting “reversed-S-shape.” Digestive gland extends for ~1 whorl. Penis simple, strap-like, tapers to a blunt distal end, not as sharply tapered as in *A. breweri*. Neither terminal papillae nor specialized penial glands observed. Testis one mass with no lobes. Seminal vesicle short and uncoiled, attaching at end of testis. Ovary an orangish mass, filling ~less than 25% of one whorl, capsule gland and albumen gland approximately equal in size, both underly and posterior to the intestine, bursa copulatrix pear shaped. Shells of individuals from Cave Creek Cave are somewhat thicker than those from Pedigo Cave and the fecal pellets are larger and more ovate in shape.

Etymology. The specific epithet *tennesseensis* is in reference to this species being from the state of Tennessee. It is also a reference to the University of Tennessee in Knoxville, where several of the authors received degrees (MLN, NSG, and ETC) or are faculty (ASE). Suggested common name is Tennessee Cavesnail.

Distribution. *Antrorbis tennesseensis* is known only from two caves developed within karst valleys near the confluence of the Clinch and Tennessee rivers and in upper Cambrian to lower Ordovician carbonate rocks of the Knox Group of the AVR of eastern Tennessee (Fig. 1). Cave Creek Cave and Eblen Cave are only 6 km apart from each other on opposite sides of a surface watershed divide, but cave passages could be hydrologically connected. In contrast, Pedigo Cave (*Antrorbis* cf. *tennesseensis*) is located to the northeast in northern Knox County. There could be additional caves with *A. tennesseensis* within the immediate karst area, but the potential for a significantly wider distribution for *A. tennesseensis* throughout eastern Tennessee is low due to the generally restrictive nature of folded and faulted nature of the karstified strata.

Ecology. Snails are largely found amongst cobble in shallow cave streams in the dark zone. At Cave Creek Cave, several snails could be observed on a single cobble, and *Caecidotea* spp. and *Crangonyx* spp. amphipods were found on the same rocks as snails. From Pedigo Cave (*Antrorbis* cf. *tennesseensis*), a single small crayfish (*Cambarus bartonii*) was observed, but no other aquatic species were seen in the cave stream. Several snails were also found in close proximity on the same rock, with up to seven individuals on a single rock. No other fauna was found in Eblen Cave, and no egg masses or other aspects of the reproductive biology of *A. tennesseensis* have been observed from any of the caves. Although annual physicochemical measurements were not acquired in this study, the parameters measured once from each system (Table 3) were similar and within the expected conditions for water flowing through carbonate rocks.

Habitat. *Antrorbis tennesseensis* has been observed on the sides and undersurface of larger cobble and flat rocks in shallow water (< 12 cm water depth) of the stream in Cave Creek Cave and more than one meter of water depth in Pedigo Cave (*Antrorbis* cf. *tennesseensis*). At Cave Creek Cave, *A. tennesseensis* has been found only from a small (55 m²) area ca. 40 m from the entrance (Fig. 4A). Snails had higher abundances among small cobble substrate and larger rocks in the cave stream near the stream bank (i.e., within 0.6 m), with an average flow rate of 0.34 m/s and depth below 8 cm. At Pedigo Cave, *Antrorbis* cf. *tennesseensis* were found throughout the cave stream, and spe-

Table 3. Examples of physicochemical measurements from each cave.

Cave	Sampling date	Temperature (°C)	pH	Specific conductance (μS/cm)
Cave Creek Cave	3 February 2019	14.5	6.95	253.6
Eblen Cave	24 March 2019	12.0	7.45	285.1
Pedigo Cave	27 January 2019	14.1	6.74	282.4

**Figure 4.** **A** Cave Creek Cave. Bottom **B** Pedigo Cave **C** Eblen Cave (NSG and ETC). Photograph credits: **A, B** NSG **C** EBP.

cifically in a riffle with several flat rocks and cobbles ca. 30 m from the entrance. They were also found in deeper pools under larger rocks (Fig. 4B). At Eblen Cave, only three snails were found within the primary stream passage accessible in the right fork ca. 100 m from the cave entrance. All snails were found on larger rocks semi-submerged in silt-bottom substrate, which was the primary substrate at the beginning of the stream.

Phylogenetic relationships. The resulting CO1 gene topology of the ML phylogeny is shown in Fig. 5. The genus *Antrorbis* clusters with the stygobitic Cochliopidae along with the recently reassigned *Phreatodrobia* (Clark 2019a) and the genus *Holsingeria*. The holotype population of *A. tennesseensis* forms a clade with *A. breweri* population, but forms a paraphyletic group with the morphologically similar Pedigo Cave population (*Antrorbis* cf. *tennesseensis*) in the maximum likelihood phylogeny. However, results of the KH and SH tests fail to reject the *a priori* topology of monophyly ($P > 0.05$ for both tests).

Conservation assessment. This species is currently only known from two caves that are within geologically and hydrologically restricted strata. However, the third cave population for *Antrorbis* cf. *tennesseensis* was incorporated in these analyses. The NatureServe rank calculated for *Antrorbis tennesseensis* is Critically Imperiled (G1).

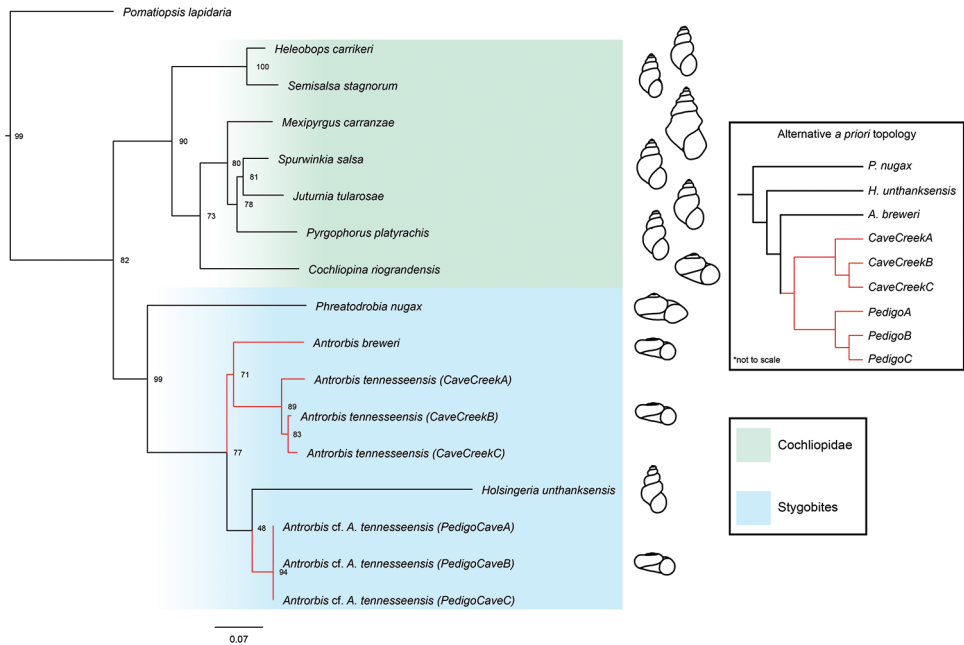


Figure 5. Maximum-likelihood phylogeny of four families within the Cochliopidae. Phylogeny is inferred by W-IQ-TREE based on mitochondrial CO1 sequences (658 bp aligned). Ultrafast bootstrap support values shown at nodes.

For the IUCN Red List assessment, *A. tennesseensis* was assessed as Endangered (EN) B1a, as the species is known from fewer than five sites and has an EOO <5,000 km². The AOO was calculated as 12.0 km² and EOO was 73.3 km². A maximum of 23 (on 3 June 2018), 54 (on 15 December 2018), and 3 individuals (on 24 March 2019) were observed at Cave Creek, Pedigo, and Eblen Caves, respectively. Mean number of snails observed at Cave Creek Cave and Pedigo Cave (for which multiple surveys were conducted) was 18.4 ± 4.3 and 36 ± 7.8 , respectively. Overall, threat impact for this species was calculated as Very High, with the two most outstanding categories of the threat assessment being Human Intrusion and Disturbance and Pollution.

Discussion

We describe a new species of stygobitic snail, *Antrorbis tennesseensis*, which is distinguished from its only congener *A. breweri* by the absence of raised tubercles on the spiral striae on the external protoconch and substantial divergence at the mitochondrial CO1 locus (holotype, Cave Creek Cave). Given the geographic proximity, geological similarity, and identical morphology, we additionally diagnose the Eblen Cave population as a second population of *A. tennesseensis*. *Antrorbis tennesseensis* and *A. breweri* form a modestly supported clade in the ML phylogeny. Individuals from the third pop-

ulation discovered in this region (Pedigo Cave), despite being morphologically similar to *A. tennesseensis*, form a paraphyletic group with *A. tennesseensis* in the ML phylogeny. In the ML phylogeny, the Pedigo Cave population shows closer genetic similarity to *Holsingeria unthankensis*, another stygobitic snail in the northern AVR that was initially thought to form a clade with *Antrorbis* due to morphological similarity (Hershler and Holsinger 1990). However, this relationship is not a strong one and given the failure to reject alternative topologies by both the KH and SH tests, we tentatively classify this third population as *Antrorbis* cf. *tennesseensis* and encourage subsequent molecular study to understand the identity of this population and the systematics of the stygobitic group. A plausible explanation may be that *Antrorbis* and *Holsingeria* are more closely related than previously understood, despite their disparate morphologies.

Within the superfamily Truncatelloidea, observing paraphyly and high intraspecific divergence among species within other gastropod families (especially subterranean groups) is common when analyzing mitochondrial genes (Wilke et al. 2013; Whelan and Strong 2016; Gladstone et al. 2019). As a result, we cautiously provide these molecular results as only one of several lines of evidence for the species designation of *A. tennesseensis* and advise for the incorporation of additional genetic data in the future. Currently, our robust morphological diagnoses provide ample distinctions between *A. breweri* and *A. tennesseensis*, in addition to their contrasting geography and ecology.

These two *Antrorbis* species are separated by ca. 250 km and occur in caves developed in different strata and in different major hydrological river basins, as *A. tennesseensis* is distributed within the Tennessee River watershed, which flows into the Ohio River, and *A. breweri* is from Manitou Cave in the Coosa River watershed that flows directly into the Gulf of Mexico. However, from the Eocene (55 million years ago) through the mid-Miocene, the ancestral Appalachian River occupied the drainage basins of the Tennessee and Coosa river and flowed through the southern AVR, across Alabama, and emptied into Mobile Bay at the Gulf of Mexico (Milici 1968; Galloway et al. 2011; Hoagstrom et al. 2013). Cave sediment records in Tennessee (Anthony and Granger 2007) and distinct changes in Gulf of Mexico delta sedimentation histories for the Mississippi and Coosa rivers in the mid-Miocene to late Pliocene point to major redistribution of the watersheds (Galloway et al. 2011). The modern drainage divide between the Tennessee and Coosa rivers occurs in northern Alabama, near the location of Manitou Cave. Although the timing of Tennessee-Coosa river divide development is not well understood, a number of processes likely contributed to the separation of the two rivers, including uplift of the southern Appalachian Mountains and subsequent incision of local streams (Gallen et al. 2013), stream downcutting to accommodate rapid base-level drops due to widespread glaciation in the northern hemisphere, and stream piracy through Walden Ridge on the edge of the Cumberland Plateau and into the karstified Sequatchie Valley in Tennessee (Johnson 1905; Clark 1989; Self 2000).

Based on the modern distribution of *Antrorbis*, the common ancestor for the two currently known species must pre-date the late Pliocene emergence of the Tennessee-Coosa drainage divide. Similar timing for the isolation of distinct genetic

lineages of the Southern Cavefish, *Typhlichthys subterraneus*, in the Tennessee and Coosa river drainages has also been proposed (Niemiller et al. 2016a). Considering the widespread modern distribution of the genus, and possible paleogeographic explanation for its distribution, it is possible that other *Antrorbis* species currently exist in caves within the modern Tennessee-Coosa river basins. It is also possible that the distinct modern cave populations of *A. breweri* in Alabama and *A. tennesseensis* in Tennessee are relict populations of a much more regionally widespread genus. In the future, evidence of their distribution and for the timing for Tennessee-Coosa river divide development could come from paleontological investigations of cave sediments with dateable material (e.g., organic matter, shell material), which could include the snails themselves.

Implications for classification

Original designation of the stygobitic genera *Antrorbis*, *Holsingeria*, and *Phreatodrobia* to Lithoglyphidae was based on soft tissue anatomy (Hershler and Thompson 1990), which was also supported by their similar morphology and subterranean ecology (Hershler and Holsinger 1990). The addition of molecular data has drastically revised our understanding of relationships among the hydrobioid lineages. The most recent molecular treatment (Wilke et al. 2013) supports the division of the former Hydrobiidae into several smaller families. The results of our phylogeny show high support for this stygobitic clade among other members of the Cochliopidae from the Wilke et al. (2013) analysis. As such, we tentatively place the genus *Antrorbis* in the family Cochliopidae.

Conservation implications

Freshwater snails have experienced significant declines globally, with nearly 93% of all recorded extinctions being narrow endemic species (Lydeard et al. 2004; Johnson et al. 2013). Many stygobitic taxa exhibit high levels of endemism, with notable sensitivity to environmental alteration (Culver and Pipan 2009; Niemiller and Ziegler 2013). There are many unique threats to subterranean environments and their associated taxa, with the conversion of the surface landcover for urban development and agriculture being most prominent (Culver and Pipan 2009). Populations of *A. tennesseensis* are found near roadways and suburban neighborhoods, and, therefore, may be at an increased risk of extirpation due to sedimentation, changes in local hydrology, and chemical effluent runoff into their cave streams. Further, despite occurring on private lands, these caves experience frequent visitation from recreational cavers. Vehicles can often be seen in proximity to Cave Creek Cave, and an array of plastics, scrap metals, and other waste materials can be found in each of the cave systems. Future consideration should be given for more deliberate protection and conservation of *A. tennesseensis*.

Acknowledgments

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Supplementary material I

Table S1. GenBank accession numbers for all taxa utilized for the phylogenetic analysis

Authors: Nicholas S. Gladstone, Kathryn E. Perez, Evelyn B. Pieper, Evin T. Carter, Katherine E. Dooley, Nathaniel F. Shoobs, Annette S. Engel, Matthew L. Niemiller
Data type: species data

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Link: <https://doi.org/10.3897/zookeys.898.46917.suppl1>

Review of the millipede genus *Orthomorpha* Bollman, 1893 (Diplopoda, Polydesmida, Paradoxosomatidae) in Vietnam, with several new records and descriptions of two new species

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Abstract

The genus *Orthomorpha* is shown to currently be represented in Vietnam by ten species or varieties, including new records of *O. arboricola* (Attems, 1937), *O. coarctata* (de Saussure, 1860), *O. rotundicollis* (Attems, 1937) and *O. scabra* Jeekel, 1964, and two new species, *O. caramel* **sp. nov.** and *O. vietnamica* **sp. nov.** A key to all eight *Orthomorpha* species and two varieties known to occur in Vietnam is provided. Although the morphological characters that have been traditionally used for *Orthomorpha* taxonomy are here considered superior to molecular ones, molecular-based phylogenetic relationships and taxon assignments within the tribe Orthomorphini are provisionally analyzed using fragments of the cytochrome c oxidase subunit I (COI) mitochondrial gene. The preferred phylograms, both rooted and unrooted, demonstrate the monophyly of the tribe Orthomorphini, but due to the special, uncertain or even controversial position of *O. coarctata*, which occurs closer to the genera *Antheromorpha* and *Hylomus*, the genus *Orthomorpha* in current usage appears to be polyphyletic. However, if *O. coarctata* is to be treated within the monotypic genus *Asiomorpha*, the monophyly of *Orthomorpha* becomes manifest. On the other hand,

a cautious approach is followed to avoid descriptions of suspicious new taxa/species. Thus, solely because the average genetic distance between *O. rodundicollis subrotundicollis* **var. nov.** and *O. rodundicollis*, as well as that between *O. scabra grandis* **var. nov.** and *O. scabra*, are both found to be negligibly small, the statuses of the sympatric and closest yet morphologically different varieties are treated only as such, i.e., infrasub-specific categories. The apparent discord observed between morphological and molecular data is obviously due to only partial and single-gene topologies used, possibly also to hybridization already known to occur in some closely related and sympatric paradoxosomatid species or even genera.

Keywords

taxonomy, variety, barcoding, phylogeny, key, map

Introduction

The Southeast Asian millipede genus *Orthomorpha* Bollman, 1893 is the largest in the tribe Orthomorphini, family Paradoxosomatidae (Nguyen and Sierwald 2013). This genus has recently been reviewed and shown to comprise as many as 54 species ranging from northern Myanmar and Thailand in the northwest to Lombok Island, Indonesia in the southeast (Likhitrakarn et al. 2011, 2014). Only one species, *O. coarctata* (de Saussure, 1860), has attained a pantropical distribution due to anthropochory.

Only six recognized species of *Orthomorpha* have hitherto been known to occur in Vietnam. Among them, *O. hydrobiologica* (Attems, 1937), *O. rotundicollis* (Attems, 1937), and *O. scabra* Jeekel, 1964 are widespread also in Laos and Cambodia (Likhitrakarn et al. 2011, 2013, 2014).

This paper is devoted to descriptions of two new species from southern Vietnam, based on the material collected by one of us (IS) in the Cat Tien, Kon Ka Kinh, Hon Ba and Bidoup Nui Ba national parks, all being priority zones for the protection of biodiversity in Vietnam (e.g., Polet and Ling 2004). In addition, we provide new records of three previously described species and a key to all eight Vietnamese species of the genus, with their distributions mapped.

