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A new species of *Pupulina* van Beneden, 1892 (Copepoda, Siphonostomatoida, Caligidae) from *Aetobatus* cf. *narinari* (Pisces, Myliobatidae) from the Pacific coast of Ecuador

Yanis Cruz-Quintana[1,2], Víctor Caña-Bozada[1], Eduardo Suárez-Morales[3], Ana María Santana-Piñeros[1,2]

1 *Departamento Central de Investigación, Universidad Laica Eloy Alfaro de Manabí, Ciudadela Universitaria, Calle 12, Vía San Mateo, Manta EC130802, Manabí, Ecuador* **2** *Grupo de Investigación en Sanidad Acuícola, Escuela de Acuicultura y Pesquería, Facultad de Ciencias Veterinarias, Universidad Técnica de Manabí, Ciudadela Universitaria, Leónidas Plaza EC131402, Bahía de Caráquez, Manabí, Ecuador* **3** *El Colegio de la Frontera Sur (ECOSUR) Unidad Chetumal. Av. Centenario Km. 5.5, Chetumal, Quintana Roo 77014, México*

Corresponding author: *Yanis Cruz-Quintana* (cqyanis@gmail.com)

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Abstract

A new caligid copepod species, *Pupulina mantensis* **sp. n.** is described based on female and male specimens collected from the gills of the myliobatid elasmobranch *Aetobatus* cf. *narinari* Euphrasen, 1790 captured off the Pacific coast of Ecuador. The new species has a unique combination of characters that diverges from its known congeners, including: (i) weakly developed posterolateral processes on the genital complex; (ii) large spines on posterior surface of maxilliped basis (iii) abdomen slender, unsegmented, approximately 1/2 length and 1/5 width of genital complex; (iv) third exopodal segment of leg II with single long naked spine adjacent to minute, naked lateral spine; (v) velum of leg II with adjacent patch of denticles; (vi) caudal rami slightly less than half the length of genital complex; (vii) post-antennal process with robust, posteriorly directed tine, sclerotized stump posterolaterally, and two multi-sensillate papillae located on or near base of process (viii) post-oral process oval. The overall prevalence of *P. mantensis* **sp. n.** on its host was 37.5% and its mean abundance was 1.87 specimens per host. This is the second record of the genus *Pupulina* from Ecuador and the second record of *Pupulina* infecting rays of the Myliobatinae genus *Aetobatus,* of the subfamily Myliobatinae, after its discovery on *A. ocellatus* in Australia, thus confirming this expansion of its previously known host range to a new elasmobranch subfamily.

Keywords
crustaceans, Eagle ray, parasites, taxonomy

Introduction

Species of *Pupulina* Van Beneden, 1892 have been reported from rays of the genera *Mobula* Rafinesque, 1810 and *Manta* Bancroft, 1829 from eastern Pacific, the Gulf of Mexico and South Africa (Wilson 1952, Dippenaar and Lebepe 2013). Members of this caligid genus appear to be restricted to species of the ray family Mobulidae (Dojiri and Ho 2013). *Pupulina* is distinguished from other caligid genera by its possession of: (1) posterolateral processes on the female genital complex , (2) a small conical processes posteromedial to dentiform maxillulary projection, (3) a dentiform or membranous process immediately posterior to the maxilliped, (4) a well-developed endopod of leg I, (5) inflated outer margin of the first and second endopodal segments of leg II and first endopodal segment of leg III, (6) distinctly 3-segmented rami of leg III, and (7) the armature of the exopod of leg III (Wilson 1952, Dojiri and Ho 2013) (8) a 2-segmented endopod of leg I armed with 0-0; 3 setae. The genus includes six valid species (Walter and Boxshall 2016): *Pupulina flores* van Beneden, 1892 from *Manta birostris* Walbaum, 1792 in Azores and Galápagos Islands; *P. brevicauda* Wilson, 1952 and *P. minor* Wilson, 1952 from *Mobula lucasana* Beebe & Tee-Van, 1938 in Santa Catalina, California and *M. diabolus* Shaw, 1804 in Trivandrum, India; *P. cliffi* Dippenaar & Lebepe, 2013 from *Mobula kuhlii* Müller & Henle, 1841 and *M. eregoodootenkee* Bleeker, 1859 in off Umdloti, South Africa; *P. merira* Dippenaar & Lebepe, 2013 from *Mobula kuhlii* and *M. eregoodootenkee* from off Karridene, South Africa, and *P. keiri* Boxshall, 2018 from *Aetobatus ocellatus* Kuhl, 1823 from Moreton Bay, Australia.

The white-spotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790) inhabits inshore areas and coral reef environments (Schluessel et al. 2010). *Aetobatus narinari* is found circumglobally throughout temperate and tropical waters; however, some studies have suggested that this nominal species may represent a species complex containing two or three species (White et al. 2010). As part of a research program on the helminth community parasitizing commercial fish of the Manabí coast, Ecuador, we found adult specimens of *Pupulina* that present an undescribed species. Based on male and female individuals, we herein describe the new species and compare it with its known congeners; and provide new data about the elasmobranch host range of the genus among the elasmobranchs.

Materials and methods

Eight white-spotted eagle rays *Aetobatus* cf. *narinari* were captured and examined between February and June 2015 from Los Esteros beach (0°56'51"S – 80°41'44"W), State of Manabí, on the Pacific Coast of Ecuador. The rays are incidentally caught by artisanal fishermen during trawling in shallow water, but are discarded because they

have no commercial value. However, some rays die during the trawling and are processed for research purposes. The rays were transported to the laboratory of Parasitology at the Universidad Laica Eloy Alfaro de Manabí (ULEAM) and digital photographs of the specimens were immediately obtained. Pictures of the dorsal spot pattern of each morphotype were prepared (Fig. 1A–B) for future identification of the individuals when the presumed species complex of *A. narinari* is solved (methodology followed Marie and Justine 2005). Copepods were obtained from the hosts by removing them with needles and then fixed in 70% ethanol for long-term preservation; they were cleared in gradually increasing concentrations of glycerol and mounted on slides sealed with glycerin jelly.

Drawings were prepared using a camera lucida attached to a CX 31 Olympus compound microscope at the laboratory of Universidad Técnica de Manabí. Unless otherwise stated, measurements are presented in micrometers (μm), and include the range and mean value in parentheses. Morphological terminology follows Boxshall et al. (2002). The ecological terms prevalence, mean abundance, and intensity were determined and used following Bush et al. (1997). Type specimens were deposited in the Zoology Museum of the Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador and the collection of Zooplankton held at El Colegio de la Frontera Sur (ECOSUR), Unidad Chetumal (ECO-CHZ), Quintana Roo, Mexico.

Two adult specimens, one female and one male, were prepared for SEM examination with a TOPCON SM-510 microscope at facilities of ECOSUR in Tapachula, Mexico. The preparation process included dehydration of specimens in progressively higher ethanol solutions (60–100%), critical point drying, and gold-palladium coating (20 nm) following standard methods.

Results

Eight white-spotted eagle rays *A.* cf. *narinari* between 94 and 157 cm total length, were examined, all specimens showed a homogeneous spotted pattern on black disc, with relatively homogeneous spot size except on the head where spots are relatively smaller. Six of them displayed fully white spots (morphotype 1) (Fig. 1A), while the remaining two individuals displayed ocellate white spots (morphotype 2) (Fig. 1B).

Order Siphonostomatoida Thorell, 1859
Family Caligidae Burmeister, 1835
Genus *Pupulina* van Beneden, 1892

***Pupulina mantensis* sp. n.**
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Type host. White-spotted eagle ray *Aetobatus* cf. *narinari* (Myliobatiformes, Myliobatidae).

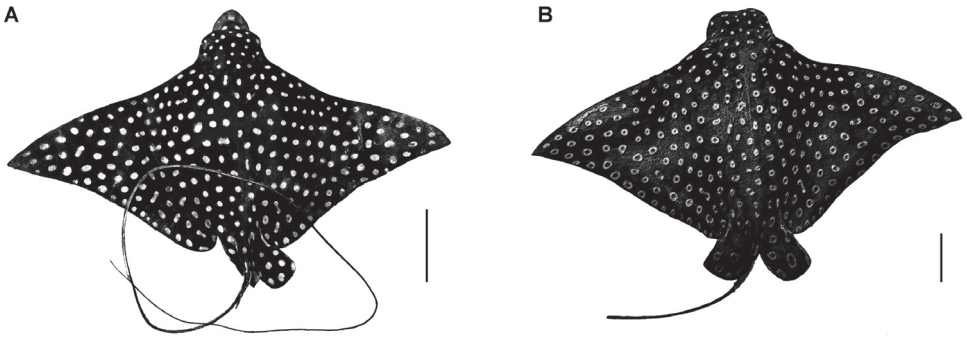

Figure 1. *Aetobatus* cf. *narinari* captured in Los Esteros, Manabí, Ecuador. **A** Morphotype 1, showing solid white spots **B** Morphotype 2, showing ocellated white spots. Scale bars: 10 cm.

Type locality. Los Esteros beach (0°56'51.43"S – 80°41'44.90"O), Manta city, State of Manabí, Pacific coast of Ecuador. The specimens of *A.* cf. *narinari* were incidentally caught by local fishermen by trawling in shallow water (depth < 5 m).

Site on host. Ventral body surface and gill filaments.

Prevalence. Overall prevalence 37.5% (n = 8). Prevalence on morphotype 1, 50% (n = 6). Prevalence on morphotype 2, 0% (n = 2).

Mean abundance. 1.87 parasites per ray (n = 8). 2.5 parasites per morphotype 1 (n = 6).

Mean intensity. 5 parasites per infected ray (n = 3).

Type material. Holotype adult female, undissected specimen preserved in 70%, ethanol vial (QCAZ No.3452); allotype adult male, undissected specimen preserved in 70% ethanol, vial (QCAZ No.3450); paratype adult male, undissected, preserved in 70% ethanol, vial (QCAZ No.3451); two paratype adult females, partially dissected, semi-permanent slides mounted in glycerin, sealed with Entellan (CO-CH-Z-10036); two paratype adult males, partially dissected, semi-permanent slides mounted in glycerin, sealed with Entellan (CO-CH-Z-10037).

Etymology. The species name is a toponym; it refers to the type locality where it was collected, Manta City, off the Ecuadorian Pacific coast.

Diagnosis. The new species shows a unique combination of characters including (i) slight posterolateral processes on the genital complex (Fig. 2A, B); (ii) large cuticular spines located posterior to base of maxilliped (Fig. 2B); (iii) abdomen nearly 1/2 length and 1/5 width of genital complex (Fig. 2A, B); (iv) third exopodal segment of leg II with a single longer naked spine followed by a minute, naked spine on lateral margin (Fig. 4B); (v) velum of leg II bearing patch of denticles (Fig. 4B); (vi) caudal rami slightly shorter than half length of the genital complex (Fig. 2A, B); and (vii) post-antennal process with posteriorly directed robust tine, sclerotized stump posterolaterally, and two multi-sensillate papillae located on or near base of process (Figs 2H, 3A).

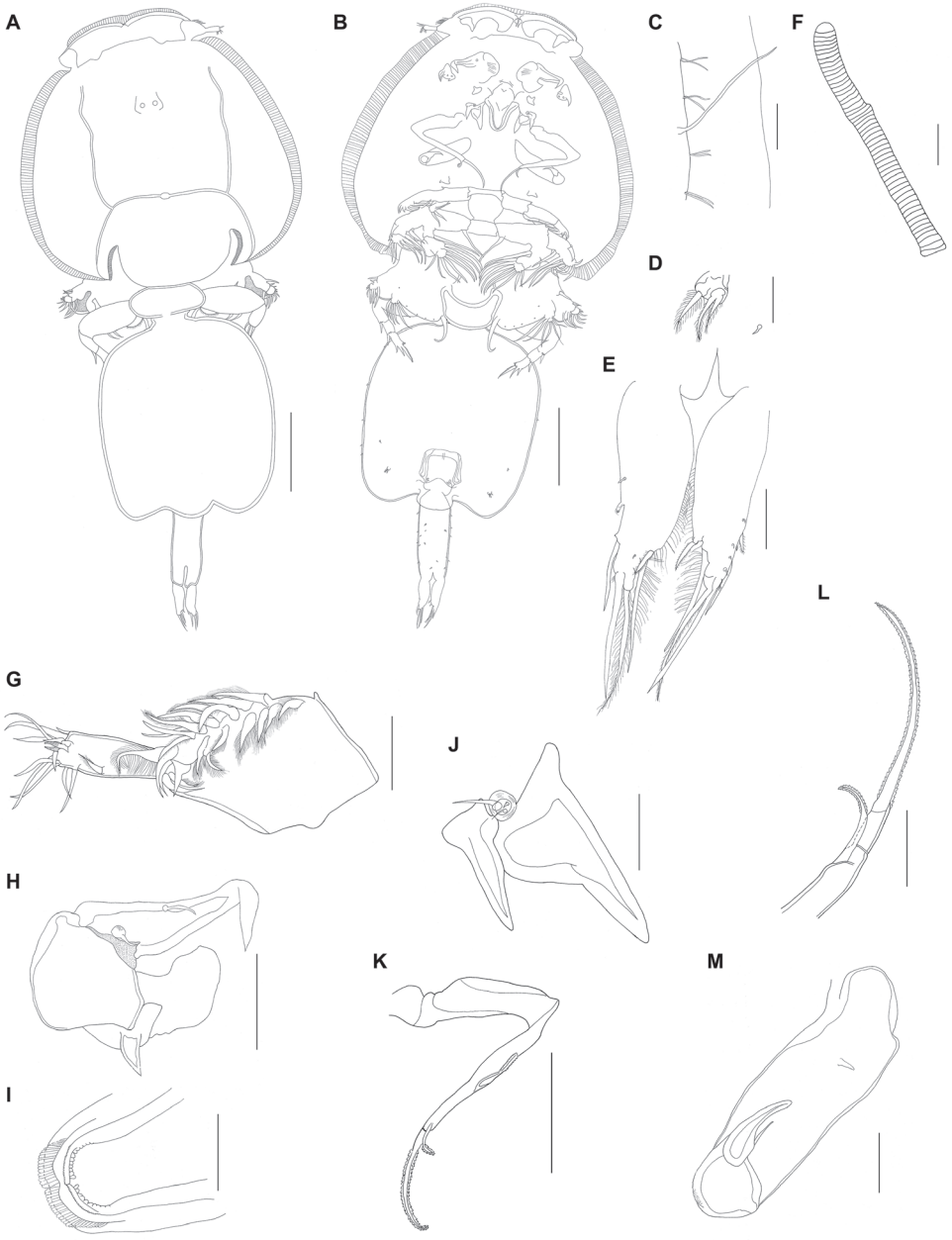

Figure 2. *Pupulina mantensis* sp. n., adult female. **A** habitus, dorsal view **B** same, ventral view **C** lateral border of cephalothorax, ventral view **D** leg V **E** caudal ramus **F** egg sac **G** antennule **H** antenna and post-antennal process **I** mandible **J** dentiform process of maxillule and post-oral process **K** maxilla **L** distal half of maxilla **M** maxilliped. Scale bars: **A, B** 800 μm; **D** 50 μm; **F** 450 μm; **H** 200 μm; **K** 400 μm; **C, E, G, I, J, L, M** 100 μm.

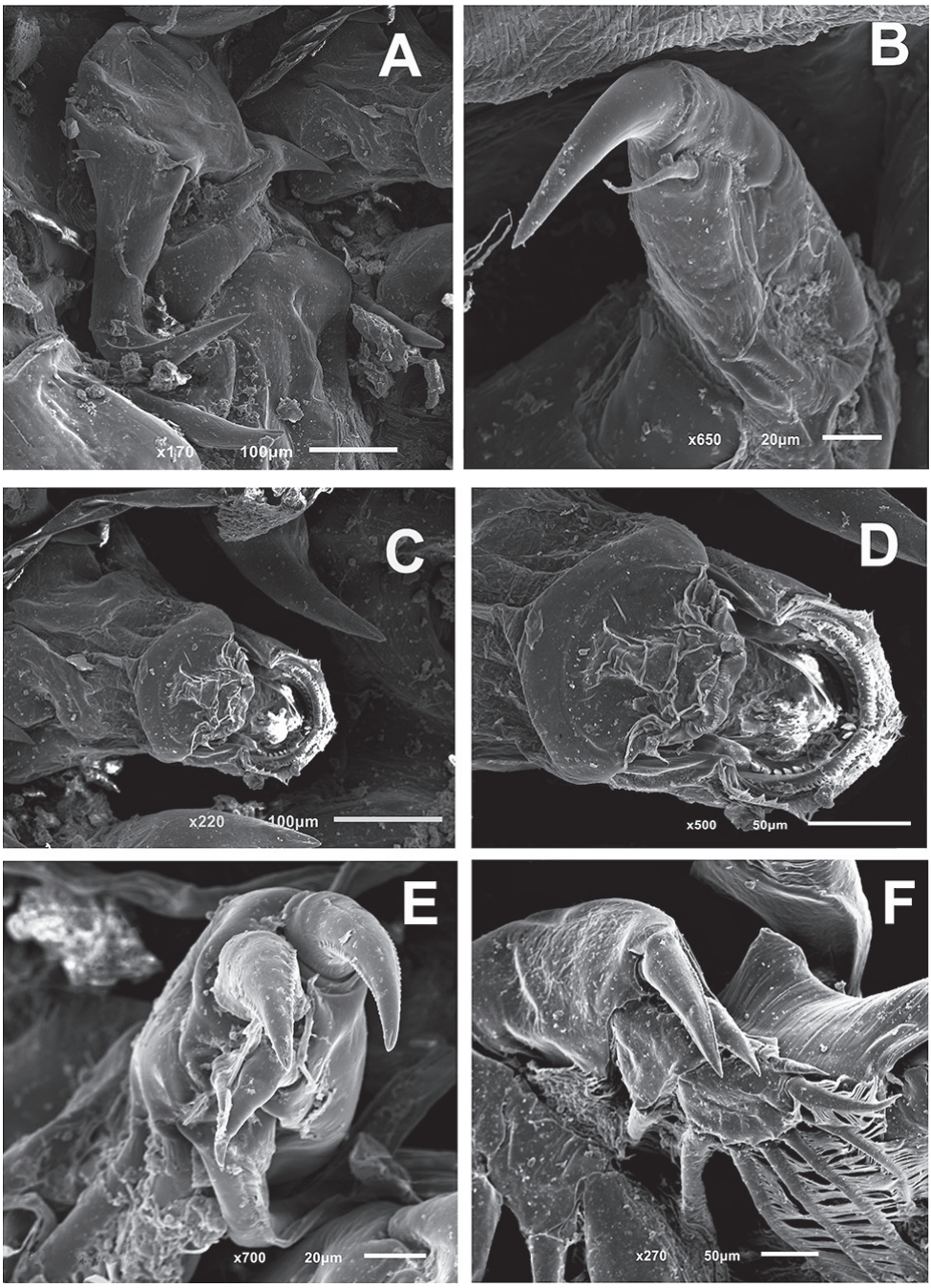

Figure 3 *Pupulina mantensis* sp. n., adult female. **A** antenna and post-antennal process **B** maxilliped **C** mouth tube **D** mandible **E** leg I **F** leg II.

Description (Figs 2–4). *Adult female.* Overall length, from anterior margin of frontal plate to distal margin of caudal rami (excluding egg sacs), 4.2–6.1 mm (5.4 mm; n = 6). Cephalothorax (2.7 mm × 2.8 mm) composed of cephalosome and first three thoracic somites (Fig. 2A–B). Carapace almost circular, slightly longer than wide, with obvious paired frontal plates lacking lunules, with shallow posterior sinuses; posterior margin convex (Fig. 2A). Anterior and lateral margins, as well as posterior sinuses of carapace, rimmed with hyaline, striated membrane (Fig. 2A). One large setule in middle portion of each side and pairs of short setules present at regular intervals along lateral margins (Fig. 2C). Antennules visible posterolaterally to frontal plate. Fourth free thoracic somite approximately twice as wide as long. Genital complex (Fig. 2A) nearly 3/4 length and 2/3 width of cephalothorax, rounded, with posterolateral corners forming slightly protruded processes; ventral surface with irregular pattern of small spinules and vestigial legs V posterolaterally (Fig. 2D). Spermatophores elongate, attached posteromedially on genital complex. Abdomen (Fig. 2A, B) indistinctly 3-segmented, almost 1/2 length and 1/5 width of genital complex; ventral surface with irregular pattern of small spinules. Caudal ramus (Fig. 2E) slender, around 1/2 length of abdomen, narrowed at apex, covered with spinules and ornamented with fringe of setules on inner margin. Armed with one pinnate outer seta nearly 2/3 from base, one naked seta outer distolaterally, one naked shorter and one large pinnate setae inner distolaterally, one pinnate and one naked setae distomedially approximately 2/3 length of caudal ramus. Egg sacs (Fig. 2F) uniseriate, each 2.9 mm long.

Antennule (Fig. 2G) 2-segmented. First segment armed with a double row of 22 stout pinnate setae inserted on anterodistal surface margin; apical segment with single pinnate seta posteromedially plus ten naked setae and three aesthetascs around apex. Antenna (Figs 2H, 3A) 3-segmented. First segment with large, posteriorly directed tine-like process; second segment subrectangular, unarmed; third segment forming curved claw, ornamented with membranous flap near distal hook, segment armed with short basal seta in basal region plus slender, naked setae inserted medially. Postantennal process (Figs 2B, 3A) weakly curved, with posteriorly directed robust tine, sclerotized stump posterolaterally, and two multi-sensillate papillae located on or near base of process. Mouth tube with intrabuccal stylet and strigil (Fig. 3C); mandible (Figs 2I, 3D) comprising four sections, bearing 12 apical teeth on inner margin. Maxillule (Fig. 2J) consisting of palp with one long and two shorter naked setae and large, subtriangular dentiform process. Sclerotized plate lateral to base of palp with a robust dentiform process directed posteriorly. Post-oral process present, consisting of raised, crescent-shaped sclerite located posteriorly to dentiform process. Maxilla (Fig. 2K) brachiform; basis with flabellum at approximately mid-length and distally with calamus and canna. Calamus nearly three times as long as canna, each rimmed with serrated membrane (Fig. 2L). Maxilliped (Figs 2M, 3B) with slender corpus, ornamented with medioventral spine; subchela (claw) slender, weakly curved, around half length of corpus, armed with relatively long naked seta on proximal 1/3. Post-maxillipedal process (Fig. 2B) present, consisting of pair of cuticular spines.

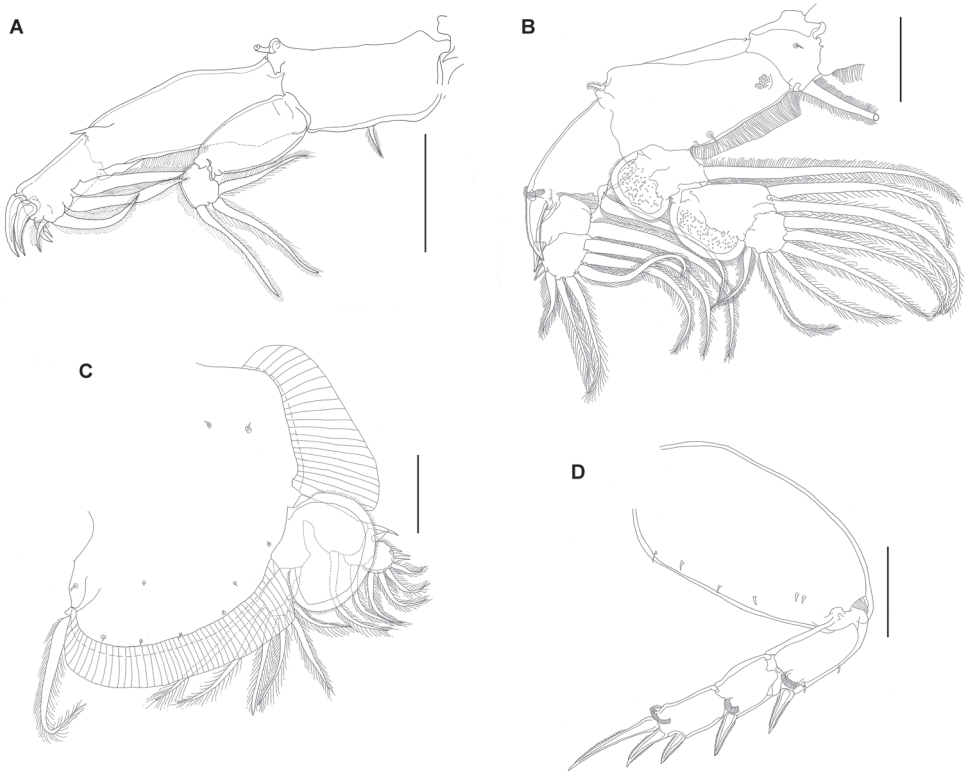

Figure 4. *Pupulina mantensis* sp. n., adult female. **A** leg I **B** leg II **C** leg III **D** leg IV. Scale bars: 200 μm.

Leg I (Figs 3E, 4A) conspicuously biramous; sympod with one outer and one inner pinnate setae. Exopod 2-segmented; first segment armed with small outer distal spine and ornamented with usual row of setules along inner margin; second segment with pinnate apical seta IV much shorter than outermost spine I. Spines I and II bilaterally serrate; spines III shorter, not serrate, with well-developed accessory process. Inner margin with three large plumose setae. Endopod 2-segmented, almost same length as first exopod segment; first endopodal segment medially expanded, robust, unarmed; second segment with three inner pinnate setae and setules around lateral and distolateral margins.

Leg II (Figs 3F, 4B) biramous; sympod armed with short outer pinnate seta distally, plus two small outer setules on proximal position, one naked inner seta distally and long inner pinnate seta proximally; with small patch of spinules on outer proximal surface and inner margin fringed with narrow membrane. Exopod 3-segmented; first segment with setules on medial margin, long, pinnate seta distomedially and long, stout, bilaterally serrate distolateral spine, with pectinate membrane at base; Second segment bearing shorter, serrate spine distolaterally and long, medial pinnate setae; third segment with six pinnate setae decreasing in length toward outer margin and one longer naked spine followed by one minute, naked spine on lateral margin. Endopod 3-segmented; first segment with long pinnate seta distomedially and velum fringed

with short setules; second segment with two long pinnate setae distomedially and velum fringed with short setules; third segment short, rounded, bearing six long pinnate setae decreasing in length toward outer margin and with few setules proximolaterally.

Leg III (Fig. 4C) biramous; sympod with large, pinnate seta medially, fringed with wide membrane along both margins, and ten sensilla scattered on medial surface. Exopod 3-segmented; first segment with slender distolateral serrate spine, distomedial pinnate seta and setules along medial margins; second segment with distolateral spine, distomedial pinnate seta and setules along inner and outer margins; third segment with three short distolateral spines, spine IV shorter than leg II, pinnate setae decreasing in length toward outer margin, and setules along inner and outer margins. Endopod 3-segmented; first segment with large rounded velum covering first two exopodal segments and most of velum inserted on second endopod segment, fringed with short setules; second segment with two long pinnate setae distomedially and small velum fringed with short setules; third segment bearing four long pinnate setae decreasing in length toward outer margin.

Leg IV (Fig. 4D) uniramous, brachiform; sympod robust, with short sensilla on inner surface. First segment with distolateral spinulate spine, pectinate membrane at base and spinules scattered along lateral margin; second segment with distolateral spine and pectinate membrane at insertion; third segment with one subapical and two apical spinulate spines, apical spine being almost twice as long as other two, one small spine and pectinate membrane at base of larger terminal spine. Leg V (Fig. 2D) located posterolaterally on ventral surface of genital complex, consisting of one short plumose seta and group of three short plumose setae on small papilliform process.

Male (Figs 5–6). Body (Fig. 5A) 3.5–3.9 mm mm long (3.7 mm; n = 5) excluding caudal setae. Cephalothorax as in female but smaller (2.0 mm × 2.0 mm). Fourth pedigerous somite two times wider than long. Genital complex somewhat oval in outline. Abdomen 2-segmented with anal somite approximately two times longer than abdominal somite. Caudal rami slender, longer than wide; armed as in female. Body surface with small spinules similar to that in female.

Antennule as in female. Antenna (Figs 5B, 6A) different from that of female, 3-segmented; first segment unarmed; second segment with spine-like process in middle region and two corrugated adhesion pads in each margin of ventral surface (Fig. 6B); terminal segment sharply pointed, claw bearing proximal robust seta with small corrugated adhesion pad, slender seta in middle region and corrugated adhesion pads in the outer margin near base (Fig. 6C). Pair of larger corrugated adhesion pads located anteromedially to antennas (Fig. 6A). Postantennal process as in female. Mouth tube and mandible, similar to female (Fig. 6D). Maxillule similar to female, but only 2 setae in male. Maxilla and Maxilliped as in female.

Legs I, III, and IV as in female (Fig. 6E, F). Leg II as in female, except the second and third exopodal spine, both blunt spines bearing small spinules (Fig. 5C). Leg V (Fig. 5D) located on medial lateral margin of genital complex; consisting of one papilla with three plumose setae along one plumose seta slightly anterior to this group. Leg VI (Fig. 5D) located posterolaterally on ventral surface of genital complex; represented by two plumose setae arising from a single papilla, in addition to one plumose seta near base of papilla.

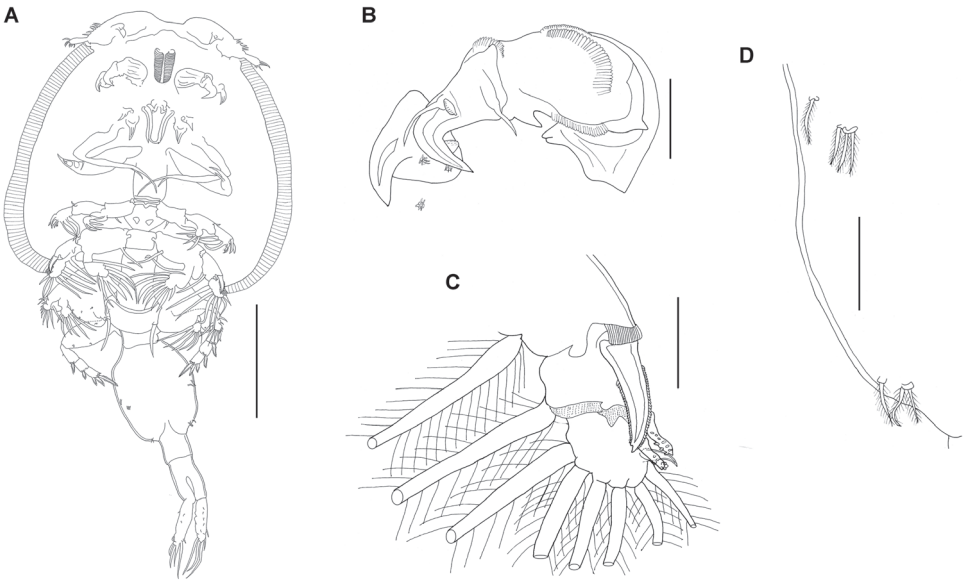

Figure 5. *Pupulina mantensis* sp. n., adult male. **A** habitus, ventral view **B** antenna and postantennal process **C** leg II **D** legs V and VI. Scale bars: **A**, 800 μm; **B–D**, 100 μm.

Remarks. The specimens were identified as belonging to the genus *Pupulina* by their possession of the diagnostic characters described by Dojiri and Ho (2013) including the presence of posterolateral processes on the genital complex of the female, the presence of a small conical process posteromedial to the dentiform projection of the maxillule, the presence of a dentiform or membranous process immediately posterior to the maxilliped, a well-developed endopod of leg I, inflated outer margin of the first and second endopodal segments of leg II and first endopodal segment of leg III, distinctly 3-segmented rami of leg III, and the armature of the exopod of leg III.

The new species, *P. mantensis* sp. n., is mainly characterized by the rounded shape of the genital complex with slight posterolateral processes. Of the six valid species of the genus *Pupulina* worldwide, only *P. merira* have very short, rounded posterolateral processes. However, this species is easily separated from *P. mantensis* sp. n. by the possession of a squarish genital complex, less than half-length and width of cephalothorax (see fig. 4A in Dippenaar and Lebepe 2013), whereas the new species possesses a larger genital complex, rounded, around 3/4 length and 2/3 width of cephalothorax. *Pupulina cliffi* and *P. keiri* differs from *P. mantensis* sp. n. by the lack of posterolateral processes in the genital complex (see fig. 1A in Dippenaar and Lebepe 2013 and fig. 73C in Boxshall 2018, respectively). *Pupulina cliffi* also differs from *P. mantensis* sp. n. by the subquadrate shape of the genital complex with anterolateral corners slightly protruded (see fig. 1A in Dippenaar and Lebepe 2013). *Pupulina keiri* also differs from *P. mantensis* sp. n. by the shape and proportion of the genital complex 1.2 times wider than long, with linear lateral margins and anterolateral corners slightly protruded (see fig. 73C in

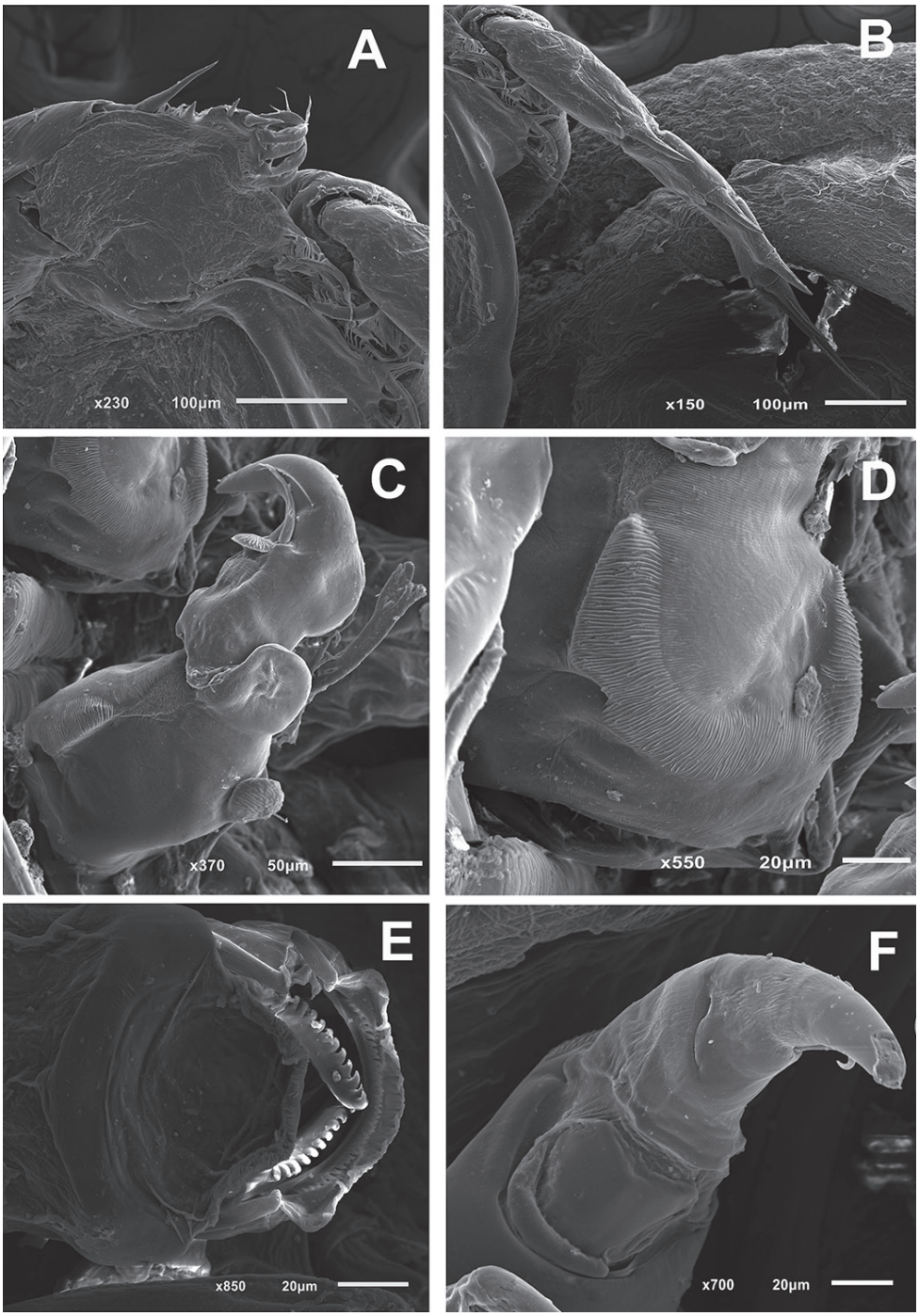

Figure 6. *Pupulina mantensis* sp. n., adult male. **A** leg III **B** leg IV **C** antenna and post-antennal process **D** details of second antennal segment showing adhesion pads **E** mouth tube and mandible **F** terminal segment of antenna showing adhesion pads.

Boxshall 2018), although the author does not mention this last characteristic, whereas in *P. mantensis* sp. n. the genital complex is 1.2 times longer than wider, rounded and without anterolateral corners protruded. According to Wilson (1952) and Dojiri and Ho (2013), the members of *Pupulina* are clearly distinguished from other caligid genera by, among others features, the possession of posterolateral processes on the genital complex. However, *P. cliffi* and *P. keiri* are currently the only species of the genus without posterolateral processes (Dippenaar and Lebepe 2013). *Pupulina flores*, *P. minor,* and *P. brevicauda* are easily separated from *P. mantensis* sp. n. by the possession of large posterolateral processes, extending approximately to midlength of abdomen in *P. flores* and *P. minor*, and beyond the caudal rami in *P. brevicauda*.

In addition to the characteristic mentioned above the new species differs from the other species by bearing sclerotized plate of the maxillule with dentiform process (without process dentiform each other except by *P. flores*), posterolateral process on genital complex not bulging (except by *Pupulina cliffi*, *P. merira,* and *P. keiri*), and sympod of leg IV with few spinules on surface (except by *Pupulina minor* and *P. brevicauda*).

Among members of the genus *Pupulina*, males have been described for four species, i.e., *P. minor*, *P. brevicauda*, *P. flores,* and *P. keiri*. The male of *P. mantensis* sp. n. differs from other species by its possession of leg II with its second and third blunt exopodal spines bearing small spinules, and the presence of corrugated adhesion pads in each margin of ventral surface of the second antennal segment, a characters absent in its male congeners except in *P. keiri*. The male of a new species is more closely related to the male of *P. keiri*, which was described from the Mobulinae ray *Aetobatus ocellatus* caught in Moreton Bay, Australia (Boxshall 2018). However, *P. mantensis* sp. n. is easily distinguished from *P. keiri* by the presence of small corrugated adhesion pads in the basis and the middle region of the terminal antennal segment, feature absent in *P. keiri* (see fig. 76D in Boxshall 2018). Furthermore, *P. mantensis* sp. n. male bears a couple of adhesion pads on the ventral anterior surface, an unusual structure hitherto undescribed in the genus.

Pupulina mantensis sp. n. female genital complex has slightly protruding posterolateral processes. It resembles that found in *P. merira* (see fig. 4A in Dippenaar and Lebepe 2013) and *P. cliffi* (see fig. 1A in Dippenaar and Lebepe 2013). According to Dippenaar and Lebepe (2013), species of this genus can be sorted by the absence, presence or shape of the posterolateral processes on the genital complex. The new species differs from its congeners by several characters, as follows *Pupulina mantensis* sp. n. has a sclerotized maxillulary plate with a dentiform process; the leg II third exopodal segment has two equally long spines; the abdomen represents almost 40% of genital complex; the sympod of leg IV bears a few spinules on ventral surface; second segment lacking distomedial seta or spine. Caudal rami are shorter than the abdomen in *P. mantensis* sp. n., thus diverging from *P. merira* (see fig. 4A–J in Dippenaar and Lebepe 2013).

In the new species, the female abdomen appears to have only one somite, which is an unusual feature in the genus. According to Dojiri and Ho (2013) and Wilson (1952) in the *Pupulina* genus, although the segmentation of the abdomen may be indistinct, it comprises 3-segments. Therefore, the number of segments as well as being a characteristic feature of the genus also can help in the identification of its species.

Identification key to adult females of *Pupulina* species modified from Dippenaar and Lebepe (2013)

1 Posterolateral processes on genital complex absent **2**
– Posterolateral processes on genital complex present **3**
2 Abdomen as long as the genital complex and approximately 3.8 times longer than wide ..... ***P. cliffi***
– Abdomen less than half the length of the genital complex and approximately 2.3 times longer than wide ..... ***P. keiri***
3 Posterolateral processes on genital complex long, extending beyond caudal rami ..... ***P. brevicauda***
– Posterolateral processes on genital complex not extending beyond caudal rami **4**
4 Posterolateral processes on genital complex very short, rounded **5**
– Posterolateral processes on genital complex longer, reaching around mid-length of genital complex **6**
5 Genital complex with a squarish shape, less than half length and width of cephalothorax; abdomen indistinctly 3-segmented; maxillule without dentiform process ..... ***P. merira***
– Genital complex rounded, large, around 3/4 length and 2/3 width of cephalothorax; abdomen in which more than one somite is indistinguishable; sclerotized plate of the maxillule with dentiform process ..... ***P. mantensis* sp. n.**
6 Posterolateral processes with rounded tips; genital complex with a squarish shape and posterior border almost straight until abrupt change into posterolateral processes; abdomen almost same length as genital complex; caudal rami longer than abdomen; sclerotised plate lateral to maxillulary palp, small, not extending to bulging area of praecoxal endite with posteriorly rounded protrusion ..... ***P. minor***
– Posterolateral processes with pointed tips; genital complex with more rounded shape and posterior border gradually extending into posterolateral processes; abdomen longer than genital complex; sclerotised plate lateral to maxillulary palp, long, sharply pointed, reaching beyond bulging area of precoxal endite.. ..... ***P. flores***

Discussion

We found *Pupulina mantensis* sp. n. parasitizing six individuals of the white-spotted eagle ray *A.* cf. *narinari*, belonging to the elasmobranch family Myliobatidae Bonaparte, 1835; subfamily Myliobatinae Bonaparte, 1835. According to Wilson (1952), Dojiri and Ho (2013), and Dippenaar and Lebepe (2013), members of the genus *Pupulina* appear to be specific for species of rays of the family Mobulidae. However, the family Myliobatidae that contains the subfamilies Mobulinae Gill, 1893, Myliobatinae and

Rhinopterinae Jordan & Evermann, 1896 (Bailly 2015) replaced the family Mobulidae (currently uncertain). Five of the six valid species of the genus *Pupulina* (*Pupulina flores* van Beneden, 1892; *P. brevicauda* Wilson, 1952; *P. minor* Wilson, 1952; *P. cliffi* Dippenaar & Lebepe, 2013; *P. merira* Dippenaar & Lebepe, 2013) have been recorded as parasites of the rays *Mobula lucasana* (Beebe and Tee-Van 1938) [= *Mobula thurstoni* (Lloyd, 1908)], *Mobula diabolus* (Shaw, 1804) [= *Mobula mobular* (Bonnaterre, 1788)], *M. kuhlii* (Müller & Henle, 1841), *M. eregoodootenkee* (Bleeker, 1859) and *Manta birostris* (Walbaum, 1792), all belonging to the subfamily Mobulinae. This finding of *P. mantensis* sp. n. as a parasite on the myliobatine ray *A.* cf. *narinari,* confirm the host range (new subfamily) expansion among elasmobranchs described recently for *P. keiri* from *Aetobatus ocellatus* Kuhl, 1823 (Boxshall 2018).

As stated above, we distinguished two morphotypes of *A.* cf. *narinari* based on its dorsal spot pattern. *Pupulina mantensis* sp. n. was found in the ray morphotype 1 only (fully white dorsal spots). *Aetobatus narinari* has been characterized by showing morphological differences related to distinct geographic regions (Compagno et al. 2005, Kyne et al. 2006); moreover, molecular data suggest that *A. narinari* is a species complex with at least two distinct species and probably also two subspecies (Richards et al. 2009). This species complex of *A. narinari* could show a distinctive parasitic fauna among morphotypes. Marie and Justine (2005) first argued that *A. narinari* could be a species complex because of differences in the diversity of parasitic monogenean helminths occurring in populations of *A. narinari* from different geographic regions. The sample size is too small to speculate and advance *P. mantensis* sp. n. as a potential specific parasite for this morphotype. However, we provide the information about each morphotype to make it available when the taxonomic status of *A. narinari* is properly solved.

Pupulina mantensis sp. n. represents the third record of parasitic copepods from *A. narinari* and the second record of the genus *Pupulina* from Ecuador (Wilson 1935, Pollerspöck and Straube 2015). Currently, the metazoan parasite fauna of *Aetobatus narinari* comprises 56 species of different groups: (Cestoda (36 sp.); Monogenea (7 sp.), Nematoda (6 sp.), Isopoda (4 sp.), and Hirudinea (1 sp.)) (Pollerspöck and Straube 2015). Only two copepods species, *Eudactylina hombosteli* Deets, 1994 (Dippenaar and Jordaan 2007) and *Euryphorus suarezi* (Morales-Serna, Rodríguez-Santiago and Gómez 2016), have been reported from *A. narinari*. The first record of *Pupulina* from Ecuador was *P. flores* van Beneden, 1892, from the giant ray *Manta birostris* from Galápagos Islands (Wilson 1935), but the genus may well be represented by other species in this geographical region because of the abundance and diversity of potential hosts belonging to the subfamilies Mobulinae and Myliobatinae (Denkinger and Vinueza 2014).

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RESEARCH ARTICLE

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The spider genus *Pterotricha* in Iran, with the description of a new genus (Araneae, Gnaphosidae)

Alireza Zamani[1], Marjan Seiedy[1], Alireza Saboori[2], Yuri M. Marusik[3,4]

1 *School of Biology, College of Sciences, University of Tehran, Tehran, Iran* **2** *Jalal Afshar Zoological Museum, Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran* **3** *Institute for Biological Problems of the North RAS, Portovaya Str. 18, Magadan 685000, Russia* **4** *Department of Zoology & Entomology, University of the Free State, Bloemfontein 9300, South Africa*

Corresponding authors: *Marjan Seiedy* (mseyyedi@ut.ac.ir); *Yuri M. Marusik* (yurmar@mail.ru)

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Abstract

The spider genus *Pterotricha* Kulczyński, 1903 (Gnaphosidae) is surveyed in Iran. To date, three species of this genus were known in the country: *P. loeffleri* (Roewer, 1955), *P. lentiginosa* (C. L. Koch, 1837) and *P. pseudoparasyriaca* Nuruyeva & Huseynov, 2016. Here two new species are described, *P. kovblyuki* Zamani & Marusik, **sp. n.** (♂, western Iran) and *P. montana* Zamani & Marusik, **sp. n.** (♀, central and southwestern Iran), and *P.* cf. *dalmasi* Fage, 1929 (from Algeria to Jordan) is reported in Iran for the first time. *Pterotricha tikaderi* Gajbe, 1983 **syn. n.** (India) and *P. loeffleri* (Roewer, 1955), **syn. n.** are synonymized with *P. strandi* Spassky, 1936 (hitherto known from Turkmenistan only). The record of *P. lentiginosa* from Iran is apparently based on misidentification. A distribution map of the genus in Iran with new provincial records is provided. In addition, *Iranotricha* Zamani & Marusik, **gen. n.**, a new genus closely related to *Pterotricha*, is described from southeastern Iran with the type species *I. lutensis* Zamani & Marusik, **sp. n.**

Keywords

Aranei, ground spiders, Iranian Plateau, *Iranotricha* gen. n., new species, new synonymy

Introduction

Gnaphosidae is a large, globally distributed family currently comprising 2196 extant species in 124 genera (WSC 2018). Of these, the Old World genus *Pterotricha* Kulczyński, 1903, currently comprises 39 valid species primarily distributed in arid and semi-arid habitats of the Middle East, North Africa, and central Asia (WSC 2018, Levy 1995). These are medium-sized (5–13 mm) Gnaphosinae spiders, which are distinguished from other genera of the subfamily by their very long, rigid cylindrical, tube-shaped anterior spinnerets extending far beyond the other spinnerets (Levy 1995). The first Iranian record of this genus was provided by Roewer (1955) who described *P. loeffleri* (sub *Bobineus l.*, Cithaeronidae) and recorded *P. lentiginosa* (C. L. Koch, 1837) for the first time from Iran. Later, *P. pseudoparasyriaca* Nuruyeva & Huseynov, 2016 was recorded in the country by Zamani et al. (2017). The goals of this paper are to survey all records of this genus in Iran, including two species new to science and one new to the Iranian fauna, and describe a closely related new genus and its type species.

Materials and methods

Specimens were photographed using an Olympus Camedia E-520 camera attached to an Olympus SZX16 stereomicroscope or to the eye-piece of an Olympus BH-2 transmission microscope and a SEM JEOL JSM-5200 scanning electron microscope. Digital images were prepared using "CombineZP" image stacking software (http://www.hadleyweb.pwp.blueyonder.co.uk/). Illustrations of internal genitalia were made after clearing in 10% KOH aqueous solution and exposure for a few minutes in an alcohol/water solution of Chlorazol Black. Lengths of leg segments were measured on the dorsal side. Leg measurements are listed as total length (femur, patella, tibia, metatarsus, tarsus). The description of the palp refers to the left one. All measurements are given in millimetres. Abbreviations not explained in the text are listed below:

ALS anterior lateral spinneret
AME anterior median eye
ALE anterior lateral eye
PME posterior median eye
PLE posterior lateral eye

Depositories

AZMI Agricultural Zoology Museum, Iranian Research Institute of Plant Protection, Tehran, Iran (A. Khalegizadeh)
EMSUM Entomological Museum of Shiraz University of Medical Sciences, Shiraz, Iran (A. Soltani)

MMUE the Manchester Museum of the University of Manchester, Manchester, UK (D. Logunov)
SMF Senckenberg Museum, Frankfurt am Main, Germany (J. Altmann)
ZMFUM Zoological Museum of Ferdowsi University of Mashhad, Mashhad, Iran (O. Mirshamsi)
ZMMU Zoological Museum of the Moscow State University, Moscow, Russia (K. Mikhailov)
ZUCT Zoological Museum of University of Tehran, Tehran, Iran (A. Sari)
ZSI National Zoological Collections, Zoological Survey of India, Calcutta, India

Taxonomy

Gnaphosidae Pocock, 1898

Pterotricha Kulczyński, 1903: 43.

Bobineus Roewer 1955: 773.
Pterotricha: Dalmas 1921: 248; Levy 1995: 944; Murphy 2007: 122–123.

Type species. *Aranea lentiginosa* C. L. Koch, 1837.

Comments. The genus belongs to Gnaphosinae, and like all other members of this subfamily has a serrated keel on chelicera. It is easily distinguished from all other Gnaphosinae by long to very long spinnerets (Figs 1c, 4a, 6a–b, 10b–c, 11g), the male palp with squarrose tibial apophysis and a heavily sclerotized (non-membranous) and pointed "conductor". Most of the species have a stylus on embolus (vs. lacking in all other genera).

Distribution. The genus is known from Spain to South Africa, to western India, with a single, doubtful record of *Pterotricha saga* (Dönitz & Strand, 1906) from Japan (most likely belonging to *Callilepis* Westring, 1874).

Pterotricha cf. *dalmasi* Fage, 1929

Figs 1, 16

Pterotricha dalmasi: Levy 1995: 948, f. 71–76 (♂♀).

Material examined. IRAN: 1♀ (ZUCT), *Hormozgan Province*: Minab, sand dunes of Minab beach, February 2018 (A. Zamani).

Diagnosis. This species closely resembles *P. conspersa* (O. Pickard–Cambridge, 1876). Males are diagnosed by the different shape of the base of the tegular apophysis (sub-circular in *P. dalmasi* vs. irregularly shaped in *P. conspersa*) and the retrolateral tibial apophysis (more massive in *P. conspersa*), while females can be distinguished by

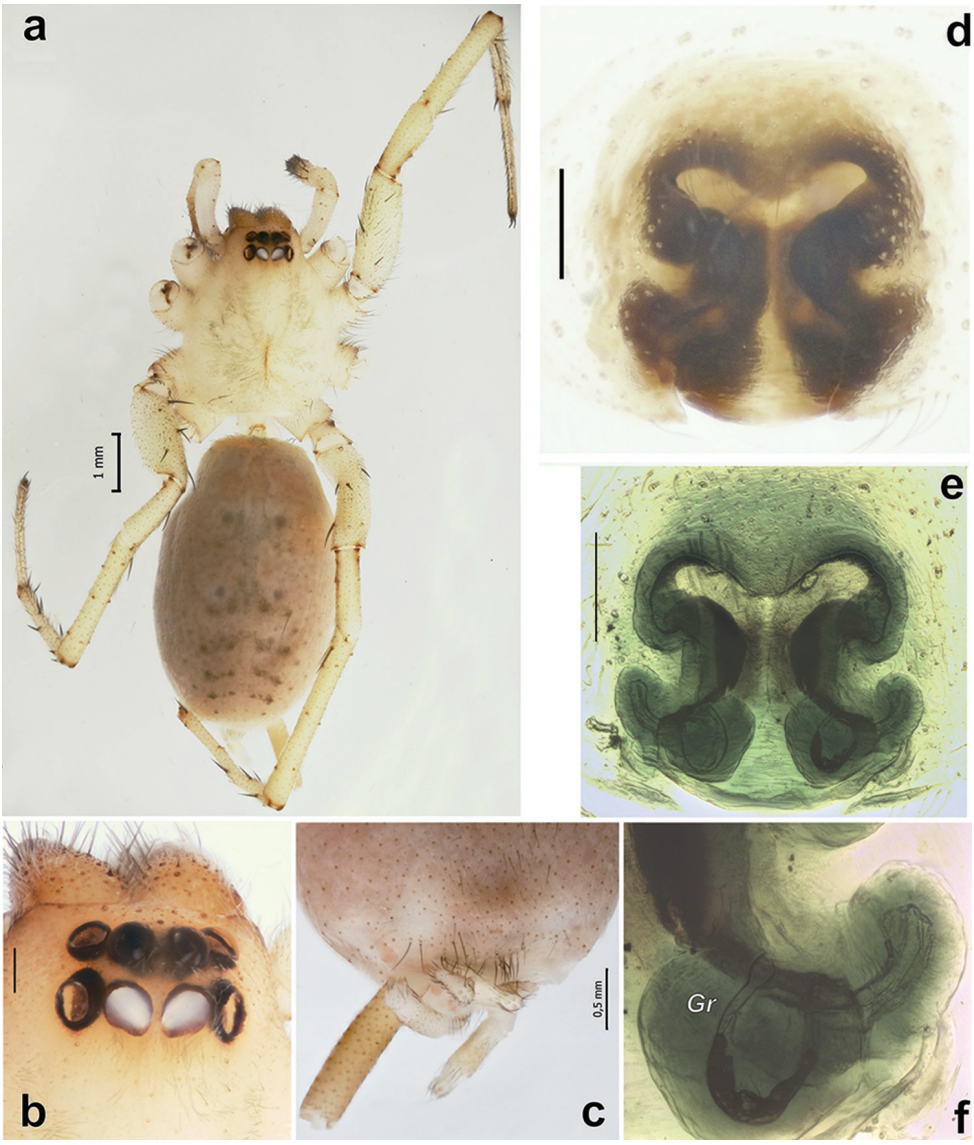

Figure 1. Female of *Pterotricha dalmasi* (?). **a** habitus, dorsal **b** cephalic part of carapace, dorsal **c** spinnerets, ventral **d, e** epigyne, ventral and dorsal **f** right receptacle, dorsal. Scale bars = 0.2 mm if not otherwise indicated. Abbreviation: *Gr* receptacular gland.

the different shape of the epigynal septum (anterior depression pointed posteriorly and median curves pointed anteriorly or anterolaterally in *P. dalmasi* (Figs 1d, e) vs. the anterior depression pointed anteriorly and median curves pointed posteriorly in *P. conspersa*) (Levy 1995).