Molecular analyses were performed to obtain a phylogram in order to visualize the phylogenetic relationships. The topology from MrBayes was consistent with the present-day morphology-based taxonomy/classification of the tribe Orthomorphini (Nguyen and Sierwald 2013).

Materials and methods

The specimens were collected as part of IS' research project on the diversity, biology and ecology of millipedes in Vietnam. Field-work by IS, including material collection, was conducted in accordance with Agreement 37/HD for the scientific cooperation between the Cat Tien National Park and the Joint Russian-Vietnamese Tropical Center; that in the Kon Ka Kinh National Park according to Agreements 432/TCLN-BTTN and 142/SNgV-VP; and that in the Bidoup Nui Ba National Park and Hon Ba

Nature Reserve according to Agreement 774/TCLN-DDPH. The Animal Care and Use Protocol Review No. 1723018 was strictly followed. Coordinates and elevations were recorded by Garmin eTrex 30 using the WGS84 datum and subsequently double-checked with Google Earth.

Live animals were photographed in their habitats using a Canon PowerShot A4000IS 16.0 MP Digital Camera and Panasonic DMC-TZ80 – LUMIX Digital Camera. Specimens were preserved in 96% ethanol, and morphological characters were studied in the laboratory using an Olympus stereo microscope. Scanning electron micrographs (SEM) of coated gonopod specimens were taken using a JEOL, JSM–5410 LV microscope. Specimens were also photographed in the laboratory as digital images assembly using automontage software techniques, while gonopods were also illustrated. All material, including the holotypes and voucher specimens for molecular analyses, is housed in the collection of the Zoological Museum, State University of Moscow (ZMUM), Russia.

In the catalogue sections, D stands for the original description, subsequent descriptive notes or appearance in a key, R for a subsequent record or records, N for giving a new name while M for a mere mention and Di stands for genetic distances in the molecular analyses.

DNA was isolated from specimens fixed in 96% ethanol using QiaAMP DNA Mini Kit (Qiagen). Sequences of the cytochrome oxidase subunit I (COI) gene were amplified using an EncycloPlus PCR kit (Evrogen, Russia) with the primer set COI-1F20 (5'-ACT CTA CTA ATC ATA AGG AT-3') and COI-1R19 (5'-TAA ACC TCC GGG TGA CCAA-3') derived from Nguyen et al. (2017). Polymerase chain reaction (PCR) products were visualized with the help of gel electrophoresis, excised, and cleaned using a SV Gel and PCR CleanUp System kit (Evrogen, Russia). The sequences were combined and aligned using ClustalX software after the addition of sequences from the GenBank (Thompson et al. 1997). MEGA 6.06 (Tamura et al. 2013) was used to calculate the genetic distances between samples. Of the trees in the post burn-in posterior distribution inferred with MrBayes version 3.2.3, a consensus tree was constructed using sumt (Huelsenbeck and Ronquist 2001). The MrBayes analysis was conducted in the CIPRES server with the evolutionary model selected based on the results of the analysis in jModelTest2 (Darriba et al. 2015). The sequences have been deposited in NCBI GenBank (Table 1). Unfortunately, as there were fixation problems with the DNA, only around a third of the COI gene became available for analyses.

Table 1. Species voucher repository and accession numbers deposited in GenBank.

Nº	Species	Location	COI sequences numbers	Voucher repository
1	<i>Orthomorpha coarctata</i>	Thac Mai	MC762236	ZMUM
2	<i>Orthomorpha rotundicollis</i> var. <i>subrotundicollis</i>	Kon Ka Kinh	MC762237	ZMUM Rd 4210
3	<i>Orthomorpha rotundicollis</i>	Thac Mai	MC762238	ZMUM Rd 4215
4	<i>Orthomorpha rotundicollis</i>	Cat Tien	MC762239	ZMUM
5	<i>Orthomorpha caramel</i>	Kon Ka Kinh	MC762240	ZMUM Rd 4198
6	<i>Orthomorpha vietnamica</i>	Kon Ka Kinh	MC762241	ZMUM Rd 4199
7	<i>Orthomorpha scabra</i>	Kon Ka Kinh	MC762242	ZMUM Rd 4213
8	<i>Orthomorpha scabra</i> var. <i>grandis</i>	Bidoup Nui Ba	MC762243	ZMUM Rd 4267
9	<i>Orthomorpha arboricola</i>	Hon Ba	MC762244	ZMUM

Taxonomic part

Family Paradoxosomatidae Daday, 1889

Tribe Orthomorphini Brölemann, 1916

Genus *Orthomorpha* Bollman, 1893

Orthomorpha arboricola (Attems, 1937)

Figs 1, 2

Pratinus arboricola Attems, 1937: 120 (D).

Pratinus arboricola – Attems 1938: 222 (D).

Orthomorpha arboricola – Jeekel 1963: 265 (M); 1964: 361 (M, D); 1968: 56 (M); Enghoff et al. 2004: 38 (M); Golovatch 1998: 42 (D); Likhitrakarn et al. 2011: 18 (D).

Old records. Vietnam, Lamdong Province, Dalat, 1,500 m a.s.l.; Lamdong Province, Langbian Mountain, Tràm Hành (= Arbret-Broyé) (Attems 1937, 1938).

New material examined. 2 ♂ (ZMUM), Vietnam, Khanh Hoa Province, Hon Ba Nature Reserve, 12°07'02"N, 108°56'45"E, 1,550 m a.s.l., mixed mossy forest on mountain ridge, on forest floor, night time, 27.VI.2018, I. Semenyuk leg.

Descriptive notes. Length 40–41 mm (♂), width of midbody pro- and metazonae 2.7–2.8 and 4.3–4.4 mm (♂), respectively.

Live colouration (Fig. 1A) and colouration in alcohol, after one year of preservation, similar, only slightly faded in fixed material, yellow-brown to brown (Fig. 1B–F), paraterga, most of mid-dorsal parts of metaterga and tip of epiproct orange-yellow to light yellow, legs and sterna light dark brown to light yellowish, antennae blackish (Fig. 1A, B).

All characters as in the available descriptions (Attems 1937; Likhitrakarn et al. 2011), except as follows. Posterior (postsulcus) transverse row of 3(4)+3(4) low, setigerous, oblong, rounded tubercles on postcollum metaterga. A prominent, tongue-shaped, rounded, setose cone or lobe between ♂ coxae 4 (Fig. 1I, J). Pleurosternal carinae complete crests only on segments 2–4 (♂) (Fig. 1B, D), each with an evident sharp denticle caudally, thereafter increasingly reduced until segment 11. Solenophore tip very faintly bidentate, with terminal tooth bearing a minute denticle at base (Fig. 2); solenomere long and flagelliform, as usual in the genus.

Remarks. This species is known not only from type material from southern Vietnam (Dalat and Peak Lang Biang, at both sites found to coexist with *O. rotundicollis* (Attems, 1937)), but also from the new samples cited above. The types have recently been redescribed by Likhitrakarn et al. (2011), while the above new material shows only minor variations.

Orthomorpha coarctata (de Saussure, 1860)

Polydesmus coarctatus de Saussure, 1860: 297 (D).

Paradesmus flavocarinatus Daday, 1889: 136 (D). Synonymized by Enghoff (2005).

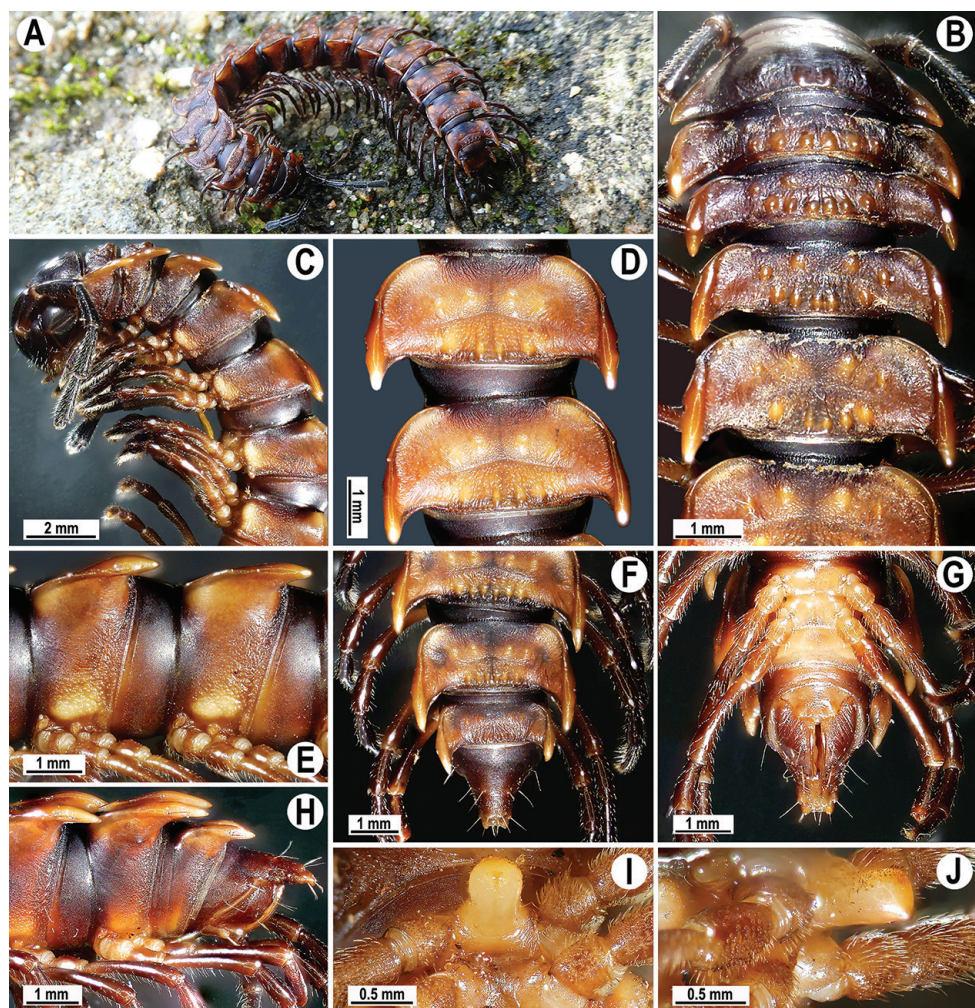


Figure 1. *Orthomorpha arboricola* (Attems, 1937), ♂ from Hon Ba National Park **A** habitus and live colouration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cone between coxae 4, subcaudal and sublateral views, respectively.

Orthomorpha coarctata – Pocock 1895: 809 (R, M, K); Attems 1937: 62 (D); Jeekel 1968: 45 (M); Likhitrakarn et al. 2011: 12 (D, R, K), Golovatch and Wesener 2016: 47 (L); et auctorum.

Orthomorpha coarctata gigas Attems, 1927: 63 (D). Synonymized by Jeekel (1968).

Asiomorpha coarctata – Verhoeff 1939: 117 (D); Nguyen and Sierwald 2013: 1236 (L); et auctorum.

Orthomorpha coarctata gigas – Jeekel 1968: 45 (M); Golovatch 1998: 43 (K); et auctorum.

New material examined. 3 ♂, 1 ♀, 2 juv. (ZMUM), Vietnam, Dong Nai Province, Cat Tien National Park, 11°25'16"N, 107°25'39"E, 120 m a.s.l., on floor between

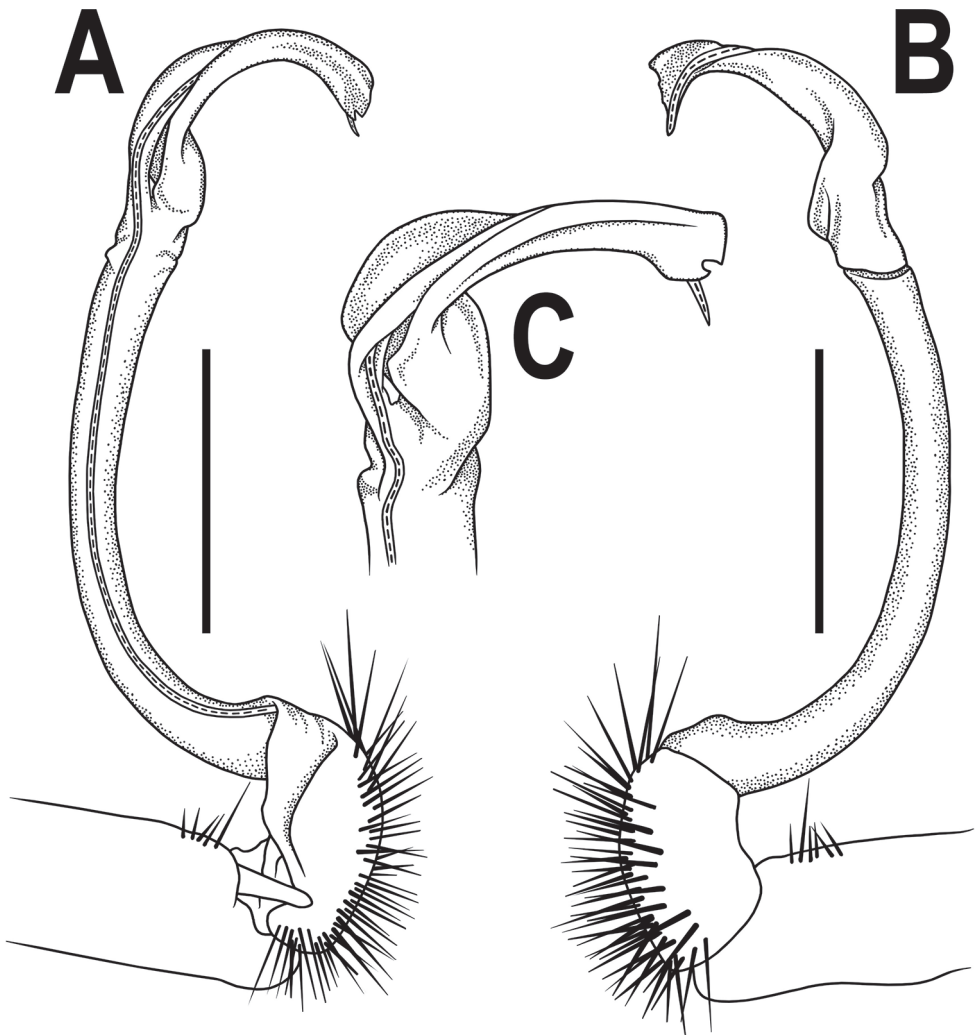


Figure 2. *Orthomorpha arboricola* (Attems, 1937), left gonopod **A**, **B** mesal and lateral views, respectively **C** tip of right gonopod, lateral view. Scale bars: 0.5 mm.

huts in the Park's headquarters, an open site in monsoon tropical forest, night time, 5 & 8.VIII.2015; 3 ♂, 2 ♀ (ZMUM), Vietnam, Dong Nai Province, Thac Mai waterfall and hot spring area, 11°06'12"N, 107°24'24"E, grassy recreation area near pond, in leaf litter, daytime, 01.06.2018, all I. Semenyuk leg.

Remarks. This pantropical anthropochore species has been redescribed several times and recently revised (Likhitrakarn et al. 2011). It is often assigned to the monotypic genus *Asiomorpha* Verhoeff, 1939 (e.g., Nguyen and Sierwald 2013), but we follow Jeekel (1968) who treated it in *Orthomorpha*. Molecular evidence, however, shows a very strong genetic isolation of *coarctata* from the other formal congeners,

thus favouring the recognition of *Asiomorpha* as a separate monobasic genus (Fig 20). This species has already been recorded from Vietnam, on sea shore north of Nhatrang (Golovatch 2017).

The new samples belong to the typical form of *O. coarctata*, whereas the only other form, *O. c. gigas* Attems, 1927, from Ambon, Indonesia, has long been synonymized under *O. c. coarctata* (see Jeekel 1968; Likhitrakarn et al. 2011).

***Orthomorpha glandulosa* (Attems, 1937)**

Pratinus glandulosus Attems, 1937: 119 (D).

Pratinus glandulosus – Attems 1938: 220 (D).

Orthomorpha glandulosa – Jeekel 1963: 265 (M); 1964: 361 (M, D); 1968: 56 (M); Hoffman 1977: 700 (M); Golovatch 1998: 42 (D, M); Enghoff et al. 2004: 38 (M, R); Likhitrakarn et al. 2011: 72 (D).

Old records. Vietnam, Dak Lak Province, near frontier with Cambodia; Khanh Hoa Province, Nhatrang, Suoidau; same Province, Hon Ba Mountain (Attems 1937, 1938).

Remarks. This species has recently been redescribed, based only on the type material (Likhitrakarn et al. 2011).

***Orthomorpha hydrobiologica* Attems, 1930**

Orthomorpha hydrobiologica Attems, 1930: 120 (D).

Orthomorpha hydrobiologica – Attems 1937: 63 (D); 1938: 215 (R); Jeekel 1963: 265 (M); 1964: 361 (M, D); 1968: 45 (M); Hoffman 1973: 362 (M); 1977: 700 (M); Golovatch 1998: 42 (M); Enghoff et al. 2004: 38 (R); Likhitrakarn et al. 2011: 53 (D); 2015: 181 (R).

Oxidus hydrobiologicus – Chamberlin 1945: 10 (R).

Old records. Vietnam, Quang Ninh Province, Hong Gai; Khanh Hoa Province, Nha Trang; Cau Da; Ba Ngoi; Ninh Thuan Province, Phan Rang; Binh Phuoc Province, Loc Ninh; Dak Lak Province, near frontier with Cambodia; Kien Giang Province, Poulo Dama (Phu Quoc Island) (Attems 1938); Cambodia, Sihanoukville Province, Ream; Kampot Province, Phnom Bokor (Attems 1938); Indonesia, East Java Province, Lumajang Regency, shore of Ranu (= lake) Bedali (Attems 1930); West Java, Mt Pangrango; Krakatau; Karimon Djawa Island (Chamberlin 1945).

Remarks. This species has recently been redescribed (Likhitrakarn et al. 2011), based both on type and non-type material. The species is widespread, probably due to anthropochory, especially along the coastal areas ranging from northern Vietnam down to southern Cambodia.

***Orthomorpha rotundicollis* (Attems, 1937)**

Figs 3–5

Pratinus rotundicollis Attems, 1937: 118 (D).*Pratinus rotundicollis* – Attems 1938: 217 (D); 1953: 179 (R).*Pratinus tuberculatus* Attems, 1937: 119 (D). Synonymized by Likhitrakarn et al. (2011).*Pratinus tuberculatus* – Attems 1938: 219 (D).*Orthomorpha rotundicollis* – Jeekel 1963: 265 (M); 1964: 361 (M, D); 1968: 56 (M);

Hoffman 1973: 363 (M); 1977: 700 (M); Golovatch 1998: 42 (M, D); Enghoff et al. 2004: 38 (M, R); Likhitrakarn et al. 2011: 61 (D).

Orthomorpha tuberculata – Jeekel 1963: 265 (M); 1964: 361 (M, D); 1968: 56 (M); Hoffman 1977: 700 (M); Golovatch 1998: 42 (M, D); Enghoff et al. 2004: 39 (M, R).

Old records. Vietnam, Lam Dong Province, Lang Biang Mountain, Tram Hanh (=Arbre-Broye), 1,500 m; Dalat, 1,500 (Attems 1937, 1938); Laos, Xiangkhoang Province, Xiangkhoang Plateau, Xiang Kuang (Attems 1953).

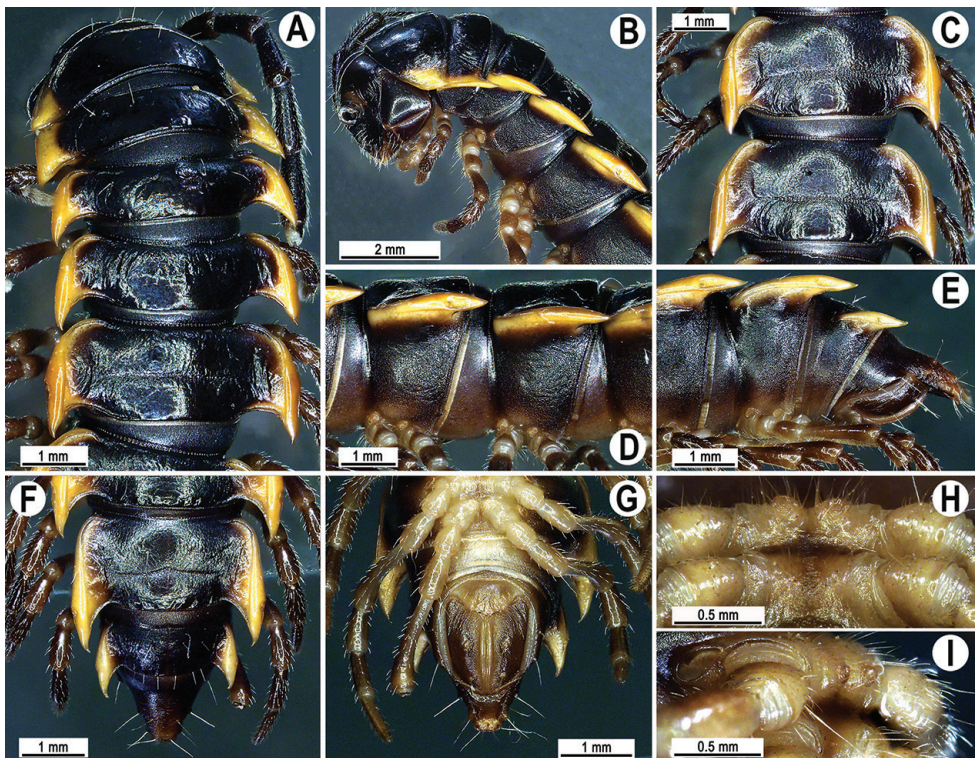


Figure 3. *Orthomorpha rotundicollis* (Attems, 1937), ♂ from Cat Tien National Park **A, B** anterior part of body, dorsal and lateral views, respectively **C, D** segments 10 and 11, dorsal and lateral views, respectively **E–G** posterior part of body, lateral, dorsal and ventral views, respectively **H, I** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

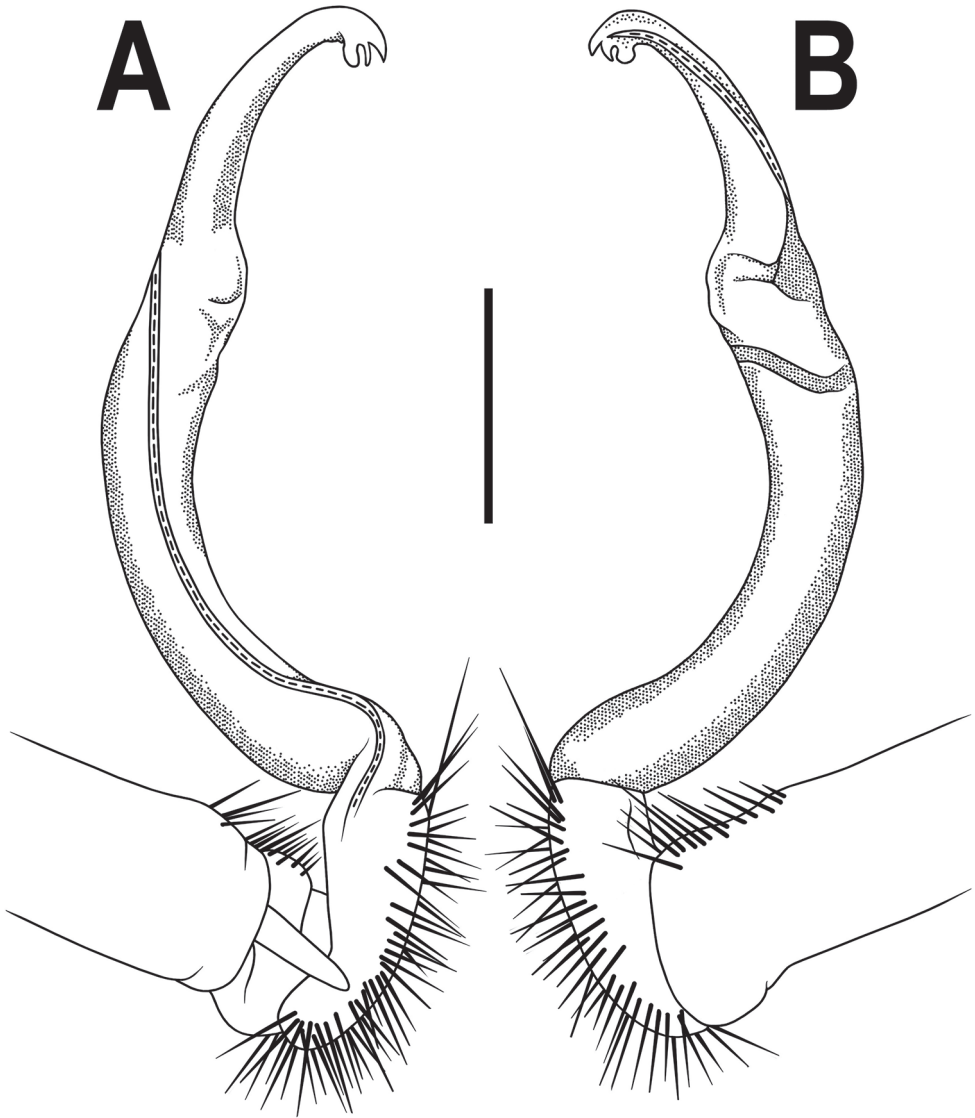


Figure 4. *Orthomorpha rotundicollis* (Attems, 1937), left gonopod **A, B** mesal and lateral views, respectively. Scale bar: 0.5 mm.

New material examined. 1 ♂ (yellow morph, ZMUM Rd 4215), Vietnam, Dong Nai Province, Cat Tien National Park, 11°25'37"N, 107°25'39"E, 140 m a.s.l., low-land monsoon tropical forest with dominating *Lagerstroemia calyculata* and *Azelia xylocarpa*, on bush, daytime, 7.X.2016; 1 ♂ (yellow morph, ZMUM Rd 4217), same locality, under log, daytime, 6.V.2015; 1 ♂ (red morph, ZMUM Rd 4218), same locality, on forest floor, daytime, 10.V.2015; 1 ♂ (red morph, ZMUM Rd 4221), same locality, on bush, daytime, 3.VI.2015; 1 ♂ (red morph, ZMUM Rd 4222), same locality, on tree trunk, night time, 29.06.2015; 1 ♂ (red morph, ZMUM), same locality, hilly

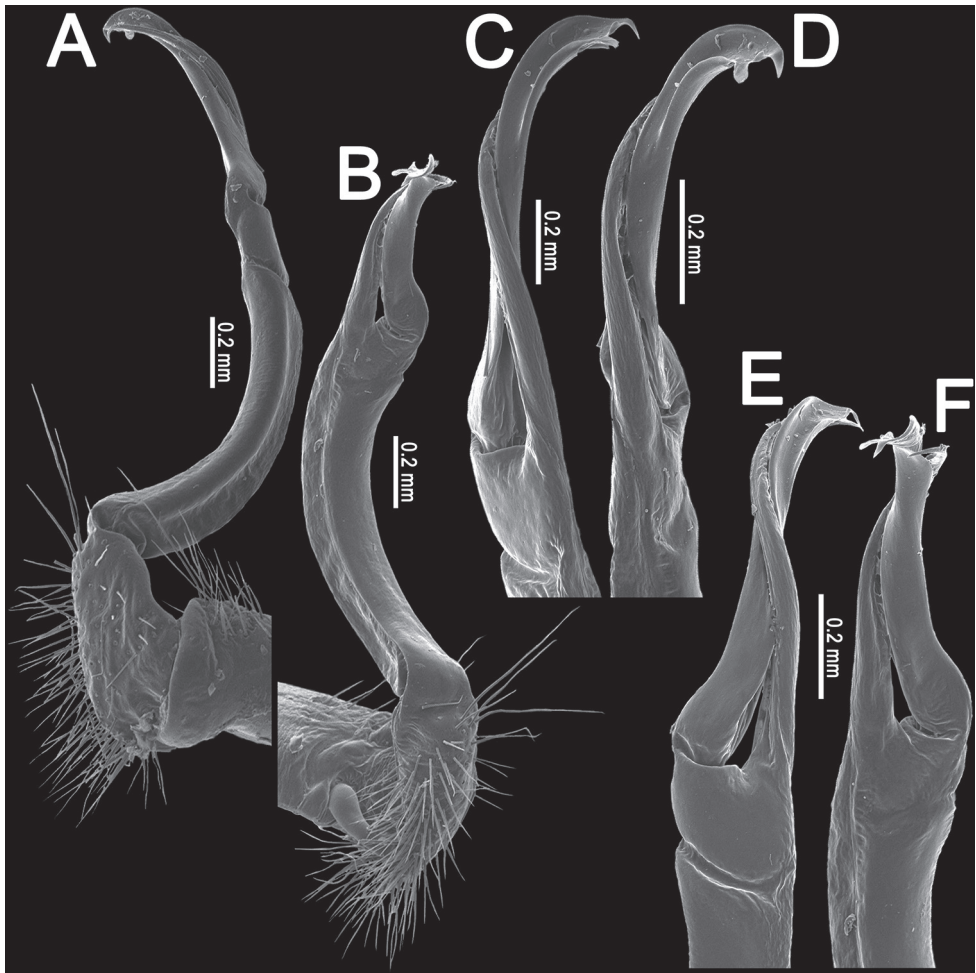


Figure 5. *Orthomorpha rotundicollis* (Attems, 1937), left gonopod **A, B** lateral and mesal views, respectively **C–F** distal part, suboral, oral, sublateral and submesal views, respectively.

area with mainly bamboo forest, 11°22'50"N, 107°13'16"E, 110 m a.s.l., in leaf litter, daytime, 29.VI.2017; 1 ♂ (red morph, ZMUM), same locality but light open forest with highly dominating *L. calyculata*, 11°24'51"N, 107°22'34"E, 130 m a.s.l., on tree trunk, daytime, 20.09.2016; 1 ♂ (red morph, ZMUM), same locality, 11°27'09"N, 107°21'57"E, lava cave, on excrements of *Hipposideros* sp.; 2 ♂, 1 ♀ (red morph, ZMUM Rd 4216), same locality, on concrete floor between huts in headquarters of National Park, 11°25'16"N, 107°25'39"E, 120 m a.s.l., night time, 4.I.2015; 1 ♀ (red morph, ZMUM Rd 4219), same locality, 11°25'37"N, 107°25'39"E, 140 m a.s.l., low-land monsoon tropical forest with dominating *Lagerstroemia calyculata* and *Afzelia xylocarpa*, on tree trunk, daytime, 20.V.2015; 1 ♀ (yellow morph, ZMUM), same local-

ity, on bush, night time, 14.VI.2015; 1 juv. (ZMUM Rd 4223), same locality, on tree trunk, night time, 9.VII.2015; 4 ♂, 2 ♀ (white form, ZMUM), Vietnam, Dong Nai Province, Thac Mai waterfall and hot spring area, 11°06'12"N, 107°24'24"E, grassy recreation area near pond, in leaf litter, daytime, 01.VI.2018, all I. Semenyuk leg.

Descriptive notes. Length 29.0–38.5 mm (♂) or 31.5–40.5 mm (♀), width of midbody pro- and metazonae 2.3–2.8 and 3.5–4.3 mm (♂) or 2.8–3.3 and 3.6–4.9 mm (♀), respectively.

Colouration in alcohol, after one year of preservation, blackish to black-brown (Fig. 3A–F), paraterga and epiproct orange-yellow to light yellow; legs and sterna light yellow to light brown; antennae yellowish to dark brownish distally (Fig. 3A). Colour polymorphism evident, colouration of paraterga generally ranging from white or yellow to red in one and the same population (see also below under Remarks).

Antennae rather long (Fig. 3A), projecting behind (♂) or reaching (♀) body segment 3 when stretched dorsally. Collum with caudal corner of paraterga dentiform, pointed, directed caudally, but not drawn past rear margin. Paraterga 2 broad, anterior edge rounded, lateral edge with two small incisions in anterior 1/3. Lateral edge of following paraterga with a small incision in anterior 1/3 (Fig. 3A, C, F) and caudal corner fully pointed, beak-like and slightly curved mesad, strongly produced behind rear tergal margin (Fig. 3A–G). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–4, followings segments 5–10 each with an evident sharp denticle caudally, the latter gradually reduced to a small tooth until segment 15 (♂, ♀) (Fig. 3B, D, E). Epiproct (Fig. 3E–G) with evident apical papillae directed ventrocaudally.

Legs long and slender, midbody ones ca. 1.3–1.4 (♂) or 0.9–1.0 (♀) times as long as body height, ♂ tarsal brushes present on legs of segments 2–10, thereafter gradually thinning out until segment 16.

Remarks. This species has recently been redescribed (Likhitrakarn et al. 2011), based on type material, and it is widespread from Luang Prabang Province, northern Laos to Cat Tien National Park, southern Vietnam (Fig. 19). The fresh specimens agree nearly fully with the available descriptions, except for the ♂ tarsal brushes being present until legs 10–14 vs. legs 5, and the pleurosternal carinae represented by small teeth gradually reduced until segment 15. These variations, as well as colour morphs, are certainly not more than infraspecific (cf. Likhitrakarn et al. 2011). One variety, *subrotundicollis* var. nov., is more disjunct morphologically, but not genetically, and is treated separately below.

The biology and behaviour of this species, referred to as *Orthomorpha* sp., has recently been described in detail in Cat Tien National Park (Semenyuk and Tiunov 2018). Millipedes are abundant almost throughout the year with a slight decline in the dry season (winter and early spring). Juveniles start swarming in the rainy season, mainly on logs or other decaying wood debris, also in suspended soil in tree holes. Swarms are active mostly in the night but can often be seen also in the daytime. Juveniles of later instars do not swarm, but still tend to group.