Description. Well described by Levy (1995).

Comments. The species was described from males. Levy (1995) was the first to describe females of this species. He provided figures of two "forms" of the epigyne (Levy 1995: figs 74–75). The epigyne illustrated on fig. 75 is rather similar to the epigyne of our specimen. Apparently, the small (tiny) receptacular gland present in the Iranian specimen was overlooked in the specimens from Israel, and perhaps the female specimens illustrated by Levy (1995) belong to two different species. A lack of samples containing both males and females does not allow us to conclude which of the two "forms" of the females are conspecific with *P. dalmasi*.

Records in Iran. Hormozgan (Fig. 16).

Distribution. From Algeria to Iran (first record), south to Sudan and Saudi Arabia (WSC 2018).

***Pterotricha kovblyuki* Zamani & Marusik, sp. n.**

http://zoobank.org/E55B2388-5DB7-4BAE-8355-5F3AB9072CD3

Figs 2, 16

Type. Holotype ♂ (AZMI), IRAN: *Ilam Province*: Mehran County, 2001 (F. Mozaffarian).

Etymology. This species is named after the Ukrainian arachnologist Mykola Kovblyuk in recognition of his contributions to the taxonomy of gnaphosid spiders.

Diagnosis. The new species is most similar to *P. dalmasi* by lacking a stylus on the embolus, the similar shape of the tegular apophysis and the tibial apophysis with a spine like tip (cf. Figs 2e–g and figs 71–73 in Levy 1995). The two species can be separated by the thinner tip of the conductor and the tegular apophysis which is longer than wide in the new species, vs. wider than long in *P. dalmasi* (cf. Fig. 2e and figs 71–73 in Levy 1995).

Description. Male. Total length 6.7. Carapace 2.8 long, 2.25 wide. Eye sizes and interdistances: AME: 0.21, ALE: 0.17, PME: 0.24, PLE: 0.20, PME–PME: 0.05. Carapace, sternum, labium, chelicerae, and maxillae light brown without any distinct patterns, with darkening in the ocular area. Abdomen light grey with distinct pale cardiac mark with three pairs of dots on either side. Legs the same colour as the carapace and without annulations. Scopula on metatarsi and tarsi indistinct. Tarsi of legs I-II (legs III and IV missing) with cuticular cracks (pseudosegmented). Leg measurements: I: 12.1 (3.1, 1.25, 2.5, 3.2, 2.05), II: 12.55 (2.95, 1.2, 2.35, 3.65, 2.4), III: absent, IV: absent.

Palp as in Figs 2c–g; patella almost as long as tibia, patella+tibia as long as cymbium; tibial apophysis with one arm, posterior part rounded, anterior part with a spine like tip; tegular apophysis (*Ta*) longer than wide with retrolateral lobe and large base; conductor (*Co*) large, tip rounded; embolus (*Em*) simple and without a stylus.

Female. Unknown.

Record in Iran. Ilam (Figure 16).

Distribution. Western Iran.

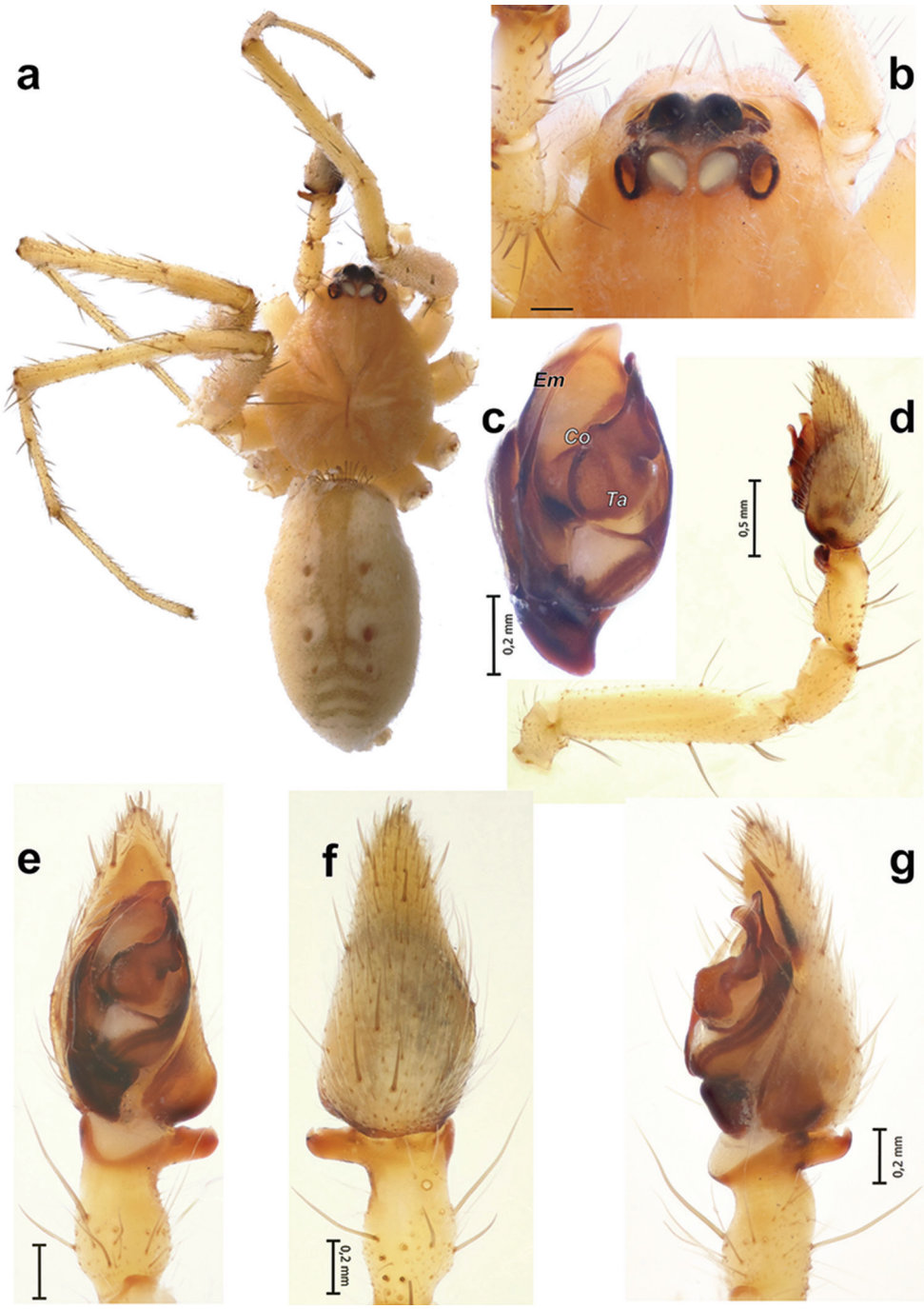

Figure 2. *Pterotricha kovblyuki* Zamani & Marusik sp. n., male. **a** habitus, dorsal **b** cephalic part of carapace, dorsal; **c** bulb, ventrolateral **d** palp, retrolateral **e–g** palp, ventral, dorsal and retrolateral. Scale bars = 0.2 mm if not otherwise indicated. Abbreviations: *Co* conductor; *Em* embolus; *Ta* tegular apophysis.

***Pterotricha lentiginosa* (C. L. Koch, 1837)**

Pterotricha lentiginosa: Roewer 1955: 772.

Comments. This species was recorded in Iran (from two localities in the provinces of East Azarbayjan and Fars) by Roewer (1955) based on two female specimens. Considering Roewer's well-known taxonomic mistakes, and that the Iranian record is considerably far from its known range (Crete is the easternmost known locality), it is probable that this species was misidentified (Mozaffarian and Marusik 2001). Unfortunately, the specimens were not located at SMF and are probably lost (Julia Altmann pers. comm.).

***Pterotricha montana* Zamani & Marusik, sp. n.**
http://zoobank.org/4C946927-3277-4247-8FAE-867F36E799BD
Figs 3, 11g, 16

Types. Holotype ♀ (MMUE), IRAN: *Kohgiluyeh & Boyer Ahmad Province*: Semoron, May 2017 (A. Hosseinpour); Paratypes: ♀ (EMSUM), IRAN: *Kohgiluyeh & Boyer Ahmad Province*: Shadegan, May 2017 (A. Hosseinpour); ♀ (ZUCT), IRAN: *Isfahan Province*: Qamsar & Barzok Protected Area, 55 km SW of Qamsar, 14 km NE Kamoo, Gargash Mountain, 33°39'59"N, 51°19'44"E, 3302 m, May 2016 (P. Ponel).

Etymology. The specific epithet refers to the montane habitat of the species.

Diagnosis. This species differs from other congeners by the epigynal plate being wider than long (vs. longer than wide in the remaining species) and the short septum (as long as receptacle length and as long as wide vs. a long septum that is longer than wide and longer than receptacle) (Figs 3d, e).

Description. Female (holotype). Total length 10.95. Carapace 4.1 long, 1.65 wide. Eye sizes and interdistances: AME: 0.14, ALE: 0.20, PME: 0.21, PLE: 0.17, PME-PME: 0.05. Carapace, sternum, labium, chelicerae, and maxillae light brown without any distinct patterns, with scattered short setae and darkening in the ocular area. Chelicerae with one anterior tooth and bifurcated posterior keel. Abdomen light grey with short grey setae and scattered dark patches dorsally. Anterior lateral spinnerets dark brown, relatively short, 3.7 x longer than wide, spaced by less than two diameters of a single ALS, with long spigots of the piriform glands. Legs yellow. Leg measurements: I: 12.85 (3.55, 1.7, 2.7, 2.7, 2.2), II: 12 (3.2, 1.50, 2.55, 2.6, 2.15), III: 11.4 (3.05, 1.45, 2.25, 3.0, 1.65), IV: 14.9 (3.9, 1.55, 3.15, 4.1, 2.2).

Epigyne as in Figs 3d–e; sclerotized part wider than long, septum short, about the length of the receptacle, as long as wide; fovea square; receptacles (*Re*) elongate oval, diverging anteriorly, receptacular gland (*Gr*) massive.

Male. Unknown.

Ecology. This species lives in the mountainous plains of Zagros Mountains.

Records in Iran. Isfahan, Kohgiluyeh & Boyer-Ahmad (Figure 16).

Distribution. Central and southwestern Iran.

Pterotricha pseudoparasyriaca Nuruyeva & Huseynov, 2016

Figs 4, 5, 16

Pterotricha pseudoparasyriaca Nuruyeva & Huseynov, 2016: 214, f. 1–5, 11–15 (♂♀); Zamani et al. 2017: 63, f. 3B (♂).

Material examined. IRAN: 1♀ (ZMFUM), *Ardebil Province*: Aghkand-Khalkhak Rd., Karoo Vil., 37°24'3.6"N 48°07'4.8"E, 30 May 2017 (A. Abedini); 1♂ 1♀ (ZUCT), *Kordestan Province*: Sanandaj, Noshur, May 2017 (A. Zamani); 2♀ (ZUCT), *Kordestan Province*: Marivan, Bardeh Bakakar, May 2017 (A. Zamani).

Diagnosis. Among Iranian *Pterotricha*, this species is most similar to *P. strandi*, which has a stylus of the embolus, a broad conductor, and a long septum. Males of the two species differ by the shape of the tibial apophysis (tapering in *P. pseudoparasyriaca* vs. rectangular in *P. strandi*), a blunt tip of conductor in *P. pseudoparasyriaca* vs. a sharply pointed tip in *P. strandi*, as well as by the shape of the tegular apophysis (with an elongate base in *P. pseudoparasyriaca* vs. unmodified in *P. strandi*) (Figs 4d, 5a–c). Females of *P. pseudoparasyriaca* are easily distinguished from those of *P. strandi* by having a looped copulatory duct and a distinct, square epigynal fovea vs. copulatory duct short, unlooped and indistinct fovea (Figure 4e, f).

Description. Well-described by Nuruyeva and Huseynov (2016).

Records in Iran. Zanjan. New records: Ardebil, Kordestan (Figure 16).

Distribution. Central eastern and southeastern Azerbaijan, western and northwestern Iran.

Pterotricha strandi Spassky, 1936

Figs 6–9, 15c, 16

Pterotricha strandi Spassky, 1936: 37, f. 1–3 (♂); Marusik 2016: 279, f. 1–13 (♂).
Bobineus löffleri Roewer, 1955: 774, f. 23a–g (♂). **Syn. n.**
Pterotricha tikaderi Gajbe, 1983: 95, f. 1A–H (♂). **Syn. n.**
Pterotricha loeffleri: Marusik et al. 2013: 349, f. 1–7, 11–16 (♂♀); Zamani 2015: 13; 2016: 225.

Type. Holotype of *Pterotricha tikaderi* (Figs 6c–f): INDIA: ♂ (ZSI), *Gujarat State*: Dwarki Dist. Jamnagar, 16.02.1975 (V.F. Srivastava).

Other material examined. IRAN: 1♂ (ZUCT), *Isfahan Province*: Shahreza County, March 2015 (A. Zamani); 2♂1♀ (ZUCT), *Hormozgan Province*: Hormuz Island, January 2014 (A. Zamani); 1♀ 1 juv. (ZUCT), *Hormozgan Province*: Parsian, January 2016 (A. Zamani); 1♂1♀ (ZUCT), *Kerman Province*: Baft, Jafriz cave, 14.10.2016 (M.J. Malek Hosseini); 1♀ (EMSUM), *Kohgiluyeh & Boyer-Ahmad Province*: Shadegan, 30°56'24"N, 50°91'99"E, April 2017 (A. Hosseinpour); 1♂ (EMSUMS), same locality and collector, May 2017; 1♂ (EMSUMS), *Kohgiluyeh & Boyer-Ahmad Province*:

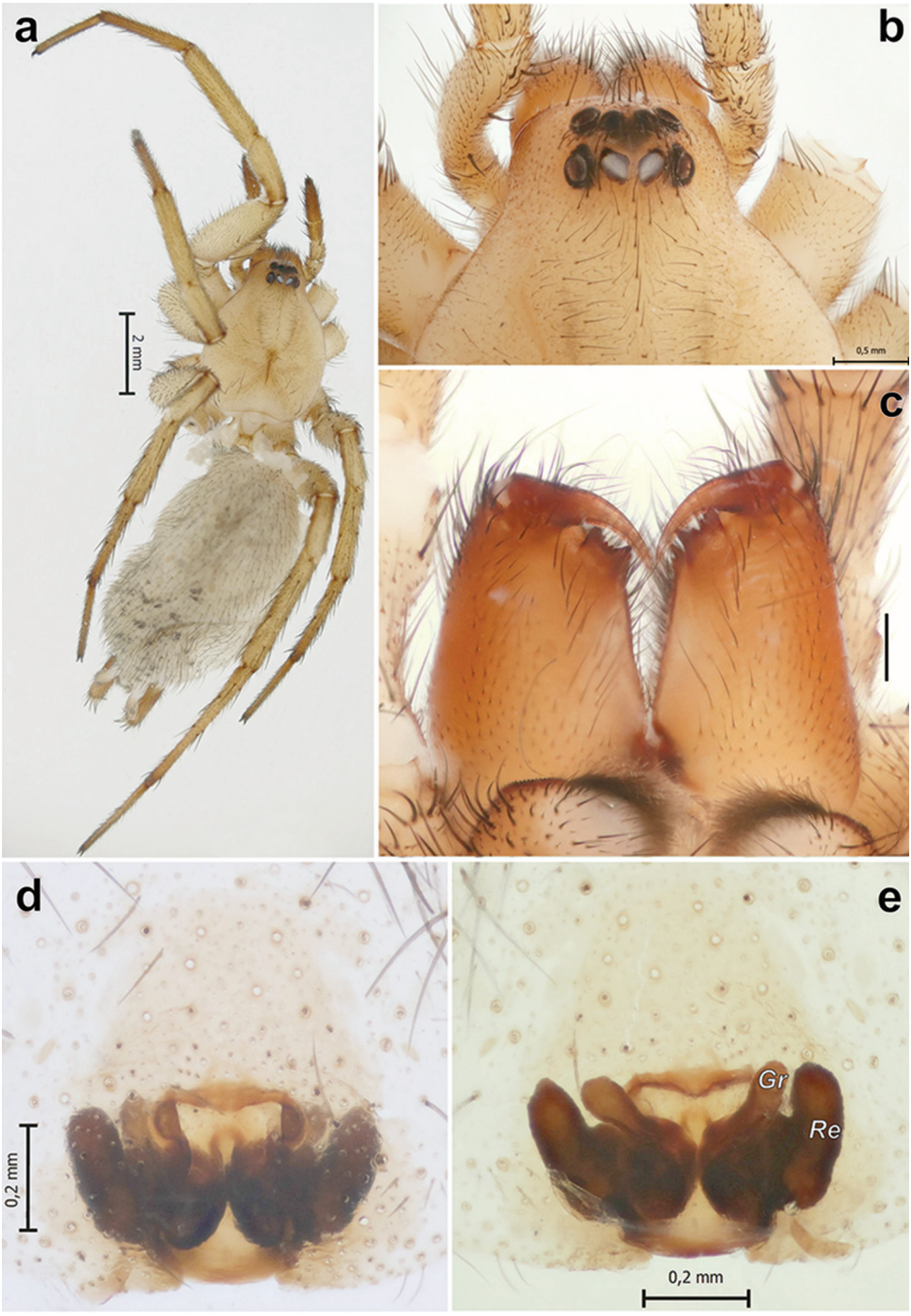

Figure 3. *Pterotricha montana* Zamani & Marusik sp. n., female. **a** habitus, dorsal **b** anterior part of prosoma, dorsal **c** chelicerae, retrolateral **d, e** epigyne, ventral and dorsal. Scale bar = 0.2 mm if not otherwise indicated. Abbreviations: *Gr* receptacular gland; *Re* receptacle.

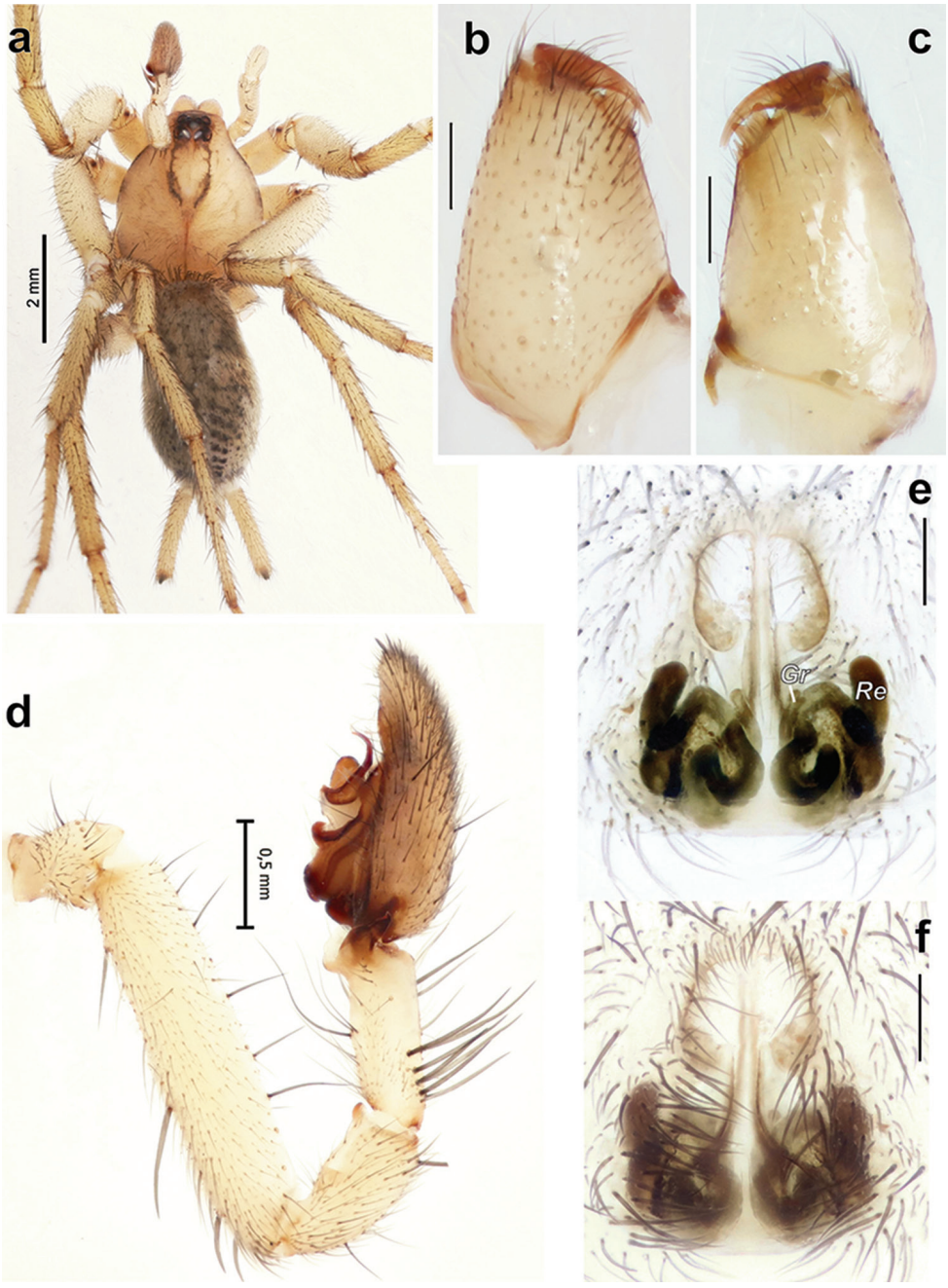

Figure 4. *Pterotricha pseudoparasyriaca*. **a** male habitus, dorsal **b–c** male chelicera, pro- and retrolateral **d** palp, retrolateral **e, f** epigyne, dorsal and ventral. Scale bars 0.2 mm if not otherwise indicated. Abbreviations: *Gr* receptacular gland; *Re* receptacle.

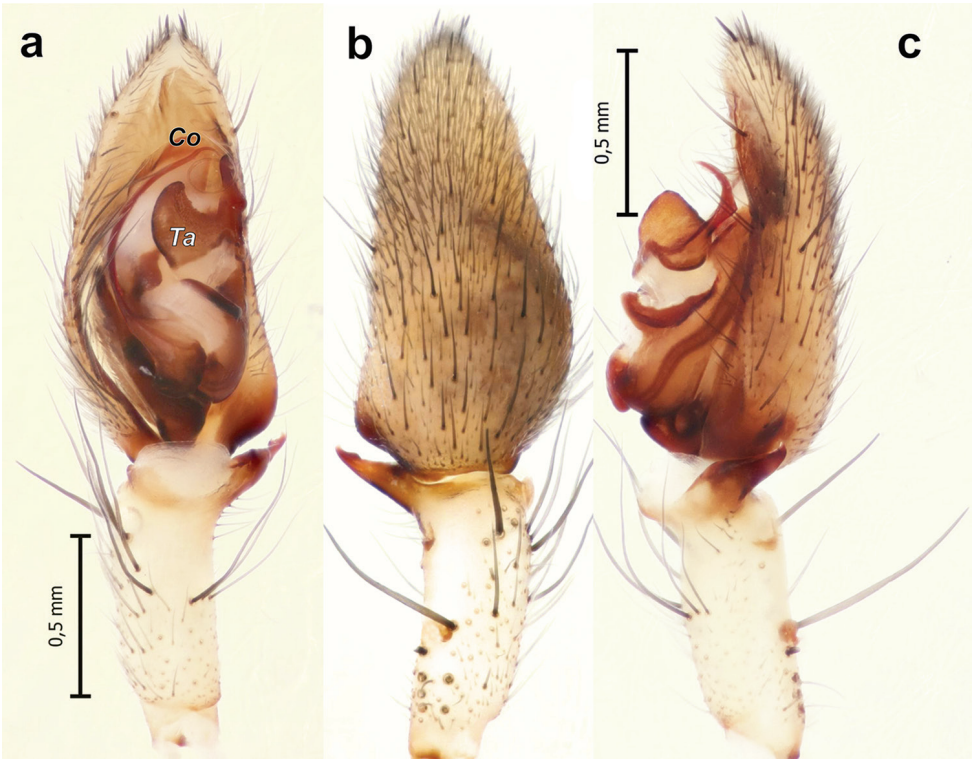

Figure 5. Male palp of *Pterotricha pseudoparasyriaca*. **a** ventral **b** dorsal **c** retrolateral. Abbreviations: *Co* conductor; *Ta* tegular apophysis.

Pasheh Kaan, 30°31'80"N, 50°81'60"E, April 2017 (A. Hosseinpour); TURKMENISTAN: 14♂ (ZMMU), SW Kopetdagh Mts, 12 km W of Kara-Kala, valley of Su River, 38°24'N, 56°07'E, mountain slope, 24.04.1991 (V.V. Dubatolov).

Diagnosis. Males of this species can be diagnosed from congeners by the square tibial apophysis with sharp corners and strongly erect spines on the palpal tibia (Figs 6c–f, 7a, b, 8a–c). Females of *P. strandi* have massive, unknot looped receptacles and long, sticklike glands that differ from most of congeners (Figure 8d, e).

Description. Well described by Marusik et al. (2013) and Marusik (2016). The male of this species has very long and widely spaced anterior lateral spinnerets, 8 × longer than wide, spaced by 2.5 diameters of a single ALS.

Comments. *Pterotricha loeffleri* was first described in *Bobineus* Roewer, 1955 (Cithaeronidae) based on the holotype male collected in Tehran Province, and later transferred to *Pterotricha* by Platnick (1991). Marusik et al. (2013) studied the type material and one female specimen collected in Bushehr Province and provisionally considered them conspecific due to the similarities in size and eye pattern and the similarities of the epigyne with the closely related *P. strandi*. Considering that the latter species is poorly illustrated and that the type material was not located, the authors

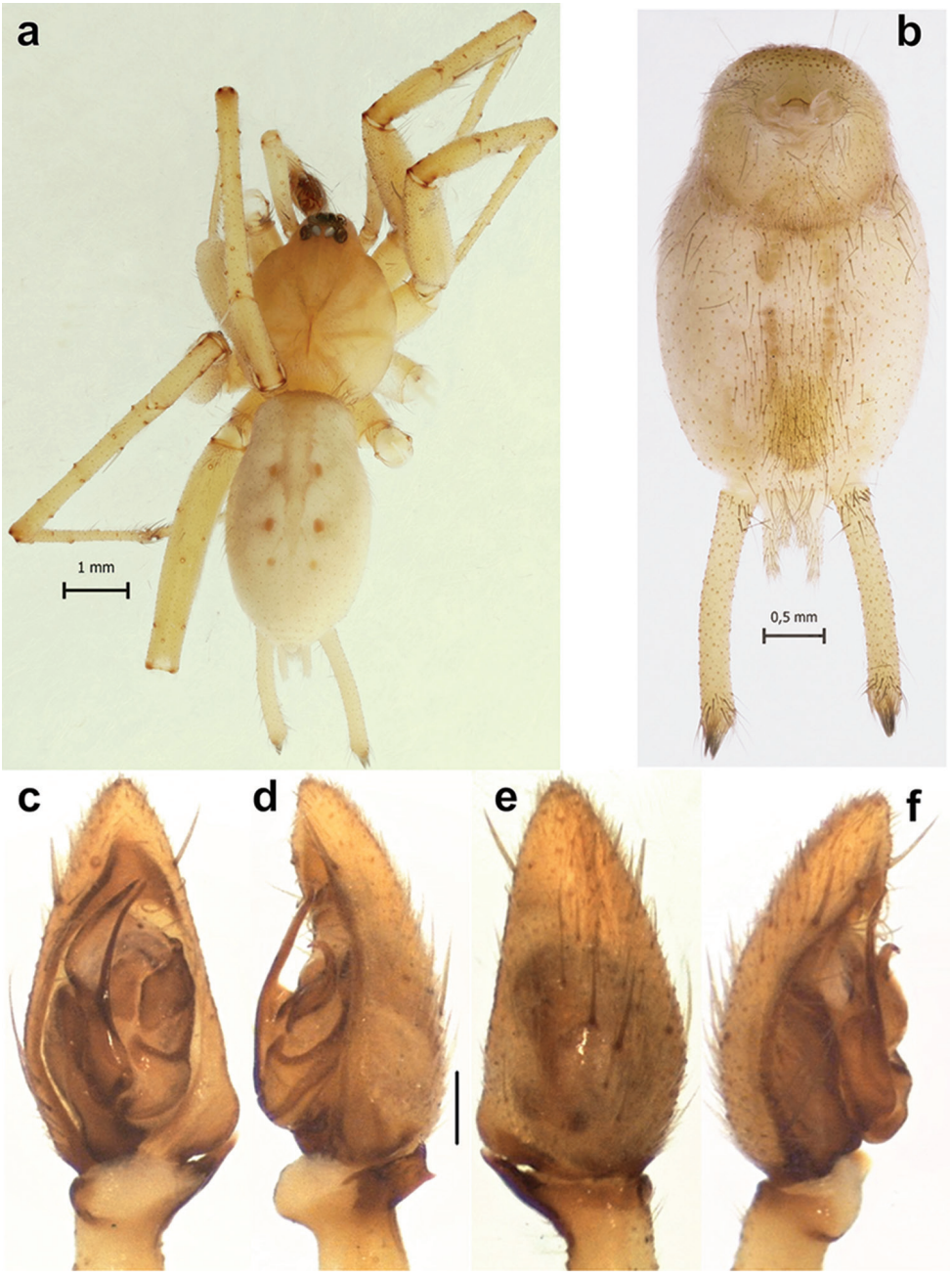

Figure 6. Habitus of male *Pterotricha strandi* (**a–b**) and male palp of the holotype of *P. tikaderi* (**c–f**). **a** whole specimen, dorsal **b** abdomen, ventral **c–f** ventral, retrolateral, dorsal and prolateral. Scale bar = 0.2 mm if not otherwise indicated.

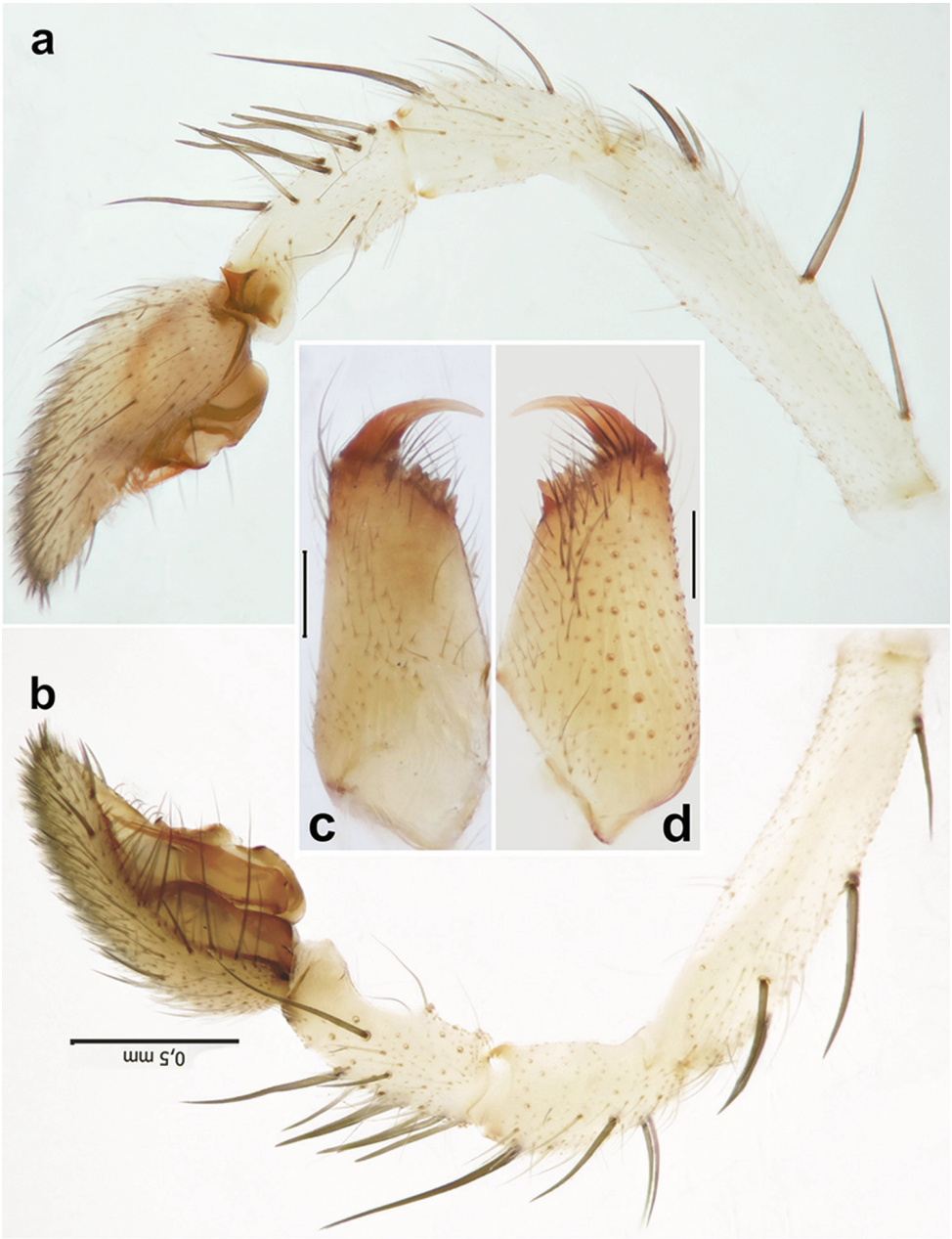

Figure 7. Male of *Pterotricha strandi*. **a, b** palp, retro- and prolateral **c, d** chelicera, retro- and prolateral. Scale bars = 0.2 mm if not otherwise indicated.

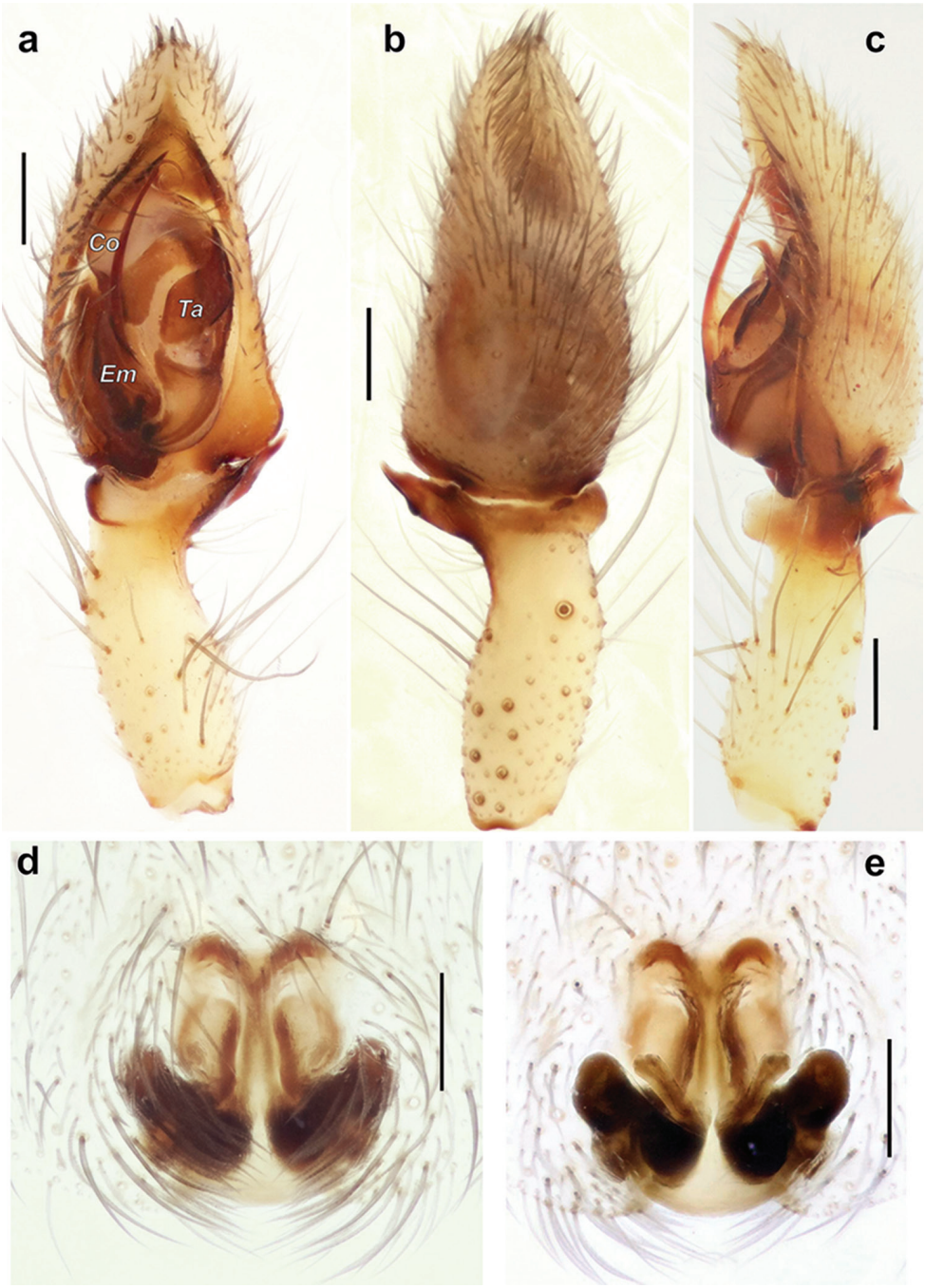

Figure 8. Copulatory organs of *Pterotricha strandi*. **a–c** male palp, ventral, dorsal and retrolateral **d, e** epigyne, ventral and dorsal. Scale bars = 0.2 mm. Abbreviations: *Co* conductor; *Em* embolus; *Ta* tegular apophysis.

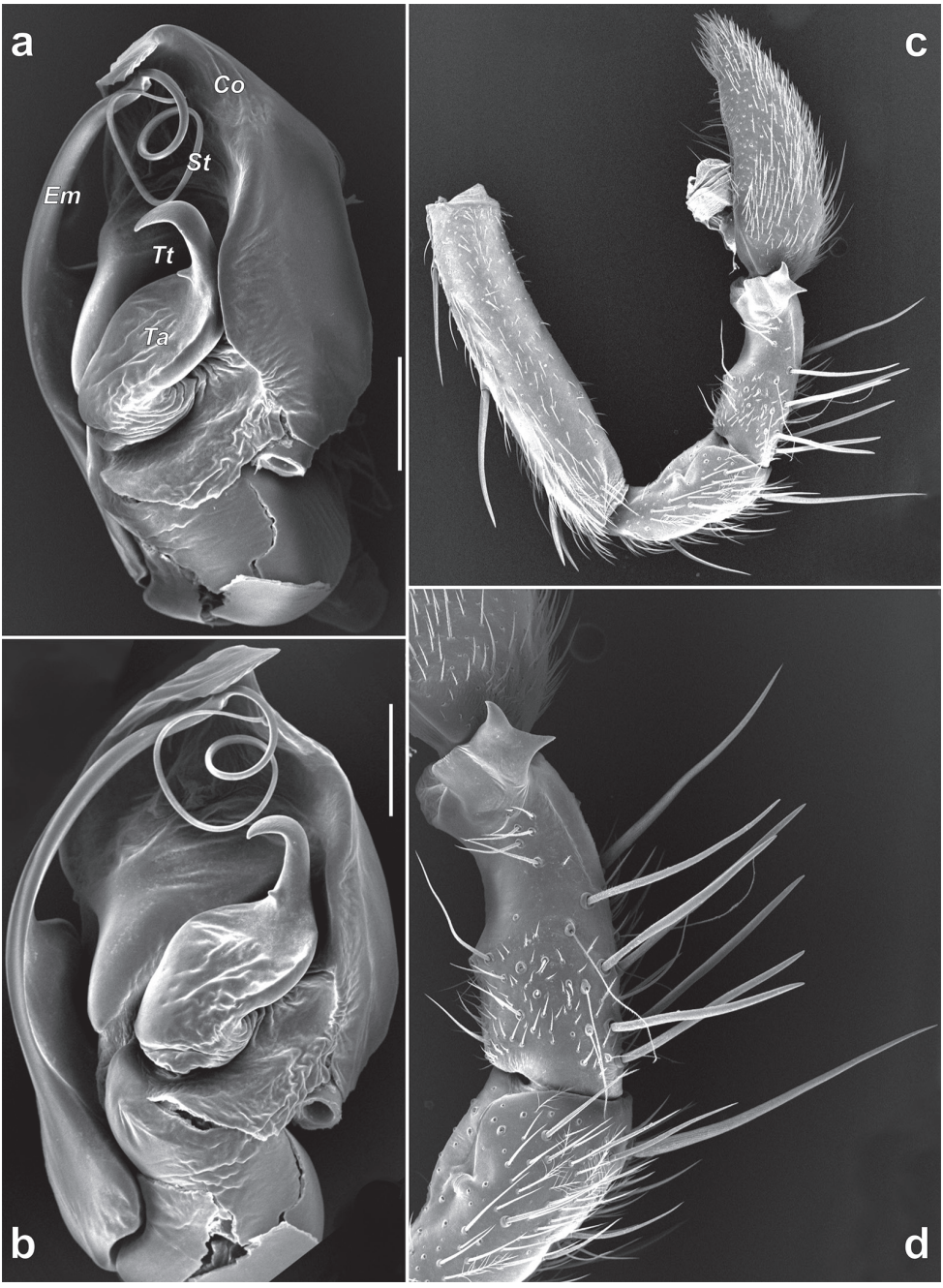

Figure 9. Male palp of *Pterotricha strandi*. **a–b** bulb, retrolateral and ventral **c** palp, retrolateral **d** palpal patella and tibia, lateral. Scale bars: 0.1 mm. Abbreviations: *Co* conductor; *Em* embolus; *St* stylus; *Ta* tegular apophysis; *Tt* tooth of tegular apophysis.

mentioned the probability of the synonymy of the two names (Marusik et al. 2013). Because we were able to collect both sexes of this species from the same localities, we can now confirm that the male and female specimens studied by Marusik et al. (2013) are conspecific. As a result of our survey, we found that this species has a rather broad distribution. Despite differences between Iranian and Turkmenian populations, we consider these as merely variations and therefore, consider *P. loeffleri* a junior synonym of *P. strandi*. Although we were unable to borrow the type material for *P. tikaderi* Gajbe, 1983 (India), based on photographs of the palp (Figure 6c–f) and habitus figures provided to us, we conclude that *P. tikaderi* is also a junior synonym of *P. strandi*.

Ecology. This is a nocturnal spider, mostly hiding beneath rocks and inside crevices during the day and hunting at night. According to our observations, this species doesn't make silken retreats. It is widespread on the Iranian Plateau, occurring in mountainous areas and sand dunes and sometimes near human dwellings, and two specimens were collected in a cave near the entrance. Mature females can probably be found throughout the year, while adult males can mostly be found from mid-autumn to late spring (Zamani 2016).

Records in Iran. Bushehr, Fars, Hormozgan, Kohgiluyeh & Boyer-Ahmad, Tehran. New records: Isfahan and Kerman (Figure 16).

Distribution. Turkmenistan, Iran, and western India.

Iranotricha Zamani & Marusik, gen. n.

http://zoobank.org/C9C70DA0-DD13-4199-B5D5-A182CC5B225F

Type species. *Iranotricha lutensis* Zamani & Marusik, sp. n.

Etymology. A combination of Iran, the type locality of the species, and "*tricha*", referring to the similarity with the genus *Pterotricha.* The gender is feminine.

Diagnosis. The genus differs from all Gnaphosinae by lacking a cheliceral keel. It is most similar to *Pterotricha* by having long anterior lateral spinnerets and the embolus similar to that of *P. cambridgei* (O. Pickard-Cambridge, 1872) and *P. levantina* Levy, 1995 by having a modified anterior part with an invagination. *Iranotricha* gen. n. differs from *Pterotricha* by lacking a cheliceral keel, having the two prolateral teeth greatly reduced and separated from each other (vs. well developed and fused at the bases in *Pterotricha*), having modified setae (long terminal setae (*Ts*), long setae (*Ls*), barbed setae (*Bs*), with longer plumage (*Ss*) on chelicera which are lacking in *Pterotricha* (cf. Figs 11a, b, 12a–c and 12d–f), an embolus with a spine (*Es*) (lacking in *Pterotricha*), a small conductor (smaller and thinner than the embolus vs. larger and wider than the embolus) and an elongate tegular apophysis lacking a large base (vs. tegular apophysis with wide base, much wider than tip).

Description. Same as for the species.

Comments. Long spinnerets and the presence of a sclerotized (non-membranous) conductor behind the embolus indicate that new genus is most probably related to

Pterotricha. *Iranotricha* gen. n. is also similar to *Scotognapha* Dalmas, 1920, a genus restricted to the Canary Islands (WSC 2018). *Scotognapha* has a greatly reduced, vestigial keel (the new genus lacks a keel) but has plumose "hairs" as in *Pterotricha* and *Iranotricha* gen. n.

Composition. Only the type species.

***Iranotricha lutensis* Zamani & Marusik, sp. n.**

http://zoobank.org/0CA60690-EB14-4484-B19C-A4DD7D102028

Figs 10–14, 15a–b, d, 16

Type material. Holotype ♂ (MMUE), IRAN: *Kerman Province*: Lut Desert, Rig-e Setareh, 30°15'26.5"N, 58°42'56.6"E, 252 m, 16.11.2016 (A. Zamani & H. Akhani).

Etymology. The specific epithet refers to the Lut Desert, the type locality of the species.

Diagnosis. The species can be easily recognized from the *Pterotricha* species with long spinnerets by lacking a cheliceral keel. The males of this species can be also recognized due to numerous strong spines on the legs (Figure 10d) and a spine on tarsus IV (Figure 11d). *Pterotricha* species have weak spines and lack a spine on tarsus IV.

Description. Male. Total length 6.45. Carapace 3.7 long, 3.1 wide. Eye sizes and interdistances: AME: 0.14, ALE: 0.21, PME: 0.12, PLE: 0.17, PME-PME: 0.08. Carapace, sternum, labium, chelicerae, and maxillae light brown without any distinct patterns, with scattered short setae and darkening in the ocular area. Chelicera lacking keel but with two strongly reduced (vestigial) teeth that are separated from each other (Figure 12c); a very long terminal seta (*Ts*), 2 long mesal setae (*Ls*), a series of barbed setae (*Bs*) along the prolateral side of the furrow and bent prolateral serrated seta (*Ss*). The barbed setae have long plumage making the wider distally (Figure 12b). Abdomen light grey with long grey setae and a light brown scutum anteriorly. Legs yellow, with numerous spines, including one spine on tarsus IV. Scopula on metatarsi and tarsi indistinct; tarsus I with more thick and thin macrosetae than tarsus IV (Figs 11c–d). Tarsi of all legs with cuticular cracks (pseudosegmented). Leg measurements: I: 15.85 (3.85, 1.9, 3.6, 4.05, 2.45), II: 17.10 (4.0, 2.0, 4.10, 4.30, 2.70), III: 16.41 (3.9, 1.70, 3.95, 4.35, 2.51), IV: 19.1 (4.3, 2.0, 4.1, 6.0, 2.70). Anterior lateral spinnerets almost 6 x longer than wide and almost as long as abdomen width.

Palp as in Figs 13–14; patella and tibia elongate, almost as long as femur and longer than cymbium; patella with very strong and long macrosetae, >1.5 x longer than tibia; tibia cylindrical, unmodified; tibia with relatively small retrolateral apophysis (not longer than diameter of tibia) with tip bent anteriorly, prolateral side with three strong and long macrosetae of equal length to the tibia; cymbium long, approx. 3 x longer than wide with three strong dorsal macrosetae; tegular apophysis elongate, almost cylindrical, with unmodified base; conductor small, partly hidden by embolus;

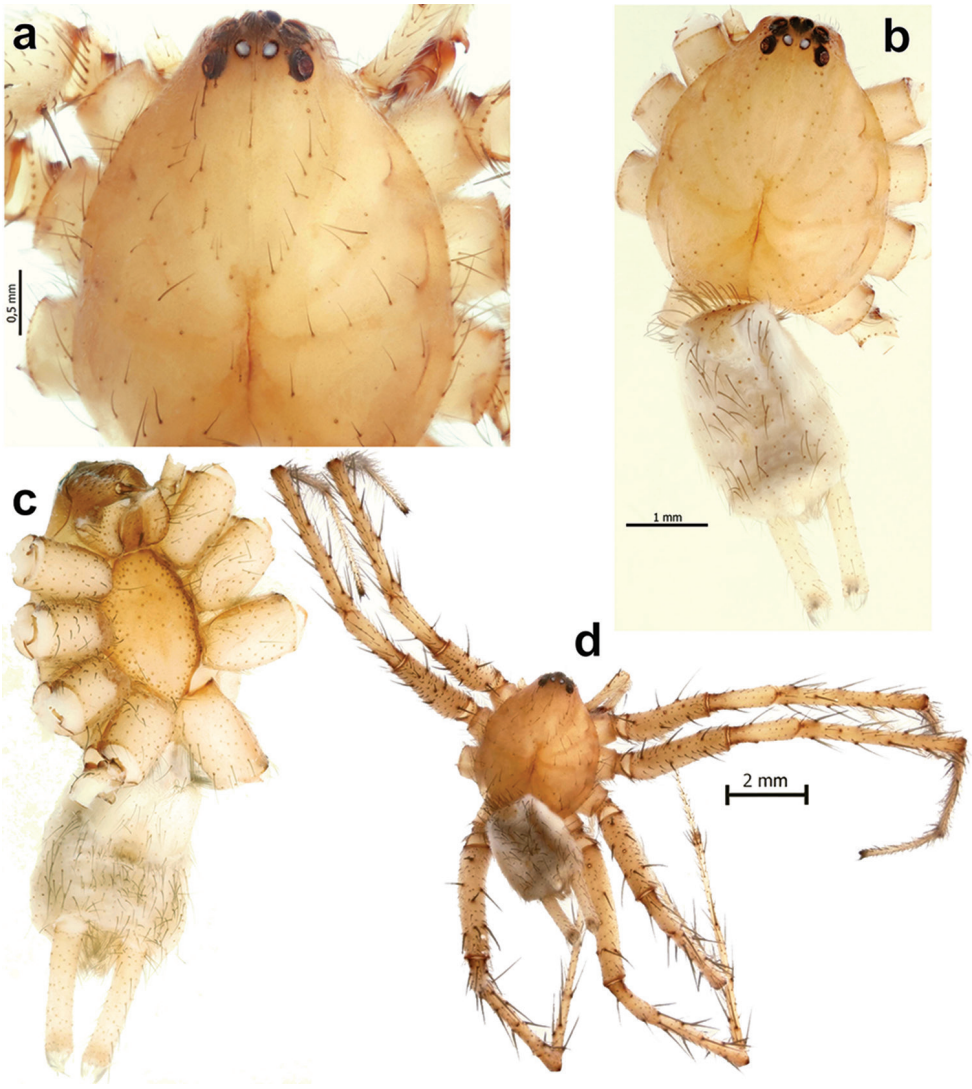

Figure 10. Habitus of *Iranotricha lutensis* Zamani & Marusik sp. n., male. **a** prosoma, dorsal **b–c** body, dorsal and ventral **d** whole specimen, dorsal.

embolus broad at the base, with a strong retrolateral spine (*Es*); anterior part of embolus modified, widened, with an invagination (*Ec*) corresponding (fitting) to conductor (*Co*), tip of embolus stylus-like, looped, directed dorsally and terminating at the tip of the conductor

Female. Unknown.

Comments. It is unclear whether the opening of the embolus is at the tip or before the loop, and as this is the only specimen available at this time, we did not dissect it.