***Orthomorpha scabra* Jeekel, 1964**

Figs 6–8

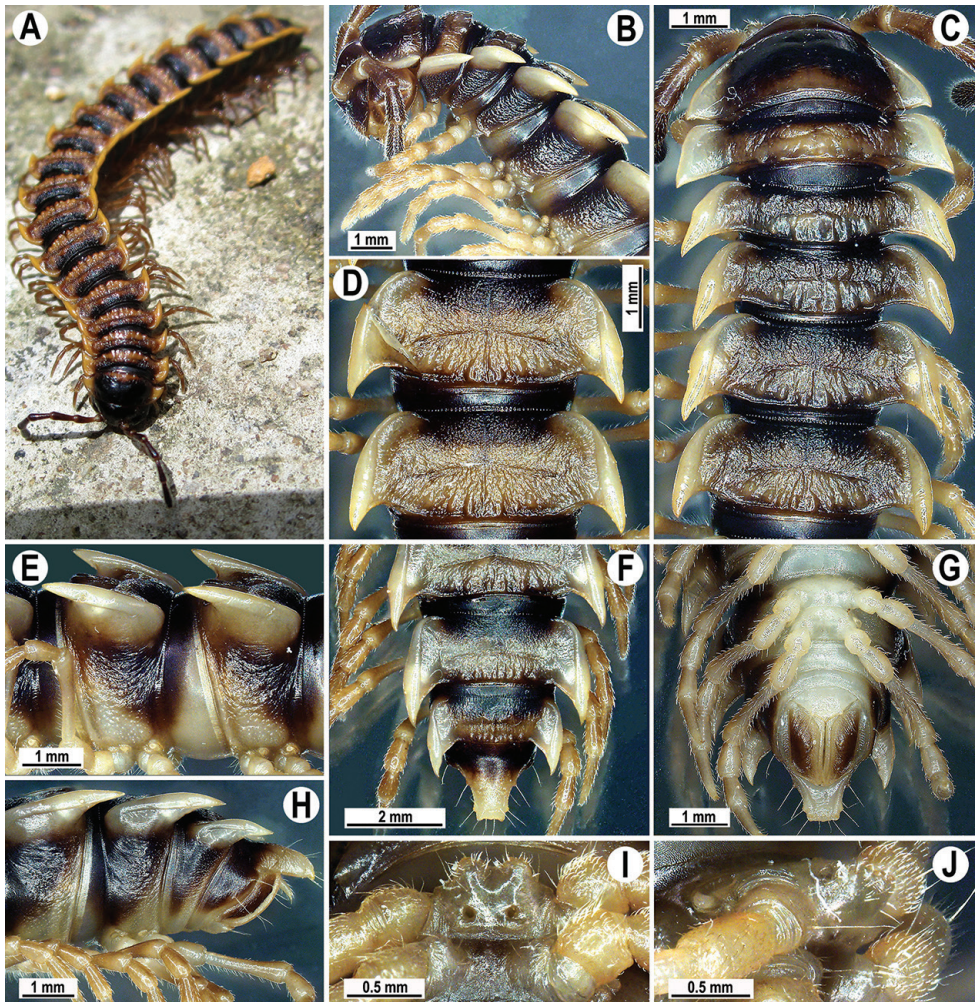
Pratinus granosus Attems, 1953: 166 (D).*Orthomorpha granosa* – Jeekel 1963: 265 (M).*Orthomorpha scabra* Jeekel, 1964: 361 (N, D). Renamed by Jeekel (1964) to avoid homonymy.*Orthomorpha scabra* – Jeekel 1968: 56 (M); Hoffman 1977: 700 (M); Golovatch 1998: 42 (M, D); Likhitrakarn et al. 2011: 58 (D).

Figure 6. *Orthomorpha scabra* Jeekel, 1964, ♂ from Kon Ka Kinh National Park **A** habitus and live colouration **B, C** anterior part of body, lateral and dorsal views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

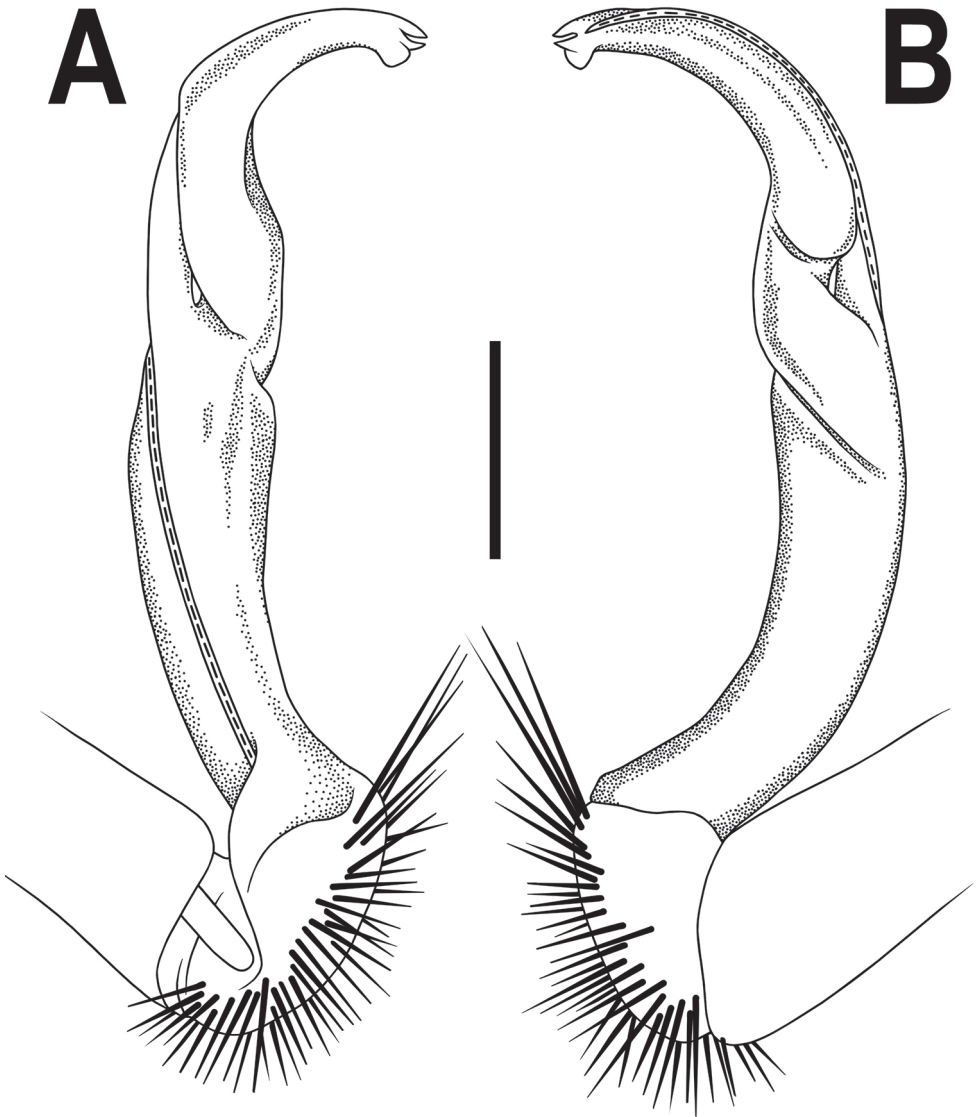


Figure 7. *Orthomorpha scabra* Jeekel, 1964, left gonopod **A, B** mesal and lateral views, respectively. Scale bar: 0.5 mm.

Old records. Vietnam, Lam Dong Province, Peak Lang Giang; Laos, Luang Prabang Province, Luang Prabang; Xiang Khouang Province, Xieng Khouang (Attems 1953).

New material examined. 1 ♂ (ZMUM Rd 4202), Vietnam, Gia Lai Province, Kon Ka Kinh National Park, forest around headquarters, 14°13'12"N, 108°19'54"E, 1,400 m a.s.l., mixed tropical forest on hill slope, under log, daytime, 26.V.2017; 2 ♂ (ZMUM Rd 4213), same locality, but near the village of Krong, 14°17'46"N, 108°26'41"E, 800 m a.s.l., disturbed tropical forest on hills with bamboo, on bushes,

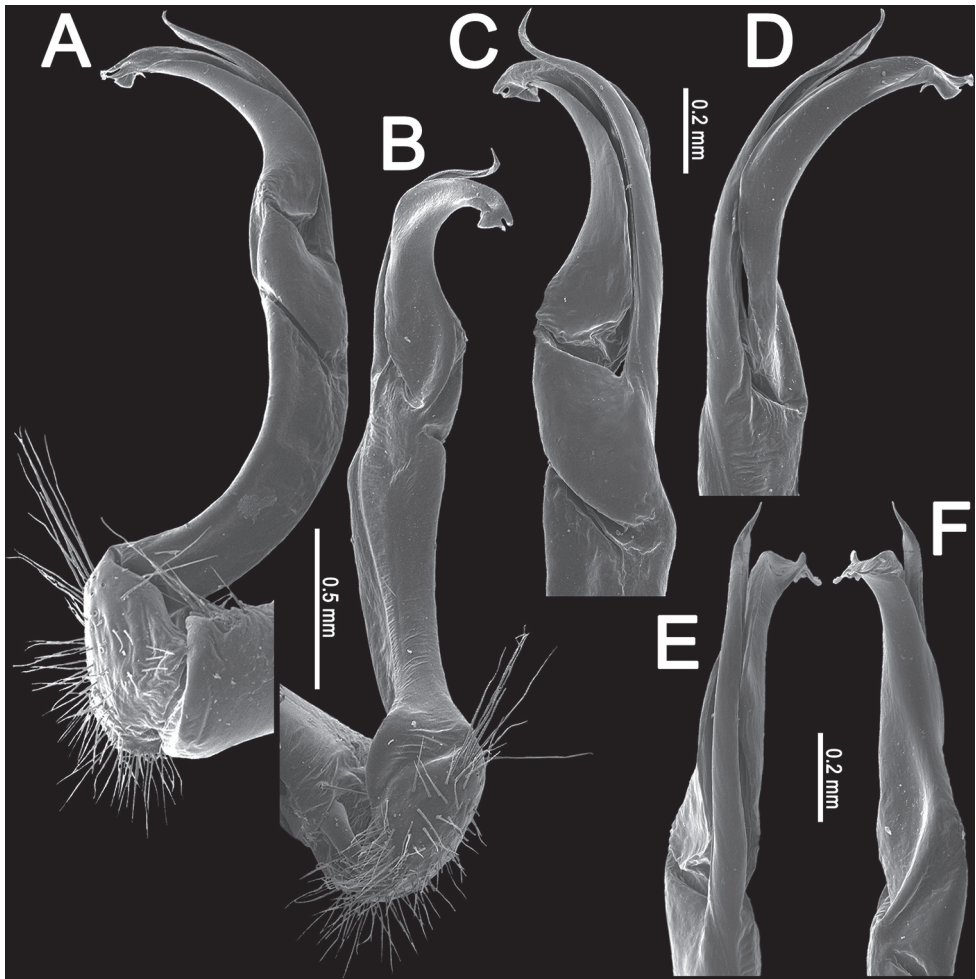


Figure 8. *Orthomorpha scabra* Jeekel, 1964, left gonopod **A, B** lateral and mesal views, respectively **C–F** distal part, sublateral, subcaudal, caudal and oral views, respectively.

daytime, 18.V.2017; 3 ♀ (ZMUM), same locality, 14°18'59"N, 108°26'26"E, 750 m a.s.l., mixed tropical forest on slopes, on tree trunk, daytime, 9.05.2017; 2 ♂ (ZMUM), Vietnam, Lam Dong Province, Bidoup Nui Ba National Park, forest near Giang Ly ranger station, 12°10'23"N, 108°40'59"E, 1,550 m a.s.l., mixed forest on slopes, in *Asplenium nidus*, daytime, 11.I.2018; 2 ♀ (ZMUM), same locality, mixed forest, 12°11'59"N, 108°40'34"E, 1,500 m a.s.l., on log, daytime, 13.I.2018; 3 ♂, 2 ♀ (ZMUM), same locality, 12°11'09"N, 108°40'43"E, 1,430 m a.s.l., mixed forest in the river valley, on forest floor, night time, 12 & 14.VI.2018, all leg. I. Semenyuk.

Descriptive notes. Length 26–46 mm (♂) or 21.5–42 mm (♀), width of mid-body pro- and metazonae 2.4–4.0 and 3.6–5.8 mm (♂) or 3.5–4.2 and 3.7–6.2 mm (♀), respectively.

Colouration of live animals (Fig. 6A) black-brownish with contrasting dark yellow to orange paraterga and epiproct, head and antennae brownish, legs pale brownish; colouration in alcohol, after one year of preservation, faded to black-brown (Fig. 6B–H), paraterga and epiproct pale whitish yellow or pale brown, legs whitish to pale brown distally.

Remarks. This species has recently been redescribed (Likhitrakarn et al. 2011), based on type material. The new specimens agree nearly fully with the available descriptions except for the ♂ tarsal brushes being present until legs 7 or 8 vs. legs 5. One variety, *grandis* var. nov., is more disjunct morphologically, but not genetically, being treated separately below.

This species seems to be widespread, occurring in Vietnam and northern Laos (Fig. 19), and in two places it was found coexisting with *O. rotundicollis* (Attems, 1937) (see also above).

According to IS' field observations, the millipedes occupy a wide range of habitats, including riparian forests with flooding occurring every year and non-flooding mixed forests on slopes. They also appear in a forestless farm area, usually being found on the forest floor and at bases of tree trunks. They occupy many microhabitats in lower forest strata. The activity is mainly restricted to the night time, but some individuals keep it up in daylight as well.

***Orthomorpha rotundicollis* (Attems, 1937), *subrotundicollis* var. nov.**

Figs 9–11

Material examined. 1 ♂ (ZMUMRd 4209), 1 ♀ (ZMUMRd 4201), Vietnam, Gia Lai Province, Kon Ka Kinh National Park, near the village of Krong, 14°18'03"N, 108°26'42"E, 600 m a.s.l., mixed tropical forest, on forest floor, night time, 9.V.2017; 1 ♂ (ZMUM Rd 4210), same locality, forest near the Park's headquarters, mixed tropical forest on hill slope, 14°11'34"N, 108°19'23"E, 1,200 m a.s.l., on forest floor, daytime, 29.V.2017; 2 ♂ (ZMUM Rd 4284, Rd 4285), same locality, on log; 1 ♀ (ZMUM Rd 4283), same locality, 14°18'24"N, 108°27'13"E, 750 m a.s.l., on forest floor, daytime, 12.V.2017, all leg. I. Semenyuk.

Name. To emphasize the strong similarity to the typical *O. rotundicollis* (Attems, 1937). Normally, no Latin names are to be applied to varieties as infrasubspecific categories, but because this new variety had first been qualified and described as a new species based on purely morphological grounds before the molecular evidence showed it to be the same as *O. rotundicollis*, we allot it the previously chosen name *subrotundicollis* and treat it separately in our analyses, key, and map.

Diagnosis. Using the latest key (Likhitrakarn et al. 2011), this new variety keys out and seems to be especially similar to the typical *O. rotundicollis*, but it differs in the smaller size (up to 23 mm (♂) or 29 mm (♀) long and 2.9–3.2 mm (♂) or 3.3–3.9 mm (♀) wide, respectively), and the pleurosternal carinae being complete crests until segment 7 (♂) or 5 (♀), each crest supplied with an evident sharp denticle caudally,

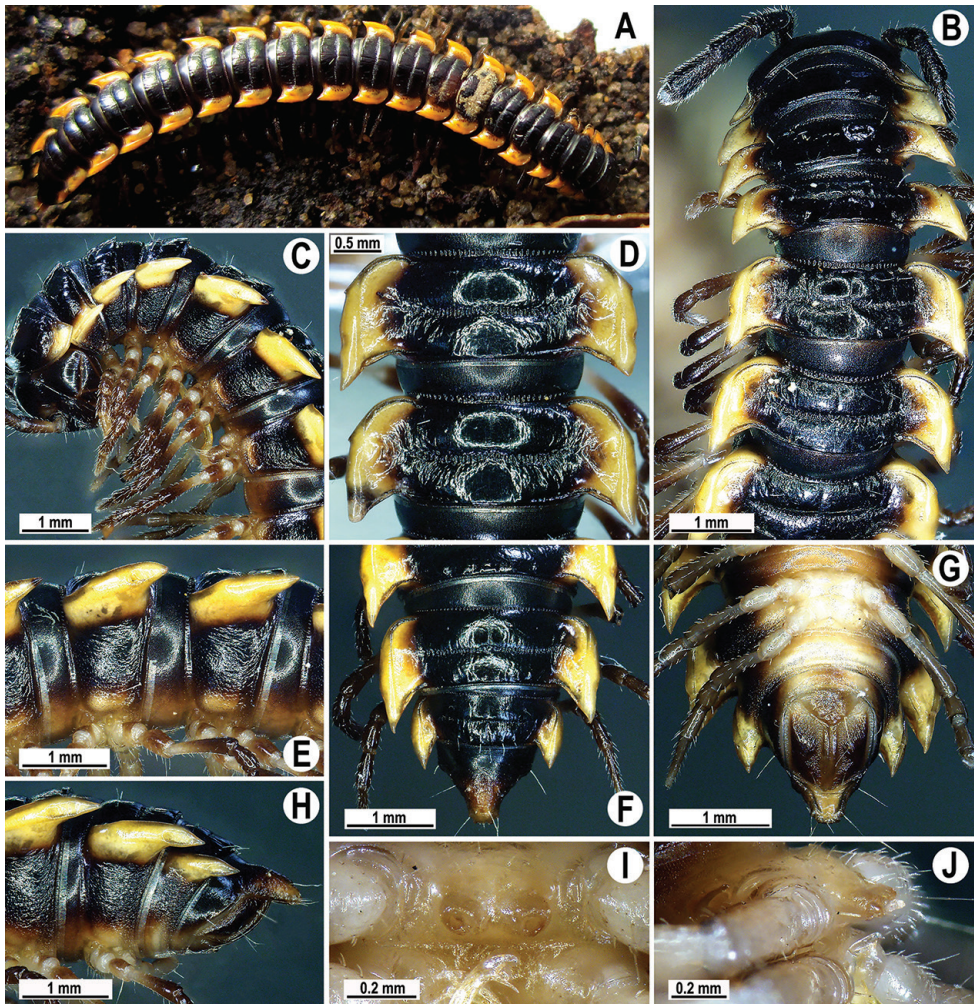


Figure 9. *Orthomorpha rotundicollis* (Attems, 1937), *subrotundicollis* var. nov., ♂ **A** habitus and live colouration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

thereafter increasingly strongly reduced until segment 16 (♂, ♀), coupled with tarsal brushes being traced until ♂ legs 11.

Description. Length 20.0–23.0 mm (♂) and 21.5–29.0 mm (♀), width of mid-body pro- and metazonae 1.7–1.9 and 2.9–3.2 mm (♂) or 2.3–2.6 and 3.3–3.9 mm (♀), respectively.

Colouration of live animals blackish (Fig. 9A), paraterga and epiproct contrasting yellow-orange, head and antennae dark brownish, legs pale brownish; colouration in alcohol, after one year of preservation, blackish or faded to black-brown (Fig. 9B–H), paraterga and epiproct pale whitish yellow to light yellow, legs and sterna light yellow to pale brown, antennae light yellow to dark brownish distally.

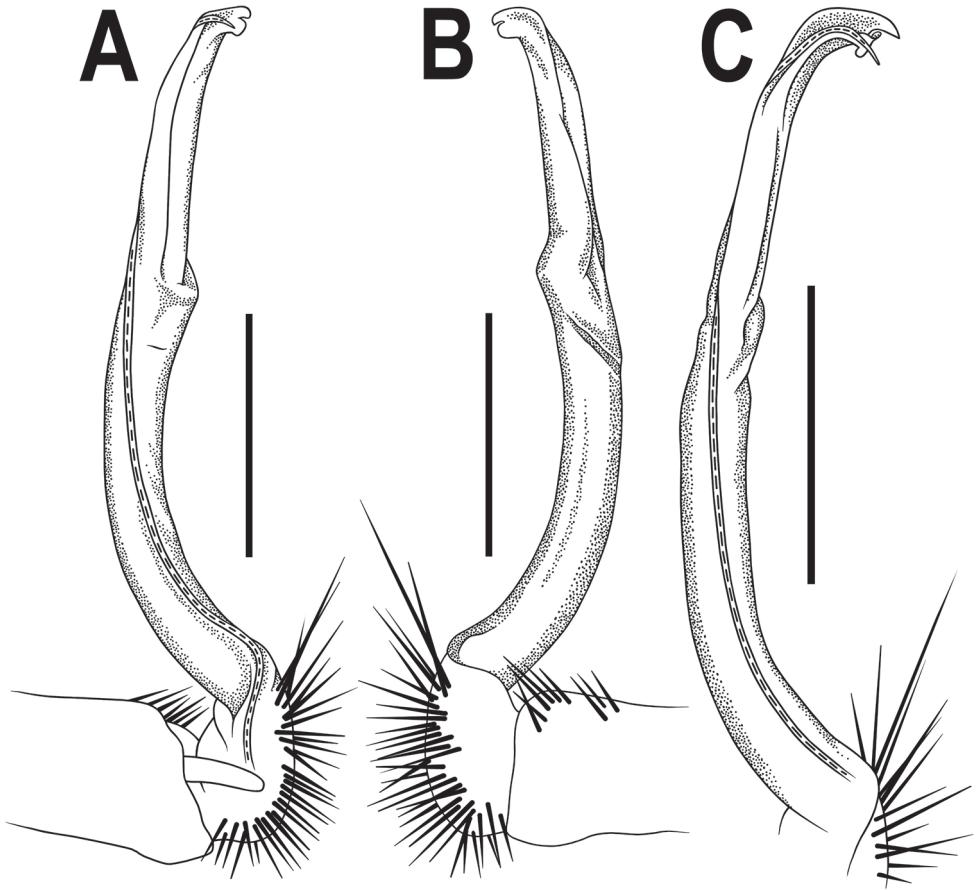


Figure 10. *Orthomorpha rotundicollis* (Attems, 1937), *subrotundicollis* var. nov., ♂, left gonopod **A**, **B** mesal and lateral views, respectively **C** distal part, submesal view. Scale bars: 0.2 mm.

Clypeolabral and vertigial regions sparsely setose; epicranial suture distinct. Antennae rather short (Fig. 9A, B), reaching behind body segment 3 when stretched dorsally, with a pair of lighter, yellowish, oblong spots above antennal sockets. In width, head < collum < segment 3 < 4 < 2 < 5–17 (♂, ♀), body gently and gradually tapering thereafter. Collum with three transverse rows of setae: 3+3 in anterior, 2+2 in intermediate, and 3+3 in posterior row; a very faint incision laterally in posterior 1/3; caudal corner of paraterga a minute, dentiform, slightly declined knob not drawn behind rear margin.

Tegument smooth and shining, prozonae finely shagreened, metaterga smooth and delicately rugulose, leathery; surface below paraterga finely microgranulate. Postcollum metaterga each with two transverse rows of setae: anterior (pre-sulcus) row with 2+2 setae traceable at least as insertion points when setae broken off; posterior (post-sulcus) row with 3+3 setae borne on minute to small tubercles growing a little larger laterally, in addition to fully obliterated knobs with insertion points of abraded setae near axial line. Tergal setae long, strong, slender, ca. 1/3 of metatergal length. Axial line visible on collum and both on following pro- and metazonae.

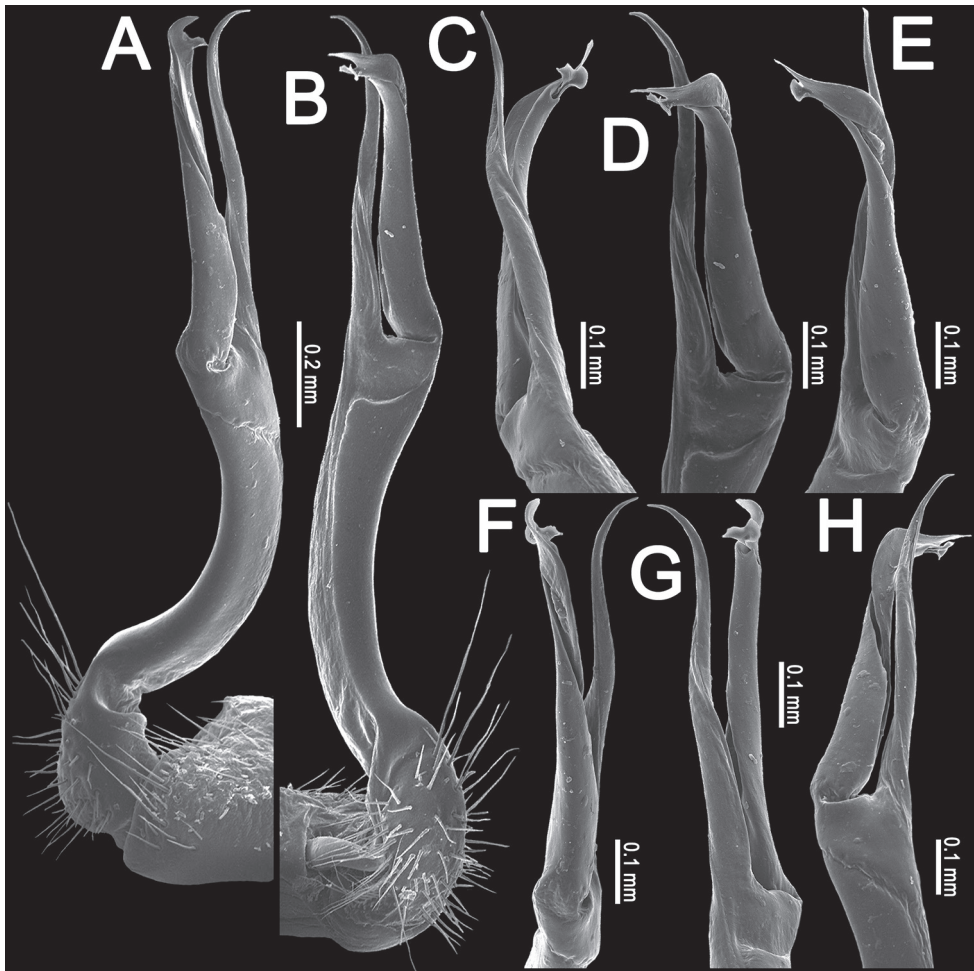


Figure 11. *Orthomorpha rotundicollis* (Attems, 1937), *subrotundicollis* var. nov., ♂, left gonopod **A, B** lateral and mesal views, respectively **C–H** distal part, caudal, mesal, suboral, oral, caudal and sublateral views, respectively.

Paraterga 2 broad, anterior edge angular, lateral edge with two small, but evident incisions in anterior 1/3; posterior edge slightly oblique (Fig. 9B, C). Following paraterga strongly developed (Fig. 9B–H), especially well so in ♂, slightly upturned caudally, all lying below dorsum, set at ca. upper 1/3 of midbody height, subhorizontal, caudal corner almost or fully pointed, increasingly spiniform and produced behind rear tergal margin; anterior edge well-developed, slightly convex to rounded, bordered and fused to callus. Lateral edge of paraterga with two small, but evident incisions, one in anterior 1/3, the other in posterior 1/3 on following poreless segments, but only one (at front 1/4) on following pore-bearing segments. Calluses on paraterga 2–4

delimited by a sulcus only dorsally, on following paraterga both dorsally and ventrally, rather narrow, modestly enlarged in pore-bearing segments, thinner in poreless ones (Fig. 9B–H). Posterior edge of paraterga clearly concave, especially well so in segments 17–19 (Fig. 9F). Ozopores evident, lateral, lying in an ovoid groove at ca. 1/3 in front of caudal corner. Transverse sulcus usually distinct (Fig. 9B, C, F), complete on metaterga 5–18, incomplete on segments 4 and 19 (♂, ♀), deep, line-shaped, nearly reaching the bases of paraterga, evidently ribbed at bottom. Stricture between pro- and metazona wide, clearly ribbed at bottom down to base of paraterga (Fig. 9B, C, F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–7 (♂) or 2–5 (♀), a front bulge and a caudal tooth until segment 10, each with a small sharp tooth caudally, thereafter tooth increasingly strongly reduced until segment 16 (♂, ♀) (Fig. 9C, E, H).

Epiproct (Fig. 9F–H) conical, rounded dorsoventrally, with two evident apical papillae; tip subtruncate; pre-apical papillae evident, lying rather close to tip. Hypoproct roundly subtriangular, setiferous knobs at caudal edge evident and well-separated.

Sterna sparsely setose, without modifications except for two rather large, fully separated, setose sternal cones between ♂ coxae 4 (Fig. 9I, J). A paramedian pair of evident tubercles in front of gonopod aperture. Legs moderately long and slender; midbody ones ca. 1.1–1.2 (♂) or 0.8–0.9 (♀) times as long as body height, prefemora without modifications, ♂ tarsal brushes present until legs 11.

Gonopods (Figs 10, 11) simple. Coxa long and slender, with several setae distoventrally. Prefemur densely setose, nearly 3 times shorter than femorite + “postfemoral” part. Femorite very slender, moderately curved, very slightly enlarged distad, “postfemoral” part demarcated by an oblique lateral sulcus; tip of solenophore small, trifid, with two subequal denticles (one lower terminal, the other middle) and a broader upper, sharp, subterminal lobule.

Remarks. Based on morphological characters alone (see Diagnosis), this variety had first been qualified and distinguished as a full new species before the molecular analyses unequivocally showed it to be genetically the same as *O. rotundicollis*. Indeed, the average genetic distance (Di) of *subrotundicollis* from the typical, morphologically closest and sympatric *O. rotundicollis* is null (Table 2). In one of the phylograms (Fig. 20), *subrotundicollis* falls out between the two individuals of *rotundicollis*, and overall the genetic variation is strikingly scant. This is one of the direct consequences of the molecular analyses accepted in our study.

Adults of this variety were found only in May during a short expedition to Kon Ka Kinh National Park, as part of IS’ research on the diversity, biology, and ecology of millipedes in Vietnam. The previous trip to the same area in 2016 failed in finding this species. In 2017, millipedes were very abundant in many types of forest ranging from native to highly disturbed ones, up to even forestless hills with farmed crops. The activity was mainly noted in the night time in forest, but walking millipedes appeared even in daylight in open areas. Mating was recorded in May.

Table 2. Average genetic distances (Di) among the available taxa, the matrix constructed using Kimura's two-parametric/pairwise model of nucleotide replacements that suggests a considerable prevalence of transitions over transversions in mitochondrial DNA. Old information is available in Nguyen et al. (2017, 2018) and GenBank, the new one is contained in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 <i>Orthomorpha coarctata</i> Chuzhou																						
2 <i>O. coarctata</i> Thac Mai	0.004																					
3 <i>Antheromorpha punatensis</i> Nghe An	0.153	0.146																				
4 <i>A. festiva</i> Dak Lak	0.210	0.202	0.203																			
5 <i>Tylopus crassipes</i> Lao Cai	0.261	0.270	0.192	0.265																		
6 <i>Oxidus gracilis</i> Onario	0.227	0.235	0.242	0.253	0.209																	
7 <i>O. rukiarius</i> Okinawa	0.171	0.165	0.184	0.249	0.229	0.144																
8 <i>Hylomus engelhoffi</i> Phong Nha	0.249	0.257	0.250	0.261	0.330	0.227	0.279															
9 <i>H. cervarius</i> Sa Pa	0.170	0.177	0.164	0.243	0.270	0.241	0.198	0.158														
10 <i>H. proximus</i> Sa Pa	0.205	0.212	0.235	0.261	0.206	0.284	0.291	0.200	0.174													
11 <i>Oxidus gigas</i> Duc Xuan	0.191	0.199	0.211	0.200	0.204	0.130	0.145	0.259	0.233	0.244												
12 <i>Piccola odontopyga</i> Bi Duop	0.164	0.170	0.198	0.217	0.201	0.199	0.141	0.265	0.204	0.221	0.179											
13 <i>Orthomorphaoides scosus</i> Bi Duop	0.176	0.183	0.198	0.218	0.171	0.227	0.199	0.273	0.249	0.241	0.178	0.128										
14 <i>Orthomorpha sabra</i> Bi Duop	0.158	0.164	0.140	0.233	0.243	0.199	0.205	0.191	0.177	0.219	0.178	0.183	0.170									
15 <i>O. glandulosa</i> Quang Nam	0.164	0.171	0.194	0.257	0.262	0.259	0.247	0.235	0.199	0.229	0.229	0.170	0.177	0.116								
16 <i>O. sabra</i> Kon Ka Kinh	0.158	0.164	0.140	0.233	0.243	0.199	0.205	0.191	0.177	0.219	0.178	0.183	0.170	0.000	0.116							
17 <i>O. sabra</i> var. <i>grandis</i> Bidoup Nui Ba	0.158	0.164	0.140	0.233	0.243	0.199	0.205	0.191	0.177	0.219	0.178	0.183	0.170	0.000	0.116	0.000						
18 <i>O. vietnamica</i> Kon Ka Kinh	0.170	0.177	0.166	0.249	0.234	0.213	0.220	0.220	0.190	0.234	0.191	0.170	0.170	0.018	0.116	0.018	0.018					
19 <i>O. arboricola</i> Hon Ba	0.164	0.170	0.190	0.224	0.261	0.243	0.236	0.205	0.198	0.233	0.226	0.184	0.170	0.076	0.046	0.076	0.076	0.076				
20 <i>O. rotundicollis</i> var. <i>subrotundicollis</i> Kon Ka Kinh	0.152	0.158	0.159	0.204	0.173	0.204	0.198	0.219	0.172	0.250	0.221	0.121	0.158	0.115	0.148	0.115	0.115	0.104	0.141			
21 <i>O. rotundicollis</i> Thac Mai	0.152	0.158	0.159	0.204	0.173	0.204	0.198	0.219	0.172	0.250	0.221	0.121	0.158	0.115	0.148	0.115	0.115	0.104	0.141	0.000		
22 <i>O. rotundicollis</i> Cac Tien	0.152	0.158	0.159	0.204	0.173	0.204	0.198	0.219	0.172	0.250	0.221	0.121	0.158	0.115	0.148	0.115	0.115	0.104	0.141	0.000	0.000	
23 <i>O. cannel</i> Kon Ka Kinh	0.158	0.164	0.166	0.234	0.201	0.241	0.219	0.218	0.185	0.241	0.243	0.139	0.164	0.121	0.105	0.121	0.121	0.110	0.099	0.032	0.032	0.032

***Orthomorpha caramel* sp. nov.**

<http://zoobank.org/0668527A-B7A6-4EE1-B5CD-7BA8B49BC540>

Figs 12–14

Type material. *Holotype* ♂ (ZMUM Rd 4197), Vietnam, Gia Lai Province, Kon Ka Kinh National Park, forest near the village Krong, 14°18'03"N, 108°26'42"E, 600 m a.s.l., mixed tropical forest on slopes to a small stream, on tree trunk, daytime, 13.V.2017, I. Semenyuk leg.

Paratypes. 1 ♂ (ZMUM Rd 4198), same locality, together with holotype; 1 ♂ (ZMUM), same locality, 14°17'46"N, 108°26'41"E, 750 m a.s.l., disturbed forest with dominating bamboo on hills, on tree trunk, daytime 18.V.2017, all leg. I. Semenyuk.

Name. A noun in apposition, to emphasize the general caramel colouration of the animals.

Diagnosis. Using the latest key (Likhitrakarn et al. 2011), distinguished from all known congeners by the tip of the solenophore being very faintly bifid, with a nearly smooth terminal lobe bearing a minute lobule at the base; in the gonopod structure it is similar to *O. tuberculifera* Likhitrakarn, Golovatch & Panha, 2011, but differs in the rather smooth and shining dorsal tegument devoid of tubercles, coupled with the particular colouration.

Description. Length of holotype 36.5 mm (♂), width of midbody pro- and metazonae 2.8 and 4.2 mm, respectively. Paratype 31.5–34.5 mm long, 2.6–2.8 and 4.0–4.1 mm wide on midbody pro- and metazonae, respectively.

Colouration of live animals dark chocolate brown (Fig. 12A); metaterga, paraterga and epiproct caramel in colour; head, antennae and legs dark brownish; colouration in alcohol after one year of preservation chocolate brown or faded to light brownish (Fig. 12B–H); metaterga, paraterga and epiproct caramel to light brownish in colour; legs and sterna light brown to pale yellow; head and antennae dark brownish to brown.