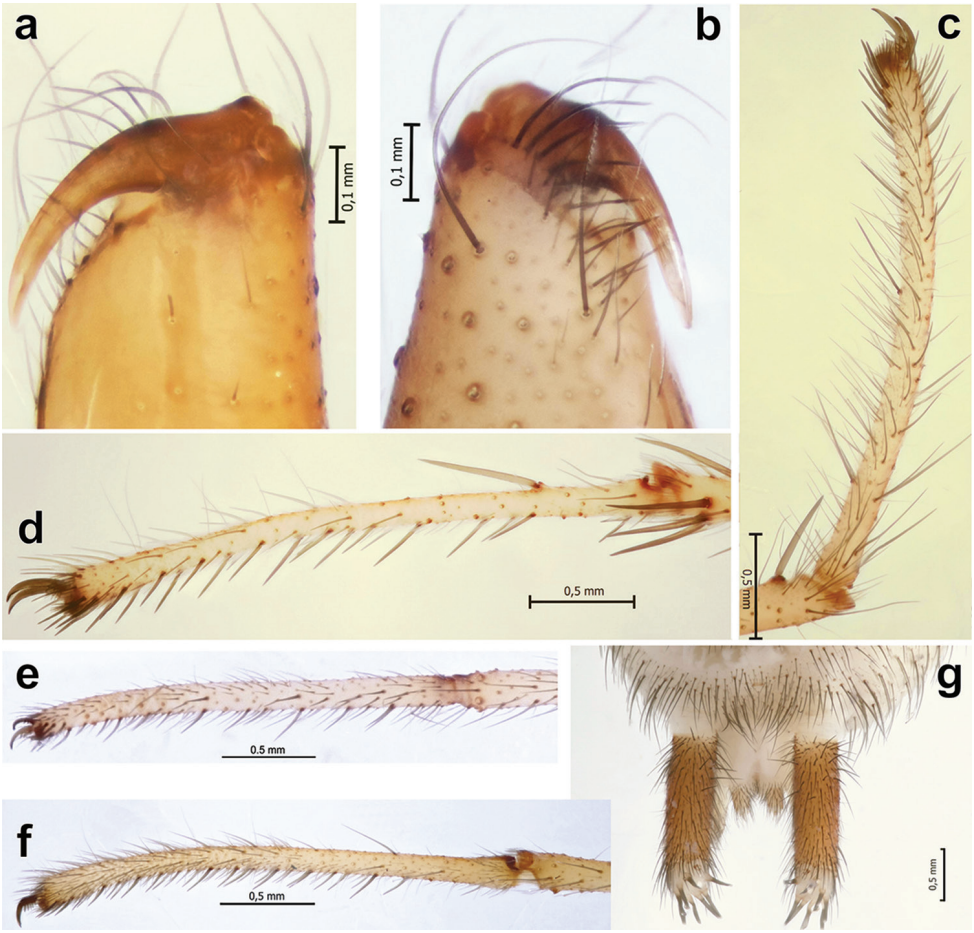

Figure 11. Somatic characters of *Iranotricha lutensis* Zamani & Marusik sp. n. (**a–d**), *Pterotricha strandi* (**e–f**) and *P. montana* (**g**). **a, b** chelicera, retrolateral and meso-prolateral **c, f** tarsus I, prolateral **d, e** tarsus IV, prolateral **g** spinnerets, ventral.

Ecology. The holotype was collected wandering on sand dunes in a habitat lacking any vegetation (Figure 15d). Two subadult specimens were also observed (but not collected) in another locality while they were taking refuge under two large stones. Recently, the hottest place inhabited by spiders was reported to be the Death Valley, Inyo, California, with the highest ground temperature measured at 56.7 °C (Mammola et al. 2017), but the sand surface of the Lut Desert, where the holotype was collected, has been recently measured at temperatures as high as 78.2 °C (Akhani and Aghakouchak pers. comm., Zamani and Marusik 2018).

Records in Iran. Kerman (Figure 16).

Distribution. Lut Desert, southeastern Iran.

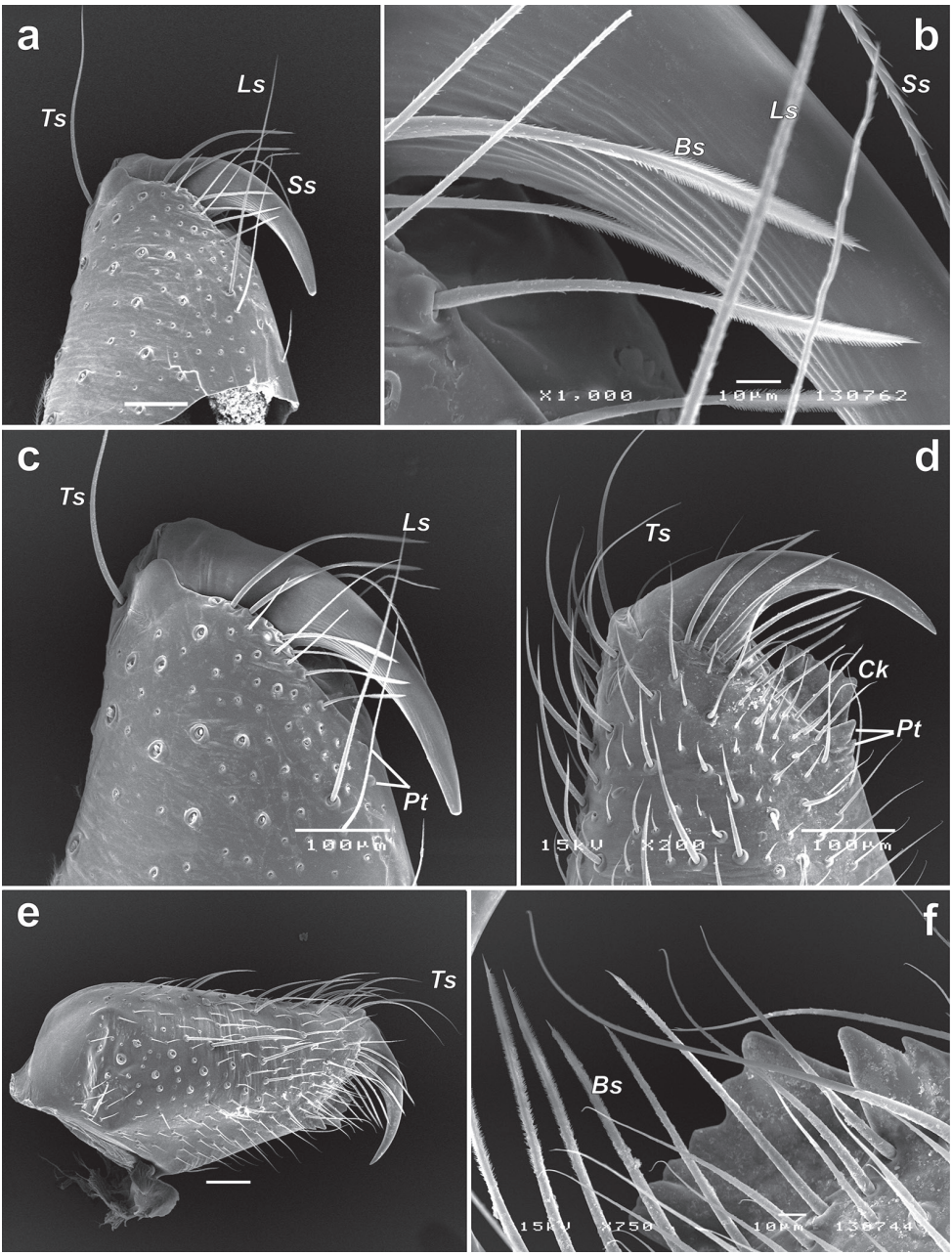

Figure 12. Chelicerae of *Iranotricha lutensis* Zamani & Marusik sp. n. (**a–c**) and *Pterotricha strandi* (**d–f**). **a, c–d** terminal part, prolateral **b, f** enlarged terminal part of chelicera showing setae and teeth; e whole chelicera, prolateral. Abbreviations: *Bs* barbed seta; *Ck* keel of chelicera; *Ls* long seta; *Pt* prolateral teeth; *Ss* serrated seta; *Ts* terminal seta.

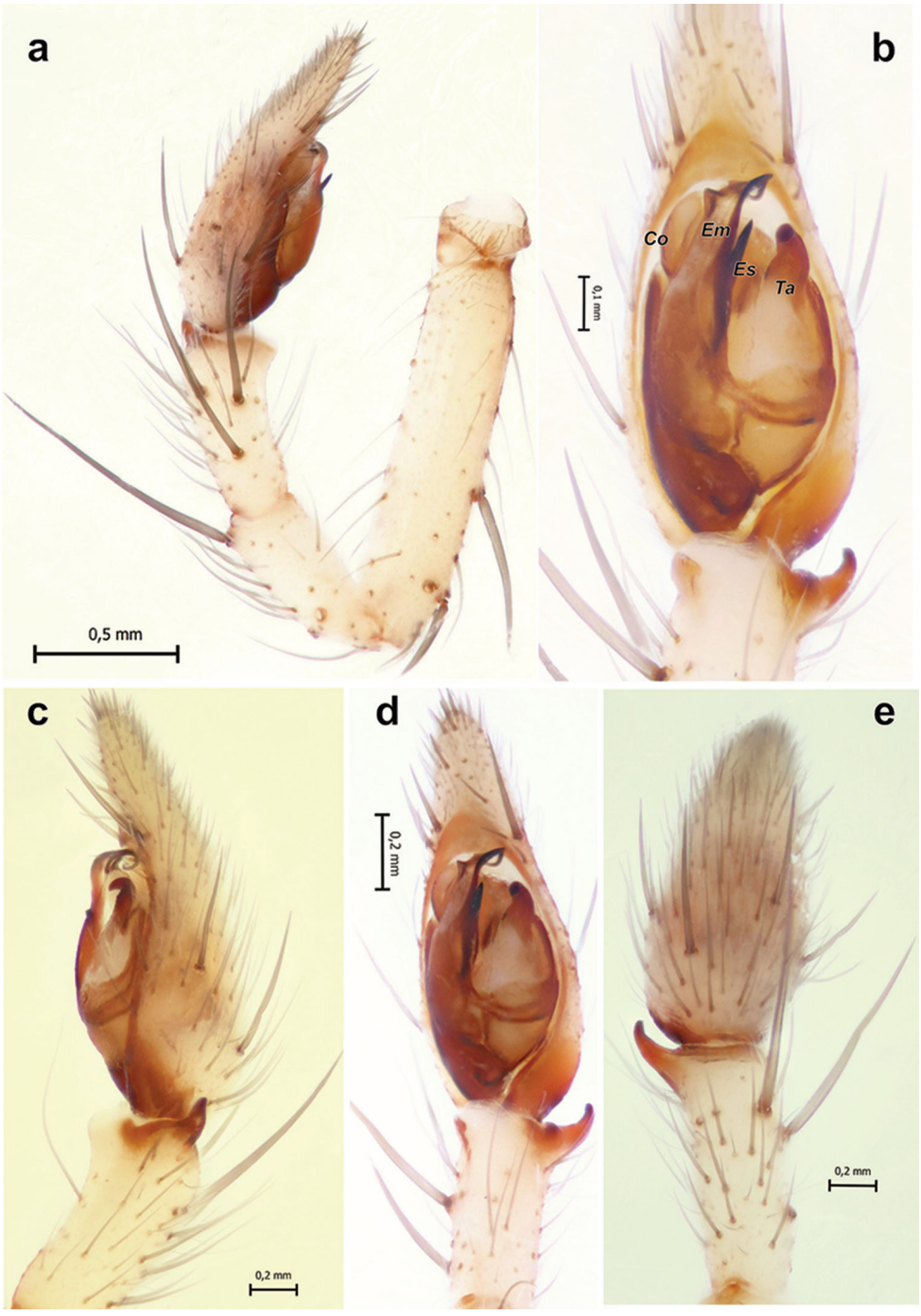

Figure 13. Male palp of *Iranotricha lutensis* Zamani & Marusik sp. n. **a** whole palp, prolateral **b, d** ventral **c** retrolateral **e** dorsal. Spine of the embolus is broken on Figure c. Abbreviations: *Co* conductor; *Em* embolus; *Es* embolic spine; *Ta* tegular apophysis.

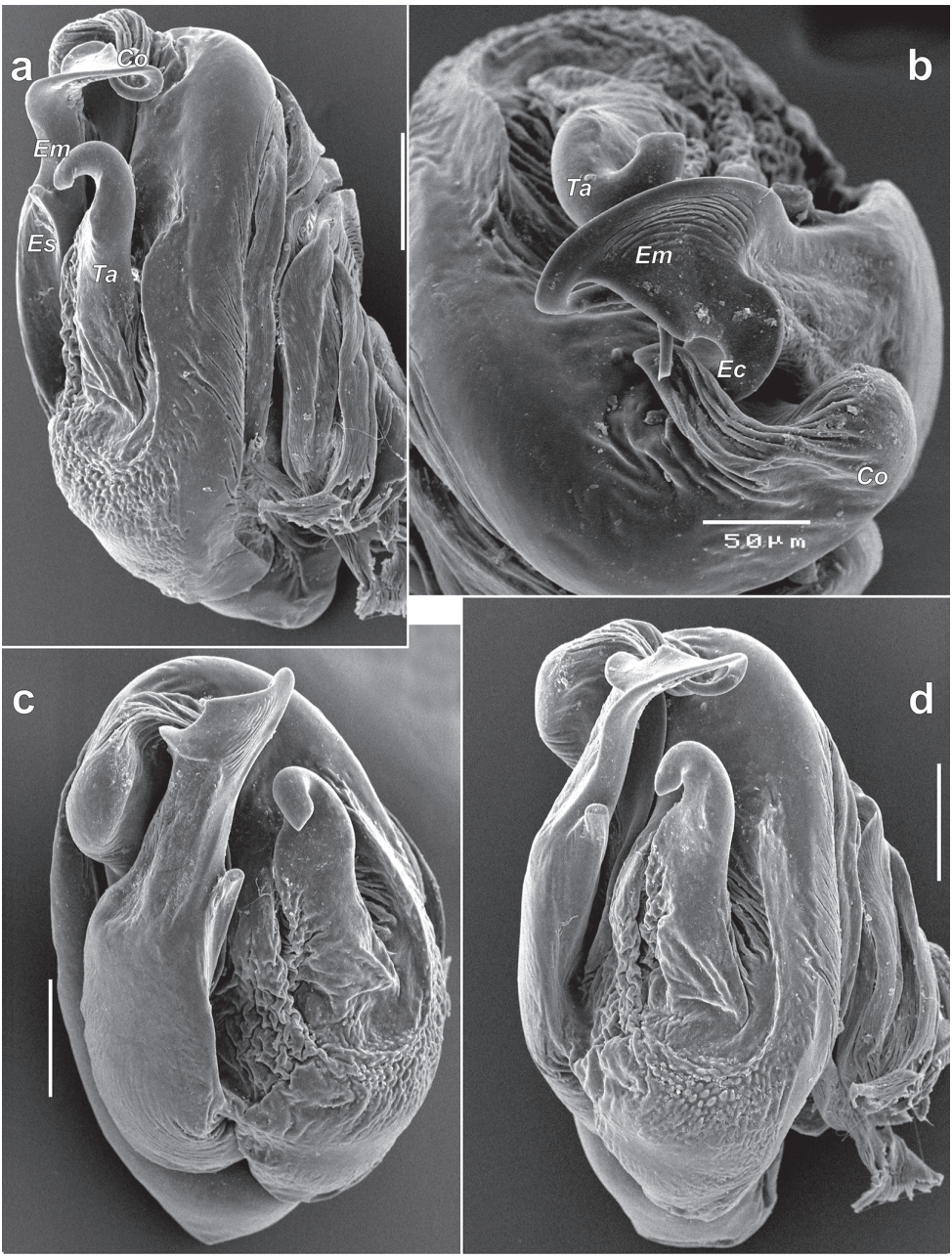

Figure 14. Bulb of *Iranotricha lutensis* Zamani & Marusik, sp. n. **a** retrolateral **b** anterior **c** ventral **d** ventro-retrolateral. Embolic spine is broken. Scale bars 0.1 mm if not otherwise indicated. Abbreviations: *Co* conductor; *Ec* embolic invagination; *Em* embolus; *Es* embolic spine; *Ta* tegular apophysis.

Figure 15. Live male specimens of *Iranotricha lutensis* Zamani & Marusik, sp. n. (**a–b**) and *Pterotricha strandi* (**c**), and type locality of *I. lutensis* Zamani & Marusik, sp. n. (**d**).

Conclusions

As a result of this study, the number of species of *Pterotricha* known from Iran increased from three (Zamani et al. 2018) to six. Two of the species are currently known only from Iran (*P. kovblyuki* Zamani & Marusik, sp. n., *P. montana* Zamani & Marusik, sp. n.), and one is known only from Iran and adjacent Azerbaijan (*P. pseudoparasyriaca*). As a result of two new synonymies, the range of *P. strandi* is broadened, representing one of the largest ranges in the genus. We assume that the actual number of species in this genus occurring in Iran is higher considering that many remote, desert habitats have not been properly investigated regarding arachnofauna.

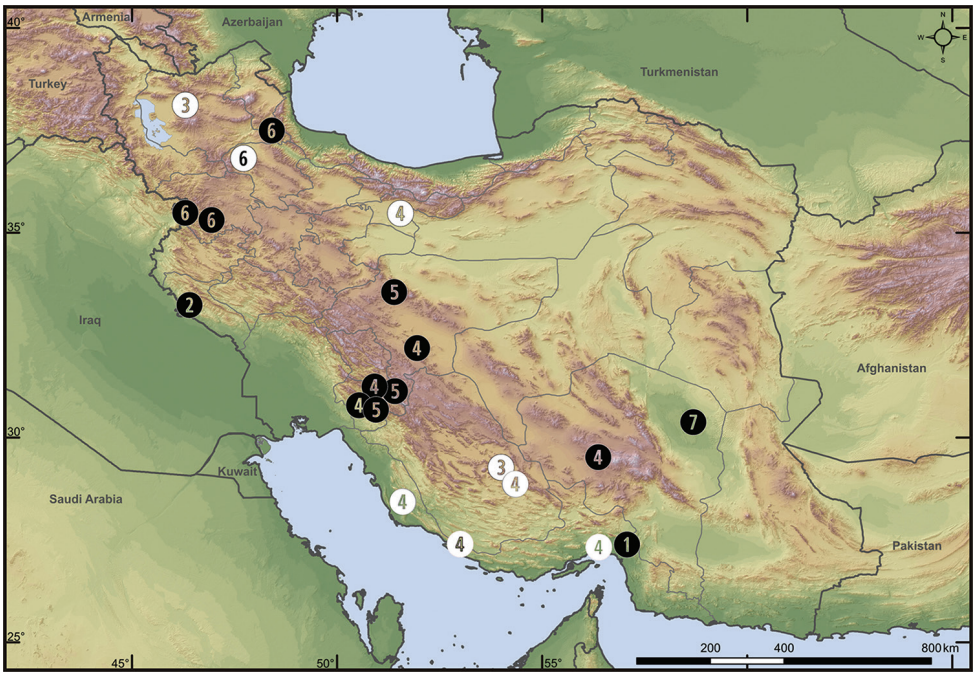

Figure 16. Distribution of *Pterotricha* spp. and *Iranotricha lutensis* Zamani & Marusik, sp. n. in Iran (white symbols refer to literature records, and black symbols refer to our new data): **1** *P.* cf. *dalmasi* **2** *P. kovblyuki* Zamani & Marusik, sp. n. **3** *P. lentiginosa* (?) **4** *P. strandi* **5** *P. montana* Zamani & Marusik, sp. n. **6** *P. pseudoparasyriaca* **7** *I. lutensis* Zamani & Marusik, sp. n.

Acknowledgments

This paper is partially the result of the Adaptation and Function of Lut Desert Biodiversity (AFLDB) research project, coordinated by University of Tehran, the SAEEDI Institute for Advanced Studies (SIAS) and University of Kashan. We are grateful to Sarah Crews for checking the language of the manuscript, Hossein Akhani, Parham Beyhaghi, Soheyl Sami and Mojtaba Ezazi for field assistance, and Jobi J. Malamel and John Caleb for their help with photographing the holotype of *P. tikaderi* in the National Zoological Collections, Zoological Survey of India.

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RESEARCH ARTICLE

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Tetrablemmidae, a spider family newly recorded from Cambodia (Arachnida, Araneae)

Yucheng Lin[1], Shuqiang Li[2], Peter Jäger[3]

1 *Key Laboratory of Bio-resources and Eco-environment (Ministry of Education), College of Life Sciences, Sichuan University, Chengdu, Sichuan 610064, China* **2** *Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China* **3** *Arachnology, Senckenberg Research Institute, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany*

Corresponding author: *Shuqiang Li* (lisq@ioz.ac.cn)

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Abstract

The family Tetrablemmidae O. Pickard-Cambridge, 1873 is reported from Cambodia for the first time. Two species belonging to the genus *Tetrablemma* O. Pickard-Cambridge, 1873 are documented as new to science: *Tetrablemma kepense* **sp. n.** (male, female) from Kep Province and *Tetrablemma sokense* **sp. n.** (male, female) from Battambang Province. Diagnoses, morphological descriptions, and comparative illustrations are provided.

Keywords

Haplogynae, Indochina, new species, taxonomy, tetrablemmids

Introduction

The family Tetrablemmidae O. Pickard-Cambridge, 1873 is a less well-known spider group compared with those medium to large spiders in subtropical and tropical regions. The type genus, *Tetrablemma* O. Pickard-Cambridge, 1873 contains 27 species

(WSC 2018) and is mainly distributed in Asia, such as China (Tong and Li 2008; Lin and Li 2010, 2014), Vietnam, Laos, Myanmar and Indonesia (Lehtinen 1981; Labarque and Grismado 2009; Lin et al. 2012), India, Nepal and Sri Lanka (Tikader 1976; Bourne 1980; Lehtinen 1981), and Angola in Africa (Brignoli 1974), Queensland, Victoria and Western Australia (Butler 1932; Burger 2008; Burger et al. 2010). Single species occur in some islands, such as Micronesia, Samoa, St. Helena, Seychelles, and Trinidad (Roewer 1963; Marples 1964; Benoit 1977; Brignoli 1978; Shear 1978; Lehtinen 1981).

Several specimens of armored spiders found in a cave and the leaf litter in Cambodia were examined, belonging to two species. Here they are described as *Tetrablemma kepense* sp. n. and *T. sokense* sp. n. Both species represent the first report of the family Tetrablemmidae from Cambodia.

Materials and methods

All type specimens were acquired by manual collection and preserved in 75% denatured ethanol solution, and are deposited in the Senckenberg Research Institute, Frankfurt, Germany (**SMF**) and the Natural History Museum of the Sichuan University in Chengdu, China (**NHMSU**).

Specimens were examined and measured under an Olympus SZX7 stereomicroscope. Further details were studied under an Olympus BX43 compound microscope. Male palp and female genitalia were examined and photographed after they were dissected and detached from the spiders' bodies. To reveal the configuration of spermathecae and the course of the spermophor in the palpal bulb, they were treated in lactic acid and embedded in Hoyer's solution before taking photos. Photographs were taken with a Canon EOS 60D wide zoom digital camera (8.5 megapixels) mounted on an Olympus BX43 compound microscope. Images were combined using Helicon Focus 3.10 software (Khmelik et al. 2006).

All measurements in the text or figures are given in millimeters. Leg measurements are provided as following: total length (femur, patella, tibia, metatarsus, and tarsus). Abbreviations used in figures are as follows:

CH	cheliceral horn;	**PA**	preanal scutum;
CP	central process;	**Pb**	palpal bulb;
Cy	palpal cymbium;	**POG**	postgenital scutum;
E	embolus;	**Sp**	spermophor;
EF	epigynal fold;	**SR**	seminal receptacle;
EP	epigynal pit;	**Ti**	palpal tibia;
Et	embolic tip;	**VD**	vulval duct;
IVP	inner vulval plate;	**VS**	vulval stem.

References to figures in the cited papers are listed in lowercase (figure or figs); figures from this paper are noted with an initial capital (Figure or Figs).

Taxonomy

Family Tetrablemmidae O. Pickard-Cambridge, 1873

Genus *Tetrablemma* O. Pickard-Cambridge, 1873

Type species. *Tetrablemma mediocula*tum O. Pickard-Cambridge, 1873 from Sri Lanka (see Lehtinen 1981).

Note. The gender of *Tetrablemma* is neuter, therefore two species names described previously are amended (see below). The ending "-ensis" denotes a place, a locality or a country. It forms an adjective with two endings: "-ensis" for genera masculine or feminine in gender, and "-ense" for genera neuter in gender.

Composition. Twenty-seven species were known before the current study: *T. alaus* Burger, Harvey & Stevens, 2010, *T. alterum* Roewer, 1963, *T. benoiti* (Brignoli, 1978), *T. brevidens* Tong & Li, 2008, *T. brignolii* Lehtinen, 1981, *T. deccanense* (Tikader, 1976), *T. extorre* Shear, 1978, *T. helenense* Benoit, 1977, *T. loebli* Bourne, 1980, *T. magister* Burger, 2008, *T. manggarai* Lehtinen, 1981, *T. marawula* Lehtinen, 1981, *T. mardionoi* Lehtinen, 1981, *T. mediocula*tum O. Pickard-Cambridge, 1873, *T. mediocula*tum *cochinense* Lehtinen, 1981, *T. mediocula*tum *gangeticum* Lehtinen, 1981, *T. menglaense* Lin & Li, 2014 (species epithet corrected, original published as *T. menglaensis*), *T. namkhan* Lin, Li & Jäger, 2012, *T. nandan* Lin & Li, 2010, *T. okei* Butler, 1932, *T. phulchoki* Lehtinen, 1981, *T. rhinoceros* (Brignoli, 1974), *T. samoense* Marples, 1964, *T. thamin* Labarque & Grismado, 2009, *T. viduum* (Brignoli, 1974), *T. vietnamense* Lehtinen, 1981, *T. ziyaoense* Lin & Li, 2014 (species epithet corrected, original published as *T. ziyaoensis*).

Distribution and habitat. Angola, Australia, Cambodia, China, St. Helena, India, Laos, Indonesia, Micronesia, Myanmar, Nepal, Queensland, Samoa, Seychelles, Sri Lanka, Trinidad, Victoria and Vietnam. These previously described species live mainly in the forest litter or in caves.

Tetrablemma kepense sp. n.

http://zoobank.org/F59316C9-5C81-47D8-BA84-13B8BDD4381D
Figs 1, 2, 6

Type material. Holotype ♂ (SMF), CAMBODIA: Kep Province, Kep, Phnom Kep, secondary forest, leaf litter, elevation 105 m, 10°28'50"N, 104°17'50"E, 4–8 July 2017, P. Jäger leg., sieving. **Paratypes** 7♂, 8♀ (5 ♂, 6♀ SMF; 2♂, 2♀ NHMSU), same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. With the exception of *T. marawula* Lehtinen, 1981, *T. brevidens* Tong & Li, 2008, *T. thamin* Labarque & Grismado, 2009, and *T. ziyaoense* Lin & Li, 2014, this new species can be distinguished from other congeners by the lack of modified

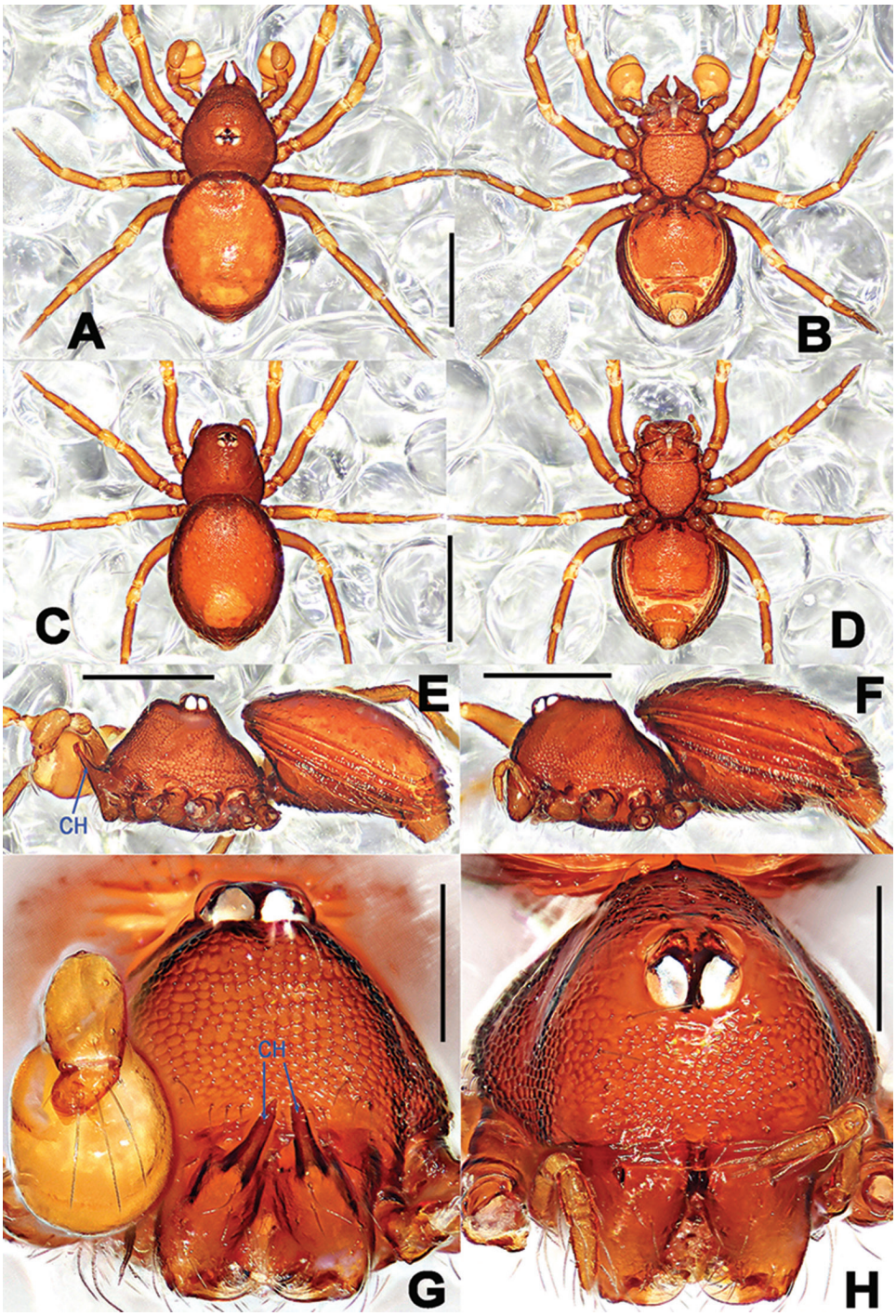

Figure 1. *Tetrablemma kepense* sp. n., male holotype (**A, B, E, G**) and female paratype (**C, D, F, H**). **A–F** habitus **G–H** prosoma. **A, C** dorsal **B, D** ventral **E–F** lateral **G–H** anterior. Abbreviations: CH = cheliceral horns. Scale bars: **A–F** 0.5 mm, **G–H** 0.2 mm.

teeth or tubercle on the clypeus or the ocular area in both sexes, the embolus furcated at proximally 1/3 position, the extra-long inner vulval plate nearly 3 × as long as the central process (Figs 1E–H, 2B–C, F–G). It differs from *T. marawula* by the wider bulb, the sharpened embolic tip and the longer straight inner vulval plate (Figure 2A, B, D, G vs. Lehtinen 1981: figs 266, 283); differs from *T. brevidens* by the more strongly coiled spermophor, the furcate embolus, the thinner long inner vulval plate, and shorter postgenital scutum (Figure 2A, C, G vs. Tong 2013: figure 97E–H); male differs from *T. thamin* by the narrower palpal tibia, the larger bulb, and the bifurcate embolic tip (trifurcate in *T. thamin*), female by the presence of a central process and the longer inner vulval plate (Figure 2A, C, D, G vs. Labarque and Grismado 2009: figs 1–3); and differs from *T. ziyaoense* by the converging cheliceral horns, the reticulated clypeus in both sexes (smooth in female of *T. ziyaoense*), the course and outlet position of spermophor, the precurved posterior margin of the pulmonary scutum, the thinner, straight inner vulval plate, the narrower vulval stem, and the lack of a distinct furrow on the preanal scutum (Figs 1A–H, 2A–G vs. Lin and Li 2014: figs 13A–H, 14A–D, 15A–C).

Description. Male (holotype). Measurements: total length 1.08; carapace 0.42 long, 0.37 wide, 0.34 high; abdomen 0.70 long, 0.58 wide, 0.35 high; clypeus 0.14 high; sternum 0.28 long, 0.29 wide. Length of legs: I 1.29 (0.43, 0.12, 0.32, 0.20, 0.22); II 1.22 (0.40, 0.11, 0.30, 0.20, 0.21); III 1.08 (0.33, 0.11, 0.25, 0.19, 0.20); IV 1.38 (0.45, 0.12, 0.36, 0.23, 0.22).

Prosoma (Figure 1A, B, E, G): reddish-brown, carapace finely reticulated, marginally rugose; four eyes in one group, in posterior half of carapace, white with black ocular base, ALE>PLE, ALE and PLE adjacent; cephalic part raised; clypeus high, sloping forward, with sparse setae, marginally round; cheliceral horns long, distal tip sharp, and tilted, cheliceral lamina developed; endites basally wide, distally narrow, labium triangular, distally blunt; sternum irregularly reticulated, scutellate, marginally strongly rugose, posterior corner truncated. Legs: yellowish-orange, cuticle striated; tibiae I–III with three trichobothria, four on tibia IV, and one on metatarsi I–IV. Opisthosoma: pale reddish-brown, dorsal scutum oval, surface nearly smooth, slightly granulated, posteriorly truncated; ventral scutum reticulated; lateral scutum I long, and exceeding beyond the posterior margin of preanal scutum; postgenital scutum straight; preanal scutum approximately oblong, slightly curved.

Palp (Figure 2A–D): femoral cuticle granulated, approx. 2.5 x longer than patella; patella normal; tibia large, swollen, approx. 1.5 x wider than femur, with a trichobothrium disto-dorsally; cymbium short, triangular from lateral view, bearing long setae; bulb pear-shaped, surface smooth; embolus tubular, distinctly sclerotized, arising from the apex of bulb; embolic tip sharply pointed, lamellar bifurcation at proximally 1/3 position; spermophor coiled into two loops, abruptly twisting to narrow, and open at the embolic tip.

Female (one paratype). Measurements: total length 1.16; carapace 0.44 long, 0.38 wide, 0.34 high; abdomen 0.72 long, 0.61 wide, 0.37 high; clypeus 0.13 high; sternum 0.28 long, 0.30 wide. Length of legs: I 1.26 (0.42, 0.12, 0.31, 0.20, 0.21); II 1.19

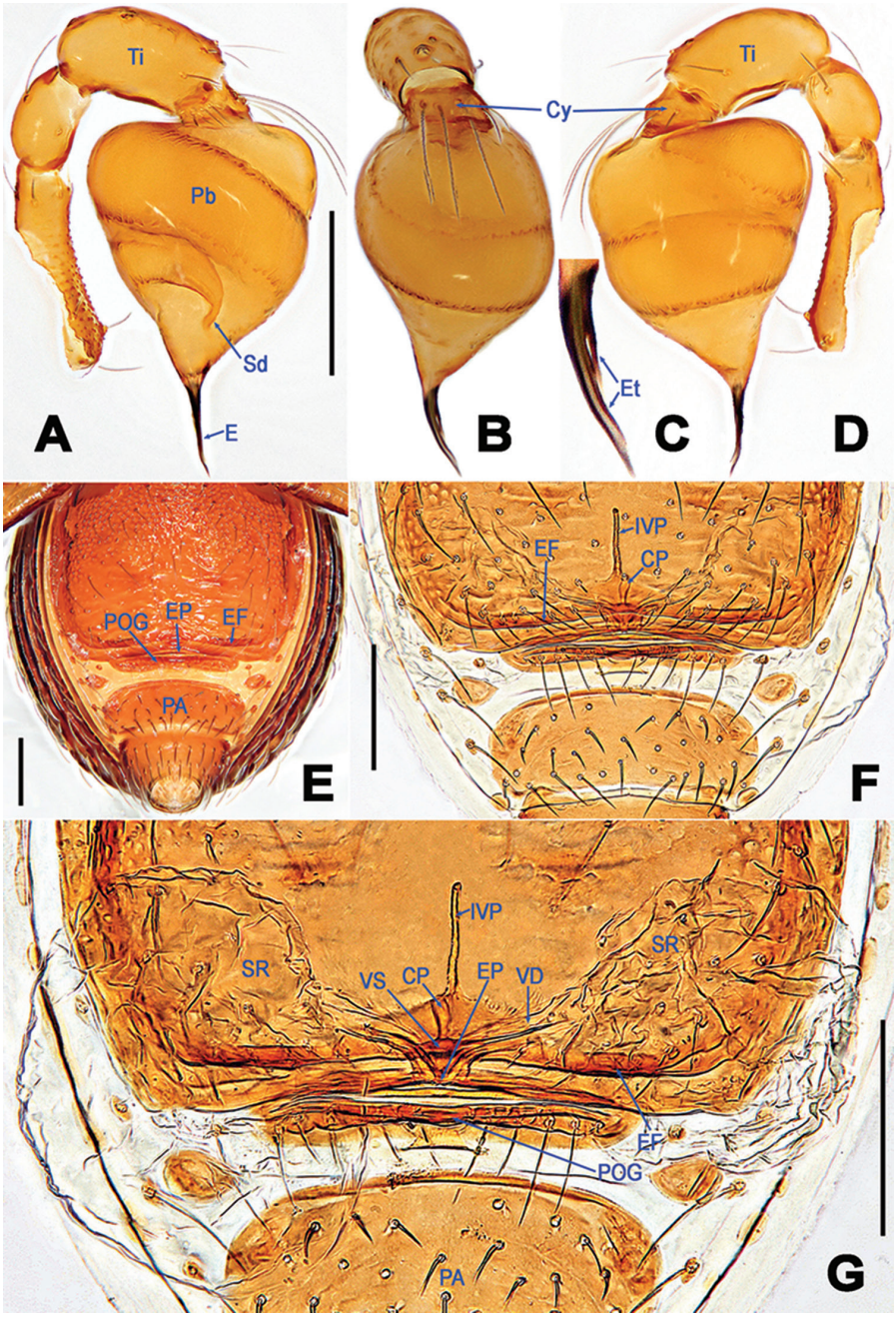

Figure 2. *Tetrablemma kepense* sp. n., male holotype (**A–D**) and female paratype (**E–G**). **A, B, D** left palp **C** embolic tip **E** genital area (untreated) **F–G** cleared vulva (lactic acid-treated). **A** prolateral **B, C** frontal **D** retrolateral **E, F** ventral **G** dorsal. Abbreviations: CP = central process; Cy = palpal cymbium; E = embolus; EF = epigynal fold; EP = epigynal pit; Et = embolic tip; IVP = inner vulval plate; PA = preanal scutum; Pb = palpal bulb; POG = postgenital scutum; Sd = spermophor; SR = seminal receptacle; Ti = palpal tibia; VD = vulval duct; VS = vulval stem. Scale bars: **A, B, D–G** 0.2 mm, **C** 0.05 mm.

(0.40, 0.11, 0.29, 0.19, 0.20); III 1.09 (0.34, 0.11, 0.26, 0.18, 0.20); IV 1.34 (0.44, 0.12, 0.35, 0.22, 0.21).

Prosoma (Figure 1C, D, F, H): coloration and modification as in male, but ocular area in anterior part of the carapace, chelicerae without long horn, only a small nodule fronto-proximally. Clypeus slightly lower than in male, palps distinctly reduced, palpal tibia with a dorsal trichobothrium. Legs as in male. Opisthosoma: dorsal and ventral scuta as in male, except for darker coloration; lateral scutum I long, extending beyond posterior margin of preanal scutum; postgenital scutum long, bearing a row of long setae, mesally narrow, laterally wide; preanal scutum more smooth, wider than long, nearly rectangular, with sparse stiff setae.

Epigyne and vulva (Figure 2F, G): epigynal fold long and obvious; epigynal pit distinct, gap-shaped, opening at the posterior margin of the pulmonary scutum; vulval stem sclerotized; vulval ducts weakly sclerotized, translucent, widely "V"-shaped, apical end connected to seminal receptacles; seminal receptacles inflated, saccular, transparent; inner vulval plate extra-long, straightly tubular, broad at base; central process short, proximally contracted, distally swollen.

Habitat. Forest leaf litter.

Distribution. Known only from the type locality (Figure 6).

***Tetrablemma sokense* sp. n.**
http://zoobank.org/34822C18-C945-4661-B08A-3528237E073D
Figs 3–6

Type material. Holotype ♂ (SMF), CAMBODIA: Battambang Province, SW Battambang, Phnom Romsay Sok, an anonymous cave, elevation 100 m, 12°57'28"N, 103°6'32"E, 19 July 2017, P. Jäger & S. Münnich leg. **Paratypes** 7♂, 20♀ (4♂, 10♀; SMF 3♂, 10♀ NHMSU), same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. This new species can be distinguished from other congeners with the exception of *T. loebli* Bourne, 1980 and *T. nandan* Lin & Li, 2010 by the protruding ocular area of carapace and the vestigial four eyespots in both sexes, the exceptionally slender bulb, and the absence of an epigynal fold in the female vulva (Figs 3A–H, 4A–F). *T. sokense* sp. n. seems similar to *T. loebli* and *T. nandan* in the appearance of habitus, the shape and configuration of genital organs, but differs from *T. loebli* by the reduced eyes without any black pigments in both sexes, the straight cheliceral horn in lateral view, the narrower bulb, the shorter, twisted embolus, the stubby inner vulval plate, and the falcate central process (Figure 3A, C, E–H vs. Bourne 1980: figs 9–10, 14, 16; Lehtinen 1981: figs 219, 221–223); and differs from *T. nandan* by the converged eyes and flat cephalic area in both sexes, the regular, not swollen palpal femur and tibia, the swollen bulb with a more distorted embolus, the shorter, fingerlike inner vulval plate and the lack of epigynal fold (Figs 3E–H, 4A–F vs. Lin and Li 2010: figs 38–39, 44–49).

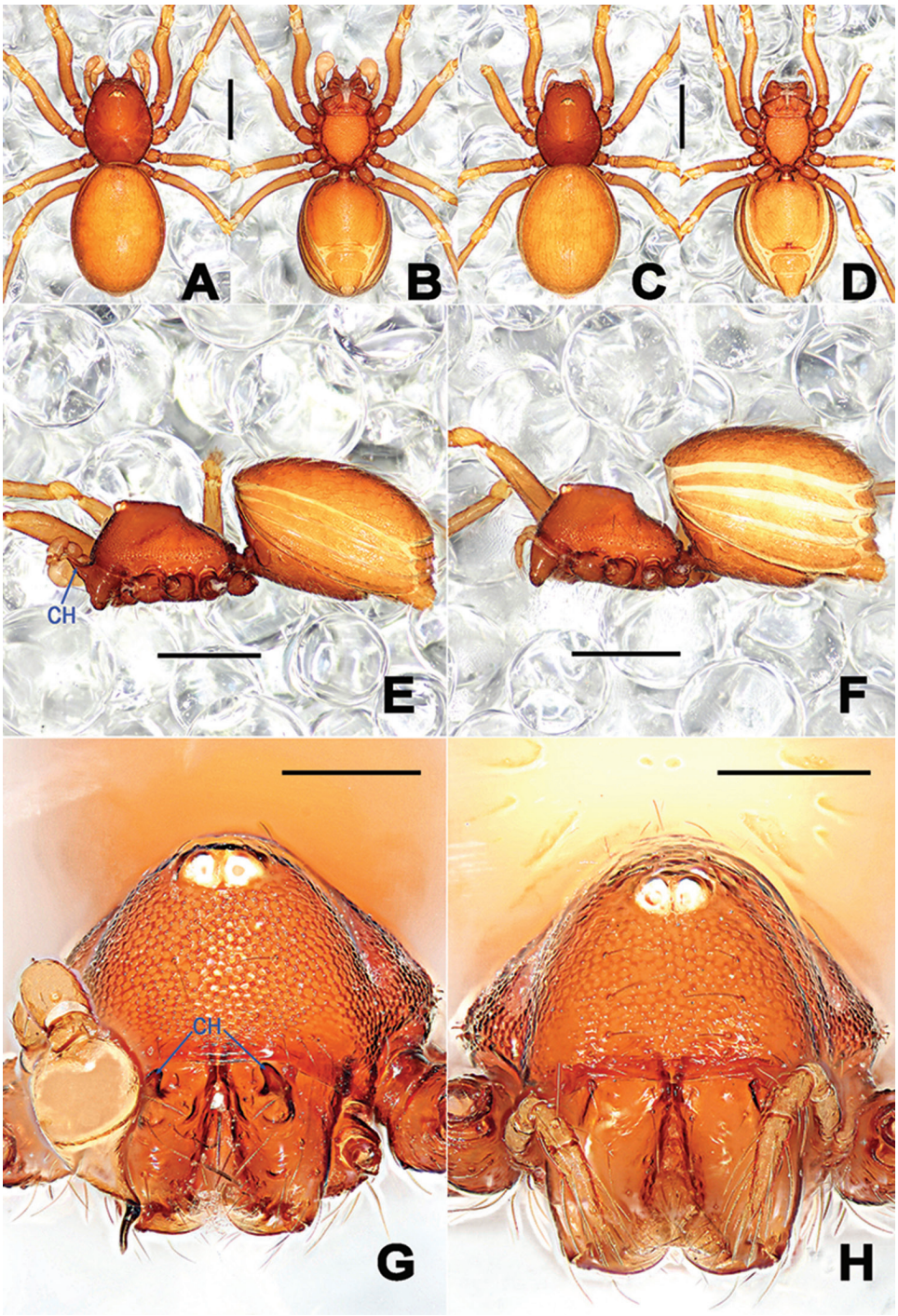

Figure 3. *Tetrablemma sokense* sp. n., male holotype (**A, B, E, G**) and female paratype (**C, D, F, H**). **A–F** habitus **G–H** prosoma. **A, C** dorsal **B, D** ventral **E–F** lateral **G–H** anterior. Abbreviations: CH = cheliceral horns. Scale bars: **A–F** 0.5 mm**, G, H** 0.2 mm.

Description. Male (holotype). Measurements: total length 1.48; carapace 0.53 long, 0.50 wide, 0.48 high; abdomen 1.07 long, 0.60 wide, 0.53 high; clypeus 0.15 high; sternum 0.31 long, 0.29 wide. Length of legs: I 1.42 (0.47, 0.13, 0.35, 0.24, 0.23); II 1.35 (0.44, 0.12, 0.34, 0.23, 0.22); III 1.15 (0.36, 0.11, 0.27, 0.20, 0.21); IV 1.44 (0.49, 0.12, 0.37, 0.23, 0.23).

Prosoma (Figure 3A–B, E, G): reddish-brown, carapace finely reticulated, marginally rugose; four white eyes, as vestigial eyespots in a group, ocular area in anterior half of carapace; ALE>PLE, ALE and PLE adjacent; cephalic part raised, flat top; clypeus high, sloping forward, with sparse setae, marginally round; cheliceral horns long, straight, distal tip sharp, cheliceral lamina developed; endites basally wide, distally narrow, labium trapezoidal, distally truncated; sternum finely reticulated, marginally strongly rugose, posterior end truncated. Legs: yellowish-orange, cuticle striated; tibiae I–III with three trichobothria, two on tibia IV, and one on metatarsi I–IV. Opisthosoma: orange, dorsal scutum long oval, surface reticulated, weakly granulated, bearing sparse long setae; ventral scutum reticulated; lateral scutum I long, and exceeding beyond the posterior margin of preanal scutum; postgenital scutum straight, banded, mesally wide and laterally narrow; preanal scutum flat, nearly oval, with long setae.

Palp (Figure 4A–C): femoral cuticle ventrally granulated, approx. 2.2 × longer than patella; patella short and smooth, distinctly longer than cymbium; tibia wide, swollen, approx. 1.2 x wider than femur, with a distal-dorsally trichobothrium; cymbium short, constricted, bearing sparse long setae; bulb long pear-shaped, surface of dilated area smooth, surface of sub-distal area rugose; embolus strongly sclerotized, starting from the apex of bulb; embolic tip cuneate, twisted, sharply pointed; spermophor coiled into a loop in bulb, abruptly twisting to narrow, and open at the embolic tip.

Female (one paratype). Measurements: total length 1.52; carapace 0.55 long, 0.49 wide, 0.47 high; abdomen 1.03 long, 0.67 wide, 0.60 high; clypeus 0.14 high; sternum 0.32 long, 0.28 wide. Length of legs: I 1.39 (0.46, 0.12, 0.37, 0.23, 0.21); II 1.30 (0.42, 0.12, 0.33, 0.22, 0.21); III 1.18 (0.37, 0.11, 0.28, 0.22, 0.20); IV 1.45 (0.48, 0.12, 0.38, 0.24, 0.23).

Prosoma (Figs 3C–D, F, H, 5): coloration and modification as in male, but instead cheliceral horns a small nodule fronto-proximally. Clypeus lower than in male, palps distinctly reduced, palpal tibia with a dorsal trichobothrium. Legs as in male. Opisthosoma: dorsal and ventral scuta as in male; lateral scutum I long, extending beyond posterior margin of preanal scutum; postgenital scutum long, straight, bearing a row of long setae, mesally wide, laterally narrow; preanal scutum weakly sculptured, wider than long, nearly rectangular, with sparse stiff setae.

Epigyne and vulva (Figure 4E–F): epigynal fold absent; epigynal pit indistinct, oval, opening at the posterior margin of the pulmonary scutum; vulval stem short, columnar, strongly sclerotized; vulval ducts wide, translucent, widely "V"-shape; seminal receptacles saccular, transparent; inner vulval plate fingerlike, distinctly sclerotized, slightly tilting; central process small, weakly sclerotized, shorter than inner vulval plate, apically falcate.

Habitat and biology. Cave. The cave entrance was ca. 80 altitudinal meters above the ground at an isolated limestone hill. Almost under every stone only one spider

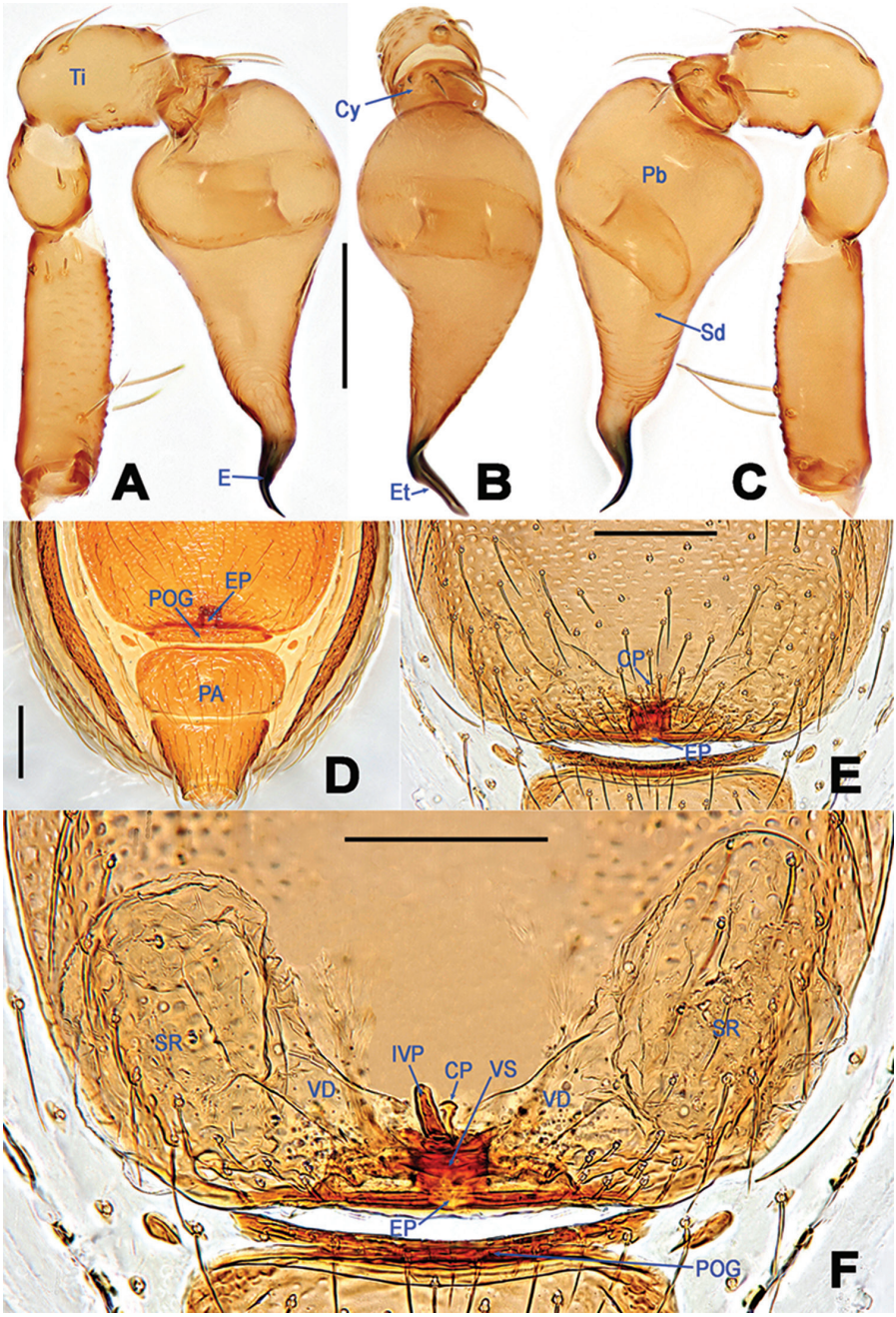

Figure 4. *Tetrablemma sokense* sp. n., male holotype (**A–C**) and female paratype (**D–F**). **A–C** left palp **D** genital area (untreated) **E, F** cleared vulva (lactic acid-treated). **A** prolateral **B** frontal **C** retrolateral **D–E** ventral **F** dorsal. Abbreviations: CP = central process; Cy = palpal cymbium; E = embolus; EP = epigynal pit; Et = embolic tip; IVP = inner vulval plate; PA = preanal scutum; Pb = palpal bulb; POG = postgenital scutum; Sd = spermophor; SR = seminal receptacle; Ti = palpal tibia; VD = vulval duct; VS = vulval stem. Scale bars: 0.2 mm.

Figure 5. *Tetrablemma sokense* sp. n., live female in cave, Cambodia (green arrows indicating silken strands, photograph by P. Jäger).

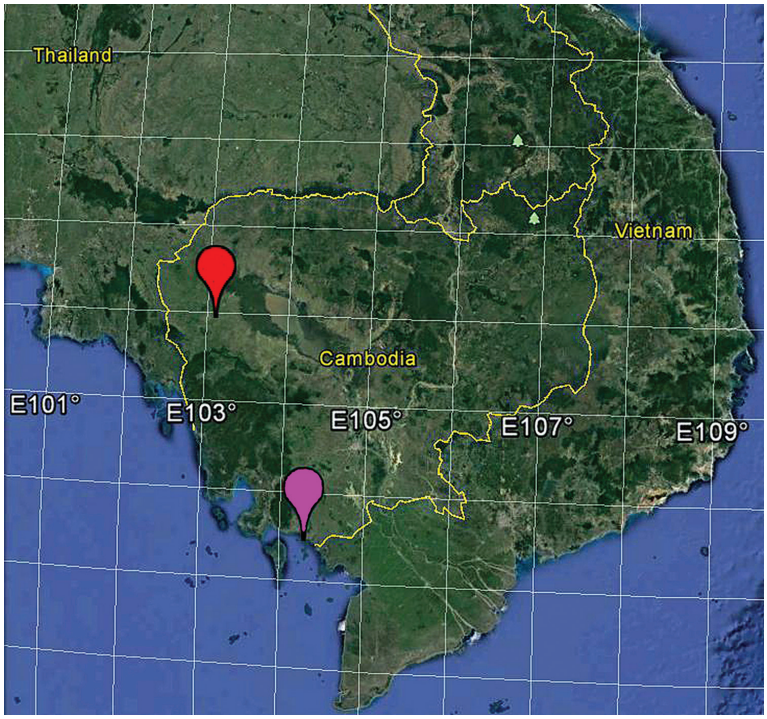

Figure 6. Distribution records of *Tetrablemma kepense* sp. n. (pink balloon) and *Tetrablemma sokense* sp. n. (red balloon) in Cambodia.

was found; silken strands used by the spiders may be the reason for this territoriality (Figure 5). It was the highest density of Tetrablemmidae observed in a cave by the last author. Besides Tetrablemmidae, there were Oonopidae (also found under stones), Pholcidae, Sparassidae, Uloboridae, Hersiliidae, Agelenidae, Amblypygi and Isopoda.