Clypeolabral region densely setose, vertigial region sparsely so; epicranial suture distinct. Antennae rather long (Fig. 12A), reaching the end of body segment 3 when stretched dorsally. In width, head < segment 3 = 4 < collum < segment 5 < 2 < 6–17, body gently and gradually tapering thereafter. Collum with three transverse rows of setae: 4+4 in anterior, 2+2 in intermediate, and 3+3 in posterior row; a slight furrow laterally in posterior 1/3; caudal corner of paraterga very narrowly rounded, slightly upturned, but not drawn behind rear margin (Fig. 12B, C).

Tegument shining, prozonae finely shagreened, metaterga rugose to rugulose, surface below paraterga finely microgranulate and rugulose. Postcollum metaterga each with two transverse rows of short, mostly abraded setae traceable only as insertion points, short wrinkles or minute tubercles: anterior (pre-sulcus) row with 2+2 mostly abraded setae traceable only as insertion points; posterior (postsulcus) row with 3+3 setae borne on minute tubercles or short wrinkles. Tergal setae long, slender, ca. 1/3 of metatergal length. Axial line rather clear, especially so on metazonae.

Paraterga very strongly developed (Fig. 12B–H), mostly upturned, all lying below dorsum, set at ca. upper 1/4 of midbody height, nearly level with dorsum on segments

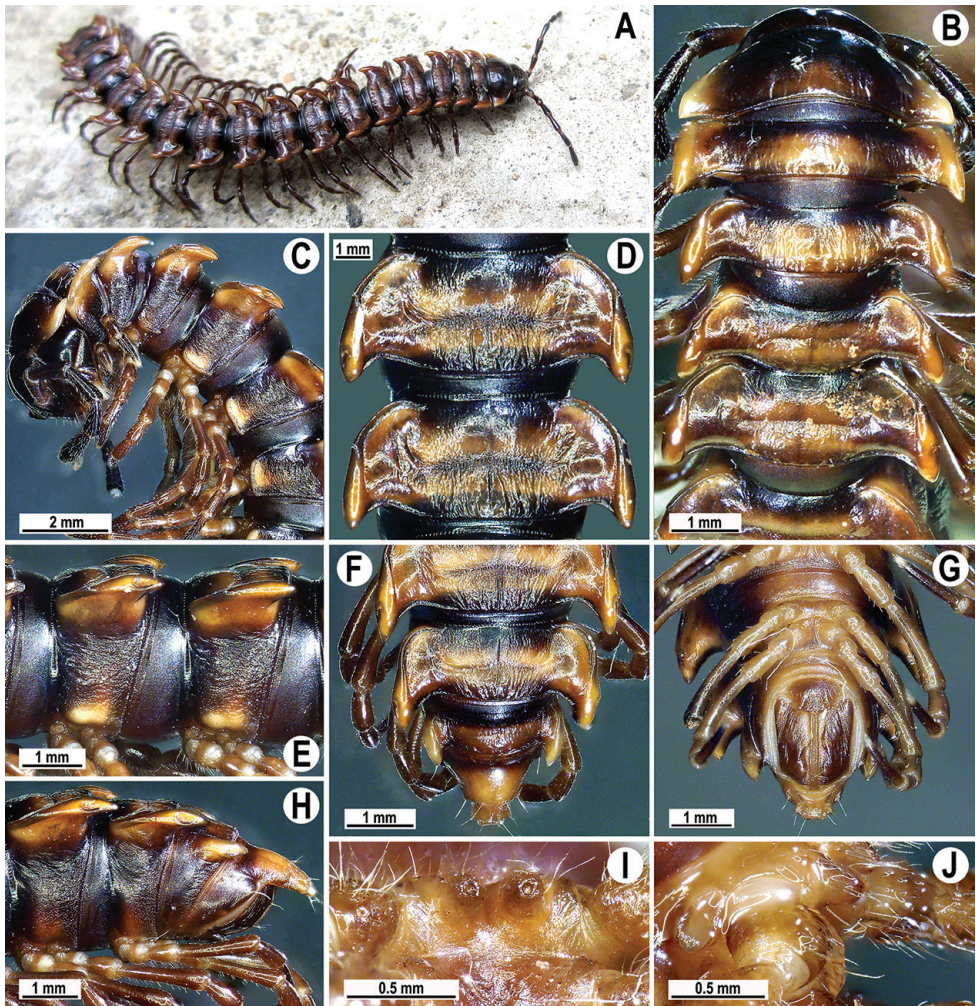


Figure 12. *Orthomorpha caramel* sp. nov., ♂ holotype **A** habitus, live colouration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

15–18, caudal corner always spiniform and narrowly rounded, extending beyond rear tergal margin; in lateral view, paraterga thinner in poreless segments and modestly enlarged in pore-bearing ones.

Paraterga 2 broad, anterior edge evidently convex, lateral edge with one larger incision in anterior 1/3, one smaller, but evident incision in the middle and a faint furrow at posterior 1/3; posterior edge oblique (Fig. 12B, D, F). Anterior edges of following paraterga strongly and regularly rounded, lateral edge with only one small, but evident incision in anterior 1/3, posterior edge clearly concave, especially strongly emarginate in segments 17–19 (Fig. 12F–H). Calluses on paraterga 2–4 strongly delimited by a sulcus only dorsally, on following paraterga both dorsally and ventrally.

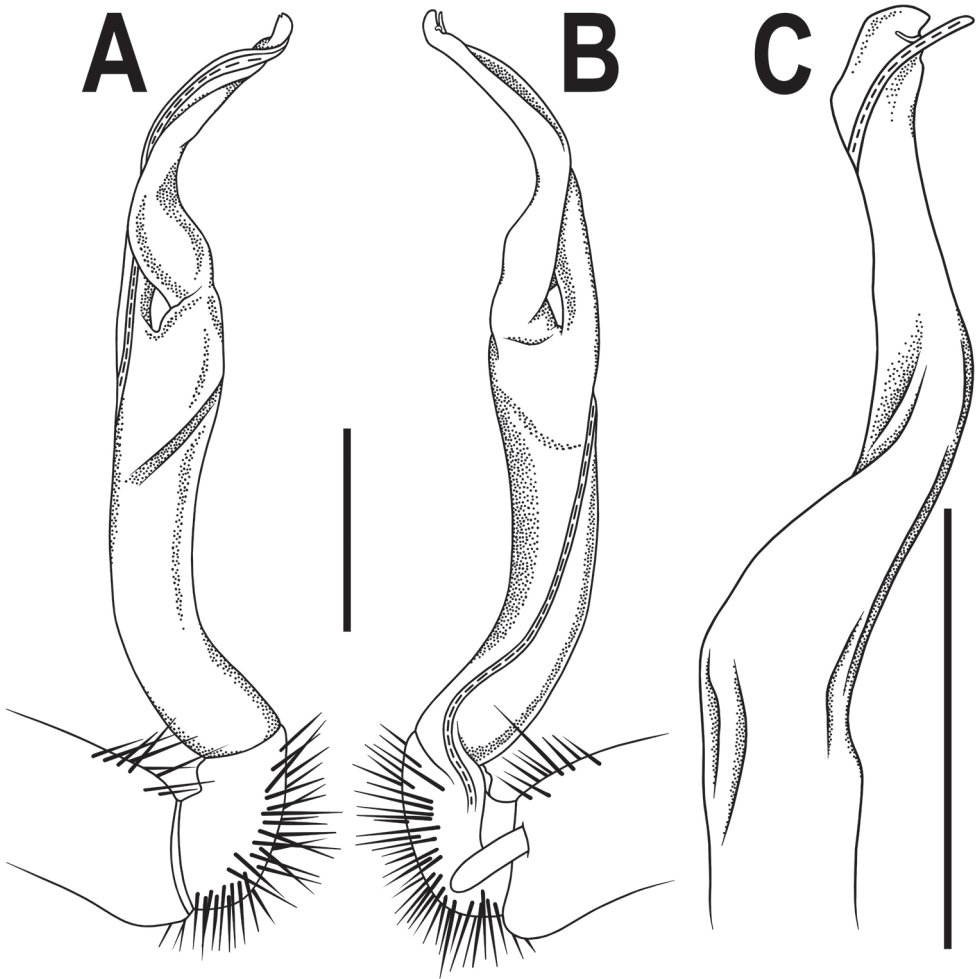


Figure 13. *Orthomorpha caramel* sp. nov., ♂ holotype, right gonopod **A**, **B** lateral and mesal views, respectively **C** distal part, suboral view. Scale bars: 0.5 mm

Ozopores evident, lateral, lying inside an ovoid groove at ca. $1/4$ in front of caudal corner. Transverse sulcus usually distinct (Fig. 12C, E, H), complete on metaterga 5–18, incomplete and nearly wanting on segments 4 and 19, wave-shaped, rather shallow, nearly reaching the bases of paraterga, ribbed at bottom. Stricture between pro- and metazona rather wide and deep, beaded at bottom down to base of paraterga (Fig. 12B, D, F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–7(8), thereafter bulged anteriorly and with a small, sharp, caudal tooth on segments 8–10, the tooth gradually reduced into small, caudally roughly granulate crests until segment 12 (Fig. 12C, E, H). Epiproct (Fig. 12F, G) conical, flattened dorsoventrally, with two evident apical papillae; tip subtruncate; pre-apical papillae small, but evident, lying rather close to tip. Hypoproct pentagonal, setiferous knobs at caudal edge evident and well-separated.

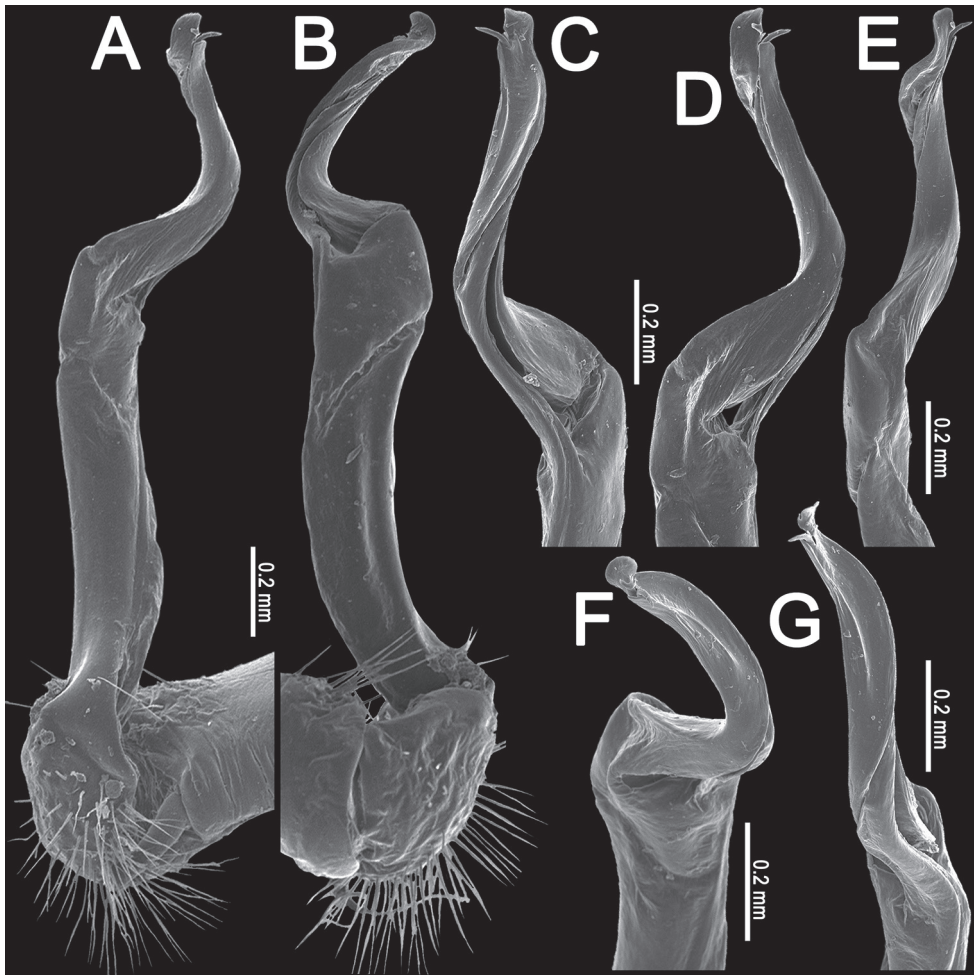


Figure 14. *Orthomorpha caramel* sp. nov., ♂ holotype, right gonopod **A, B** mesal and lateral views, respectively **C–G** distal part, caudal, mesal, oral, submesal and subcaudal views, respectively.

Sterna sparsely setose, without modifications except for two rather large and long, fully separated, sternal cones between ♂ coxae 4 (Fig. 12I, J). A paramedian pair of evident tubercles in front of gonopod aperture. Legs long and slender, midbody ones ca. 1.2–1.4 times as long as body height, prefemora without modifications, ♂ tarsal brushes present until legs 15.

Gonopods (Figs 13, 14) simple. Coxa slender and long, with several setae distoventrally. Femorite ca. 2 times as long as prefemoral (= strongly setose) part. Femorite slender, suberect to slightly curved, “postfemoral” portion demarcated by an oblique lateral sulcus; solenophore moderately twisted and curved, tip of solenophore very faintly bifid, with a nearly smooth terminal lobe bearing a minute lobule at base; solenomere long and flagelliform, as usual.

Remarks. The biology and behaviour of this species are very similar to those of *O. vietnamica* sp. nov. During field observations in May 2017, millipedes occurred mainly on tree trunks. Mating was also recorded, but no females were collected.

***Orthomorpha vietnamica* sp. nov.**

<http://zoobank.org/D9F27912-213D-4AEB-AE74-38FFFFA0F66B>

Figs 15, 16

Type material. Holotype: ♂ (ZMUM Rd 4199), Vietnam, Gia Lai Province, Kon Ka Kinh National Park, near the village of Krong, 14°18'03"N, 108°26'42"E, 600 m a.s.l., mixed tropical forest, on tree trunk, night time, 9.V.2017, I. Semenyuk leg.

Paratype: 1 ♀ (ZMUM Rd 4200), same locality, together with holotype.

Name. Adjective to refer to the country of origin.

Diagnosis. This species seems to be especially similar to *O. caramel* sp. nov., but differs from all congeners (Likhitrakarn et al. 2011) in the presence of a conspicuous,

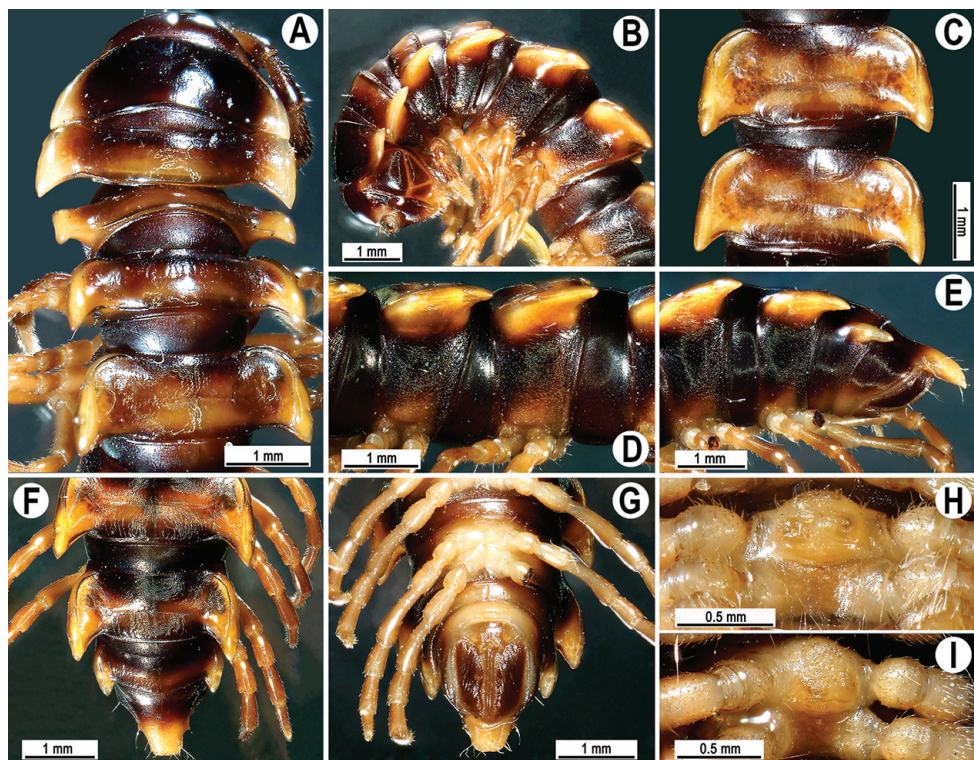


Figure 15. *Orthomorpha vietnamica* sp. nov., ♂ holotype **A, B** anterior part of body, dorsal and lateral views, respectively **C, D** segments 10 and 11, dorsal and lateral views, respectively **E–G** posterior part of body, lateral, dorsal and ventral views, respectively **H, I** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