Distribution. Known only from the type locality (Figure 6).

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RESEARCH ARTICLE

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A review of the Cholevinae from the island of Borneo (Coleoptera, Leiodidae)

Menno Schilthuizen[1,2,3,4], Michel Perreau[5], Iva Njunjić[1,3,6]

1 *Naturalis Biodiversity Center, Darwinweg 2, 2333CR Leiden, The Netherlands* **2** *Institute for Biology Leiden, Leiden University, Sylviusweg 72, 2333BE Leiden, The Netherlands* **3** *Taxon Expeditions, Rembrandtstraat 20, 2311 VW Leiden, The Netherlands* **4** *Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, Kota Kinabalu, Malaysia* **5** *IUT Paris Diderot, Université Paris Diderot, Sorbonne Paris cité, case 7139, 5 rue Thomas Mann, 75205 Paris cedex 13, France* **6** *Institut de Systématique, Évolution et Biodiversité, Muséum National d'Histoire naturelle, Sorbonne Universités, Paris, France*

Corresponding author: *Menno Schilthuizen* (menno.schilthuizen@naturalis.nl)

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Abstract

The available knowledge of the round fungus beetle subfamily Cholevinae (Leiodidae) from the island of Borneo is reviewed, and the results of newly studied material presented. The currently known 30 species (of which 14 are newly described herein) represent the genera *Micronemadus* (one species), *Catops* (one species), *Baryodirus* (one species), *Ptomaphaginus* (14 species), and *Ptomaphaminus* (13 species). The following new species are described: *Micronemadus sondaicus* Schilthuizen & Perreau, **sp. n.**, *Ptomaphaginus grandis* Schilthuizen & Perreau, **sp. n.**, *P. louis* Schilthuizen & Perreau, **sp. n.**, *P. muluensis* Schilthuizen & Perreau, **sp. n.**, and *P. isabellarossellini* Schilthuizen, Njunjić & Perreau, **sp. n.**, and *Ptomaphaminus kinabatanganensis* Njunjić, Schilthuizen & Perreau, **sp. n.**, *P. testaceus* Schilthuizen & Perreau, **sp. n.**, *P. nanus* Schilthuizen & Perreau, **sp. n.**, *P. marshalli* Schilthuizen & Perreau, **sp. n.**, *P. hanskii* Schilthuizen & Perreau, **sp. n.**, *P. sarawacensis* Schilthuizen & Perreau, **sp. n.**, *P. layangensis* Schilthuizen & Perreau, **sp. n.**, *P. microphallus* Schilthuizen & Perreau, **sp. n.**, and *P. alabensis* Schilthuizen & Perreau, **sp. n.** It is expected that the cholevine biodiversity of Borneo is still far from completely known. Nonetheless, provisional identification keys to all species known so far are presented.

Keywords

caves, Indonesia, Malaysia, scavenging beetles, taxonomy

Introduction

Borneo is, after New Guinea, the second-largest tropical island of the world. It has never been strongly isolated, having formed part of a larger land mass, known as Sundaland, during marine transgressions in the Pleistocene (Hall and Holloway 1998). Sundaland comprises the present-day Malay Peninsula, the islands of Sumatra, Java, and Borneo, as well as the shallow seas in between. Recent paleoclimatic modelling (Raes et al. 2014) suggests that even during cooler periods of marine regression, evergreen wet forests dominated the area that now comprises Borneo. This, and the fact that the island, because of its mountainous character (with Gunung Kinabalu reaching almost 4,100 m) contains a great variety of habitats, has generated and maintained a rich biodiversity, not least in its soil and litter-dwelling invertebrate fauna (e.g., Hanski and Hammond 1986, Rahman et al. 2002, Liew et al. 2010).

The beetle subfamily Cholevinae (Coleoptera, Staphylinoidea, Leiodidae) consists mostly of small, soil-dwelling scavengers, well represented in the litter fauna of all tropical regions. Szymczakowski (1964) provided the first overview of the Cholevinae of South Asia, but the large number of new species described since then (Perreau 2000, and unpublished checklists) mean that this work is severely outdated by now. In recent years, several semi-comprehensive studies have appeared, either limited to a certain region (e.g., Wang and Zhou 2015) or to a certain habitat (e.g., Perreau 2009).

In this paper, we provide an overview of the species of Cholevinae currently known from the island of Borneo. By necessity, this is a very preliminary overview, since it is based on comparatively little information. Jeannel (1936) mentions only one species from Borneo. Szymczakowski (1961) mentions one more, and Peck (1981) and Perreau (2000) describe two more. In 2008, we (Schilthuizen and Perreau 2008) described seven new species and two new records from Borneo, bringing the total cholevine fauna to 13 species. However, more recent work (e.g., Merckx et al. 2015), as well as study of existing material in the Natural History Museum (London), deriving from the 1978 Mulu expedition (Hanski 1983, Hanski and Hammond 1986), and in Naturalis Biodiversity Center (Leiden), have revealed many additional new species. In our opinion, the 30 species that we recognize in the present paper form a sufficient basis to produce a first overview of our current, but doubtlessly still very incomplete, knowledge of the cholevine fauna of Borneo.

We provide a brief description for all previously described genera and species, and more extensive descriptions for newly-described species, as well as differential diagnoses for new species that have close congeners in Borneo. Where available, we also refer to DNA sequences in the Barcode of Life Database (BOLD, http://boldystems.org) and to so-called Barcode Index Numbers (BINs; Ratnasingham and Hebert 2013). We also give preliminary identification keys. However, given the fact that this overview is probably still far from complete, these keys should be used with caution: any sample collected in Borneo is likely to contain previously unrecognised species, and we hope this paper will stimulate further taxonomic and faunistic work.

The collection abbreviations used in the lists of examined material are as follows:

BORN Borneensis Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia;
FRCS Forest Research Centre, Sepilok, Malaysia;
HNHM Hungarian Natural History Museum, Budapest, Hungary;
JRUC collection of Jan Růžička, Prague, Czech Republic;
MHNG Muséum d'Histoire Naturelle de Genève, Switzerland;
NHMUK Natural History Museum, London, UK (formerly British Museum (Natural History));
RMNH Naturalis Biodiversity Center, Leiden, The Netherlands (comprising the collections of the Rijksmuseum van Natuurlijke Historie, Leiden and the Zoölogisch Museum, Amsterdam).
TXEX Taxon Expeditions, Leiden, The Netherlands.
CMPR Collection Michel Perreau, Paris.

Male genitalia were mounted in Euparal after dissection and dehydration in ethanol 95%. Female genitalia were cleared in hot KOH 10% and stained with Azoblack before mounting in DMHF (2,5-DiHydroxyMethylFurane). Photographs of genitalia were taken on a Leitz Diaplan microscope using a Spot Insight IN1820 or a Leica MC170HD camera. High-resolution photonic pictures of external morphological details (Figure 14a–e) were taken with a Keyence VHX5000 microscope and a VH-Z250T lens. The outline of the map was built from SRTM3 data (Shuttle Radar Topography Mission) of NASA with the software QGIS. They were completed by the global administrative areas database GDAM (www.gdam.org) and the hydrographic networks of Natural Earth (http://www.naturalearthdata.com/). All images and descriptions will be uploaded to the Cholevidae of the World website (http://cholevidae.myspecies.info/).

Systematics

Tribe: ANEMADINI Hatch

Genus: *Micronemadus* Jeannel, 1936

Description. Small, 1.4–2.6 mm. Oval habitus, with the apex of the elytra rounded. Head and pronotum punctate, elytra with transverse strigae. Antenna with antennomeres 4 and 5 very short and wide. Mesosternum with a longitudinal mesoventral process. The four first protarsomeres and the first mesotarsomere dilated in the male. Aedeagus: median lobe triangular, parameres longer than the median lobe, and bent inward.

***Micronemadus sondaicus* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/8AA2A703-76B4-4DCE-BFD3-8E19943EA8BA
Figure 1a, c–f

Material. Holotype: Malaysia, Sabah, Crocker Range Park, Inobong, 5°51.265'N, 116°08.363'E, 500 m elev., 21–23.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555641), male. **Paratypes**: *Sabah.* Crocker Range Park, Inobong, 5°51.3'N, 116°08.4'E, 500 m elev., 21–23.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555640, 555642), 2 individuals; Crocker Range, Gunung Alab, xii.2009 (leg. M. Schilthuizen, RMNH.INS.63291, 63310, 63295), 3 individuals; Crocker Range, along the road from Kota Kinabalu to Tambunan, near Rafflesia Park, 5°46.4'N, 116°20.8'E, 1350 m elev., baited pitfall trap, 2001 (leg. M. Schilthuizen, RMNH.INS.549293–549295), 3 individuals; Kinabalu Park, Headquarters Area, Liwagu Trail, 6°0.487'N, 116°32.7'E, pitfall with chicken, 2.iv.2016 (leg. M. Schilthuizen, I. Njunjić & F. Feijen, BORN, RMNH.INS.1086143–1086158), 36 individuals. Kinabalu Park, Sayap, ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, BOR/COL/14178–14193), 16 individuals. *Sarawak.* Gunung Mulu National Park, many localities between 100 and 950 m elev., iii–viii.1978 (leg. P. M. Hammond & J. E. Marshall, NHMUK BM 1978–49), 131 specimens.

Description. Length: 2.0–2.6 mm. Colouration: in fully coloured individuals dark brown to black, margins of pronotum and front half of the elytra reddish brown, entirely covered in reddish brown setae; legs, palps, and basal three and final antennomeres light reddish brown; antennomeres 4–10 darker (Figure 1a). Pronotum: small, much narrower than the elytra, ca. 2 times as broad as wide, with the greatest width slightly frontal of the caudal angles; basal margin gently emarginated near the angle, and with an angular sinuosity in the centre, on either side of the scutellum. Elytra: rounded at the apex, 1.25 times as long as jointly wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Winged. Male protarsi: slightly narrower than the protibia, segments 1–4 as long as wide. Aedeagus: median lobe pointed, nearly perfectly triangular, parameres slender, extending far beyond the tip of the median lobe (Figure 1c). Female sternite VIII caudally broadly rounded, rostrally tapering into a narrow tip.

Differential diagnosis. Similar to *M. pusillimus* (Kraatz, 1877), described from Japan, but compared with Japanese specimens of *M. pusillimus* that we have seen, *M. sondaicus* is larger, more uniformly coloured (Figure 1a; Japanese *M. pusillimus* have a more strikingly dark pronotum), has a simple triangular shape of the median lobe of the aedeagus (in *M. pusillimus*, the apex is separately acuminate; see Figure 1b), and more slender parameres (Figure 1c). The female sternite VIII in *M. pusillimus* is more slender and rostrally not as narrowly tapered as in *M. sondaicus*. *M. ruzickai* Perreau, 2004 differs by the parameres that are even more massive than in *M. pusillimus*.

DNA-barcodes. In the BOLD database, COI sequences are available for the holotype (RMNH.INS.555641) and two paratypes (RMNH.INS.555640, 555642) from

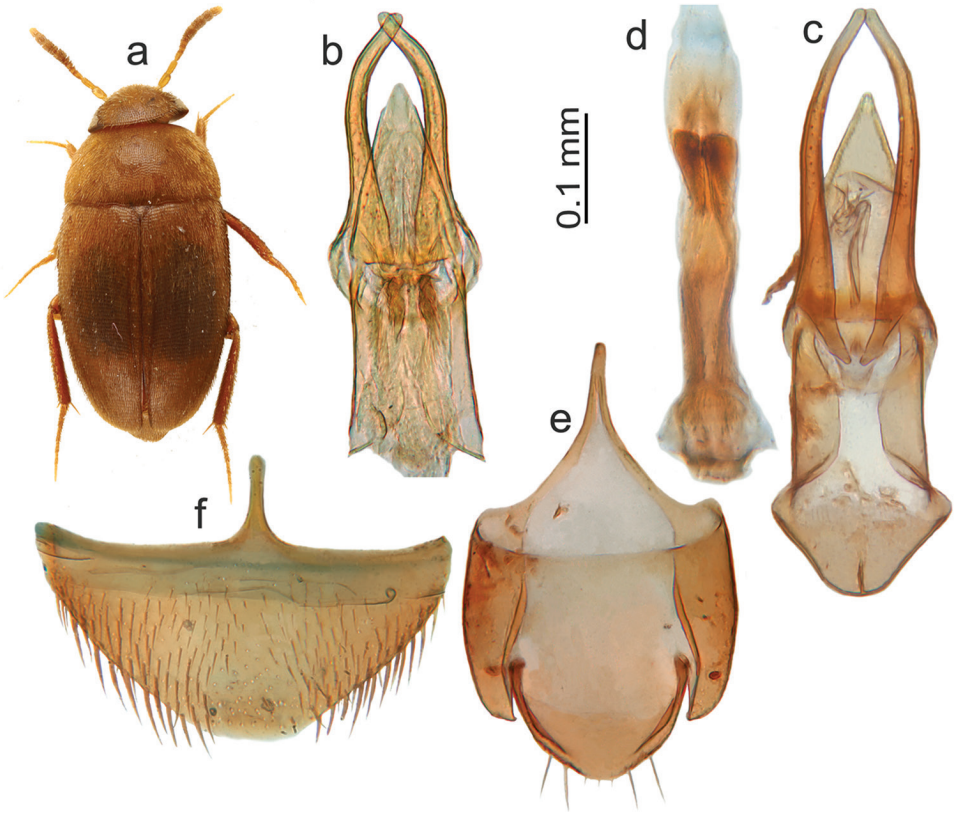

Figure 1. *Micronemadus*. **a** *M. sondaicus* sp. n. habitus (paratype female, Sarawak, Gunung Mulu) **b** *M. pusillimus* (Kraatz) aedeagus, Sarawak, Gunung Mulu **c** *M. sondaicus* sp. n. aedeagus Sarawak, Gunung Mulu **d** *M. sondaicus* sp. n. endophallus, Sarawak, Gunung Mulu **e** *M. sondaicus* sp. n. male urite IX, Sarawak, Gunung Mulu **f** *M. sondaicus* sp. n. female sternite VIII, Sarawak, Gunung Mulu.

Inobong (Crocker Range) and also for the paratypes RMNH.INS.549293–549295 from Gunung Alab (Crocker Range). See also under Remarks.

Habitat and distribution. Very common and widespread, in primary and secondary forest, 0–1850 m elev. In addition to the type material, we have seen seemingly conspecific material from many other localities in Sundaland, (Sabah, Sarawak, Peninsular Malaysia, Mindanao, Java, Bali) and also from Vietnam. Nishikawa's (1989) records of *M. pusillimus* from Peninsular Malaysia, Sabah, Sarawak, Java, and Bali (which we did not see) may also refer to *M. sondaicus*. This overview suggests that *M. sondaicus* is widespread in Southeast Asia (but see below under remarks).

Remarks. For many years, we considered this Borneo *Micronemadus*, which is usually the commonest leiodid in baited traps, as identical to *M. pusillimus*. However, DNA-barcodes for Japanese individuals (BOLD BIN ABU9390) and Bornean individuals (BOLD BINs ABU9391 and ACK0008) display a 17% sequence divergence, strongly suggesting that, despite the only slight morphological differences,

these belong to separate, not closely related species. We suspect that *M. pusillimus*, previously considered a very widespread Asian species (Szymczakowski 1964), may represent a complex of genetically strongly differentiated, but morphologically very similar taxa. In fact, among the DNA-barcoded specimens of *M. sondaicus* from Sabah's Crocker Range, we already see a 2.7% sequence divergence between highland and lowland populations, which has led the BOLD algorithm to place them into separate BINs (ABU9391 and ACK008, respectively). At the moment, however, we consider ABU9391 and ACK008 as conspecific.

Etymology. The name refers to the Sunda region, of which Borneo forms part (*sondaicus* (L.) = from Sunda). We used the spelling *sondaicus*, rather than *sundaicus*, to conform with other specific epithetons, such as *Rhinoceros sondaicus* Desmarest, 1822.

Tribe: CHOLEVINI Kirby, 1837

Genus: *Catops* Paykull, 1798

Description. Fairly robust cholevines of sizes that range from just longer than 2 mm to almost 10 mm. Body fairly convex, pronotum relatively large, but usually narrower than the elytra. Elytra sometimes with traces of parallel longitudinal striae. Antennae with the 8th antennomere usually broader than long. In the male, the four first protarsomeres and the first mesotarsomere are dilated; also, the protibiae often are sexually dimorphic. Aedeagus: median lobe usually symmetric, elongated, lance-shaped, terminally rounded, truncate, acute, or two-pronged. Parameres usually thin, hair-like.

Catops pruinosus Schweiger, 1956

Figure 2

Catops pruinosus Schweiger, 1956: 538, fig. 5; type from Kuatun, Fukien, China.
Catops solitarius Szymczakowski, 1961: 129, figs 16–19; type from Sandakan, Sabah, Borneo (in NHMUK).

Material. *Sabah.* Sandakan (leg. W.B. Pryer, NHMUK 1925–264). Holotype of *C. solitarius* Szymczakowski (examination based on a photograph taken by Jan Růžička).

Description. Length: 3.9 mm. Habitus slender and elongated, somewhat flattened. Body reddish brown; head, centre of the pronotum, and centre of the elytra dark brown. Entire dorsum covered in orange setae. Antenna robust, 7th antennomere as wide as long, 6th, 8th, 9th, and 10th wider than long. Pronotum 1.54 times as wide as long, frontal and caudal margins straight, lateral margins curved, more strongly rostrad than caudad (greatest width of the pronotum slightly behind the centre), caudal angles broadly rounded; surface with dense, rasp-like punctuation and somewhat matte due

Figure 2. *Catops pruinosus* Schweiger, habitus of the female holotype of *C. solitarius* Szymczakowski from Sandakan (photograph Jan Růžička).

to microsculpture. Elytra with fine punctuation, shagreened, and with slight indications of longitudinal striae, 1.27 times as wide as the pronotum, 1.3 times as long as jointly wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Male unknown.

Habitat and distribution. *Catops pruinosus* is known from a large latitudinal expanse along the East Asian coast: Shanghai, Fujian, and North Borneo. The only known record from Borneo (Sabah: Sandakan) is the female holotype of *C. solitarius*, later synonymized with *C. pruinosus* (Szymczakowski 1964).

Remarks. *Catops pruinosus* is a member of the *C. hilleri* group (Szymczakowski 1964), represented by ca. 30 species, primarily from central and eastern Asia (Perreau 2000). The diagnosis above is based on a photograph (Figure 2) of the holotype of *C. solitarius*, as well as the description of *C. solitarius* by Szymczakowksi (1961). In the absence of males, we are unsure whether the Borneo specimen is indeed conspecific with *C. pruinosus*. Indeed, we also doubt that the specimen truly derives from Borneo: despite many years of work in Borneo, we have never come across any Cholevini. If members of such temperate-region groups exist in Borneo, we would expect them to occur in the highlands, rather than in coastal locations such as Sandakan. In fact, it is not impossible that the Sandakan specimen is a mislabelled Chinese specimen, as the collector, William Burgess Pryer, was active in Shanghai (where *C. pruinosus* is known to occur) immediately before moving to Sandakan (Tregonning 1954).

Tribe: PTOMAPHAGINI Jeannel, 1911

Genus: *Baryodirus* Perreau, 2000

Description. Length: 2.2 mm. Winged and with fully developed eyes (Figure 3a). Body uniformly brown, eyes black. Dorsal surface with transverse strigae. Pronotal and elytral surface with two types of setation: one dense, long, and recumbent aligned on the transverse strigae, and one sparse, long and erected, roughly aligned along longitudinal rows (Figure 3b). Head with a high and robust occipital carina. Pronotum convex and transverse, slightly wider than the elytra at the shoulders, 1.9 times as wide as long, the lateral sides rounded, the largest width near the anterior third of the length. Basal margin without a marginal gutter, slightly sinuate near the slightly drawn-out lateral angles. Elytra exactly as long as wide, the largest width at the base. Elytral sides nearly straight, weakly arcuate, giving the elytra a triangular shape. The sutural stria is the only recognizable elytral stria. Mesoventral process strikingly wide and high, anteriorly angular, with flat and setose ventral side, posteriorly widely expanded above the metasternum (Figure 3c). Protibiae with a lateral row of spines along the external edge and with smaller spines randomly arranged on the ventral side (Figure 3d). Mesotibiae and metatibiae with a circular row of spines around the apex. Female protarsi tetramerous and strikingly expanded with dense setae on the ventral side. Male unknown. Spermatheca elongated with a succession of rings along the entire length (Figure 3e; a somewhat similar condition is found in *Ptomaphaminus latescens* Szymczakowski, 1964 and *P. testaceus* sp. n.).

Baryodirus hammondi Perreau, 2000

Figure 3a–e

Baryodirus hammondi Perreau, 2000 19–20, figs 1–10; type from Mulu, Sarawak (in NHMUK).

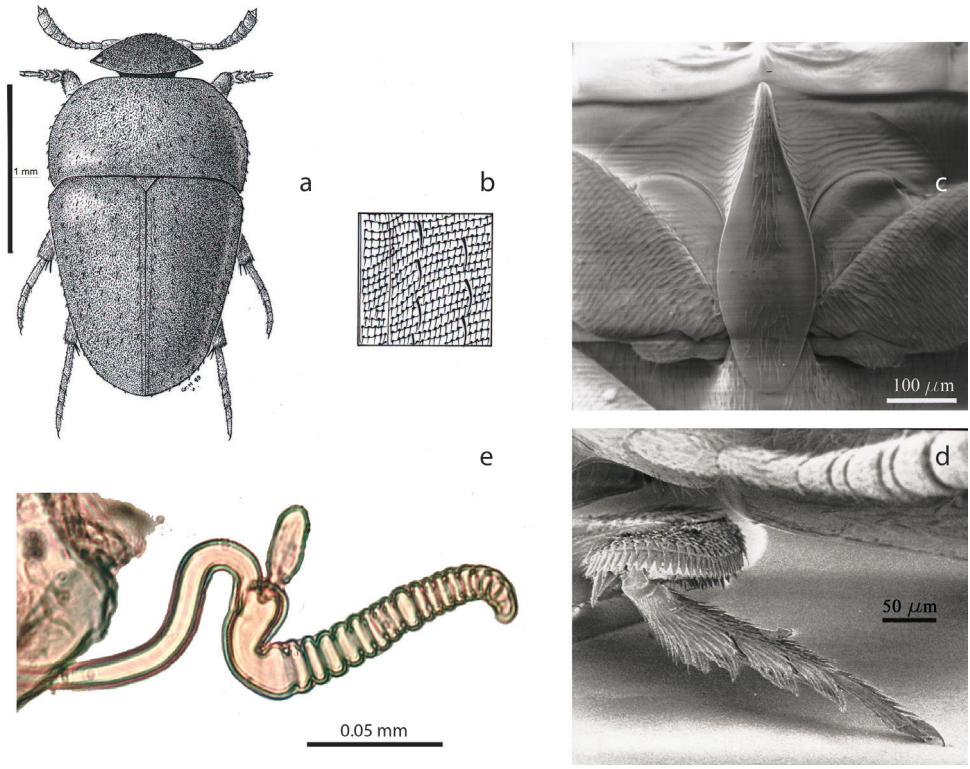

Figure 3. *Baryodirus hammondi* Perreau (holotype female, Sarawak, Gunung Mulu; after Perreau 2000). **a** habitus (drawing by G. Hodebert) **b** detail of double setation on elytra **c** mesoventral process, ventral view **d** protarsus **e** spermatheca.

Description. See genus description above: the genus is monotypic, and the holotype is the only known specimen of the species.

Habitat and distribution. The biotope and ecology of this species are unknown, but several characters suggest that it could be a commensal of hymenopterans. The compact habitus and the double setation are observed (almost exclusively) in many myrmecophilous leiodid genera or subgenera, such as *Ptomaphagus* (*Echinocoleus*) Horn in North America, and *Synaulus* in North Africa (our observations).

Genus: *Ptomaphaginus* Portevin, 1914

Description. In Borneo, *Ptomaphaginus* consists of relatively large Ptomaphagini with four dilated male protarsomeres, distinguishable from *Ptomaphaminus* by the ventral spines of the protibiae being aligned along the latero-external row of equal spines, making a second, more widely spaced row next to the external one, as well as by the metaventral sutures, which are roughly parallel to the axis of the body. Also,

in the female, the gonocoxites are elongated, whereas in most *Ptomaphaminus*, they are reduced.

With *Ptomaphaminus* Perreau (see below), *Ptomaphaginus* Portevin makes up the vast majority of the Borneo cholevine diversity. We currently recognise 14 species. However, more diversity is to be expected, both cryptic (e.g., DNA-analysis suggests additional diversity in *P. bryanti* and related species; Merckx et al. 2015) and non-cryptic (each field project in previously unexplored regions in Borneo results in new discoveries).

Ptomaphaginus anas Schilthuizen & Perreau, 2008

Figures 4a, 6i–j, 9a

Ptomaphaginus anas Schilthuizen & Perreau, 2008: 199, figs 16–17; type from Gombak, Selangor, Peninsular Malaysia (in RMNH).

Material. (In addition to that given in Schilthuizen and Perreau (2008)): *Sarawak*. Kuching, Semongok, 1°24.7'N, 110°19.3'E, 16.i.1978, (RMNH.INS.549311) 1 male.

Description. (Adapted from Schilthuizen and Perreau (2008)). Medium-sized (2.3–2.9 mm) and dark-coloured species. Pronotum 1.65 times as wide as long, as wide as the elytra. Elytra 1.1 times as wide as their combined length (length measured from the caudal tip of the scutellum to the apex of the elytra). Winged. Aedeagus in dorsal view gradually narrowing towards the apex. The tip is triangular and subtly asymmetric. A broad medial furrow runs over the dorsal side of the aedeagus, and dissolves just short of the apex. In lateral view, the median lobe is strongly curved, almost semicircular, and distinctly thickened at the point of strongest curvature.

Differential diagnosis. The aedeagus is characteristically shaped: strongly curved, distally tapering into a narrow, flattened, and slightly upturned apex. *Ptomaphaginus louis* and *P. muluensis* have a similar aedeagus, which, however, is less strongly curved in the terminal half.

DNA barcodes. One individual (RMNH.INS.549311; see under Examined material) is available in BOLD, but no DNA has been successfully sequenced from this specimen.

Habitat and distribution. Lowland and lower montane forest, up to 1,500 m. Sabah: Batu Punggul, Kinabalu Park HQ, Kibongol; Sarawak: Semongok. Peninsular Malaysia: Gombak, Cameron Highlands.

Ptomaphaginus bryanti Jeannel, 1936

Ptomaphaginus Bryanti Jeannel, 1936: 56–59, figs 63–66; type from Mt. Matang, Sarawak, Borneo (in NHMUK).

Description. Length 2.8 mm. Winged. Slender build (pronotum 1.56 times wider than long), as wide as the elytra. Aedeagus subterminally with two lateral extensions

Figure 4. *Ptomaphaginus*, habitus, dorsal. **a** *P. anas* Schilthuizen & Perreau, Ulu Gombak, male (RMNH) **b** *P. bryantioides* Schilthuizen & Perreau, Gunung Mulu, male (NHMUK) **c** *P. caroli* Schilthuizen & Perreau, Gunung Mas, holotype, male (RMNH) **d** *P. grandis* sp. n., Gunung Mulu, paratype, male (NHMUK) **e** *P. kinabaluensis* Schilthuizen & Perreau, Gunung Kinabalu, paratype, male (RMNH) **f** *P. kinabaluensis* Schilthuizen & Perreau, Gunung Kinabalu, paratype, female (RMNH.INS.1086205).

and a long median processus (the image given by Jeannel [1936] is erroneous, due to mounting error [Schilthuizen and Perreau 2008]).

Differential diagnosis. Very similar to *P. bryantioides*, from which it differs chiefly (as far as can be discerned from the single *P. bryanti* individual available) by its more slender habitus.

DNA barcodes. In the BOLD database, COI barcodes are available for RMNH.INS.555591 and 555594, two specimens that possibly belong to this species (See under Habitat and distribution).

Habitat and distribution. To date only known from the type location, Mt. Matang in Sarawak. However, given the great molecular distances (Merckx et al. 2015) that we find among Sabah populations of *P. bryantioides*, a more robust species with an aedeagus nearly indistinguishable from *P. bryanti* (see below), we suspect that some specimens assigned to that species, especially those from Sugud (BOLD BIN ACJ9515, RMNH.INS.555591 and 555594), may in fact belong to *P. bryanti* (although they are not as slender as the holotype of *P. bryanti*).

Ptomaphaginus bryantioides Schilthuizen & Perreau, 2008

Figures 4b, 6c–d, 9b, 10a

Ptomaphaginus bryantioides Schilthuizen & Perreau, 2008: 192–193, figs 20–21; type from Danum Valley, Sabah, Borneo (in RMNH).

Material. (In addition to that given in Schilthuizen and Perreau (2008)): *Sabah.* Sandakan, Sungai Lokam (logged forest), flight interception trap, iii.1997 (leg. A.Y.C. Chung, FRCS), 1 male; Sandakan, Sepilok (primary forest), flight interception trap, x.1996 (leg. A.Y.C. Chung, FRCS), 1 female. Kinabalu Park, Poring Hot Springs, 6°02.894'N, 116°41.957'E, 625 m elev., in baited pitfall traps, 15–20.ix.2012, (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555625–555628), 4 individuals; Crocker Range Park, Inobong, 5°51.265'N, 116°08.363'E, 500 m elev., 21–23.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555637), 1 individual; Kiansom Waterfall, 5°58.444'N, 116°12.526'E, 300 m elev., 5–7.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555598–555600), 3 individuals; Kiansom Waterfall, 5°58.444'N, 116°12.526'E, 300 m elev., 21–28.xii.2009 (leg. M. Schilthuizen, RMNH.INS.555644–555645, 549278, 63309, 63289–63290), 6 individuals; Crocker Range, Kota Kinabalu–Tambunan road (km 56), 1350 m elev., fish and human excrement traps, 21–24.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086159), 1 male; Kota Kinabalu, Tun Fuad Stephen Park, 20.iv.2003 (leg. Ng Kok Kit, RMNH.INS.63303, 63298, 549268–549271), 6 individuals; Kota Kinabalu, Tun Fuad Stephen Park, 5°56.717'N, 116°06.709'E, 75 m elev., baited pitfall traps, 23–29.xii.2009 (leg. M. Schilthuizen, RMNH.INS.555646–555677, 63285–63286, BOR/COL/14194–14205), 46 individuals. *Sarawak*. 4th Division, Gunung Mulu National Park, many localities between 100 and 800 m elev., iii–viii.1978 (leg. P. M. Hammond & J. E. Marshall, NHMUK BM 1978–49), 102 males, 116 females. *Kalimantan Timur*. Balikpapan env., ca. 25 km by road Sungain Wain reserve, camp Djamaludin, baited traps in primary dipterocarp forest, a clearing next to small stream, 14–17.ii.2010 (leg. P. Šipek, H. Šipkovà, JRUC), 1 male, 2 females.

Description. Habitus broad, rectangular, flat, very variable in size, 2.1–3.5 mm. Pronotum on average 1.8 times as wide as long, as wide as the elytra. Elytra as long as wide (length measured from the caudal tip of the scutellum to the apex of the

elytra). Winged. Aedeagus with two apical, laterally directed extensions and a long terminal processus. (It appears that in *P. bryanti*, the lateral extensions may be directed even more ventrad, and the median processus is more widened apically than in *P. bryantioides*, but the significance of these differences needs to be substantiated.) Male forelegs with long setae on the ventral sides of the femur and tibia. The 3rd, 4th, and 5th visible abdominal ventrite of the male carry a slight central notch and show a depression around these notches. Spermatheca simple, inflated, semicircular (Figure 10a), similar to that of *P. louis*.

Differential diagnosis. Distinguishable from other Bornean *Ptomaphaginus* species with the same aedeagus structure by the more elongated aedeagus with long, narrow processus, and the long setae on the male femur and tibia.

DNA barcodes. For the following specimens, COI barcodes are available in BOLD: RMNH.INS.549278 (Kiansom), RMNH.INS.63289 (Kiansom), RMNH.INS.555644–555645 (Kiansom), RMNH.INS.555598–555600 (Kiansom), RMNH.INS.63285–63286 (Kota Kinabalu), RMNH.INS.549268–549271 (Kota Kinabalu), RMNH.INS.555677 (Kota Kinabalu), RMNH.INS.555625–555628 (Poring Hot Springs), and RMNH.INS.555637 (Inobong). Although these sequences fall into several separate BINs, for the moment we consider them all conspecific (see under Habitat and distribution).

Habitat and distribution. Widely distributed in Sabah and northern Sarawak, in primary and secondary lowland forest (usually up to 500 m, one exceptional record at 1350 m). Sabah: Kota Kinabalu, Kiansom, Sugud, Kinabalu Park (Poring), Crocker Range Park (Inobong, KK–Tambunan road km 56), Danum Valley, Batu Punggul; Sarawak: Mulu National Park. DNA sequencing (Merckx et al. 2015) shows that within Sabah, several lineages exist. The most widely divergent of these are from Sugud and may represent a separate species (possibly *P. bryanti*; see above). Additionally, an approximate 4% COI-distance can be observed between the populations on the east and west slopes of the Crocker Range (BOLD BINs ACJ9516+ACJ9517 and ABU8889+ABU8890, respectively), but morphologically these populations are indistinguishable. For the time being, we consider all these BINs as conspecific.

Ptomaphaginus burckhardti Schilthuizen & Perreau, 2008

Figures 5f, 7g, h, 9c

Ptomaphaginus burckhardti Schilthuizen & Perreau, 2008: 202–203, figs 7–8; type from Gunung Kinabalu, Sabah, Borneo (in MHNG).

Description. (Adapted from Schilthuizen and Perreau (2008)). Length 2.5 mm. Habitus slender, ovoid. Pronotum 1.7 times as wide as long, slightly broader than the elytra. Elytra slender, 1.25 times as long as their combined width (length measured from the caudal tip of the scutellum to the apex of the elytra). Uniformly light brown. Wingless. Eyes reduced. Elytra laterally not curved, narrowed caudad in an approximately

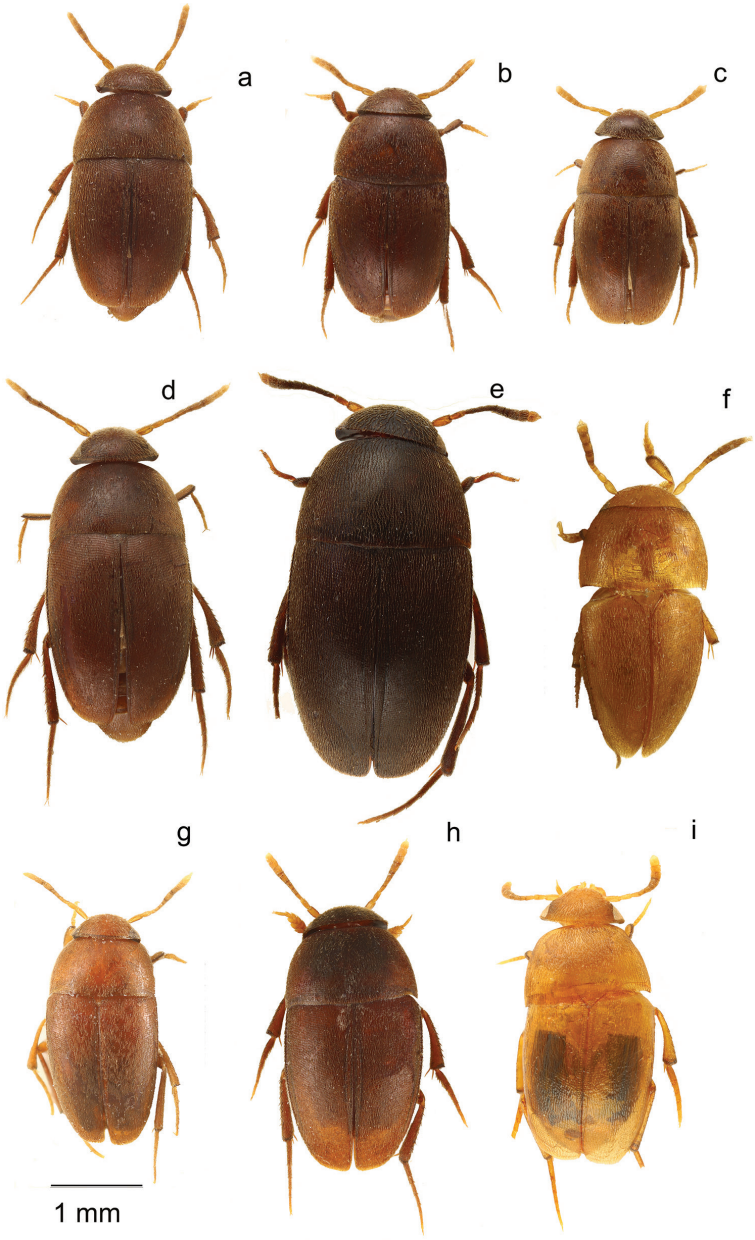

Figure 5. *Ptomaphaginus*, habitus, dorsal. **a** *P. louis* sp. n., Gunung Mulu, paratype, male (NHMUK) **b** *P. muluensis* sp. n., Gunung Mulu, paratype, male (NHMUK) **c** *P. scaphaner* Szymczakowski, Gunung Mulu, male (NHMUK) **d** *P. similipes* Schilthuizen & Perreau, Gunung Mulu, male (NHMUK) **e** *P. isabellarossellini* sp. n., Gunung Kinabalu, paratype, female (RMNH.INS.1086164) **f** *P. burckhardti* Schilthuizen & Perreau, Gunung Kinabalu, male, holotype (MNHG) **g** *P. sabahensis* Schilthuizen & Perreau, Gunung Kinabalu, male, holotype (MNHG) **h** *P. latimanus* Schilthuizen & Perreau, Gunung Trus Madi, holotype, male (RMNH) **i** *P. latimanus* Schilthuizen & Perreau, Gunung Trus Madi, paratype, female (RMNH.INS.1086206).

straight line. Male with a large and deep semicircular depression extended on the 5th and 6th visible abdominal sternites, bordered on the front half with long and dense setae, and a central notch on the apical edge of the 6th. Aedeagus slender. The apex is tapered terminally and ends in a flattened, duck-bill-shaped processus. It carries several long, curved, lateral setae.

Differential diagnosis. Unique among the Bornean *Ptomaphaginus* because of its small, slender build, reduced eyes, and long, slender aedeagus.

Habitat and distribution. Only two specimens known (holotype and paratype), from upper montane forest at 2600 m elev. on Gunung Kinabalu.

Ptomaphaginus caroli Schilthuizen & Perreau, 2008

Figures 4c, 8a, b

Ptomaphaginus caroli Schilthuizen & Perreau, 2008: 193, figs 14–15, 26; type from Gunung Mas, Sabah, Borneo (in RMNH).

Description. (Adapted from Schilthuizen and Perreau (2008)). Length 2.7 mm. Habitus relatively slender and narrow, flat. Pronotum 1.62 times as long as wide, slightly narrower than the elytra. Elytra 1.41 times as long as their combined width (length measured from the caudal tip of the scutellum to the apex of the elytra). Winged. Long setae on the ventral side of the male profemur and protibia absent. Aedeagus apically with two short 'wings' and a very small, indistinct terminal processus. *Spiculum gastrale* long-triangular, the apex nearly truncate, with a small central projection; similar in shape to *P. latimanus* and *P. similipes*.

Differential diagnosis. *Ptomaphaginus caroli* has a similar aedeagus as *P. bryanti*, *P. similipes*, and *P. bryantioides*. However, it differs in having a distinctly elongated habitus (elytral index of 1.41) and very short apical 'wings' on the aedeagus.

Habitat and distribution. So far, only known from the type specimen, collected in lower montane forest at 1350 m in the Crocker Range of Sabah. The aedeagal shape shows that it belongs within the "*bryanti*-group".

Remarks. The aedeagus of the holotype has been lost shortly after it was first collected and studied (in 2000). Before the loss, sketches were made of the dorsal and lateral view of the aedeagus, which form the basis for the line drawing in Figure 8 and in Schilthuizen and Perreau (2008).

Ptomaphaginus grandis Schilthuizen & Perreau, sp. n.

http://zoobank.org/1995F69B-A8D0-44E7-B4D5-A8BA57C2235C

Figures 4d, 6k, l, 9d, 10b

Material. Holotype: Malaysia, Sarawak, Mulu National Park, Slope, TPS 7–9, 29.iv.1978 (P.M. Hammond & J.E. Marshall leg., NHMUK, B.M. 1978–49), male.

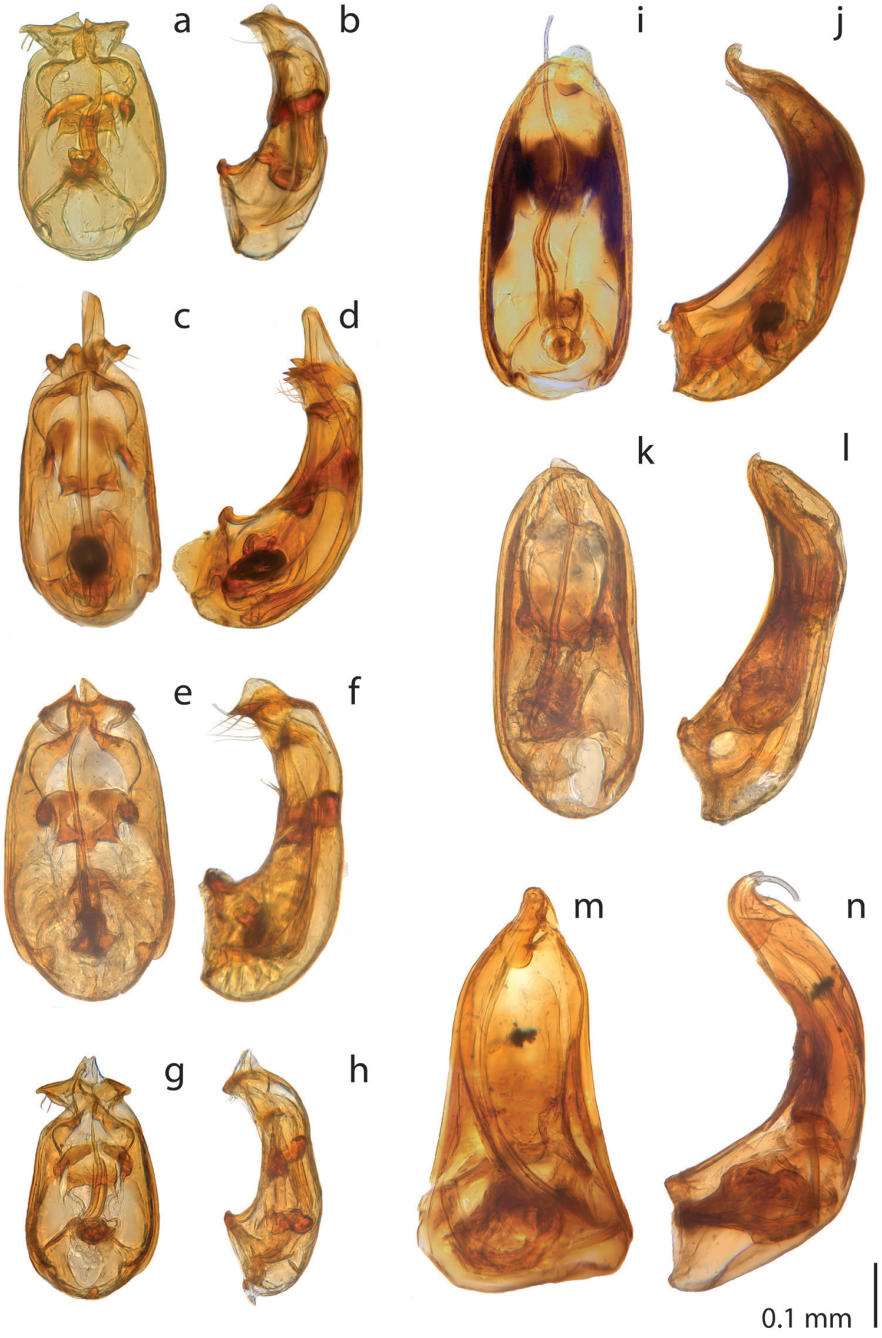

Figure 6. *Ptomaphaginus*, aedeagus, dorsal (left) and lateral (right) view. **a, b** *P. kinabaluensis* Schilthuizen & Perreau, Gunung Kinabalu (RMNH.INS.63302) **c, d** *P. bryantioides* Schilthuizen & Perreau **e, f** *P. similipes* Schilthuizen & Perreau, Gunung Mulu (NHMUK) **g, h** *P. latimanus* Schilthuizen & Perreau Gunung Trus Madi, holotype (RMNH) **i, j** *P. anas* Schilthuizen & Perreau, Semongok (RMNH) **k, l** *P. grandis* sp. n. Gunung Mulu, paratype (NHMUK) **m, n** *P. louis* sp. n. Gunung Mulu, paratype (NHMUK).

Paratypes: Sarawak. Mulu National Park, Slope, TPS 7–9, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 5 males, 7 females; Mulu National Park, Slope, TPS 10–12, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 male, 5 females.

Description. Habitus: very large (3.4–4.0 mm), dark reddish brown, the elytra deeper red than the pronotum, basis and tip of the antenna pale, antennomeres 5–10 much darker; relatively parallel-sided and somewhat convex, head relatively narrow, pronotum 1.67 times as wide as long, slightly wider than the elytra, caudal angles clearly extended. Elytra of moderate length, convex, broadest at the shoulders, in the caudal one-third gently rounded towards the apex, jointly ca. 1.5 times as long as wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Body entirely covered in dense pale yellow setation. Wings present. Antennae slender, 4th antennomere longer than wide, 9th and 10th antennomere square. Male protarsi only slightly dilated, the first four tarsomeres jointly ca. 4 times as long as wide. Aedeagus short and broad, in lateral view only very slightly bent ventrad with a barely perceptible upturned tip at the end, in dorsal view narrowing (in rounded fashion) towards the blunt apex. Stylet short and straight. *Spiculum gastrale* long, narrow-triangular, with the caudal part rounded. Spermatheca U-shaped, with ca. 6 distinct narrow rings on the proximate leg of the "U", and ca. 6 additional, indistinct, broader rings on the remainder. Spermiduct long, thin, consisting of 5–6 360° coils.

Differential diagnosis. Externally distinctive by its large size and the colour pattern of the antennae. From equally large *P. bryantioides*, it may be distinguished by the narrower male protarsi and the longer elytra. Aedeagus cannot be confused with that of any other known Bornean species, but is similar in shape to the one of *P. nitens* Jeannel, 1936 from Sri Lanka (which, however, is smaller and has much more condensed antennae) and of several species described from China and Taiwan (especially *P. pingtungensis* Perreau, 1996, *P. guangxiensis* Wang & Zhou, 2015, *P. perreaui* Wang & Zhou, 2015, and *P. yui* Wang & Zhou, 2015), from which *P. grandis* is distinguished by the unique combination of body size, antennomere proportions, and details of the *spiculum gastrale*, spermatheca, and aedeagus shape.

Habitat and distribution. Only known from Mulu National Park in Sarawak.

Etymology. Named *grandis* for its large size.

***Ptomaphaginus isabellarossellini* Schilthuizen, Njunjić & Perreau, sp. n.**
http://zoobank.org/87C3F9D7-6CBD-4351-B96F-307A65F0716D
Figures 5e, 7a, b, 9e, 10c

Material. Holotype: Malaysia, Sabah, Mt. Kinabalu National Park, Bukit Ular Trail (low), 1800 m elev., multistratum evergreen forest, 2 fish traps, 07–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086160), male. **Paratypes**: Sabah. Mt. Kinabalu National Park, Bukit Ular Trail (low), 1800 m elev., multistratum evergreen for-

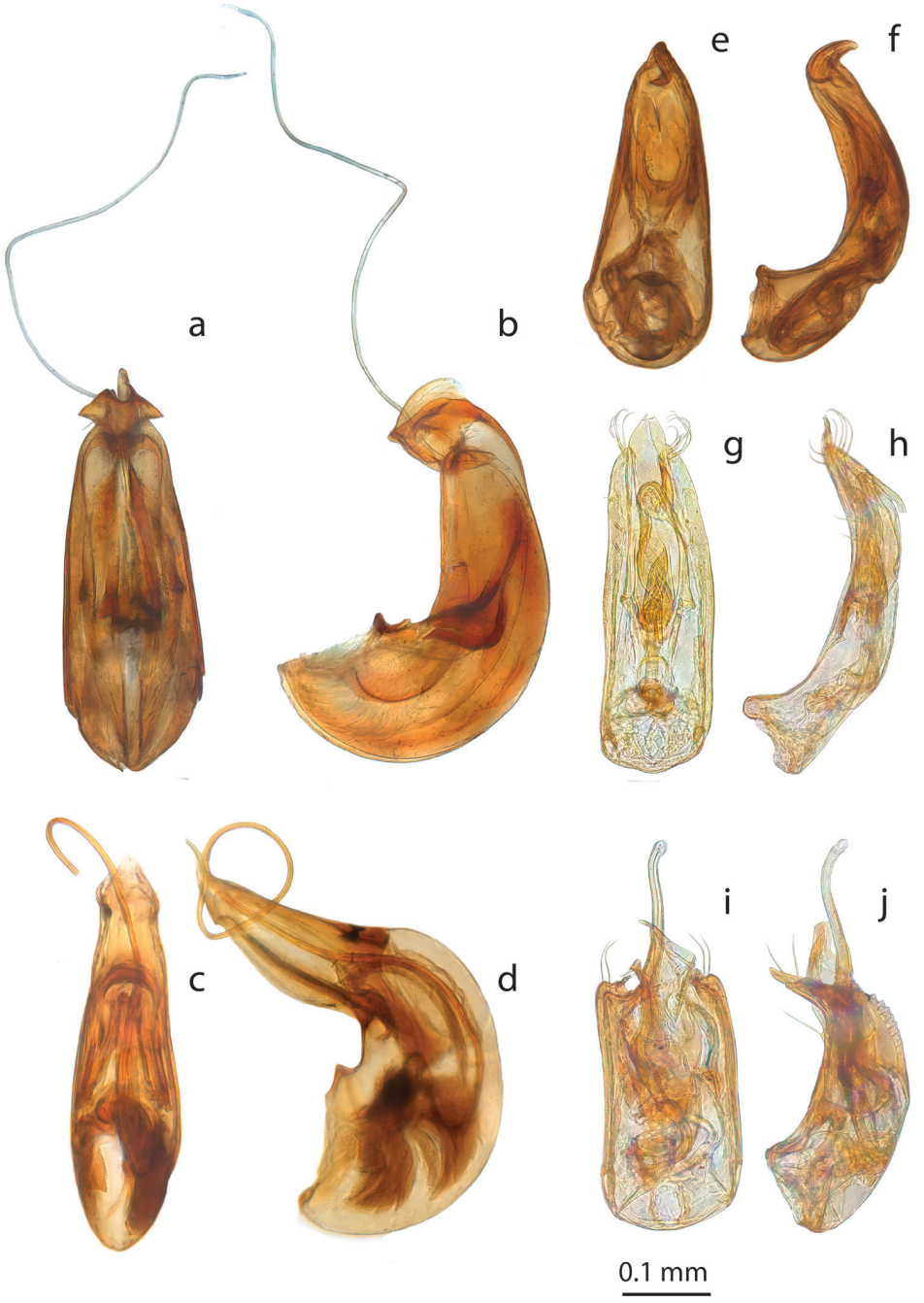

Figure 7. *Ptomaphaginus*, aedeagus, dorsal (left) and lateral (right) view. **a, b** *P. isabellarossellini* sp. n. Gunung Kinabalu, holotype (RMNH.INS.1086160) **c, d** *P. scaphaner* Szymczakowski, Gunung Mulu (NHMUK) **e, f** *P. muluensis* sp. n. Gunung Mulu, paratype (NHMUK) **g, h** *P. burckhardti* Schilthuizen & Perreau, Gunung Kinabalu, holotype (MHNG) **i, j** *P. sabahensis* Schilthuizen & Perreau, Gunung Kinabalu, holotype (MHNG).

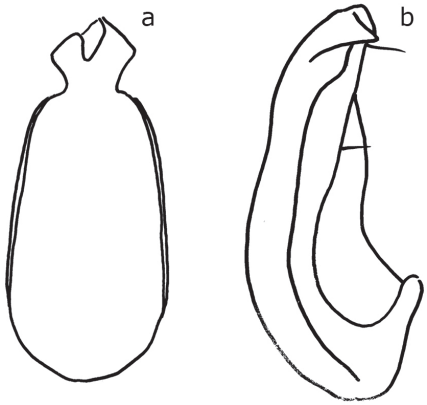

Figure 8. *Ptomaphaginus caroli*, aedeagus, Crocker Range, holotype (RMNH). **a** dorsal view **b** lateral view (after Schilthuizen & Perreau, 2008). Scale line absent as the drawing is based on a rough sketch made before the aedeagus of the holotype was lost; see text.

est, 2 fish traps, 07–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086161–1086164), 4 females.

Description. Large (3.3–4.0 mm), winged. Elytra, legs and basis and tip of the antennae dark reddish brown, pronotum, head and antennomeres 5–10 nearly black. Pronotum 1.6 times as wide as long, caudal angles clearly extended, as wide as the elytra at the shoulders. Elytra slender, slightly convex, 1.5 times as long as wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Elytral apex in the female gradually rounded and joining the suture at a right angle; in the male more acute, meeting the suture at a sharp angle, and with a distinct bunch of thick, black, outwardly-curved, spine-like setae. Wings present. Body otherwise covered with dense light grey setation. Male tarsi strongly dilated, tarsomeres 1–4 jointly twice as long as wide. Female tarsi not dilated. Aedeagus very strongly curved ventrad, very convex, with a distinct dorsal keel; apex trilobate; stylet very long and thin, hair-like. Spermatheca semicircular, spermiduct extremely long (in extended condition probably at least 5 mm), consisting of ca. 30 360° loops.

Differential diagnosis. Among Sabah *Ptomaphaginus*, and more generally, very distinctive by its large size, dark colouration (but see below under Remarks), the spine-like setae on the male elytral apex, and the uniquely shaped aedeagus (the basic design of which, with two lateral flaps at the apex, resembles that of the *P. bryanti* group, as well as non-Bornean species like *P. sinuatus* Schilthuizen, 1984). The conspicuous bunch of spines at the elytral apex in the male is shared with three other non-Bornean species, viz. *P. riedeli* Perreau, 1995, *P. pilipennis* Perreau, 1991 and *P. pilipennoides* Perreau, 1991, which, however, differ strongly from *P. isabellarossellini* in aedeagal shape. In other Bornean species, *P. bryantioides* and *P. similipes*, stronger setae at the male elytral apex can also be discerned, but never as conspicuous as in *P. isabellarossellini*.

Habitat and distribution. Only known from the lower montane forest around Kinabalu Park Headquarters.

Remarks. It should be noted that specimens of the normally rusty-coloured *P. scaphaner* Szymczakowski, 1972 from the same collection sample as *P. isabellarossellini* are also nearly black. This may mean that the dark colouration of *P. isabellarossellini* is a preservation artefact.

Etymology. Named in honour of the actress and biologist Isabella Rossellini, whose short movies and stage performances on animal reproduction have popularized theories on the evolution of genitalia. In *P. isabellarossellini*, the extremely long penis stylet in the male and similarly long spermiduct in the female suggest a long history of sexually antagonistic coevolution, one of the types of selection that appears in Rossellini's 'Green Porno' series on SundanceTV (Schilthuizen 2014).

Ptomaphaginus kinabaluensis Schilthuizen & Perreau, 2008

Figures 4e–f, 6a–b, 9f, 10g

Ptomaphaginus kinabaluensis Schilthuizen & Perreau, 2008: 195, figs 24–25, 29–30; type from Gunung Kinabalu, Sabah, Borneo (in RMNH).

Material. (In addition to that given in Schilthuizen and Perreau (2008)): *Sabah.* Kinabalu Park, HQ, 1540 m elev., pitfall with Limburg cheese, 10–14.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555601–555606), 6 males; Kinabalu Park, HQ, 2003 (leg. Ng Kok Kit, RMNH.INS.63302, 63299, 549265–549267), 5 individuals; Kinabalu Park, Silau Silau (low), 1530 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086165–1086194), 15 males, 15 females; Kinabalu Park, Silau Silau trail (high), 1600 m elev., human excrement trap, 12–17.i.1986 (leg. J. Krikken, RMNH.INS.1086195), 1 female; Kinabalu Park, Bukit Ular trail (low), 1800 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086196–1086197), 2 females; Kinabalu Park, Mempening trail, 1700 m elev., fish traps, 15–22.i.1986 (leg. J. Krikken, RMNH.INS.1086198), 1 male; Kinabalu Park, Mempening trail (high), 1700 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086199), 1 female; Kinabalu Park, Silau Silau (canteen slope), 1540 m elev., fish traps, 16–23.i.1986 (leg. J. Krikken, RMNH.INS.1086200), 1 male; Kinabalu Park, Tempat Pelandok, 1650 m elev., human excrement traps, 9–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086201–1086204), 1 male, 3 females; Crocker Range Park, Gunung Alab, 1930 m elev., pitfall with Limburg cheese, 17–22.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555629–555631), 2 males, 1 female.

Description. Length 2.3–3.0 mm. Habitus slender, ovoid. Pronotum 1.68–1.86 times as wide as long, as wide as the elytra. Elytra 1.2–1.3 times as long as their combined width (length measured from the caudal tip of the scutellum to the apex of

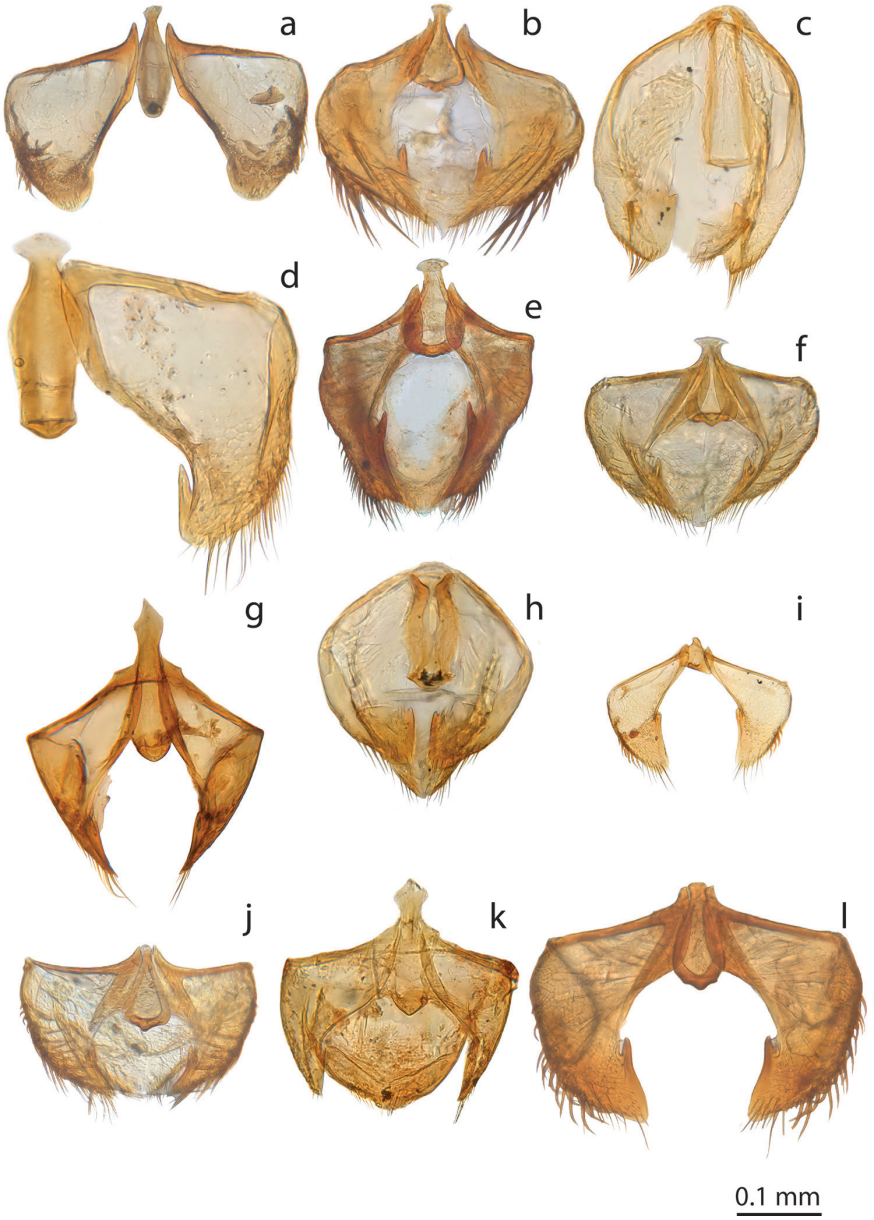

Figure 9. *Ptomaphaginus*, male genital segment (urite IX), dorsal view. **a** *P. anas* Schilthuizen & Perreau, Ulu Gombak (RMNH) **b** *P. bryantioides* Schilthuizen & Perreau **c** *P. burckhardti* Schilthuizen & Perreau, Gunung Kinabalu, holotype (MHNG) **d** *P. grandis* sp. n., Gunung Mulu, paratype (NHMUK), left pleurite missing **e** *P. isabellarossellini* sp. n., Gunung Kinabalu, holotype (RMNH.INS.1086160) **f** *P. kinabaluensis* Schilthuizen & Perreau, Gunung Kinabalu, paratype (RMNH.INS.63302) **g** *P. muluensis* sp. n., Gunung Mulu, paratype (NHMUK) **h** *P. sabahensis* Schilthuizen & Perreau, Gunung Kinabalu, holotype (MHNG) **i** *P. scaphaner* Szymczakowski, Gunung Mulu (NHMUK) **j** *P. latimanus* Schilthuizen & Perreau, Gunung Trusmadi (RMNH) **k** *P. louis* sp. n., Gunung Mulu, paratype (NHMUK) **l** *P. similipes* Schilthuizen & Perreau, Gunung Mulu (NHMUK). Scale bar represents 0.05 mm for Figure 9e.

the elytra). Winged. Aedeagus short and wide, with two elongated apical, laterally directed 'wings' and a short terminal processus. Spermatheca thin, broadly bent over a 90° angle, slightly bulbous at the basis and with several indistinct annulations at the terminus. Spermiduct long, narrow, with numerous coils. Antennae short, as long as the width of the head. Long setae on the ventral side of the male profemur and protibia absent. Female elytral apices drawn out, male elytral apices rounded, not truncated. Male with a central extension on the 4th visible abdominal sternite.

Differential diagnosis. Similar in aedeagal shape to *P. bryantioides*, but very different in habitus, which is more slender in *P. kinabaluensis*. Furthermore, *P. kinabaluensis* has only slightly dilated male protarsi, no setae on the male profemur and protibia, and extended elytral apices in the female.

DNA barcodes. For the following specimens, DNA barcodes are available in BOLD: RMNH.INS.555601–555606 (Kinabalu Park HQ), RMNH.INS.555629, 555631 (Gunung Alab). RMNH.INS.549265–549267 are available in BOLD, but we have not yet succeeded in obtaining DNA sequences for them.

Habitat and distribution. In montane forest at 1400–1930 m. Sabah: Kinabalu Park (around Park HQ), Crocker Range Park (Gunung Alab and km 51 KK-Tambunan road). The Crocker Range and Kinabalu populations are genetically very similar (BOLD BIN ACK0160).

Ptomaphaginus latimanus Schilthuizen & Perreau, 2008

Figures 5i, 6g, h, 9j, 10h

Ptomaphaginus latimanus Schilthuizen & Perreau, 2008: 196, figs 22–23; type from Gunung Trus Madi, Sabah, Borneo (in RMNH, RMNH.INS.1086293).

Description. (Adapted from Schilthuizen and Perreau (2008)). Length 2.3–2.9 mm. Habitus slender, ovoid. Pronotum 1.60–1.75 times as wide as long, as wide as the elytra. Elytra 1.15–1.25 times as long as their combined width (length measured from the caudal tip of the scutellum to the apex of the elytra). Winged. Aedeagus short and wide, with two elongated apical, laterally-directed 'wings' and a short terminal processus. Spermatheca narrow, annulated, and bent over a rounded 90° angle, quite similar to that of *P. kinabaluensis*. Spermiduct long and narrow, with numerous coils. Antennae short, as long as the width of the head. Long setae on the ventral side of the male profemur and protibia absent. Male with broad and indistinct central notches on the 5th and 6th visible abdominal sternite. Male protarsi strongly dilated.

Differential diagnosis. *Ptomaphaginus latimanus* is closely related to *P. kinabaluensis*, but differs in the habitus, which is much more stocky in *P. latimanus*. Also, *P. kinabaluensis* has extended elytral apices in the female, less strongly dilated male protarsi, and a central extension on the male 4th abdominal sternite.

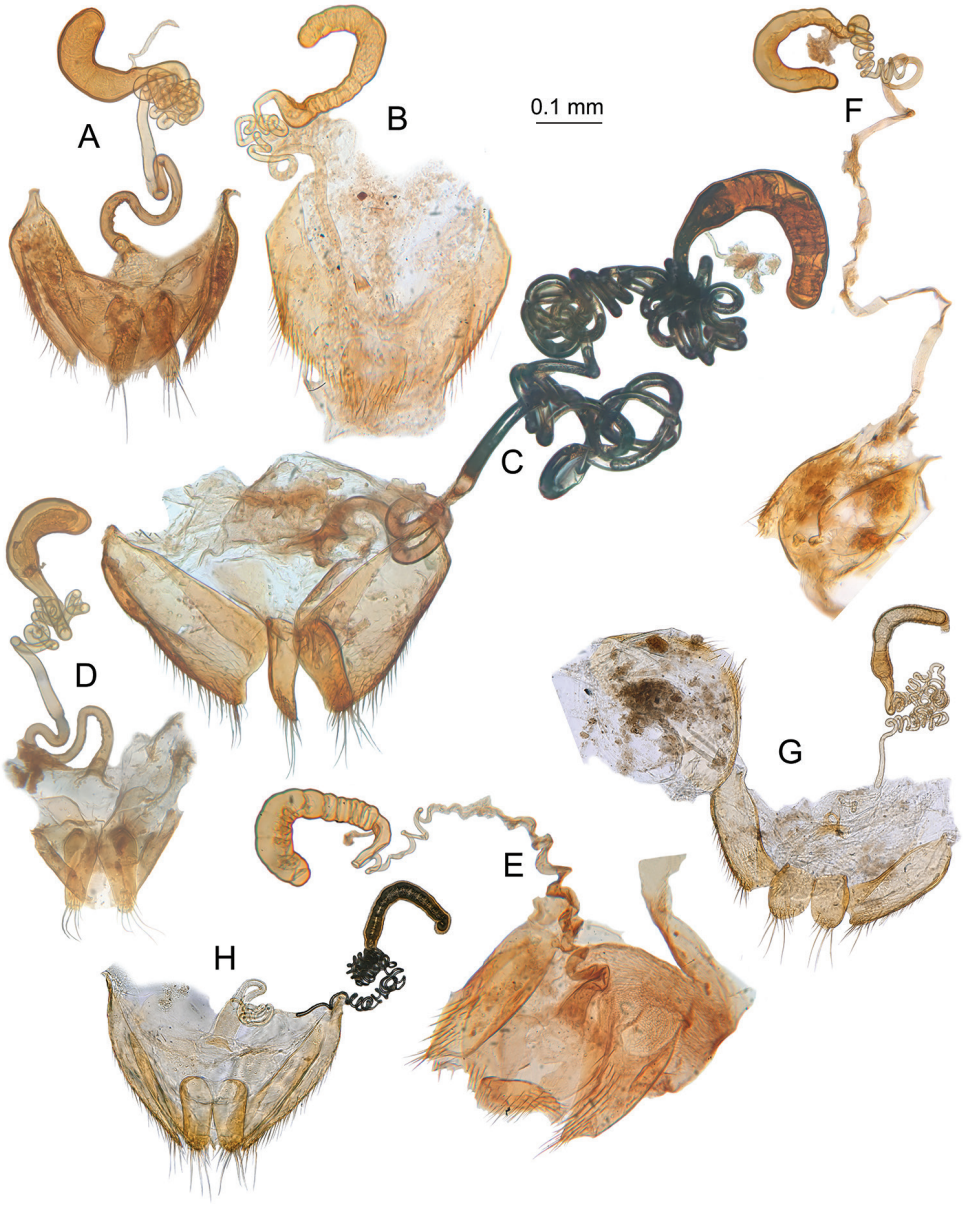

Figure 10. *Ptomaphaginus*, female spermiduct and spermatheca. **a** *P. bryantioides* Schilthuizen & Perreau, Gunung Mulu (NHMUK) **b** *P. grandis* sp. n., Gunung Mulu, paratype (NHMUK) **c** *P. isabellarossellini* sp. n., Gunung Kinabalu, paratype (RMNH.INS.1086161) **d** *P. louis* sp. n., Gunung Mulu, paratype (NHMUK) **e** *P. muluensis* sp. n., Gunung Mulu, paratype (NHMUK) **f** *P. scaphaner* Szymczakowski, Gunung Mulu (NHMUK) **g** *P. kinabaluensis* Schilthuizen & Perreau, Gunung Kinabalu (TXEX) **h** *P. latimanus* Schilthuizen & Perreau, Gunung Trus Madi, paratype (RMNH).

Habitat and distribution. Only known from montane forest at Gunung Trusmadi in Sabah, at 1400 m elev. One *bryanti*-group female (RMNH.INS.555611) from Sayap substation on Gunung Kinabalu is genetically unique (BOLD BIN: ACK0183) and might also belong to this species.

***Ptomaphaginus louis* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/67975FC1-077B-4348-86EA-159B147E148C
Figure 5a, 6m, n, 9k, 10d

Material. Holotype: Malaysia, Sarawak, Mulu National Park, TPS 7–13, 4.v.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), male. **Paratypes**: *Sarawak.* Mulu National Park, TPS 7–13, 4.v.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 12 males, 14 females; Mulu National Park, Kerangas?, 7.iv.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 4 males, 2 females; Mulu National Park, mixed dipterocarp forest litter, TPS 1–2, iv–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 3 males, 4 females; Mulu National Park, slope, baited traps, 7.iv.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 male, 1 female; Mulu National Park, mixed dipterocarp forest litter, TPS 3–4, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 2 females; Mulu National Park, mixed dipterocarp forest litter, TPS 7–10, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 female; Mulu National Park, alluvial forest 100 m, iii–v.1978 (leg. I. Hanski, NHMUK, B.M. 1978–524), 5 females; Mulu National Park, Limestone 6.4, Tp 113, 400 m, 6.iv.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 female; Mulu National Park, mixed dipterocarp forest litter Tp 7, 21.iv.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 male. **Other examined material (not included in the type series)**: *Sarawak.* Mulu National Park, slope, baited traps, 7.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 2 females.

Description. Length 2.0–2.8 mm. Habitus: Light to dark reddish brown; flattened and relatively short and broad, head broad, pronotum 1.6–1.7 times as wide as long, narrower than the elytra, caudal angles almost not extended. Elytra short, gently convex, jointly ca. 1.2 times as long as wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Body entirely covered in dense golden-yellow setation. Wings present. Antennae slender, 4th, 9th, and 10th antennomeres almost as long as wide. Male protarsi slightly dilated, the first four tarsomeres jointly ca. 3.5 times as long as wide. Aedeagus gently bent ventrad, flattened, apically broad and convex but subapically tapering in a rounded fashion into a broad but sharp upturned tip. Stylet long and thin, hair-like; stored in a wide loop in the basal part of the aedeagus. *Spiculum gastrale* elongate-ovoid, with the caudal part button-shaped, truncated. Spermatheca semicircular, thick, otherwise featureless, "sausage-shaped". Spermiduct long, thin, consisting of ca. 4–6 360° coils.

Differential diagnosis. Aedeagus in dorsal view very similar to that of *P. tarsalis* Symczakowski, 1964 from Sumatra, but in lateral view apically clearly more convex and with a shorter stylet. Moreover, the habitus and appendages of *P. tarsalis* are very stout and thick, whereas those in *P. louis* are much more slender. Also very similar to *P. muluensis*, but externally distinguished by the smaller size and more stocky habitus, with shorter elytra, narrower pronotum and the absence of drawn-out caudal pronotal angles. Aedeagus in dorsal view tapering abruptly towards the apex, not as gradually as in *P. muluensis*; in lateral view, the apex is more convex. Spermatheca distinguished from *P. muluensis* by the semicircular shape without any distinctive rings.

Habitat and distribution. Only known from Mulu National Park, Sarawak.

Remarks. Two females from the Mulu locality "Slope" have several rings at the basis of the spermatheca. As they are externally identical to other females of this species, they have been provisionally included in this species, but excluded from the type series. Several specimens infected on the elytra and pygidium with black Laboulbeniales.

Etymology. We name this species after our friend and colleague Dr. Louis Deharveng (MNHN), in recognition for his logistic and emotional support during the preparation of this paper. The specific epithet is given as a noun in apposition.

***Ptomaphaginus muluensis* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/0A383A2B-9730-409A-98F0-7EAAF851B15F
Figures 5b, 7e, f, 9g, 10e

Material. Holotype: Malaysia, Sarawak, Mulu National Park, Mixed dipterocarp forest, TPS 7–10, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), male. **Paratypes**: *Sarawak*. Mulu National Park, mixed dipterocarp forest, TPS 7–10, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 4 males, 5 females; Mulu National Park, Slope, TPS 13–16, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 9 males, 6 females; Mulu National Park, Slope, TPS 17–21, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 4 males, 5 females; Mulu National Park, Slope, TPS 5–6, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 male.

Description. Length 2.5–3.1 mm. Habitus: reddish brown; relatively parallel-sided and somewhat flattened, head broad, pronotum 1.6 times as wide as long, as wide as the elytra, caudal angles clearly extended. Elytra of moderate length, gently convex, in the caudal one-third gently rounded towards the apex, jointly ca. 1.4 times as long as wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Body entirely covered in dense golden-yellow setation. Wings present. Antennae slender, 4th, 9th, and 10th antennomeres slightly wider than long. Male protarsi slightly dilated, the first four tarsomeres jointly ca. three times as long as wide. Aedeagus gently bent ventrad, in lateral view apically flattened and ending in a bulbous upturned tip, in dorsal view gradually narrowing towards the apex. Stylet long and thin, hair-like.

Spiculum gastrale long-ovoid, with the caudal part truncated. Spermatheca J-shaped, with 7–10 narrow rings on the long shaft of the "J", and 5–7 broader rings on the curved part. Spermiduct long, thin, consisting of at least ten 360° coils.

Differential diagnosis. Very similar to *P. louis*, but externally distinguished by the larger size and more slender habitus, with longer elytra, broader pronotum and distinctly drawn-out caudal pronotal angles. Aedeagus in dorsal view tapering gradually towards the apex, not as abruptly as in *P. louis*; in lateral view, the apex is not as convex. Spermatheca distinguished from *P. louis* by the J-shape with distinctive rings.

Habitat and distribution. Only known from Mulu National Park, Sarawak. Several specimens infected with black Laboulbeniales on the elytra and the pygidium.

Etymology. Named after Mulu National Park, to date the only locality from which this species is known.

Ptomaphaginus sabahensis Schilthuizen & Perreau, 2008

Figures 5g, 7i, j, 9h

Ptomaphaginus sabahensis Schilthuizen & Perreau, 2008: 202, figs 11, 12; type from Gunung Kinabalu, Sabah, Borneo (in MHNG).

Description. (adapted from Schilthuizen and Perreau (2008)). Length 2.4 mm. Habitus elongated, parallel-sided. Pronotum short, 2.3 times as wide as long, nearly as wide as the elytra. Elytra 1.35 times as long as their combined width. Aedeagus quadrangular with a sinuous apical expansion. Internal stylus short and moderately thick. Female unknown.

Differential diagnosis. The elongated habitus combined with the rectangular and stocky aedeagus are unique features among the Bornean *Ptomaphaginus*.

Habitat and distribution. Only known from the male holotype, collected on Gunung Kinabalu at 1580 m elevation.

Ptomaphaginus scaphaner Szymczakowski, 1972

Figures 5c, 7c, d, 9i, 10f

Ptomaphaginus scaphaner Szymczakowski, 1972: 279–300, figs 28–33); type from Cue phuong Ninh binh, Vietnam (in HNHM).

Material. (in addition to that given in Schilthuizen and Perreau (2008)): *Sabah.* Kinabalu Park, Silau-Silau (low), 1530 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086209–1086214), 5 males, 1 female; Kinabalu Park, Bukit Ular trail (low), 1800 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086224–1086231), 3 males, 5 females; Kinabalu Park, Mempening trail (high), 1700 m elev., human excrement traps, 7–11.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086233), 1 male; Crocker Range, Kota Kina-

balu-Tambunan road (km 56), 1350 m elev., fish traps, 21–24.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086215–1086223), 2 males, 7 females; Kinabalu Park, Headquarters Area, Liwagu Trail, 6°00'29.2"N 116°32'43.8"E, pitfall with chicken, 2.iv.2016 (leg. M. Schilthuizen, I. Njunjić & F. Feijen) 2 males (BORN), 1 male and 1 female (RMNH.INS.1086232). *Sarawak*. Mulu National Park, Limestone 6.4, Tp 113, 400 m elev., 6.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 male; Mulu National Park, Limestone 6.4, Tp 110, 650 m elev., 6.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 male, 2 females; Mulu National Park, mixed dipterocarp forest litter, TPS 5–6, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 4 males, 1 female; Mulu National Park, mixed dipterocarp forest litter, Tp 7, 21.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 male; Mulu National Park, slope, baited traps, 7.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 3 females; Mulu National Park, slope, TPS 4–6, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 female; Mulu National Park, TPS 7–13, 4.v.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 female.

Description. Length 1.8–2.5 mm. Habitus broad and short, colouration light reddish-brown. Pronotum 1.75 times as wide as long, slightly narrower than the elytra. Elytra 1.2 times as long as jointly wide (length measured from the caudal tip of the scutellum to the caudal tip of the elytra). Wings present. Antennae very broad and short, with antennomeres 9 and 10 twice as broad as long. Aedeagus strongly curved, extremely convex and swollen, ending in a flattened "beak"; stylet long and thin, hair-like, running along the inside of the roof of the convex part of the aedeagus. *Spiculum gastrale* short, triangular, as long as wide. Spermatheca U-shaped, with 6–7 broad rings along the proximal part, and ca. 5 much narrower rings in the terminal one-quarter. Spermiduct very long and very thin.

Differential diagnosis. Unique among the Bornean *Ptomaphaginus* by the condensed antennae and the inflated aedeagus with flattened "beak" and long stylet.

Habitat and distribution. This appears to be a very widespread species, now known from Vietnam, Peninsular Malaysia, Borneo, and Java. It is possible, however, that the species consists of a complex of closely related species, given the geographic variation in secondary sexual characters (Schilthuizen and Perreau 2008).

Ptomaphaginus similipes Schilthuizen & Perreau, 2008

Figures 5d, 6e, f, 9l

Ptomaphaginus similipes Schilthuizen & Perreau, 2008: 193–194, figs 18–19, 27–28; type from Crocker Range Park, Sabah, Borneo (in RMNH).

Material. (In addition to that given in Schilthuizen and Perreau (2008)): *Sabah*. Kinabalu Park, Sayap substation, 950 m elev., 11–16.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555608–555610, 555612–555614,

555616–555617), 8 individuals; Kinabalu Park, Headquarters Area, Liwagu Trail, 6°00'29.2"N 116°32'43.8"E, pitfall with chicken, 2.iv.2016 (leg. M. Schilthuizen, I. Njunjić & F. Feijen, RMNH.INS.1086234 and BORN), 3 males; Crocker Range, Sugud Forest Reserve, 5°50.361'N, 116°07.084'E, 360 m elev., 1–4.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555592, 555593, 555595), 3 individuals; Crocker Range, Sugud Forest Reserve, 5°50.361'N, 116°07.084'E, 360 m elev., 25.xii.2009 – 01.i.2010 (leg. M. Schilthuizen, RMNH.INS.555678–555685, RMNH.INS.63287–63288, RMNH.INS.549296–549299 and BORN), 14 individuals; Crocker Range, Sugud Forest Reserve, 5°50.361'N, 116°07.084'E, 360 m elev., 10–15.iv.2011 (leg. M. Schilthuizen, RMNH.INS.549263), 1 individual; Crocker Range, Kota Kinabalu-Tambunan road (km 56), 1350 m elev., fish and human excrement traps, 21–24.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086239–1086252), 10 males, 8 females; Crocker Range, Keningau-Kimanis road, km 25, 1300 m elev., human excrement traps, 18–23.xi.1987 (leg. Krikken & Rombaut, RMNH.INS.1086235–1086238), 4 individuals. *Sarawak*. Mulu National Park, mixed dipterocarp forest litter, TPS 1–2, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 3 males, 5 females; Mulu National Park, mixed dipterocarp forest litter, TPS 5–6, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 6 males, 8 females; Mulu National Park, mixed dipterocarp forest litter, TPS 7–10, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 4 males, 1 female; Mulu National Park, slope, TPS 4–6, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 2 males; Mulu National Park, slope, TPS 7–9, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 2 males, 2 females; Mulu National Park, slope, TPS 10–12, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 2 females; Mulu National Park, slope, TPS 13–16, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 4 males, 3 females; Mulu National Park, slope, TPS 17–21, 29.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 2 males; Mulu National Park, slope, baited traps, 7.iv.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 female; Mulu National Park, camp 2, ca. 500 m elev., v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, B.M. 1978–49, NHMUK), 1 female.

Description. Length 2.4–3.0 mm. Pronotum 1.69–1.80 times as wide as long, as wide as the elytra. Elytra 1.19–1.23 times as long as wide (length measured from the caudal tip of the scutellum to the apex of the elytra). Wings present. Aedeagus short and broad, with two short apical, laterally directed 'wings' and a short terminal processus. Male forelegs usually with long setae on the ventral side of the femur and tibia. Male protarsus completely not dilated, of the same width as in the female. The 3rd, 4th, and 5th visible abdominal ventrite of the male carry a slight central notch and show a depression around these notches. Spermatheca narrow, V-shaped, with ca. 10 indistinct rings. Spermiduct long and thin, consisting of ca. 6 360° loops.

Differential diagnosis. Among other members of the *P. bryanti* complex, distinguished by the not dilated male protarsi, thin, annulated spermatheca, the relatively small size, and the short and squat aedeagus.

DNA barcodes. COI barcodes are available for the following specimens: RMNH.INS.63287 (Sugud), RMNH.INS.549263 (Sugud), RMNH.INS.555592–555593 (Sugud), RMNH.INS.555680–555681 (Sugud), RMNH.INS.555685 (Sugud), RMNH.INS.555609–555610 (Sayap), RMNH.INS.555612 (Sayap), RMNH.INS.555616 (Sayap). For RMNH.INS.63288, only the 3' section of COI is available. For the specimens RMNH.INS.549296–549299 there are entries in BOLD, but we have not yet been able to extract amplifiable DNA from these.

Habitat and distribution. Appears to be widespread on the west coast of Sabah and Sarawak, at elevations between 350 and 1400 m. Some deep molecular divergences are apparent: the specimens collected at Sayap fall in a different DNA barcode BIN than the ones from Sugud (BOLD BINs ACK0140 and ACK0141+ABV4636).

Remarks. The male protarsi were slightly dilated in the one male from the Kinabalu Headquarters area.

Genus: *Ptomaphaminus* Perreau, 2000

Ptomaphaminus Perreau, 2000: 20; type species *Ptomaphaginus tantillus* Szymczawski, 1964 (original designation).

Notes. During the study of this Bornean material, we have refined our concept of the genus *Ptomaphaminus*, which is why the genus description below is more extensive than for the previous genera.

Description. Species of small size, not exceeding 2 mm. Colour generally brown, partly yellowish or light brown, rarely darker. Dorsal surface covered with short recumbent setae inserted along transverse strigae which also cover the whole dorsum of the body. Head with more or less developed eyes. A significant eye reduction is observed in species living in subterranean environments. Antennae generally slender, the apical club weakly marked. Pronotum transverse, the largest width generally at the base, the sides of the pronotum and the elytra continuously arcuate, of equal width. Elytra generally elongate, the posterior sutural angles rounded in males (Figure 14a), in females either rounded (Figure 14b), or simply angular (Figure 14c), or sharply protruding backwards (Figure 14d–e). Surface of elytra with transverse oblique strigae and a single longitudinal sutural stria. Flight wings generally present and functional, even in species living in subterranean environments. (The few apterous or brachypterous species of the genus do not live in Borneo.) Mesoventral process low, narrow, and rounded. Metasternal sutures incomplete and convergent towards the central axis of the body. Protibiae with a lateral row of spines along the external edge and with smaller spines randomly dispersed on the ventral side. Mesotibiae and metatibiae with a circular row of spines around the apex. Male protarsi with four protarsomeres expanded, female protarsi unexpanded. Male and female mesotarsi and metatarsi unexpanded. Male genital segment (urite IX) with a long *spiculum gastrale*, significantly extending beyond the anterior margin of the epipleurites and sometimes expanded into a paddle shape in the distal half. The size of the aedeagus (relatively to

the body length) is highly variable: from 3.0 (*P. latescens*) to 5.7 (*P. marshalli*) times smaller than the body length. The left apical expansion of the median lobe generally (in Borneo species) with a more or less developed, ventrally deflexed and sometimes retroverted apical hook, clearly visible in lateral view, more rarely simple (*P. latescens*, *P. testaceus* sp. n.). Endophallus with a long and weakly sinuate stylus and with a basal symmetric (Figures 12a, 12c) or asymmetric (Figures 12f, h, j, l, m, o, q, s, w, y) loop. When asymmetric, the loop is expanded on the left side in dorsal view (which appears on the right side on pictures which are traditionally illustrated with the caudal side up). Female genital segment either with long gonocoxites, more than three times as long as wide (*P. latescens*: Figure 13b; *P. testaceus* sp. n.: Figure 13d), or gonocoxites reduced to small subsquare sclerites (Figures 13f, h, j, n, p, s, u). Spermatheca generally bilobate, with (*P. ater* Perreau, 2009: Figure 13f) or without an apical sclerified plate. A single lobe, weakly sclerotised and transversally ringed occurs in *P. latescens* (Figure 13b) and *P. testaceus* (Figure 13d). Spermiduct less sclerotised, but generally with a fixed morphology, sometimes wrapped in a helical shape, rarely entirely membranous, without structured morphology (*P. hanskii* sp. n., *P. sarawacensis* sp. n.: Figures 13h–13j).

Remarks. The two species *P. latescens* and *P. testaceus* sp. n. have significantly different morphological characters from other species of *Ptomaphaminus* (not limited to Borneo): a short stylus of the endophallus (limited to half the length of the median lobe) with a symmetric basal loop, female gonocoxites long (more than three times longer than wide), a weakly sclerified spermatheca with a set of transversal rings (similar to structures preventing a collapse under depression, like for the respiratory trachea). Other species have a long stylus developed on most of the length of the aedeagus, female gonocoxites short, sub-square and a more sclerified spermatheca without reinforcing transversal rings. These two species form a distinct species group which possibly represents another genus.

Biology. Little information is available on the biology of *Ptomaphaminus*. Two methods of sampling are successful in obtaining specimens: trapping with pitfall traps baited with meat, cheese, or human excrement (either in epigean or in cave environments) and manual collecting in caves. Species collected in epigean conditions generally have fully developed eyes and flight wings while specimens from caves often have reduced eyes (although presently no anophthalmic *Ptomaphaminus* are known). The eye reduction observed in species recorded from caves is not correlated with the flight wing reduction, in contrast to palaearctic and nearctic subterranean species of Cholevinae (Leptodirini; *Ptomaphagus* (*Adelops*)). Flight wings of *P. fagei* Perreau, 2009 and *P. latescens* Szymczakowski, 1964, for example, remain fully functional as observed in Gua Sedepan (Eastern Kalimantan) and caves in the Kinabatangan valley (Sabah) where specimens flew up when lighted by headlamps even in the dark zone deep inside caves. A similar observation was reported by Peck (1981) for *P. chapmani* Peck, 1981.

Species are very similar externally. For each of the species below, we provide only specific diagnoses, without listing any shared generic characters.

***Ptomaphaminus latescens* (Szymczakowski, 1964)**
Figures 12a, b, 13a, b

Ptomaphaginus latescens Szymczakowski, 1964: 140–144, figs 122–132; type from Cave of Durian, Padang Highlands, Sumatra (in RMNH).

Material. *Sabah*. Kinabalu Park, Poring Hot Springs, 6°02.894'N, 116°14.957'E, 625 m elev., 15–20.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, in RMNH.INS.1086253), 1 female; Kinabalu Park Headquarters, 6°00.394'N, 116°32.654'E, 1540 m elev., 10–14.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555607) 1 male; Tinahas Cave, v.2005 (leg. M. Schilthuizen, in RMNH.INS.1086254), 1 male; Crocker Range, Inobong Station, 5°51.265'N, 116°08.363'E, 500 m elev., 21–23.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555643), 1 male; Crocker Range, Gua Laing, 5°28.701'N, 116°10.517E, 613 m elev. (leg. M. Schilthuizen & I. Njunjić, RMNH.INS.1086255–1086257), 3 females; Lower Kinabatangan, Batu Batangan, Gua Ular, 5°27.566'N, 118°06.126'E, 24–28.ii.2017 (leg. M. Schilthuizen, RMNH. INS.5081737, 5081740, 5081743, BOR/COL/14209–14210), 3 males, 2 females; Lower Kinabatangan, Batu Batangan, Gua Kolam, 5°27.557'N, 118°06.118'E, 24.ii–1. iii.2016 (leg. M. Schilthuizen, RMNH.INS. 5081738, 5081741–5081742, 1086284, BOR/COL/14211–14214, 14217), 6 males, 2 females; Lower Kinabatangan, Batu Batangan, Gua Ikan, 5°27.558'N, 118°05.891'E, 24–28.ii.2016 (leg. M. Schilthuizen, RMNH.INS.5081739) 1 male; Lower Kinabatangan, Batu Batangan, Gua Merayap 5°27.573'N, 118°06.075'E, 24–29.ii.2016 (leg. M. Schilthuizen, BOR/COL/14206), 1 female; Lower Kinabatangan, Batu Batangan, Gua Ikan, 5°27.558'N, 118°05.891'E, 18.iii.2015 (leg. M. Schilthuizen & I. Njunjić, RMNH.INS.1086272–1086283), 3 males, 9 females; Lower Kinabatangan, Batu Batangan, Gua Babi, N 5°27.570'N, 118°06.088'E, 24–28.ii.2016 (leg. M. Schilthuizen, RMNH.INS.1086285–1086287 and BOR/COL/14207–14208), 2 males, 3 females; Lower Kinabatangan, Gua Fico, 5°27.135'N, 118°08.769'E, 1–7.iii.2016 (leg. M. Schilthuizen, BOR/COL/14215–14216), 2 males; Lower Kinabatangan, Gua Fico, 5°27.135'N, 118°08.769'E, 20.iii.2015 (leg. M. Schilthuizen & I. Njunjić, RMNH.INS.1086258–108671), 14 males. *Sarawak*. Bau, Gunung Jambusan, 1.401N 110.191E, 24.ii.1980 (RMNH. INS.549312–549316), 2 males, 3 females; Gunung Mulu, mixed dipterocarp forest litter, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK), 2 males, 2 females; Gunung Mulu, Limestone 6.4 400 m Tp 113, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK), 3 males, 2 females; Gunung Mulu, pitfall-trap fish bait, alluv. for. ca. 100 m, iii–v.1978 (leg. I. Hanski, NHMUK), 1 female; Gunung Mulu, 4.5.78 Tps 7–13, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK), 2 females; Gunung Mulu, Limestone 6.4 650 m Tp 110, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK), 2 females; Gunung Mulu, Slope 7.4.78, baited traps, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK), 1 female. *Sumatra*. Cave of Durian (Padang Highlands), 800 m, from excrements of bats, viii.1924, Ptomaphaginus latescens Szym-

czakowski, 1964 ZMAN type COLE.0754.1, ZMA.INS.1229114 (leg. E. Jacobson, RMNH), holotype, male; Cave of Durian (Padang Highlands), 800 m, from excrements of bats, viii.1924 (leg. E. Jacobson, ZMA.INS.1229106, 1229112, 1229124, 1229126, 1229128, 1229135, 1229147–1229149, 1229151, 1229153, 1229154), 12 paratypes.

Description. Length 1.45–1.75 mm. General colour dark brown. Winged. Eyes normally developed. Pronotum 1.56 times as wide as long. Elytra 1.35 times as long as wide. Female sutural angle of elytra expanded backwards into a sharp tooth. Male protarsi 0.5 times as wide as the protibia. Male genital segment with a very elongate and thin *spiculum gastrale* (Figure 13a). Aedeagus three times shorter than the body length, strikingly elongate and parallel-sided (Figure 12b). Apex of the median lobe rounded, with two overlapping apical right and left expansions in dorsal view (Figure 12b), regularly arcuate and without apical hook in lateral view (Figure 12a). Two lateral setae on each side, orthogonal to the plane of the aedeagus. Internal stylus of the endophallus short and strongly sinuate, confined to the apical half of the length of the median lobe. Female with normally developed gonocoxites (Figure 13b). Spermiduct irregularly wound, not clearly helical. Spermatheca weakly sclerotised, the apical capsule with a set of transversal rings and without apical sclerotised plate (Figure 13b).

Differential diagnosis. Larger than most other Bornean *Ptomaphaminus*, with spiniform elytral apices in the female, and a very narrow urite IX in the male; differing from the otherwise similar *P. testaceus* by the darker head and discus of the elytra, as well as slight differences in the aedeagus.

DNA barcodes. COI barcodes are available for the following specimen: RMNH.INS.555607 (Kinabalu Park HQ), BIN: ACJ9972. The specimens RMNH.INS.549312–549316 have entries in BOLD, but we have so far been unable to extract amplifiable DNA from them.

Habitat and distribution. Widely distributed in South East Asia. Indonesia: Sumatra (type locality); Kalimantan (Gunung Marang). Malaysia: Continental Malaysia (Batu Caves in Selangor), Sabah (Kinabalu; Lower Kinabatangan), Sarawak (Gunung Jambusan; Gunung Mulu). It has been found in many caves, but also in forest litter and pitfall traps.

Remarks. Variations can be observed in the curvature of the aedeagus. In the type series from Sumatra, the aedeagus is moderately curved, similarly to the population of Marang Mountains, while the population from Continental Malaysia have a more pronounced curvature. We consider that these differences do not exceed intraspecific variation.

Ptomaphaminus testaceus Schilthuizen & Perreau, sp. n.

http://zoobank.org/B7A6C3B9-48F7-4D19-A217-A47B4B05D6AA
Figures 11e, 12c, d, 13c, d

Material. Holotype: Malaysia, Sarawak, 4th Division, Gunung Mulu National Park, mixed dipterocarp forest, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK,

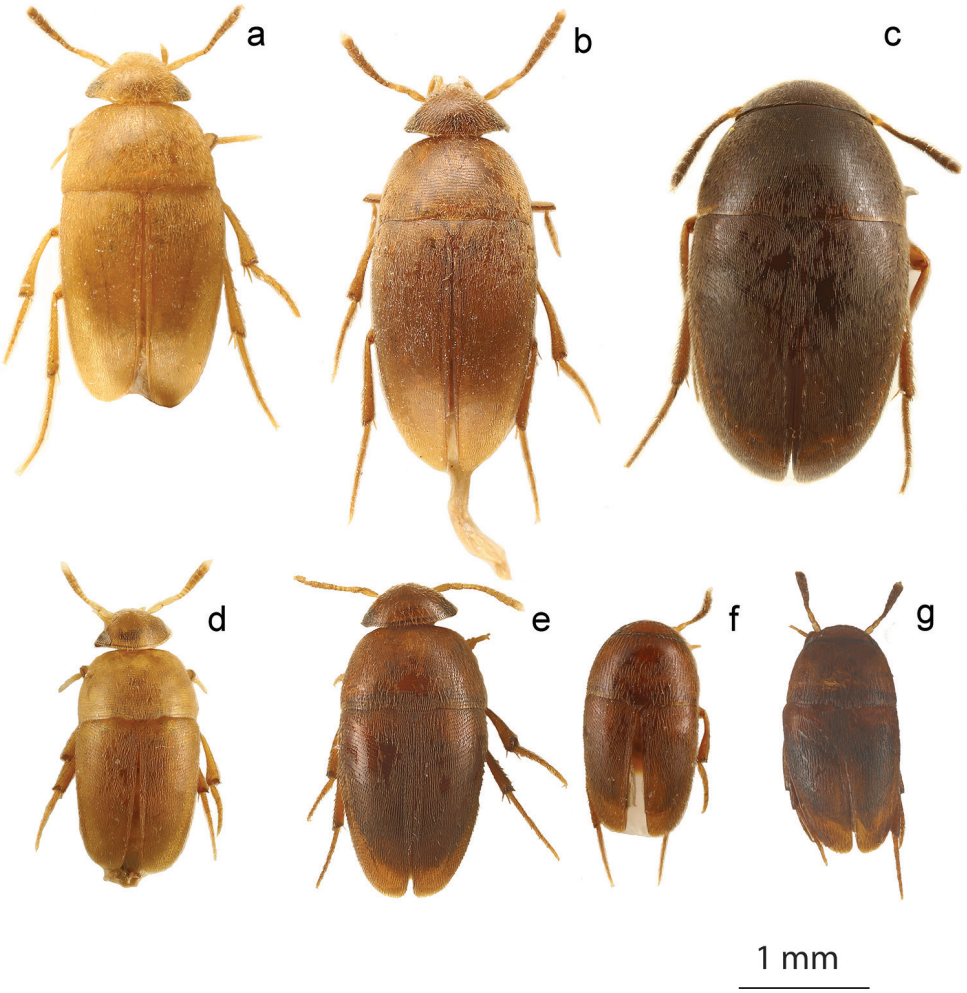

Figure 11. *Ptomaphaminus*, habitus, dorsal. **a–g** *P. hanskii*, *sarawacensis*, *layangensis*, *kinabatanganensis*, *testaceus*, *microphallus*, *alabensis*.

B.M. 1978–49), male (aedeagus on separate microscope slide). **Paratypes**: *Sarawak*. Gunung Mulu National Park, pitfall-trap, fish bait, alluv. for., ca. 100 m, iii–v.1978 (leg. I. Hanski, NHMUK, B.M. 1978–524), 2 males, 4 females; Gunung Mulu National Park, mixed dipterocarp forest, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 female; Gunung Mulu National Park, 4.5.78, Tps 7–13, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M. 1978–49), 1 female.

Description. Length: 1.4–1.8 mm. General colour light reddish brown; legs, antenna, and mouthparts yellowish. Winged. Eyes well developed. Pronotum 1.45 times as wide as long. Elytra 1.45 times as long as wide. Female sutural angle of elytra expanded backwards into a sharp tooth. Male protarsi 0.4 times as wide as the apex of protibia. Male genital segment with a very elongate thin *spiculum gastrale* (Figure 13c).

Aedeagus approximately 3.25 times shorter than the body length, elongate and parallel-sided, apex rounded, with two overlapping apical right and left expansions in dorsal view (Figure 12d), regularly arcuate from base to apex, without apical hook in lateral view (Figure 12c). Two lateral setae on each side, orthogonal to the plane of the aedeagus. Internal stylus of the endophallus short and strongly sinuate, confined to the apical half of the length of the median lobe (Figure 12c). Female genital segment with normally developed gonocoxites. Spermiduct slightly helical. Spermatheca weakly sclerified, with a set of transverse rings and without apical sclerotised plate (Figure 13d).

Differential diagnosis. Very similar to *P. latescens*, but distinct in the external morphology by its significantly smaller size, and its lighter colour. The spermiduct is slightly helical, which is not the case in *P. latescens*.

Habitat and distribution. Known only from the lowland forest of Gunung Mulu, Sarawak, Malaysia.

Etymology. Named for its light brown colour (*testaceus* = brick-coloured).

Ptomaphaminus ater Perreau, 2009

Figures 12e, f, 13e, f, 14d

Ptomaphaminus ater Perreau, 2009: 5, fig. 5; type from Gunung Kinabalu, Sabah, Borneo (in MHNG).

Ptomaphaginus ater: Merckx et al., 2015: extended data figs 2, 6.

Material. (In addition to that listed in Perreau 2009): *Sabah.* Kinabalu Park, Paka Cave, 3080 m elev., 14–19.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH), 10 individuals (incl. RMNH.INS.555623–555624, RMNH.INS.1086288–1086290).

Description. Length 1.75–2.00 mm. Large species, dark brown, winged. Eyes reduced, with 25 ommatidia. Pronotum ca. 1.5 times wider than long. Elytra approximately 1.2 times longer than wide. Female apex of the elytra with a sharp sutural angle expanded posteriorly (Figure 14d). Male protarsi approximately 0.6 times as wide as the apex of protibia. Male genital segment with long and apically expanded *spiculum gastrale*, widely dilated into a kind of paddle (Figure 13e). Aedeagus long, 3.5 times shorter than the body length, parallel-sided, straight, shortly narrowed near the apex in dorsal view (Figs 12f), ventrally bent on the last quarter of its length and with an apical hook clearly retroverted ventrally (Figure 12g). Stylet of the endophallus long and straight. Female genital segment with reduced gonocoxites. Spermiduct helical. Spermatheca long, bilobate, rounded at the apex, but with an apical sclerotised plate (Figure 13f).

DNA barcodes. For two individuals, RMNH.INS.555623–555624, COI barcodes are available in BOLD, which form the BIN ACK0013.

Differential diagnosis. Externally recognizable by its large size, dark colouration, and strongly cuneiform habitus. Apex of the female elytra spiniform. Spermatheca with a sclerotised plate at its apex. Aedeagus blunt-ended.

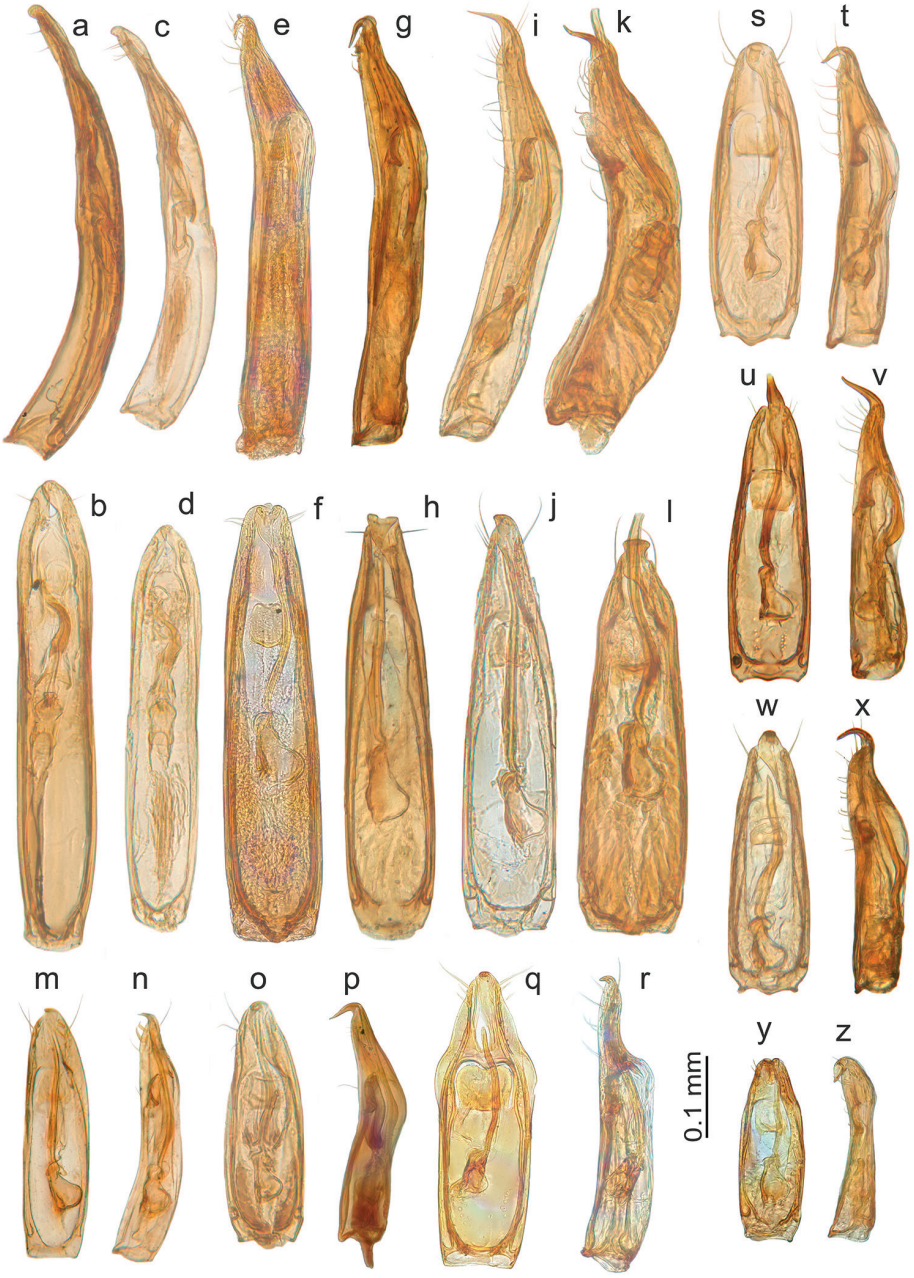

Figure 12. *Ptomaphaminus*, aedeagus. **a, c, e, g, i, k, n, p, r, t, v, x, z** lateral view **b, d, f, h, j, l, m, o, q, s, u, w, y** dorsal view. **a, b** *P. latescens* **c, d** *P. testaceus* sp. n., Sarawak, Gunung Mulu **e, f** *P. ater*, paratype (CMPR). **g, h** *P. chapmani*, Sarawak, Gunung Mulu **i, j** *P. sarawacensis* sp. n., Sarawak, Gunung Mulu **k, l** *P. hanskii* sp. n., Sarawak, Gunung Mulu **m, n** *P. nanus* sp. n., Sarawak, Gunung Mulu **o, p** *P. marshalli* n. sp., Sarawak, Gunung Mulu **q, r** *P. fagei* holotype (CMPR) **s, t** *P. layangensis* sp. n., Sabah, Gunung Kinabalu, Layang-Layang **u, v** *P. kinabatanganensis* sp. n., Sabah, Kinabatangan valley, Gua Ikan **w, x** *P. alabensis* sp. n., Sabah, Gunung Alab **y, z** *P. microphallus* sp. n., Sabah, Kinabalu, Poring Hot Springs.

Habitat and distribution. Known from high altitude on Gunung Kinabalu, above 3000 m. Some specimens were taken under a rocky overhang (Paka cave), others in Panar Laban (type locality) and Gunting Lagadan, without detail on collecting conditions.

Remarks. The only species in Borneo with an apical sclerotised plate at the apex of the spermatheca (which occurs in several other species outside Borneo).

Ptomaphaminus kinabatanganensis **Njunjić, Schilthuizen & Perreau, sp. n.**
http://zoobank.org/ED299A72-768F-4F5E-8EB8-60CDD927ED6F
Figures 11d, 12u, v, 13m, n

Material. Holotype: Malaysia, Sabah, Lower Kinabatangan, Batu Batangan, Gua Kolam, 5°27.557'E, 118°06.118'E, 24.ii–1.iii.2016 (leg. I. Njunjić et al., BOR/COL/14218), 1 male. **Paratypes**: *Sabah*. Lower Kinabatangan, Batu Batangan, Gua Babi, 5°27.570'N, 118°06.088'E, 24–28.ii.2016 (leg. field course students, BOR/COL/14219–14220), 2 individuals; Lower Kinabatangan, Gua Fico, 5°27.135'N, 118°08.769'E, 18.iii.2015 (leg. I. Njunjić et al., CMPR), 1 female; Lower Kinabatangan, Batu Batangan, Gua Babi, N 5°27.570'N, 118°06.088'E, 24–28.ii.2016 (leg. I. Njunjić et al., CMPR), 1 female; Lower Kinabatangan, Batu Batangan, Gua Ikan, 5°27.558'N, 118°05.891'E, 18.iii.2015 (leg. I. Njunjić et al., CMPR), 2 males.