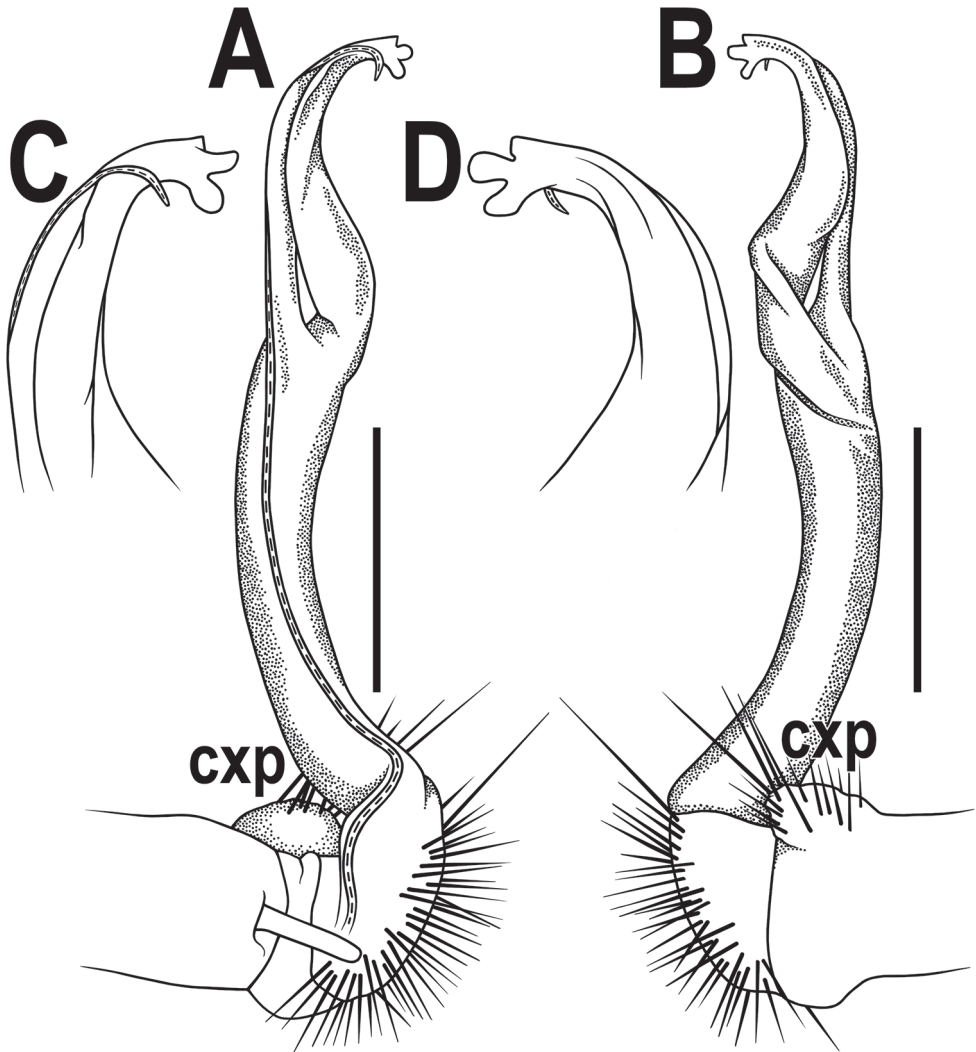


Figure 16. *Orthomorpha vietnamica* sp. nov., ♂ holotype, left gonopod **A, B** mesal and lateral views, respectively **C, D** tip of gonopod, submesal and sublateral views, respectively. Abbreviation: **cxp**, coxal tubercle. Scale bars: 0.5 mm.

densely setose, rounded tubercle (Fig. 16, **cxp**) on the gonocoxa and the evident trifid tip of the solenophore, as well as the ♂ tarsal brushes showing until segment 16, coupled with the pleurosternal carinae present as complete crests with a sharp caudal tooth on segments 2–4.

Description. Length 27.5 mm (♂) or 29.5 mm (♀), width of midbody pro- and metazonae 2.0 and 3.0 mm (♂) or 2.7 and 3.6 mm (♀), respectively.

Colouration of alcohol material after one year of preservation dark brown (Fig. 10B–H); metaterga brown to light brownish; paraterga and epiproct light yellow to yellowish; legs and sterna light brown to pale yellow; head, collum, and antennae dark brownish to brown. Bases of paraterga marbled (Fig. 15C).

All characters as in *O. caramel* sp. nov., except as follows: clypeolabral region sparsely setose, vertigial region bare. Antennae rather short, reaching behind body segment 3 (♂, ♀) when stretched dorsally. In width, head < collum < segment 3 < 4 < 5 < 2 < 6–17 (♂) or head < collum < segment 3 < 4 < 2 < 5–17 (♀), body gently and gradually tapering thereafter.

Tegument rather dull, prozonae finely shagreened, metaterga rugose to rugulose, surface below paraterga finely microgranulate and faintly rugulose (Fig. 15A–F).

Axial line visible on collum and both on following pro- and metazonae.

Transverse sulcus usually distinct (Fig. 15C, E, H), complete on metaterga 5–18, incomplete and nearly wanting on segments 4 and 19, nearly line-shape, rather shallow, almost reaching the bases of paraterga, at most very faintly beaded at bottom.

Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–4 (♂) (Fig. 15B) or nearly complete crests with a sharp caudal tooth on segment 4 (♀), thereafter bulged anteriorly and with a small sharp caudal tooth until segment 8, the tooth gradually reduced into small, caudally roughly granulate crests until segment 12 (♂, ♀). Epiproct (Fig. 15F, G) conical, flattened dorsoventrally, tip subtruncate; with two evident, sharp, apical teeth directed ventrocaudally (♂, ♀); pre-apical papillae very small, located close to tip. Hypoproct roundly subtriangular, setiferous knobs at caudal edge evident and well-separated (Fig. 15G).

Sterna sparsely setose, without modifications except for an evident, rounded, sparsely setose bulge directed anteroventrally between ♂ coxae 4 (Fig. 15I, J). A paramedian pair of evident, high tubercles in front of gonopod aperture. Legs rather long and slender, midbody ones ca. 1.2–1.3 (♂) or 0.8–0.9 (♀) times as long as body height, prefemora without modifications, ♂ tarsal brushes present until legs of segment 16.

Gonopods (Fig. 16) somewhat more complex than usual. Coxa long and slender, with a conspicuous, high, laterally densely setose, rounded tubercle (Fig. 16A, B, cxp). Femorite ca. 2 times as long as prefemoral (= strongly setose) part. Femorite slender, slightly curved and enlarged distad, “postfemoral” portion demarcated by an oblique lateral sulcus; solenophore with a tridentate tip, two subequal, rounded lobules (middle and ventral) and a shorter apicodorsal lobule; solenomere long and flagelliform, as usual.

Remarks. We assume the apicodorsal lobule of the solenophore to be broken off, considering the structure of the solenophore tip in the other *Orthomorpha* spp.

The ecology of this species is very similar to that of *O. caramel* sp. nov. These two species are syntopic and share the same microhabitats.

Orthomorpha scabra Jeekel, 1964, *grandis* var. nov.

Figs 17, 18

Material examined. 4 ♂ (ZMUM Rd 4268, Rd 4266, Rd 4267, Rd 4269), Vietnam, Lam Dong Province, Bidoup Nui Ba National Park, Mount Bidoup, 12°05'58"N, 108°39'30"E, 2,000 m a.s.l., mixed cloudy mossy forest on mountain top, on forest floor, night time, 16.VI.2018, I. Semenyuk leg.

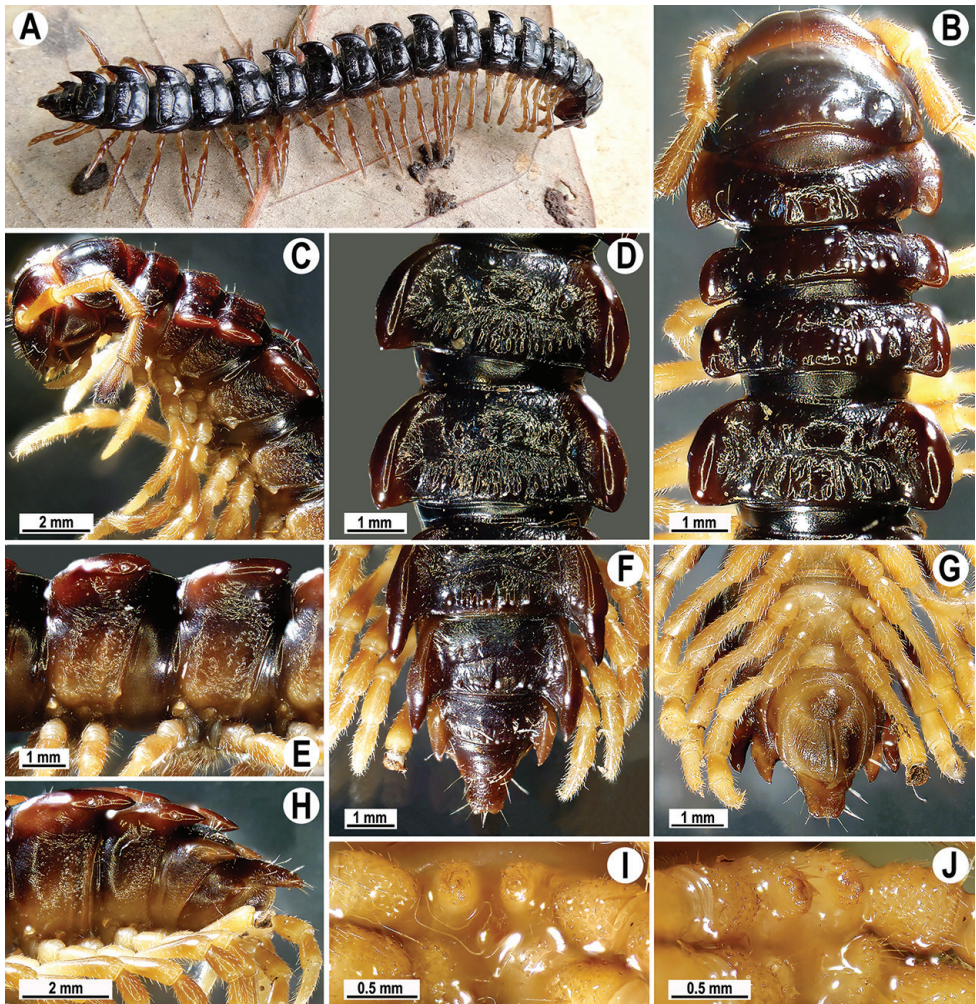


Figure 17. *Orthomorpha scabra* Jeekel, 1964, *grandis* var. nov., ♂ **A** habitus and live colouration **B, C** anterior part of body, dorsal and lateral views, respectively **D, E** segments 10 and 11, dorsal and lateral views, respectively **F–H** posterior part of body, dorsal, ventral and lateral views, respectively **I, J** sternal cones between coxae 4, subcaudal and sublateral views, respectively.

Name. Adjective to emphasize the unusually large size of the animals. Normally, no Latin names are to be applied to varieties as infrasubspecific categories, but because this new variety had first been qualified and described as a new species based on purely morphological grounds before the molecular evidence showed it to be the same as *O. scabra*, we allot it the previously chosen name *grandis* and treat it separately in our analyses, key, and map. This is also one of the direct consequences of the molecular analyses accepted in our study.

Diagnosis. Distinguished from all known congeners or varieties by the particularly large size, coupled with the clearly tuberculate metaterga, caudolaterally rounded paraterga 1–14, and the relatively short gonopodal femorite.

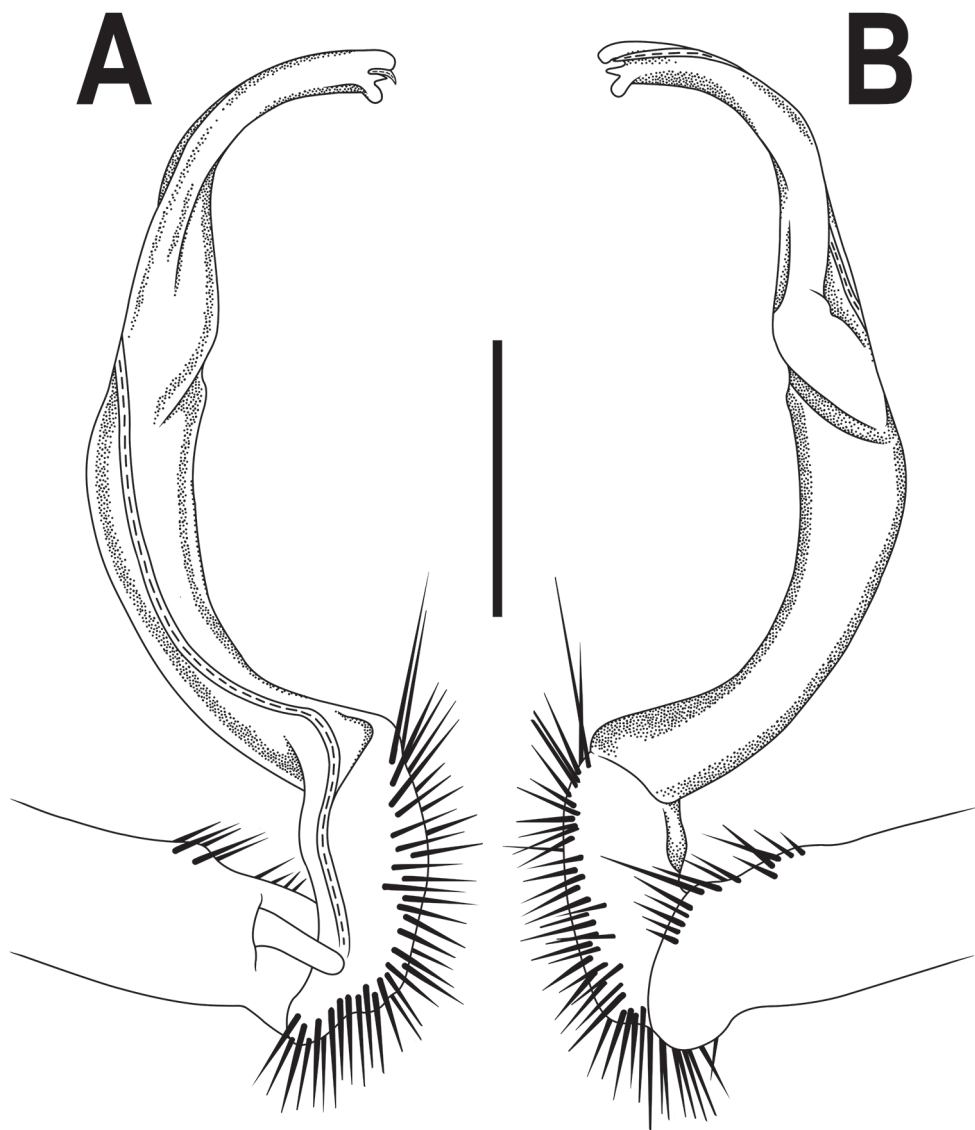


Figure 18. *Orthomorpha scabra* Jeekel, 1964, *grandis* var. nov., ♂, left gonopod **A, B** mesal and lateral views, respectively. Scale bar: 0.5 mm.

Description. Length 44–50 mm, width of midbody pro- and metazonae 3.5–3.8 and 5.2–5.6 mm wide on midbody pro- and metazonae, respectively (♂).

Colouration in alcohol after ten months of preservation dark brown (Fig. 17A–G); metaterga, paraterga and epiproct red-brown to dark brown; legs, antennae and sterna light brown to light yellow; head brownish to brown.

Clypeolabral region densely setose, vertigial region sparsely so; epicranial suture distinct. Antennae rather long (Fig. 17B), reaching the end of body segment 3 when stretched dorsally. In width, head < segment 3 < 4 < collum < segment 5 < 2 < 6–14,

body gently and gradually tapering thereafter. Collum with three transverse rows of setae: 3+3 in anterior, 2+2 in intermediate, and 4+4 in posterior row; a slight furrow laterally in posterior 1/3; caudal corner of paraterga very broadly rounded, slightly upturned, but not drawn behind rear margin (Fig. 17A, B).

Tegument shining, prozonae finely shagreened, postcollum metaterga rugose to rugulose and clearly tuberculate, surface below paraterga finely microgranulate and rugulose. Postcollum metaterga each with two transverse rows of abraded setae: anterior (pre-sulcus) row with 2(3)+2(3) mostly minute tubercles, short wrinkles or traceable only as insertion points, posterior (postsulcus) row with 3–5+3–5 setae borne on low, oblong, rounded tubercles or minute knobs. Tergal setae long, slender, ca. 1/3 of metatergal length. Axial line rather clear, especially so on metazonae.

Paraterga 2 broad, anterior edge evidently convex, lateral edge with three minute incisions in anterior 1/4 to half; posterior edge oblique (Fig. 17A). Anterior edges of following paraterga regularly rounded, lateral edge without incisions, posterior edge oblique to regularly concave, especially strongly concave in segments 14–19 (Fig. 17E–G). Calluses on paraterga 2–4 strongly delimited by a sulcus only dorsally, on following paraterga both dorsally and ventrally.

Following paraterga very strongly developed (Fig. 17A–F), upturned, lying below dorsum until segment 4, following ones above dorsum, caudal corner ranging from obtuse-angular to subrectangular, always and increasingly extending behind rear tergal margin (Fig. 17A–C), from segment 15 on spiniform, long and pointed; in lateral view, paraterga thinner in poreless segments and modestly enlarged in pore-bearing ones.

Ozopores evident, lateral, lying inside an ovoid groove at ca. 1/4 in front of caudal corner. Transverse sulcus usually distinct (Fig. 17A, C, F), complete on metaterga 5–18, incomplete on segment 4, wave-shaped, rather shallow, nearly reaching the bases of paraterga, very faintly ribbed at bottom. Stricture between pro- and metazona rather wide and deep, very faintly ribbed at bottom down to base of paraterga (Fig. 17A, C, F). Pleurosternal carinae complete crests with a sharp caudal tooth on segments 2–4(8), thereafter bulged anteriorly and with a small, sharp, caudal tooth on segments 8–13, the tooth gradually reduced into small, caudally roughly granulate crests until segment 16 (Fig. 17B, D, E). Epiproct (Fig. 17F, G) conical, flattened dorsoventrally, with two evident apical papillae; tip subtruncate; pre-apical papillae very small, but traceable, lying rather close to tip. Hypoproct subtriangular, setiferous knobs at caudal edge evident and well-separated.

Sterna sparsely setose, without modifications except for two rather large and long, fully separated, sternal cones between ♂ coxae 4 (Fig. 17H, I). A paramedian pair of small tubercles in front of gonopod aperture. Legs long and slender, midbody ones ca. 1.3–1.4 times as long as body height, prefemora without modifications, ♂ tarsal brushes present until legs 7.

Gonopods (Fig. 18) simple. Coxa slender and long, with several setae distoventrally. Femorite relatively short, ca. 2 times as long as prefemoral (= strongly setose) part. Femorite slender, moderately curved, “postfemoral” portion demarcated by an oblique lateral sulcus; solenophore with a tridentate tip, middle denticle shorter than terminal

tooth, but longer than a small subterminal lobule; solenomere long, flagelliform, tip barely exposed.

Remark. This species was found only on Mount Bidoup in the summit area, while none of the inspected adjacent forests, even those located at the same altitudes, including a very similar forest on Mount Hon Giao, failed to reveal these millipedes. On Mount Bidoup, this species was quite abundant, occurring mainly on the forest floor, on logs and at bases of tree trunks in the night time, as well as under logs in the daytime.

Key to the species and varieties of *Orthomorpha* currently known to occur in Vietnam, based on ♂ characters (constructed on the key by Likhitrakarn et al. 2011).

- 1 Colouration not strikingly contrasting, calluses being only inconspicuously paler than a dark remaining background (Figs 1A–F, 6A–H, 12A–H, 15A–G, 17A–H)2
- Colouration of metaterga more or less strongly contrasting, with very pale calluses against a very dark remaining background (Figs 3A–G, 9A–H)6
- 2 Each metatergum at least with one, rather evident, transverse row of tubercles near caudal margin (Figs 1A–C, F, 6A–D, F, 17A–C, F)3
- Metaterga smooth and shining, at most faintly rugulose (Figs 12A–D, F, 15A–C, F)5
- 3 Paraterga 1–14 clearly rounded caudolaterally (Fig. 17A–D).....*O. scabra grandis* var. nov.
- All paraterga clearly sharpened and pointed caudolaterally (Figs 1A–D, 6A–E).4
- 4 A single sternal cone between ♂ coxae 4 (Fig. 1H, I). Distal part of gonopod evidently curved and tip bifid (Fig. 2) *O. arboricola*
- Two separated sternal cones between ♂ coxae 4 (Fig. 6I, J). Distal part of gonopod slightly curved and tip trifid (Figs 7, 8)*O. scabra*
- 5 Pleurosternal carinae complete and high crests, each with a sharp caudal tooth on segments 2–7 (♂) (Fig. 12C, E, H). Tarsal brushes present until segment 10 (♂). Tip of gonopod very faintly bifid, with a minute lobule at base (Figs 13, 14)*O. caramel* sp. nov.
- Pleurosternal carinae complete high crests, each with a sharp caudal tooth on segments 2–4 (♂, ♀) (Fig. 15B, D, E). Tarsal brushes present until segment 16 (♂). Tip of gonopod evidently trifid and coxa with a conspicuous, densely setose, rounded, distoventral tubercle (cxp) (Fig. 16A, B).....*O. vietnamica* sp. nov.
- 6 Gonopod tip a single, very small, rounded lobule. Virtually no modifications between ♂ coxae 4. Pantropical..... *O. coarctata*
- Gonopod tip trifid (Figs 4, 5, 10, 11). Modifications between ♂ coxae 4 mostly present (Figs 3H, I, 9I, J)7
- 7 Paraterga largely level with or even elevated above dorsum. Sternal cone between ♂ coxae 4 single, large. Distal part of gonopod evidently curved ... *O. glandulosa*
- All paraterga set below dorsum. Two small, separated, sternal cones between ♂ coxae 4 (Figs 3I, J, 9I, J). Distal part of gonopod slightly curved.....8

- 8 Tarsal brushes present on ♂ legs 1–7. Transverse sulcus complete and distinct until metatergum 17. Sternal cone between ♂ coxae 4 very low. Gonopod telopodite very slender..... ***O. hydrobiologica***
- Tarsal brushes present also past ♂ leg 10. Transverse sulcus complete and distinct until metatergum 18. Sternal cone between ♂ coxae 4 high (Figs 3I, J, 9I, J). Gonopod rather stout (Figs 4, 5, 10, 11)..... **9**
- 9 Larger (29–38.5 (♂) or 31–40.5 mm (♀) long and 3.5–4.3 (♂) or 3.6–4.9 mm (♀) wide, respectively). Pleurosternal carinae complete crests on segments 2–4 (♂, ♀), each with an evident sharp denticle caudally, thereafter increasingly strongly reduced until segment 10 (♂). Tarsal brushes present until legs of ♂ segment 10 ***O. rotundicollis***
- Smaller (up to 23 (♂) or 29 mm (♀) long and 2.9–3.2 (♂) or 3.3–3.9 mm (♀) wide, respectively). Pleurosternal carinae complete crests until segment 7 (♂) or 5 (♀), each with an evident sharp denticle caudally, thereafter increasingly strongly reduced until segment 16 (♂, ♀). Tarsal brushes present until ♂ legs 11..... ***O. rotundicollis subrotundicollis* var. nov.**

Conclusions

The phylogenetic analyses performed here are considered as supporting to the traditional morphological taxonomy since it is a single-gene topology. While it should provide some resolution to disentangling *Orthomorpha* evolutionary history, the limitations of using just one gene are evident. The more so as, due to fixation problems with the DNA, we have only been able to get approximately one-third of the COI gene. In addition, not only sympatric and closely related species, but even certain genera of Paradoxosomatidae sometimes seem to show hybridization (Decker 2018).

As our study shows (Tables 1, 2, Fig. 20), within the tribe Orthomorphini, almost all particularly closely related species belong to the genus *Orthomorpha*. Only *O. coarctata* is set apart and appears to be closer to other genera (Table 2). This is clearly seen also in Figure 20. Again only *O. coarctata* shows a special position clustering closer to *Antheromorpha* Jeekel, 1968 and *Hylomus* Cook & Loomis, 1924 than to other formal congeners. This is hardly surprising though, because that species is often treated as the sole constituent member of a separate genus, *Asiomorpha* Verhoeff, 1939 (cf. Nguyen and Sierwald 2013). However, we prefer to stick here to the traditional, purely morphologically based concept of the Orthomorphini and *Orthomorpha*, taking most of our and all previous molecular evidence as only subordinate, provisional, and auxiliary.

Based on a different genetic marker (16S ribosomal gene), Nguyen et al. (2018) showed that *Antheromorpha* appears as sister group to *Orthomorpha* + *Nesorthomorpha*. The results of our analysis (Fig. 20) suggest, however, that *Orthomorpha* (minus *coarctata*) is sister to *Antheromorpha* + *coarctata* + *Hylomus* (NB: Nguyen et al. (2018) treated *Hylomus* as *Desmoxytes* Chamberlin, 1923).

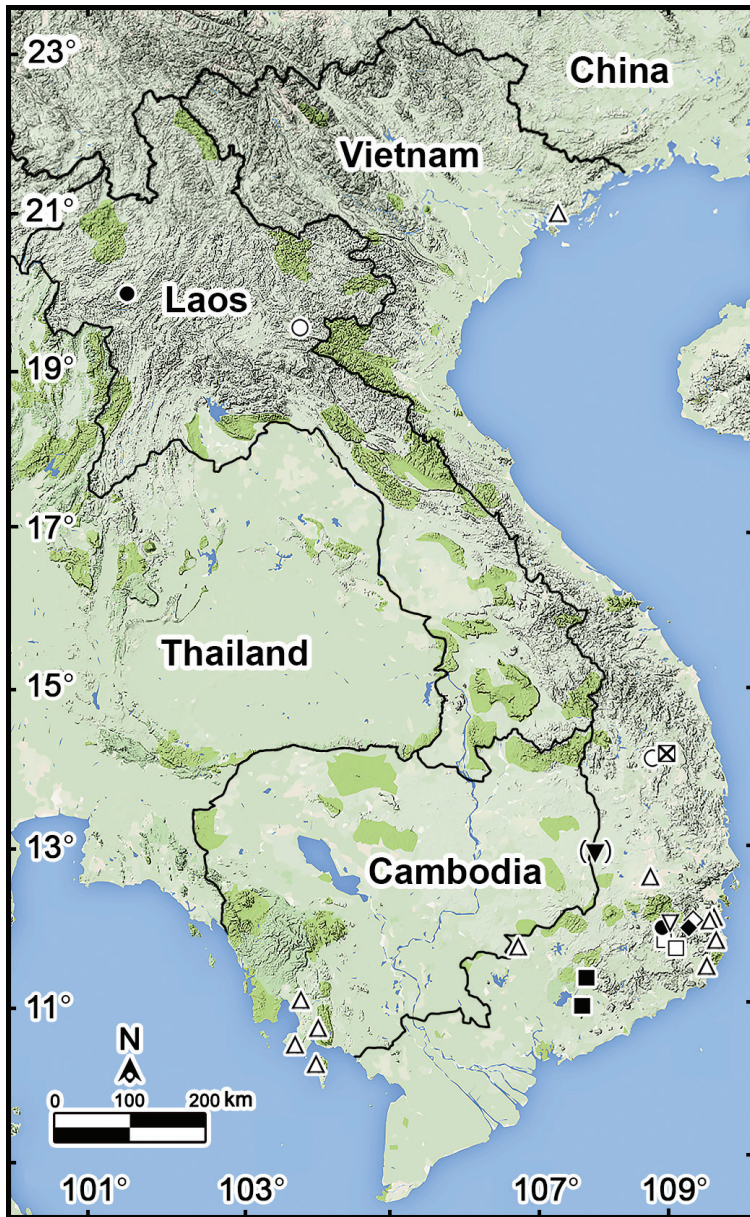


Figure 19. Distributions of *Orthomorpha* species (nine species or varieties, excluding the pantropical anthropochore *O. coarctata* (de Saussure, 1860)) recorded in Vietnam. **Open triangle** *O. hydrobiologica* Attems, 1930 **Filled circle** *O. scabra* Jeekel, 1964 **Open circle** *O. scabra, grandis* var. nov., *O. scabra* Jeekel, 1964 and *O. rotundicollis* (Attems, 1937) **Crossed square** *O. rotundicollis, subrotundicollis* var. nov., *O. caramel* sp. nov. and *O. vietnamica* sp. nov. **Filled Inverted triangle** *O. glandulosa* (Attems, 1937) **Opened Inverted triangle** *O. scabra* Jeekel, 1964 and *O. scabra, grandis* var. nov. **Open diamond** *O. glandulosa* (Attems, 1937) and *O. hydrobiologica* Attems, 1930 **Filled diamond** *O. glandulosa* (Attems, 1937) **Open square** *O. arboricola* (Attems, 1937) and *O. rotundicollis* (Attems, 1937) **Filled square** *O. rotundicollis* (Attems, 1937) and *O. coarctata* (de Saussure, 1860).

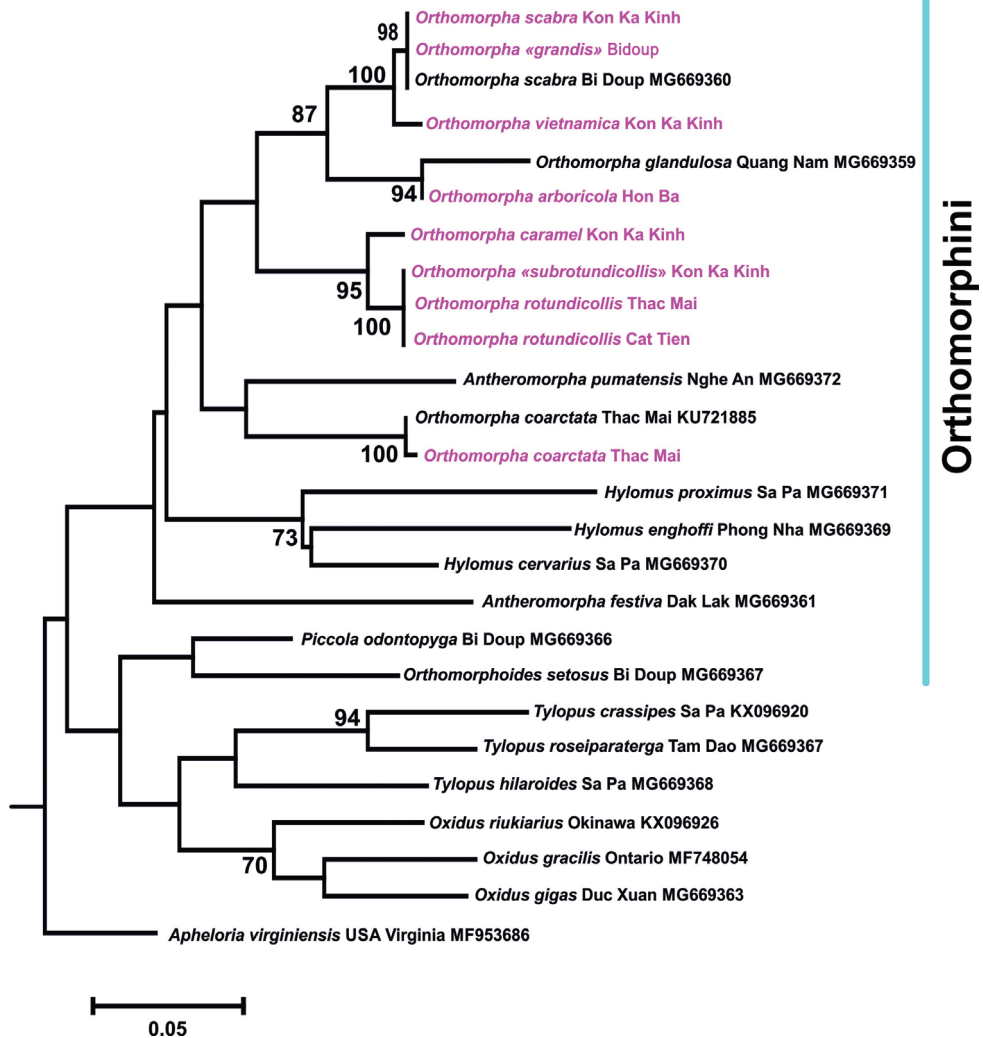


Figure 20. A rooted phylogram based on COI sequences obtained from the relevant literature on Paradoxosomatidae (Nguyen et al. 2017, 2018) and available in GenBank (all given in black, yet with several name updates according to modern taxonomy), combined with new haplotypes (six species and two varieties, these latter put in quotation marks and all highlighted in red). Tree topology was reconstructed using MrBayes software. The values of statistical support are given above the branches only when these exceed 65%.

We present here only a phylogram rooted in *Apheloria virginiensis* (Drury, 1770) (Xystodesmidae) as perhaps the closest outgroup currently available (Fig. 20). Even though the presence or absence of a root can drastically change tree topology, because our unrooted trees completely failed to alter the picture, they have been omitted. The same applies to a number of other rooted phylograms.

However, as noted above, two important taxonomic changes have been accepted following solely our molecular analyses and trees. We simply follow a cautious approach to avoid descriptions of suspicious new taxa/species. These changes concern the

admittance of two morphologically distinct (especially so in body size), but genetically unsupported varieties, *O. rotundicollis subrotundicollis* var. nov. and *O. scabra grandis* var. nov. Because neither is distinguished from their typical forms by average genetic distances (Table 2), they have been allotted no taxonomic status. The other results, however, clearly suggest that more molecular and morphology-based taxonomic work should be paid to *Orthomorpha* in the future. The animals are large-sized, often vividly coloured and readily exposed, thus being easy to spot and collect. In addition, *Orthomorpha* enjoys a recent, colourful, open-access, monographic treatment with an identification key to species (Likhitrakarn et al. 2011).

In any event, although the trees both in Nguyen et al. (2017, 2018) and our present research must only be taken as provisional, they provide a basis for future phylogenetic analyses implementing additional gene regions. Further efforts, both morphology- and molecular-based, are required to reveal and refine the relationships between Orthomorphini (and not only) genera and species. At least for the time being, the Orthomorphini seems to be a monophyletic tribe of Paradoxosomatidae, whereas *Orthomorpha* remains polyphyletic and *Antheromorpha* is paraphyletic (Fig. 20).

A total of eight species and two morphologically distinct varieties of *Orthomorpha* is currently recognized in the fauna of Vietnam, including two new congeners: *O. caramel* sp. nov. and *O. vietnamica* sp. nov. Both new species come from national parks and surrounding areas, thus priority zones for the protection of biodiversity in Vietnam. Several, often two or three species co-exist in one place and are strictly syntopic, this having been observed, e.g., in the pristine tropical forest of the Kon Ka Kinh National Park (Fig. 19).

Most of the Vietnamese species tend to be restricted to the southern parts of Vietnam, except for the likely anthropochore *O. hydrobiologica* which ranges from Hong Gai, Quảng Ninh Province, northern Vietnam to southern Cambodia. The range of *O. coarctata* in Vietnam must be even greater, covering most of the country in man-made habitats. No native species seem to exist in northern Vietnam. A similar distribution pattern concerns Laos where no native *Orthomorpha* seem to populate the northern parts of the country (Likhitrakarn et al. 2014).

There can be little doubt that further new *Orthomorpha* species and/or records await discovery in Indochina, including Vietnam. This seems particularly topical in the still persisting forested areas of that huge region.

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