Description. Length: 1.45–1.60 mm. General colour brown; antenna, mouthparts, and protarsi yellowish, the other tarsi light brown. Winged. Eyes well developed. Pronotum 1.55 times wider than long. Elytra 1.25 times longer than wide (slightly wider in males than in females). Female sutural apex of elytra angular but not protruding backwards. Male protarsi 0.65 times as wide as the apex of protibia. *Spiculum gastrale* of the male genital segment shortly protruding beyond the apex of epipleurites, significantly dilated (Figure 13m). Aedeagus approximately 4 times smaller than the body length, parallel on the first third of its length, then regularly narrowed, the sides linearly convergent towards the apex in dorsal view (Figure 12u), straight in lateral view (Figure 12v). Apex of the median lobe with a long hook deflexed towards the ventral side, but not retroverted in lateral view (Figure 12v). Six lateroventral preapical setae on each side. Internal stylus of the endophallus long and moderately sinuate. Female genital segment with reduced gonocoxites. Spermiduct not helical. Spermatheca rounded at the apex without sclerotised plate (Figure 13n).

Differential diagnosis. Female with spiniform elytra; male with long apical hook of the (relatively short but straight) aedeagus, which, however, is not retroverted.

Habitat and distribution. Known exclusively from three caves in the lower Kinabatangan valley: Gua Babi, Gua Fico, and Gua Ikan.

Etymology. Named after the lower Kinabatangan valley, in which the specimens were collected.

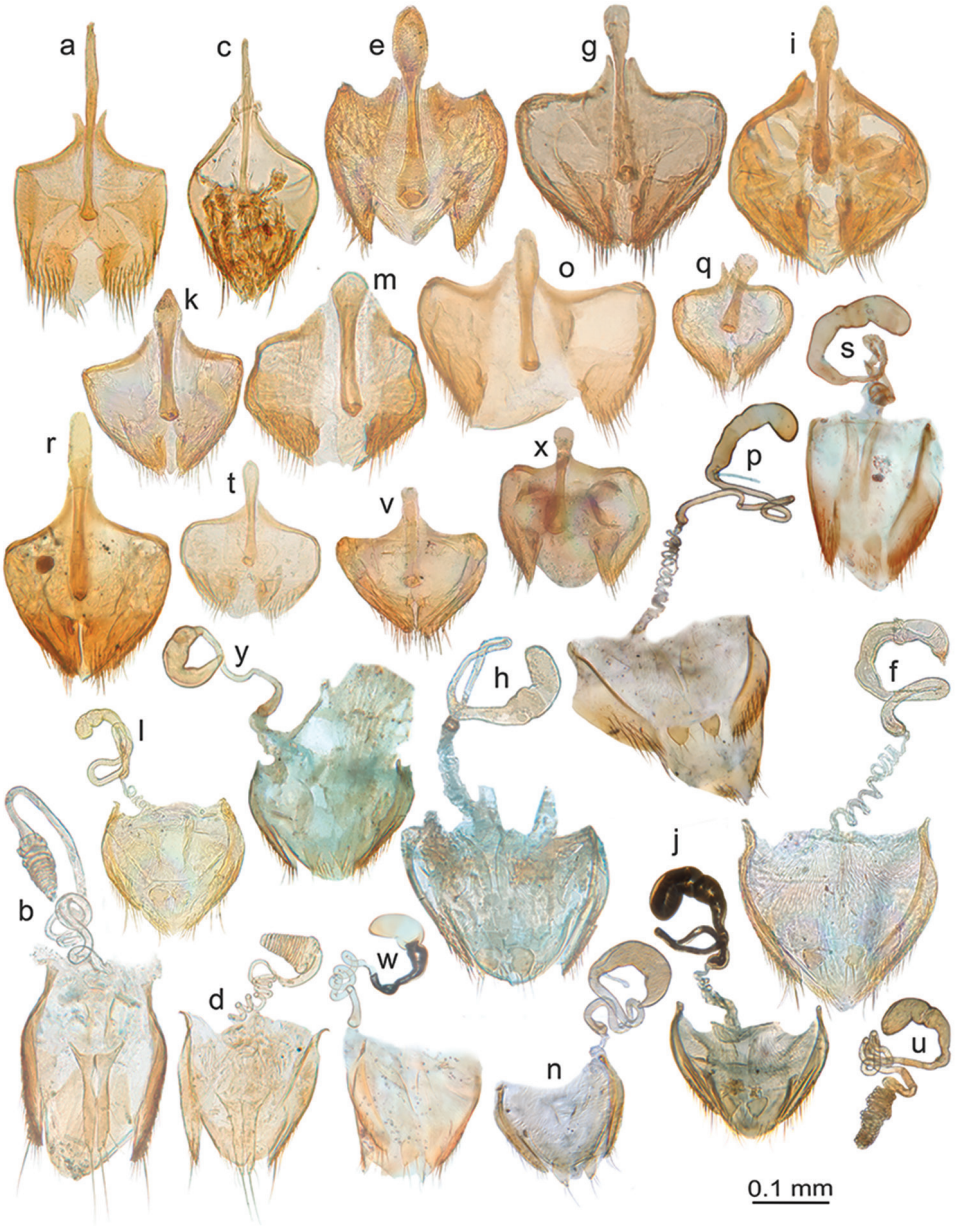

Figure 13. *Ptomaphaminus*, **a, c, e, g, i, k, n, o, r, t, v, x** male genital segments **b, d, f, h, j, l, n, p, q, s, u, w, y** female genital segments. **a, b** *P. latescens* **c, d** *P. testaceus* sp. n. **e, f** *P. ater*, paratype (CMPR) **g, h** *P. sarawacensis* sp. n., Sarawak, Gunung Mulu **i, j** *P. hanskii* sp. n., Sarawak, Gunung Mulu **k, l** *P. fagei*, paratype (CMPR) **m, n** *P. kinabatanganensis* sp. n. Sabah, Lower Kinabatangan, Gua Fico **o, p** *P. layangensis* sp. n. Sabah, Gunung Kinabalu, Layang-Layang **q** *P. microphallus* sp. n., Sabah, Kinabalu, Poring Hot Springs **r, s** *P. chapmani*, Sarawak, Gunung Mulu **t, u** *P. nanus* sp. n., Sarawak, Gunung Mulu. **v, w** *P. alabensis* sp. n., Sabah, Gunung Alab. **x, y** *P. marshalli* sp. n., Sarawak, Gunung Mulu.

***Ptomaphaminus chapmani* (Peck, 1981)**
Figures 12g–h, 13r–s, 14e

Ptomaphaginus chapmani Peck, 1981. Peck (1981: 222, fig. 1–4); type from Mulu, Sarawak, Borneo (in NHMUK).

Material. Sarawak. Mulu, Mayday Cave, rotten prawn bait, 24.vii.1980 (RMNH.INS.634810, 634795), 2 individuals; Mulu, Clearwater Cave, Snake Track passage, mice-rat bait, 5.i.1981 (RMNH.INS.634763, 634819, 634784), 3 individuals; Mulu, Clearwater Cave, 9.v.1978 (leg. P. Chapman, RMNH.INS.634799), 1 paratype; Mulu, Mayday Cave, rotted prawn bait, 24.vii.1980 (CMPR), 7 individuals.

Description. Length 1.40–2.0 mm. Colour light brown. Winged. Eyes with ten ommatidia. Pronotum 1.47 times as wide as long, elytra 1.84 times as long as wide. Female sutural angle of elytra expanded in a sharp apical tooth (Figure 14e). Protarsi 0.8 times as wide as the protibia. *Spiculum gastrale* of the male genital segment moderately dilated in a parallel-sided spatula (Figure 13r). Aedeagus long, approximately 3.3 times smaller than the body length, parallel, weakly arcuate in lateral view and shortly narrowed on the apical quarter of its length, rectangular at the apex, with an apical hook strongly retroverted ventrally (Figure 12g, h). Internal stylus of the endophallus long and straight. Female genital segment with reduced gonocoxites. Spermiduct not helical. Spermatheca rounded at the apex without sclerotised plate (Figure 13s).

Differential diagnosis. Unique among Bornean *Ptomaphaminus* in showing a combination of troglomorphic features: reduced eyes and elongated habitus. Aedeagus very similar to that of *P. ater*, which, however, is darker and has a more strongly cuneiform habitus.

Habitat and distribution. Known only from a single cave (Clearwater cave) in Gunung Mulu, Sarawak, Malaysia.

***Ptomaphaminus fagei* Perreau, 2009**
Figures 12q–r, 13k–l

Ptomaphaminus fagei Perreau, 2009. Perreau (2009: 2, fig. 4); type from Gunung Marang, Kalimantan, Borneo (in CMPR).

Material. *Kalimantan Timur*. Kebupaten Kutai Timur, karst of Mangkalihat, Mt Marang, Gua Sedepan, 8.vi.2002 (leg. M. Perreau, Expédition du Kalimanthrope, TXEX), 1 male, 1 female paratypes.

Description. Length 1.50–1.90 mm. Colour light brown. Winged. Eyes with 15 ommatidia. Body very elongate, parallel-sided. Pronotum approximately 1.6 times wider than long. Elytra approximately 1.4 times longer than wide. Female sutural angle of elytra expanded backwards in a sharp tooth. Male protarsi 0.75 times as wide as the apex of protibia. *Spiculum gastrale* of the male genital segment expanded, with

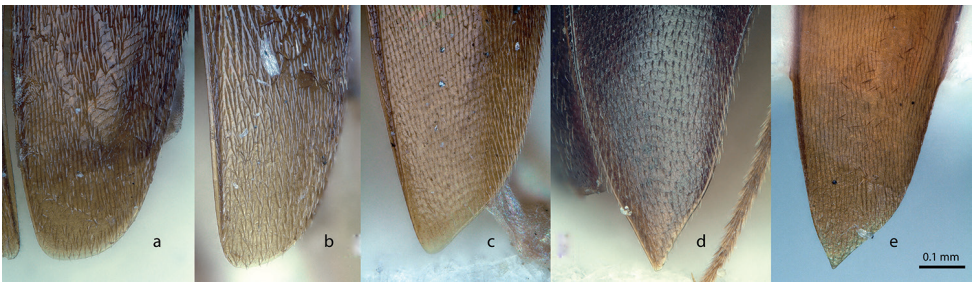

Figure 14. *Ptomaphaminus*, elytral apices. **a** *P. marshalli*, male, Sarawak, Gunung Mulu **b** *P. marshalli*, female, Sarawak, Gunung Mulu **c** *P. sarawacensis*, female Sarawak, Gunung Mulu **d** *P. ater* female paratype (CMPR) **e** *P. chapmani* female Sarawak, Gunung Mulu.

a triangular apical part (Figure 13k). Aedeagus 4.8 times as long as the body length, parallel-sided at the base, triangularly narrowed in the last third of the length in dorsal view (Figure 12q), thick at the base, abruptly thinned in the two apical third of its length and ending with a short ventrally deflexed hook in lateral view (Figure 12r). Five lateroventral lateral external setae and three more ventral central setae on each side. Internal stylus of the endophallus straight. Parameres with five apical external and three apical internal setae. Female genital segment with reduced gonocoxites, spermatheca bilobate, with helicoidal spermiduct, and without apical sclerotised plate (Figure 13l).

Differential diagnosis. Among the species with similarly reduced eyes and/or spiniform female elytral apices, *P. fagei* is unique in having an aedeagus that shows an abrupt narrowing (in lateral view) in the apical third.

Habitat and distribution. Known from two caves of Gunung Marang, Kalimantan, Indonesia: Gua Sedepan and Gua Gala.

Ptomaphaminus nanus Schilthuizen & Perreau, sp. n.

http://zoobank.org/78CBED84-54FD-4632-89F7-FAA3944D5921
Figures 12m–n, 13t–u

Material. Holotype: Malaysia, Sarawak, 4th Division, Gunung Mulu National Park, mixed dipterocarp forest litter, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, in NHMUK, B.M.1978–49), 1 male. **Paratypes:** *Sarawak*. Gunung Mulu National Park, 4.5.78 Tps 7–13, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 7 males, 4 females; Gunung Mulu National Park, mixed dipterocarp forest litter, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 2 males; Gunung Mulu National Park, limestone 6.4, 650 m, tp 110, v–viii.1978 (leg. P. E. Hammond & J. E. Marshall, B. M. 1978–49, NHMUK), 1 female.

Description. Length: 1.28–1.50 mm. General colour brown; tarsi, antenna, mouthparts yellowish. Winged. Eyes well developed. Pronotum1.6 times as wide as long. Elytra 1.2 times as long as wide. Elytral internal angle rounded in male and in female, without noticeable sexual dimorphism. Male protarsi 0.6 times as wide as the protibia. *Spiculum gastrale* of

the male genital segment dilated into a narrow spatula (Figure 13t). Aedeagus approximately 4.7 times smaller than the body length, slightly arcuate in lateral view and the sides slightly arcuate in dorsal view, the apex with a short ventrally deflexed hook (Figures 12m, 2n). Internal stylus of the endophallus long and nearly straight. On each side one lateroventral preapical seta, one lateroapical, and one seta located at the apical third of the length of the aedeagus. The lateroapical seta is pointing forward, the other orthogonally to the plane of the aedeagus. In addition, there are two very strong preapical setae on each side, which have no equivalent in other species. Female genital segment with reduced gonocoxites. Spermiduct helical with a very large number of tightly compacted coils. Apex of the spermatheca rounded, without apical sclerotised plate (Figure 13u).

Differential diagnosis. Small-sized species with normally developed eyes and non-spiniform female elytra. Spermiduct tightly coiled; aedeagus small; distinguishable from *P. marshalli*, which has an equally small aedeagus, by the very short hook.

Habitat and distribution. Known from lowland forests of Gunung Mulu, Sarawak, Malaysia.

Remarks. A very small species, one of the smallest species of the genus.

Etymology. Named for its very small size (*nanus* = dwarf).

Ptomaphaminus marshalli Schilthuizen & Perreau, sp. n.

http://zoobank.org/B09BB75F-114E-42C4-B3FD-B6490A445EB5

Figures 12o, p, 13x, y, 14a, b

Material. Holotype: Malaysia, Sarawak, 4th Division, Gunung Mulu National Park, Slope, 29.4.78, Tps 4–6, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, in NHMUK, B.M.1978–49), 1 male. **Paratypes**: Sarawak. Gunung Mulu National Park, Slope, 29.4.78, Tps 4–6, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 2 males, 1 female; Gunung Mulu National Park, Slope, 29.4.78, Tps 1–3, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 6 males, 7 females; Gunung Mulu National Park, Slope, 7.4.78, baited traps, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 1 female. *Sabah*. Crocker Range Park, Inobong Station, 5°51.265'N, 116°06.363'E, 500 m elev., 21–23.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555639), 1 male.

Description. Length: 1.50–1.90 mm. General colour brown; the tarsi, the two first antennomeres, the base of the third antennomere, and of the tibiae yellowish. Winged. Eyes well developed. Pronotum 1.65 times as wide as long. Elytra 1.25 times as long as wide. Female sutural apex of elytra rounded (Figure 14b), similar to the male (Figure 14a). *Spiculum gastrale* of the male genital segment apically dilated into a short discoid expansion (Figure 13x). Aedeagus approximately 5.7 times shorter than the body length, the sides regularly arcuate in dorsal view (Figure 12o), moderately arcuate ventrally and obtusely angular dorsally in lateral view (Figure 12p). Apex of the median lobe with a large ventrally deflexed but not retroverted hook. Four lateroventral setae spaced from the apical third of the aedeagus and the apex. Internal stylus of the

Figure 15. Map of Borneo, with the areas that feature in this paper indicated.

endophallus moderately sinuate. Female genital segment with reduced gonocoxites. Spermiduct not helical. Apex of the spermatheca conically narrowed, the apex shortly rounded, without apical sclerotised plate (Figure 13y).

Differential diagnosis. Females of this species can be recognized by the apex of the spermatheca, which is conically narrowed, a very distinct morphology compared to all other species, which have a spermatheca with a widely rounded apex.

Habitat and distribution. Known from lowland forests of Gunung Mulu, Sarawak, and of Gunung Kinabalu, Sabah, Malaysia.

Etymology. Dedicated to J. E. Marshall, one of the collectors of the species during the expedition of the Natural History Museum of London in Sarawak.

***Ptomaphaminus hanskii* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/375C731A-B3B0-49DF-A150-51FA4F0D7A41
Figure 11a, 12k, l, 13i, j

Material. Holotype: Malaysia, Sarawak, 4th Division, Gunung Mulu National Park, Slope, 4.5.78, 9.1, 9.3, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, in NHMUK, B.M.1978–49), 1 male. **Paratypes**: *Sarawak*. Gunung Mulu National Park, Slope, 4.5.78, 9.1, 9.3, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 5 males, 8 females.

Description. Length: 1.6–2.1 mm. General colour brown; the tarsi and two first antennomeres yellowish. Winged. Eyes well developed. Pronotum 1.65 times as wide as long. Elytra 1.30 times as long as wide. Sutural angle of female elytra angular. Apex of the *spiculum gastrale* of the male genital segment dilated into a diamond-like form (Figure 13i). Aedeagus elongated, approximately 3.5 times shorter than the body length. Median lobe regularly narrowed from base to the apex in dorsal view (Figure 12l), thick and strongly arcuate, with a long ventrally deflexed but not retroverted apical hook in lateral view (Figure 12k). Six lateroventral preapical setae and one lateroapical seta on each side. Internal stylus of the endophallus moderately sinuate. Female genital segment with reduced gonocoxites. Spermiduct membranous, vaguely helical at least near the base of the spermatheca. Apex of the spermatheca rounded, without apical sclerotised plate (Figure 13j).

Differential diagnosis. Species with normally developed eyes and a long aedeagus. Very similar to *P. sarawacensis*, from which it cannot be confidently distinguished in the female sex. Males of *P. hanskii* have a thicker median lobe of the aedeagus than *P. sarawacensis*.

Habitat and distribution. Known from lowland forests of Gunung Mulu, Sarawak, Malaysia.

Remarks. The external morphology and the female genital morphology are extremely similar to *P. sarawacensis*, so that females are nearly impossible to distinguish. However, the male aedeagi of these species are very different.

Etymology. Named in honour of Ilkka Hanski, the Finnish ecologist who played an important role in the Royal Geographical Society expedition to Mulu of 1978, and who passed away in 2016.

***Ptomaphaminus sarawacensis* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/B1280A81-B7FC-48B2-9997-9133EF5B4D85
Figures 11b, 12i, j, 13g, h, 14c

Material. Holotype: Malaysia, Sarawak, 4th Division, Gunung Mulu National Park, Slope, 4.5.78, 9.1, 9.3, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, in NHMUK, B.M.1978–49), 1 male. **Paratypes**: *Sarawak*. Gunung Mulu National Park,

Slope, 4.5.78, 9.1, 9.3, v–viii.1978 (leg. P.M. Hammond & J.E. Marshall, NHMUK, B.M.1978–49), 5 males, 12 females.

Description. Length: 1.90–2.35 mm. General colour brown; the tarsi and two first antennomeres yellowish. Winged. Eyes well developed. Pronotum 1.6 times as wide as long. Elytra 1.4 times as long as wide. Sutural angle of female elytra angular (Figure 14c). Apex of the *spiculum gastrale* of the male genital segment dilated into a paddle-like shape (Figure 13g). Aedeagus approximately four times shorter than the body length. Median lobe parallel-sided in the first half, then regularly narrowed from the middle of its length, with a preapical constriction in dorsal view (Figure 12j), obtusely angular ventrally after the middle, with a long apical ventrally deflexed but not retroverted hook in lateral view (Figure 12i). Six lateroventral preapical setae and one lateroapical seta on each sides. Internal stylus of the endophallus nearly straight. Female genital segment with reduced gonocoxites. Spermiduct membranous, vaguely helical at least near the base of the spermatheca. Apex of the spermatheca rounded, without apical sclerotised plate (Figure 13h).

Differential diagnosis. See under *P. hanskii* (above).

Habitat and distribution. Known from lowland forests of Gunung Mulu, Sarawak, Malaysia.

Remarks. Extremely similar to *P. hanskii*, except in aedeagus shape.

Etymology. Named for the Malaysian state of Sarawak, where the type locality lies.

***Ptomaphaminus layangensis* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/A840208F-B55E-486C-887F-A26A62243AEB
Figures 11c, 12s, t, 13o, p

Ptomaphaginus sp. n. *bryanti* complex Merckx et al., 2015: extended data fig. 6.

Material. Holotype: Malaysia, Sabah, Kinabalu Park, Layang-Layang, 2750 m elev., 6°02.748'N, 116°33.632'E, 13–18.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH.INS.555619), 1 male. **Paratypes**: *Sabah*. Kinabalu Park, Layang-Layang, 6°02.748'N, 116°33.632'E, 2750 m elev., 13–18.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, CMPR, RMNH, incl. RMNH.INS.555618–555622), 11 paratypes.

Description. Length: 1.6–2.5 mm. General colour dark brown; the tarsi and two first antennomeres lighter. Winged. Eyes well developed. Pronotum 1.6 times as wide as long. Elytra 1.45 times as long as wide. Sutural angle of female elytra rounded, without noticeable sexual dimorphism. Male protarsi 0.75 times as wide as the protibia. *Spiculum gastrale* of the male genital segment short, moderately dilated at the apex (Figure 13o). Aedeagus 5.4 times shorter than the body length, the sides regularly arcuate in dorsal view (Figure 12s), ventrally straight and dorsally obtusely angular in lateral view. Apex of the median lobe with a ventrally deflexed, arcuate hook in lateral

view (Figure 12t). Six lateroventral preapical setae and one lateroapical seta on each side. Internal stylus of the endophallus significantly sinuate. Female genital segment with reduced gonocoxites. Spermiduct long and helical (Figure 13p). Apex of spermatheca rounded, without apical sclerotised plate.

Differential diagnosis. Normal-sized species with unreduced eyes and non-spiniform female elytra. Aedeagus with a long, retroverted apical hook. Distinguishable from *P. alabensis* by the anteriorly widened *spiculum gastrale* and the broader apex of the median lobe of the aedeagus. Females are distinguishable from *P. nanus* by their larger size.

DNA barcodes. COI barcodes are available in BOLD for the holotype, RMNH.INS.555619, as well as for the paratypes RMNH.INS.555618 and 555620–555622, jointly forming the BIN ACK0070.

Habitat and distribution. Known from high altitude (above 2000 m) on Gunung Kinabalu, Sabah, Malaysia.

Etymology. Named for the type locality on Gunung Kinabalu.

***Ptomaphaminus microphallus* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/F32A3991-EC96-4F68-8C61-464F62432FAF
Figures 11f, 12y, z, 13q

Material. Holotype: Malaysia, Sabah, Kinabalu Park, Poring Hot Springs, 6°02.894'N, 116°41.957'E, 625 m elev., in baited pitfall traps, 15–20.ix.2012, (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition), 1 male in RMNH (RMNH.INS.1086291). **Paratypes**: *Sabah*. Kinabalu Park, Poring Hot Springs, 6°02.894'N, 116°41.957'E, 625 m elev., in baited pitfall traps, 15–20.ix.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition), 1 male paratype in RMNH (RMNH.INS.1086292).

Description. Length: 1.2 mm. General colour dark brown; the tarsi and two first antennomeres lighter. Winged. Pronotum 1.55 times as wide as long. Elytra 1.15 times as long as wide. Male protarsi 0.6 times as wide as the protibia. *Spiculum gastrale* of the male genital segment apically dilated into a short discoid expansion (Figure 13q). Aedeagus very small, 5.5 times shorter than the body length. Lateral sides regularly arcuate in dorsal view (Figure 12y), flattened in the middle and with a short ventrally retroverted expansion in lateral view (Figure 12z). On each side, six latero-preapical pointing ventral setae and one apical seta pointing forward. Internal stylus of the aedeagus weakly sinuate.

Differential diagnosis. The female is unknown, but the male aedeagus shares several features with other species, such as *P. marshalli*, *P. nanus*, and *P. alabensis* (i.e., a relatively short aedeagus with retroverted hook). However, *P. microphallus* is unique among Borneo *Ptomaphaminus* by its extremely short (0.22 mm) aedeagus.

Habitat and distribution. Known from the type locality, in Kinabalu Park, Sabah, Malaysia.

Remarks. Female unknown.

Etymology. Named for the relatively small male genitalia.

***Ptomaphaminus alabensis* Schilthuizen & Perreau, sp. n.**
http://zoobank.org/1F9CBD47-54C9-4F92-B7D3-DE35E2DEAF20
Figures 11g, 12w, x, 13v, w

Ptomaphaginus nr. *fagei* Merckx et al., 2015: extended data figs 2, 6.

Material. Holotype: Malaysia, Sabah, Crocker Range, Gunung Alab, 5°47.766'N, 116°20.504'E, 1930 elev., baited pitfall trap, 17–22.iv.2012 (leg. M. Schilthuizen, RMNH.INS.555632)**. Paratype**: *Sabah*. Crocker Range, Gunung Alab, 5°47.766'N, 116°20.504'E, 1930 elev., baited pitfall trap, 17–22.iv.2012 (leg. M. Schilthuizen, Crocker Range / Kinabalu Expedition, RMNH, CMPR), 3 males, 3 females (including RMNH.INS.555633).

Description. Length: 1.5–1.6 mm. General colour dark brown; the tarsi and two first antennomeres yellowish. Winged. Pronotum 1.6 times as wide as long. Elytra 1.33 times as long as wide. Sutural angle of female elytra rounded, without noticeable sexual dimorphism. Male protarsi 0.8 times as wide as the apex of protibia. *Spiculum gastrale* of the male genital segment straight, without apical dilation. Median lobe of the aedeagus 4.7 times shorter than the body length. Apex of the median lobe with a ventrally deflexed, arcuate hook. Aedeagus regularly narrowed from base to apex in dorsal view, ventrally straight (Figure 12w) and dorsally obtusely arcuate in the middle in lateral view (Figure 12x). Six lateroventral preapical setae and one lateroapical seta on each side. Internal stylus of the aedeagus weakly sinuate. Spermiduct extremely short. Spermatheca bilobate, with a very small basal lobe, base of the spermatheca helical (Figure 13w).

Differential diagnosis. Females are easily recognized by the spermatheca which has a helical base and the spermiduct short, not helical. When helical structures occur in the female genitalia in other species, this affects the spermiduct, and not the spermatheca.

DNA barcodes. In BOLD, COI barcodes area available for the holotype, RMNH.INS.555632, and one paratype, RMNH.INS.555633, together forming the BIN ACJ9598.

Habitat and distribution. Known from the type locality, on Gunung Alab, Crocker Range, Sabah, Malaysia.

Etymology. Named for the type locality, Gunung Alab in the Crocker Range.

Identification keys to genera and species

Key to the genera

1 Mesocoxal cavities attached to one another. Protibiae without a long row of equal spines along the external side. Male first mesotarsomere dilated. Epistomal suture absent **2**

– Mesocoxal cavities separated by a mesoventral process. Protibiae with a long row of equal spines along the external side. Male first mesotarsomere undilated. Epistomal suture present (Ptomaphagini) **3**

2 Elytral surface with punctuation aligned in transverse strigae. Male urite IX entire (Anemadini, Nemadina) ..... ***Micronemadus sondaicus*** **sp. n.**

– Elytral surface with uniformly spaced punctuation, without transverse strigae. Male urite IX reduced (Cholevini, Catopina) ..... ***Catops pruinosus*** **Schweiger**

3 Female protarsi tetramere and widely dilated (Figure 3d), approximately as wide as the apex of the protibia. Mesoventral process extremely wide and high with a flat ventral side (Figure 3c). Pronotal and elytral setae of two kinds, one long and erect, the other short and recumbent (Figure 3a) (Baryodirina) ..... ***Baryodirus hammondi*** **Perreau**

– Female protarsi pentamere and undilated. Mesoventral process narrow, the ventral side sharp-edged (Ptomaphaginina) **4**

4 Ventral spines of protibiae randomly arranged. Metaventral sutures convergent towards the central axis of the body..... ***Ptomaphaminus*** **Perreau**

– Ventral spines of protibiae aligned along the latero-external row of equal spines, making a second, more widely-spaced row next to the external one. Metaventral sutures roughly parallel to the axis of the body ..... ***Ptomaphaginus*** **Portevin**

Key to the species of *Ptomaphaginus*

1 Body length more than 3.3 mm..... **2**

– Body length less than 3.1 mm..... **4**

2 Elytra more than two times as long as the pronotum **3**

– Elytra not more than two times as long as the pronotum..... ***P. bryantioides*** **Schilthuizen & Perreau** (exceptionally large individuals)

3 Female: apical capsule of spermatheca annulated, U-shaped, spermiduct not extremely long, consisting of 5–6 coils (Figure 10b); male: aedeagus slightly bent ventrad and relatively flat, at the apex blunt, nearly rounded, stylet short and broad (Figure 6k–l), elytral apex without a distinct tuft of spine-like setae ..... ***P. grandis*** **sp. n.**

– Female: apical capsule of spermatheca not annulated, semicircular, spermiduct extremely long, consisting of ca. 30 coils (Figure 10c); male: aedeagus strongly curved ventrad and strongly convex, keeled, at the apex trilobate, stylet very long and thin, hair-like (Figure 7a–b), elytral apex with a distinct tuft of spine-like setae ..... ***P. isabellarossellini*** **sp. n.**

4 Aedeagus with two lateral "flaps" at the apex and usually a median processus, the apex thereby appearing bilobate or trilobate (Figs 6a, c, e, g, 8a) **5**

– Aedeagus tip upturned or flattened, sometimes with a median processus, but not clearly bi- or trilobate (Figs 6i, m, 7c, e, g, i) **10**

5 Habitus narrow and elongated, relatively flat. Pronotum 1.5–1.6 times as wide as long, narrowing in a more rectilinear fashion from caudal to rostral (Figure 4c) **6**

– Habitus broader. Pronotum 1.7–1.9 times as wide as long, narrowing in a gradual curve from caudal to rostral **7**

6 Aedeagus apically with two long lateral flaps that jointly are more than half the width of the basal part of the aedeagus, and a long median processus. Female unknown ..... ***P. bryanti*** **Jeannel**

– Aedeagus apically with two short, triangular lateral flaps, jointly less than half the width of the basal part of the aedeagus, without a clear median processus (Figure 8a). Female unknown ..... ***P. caroli*** **Schilthuizen & Perreau**

7 Aedeagus in dorsal view slender, more than two times as long as wide, at the apex with a long (longer than each of the lateral flaps), caudally pointing, median processus (Figure 6c); spermatheca without multiple, ring-shaped constrictions (Figure 10a) ..... ***P. bryantioides*** **Schilthuizen & Perreau**

– Aedeagus in dorsal view short and broad, less than two times as long as wide, if at the apex with a caudally pointing median processus, then this is shorter than each of the lateral flaps; spermatheca sometimes with ring-shaped constrictions **8**

8 Male protarsi not dilated, less than one-third the width of the apex of the protibia; as narrow as in the female; spermatheca with multiple, ring-shaped constrictions ..... ***P. similipes*** **Schilthuizen & Perreau**

– Male protarsi moderately to strongly dilated, at least half the width of the apex of the protibia; spermatheca unknown **9**

9 Male protarsi moderately dilated, about half as wide as the apex of the protibia; elytral apices rounded (male) or drawn out (female) ..... ***P. kinabaluensis*** **Schilthuizen & Perreau**

– Male protarsi strongly dilated, as wide as the apex of the protibia; elytral apices truncated in both sexes ..... ***P. latimanus*** **Schilthuizen & Perreau**

10 Antennae short and broad, antennomeres 9 and 10 twice as long as wide; aedeagus inflated and strongly convex; spermatheca with multiple ring-shaped constrictions (Figure 10f) ..... ***P. scaphaner*** **Szymczakowski**

– Antennae slender, antennomeres 9 and 10 square or only slightly wider than long; aedeagus not inflated and highly convex; (spermatheca not known for all species) **11**

11 Eyes reduced (each eye only one-tenth of the width of the head), wingless; female unknown ..... ***P. burckhardti*** **Schilthuizen & Perreau**

– Eyes normally developed (each eye ca. one-sixth of the width of the head), winged **12**

12 Aedeagus in dorsal view quadrangular, two times as long as wide (Figure 7i); female unknown ..... ***P. sabahensis*** **Schilthuizen & Perreau**

– Aedeagus in dorsal view narrowed caudally, either gradually or abruptly pointed, more than two times as long as wide **13**

13 Upturned tip of the aedeagus sharp, pointed (Figs 6m, 7e) **14**

– Upturned tip of the aedeagus broadly flattened and rounded (Figure 6i)..... ..... ***P. anas*** **Schilthuizen & Perreau**

14 Apex of the aedeagus abruptly narrowed (Figure 6m); pronotum narrower than the elytra at the shoulders, caudal angles hardly drawn out (Fig. 5a); spermatheca without multiple ring-shaped constrictions (Figure 10d) .... ***P. louis*** **sp. n.**

– Apex of the aedeagus gradually narrowed; pronotum as wide as the elytra at the shoulders, caudal angles distinctly drawn out (Figure 5b); spermatheca with multiple ring-shaped constrictions (Figure 10e) ..... ***P. muluensis*** **sp. n.**

Key to the species of *Ptomaphaminus*

1 Basal loop of the endophallus symmetric and stylus short and more strongly sinuate, located in the apical half of the median lobe (Figure 12b–d). Urite IX of the male with an extremely long and thin *spiculum gastrale*, not transversally expanded (Figure 13a–c). Aedeagus without apical hook in lateral view (Figure 12a–c). Female gonocoxites long, more than three times as long as wide (Figure 13b–d). Spermatheca weakly sclerified, the apical capsule with a set of transversal rings (Figure 13b–d). Female sutural apex of elytra spiniform **2**

– Basal loop of the endophallus asymmetric and stylus long and weakly sinuate, extended over most of the length of the median lobe. Anterior half of the *spiculum gastrale* of the male genital segment generally dilated into a paddle-shape (except *P. alabensis* sp. n.). Apex of aedeagus with a more or less developed hook-shaped expansion visible in lateral view. Female gonocoxites short, approximately as wide as long. Female sutural apex of elytra rounded, angular or spiniform..... **3**

2 Head and discus of the elytra noticeably darker brown than the rest of the body. Male protarsi more expanded, 0.5 times as wide as the apex of protibia. Spermiduct irregular ..... ***P. latescens*** **Szymczakowski**

– Entire body light reddish brown. Male protarsi less expanded, 0.4 times as wide as the apex of protibia. Spermiduct slightly helical..... ***P. testaceus*** **sp. n.**

3 Protarsus dilated (males) **4**

– Protarsus undilated (females) **14**

4 Eyes reduced (<50 ommatidia)..... **5**

– Eyes normally developed (>100 ommatidia) **7**

5 Aedeagus long (more than 0.5 mm). Apical hook of the aedeagus long and retroverted (Figure 12e–12g)..... **6**

– Aedeagus short (~0.35 mm). Median lobe abruptly narrowed in lateral view on the apical third of its length, with a short apical hook. (Figure 12r) .... ***P. fagei*** **Perreau**

6 Apex of the aedeagus rectangular, the lateral angles sharp (Figure12h) ..... ***P. chapmani* Peck**

– Lateral angles of the apex of the aedeagus rounded (Figure 12f) ..... ***P. ater* Perreau**

7 Aedeagus long, more than 0.5 mm **8**

– Aedeagus short, less than 0.4 mm **9**

8 Median lobe of the aedeagus thicker, regularly arcuate along its whole length (Figure 12k), the endophallic stylus sinuate in dorsal view (Figure 12l)..... ***P. hanskii* sp. n.**

– Median lobe of the aedeagus thinner, slightly angular at the second third of its length (Figure 12i), the endophallic stylus strait in dorsal view (Figure 12j) .. ***P. sarawacensis* sp. n.**

9 Apical hook of the median lobe of aedeagus short (Figure 12n) ..... ***P. nanus* sp. n.**

– Apical hook of the median lobe of aedeagus longer **10**

10 Apical hook of the aedeagus retroverted **11**

– Apical hook of the aedeagus not retroverted (Figure 12v) ..... ***P. kinabatanganensis* sp. n.**

11 Apical hook of the median lobe of the aedeagus thick (Figure 12z). Aedeagus extremely small (0.22 mm) (Figure 12y–z)..... ***P. microphallus* sp. n.**

– Apical hook of the median lobe of the aedeagus thin **12**

12 Apical hook of the median lobe of aedeagus angular (Figure 12p) ..... ***P. marshalli* sp. n.**

– Apical hook of the median lobe of aedeagus roundish **13**

13 *Spiculum gastrale* of the male genital segment slightly expanded in the anterior part (Figure 13o). Median lobe of aedeagus widely rounded at apex in dorsal view (Figure 12s) ..... ***P. layangensis* sp. n.**

– *Spiculum gastrale* of the male genital segment not expanded in the anterior part (Figure 13v). Median lobe of aedeagus more or less triangularly narrowed at the end in dorsal view, the apex narrowly rounded (Figure 12w)..... ***P. alabensis* sp. n.**

14 Sutural apex of elytra sexually dimorphic, rounded in males, angular or spiniform in females (Figure 14c–e) **15**

– Sutural apex of elytra not sexually dimorphic, rounded in females as in males (Figure 14b)..... **19**

15 Eyes reduced (<50 ommatidia). Sutural apex of elytra spiniform (Figure 14d–e)..... **16**

– Eyes normally developed (>80 ommatidia). Sutural apex of elytra simply angular (Figure 14c) **18**

16 Spermiduct not helical (Figure 13s) ..... ***P. chapmani* Peck**

– Spermiduct helical **17**

17 Spermatheca with an apical sclerotised plate (Figure 13f) ..... ***P. ater* Perreau**

– Spermatheca without apical plate (Figure 13l)..... ***P. fagei* Perreau**

18	Spermiduct not helical (Figure 13n).....***P. kinabatanganensis* sp. n.**
–	Spermiduct membranous, vaguely helical near the base of the spermatheca (Figure 13h–j).....***P. hanskii* sp. n. and *P. sarawacensis* sp. n.**
19	Spermiduct not helical.....**20**
–	Spermiduct helical.....**21**
20	Terminal lobe of spermatheca regularly narrowed, the apex conical (Figure 13y).....***P. marshalli* sp. n.**
–	Apex of spermatheca rounded, base of the spermatheca helical (but not the spermiduct) (Figure 13w).....***P. alabensis* sp. n.**
21	Very small size, <1.3 mm. Spermiduct with many coils tightly compacted (Figure 13u).....***P. nanus* sp. n.**
–	Normal size, >1.5 mm. Spermiduct with coils regularly spaced, not tightly packed (Figure 13p).....***P. layangensis* sp. n.**

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RESEARCH ARTICLE

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An enigmatic new species of *Panorpa* Linneaus from the Bashan Mountains (Mecoptera, Panorpidae)

Yuan Hua[1], Shi-Heng Tao[1], Bao-Zhen Hua[2]

1 *College of Life Sciences, Northwest A&F University, Yangling, Shaanxi 712100, China* **2** *Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, Entomololgical Museum, Northwest A&F University, Yangling, Shaanxi 712100, China*

Corresponding authors: *Bao-Zhen Hua* (huabzh@nwafu.edu.cn); *Shi-Heng Tao* (shihengt@nwafu.edu.cn)

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Abstract

A new species of Panorpidae, *Panorpa bashanicola* **sp. n.**, is described and illustrated from the Bashan Mountains in central China. The new species is characterized by the following characters: vertex black, with two pale longitudinal stripes and four pale rounded spots; vein 1A ending before the origin of Rs; meso- and metanotum pale, and the pale color extending to tergum III in V-shape; male epandrium emarginate distally in deep U-shape; hypovalves without basal stalk, completely represented by a pair of short hypovalves, extending to distal third of gonocoxite, with five black stout setae in distal portion; paramere simple, S-shaped; a bundle of long hairs between dorsal and ventral valves of aedeagus; dorsal valves of aedeagus much longer than ventral valves and curved ventrally, with distal portion foot-shaped; female medigynium twice as long as wide, with stout axis extending over one-third its length beyond main plate.

Keywords

China, Hubei, Oriental Region, Mecoptera, *Panorpa*, Panorpidae, Shaanxi

Introduction

Panorpidae is the largest family of Mecoptera, with more than 420 described extant species, which are assigned to seven genera (Gao et al. 2016). *Panorpa* Linnaeus, 1758 is the most species-rich genus in Panorpidae, and is widely distributed in Asia, Europe and North America (Esben-Petersen 1921; Cheng 1957), with approximately 270 species in the world (Penny and Byers 1979) and 229 species in China (Wang and Hua 2017, 2018).

The current generic taxonomy of Panorpidae strongly relies on the status of vein 1A to a large extent as well as the presence or absence of anal horn(s) on the posterior margin of tergum VI in males, apart from the male and female genitalia (Carpenter 1938). Vein 1A ends at the anal margin of wings far beyond the origin of Rs in *Panorpa* Linneaus, 1758 (Fig. 1A), but before the origin of Rs in *Neopanorpa* van der Weele, 1909 (Fig. 1B) (Esben-Petersen 1921; Cheng 1957; Rust and Byers 1976; Chau and Byers 1978). The number of cross veins between veins 1A and 2A of forewings are also used as a generic character: two in *Panorpa*, but one in *Neopanorpa* (Esben-Petersen 1921; Chau and Byers 1978). *Panorpa* is also separated from *Neopanorpa* by a series of morphological characters (Ma et al. 2012) and anatomical characters, such as salivary glands (Ma et al. 2011), female genital plate (Ma et al. 2012), and female reproductive system (Hou and Hua 2008). Eggshell (Ma et al. 2009) and larvae (Yie 1951) can also provide useful characters.

However, some Chinese Panorpidae, such as *Panorpa fulvastra* Chou and *P. chengi* Chou (Chou et al. 1981), have vein 1A ending just at the level of the origin of Rs (Cai et al. 2008), making vein 1A not so credible as a diagnosis to differentiate *Panorpa* from *Neopanorpa*.

Further complicating the issue is an enigmatic undescribed species from the Bashan Mountains in central China. Its wing venation belongs to the pattern of *Neopanorpa* with 1A ending before the origin of Rs and one cross-vein between veins 1A and 2A (Fig. 1C), while other characters, especially the male and female genitalia, correspond to the genus *Panorpa*. In this paper, we describe the new species in *Panorpa* Linneaus, 1758 mainly based on the characters of genitalia, and briefly discuss the current criteria of the generic diagnoses of *Panorpa* and *Neopanorpa*.

Materials and methods

The specimens were collected from the Bashan Mountains in central China, and are preserved in 70% alcohol at the Entomological Museum, Northwest A&F University, China (**NWAU**). Observations were made under a Nikon SMZ1500 stereoscopic zoom microscope. Photographs were taken with a Nikon CoolPix5000 digital camera attached to the microscope.

For scanning electron microscopy, samples were cleaned in an ultrasonic cleaner for 30 s and dehydrated in a graded ethanol series. The materials were then dried in a CO_2 critical-point drier, gold-coated in a sputter coater and examined in a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 15 kV.

Taxonomy

***Panorpa bashanicola* sp. n.**
http://zoobank.org/95659BA8-69DE-4EFA-A507-565E3D14FDD4
Figs 1–6

Type material. Holotype: ♂, CHINA: Shaanxi: Nangongshan (32°14'N, 109°04'E), 1200–2025 m, Langao County, 24–25 June 2007, BZ Hua and JL Tan. **Paratypes:** 26♂22♀, same data as holotype; 12♂23♀, Nangongshan, 17–18 Aug. 2010, BZ Hua, J Huang, J Chen, JX Zhang; 40♂62♀, Nangongshan, 17–19 July 2011, BZ Hua, QH Gao, M Wang, B Xu; 24♂63♀, Nangongshan, 17–18 June 2012, BZ Hua, N Ma, B Xu, QH Gao, YY Feng; 2♂, Hubei, Hongping (31°20'N, 110°22'E), Shennongjia, 28 June 2007, BZ Hua and JL Tan.

Diagnosis. The new species can be readily distinguished from its congeners by the following characters: vertex black, with two pale longitudinal stripes and four pale rounded spots; vein 1A ending before the origin of Rs; one cross-vein between veins 1A and 2A; meso- and metanotum pale, and the pale color extending to tergum III in a V-shape; male epandrium emarginate distally in a deep U-shape; hypovalves extending to the distal third of gonocoxite, with five stout black setae on the distal portion; paramere simple, S-shaped; a bundle of long hairs between the dorsal and ventral valves of aedeagus; dorsal valves of aedeagus much longer than ventral valves and curved ventrally, with distal portion foot-shaped; female medigynium twice as long as wide, with stout axis extending over one-third its length beyond main plate.

Description of male (Fig. 2A). Vertex black, with two pale submedian stripes and two eye-shaped speckles on lateral regions. Two suborbicular spots beyond the protuberant area laterally (Fig. 3A). Ocellar triangle black. Compound eyes dark grey. Rostrum uniformly yellowish, mandible dark brown; labial and maxillary palps yellow with distal segments dark brown. Antennae long, filiform, with 39–40 flagellomeres.

Thorax. Pronotum light brown, with 12 black setae along anterior margin; meso- and metanotum pale with both sides grayish yellow. Pleura light grayish yellow. Legs pale yellow, tibia with a pair of apical spurs; tarsi light yellowish brown.

Wings. Forewing length 13.0–13.2 mm, width 2.9–3.1 mm. Wing membrane hyaline, almost without markings. Apical band greatly reduced, only indicated by a narrow dark gray trace at apical region; pterostigma prominent. Vein R_2 bifurcate; vein 1A ending before the origin of Rs; one cross-vein between veins 1A and 2A (Fig. 1C). Hindwings similar to forewings (Fig. 2A).

Abdomen. Terga I–V brownish black except for a narrowing pale V-shaped median stripe on terga I–III. Notal organ of tergum III very short, not prominent. Tergum VI without anal horns on posterior margin. Segments VII and VIII elongate and uniformly yellowish brown, with basal half slightly constricted and slightly wider toward apices (Fig. 3B).

Male genitalia. Genital bulb globular, yellowish brown (Fig. 3C, D). Epandrium (tergum IX) broad at base, slightly narrower toward apex, with a deep broad U-shaped

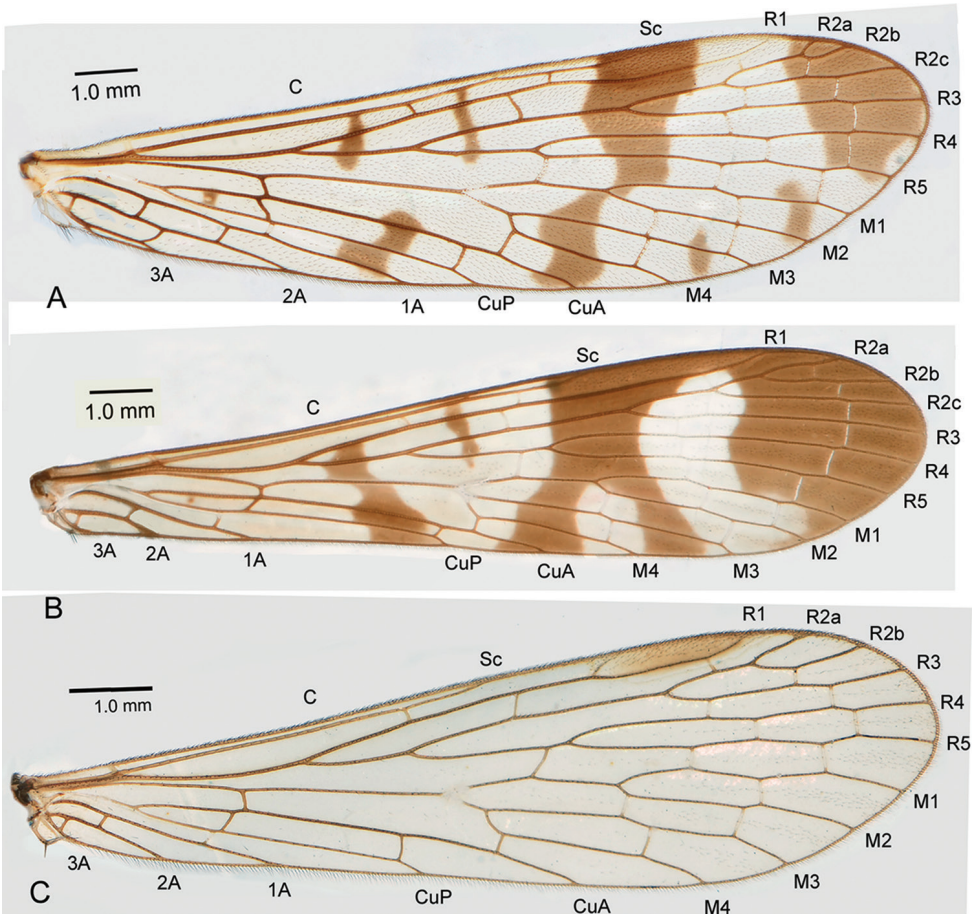

Figure 1. Forewings of male Panorpidae. **A** *Panorpa communis* **B** *Neopanorpa pulchra* **C** *Panorpa bashanicola* sp. n.

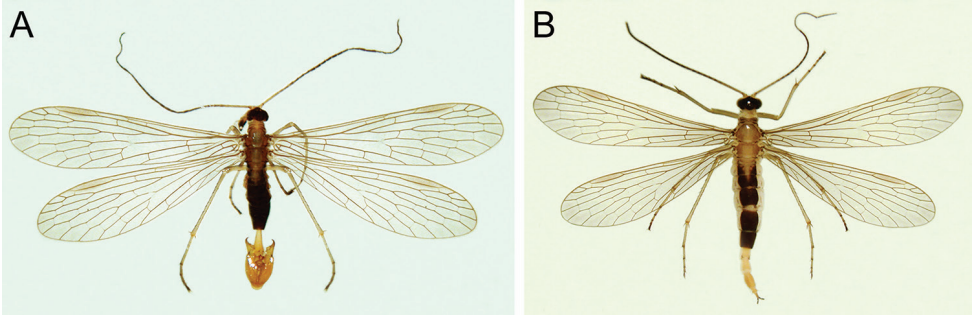

Figure 2. *Panorpa bashanicola* sp. n., adults in dorsal view. **A** Male **B** Female.

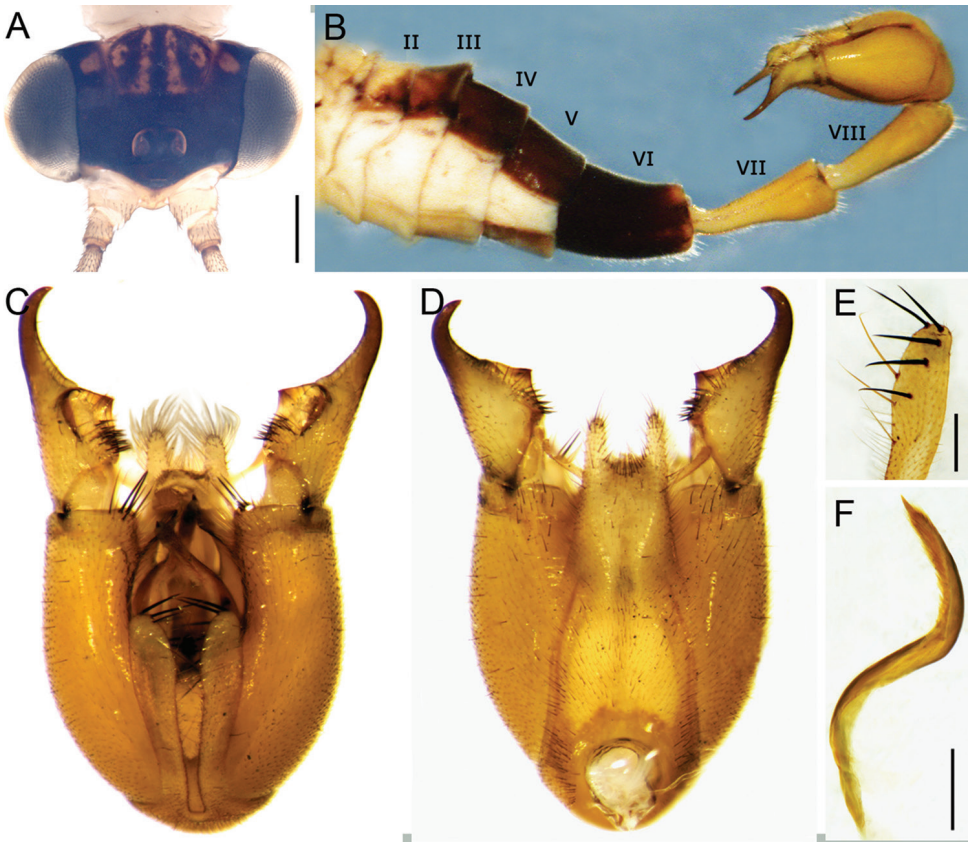

Figure 3. *Panorpa bashanicola* sp. n., male. **A** Head in dorsal view **B** Abdomen in lateral view **C, D** Genital bulb in ventral and dorsal views **E** Distal part of left hypovalves in dorsal view **F** Left paramere in ventral view. Scale bars: 0.5 mm (**A**); 0.2 mm (**E, F**).

emargination distally; epandrial lobes with dense setae. Cercus elongate and expanded apically (Fig. 4A), with five campaniform sensilla on dorsal surface (Fig. 4B). Hypandrium (sternum IX) without basal stalk, completely represented by a pair of parallel hypovalves, reaching two-thirds of gonocoxite (Fig. 3C). Hypovalve with five stout black setae on distal portion and three yellow setae on dorsal side (Fig. 3E). Gonocoxite bearing a cluster of black bristles on inner apex (Fig. 3C). Gonostylus broad in basal half and slender in distal half, with a large median concave area; a cluster of stout black setae basal to the concave region (Fig. 3C). Parameres distinctly twisted in S-shape and bearing short setae along inner margin on distal part (Fig. 3F). Aedeagus weakly sclerotized; dorsal valves slender and curved ventrally, with distal part foot-shaped; ventral valves greatly shortened; a bundle of long hairs between ventral and dorsal valves (Fig. 4C, D). A short broad lateral process from basal part of dorsal valves (Fig. 4C, E).

Description of female. Head, thorax and abdominal segments I–V similar to those of male (Fig. 2B). Abdominal segments VII and VIII pale yellow, segment IX

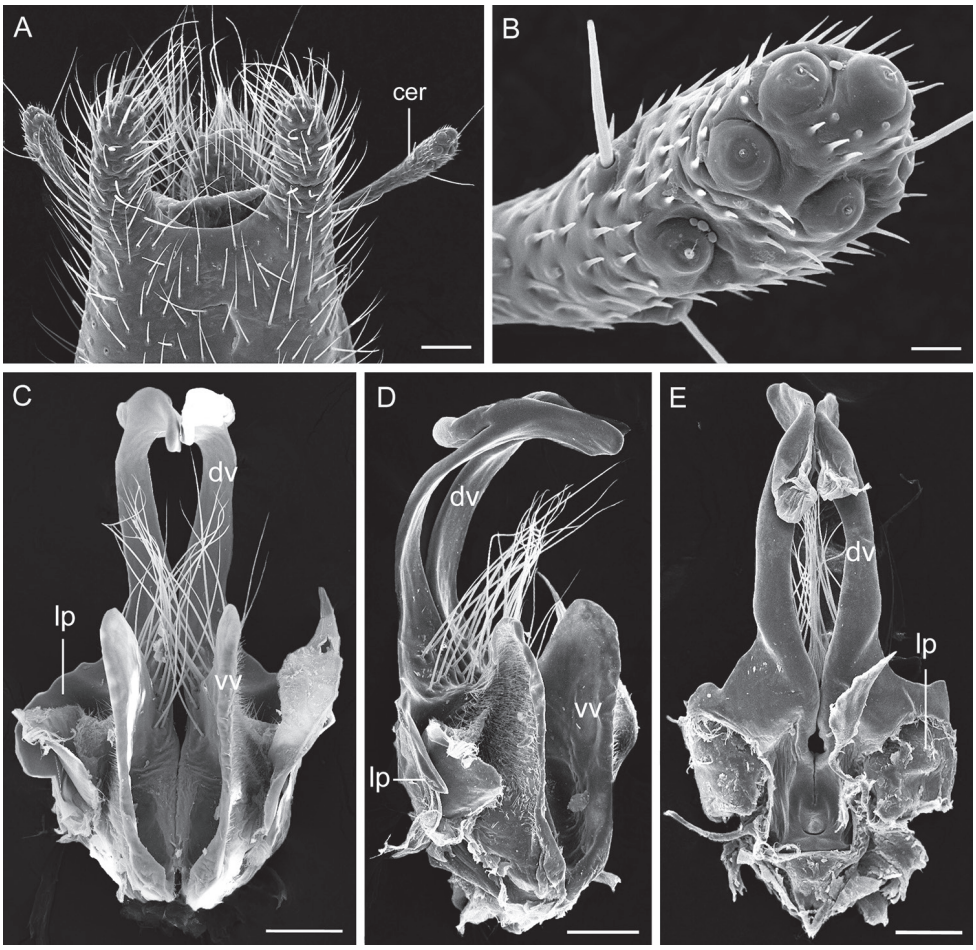

Figure 4. SEM micrographs of the male genitalia of *Panorpa bashanicola* sp. n. **A** Distal part of epandrium in dorsal view **B** Magnification of distal part of cercus **C–E** Aedeagus in ventral, lateral and dorsal views. Abbreviations: **cer** cercus; **dv** dorsal valve of aedeagus; **lp** lateral process; **vv** ventral valve of aedeagus. Scale bars: 1 mm (**A, B**); 100 μm (**C–E**).

yellowish brown (Fig. 5A). Cerci black, two-segmented, arising from distal end of abdomen. Wing pattern similar to that of male (Fig. 2B).

Female genitalia. Subgenital plate broad subbasally and narrowing toward apex, with long setae on lateral distal part (Fig. 5A). Medigynium with main plate twice as long as wide and infolded medially. Paired posterior arms forming a broad U-shape emargination. Median axis stout, extending anteriorly over one-third its length beyond main plate (Fig. 5B–D), with anterior end broadly furcate. Posterior end of axis with sculptured region, with orifice of spermathecal duct at terminal end (Fig. 6A–C).

Etymology. The specific epithet, *bashanicola*, refers to its type locality, Bashan Mountains.

Distribution. China (Shaanxi and Hubei).

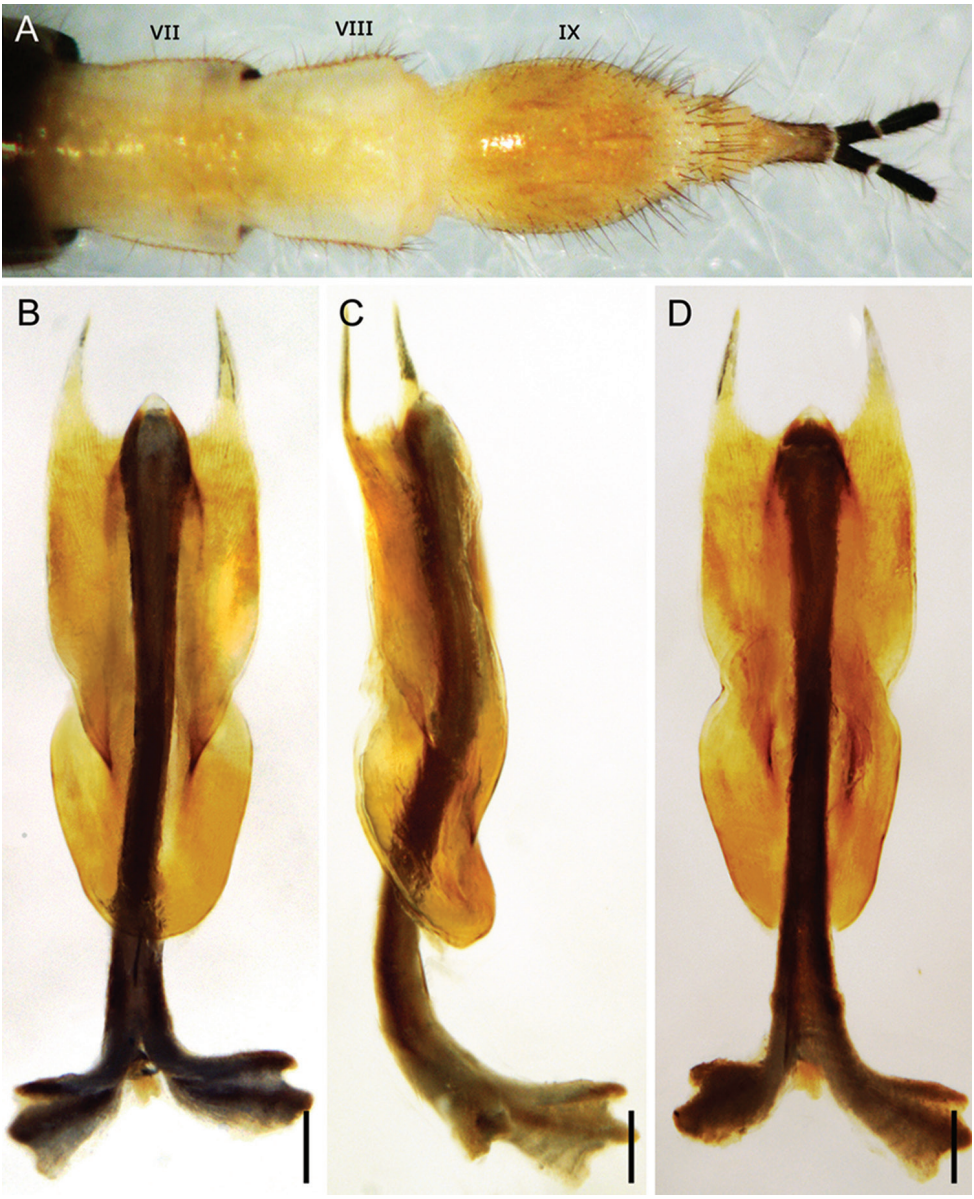

Figure 5. *Panorpa bashanicola* sp. n., female. **A** Distal part of abdomen in ventral view **B–D** Medigynium in ventral, lateral and dorsal views. Scale bars: 0.1 mm.

Remarks. The new species resembles *P. chengi* Chou, 1981 from the Qinling Mountains, Shaanxi Province in pale nota and brownish body coloration as well as broad hypovalves. It can be readily recognized from the latter by the following characters: 1) vein 1A ending before the origin of Rs; 2) abdominal terga I–III brownish black except for a V-shaped pale median stripe; 3) parameres bearing dense setae along inner margin of distal portion; and 4) dorsal valves of aedeagus slender and foot-shaped in distal portion.

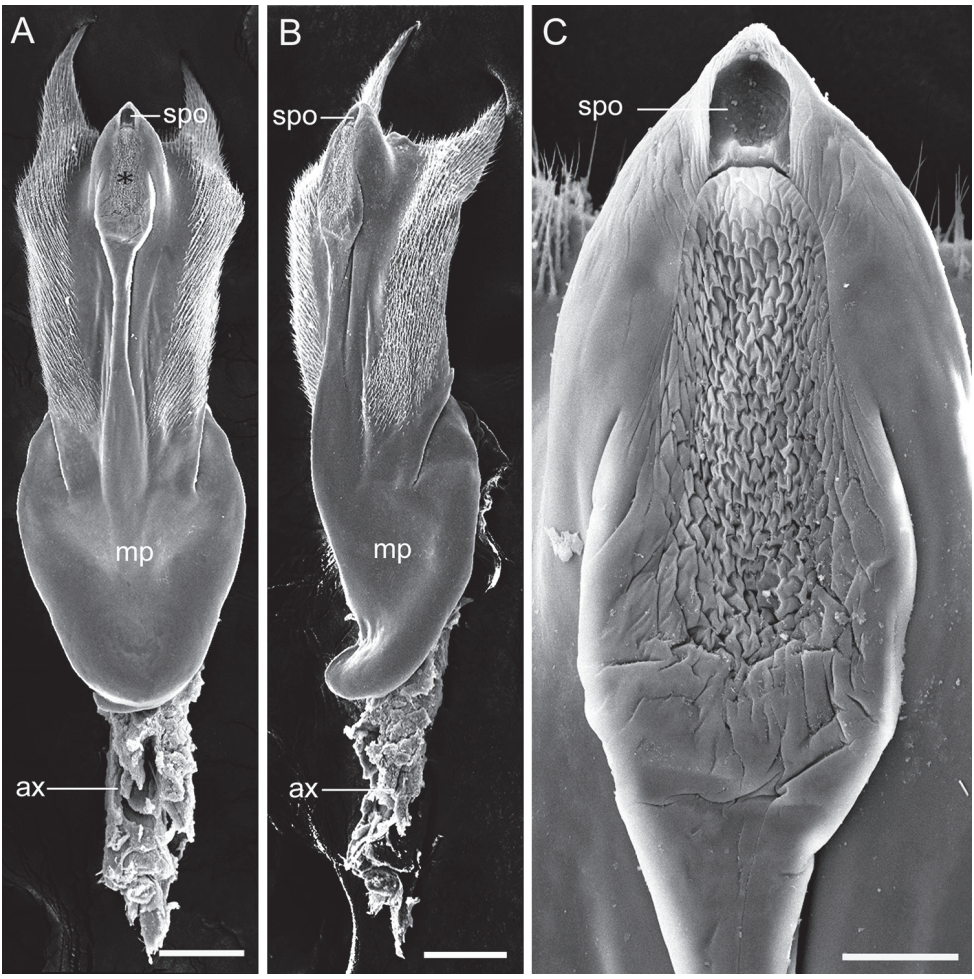

Figure 6. SEM micrographs of the female medigynium of *Panorpa bashanicola* sp. n. **A, B** Medigynium in ventral and latero-ventral views **C** Magnification of the sculpturing part of the main plate (asterisk), showing the orifice of spermathecal duct. Abbreviations: **ax** axis; **mp** main plate; **spo** orifice of spermathecal duct. Scale bars: 100 μm (**A, B**); 25 μm (**C**).

Discussion

We assigned the new species to *Panorpa* Linneaus based on the following characters: notal organ on tergum III in male not prominent; hypandrium of male genitalia without basal stalk; female medigynium with long axis extending anteriorly beyond main plate by one third length.

However, vein 1A terminates at the hind margin of wings before the origin of Rs in the new species. Strictly speaking, this character is not in accord with the generic definition of *Panorpa* Linnaeus, but conforms to the genus *Neopanorpa* van der Weele (Esben-Petersen 1921; Chau and Byers 1978; Cheng 1957). Because vein 1A varies

considerably among the species of Panorpidae, taxonomists should be cautious to assign a species to the suitable genus based mainly on the character of vein 1A. Instead, it is more reliable for them to consult more characters, especially the male and female genital characters (Carpenter 1938). In other words, the genus *Neopanorpa* needs to be redefined accordingly.

Acknowledgements

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RESEARCH ARTICLE

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A newly discovered biodiversity hotspot of many-plumed moths in the Mount Cameroon area: first report on species diversity, with description of nine new species (Lepidoptera, Alucitidae)

Peter Ustjuzhanin[1], Vasily Kovtunovich[2], Szabolcs Sáfián[3], Vincent Maicher[3,4], Robert Tropek[3,5]

1 *Altai State University, Lenina 61, Barnaul, 656049, Russia* **2** *Moscow Society of Nature Explorers, Bolshaya Nikitskaya 6, Moscow, RU–103009, Russia* **3** *Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, CZ-37005 České Budějovice, Czechia* **4** *Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Branišovská 31, CZ-37005 České Budějovice, Czechia* **5** *Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Prague, Czechia*

Corresponding author: *Robert Tropek* (robert.tropek@gmail.com)

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Abstract

Fifteen species of many-plumed moths are recorded from the Mount Cameroon area, SW Cameroon, West Africa. Nine species: *Alucita longipenis* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. lidiya* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. ludmila* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. escobari* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. mischenini* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. fokami* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. janeceki* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. besongi* Ustjuzhanin & Kovtunovich, **sp. n.,** and *A. olga* Ustjuzhanin & Kovtunovich, **sp. n.,** are described as new for science. Four species are recorded as new from Cameroon: *A. acalyptra*, *A. chloracta*, *A. coffeina,* and *A. spicifera*. By these records, the Mount Cameroon area has become the richest known Afrotropical locality for the Alucitidae, highlighting its tremendous value for biodiversity conservation.

Keywords

Alucitidae, biodiversity, Cameroon, many-plumed moths, Mount Cameroon, new species, new records, tropical rainforest

Introduction

Many-plumed moths (Alucitidae) differ from other Lepidoptera by the structure of their wings, which are each split into six lobes, with the exception of the oriental genus *Triscaedecia* Hampson, 1905, which has seven-lobed hind wings. These moths are active at night, and relatively well attracted to light. Most of their diversity is currently known from the Palearctic region, where their caterpillars usually live concealed in plant tissue, some make leafmines, others feed in flowers and buds of various species in the honeysuckle family (Caprifoliaceae). However, the biology of the African many-plumed moths is virtually unstudied.

The taxonomy and distribution of the many-plumed moths are seriously understudied in the Afrotropical Region, despite recent publications of material originating from South Africa, Zimbabwe, and Malawi (Ustjuzhanin and Kovtunovich 2011, 2016). Altogether, 58 species are known from all of the Afrotropics (De Prins and De Prins 2018). Most of the previously described species originate from southern and eastern Africa (Meyrick 1908, 1911, 1913, 1920, Hering 1917, Viette 1958), whereas only 12 species were known to occur in the Guineo-Congolian forest zone, virtually each of them from a few records only (De Prins and De Prins 2018). Nevertheless, this region includes two of the recognised biodiversity hotspots of Africa (Myers et al. 2000) and is thus also expected to harbour many more species of Alucitidae. This is reflected in recent unpublished collections by Sz. Sáfián, who collected several species in Ghana and Liberia.

Since 2014, the last three authors have been coordinating an extensive study of the biodiversity of Lepidoptera on Mount Cameroon, Southwest Province, Cameroon. Its aim was to survey butterfly and moth communities in different altitudinal forest zones on the south-western slopes of the mountain. Originally, Alucitidae were not included in the target groups (which are mainly various groups of Bombycoidea, Noctuoidea, and Geometroidea), but during the first collecting hours, the authors realised how species-rich the family appeared in the study area. Consequently, all Alucitidae specimens were systematically collected during each sampling night. The collected material was sent to the first two authors for identification and further taxonomic work. This paper presents the first results of the study, including descriptions of nine new species, a staggering increase in the known species of Alucitidae from West Africa.

Materials and methods

Abbreviations

NHM	Natural History Museum, London, UK.
CUK	personal collections of P. Ustjuzhanin and V. Kovtunovich, Novosibirsk and Moscow, Russia.
NECJU	Nature Education Centre, Jagiellonian University, Kraków, Poland.

MNHN Muséum national d'Histoire naturelle, Paris, France.
TMSA Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa.
ZMHB Museum für Naturkunde, Berlin, Germany.
ZISP Zoological museum of St. Petersburg, Russia.

Sampling localities

All the presented material was sampled in rainforests of the Mount Cameroon National Park and in the littoral forest of the nearby Bimbia-Bonadikombo Community Forest, both lying in the Southwest Province, Cameroon (Fig. 1). This paper presents data from the first two field expeditions, when mostly the lower altitudinal zones were sampled, with the exception of mountain forests around the Elephant Camp. The two reported field trips comprised sampling in a transition from wet to dry seasons (November/December 2014 – Bamboo Camp, Drinking Gari Camp, Elephant Camp, PlanteCam), a full dry season (December 2014/January 2015 – Bimbia-Bonadikombo), and a transition from dry to wet seasons (April/May 2015 – Bamboo Camp, Drinking Gari Camp, Bimbia-Bonadikombo, PlanteCam). All the sampled localities are listed here:

Bamboo Camp – Bamboo Camp (350 m a.s.l.), Mount Cameroon (SW slope), N4.08791°, E9.05051°; a lowland forest with historical disturbances by selective logging.
Bimbia-Bonadikombo – Mexico Camp (30 m a.s.l.), Bimbia-Bonadikombo Community Forest, N3.98183°, E9.26250°; a littoral forest in the formally non-intervention part of the Community forest, but with intensive current logging (Ferenc et al. in press)
Drinking Gari – Drinking Gari Camp (650 m a.s.l.), Mount Cameroon (SW slope), N4.10144°, E9.06100°; a lowland forest with a presumably closed canopy layer.
Elephant Camp – Elephant Camp (1850 m a.s.l.), Mount Cameroon (SW slope), N4.11700°, E9.07292°; a montane forest with a highly sparse canopy layer, as a consequence of intensive natural disturbances by forest elephants.
PlanteCam – PlanteCam Camp (1100 m a.s.l.; also misspelled as "Planticamp"), Mount Cameroon (SW slope), N4.11750°, E9.07094°; an upland forest in the transition between lowland and montane zones, its canopy layer is substantially opened by natural disturbances by forest elephants.

Sampling methods

In each of the above-listed localities, three sampling plots were established to partially cover the heterogeneity of local forest habitats. In each plot, moths were collected during two full nights (from dusk till dawn) in each sampled season. All specimens were captured at an artificial light (a single energy saving bulb: 4100 K, 5300 lm,

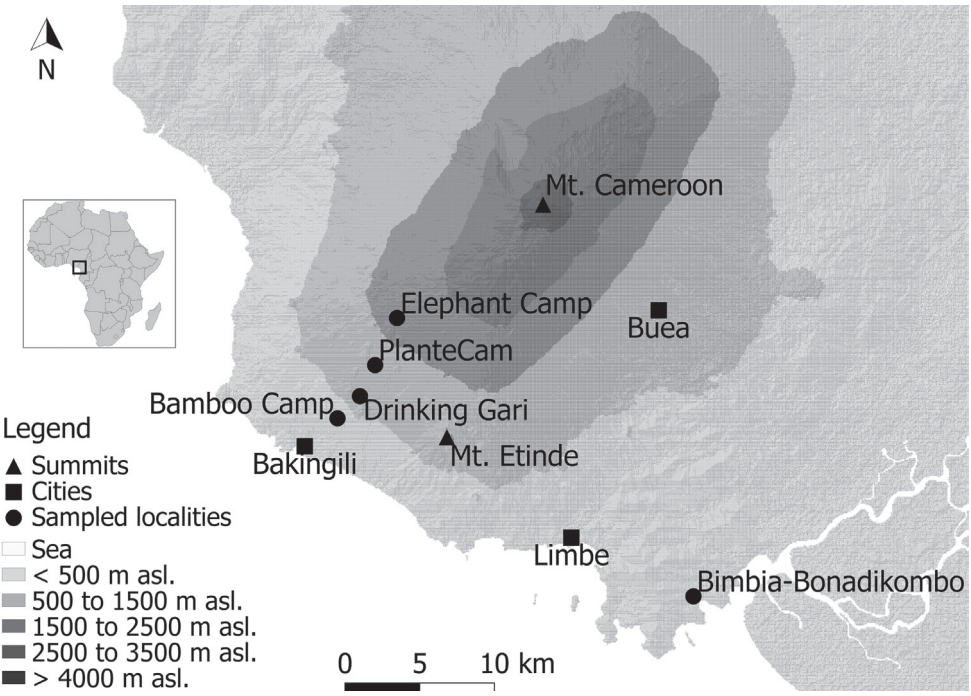


Figure 1. Map of the study area and localities.

105 W, 5 U), powered by a portable generator. The bulb was set in the centre of two perpendicularly placed white sheets (1.5 × 1.5 × 1.8 m, the cloth type B, produced by Entosphinx, Czechia). Specimens were killed by ammonia vapours and either pinned in situ or temporarily stored in glassine envelopes, all dried by silica gel. Later, all specimens were properly mounted in the lab.

Genitalia preparations

The preparation of genitalia slides is necessary for the identification of Alucitidae. Normally, abdomens were boiled in a 10–15% solution of potassium hydroxide until semi-transparent. After this, they were rinsed in water thoroughly for the preparation of permanent slides. On the mount, genitalia were put in a small drop of Euparal after being dehydrated in 100% ethanol. The mounts were then covered with a cover glass. In case the genitalia structures were not well sclerotised, they were stained with Chlorazol Black for greater contrast. Permanent preparations were dried for at least two weeks before being studied. Each permanent preparation received its unique code under which it is searchable in the collections where they are stored; the relevant numbers are also mentioned in captions of the genitalia figures.

Results

Recorded species

Altogether 15 species of Alucitidae were recorded on Mount Cameroon during the reported two field expeditions: nine of them proved to be new for science, and four others were new country records for Cameroon (marked with *), only two had been recorded previously. The morphological terminology follows Zagulajev (1986). The distribution of individual species follows the Afromoths database (De Prins and De Prins 2018).

******Alucita acalyptra* **(Meyrick, 1913)**

Orneodes acalyptra Meyrick, 1913: 269. Type locality: Barberton, Republic of South Africa. Holotype: male, TMSA, examined by the authors.

Material examined. Bamboo Camp, 1 female, (CUK), 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the mottled grey colour of the wings with contrast zigzag bands, this species is close to *A. agassizi* Ustjuzhanin & Kovtunovich, 2018. In the male genitalia, the shape of the phallus and the lanceolate uncus are similar to *A. hemicyclus* (Hering, 1917), but it differs by the blunt gnathos and the basally narrow valves.

Distribution. Malawi, Republic of South Africa, Cameroon.

******Alucita chloracta* **(Meyrick, 1908)**

Orneodes chloracta Meyrick, 1908: 507. Type locality: Benin. Holotype: female, BMNH, examined by the authors.

Material examined. PlanteCam, 5 ex., (CUK, NECJU), 11–18.XII.2014; **Elephant Camp,** 18 ex., 19–24.XI.2014; **Bamboo Camp,** 7 ex., (CUK, NECJU), 17–23. IV.2015; **Drinking Gari,** 1 male, (CUK), 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the female genitalia, the shape of the bursa copulatrix and the round signum, resemble those of *A. entoprocta* (Hering, 1917), from which it differs by the wide ductus, the narrow antrum, and by the wings pattern.

Distribution. Benin, Cameroon.

**Alucita coffeina* (Viette, 1958)

Orneodes coffeina Viette, 1958: 457. Type locality: Oubangui-Chari, Boukoko, [Central African Republic]. Holotype: female, MNHN, examined by the authors.

Material examined. PlanteCam, 1 male, (CUK), 11–18.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The bright orange wings with dark, almost black bases and the large size (about 20 mm), are unique for this species. In the male genitalia, the blunt apex of the uncus and the narrow anellus arms, are close to *A. crococyma* (Meyrick, 1937), from which it differs by the short triangular valves, the narrow gnathos and the needle-like clusters of cornuti in the distal part of the phallus.

Distribution. Central African Republic, Cameroon.

Alucita megaphimus (Hering, 1917)

Orneodes megaphimus Hering, 1917: 191. Type locality: Cameroon. Holotype: male, ZMHB, examined by the authors.

Material examined. Bamboo Camp, 6 ex., (CUK, NECJU), 17–23.IV.2015; **PlanteCam**, 5 ex., (CUK, NECJU), 09–14.IV.2015; **Drinking Gari**, 3 ex., (CUK, NECJU), 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the mottled colour of the wings with zigzag white bands, the species is similar to *A. seychellensis* (Fletcher, 1910), but differs by the larger size and the elongated fore wings. In the male genitalia, it differs from *A. seychellensis* by the notch at the apex of the uncus, more narrow valves, and robust serrated saccular processes.

Distribution. Cameroon.

**Alucita spicifera* (Meyrick, 1911)

Orneodes spicifera Meyrick, 1911: 221. Type locality: Pretoria, Republic of South Africa. Holotype: male, TMSA, examined by the authors.

Material examined. PlanteCam, 1 male, (NECJU), 11–18.XII.2014, 4 males, (CUK, NECJU), 09–14.IV.2015; **Elephant Camp**, 7 males, (CUK, NECJU), 19–24.XI.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the male genitalia, the species is close to the Palaearctic species of *Alucita*. In particular, in its crown-shaped uncus, narrow membranous valves and long anellus arms, the species is similar to *A. cinnerethella* (Amsel, 1935), known from Iran, Turkey and Israel. However, it is distinctive in the shorter phallus, in the widened, almost round apex of the gnathos, and also in the wing colour.

Distribution. Republic of South Africa, Malawi, Tanzania, Cameroon.

Alucita zinovievi Kovtunovich & Ustjuzhanin, 2016

Alucita zinovievi Kovtunovich & Ustjuzhanin, 2016: 299. Type locality: PlanteCam, Moutn Cameroon, Cameroon. Type: male, ZISP, examined by the authors.

Material examined. PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), N4.1175000°, E9.0709440°, 11–18.XII.2014. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the male genitalia, the shape of the uncus, gnathos, and phallus, this species is similar to *A. aarviki* Ustjuzhanin & Kovtunovich, 2016. These species differ from each other by the wider valves, long anellus arms and cornuti. The new species is also distinctive in the wing colour: in *A. aarviki* the wings are yellow with white transverse bands, while in *A. zinovievi*, the wings are white with wide dark brown bands (Kovtunovich and Ustjuzhanin 2016).

Distribution. Cameroon.

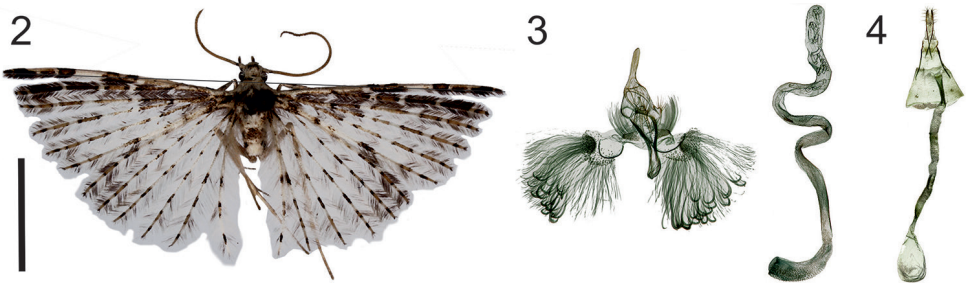
Alucita longipenis Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/0C5D41E9-38EE-4A7C-BB72-56855C9066D7
Figs 2–4

Type material. Holotype, male, (NECJU 201801) **CAMEROON**, **Elephant Camp**, 1850 m a.s.l., Mount Cameroon (SW slope), N4.11700°, E9.07292°, 19–24.XI.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 4 males, 2 females (NECJU, CUK) same data as holotype; 1 male (CUK), **PlanteCam**, 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the wings' colour and the male genital structure, the new species is unique, with no analogues among known African Alucitidae. The phallus length, disproportionate in relation to the entire genital structure, distinguishes this species from all the known species of this family.

External characters. Head with white spiky hairs, thorax, and tegula white with portions of brown strokes. Labial palpus thin, straight, 2 × longer than longitudinal eye diameter; brown on the outside, white on the inside. Third segment thin, narrow, tapered to apex. Antenna white, scape laterally thickened. Wingspan 18–23 mm, of holotype 22 mm. Wings white, with patches of brown strokes and spots. Small, dark brown rectangular spot in basal part of first lobe of fore wing. Larger, pale brown elongated spot with triangle cut in middle part of lobe. Alternating white, pale brown, and dark brown patches in the distal part of the first lobe. Apical part darkened with black scales. Dark brown elongated patches separated by narrow white bands on second lobe. Alternating brown and white elongated portions of scales on other four lobes of fore wing. Lobes of hind wing white, with patches of elongated brown strokes and spots. Fringe on wing pale, between first and second lobe of fore wing fringe with portions of dark brown scales. Abdomen white, with small spots of dark brown scales. Hind leg pale yellow.



Figures 2–4. *Alucita longipenis* Ustjuzhanin & Kovtunovich, sp. n. **2** Adult male, Holotype, NECJU **3** Male genitalia, Holotype, NECJU, preparation slide no. 201801 **4** Female genitalia, Paratype, NECJU, preparation slide no. 201810. Scale bar: 5 mm.

Male genitalia. Uncus long, equally wide along entire length. Gnathos longer than uncus, sharply thickened at end. Gnathos arms narrow, tapered to apices. Valva reduced, poorly expressed. Anellus arms long, narrow, slightly widened at apices. Saccus very long, elongated, smoothly curved in distal part. Phallus extremely long: 5 × longer than the entire genital structure, sharp arched bands in middle part, without cornuti.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses straight, thin, long. Anterior apophyses equal in length to posterior apophyses, but slightly thicker and undulated. Antrum narrow, tubulate, length almost equal to posterior apophyses. Ductus corrugated, thin, very long: 4 × longer than antrum. Bursa copulatrix small, oval, barely exceeds length of antrum, without signa.

Distribution. Cameroon.

Flight period. April, November.

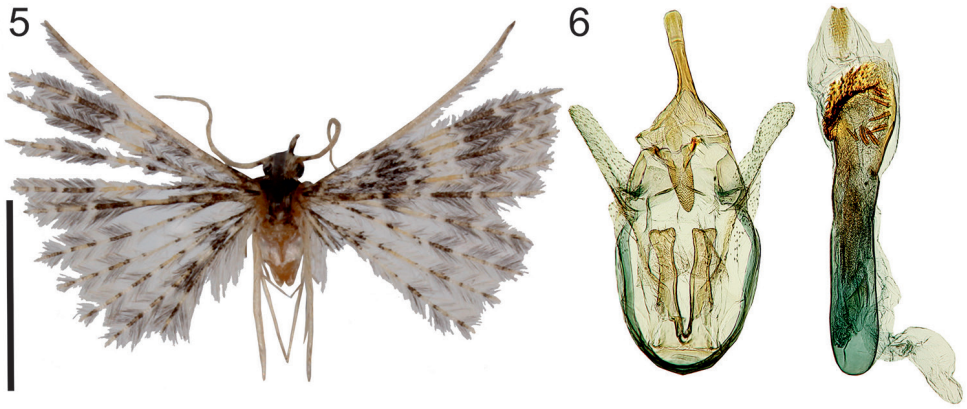
Etymology. The species is named after the morphological peculiarity of the phallus; the species name is a noun in apposition.

Alucita lidiya Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/0149F089-D5B7-47BD-BF49-B8A5FAF14FC1
Figs 5–6

Type material. Holotype, male, (NECJU 201802) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male (CUK), **Drinking Gari**, 11–23.IV.2015; 2 males (NECJU, CUK), **PlanteCam**, 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled pattern of the wings and position of the bands of the new species is similar to *A. chloracta* (Meyrick, 1908). These species differ from each other by the pale yellow median band in *A. lidiya*, while in *A. chloracta* the band is brown. *A. lidiya* has paler hind wings, without saturated dark grey portions of fringe, as in *A. chloracta.* Male genitalia of the new species also have some similarity to *A. chloracta*,



Figures 5–6. *Alucita lidiya* Ustjuzhanin & Kovtunovich, sp. n. **5** Adult male, Holotype, NECJU **6** Male genitalia, Holotype, NECJU, preparation slide no. 201802. Scale bar: 5 mm.

but there are significant differences in the shape of the narrow valva, the wide gnathos and the wide anellus arms of *A. lidiya*; while in *A. chloracta* the valva is significantly wider and rounded distally, the gnathos is thin, and the anellus arms are narrow.

External characters. Head, thorax and tegula with dark grey clinging hairs. Labial palpus dark grey, short, slightly longer than longitudinal eye diameter. Third segment thin, short, white, tapered to apex. Antenna pale grey. Wingspan 14–15 mm, of holotype 14 mm. Wing greyish brown. Base of fore and hind wing coloured with dark brown scales. Wide pale yellow band in median part, wide dark brown band in distal part of wing. Fringe on wing with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus quite long, narrow, slightly widened distally. Gnathos short, wide, shorter than uncus. Gnathos arms thin, undulate, widened to apices. Valva narrow, quite long, poorly sclerotised. Anellus arms long, wide, equal to valva in length. Phallus short, almost straight, group of various cornuti in the distal part: fine needle-shaped and large, with serrated edges.

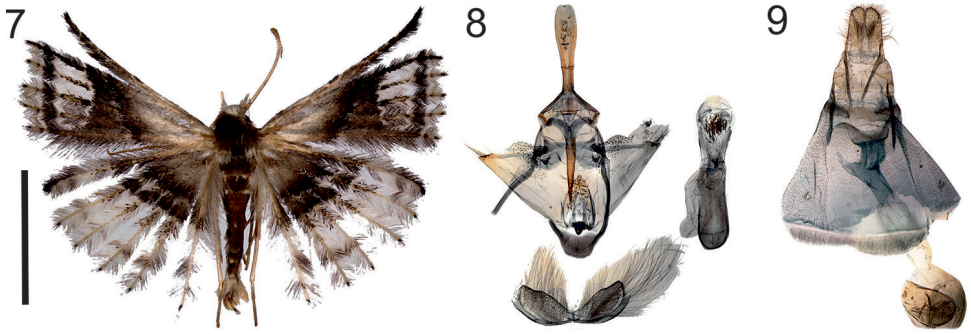
Distribution. Cameroon.

Flight period. April.

Etymology. The species name is a noun in apposition in honour of Lidiya Bezverkhova.

***Alucita ludmila* Ustjuzhanin & Kovtunovich, sp. n.**
http://zoobank.org/6B6DA5D1-494E-47E5-A362-9DB51258D5EC
Figs 7–9

Type material. Holotype, male, (NECJU 201803) **CAMEROON**, **Bamboo Camp** (350 m a.s.l.), Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015.



Figures 7–9. *Alucita ludmila* Ustjuzhanin & Kovtunovich, sp. n. **7** Adult male, Holotype, NECJU **8** Male genitalia, Holotype, NECJU, preparation slide no. 201803 **9** Female genitalia, Paratype, CUK, preparation slide no. 451. Scale bar: 5 mm.

V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male (NECJU), **Bamboo Camp,** 12–20.XII.2014; 1 male (CUK), **PlanteCam,** 11–18.XII.2014; 1 male (CUK), **Drinking Gari**, 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; 1 male (NHM), **NIGERIA**, **Forest Sapobc** (?), 17.IV.1976, M.A. Comes; 1 male (NHM), **NIGERIA**, **Gambari Forest**, Oyo State, 2.X.1976, M.A. Comes; 1 male (NHM), **NIGERIA**, **Gambari Forest**, Oyo State, 8.X.1977, J. Riley; 1 female (NHM), **NIGERIA**, **Port Harcourt**, Rivers, 2.VI.1958, B.J. MacNutly; 1 male (NHM), **NIGERIA**, Crin, 30.VII.1976, M.A. Comes; 1 female (CUK), **GHANA**, **Bunso Arboretum**, Eastern Region, 16–18.XI.2011, Sz. Sáfián, F. Pühringer.

Diagnosis. In the wing colour, this new species is unique among the African Alucitidae. In the male genitalia structure, the wing-shaped valva and shape of the phallus are similar to *A. aarviki* Ustjuzhanin & Kovtunovich, 2016, but it differs from that by the shape of the uncus, the tapered apices of the valva, the narrow arms of the anellus and the cluster of needle-shaped cornuti in the distal part of the phallus.

External characters. Head, thorax, and tegula with greyish white clinging hairs. Labial palpus greyish white, almost 2 × longer than longitudinal eye diameter. Third segment thin, short, white, tapered to apex. Antenna pale brown. Wingspan 16–23mm, of holotype 17 mm. Wing colour greyish white. Base of wing pale grey, wide brownish grey band in median part. Well pronounced pale elongated patch, framed by dark brown band in distal part. Portions of dark brown hairs in distal part of hind wing. Fringe on wing with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus long, paddle-like, with even edge of apex. Gnathos longer than uncus, narrow, tapered to apex. Gnathos arms short, wide. Valva wing-like, triangle, long needle-shaped bristles in apical part. Anellus arms short, narrow. Saccus short, with even outer edge. Phallus quite short, almost straight, cluster of small needle-shaped cornuti in distal part.

Female genitalia. Papilla analis wide, elongated. Posterior apophyses straight, short, slightly longer than the papilla analis. Anterior apophyses thicker than posterior ones, equal to them in length. Ostium wide, cupped. Antrum tubulate, short, wide,

sclerotised, almost equal to length of posterior apophyses. Ductus wide at confluence to antrum, twice as wide as antrum, ductus seminalis short. Bursa copulatrix round, without signa.

Distribution. Cameroon, Nigeria, Ghana.

Flight period. From April to December.

Etymology. The species name is a noun in apposition in honour of the first author's wife, Ludmila Ustjuzhanina.

***Alucita escobari* Ustjuzhanin & Kovtunovich, sp. n.**
http://zoobank.org/D1CF050D-CB13-4283-87C2-5DE4D082E730
Figs 10–12

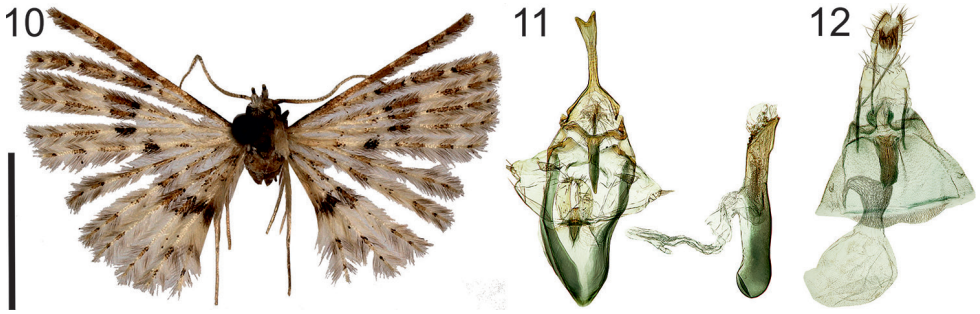
Type material. Holotype, male, (NECJU 201804) **CAMEROON**, PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), N4.11750°, E9.07094°, 11–18.XII. 2014. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 female (CUK), same data as holotype; 2 males (NECJU, CUK), **Bamboo Camp,** 12–20.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour and the median arched band on the wings of the new species is similar to *A. mischenini*. The new species is distinguished by the brown spot of scales on the sixth lobe of the fore wing, declining from the correct arc and shifting towards the basal part of the lobe. In the male genital structure, the uncus with the apical triangle cut and the phallus obliquely cut at apex of the new species are similar to *A. balioxantha* Meyrick, 1921. These species differ from each other by the valva in the shape of a wide-triangle valva, the elongated saccus, and the tapered gnathos in *A. escobari*.

External characters. Head with white spiky hairs, thorax, and tegula white. Labial palpus quite wide, short, 1.5 × longer than longitudinal eye diameter, slightly bent upwards, painted with brown scales inside and outside. Third segment short, white on apex. Antenna yellowish brown, scape thickened. Wingspan 14–16 mm, of holotype 15.5 mm. Wing yellowish brown. Transverse brown arched band well expressed in median part of both wings. On sixth lobe of fore wing, patch of scales declining from correct arc and shifting towards basal part of lobe. Wing base pale, interspersed with small brown scales. Alternating brown and white elongated portions of scales in distal part of fore wing. Fringe on wing yellow with rare portions of brown hairs. Hind leg yellow.

Male genitalia. Uncus long, widened distally, triangle cut apically. Gnathos slightly shorter than uncus, thick, tapered to apex. Gnathos arms short, thick, smoothly bent inwards. Valva short, wide-triangle, apically with bunch of thin needle-shaped bristles. Anellus arms wide, slightly shorter than gnathos, slightly bent inwards, narrowed apically. Saccus elongated, narrow-triangle, sharp outer edge. Phallus almost straight, apex obliquely cut, small needle-shaped cornuti medially and distally.

Female genitalia. Papilla analis narrow, triangle. Posterior apophyses straight, long, thin. Anterior apophyses thicker than posterior, equal to them in length. An-



Figures 10–12. *Alucita escobari* Ustjuzhanin & Kovtunovich, sp. n. **10** Adult male, Holotype, NECJU **11** Male genitalia, Holotype, NECJU, preparation slide no. 201804 **12** Female genitalia, Paratype, CUK, preparation slide no. 452. Scale bar: 5 mm.

trum tubulate, sclerotised, length equal to posterior apophyses. Ductus wide at confluence with antrum, twice as wide as antrum, ductus seminalis short. Bursa copulatrix round, without signa.

Distribution. Cameroon.

Flight period. December.

Etymology. The authors name the species in recognition of Francis Luma Ewome, locally well known as 'Escobar', a very well trained guide on Mount Cameroon. Over the years, he became instrumental in organising and implementing the field expeditions, and also became a good friend to the last three authors of this paper. It could be stated that the research would have been extremely difficult without the selfless help of Escobar.

Alucita mischenini Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/ACC44B4D-76B6-4364-86CB-90BA6665C3B6
Figs 13–14

Type material. Holotype, male, (NECJU 201805) **CAMEROON**, **Bimbia-Bonadikombo**, 30 m a.s.l., Mexico Camp, Bimbia-Bonadikombo Community Forest, N3.98183°, E9.26250°, 07–12.V.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes:** 2 males (NECJU, CUK), **PlanteCam**, 11–18.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour and the transverse arched band on the wings of *A. mischenini* are similar to *A. escobari*. These species differ from each other by the brown spot of scales on the sixth lobe of the fore wing, declining from the arc to the distal part of the lobe. In the male genital structure, the shape of the valva and the phallus is also similar to *A. escobari*. These species differ from each other by the shape of the uncus, the longer gnathos, the saccus wide in the base, and narrower, longer anellus arms in *A. mischenini*.

External characters. Head, thorax and tegula with white clinging scales. Labial palpus short, 1.5 × longer than longitudinal eye diameter, directed forward, white on

Figures 13–14. *Alucita mischenini* Ustjuzhanin & Kovtunovich, sp. n. **13** Adult male, Holotype, NECJU **14** Male genitalia, Holotype, NECJU, preparation slide no. 201805. Scale bar: 5 mm.

inside, coloured with small brown scales on outside. Third segment short, middle part framed in narrow brown band, apex tapered. Antenna yellow. Wingspan 12–15 mm, of holotype 12 mm. Wing mottled, median transverse band of brown elongated spots of scales developed on first five lobes of fore wing. Similar spot on sixth lobe, declining from band and shifted to distal part of lobe. Median transverse band on hind wing forms correct arc. Small dark brown scales in basal part of fore and hind wing. Alternating portions of brown and yellow scales in distal part. Fringe on wing yellow, with alternating rare portions of brown hairs. Hind leg white.

Male genitalia. Uncus long, basally narrow, distally wide, with poorly expressed cut at apex. Gnathos significantly longer than uncus, narrow, tapered to apex. Gnathos arms short, thick, smoothly bent inwards. Median process between gnathos arms well developed. Valva wing-like, short, wide. Anellus arms long, slightly shorter and noticeably wider than gnathos. Saccus short, basally wide, small oval cut on outer edge. Phallus short, slightly bent in middle, distally with small needle-shaped cornuti.

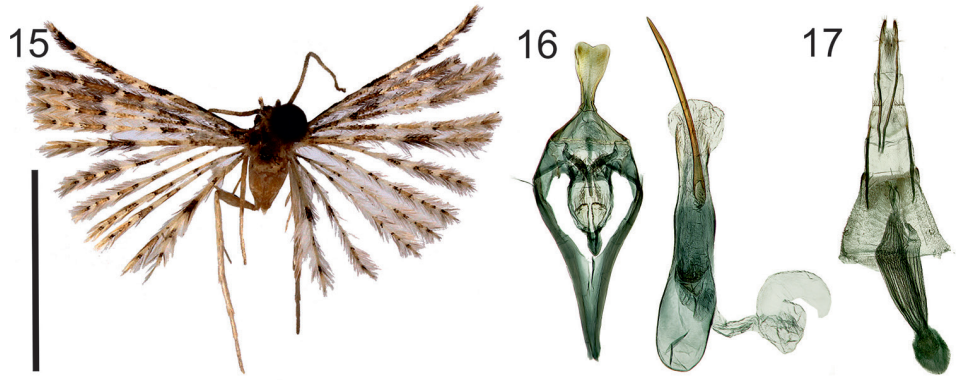
Distribution. Cameroon.

Flight period. May, December.

Etymology. The species is named after the Novosibirsk biologist and naturalist Sergei Ivanovich Mischenin.

***Alucita fokami* Ustjuzhanin & Kovtunovich, sp. n.**
http://zoobank.org/A61D9EE8-F9A8-4A57-97AA-F21CAC659328
Figs 15–17

Type material. Holotype, male, (NECJU 201806) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 female (NECJU), same data



Figures 15–17. *Alucita fokami* Ustjuzhanin & Kovtunovich, sp. n. **15** Adult male, Holotype, NECJU **16** Male genitalia, Holotype, NECJU, preparation slide no. 201806 **17** Female genitalia, Paratype, NECJU, preparation slide no. 201811. Scale bar: 5 mm.

as holotype; 1 male (CUK), **PlanteCam,** 11–18.XII. 2014; 2 males, 1 female (NECJU, CUK), **Drinking Gari,** 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour of the wings and the median arched band on the fore wing in *A. fokami*. is similar to *A. escobari*. *A. fokami* is characterised by the absence of such a band on the hind wings and by the base of the wings darkened with brown scales. In the male genitalia, the absence of the valva in the new species is similar to *A. janeceki.* These species differ from each other by the long needle-shaped cornutus, narrow elongated saccus, and the shape of the uncus in *A. fokami.*

External characters. Head with pale yellow spiky hairs, thorax and tegula pale brown. Labial palpus yellow-brown, 1.5 × longer than eye diameter. Antenna yellow. Wingspan 12–13 mm, of holotype 12 mm. Wing yellowish brown with three white transverse bands. Wing base darkened with brown scales. Fringe on wing yellow. Hind leg white.

Male genitalia. Uncus basally narrow, distally wide, apex with small oval cut. Gnathos short, 3 × smaller than uncus, narrow, slightly tapered to apex. Gnathos arms thick, long, undulate, apically tapered. Median process between gnathos arms well developed. No valva. Anellus arms very short, in shape of wide lobes, equal to gnathos in length. Saccus narrow, elongated, exceeds length of uncus with tegumen. Phallus short, almost straight, distally with long needle-shaped cornutus exceeding total length of phallus.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses very long, slightly undulated. Anterior apophyses straight, long, slightly shorter than posterior apophyses. Antrum narrow, short. Ductus long, corrugated, with well-expressed longitudinal cords. Ductus narrow at confluence to bursa copulatrix. Ductus seminalis short, wide. Bursa copulatrix oval, small, equal to papilla analis, without signa.

Distribution. Cameroon.

Flight period. April, December.

Etymology. The authors name this species in recognition of Dr. Eric Bertrand Fokam, the current head of the Department of Zoology and Animal Physiology, Uni-

versity of Buea. Eric is a renowned ecologist and a keen field scientist. He has not only been an active collaborator during the field research on Mount Cameroon, but has also brought up a new generation of young Cameroonians to continue the scientific work on insects and other animal groups in Cameroon.

***Alucita janeceki* Ustjuzhanin & Kovtunovich, sp. n.**
http://zoobank.org/2753F767-627A-4882-B138-E8DB95800AE7
Figs 18–20

Type material. Holotype, male, (NECJU 201807) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male, 1 female (NECJU, CUK), same data as holotype; 1 male (CUK), **Drinking Gari,** 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The wings colour and the absence of the valva in the male genitalia of the new species is similar to *A. fokami*. In the male genitalia, *A. janeceki* is characterised by the oval saccus, the long uncus slightly tapered to apex, the long and wide phallus without a large needle-shaped cornutus. In the female genitalia, the new species is characterised by the oval bursa copulatrix with the ductus seminalis inside, and by the very long posterior apophyses.

External characters. Head, thorax and tegula yellowish white, interspersed with fine brown scales. Labial palpus white, 2 × longer than eye diameter, slightly bent upwards. Third segment thin, tapered to apex. Antenna pale brown. Wingspan 10–12 mm, of holotype 12 mm. Wing greyish white. Wing base darkened with brown scales. Well expressed elongated brown strokes separated by yellowish portions on first lobe. Apical part of lobe brown, sharp. Second and other lobes repeat the pattern of first but with less contrast. Fringe on wing with alternating pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus very long, distally wide, apically slightly tapered. Gnathos not expressed. Valva reduced. Anellus arms straight, wide, twice as short as uncus. Saccus oval. Phallus long and wide, 1.5 × longer than uncus, almost straight, medially and distally with clusters of small spiny cornuti.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses very long, thin. Anterior apophyses straight, very long, equal to posterior apophyses. Antrum short, V-shaped. Ductus wide, corrugated, with longitudinal cords and clusters of small signa. Ductus seminalis inside bursa copulatrix, long, distally widened. Bursa copulatrix big, oval, with impregnation of small spiny signa.

Distribution. Cameroon.

Flight period. April.

Etymology. The species is named after Dr. Štěpán Janeček, an experienced botanist who accompanied all our field expeditions and crucially helped us with many things, including the collection of a substantial part of the presented specimens.

Figures 18–20. *Alucita janeceki* Ustjuzhanin & Kovtunovich, sp. n. **18** Adult male, Holotype, NECJU **19** Male genitalia, Holotype, NECJU, preparation slide no. 201807 **20** Female genitalia, Paratype, CUK, preparation slide no. 453. Scale bar: 5 mm.

Alucita besongi Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/2753F767-627A-4882-B138-E8DB95800AE7
Figs 21–23

Type material. Holotype, male, (NECJU 201808) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 2 females (NECJU, CUK), same data as holotype.

Diagnosis. The yellowish brown wings and the small size of the new species are similar to *A. certifica* Meyrick, 1909. These species differ from each other by the absence of the wide pale-brown band in the median portion of the fore wing in *A. besongi*. In the male genitalia, the shape of the uncus and the gnathos of the new species have some similarities to those of *A. acalyptra* Meyrick, 1913; these species differ from each other by the elongated saccus, the peculiar shape of the valva and the phallus with large needle-shaped cornuti in *A. besongi*.

External characters. Head, thorax, and tegula with white clinging scales. Labial palpus white, interspersed with small brown scales, 2 × longer than longitudinal eye diameter, bent upwards. Third segment thin, framed with narrow brown band at base. Antenna yellow. Wingspan 8–10 mm, of holotype 9 mm. Wing yellowish brown. Wing base interspersed with small brown scales. White longitudinal strokes separated by pale brown portions well expressed on first lobe. Poorly noticeable series of white bands from wing base to apical area. Fringe on wing yellowish brown. Hind leg pale yellow.

Male genitalia. Uncus long, distally wide, apically slightly tapered. Gnathos narrow, long, tapered to apex. Valva basally wide, then smoothly narrowing. Anellus arms straight, long. Saccus elongated, oval. Phallus thick, long, almost twice as long as entire genital structure, with cluster of large spiny cornuti.

Figures 21–23. *Alucita besongi* Ustjuzhanin & Kovtunovich, sp. n. **21** Adult male, Holotype, NECJU. **22** Male genitalia, Holotype, NECJU, preparation slide no. 201808. **23** Female genitalia, Paratype, NECJU, preparation slide no. 201812. Scale bar: 5 mm.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses long, thin. Anterior apophyses straight, equal to posterior apophyses. Antrum short, V-shaped. Ductus short, corrugated, with longitudinal cords, smoothly turning into bursa copulatrix. Ductus seminalis inside bursa copulatrix. Bursa big, oval, with long ribbon-like signa and impregnation of small spiny signa.

Distribution. Cameroon.

Flight period. April.

Etymology. The species is named after Simon B. Besong, the current main conservator of the Mount Cameroon National Park, who helped our research by various means of support.

***Alucita olga* Ustjuzhanin & Kovtunovich, sp. n.**
http://zoobank.org/461C9B8A-5BF5-46B9-9A1A-CB04F656358A
Figs 24–26

Type material. Holotype, male, (NECJU 201809) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17.-23.IV.2015. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male, 2 females (NECJU, CUK), same data as holotype; 1 male (CUK), **PlanteCam,** 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled yellowish brown wings of the new species have some similarity to *A. lidiya*, but these species differ from each other by the narrow medial band and the dark-brown spots in the apical parts of the lobes in *A. olga*. In the male genitalia, the shapes of the uncus, saccus and phallus of *A. olga* are similar to *A. spicifera* Meyrick, 1911. These species differ from each other by the wide, oval gnathos and the short valva not widened distally, in *A. olga*, and by the gnathos and valva widened at the apices in *A. spicifera*.

Figures 24–26. *Alucita olga* Ustjuzhanin & Kovtunovich, sp. n. **24** Adult male, Holotype, NECJU **25** Male genitalia, Holotype, NECJU, preparation slide no. 201809 **26** Female genitalia, Paratype, NECJU, preparation slide no. 201813. Scale bar: 5 mm.

External characters. Head, thorax and tegula with brown-yellow clinging scales. Labial palpus spotty, with alternating white and black scales, 2 × longer than longitudinal eye diameter, bent upwards. Third segment long, thin, tapered to apex. Antenna yellow, interspersed with dark brown scales. Wingspan 10–11 mm, of holotype 11 mm. Wing mottled, yellowish brown. Wing base coloured with dark brown scales. First lobe of fore wing with well-expressed orange elongated spots, alternating with dark brown elongated spots separated by white bands. Alternation of orange and dark brown spots on other lobes of both wings. Apical area of all lobes ends with dark brown spot. Fringe on wing yellowish brown, with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus medially narrow, distally widened, apex with four claw-like processes forming a kind of rake. Gnathos wide, oval. Gnathos arms straight, narrow, apically tapered. Valva quite wide, short, membranous, poorly sclerotised. Anellus arms long, wide. Saccus slightly elongated, oval. Phallus narrow, elongated, longer than entire genital structure, with one well-expressed narrow long cornutus and cluster of small needle-shaped cornuti distally.

Female genitalia. Papilla analis elongated, narrow triangle. Posterior apophyses thin, straight. Anterior apophyses thin, slightly longer than posterior apophyses. Antrum wide, funnel-shaped, sclerotised. Ductus wide, short, narrow at confluence to bursa copulatrix. Ductus seminalis short, wide. Bursa copulatrix big, oval, with two narrow longitudinal ribbon-like signa, impregnation of many small spines inside the whole bursa.

Distribution. Cameroon.

Flight period. April.

Etymology. The species name is a noun in apposition in honour of Olga Birichevskaya.

Discussion

Our report, although covering just the first part of the sampled material, has revealed that the Mount Cameroon area is the richest known locality for Alucitidae in the whole Afrotropical Region. To the best of our knowledge, maximally only a few species are

known from elsewhere in the region; they are met extremely rarely and very locally in other biogeographic areas as well. Partly, this is an artefact of incomplete sampling and relatively less attention to the group during many biodiversity surveys. On the other hand, Alucitidae were specifically focused by various lepidopterists in many places in the Afrotropics in the recent years, never resulting in such rich local biodiversity. By its 15 reported species, Mount Cameroon outnumbers all the other localities in biodiversity of many-plumed moths. The Mount Cameroon area is known to host an exceptional diversity of some other groups of organisms, including Lepidoptera (Ballesteros-Mejia et al. 2013, Maicher et al. 2016, Ferenc et al. in press). Its tremendous biodiversity is considered to be the result of its location on the border between the West African Forests and the Congolese Basin, combining species pools of both these species-rich regions, together with its own endemics (Myers et al. 2000, Maicher et al. 2016). Moreover, its complete altitudinal forest gradient from seashore to timberline comprises a few steep gradients of environmental conditions known to support high species richness.

Our results have also highlighted the poor knowledge of Lepidoptera of the studied region, despite its high importance for biodiversity and its conservation. This paper increased the known Cameroonian fauna of Alucitidae from three (De Prins and De Prins 2018) to 16 species. The nine new species of *Alucita* described in this study can be supplemented by numerous recent descriptions of new species from various lepidopteran groups (e.g., Przybyłowicz 2013, Yakovlev and Sáfián 2016, Sáfián and Tropek 2016). Moreover, our lack of knowledge is further evidenced by the faunistic importance of some of our findings. Three species reported as new for the country had their nearest known localities thousands of kilometers away, in different biogeographic regions. A comparable pattern has already been reported in Erebidae by Maicher et al. (2016). It is highly unlikely that Mount Cameroon would be a refugium for so many species of Lepidoptera occurring in different Afrotropical areas. We thus rather hypothesise that at least some of the mentioned species have a more continuous distribution area, but are just insufficiently explored.

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Supplementary material 1

Table of localities

Authors: Peter Ustjuzhanin, Vasily Kovtunovich, Szabolcs Sáfián, Vincent Maicher, Robert Tropek

Data type: occurence

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RESEARCH ARTICLE

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Cryptic species diversity in the *Hypsolebias magnificus* complex, a clade of endangered seasonal killifishes from the São Francisco River basin, Brazilian Caatinga (Cyprinodontiformes, Aplocheilidae)

Wilson J. E. M. Costa[1], Pedro F. Amorim[1], José Leonardo O. Mattos[1]

1 *Laboratory of Systematics and Evolution of Teleost Fishes, Institute of Biology, Federal University of Rio de Janeiro, Caixa Postal 68049, CEP 21941-971, Rio de Janeiro, Brazil*

Corresponding author: *Wilson J. E. M. Costa* (wcosta@acd.ufrj.br)

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Abstract

A great diversity of animal species adapted to life in the semi-arid Caatinga of northeastern Brazil, including seasonal killifishes, has been reported in the last three decades. More recently, field and molecular data have shown a high occurrence of cryptic species. The killifish group herein analysed, the *Hypsolebias magnificus* species complex, is endemic to the middle and southern portion of the Caatinga, occupying about 120 km along the floodplains of the middle São Francisco River and some adjacent tributaries. Species of this complex are rare and presently considered threatened with extinction, being uniquely found in pools protected by trees and bushes. Single-locus delimitation methods were used to test species limits of populations displaying different colour patterns along the whole distribution of the complex. All analyses consistently supported the three nominal species and two new, herein described: *H. gardneri* Costa, **sp. n.**, from the floodplains of the middle São Francisco River and *H. hamadryades* Costa, **sp. n.**, from the Gorotuba River floodplains. The phylogenetic analysis highly supports *H. hamadryades* as sister to a clade comprising *H. gardneri* and *H. harmonicus*. Our field observations suggest that *H. hamadryades* is a miniature species. This study indicates that the *H. magnificus* complex comprises cryptic species apparently endemic to small areas and extremely vulnerable to environmental changes, deserving high concern.

Keywords

Biodiversity, conservation, molecular taxonomy, species delimitation, systematics

Introduction

Recent studies on the fauna of the Caatinga, a biogeographical province of northeastern Brazil, have revealed a high diversity of species adapted to survive in semi-arid conditions, including small terrestrial vertebrates (Rodrigues 2003; Nascimento et al. 2013; Werneck et al. 2015) and seasonal killifishes (Costa 2001; Rosa et al. 2003; Costa et al. 2012, 2018). Seasonal killifishes live in temporary pools formed at rainy seasons, where they complete their entire life cycle, surviving as resistant eggs during dry periods (Wourms 1972; Costa 1995). In the Caatinga, pools disappear during a long dry season, frequently between May and October in most of the southern and central part of the Caatinga, which concentrates the great diversity of seasonal killifish species, but a short dry period may also occur between January end and February, with most pools drying again (Costa 2017).

Hypsolebias Costa, 2006 is the most species rich and morphologically diverse seasonal killifish genus in the Caatinga, where it is represented by two clades highly supported by morphological and molecular data (Costa 2006; Costa et al. 2017), the *H. antenori* group (Costa 2007; Costa et al. 2014, 2018) and the *H. magnificus* group (Costa 2007). Among species of this clade is *H. magnificus* (Costa & Brasil, 1991) and two closely related species, *H. picturatus* (Costa, 2000) and *H. harmonicus* (Costa, 2010) (Costa 2007, 2010), which together form a species complex, herein called the *H. magnificus* complex (hereafter HMC), distinguished from all other congeners by the presence of a narrow black margin on unpaired fins and pectoral fin in males (vs. black margin absent) and unpaired fins rounded or slightly pointed (vs. sharply pointed) (Costa 2010). Like other closely related congeners, HMC species live only in shadowed parts of the pools, protected by dense concentration of shrubs and trees (pers. obs. 1994–2018).

The first species of HMC to be described was *H. magnificus*, collected in the São Francisco River floodplains near the village of Mocambinho (Costa and Brasil 1991). With the discovery of *H. picturatus* and more frequent field studies between 1999 and 2005, the distribution of the complex was amplified to include records about 420 km N from the type locality of *H. magnificus* (Costa, 2007). During field studies between 2005 and 2010, a strong decline of natural habitats was progressively recorded, resulting in extinction of several populations of seasonal killifishes (Costa et al. 2012; Costa 2017). During this same period, a third species, *H. harmonicus*, was recognised and described (Costa 2010). However, the identity of two populations remained dubious. The first one, sharing a similar colour pattern with *H. harmonicus*, was collected in 2010 only about 40 km from the type locality of this species. The second one was tentatively identified as *H. magnificus* (Costa, 2017), but collected about 120 km from its type locality, at the upper Rio Gorotuba floodplains in 2017. However, fish from both populations exhibited a few distinct morphological characters suggesting that they are cryptic species (sense Bickford et al. 2006). Herein we analyse a segment of the mitochondrial gene cytochrome b for representatives of all nominal species of HMC and the two putative cryptic species, under different single-locus methods of species delineation in order of to provide a more accurate picture about species diversity in the complex.

Material and methods

Specimens were captured with small dip nets (40 × 30 cm) and were euthanized soon after collection, using a buffered solution of tricaine methanesulfonate (MS-222) at a concentration of 250 mg/l, for a period of about 10 minutes (i.e. until opercular movements ceased). Representative live specimens were kept alive for about 24 hours, photographed, and then euthanized as described above. Specimens were fixed in 10 % formalin for a period of 10 days, and then transferred to 70 % ethanol, except for those used in the molecular analysis, fixed and preserved in 98 % ethanol. Collections were made with permits provided by ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade; permit numbers: 34270-4, 20618-1, 57099-1) and methods for euthanasia were approved by CEUA-CCS-UFRJ (Ethics Committee for Animal Use of Federal University of Rio de Janeiro; permit number: 01200.001568/2013-87). Material is deposited in the ichthyological collections of: Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ) and Centro de Ciências Agrárias e Ambientais, Universidade Federal do Maranhão, Chapadinha (CICCAA). In lists of material, the abbreviation C&S indicates specimens prepared for osteological analysis and preserved in glycerine (see below), and DNA indicates specimens fixed and preserved in 98% ethanol. List of specimens used in the molecular analysis and their respective GenBank accession numbers appears in Table 1.

Descriptions of colouration in living fish were based on photographs of both sides of individuals. Photographs of at least two males and two females were taken in small aquaria about 24 hours after collection. Additional direct observations were made with fish in small transparent plastic bottles just after collection. Measurements and counts follow Costa (1988). Measurements are presented as percentages of standard length (SL), except for those related to head morphology, which are expressed as percentages of head length. Measurements were made only in well preserved adult specimens; juvenile specimens (less than 20 mm SL) and specimens presenting deformities were not measured. Fin-ray counts include all elements. At least four specimens, two males and two males, were cleared and stained for osteological analysis using Taylor and Van Dyke's (1985) protocol. Terminology for osteological structures followed Costa (2006), for frontal squamation Hoedeman (1958), and for cephalic neuromast series Costa (2001). Osteological characters used in species descriptions are those that show informative variability in *Hypsolebias* (e.g., Costa 2006).

Total genomic DNA was extracted from muscle tissue of the right side of the caudal peduncle using the DNeasy Blood & Tissue Kit (Qiagen) according to the manufacturer instructions. To amplify a fragment of the mitochondrial DNA gene cytochrome b (cytb), we used the primers L14724 and H15149 (Kocher et al. 1989; Meyer et al. 1990). Polymerase chain reaction (PCR) was performed in 15 µl reaction mixtures containing 5× Green GoTaq Reaction Buffer (Promega), 3.2 mM $MgCl_2$, 1 µM of each primer, 75 ng of total genomic DNA, 0.2 mM of each dNTP and 1 U of Taq polymerase. The thermocycling profile was: (1) 1 cycle of 4 minutes at 94 °C; (2) 35 cycles of

Table 1. List of specimens used in the molecular analysis, with their respective catalogue numbers, coordinates of the collecting site, and GenBank accession numbers for cytb sequences.

Species	Catalogue number	Coordinates	Cytb
Hypsolebias carlettoi	UFRJ 6780.2	14°13'42"S, 42°55'12"W	MH048856
Hypsolebias fulminantis	UFRJ 6726.1	14°12'21"S, 42°45'42"W	MH048854
Hypsolebias gardneri	UFRJ 6796.1	14°17'39"S, 43°42'32"W	MH048861
Hypsolebias gardneri	UFRJ 6796.3	14°17'39"S, 43°42'32"W	MH048862
Hypsolebias gardneri	UFRJ 6796.4	14°17'39"S, 43°42'32"W	MH048863
Hypsolebias hamadryades	UFRJ 11473.1	15°48'06"S, 43°19'19"W	MH048860
Hypsolebias hamadryades	UFRJ 11473.2	15°48'06"S, 43°19'19"W	MH048859
Hypsolebias hamadryades	UFRJ 11473.3	15°48'06"S, 43°19'19"W	MH048858
Hypsolebias hamadryades	UFRJ 11473.4	15°48'06"S, 43°19'19"W	MH048857
Hypsolebias harmonicus	UFRJ 6705.3	13°15'42"S, 43°31'00"W	MH048864
Hypsolebias harmonicus	UFRJ 6705.4	13°15'42"S, 43°31'00"W	MH048865
Hypsolebias hellneri	UFRJ 6700.2	15°04'50"S, 44°04'40"W	MH048855
Hypsolebias magnificus	UFRJ 6712.1	14°55'20"S, 43°29'56"W	MH048866
Hypsolebias magnificus	UFRJ 6712.2	14°55'20"S, 43°29'56"W	MH048867
Hypsolebias picturatus	UFRJ 6708.1	11°28'03"S, 43°17'10"W	MH048868

1 minute at 92 °C, 1 minute at 44–54 °C and 1 minute at 72 °C; and (3) 1 cycle of 4 minutes at 72 °C. In all PCR reactions, negative controls without DNA were used to check for contaminations. Amplified PCR products were purified using the Wizard SV Gel and PCR Clean-Up System (Promega). Sequencing reactions were made using the BigDye Terminator Cycle Sequencing Mix (Applied Biosystems). Cycle sequencing reactions were performed in 10 µl reaction volumes containing 1 µl BigDye 2.5, 1.55 µl 5× sequencing buffer (Applied Biosystems), 2 µl of the amplified products (10–40ng), and 2 µl primer. The thermocycling profile was: (1) 35 cycles of 10 seconds at 96 °C, 5 seconds at 54 °C and 4 minutes at 60 °C. The sequencing reactions were purified and denatured and the samples were run on an ABI 3130 Genetic Analyzer. Sequences were edited using MEGA 6 (Tamura et al. 2013) and aligned using ClustalW (Chenna et al. 2003); alignments were subsequently translated into amino acids residues to check premature stop codons or indels. List of specimens used in the molecular analysis and their respective GenBank accession numbers appear in Table 1.

Analyses were performed with a cytb fragment (463 bp), which has been efficiently used for delimitating cryptic species of different aplocheiloid killifish groups (Sonnenberg et al. 2006; Sonnenberg 2007; Van der Zee and Sonnenberg 2011; Costa et al. 2012, 2014; Agnèse et al. 2013). Terminal taxa were 12 specimens of five populations representing all nominal species of the HMC; out-groups comprised *H. carlettoi* (Costa & Nielsen, 2004) and *H. fulminantis* (Costa & Brasil, 1993), two species closely related to HMC (Costa 2006; Costa et al. 2017), and *H. hellneri* (Berkekamp, 1993), which was sister to all other members of the *H. magnificus* group (Costa 2006; Costa et al. 2017), was used to root the phylogeny. The best-fit model of sequence

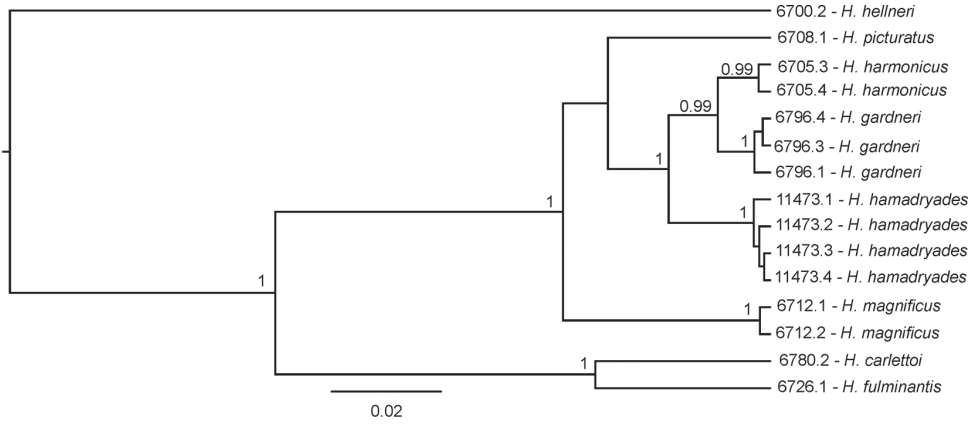

Figure 1. Bayesian phylogeny used to delimit species of the *Hypsolebias magnificus* complex inferred by using sequences of the mitochondrial gene cytochrome b, 463 bp. Numbers above nodes are posterior probability values above 95 %; numbers before species names are catalogue numbers for specimens.

evolution was calculated by jModelTest 2.1.7 (Darriba et al. 2012), which indicated the general-time reversible model with a gamma frequency distribution of categories among sites (GTR + G). We inferred tree topology using Bayesian reconstruction performed with BEAST v.1.8 (Drummond et al. 2012), using an uncorrelated relaxed lognormal model and other parameters set as default; the MCMC length was 30,000,000 runs with sampling every 1000 runs. The quality of the MCMC chains was evaluated in Tracer 1.5 (Rambaut et al. 2013); a 25% burn-in was removed and the final tree was obtained using TreeAnnotator v.1.5 from BEAST v.1.8 package; support values of the Bayesian inference (BI) analysis were calculated by posterior probability. The following single-locus models for species delimitation were used: the Generalized Mixed Yule-Coalescent (GMYC) (Fujisawa and Barraclough 2013), independently applying both single and multiple-threshold, and the Bayesian implementation of Poisson Tree Process (bPTP) (Zhang et al. 2013), with 500,000 Markov chain Monte Carlo (MCMC) generations, thinning set to 100 and a burn-in of 25% initial samples, checking both Maximum likelihood and Bayesian solutions. All analyses were carried on the Exelixis Lab's web server (GMYC at http://species.h-its.org/gmyc/; bPTP at http://species.h-its.org/ptp/).

Results

BEAST analysis generated a tree with most branches supported by high posterior probability values (0.99–1; Fig. 1). All methods of species delimitation yielded identical results, supporting a total of five species within the HMC, including two new species below described. Both new species appear as closely related to *H. harmonicus* in a well-supported clade.

Taxonomic accounts

***Hypsolebias gardneri* Costa, sp. n.**
http://zoobank.org/1924252C-19C9-42B2-B502-9F2BF8C5867F
Figure 2, Table 2

Material examined. Holotype. UFRJ 11859, male, 36.9 mm SL; Brazil: Bahia state: Malhada municipality: temporary pool near road BR-030, about 8 km NE of the village of Malhada, São Francisco River floodplains, 14°17'39"S, 43°42'32"W, altitude about 440 m above sea level (a.s.l.); W. J. E. M. Costa et al., 31 January 2010. **Paratypes.** UFRJ 6797, 3 males, 29.7–36.1 mm SL, 2 females, 27.9–30.0 mm SL; UFRJ 11860, 2 males, 30.6–33.0 mm SL, 2 females, 26.6–27.9 mm SL (C&S); UFRJ 6796, 3 males, 32.6–36.8 mm SL, 4 females, 26.5 – 29.3 mm SL (DNA); CICCAA02038, 2 males, 32.9–33.6 mm SL; all collected with holotype.

Diagnosis. *Hypsolebias gardneri* differs from all other species of the *H. magnificus* complex, except *H. harmonicus*, by the following combination of character states relative to the male colour pattern: anterior part of the flank with three dark greenish grey bars (vs. dark greenish grey bars absent in *H. hamadryades*); dorsal fin with transverse blue stripes and one basal row of blue dots (vs. rows of blue dots on the whole fin in *H. picturatus*); anal fin with dots and short vermiculate marks irregularly arranged on the anterior part of the fin (vs. dots on the entire fin in *H. picturatus*, and transverse blue stripes on most fin in *H. magnificus* and *H. hamadryades*); and anterior half of caudal fin with transverse rows of blue dots, posterior half with transverse blue bars (vs. blue bars on most fin in *H. magnificus* and dots on the entire fin in *H. picturatus*). *Hypsolebias gardneri* is distinguished from *H. harmonicus* by having the caudal fin with 23 or 24 rays, subtruncate and longer in males, measuring 34.5–36.4% SL (vs. with 22 or 22 rays, round, measuring 31.2–33.2% SL), and from *H. hamadryades* by having the dorsal-fin origin just posterior to anal-fin origin in males (vs. anterior) and between the base of 3rd and 5th anal-fin rays in females (vs. between the base of 1st and 3rd anal-fin rays), and the second proximal radial of the dorsal fin between neural spines of the 7th and 8th vertebrae in males (vs. between neural spines of the 5th and 7th).

Description. Morphometric data appear in Table 2. Body relatively deep, compressed. Greatest body depth at vertical just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Head narrow, sub-triangular in lateral view. Jaws short, teeth numerous, conical, irregularly arranged; outer teeth hypertrophied, inner teeth small and numerous. Vomerine teeth absent. Gill-rakers on first branchial arch 3 + 9, gill-rakers long, straight, without denticles. Urogenital papilla conical in males, pocket-shaped in females, slightly projecting over anterior part of anal fin.

Dorsal and anal fins relatively short, extremities rounded to slightly pointed in both sexes, without filamentous rays. Caudal fin subtruncate in males, rounded in females. Pectoral fin elliptical, posterior margin reaching between base of 6th and 9th anal-fin ray in males, reaching anus in females. Pelvic fin small, tip reaching between

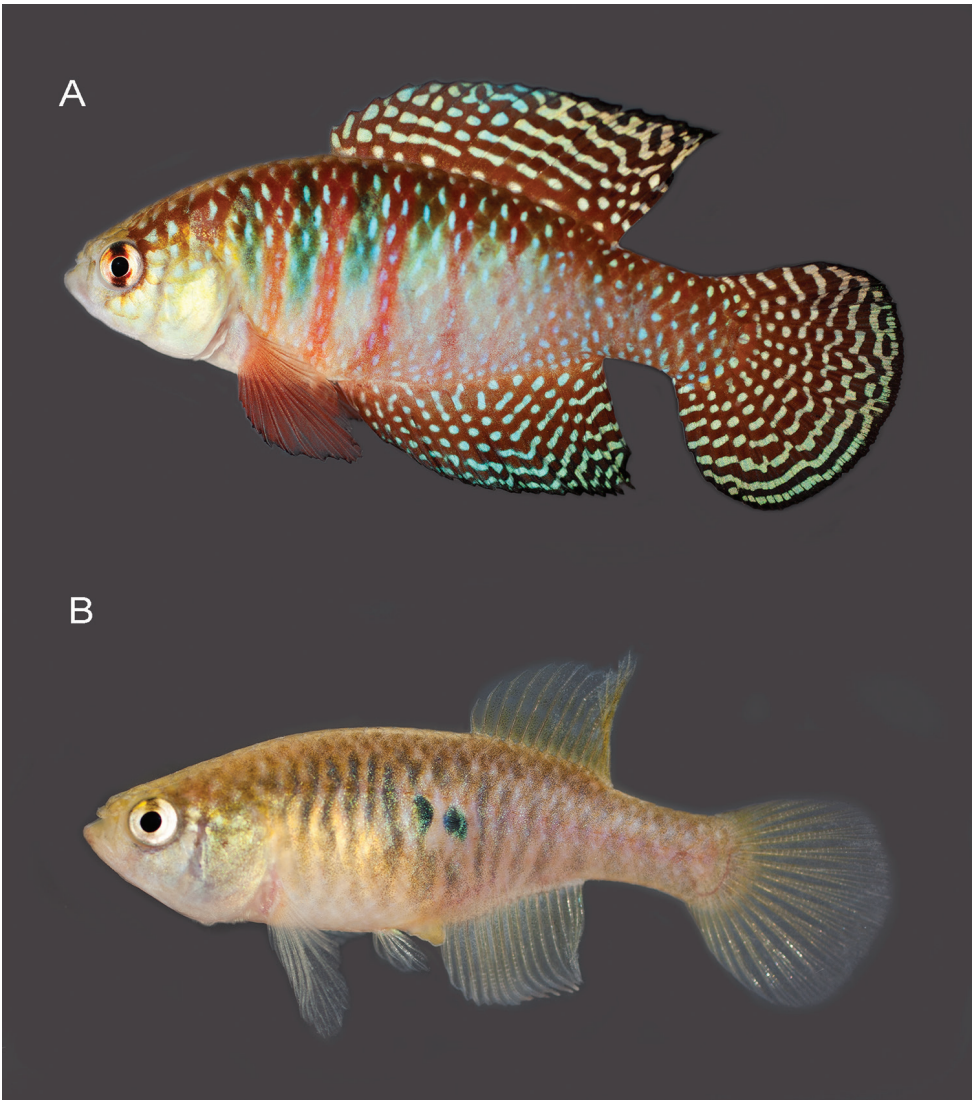

Figure 2. *Hypsolebias gardneri* sp. n. **A** live holotype, UFRJ 11859, male, 36.9 mm SL **B** live paratype, UFRJ 6797, female, 30.0 mm SL. Photographs by WJEM Costa.

base of 3rd and 5th anal-fin rays in males, reaching base of 1st anal-fin ray in females; pelvic-fin bases medially united. Dorsal-fin origin at vertical between base of 1st and 2nd anal-fin rays in males, between base of 3rd and 5th anal-fin rays in females. Dorsal-fin rays 22–24 in males, 15–17 in females; anal-fin rays 21–22 in males, 17–19 in females; caudal-fin rays 23–24; pectoral-fin rays 12–; pelvic-fin rays 5–6. In males, minute papillate contact organs on inner surface three dorsal-most pectoral-fin rays. Second proximal radial of dorsal fin between neural spines of 7th and 8th vertebrae in males, between neural spines of 11th and 12th vertebrae in females; first proximal radial of anal

Table 2. Morphometric data of *Hypsolebias gardneri* sp. n.

	Holotype	Paratypes	
	male	males (6)	females (4)
Standard length (mm)	**36.9**	**29.7–36.1**	**26.6–30.0**
Percent of standard length			
Body depth	36.7	36.4–38.5	33.9–38.4
Caudal peduncle depth	16.4	16.8–17.3	16.0–16.9
Pre-dorsal length	43.1	42.0–47.2	61.1–61.8
Pre-pelvic length	42.8	43.5–45.2	51.9–52.7
Length of dorsal-fin base	45.9	43.4–46.2	24.1–25.9
Length of anal-fin base	43.1	41.1–43.6	23.4–25.4
Caudal-fin length	34.5	34.7–36.4	33.3–36.8
Pectoral-fin length	25.5	26.9–28.8	22.7–26.9
Pelvic-fin length	10.2	10.1–11.7	9.4–11.9
Head length	27.6	27.3–29.8	29.0–31.6
Percent of head length			
Head depth	115.6	108.6–121.9	100.1–104.5
Head width	62.2	65.0–71.5	67.3–71.8
Snout length	15.9	13.4–16.3	13.3–14.3
Lower jaw length	20.5	18.8–21.2	15.7–16.8
Eye diameter	30.5	27.9–33.8	30.5–31.6

fin between pleural ribs of 6th and 8th vertebrae in males, between pleural ribs of 8th and 9th vertebrae in females; total vertebrae 26–27.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 20% of caudal-fin base and gently extending on middle portion of anal-fin base; no scales on dorsal and pectoral-fin bases. Frontal squamation E-patterned; E-scales overlapping medially; no row of scales anterior to G-scale; supraorbital scales 1–2. Longitudinal series of scales 25–26; transverse series of scales 10; scale rows around caudal peduncle 12. One minute contact organ per scale of ventral portion of flank. Cephalic neuromasts: supraorbital 11–14; parietal 2; anterior rostral 1, posterior rostral 1; infraorbital 2 + 20–24; preorbital 3–4; otic 1–2, post-otic 2–3; supratemporal 1; median opercular 1, ventral opercular 2; pre-opercular 15–17, mandibular 10; lateral mandibular 4, paramandibular 1.

Colouration in life. Males. Flank light blue on middle, light pink ventrally, and dark reddish orange dorsally and posteriorly; six to eight light red bars between humeral region and anterior part of caudal peduncle, more conspicuous anteriorly, three anterior-most red bars alternating with three dark greenish grey bars; minute vertically elongated metallic blue spots per scale, on whole flank. Dorsum pale reddish orange, venter white. Head light blue, margin of scales of dorso-posterior region reddish orange to golden. Iris yellow, with dark reddish brown bar through orbit centre. Unpaired fins dark red with bright blue marks, narrower than interspace, including six to nine transverse stripes and one basal row of dots on dorsal fin, stripes often

interrupted and substituted by dots on posterior portion of sub-basal portion; dots and short vermiculate marks irregularly arranged on anterior portion of anal fin and transverse stripes on posterior portion; and seven or eight transverse rows of dots on caudal fin, coalesced to form bars on posterior half of fin; each unpaired fin with black line along distal margin. Paired fins red with black margin; minute light blue dots on pelvic fin. **Females.** Flank pale brownish grey, with faint vertically elongated grey spots and short bars along flank and one or two small black spots on flank centre at vertical between anus and anal-fin origin; anterior portion of flank pale golden. Dorsum pale brown, venter white. Head side pale blue with pale golden iridescence on opercle. Iris silver, with dark brownish grey bar through orbit centre. Fins hyaline.

Colouration in alcohol. Males with similar colour pattern as in life, but iridescence is lost and red marks substituted by grey or inconspicuous. Females with similar colour pattern as in life, but iridescence in head is lost.

Distribution. *Hypsolebias gardneri* is known only from the type locality (14°17'39"S, 43°42'32"W, altitude about 500 m a.s.l.; Fig. 3), a wide temporary pool, with dense aquatic vegetation in open areas and bushes concentrated on part of the pool bank. Specimens of *Hypsolebias pterophyllus* Costa, 2012 were common in all parts of the pool, whereas specimens of *H. gardneri* have their distribution restricted to shadow areas, under marginal bushes. The pool was sampled a single time (31 January 2010), when the whole type series was collected. No similar pools were found in the region, thus it is not possible to evaluate its conservation status.

Etymology. The name *gardneri* in honour of Scottish naturalist George Gardner, who was in the Caatinga during his trip to Brazil between 1836 and 1841, making rich natural history collections. His reports on the region, and the numerous plant species and Cretaceous fossil fish collected by him represent important landmarks of our knowledge about Caatinga biodiversity.

***Hypsolebias hamadryades* Costa, sp. n.**
http://zoobank.org/9057BBBC-39AA-4BD9-B84B-005499635FCD
Figure 4, Table 3

Holotype. UFRJ 6893, male, 26.9 mm SL; Brazil: Minas Gerais state: Janaúba municipality: temporary pool near road MG-401 at the town of Janaúba, floodplains of Gorutuba River, Verde Grande River drainage, São Francisco River basin, 15°48'06"S, 43°19'19"W, altitude about 530 m a.s.l.; W. J. E. M. Costa et al., 17 January 2017.

Paratypes. UFRJ 6895, 4 males, 17.4–26.1 mm SL, 1 female, 21.2 mm SL; UFRJ 6894, 3 males, 22.6 – 26.1 mm SL, 2 females, 15.9–21.0 mm SL (C&S); UFRJ 11473, 4 males, 15.5–17.9 mm SL (DNA); collected with holotype. – UFRJ 6892, 2 females, 21.0–23.7 mm SL; same locality and collectors, 21 April 2017.

Diagnosis. *Hypsolebias hamadryades* is distinguished from all other species of the *H. magnificus* complex by the absence of dark greenish grey bars on the anterior portion of the flank in males (vs. presence) and presence of transverse blue stripes on the unpaired

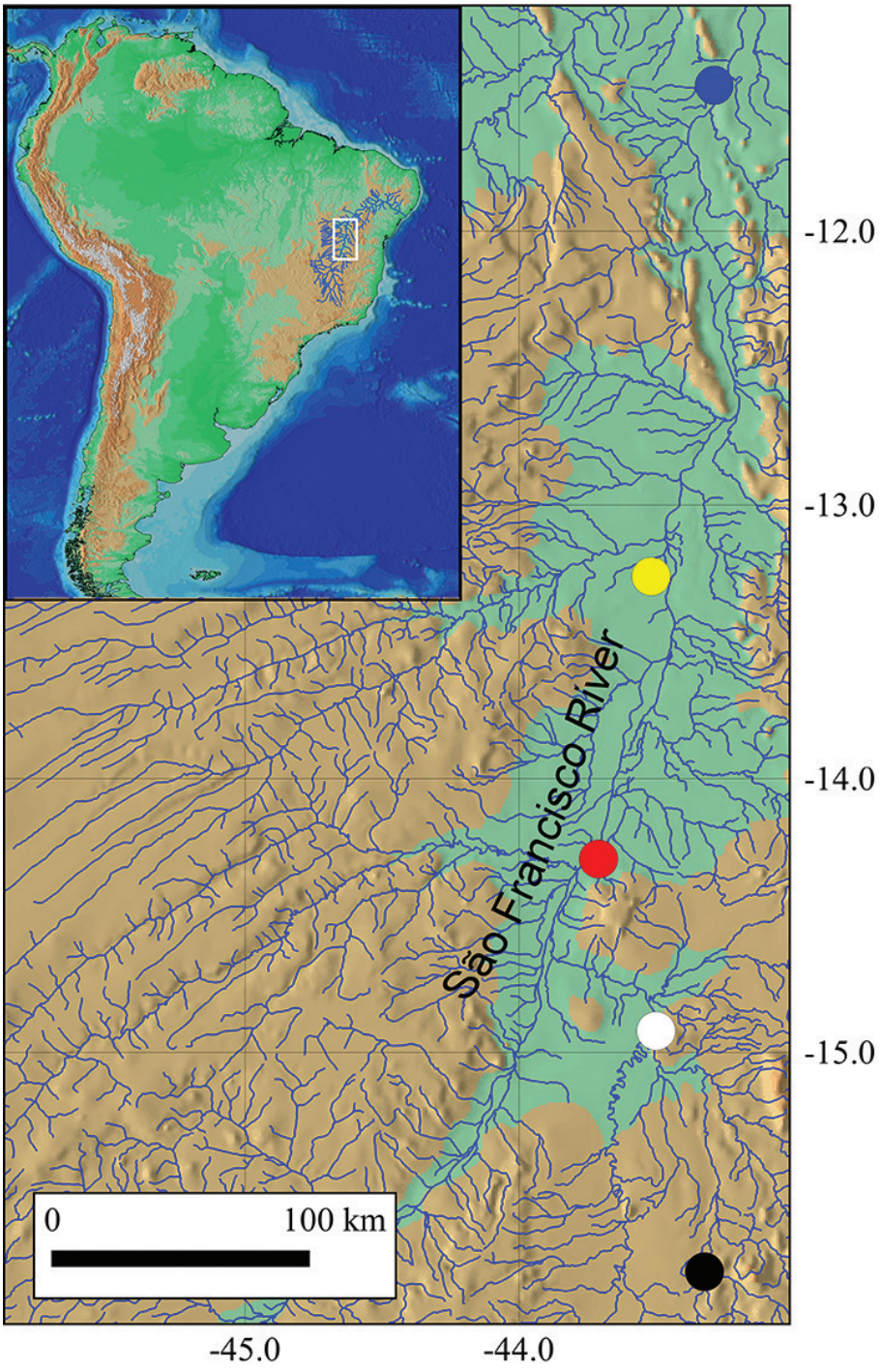

Figure 3. Localities of specimens belonging to species of the *Hypsolebias magnificus* complex used in this study: black dot, *H. hamadryades*; white dot, *H. magnificus*; red dot, *H. gardneri*; yellow dot, *H. harmonicus*; blue dot, *H. picturatus*.

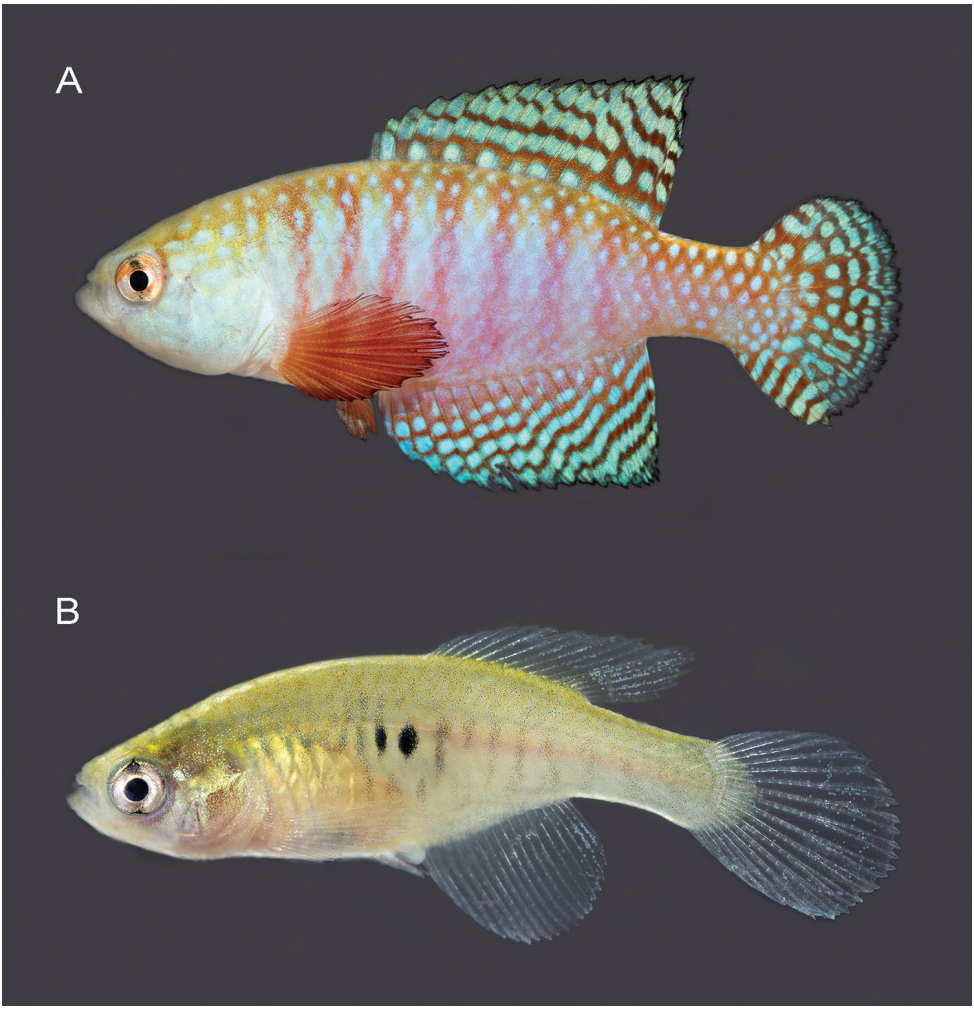

Figure 4. *Hypsolebias hamadryades* sp. n. **A** live holotype, UFRJ 6893, male, 26.9 mm SL (caudal fin damaged and regenerated) **B** live paratype, UFRJ 6895, female, 21.2 mm SL. Photographs by WJEM Costa.

fins in males wider than interspace (vs. transverse series of dots or stripes narrower than interspace). It also differs from all other species of the complex by the following combination of character states relative to the male colour pattern: dorsal fin with transverse blue stripes and one basal row of blue dots (vs. rows of blue dots on the whole fin in *H. picturatus*); anal fin with transverse blue stripes on most portion of the fin (vs. dots and short vermiculate marks arranged on most part of the fin in *H. gardneri*, *H. harmonicus* and *H. picturatus*); and most portion of caudal fin with blue bars (vs. anterior half of caudal fin with transverse rows of blue dots, posterior half with transverse blue bars in *H. gardneri* and *H. harmonicus*, or dots on the entire fin in *H. picturatus*), and the presence of eight to ten light red bars between humeral region and the anterior part of the caudal peduncle (vs. six or seven in *H. magnificus*, *H. harmonicus* and *H. gardneri*).

Hypsolebias hamadryades is further distinguished from *H. gardneri* and *H. picturatus* by having the dorsal-fin origin anterior to anal-fin origin in males (vs. just posterior anterior) and from *H. harmonicus* by having 23 or 24 caudal-fin rays (vs. 21 or 22).

Description. Morphometric data appear in Table 3. Body relatively deep, compressed. Greatest body depth at vertical just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Head narrow, sub-triangular in lateral view. Jaws short, teeth numerous, conical, irregularly arranged; outer teeth hypertrophied, inner teeth small and numerous. Vomerine teeth absent. Gill-rakers on first branchial arch 3 + 9, gill-rakers short, straight, without denticles. Urogenital papilla conical in males, pocket-shaped in females, slightly projecting over anterior part of anal fin.

Dorsal and anal fins relatively short, extremities rounded to slightly pointed in both sexes, without filamentous rays. Caudal fin rounded. Pectoral fin elliptical, posterior margin reaching base of 7th anal-fin ray in males, reaching anus in females. Pelvic fin small, tip reaching between base of 2nd and 3rd anal-fin rays in males, reaching urogenital papilla in females; pelvic-fin bases medially united. Dorsal-fin origin anterior to anal-fin origin in males, anal-fin origin at vertical between base of 1st and 3rd dorsal-fin rays; dorsal-fin origin posterior to anal-fin origin in females, dorsal-fin origin at vertical between base of 1st and 3rd anal-fin rays in females. Dorsal-fin rays 22–26 in males, 15–17 in females; anal-fin rays 20–23 in males, 18–19 in females; caudal-fin rays 23–24; pectoral-fin rays 12–13; pelvic-fin rays 5–6. In males, minute papillate contact organs on inner surface of dorsal-most pectoral-fin ray. Second proximal radial of dorsal fin between neural spines of 5th and 7th vertebrae in males, between neural spines of 10th and 12th vertebrae in females; first proximal radial of anal fin between pleural ribs of 7th and 9th vertebrae in males, between pleural ribs of 8th and 10th vertebrae in females; total vertebrae 27–29.

Scales small, cycloid. Body and head entirely scaled, except anterior ventral surface of head. Body squamation extending over anterior 25% of caudal-fin base; no scales on dorsal, anal and pectoral-fin bases. Frontal squamation E-patterned; E-scales overlapping medially; no row of scales anterior to H-scale; one supraorbital scale. Longitudinal series of scales 26; transverse series of scales 11; scale rows around caudal peduncle 12. One minute contact organ per scale of anteroventral portion of flank. Cephalic neuromasts: supraorbital 14–16; parietal 2; anterior rostral 1, posterior rostral 1; infraorbital 2 + 18–20; preorbital 2; otic 2–3, post-otic 2; supratemporal 1; median opercular 1, ventral opercular 1; pre-opercular 12–15, mandibular 10; lateral mandibular 5, paramandibular 1.

Colouration in life. Males. Flank light blue on middle, light pink ventrally, and pale reddish orange dorsally and posteriorly; eight to ten light red bars between humeral region and anterior part of caudal peduncle, more conspicuous anteriorly; minute vertically elongated metallic blue spots per scale, on whole flank. Dorsum pale reddish orange, venter white. Head light blue, margin of scales of dorso-posterior region reddish orange. Iris yellow, with dark reddish brown bar through orbit centre. Unpaired fins red with bright blue transverse stripes, sometimes interrupted, including four or five on dorsal and anal fins, and six or seven on caudal fin; stripes broader than inter-

Table 3. Morphometric data of *Hypsolebias hamadryades* sp. n. Caudal fin of holotype damaged and regenerated, thus not measured.

	Holotype	Paratypes	
	male	males (3)	females (3)
Standard length (mm)	**26.9**	**24.4–26.1**	**21.0–23.7**
Percent of standard length			
Body depth	36.0	33.9–35.0	33.9–34.6
Caudal peduncle depth	15.3	14.2–14.8	12.9–14.9
Pre-dorsal length	45.6	44.7–45.1	61.1–61.5
Pre-pelvic length	44.3	42.6–44.4	52.8–53.6
Length of dorsal-fin base	44.7	40.1–45.5	23.7–25.2
Length of anal-fin base	41.1	36.7–41.7	22.6–23.9
Caudal-fin length	-	33.0–33.9	32.7–34.9
Pectoral-fin length	25.0	25.5–28.0	23.9–26.5
Pelvic-fin length	9.6	8.2–10.6	8.5–11.9
Head length	29.1	28.1–30.4	28.3–31.1
Percent of head length			
Head depth	101.3	99.7–102.6	97.1–100.6
Head width	63.6	59.8–61.5	66.5–70.5
Snout length	14.2	13.7–15.8	11.9–13.9
Lower jaw length	19.4	16.5–18.8	14.1–16.5
Eye diameter	31.1	31.6–33.9	34.2–36.1

space; each unpaired fin with one row of small bright blue spots along basal portion and black line along distal margin. Paired fins red with black margin; faint blue dots on pelvic fin. **Females.** Flank light grey, with faint vertically elongated grey spots and one or two small black spots on flank centre, at vertical between pelvic-fin base and urogenital papilla; scale border pale yellow on dorsal portion of flank and head. Dorsum light grey, venter white. Head side pale grey with pale golden iridescence on opercle. Iris silver, with dark grey bar through orbit centre. Fins hyaline.

Colouration in alcohol. Males with similar colour pattern as in life, but iridescence is lost and red marks substituted by grey or inconspicuous. Females with similar colour pattern as in life, but iridescence in head is lost.

Distribution and conservation. *Hypsolebias hamadryades* is only known from a pool in the floodplains of the Gorutuba River, within the town of Janaúba, Minas Gerais, Brazil (15°48'06"S, 43°19'19"W, altitude about 530 m a.s.l.; Fig. 3). This area has been studied since January 2002 (Costa, 2006), but *H. hamadryades* was first collected only in 2017. Previous field studies revealed two endemic seasonal killifishes, *H. janaubensis* (Costa, 2006) and *Cynolebias gorotuba* Costa, 2017, as well as an intense process of urbanization which result in the complete extirpation of all temporary pools studied between 2002 and 2010 (Costa 2017). The type locality pool of *H. hamadryades* was only found in January 2017, since it was hidden by a dense Caatinga forest. The pool occupied an area of about 100 m^2 and was about 1 m deep. The whole pool was densely populated by adult specimens of *H. janaubensis*, whereas individuals of *H. hamadryades*, mostly

juvenile specimens below 20 mm SL including, were found only in a small part of the pool containing shaded zones, near the pool margins, where bushes were concentrated. The largest males exhibited damaged caudal fins, indicating possible territorial disputes as commonly occurring in other seasonal killifishes. A new collecting trip was made in April 2017, when physical conditions of the pool were nearly identical to the first collection, except that the pool was shallower (about 0.5 m at deepest places). At that time, however, only two females and no males of *H. hamadryades* were found. According to local people, pools in the region did not dry between January and the period of the second collection.

Etymology. The name *hamadryades* is an allusion to the occurrence of the new species in the forested part of a Caatinga temporary pool. This name was used by the Bavarian naturalist Karl Friedrich Philipp von Martius for the Caatinga in his classification of vegetation formations of Brazil, in which he used names of Greek mythological beings to name each Brazilian phytogeographical province. The name is opportune by referring to *hamadryades*, a particular kind of Greek nymph entity that is believed to be associated to trees, vanishing when trees die. Similarly, field studies have shown that populations of species of the *H. magnificus* group became extinct after marginal deforestation (see discussion below).

Discussion

The two new species here described, *H. gardneri* and *H. hamadryades*, are respectively most similar in colour pattern to *H. harmonicus* and *H. magnificus*, what is mostly evident in the male caudal fin (Fig. 5). In both *H. gardneri* and *H. harmonicus*, the caudal fin of males is blue-dotted on its proximal portion and has light blue bars on the distal one (Figs 2A, 5A, B), and in *H. hamadryades* and *H. magnificus* there are light blue bars scattered over the whole fin (Fig. 5C–E), thus contrasting with the entire blue-dotted fin in *H. picturatus* (Fig. 5F). Whereas the molecular analysis corroborates *H. gardneri* and *H. harmonicus* as sister species (Fig. 1), *H. hamadryades* is not supported as closer to *H. magnificus*, but to *H. gardneri* and *H. harmonicus*. *Hypsolebias gardneri* and *H. harmonicus* share a similar colour pattern on the caudal fin, unique among congeners, but the former species has a proportionally larger fin (34.5–36.4% SL) that is subtruncate (Figs 2A, 5B) and bears more rays (23–24), whereas the fin is conspicuously smaller (31.2–33.2% SL) and rounded (Fig. 5A), besides having fewer rays (21–22). In contrast to all other species of HMC, in *H. hamadryades* the bars on the caudal fin are wider than the dark red interspace (Fig. 5C).

Little is presently known about the maximum length that seasonal killifishes endemic to the Caatinga may reach. According to field data, species of the genus *Cynolebias* Steindachner, 1876 may reach about 135 mm SL (Costa 2001), whereas species of the *H. antenori* group reach about 75 mm SL (Costa 2007), but species of the *H. magnificus* group do not surpass about 45 mm SL (Costa 2007). Among species of HMC, *H. gardneri*, *H. magnificus*, and *H. picturatus* may reach between 42–45 mm SL, but *H. hamadryades* and *H. harmonicus* seem to be smaller. *Hypsolebias hamadryades* was first collected in January

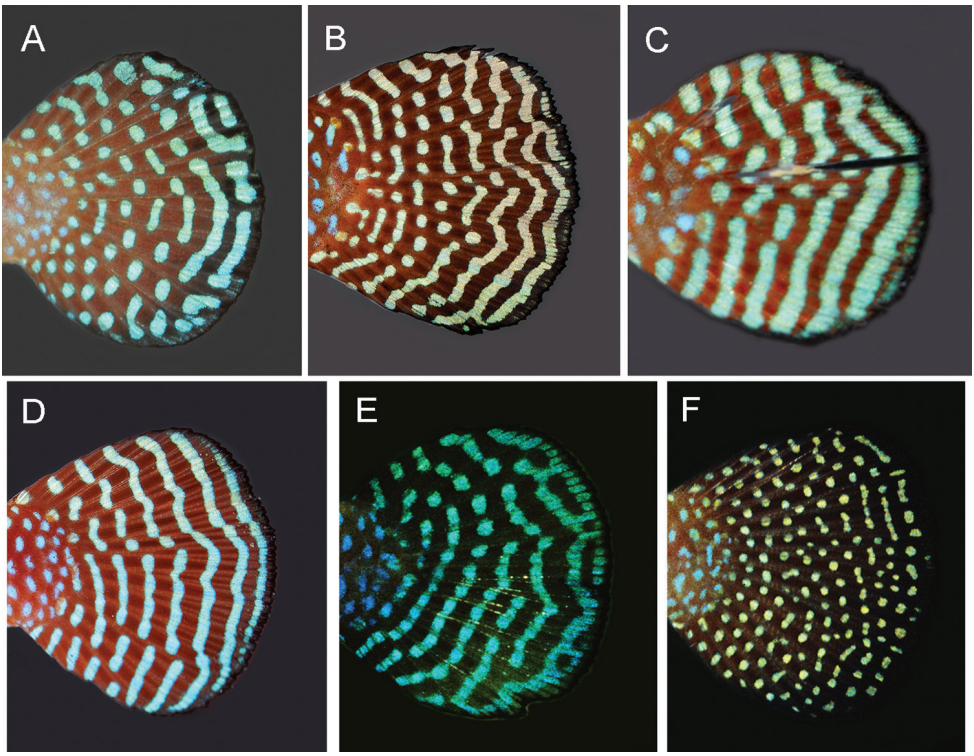

Figure 5. Caudal fin of live males of the *Hypsolebias magnificus* species complex. **A** *H. harmonicus*, holotype, UFRJ 6696, 29.4 mm SL **B** *H. gardneri* sp. n., paratype, UFRJ 6797, 34.4 mm SL **C** *H. hamadryades* Costa sp. n., paratype, UFRJ 6895, 24.8 mm SL **D** *H. magnificus*, specimen from Gado Bravo, UFRJ 4959, 31.2 mm SL **E** *H. magnificus*, topotype not preserved, about 25 mm SL **F** *H. picturatus*. Paratype, UFRJ 5053, 38.6 mm SL. Photographs by WJEM Costa.

2017, when specimens found were always small, males reaching a maximum size of 27 mm SL and females 21 mm SL. A new collection was made three months after, just before the long dry period. However, only females were found, which exhibited approximately the same size as in January, although local people reporting that pools had not dried between the two trips. The only other seasonal fish found in sympatry, *H. janaubensis,* measured about 50 mm SL, the largest size recorded for this species, suggesting that seasonal killifishes of the pool were at their maximum size. These data suggest that *H. hamadryades* is a miniature species, probably constituting the smallest species of the genus.

Although our phylogeny was based in a short fragment of a single mitochondrial gene and relatively low number of individuals, the concordance between molecularly delimited (i.e., exclusive lineages supported by high Bayesian posterior probabilities) and morphologically diagnosable (i.e., exhibiting unique combination of morphological character states) highly supports recognition of five distinct species. In addition, the naturally fragmented distribution pattern of recognised species due to their ecologically specialised nature in uniquely inhabiting pools under dense concentration of shrubs

and trees, which is not a common habitat in the Caatinga, also reinforces hypotheses of genetic isolation among these species.

Continuous field studies in the Caatinga have revealed a high diversity of seasonal killifish species, but they have also reported rapid environmental decline caused by deforestation, new roads and draining projects for agricultural proposals, extirpating natural habitats many killifish populations (Costa 2002, 2017; Costa et al. 2012). As a consequence, several of these species have appeared in lists of endangered species (e.g., http://www.icmbio.gov.br/portal/especies-ameacadas-destaque). However, our field studies have clearly shown that species of the *H. magnificus* group are much more susceptible to extinction than most other seasonal killifishes of the region. Besides being rarer, occurring only in areas where terrestrial marginal vegetation is taller, they are highly sensitive to deforestation, tending to disappear just after original vegetation is removed, whereas species of the *H. antenori* group and *Cynolebias* may survive in areas highly exposed to sunlight (pers. observ. 2002–2018). This study therefore indicates that HMC comprises cryptic species apparently endemic to small areas and extremely vulnerable to environmental changes, deserving high concern.

Acknowledgements

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