

Notaulax yamasui sp. n. (Annelida, Sabellidae) from Okinawa and Ogasawara, Japan, with notes on its ecology

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Abstract

The polychaete *Notaulax yamasui* sp. n. (Sabellidae) is described from Okinawa and Ogasawara, south Japan, where it was found living embedded in a dead skeleton of the coral *Porites* sp. The new species is characterized by the presence of a pigmented sub-distal swelling on the tips of the crown radioles, a unique feature among species of the genus. Besides, its collar chaetae have an L-shape orientation, and the dorsal basal flanges of the branchial lobes are long and have a dorsal joint.

Keywords

Boring species, coral reef, new species description, Polychaeta, taxonomy, worms

Introduction

A revision of the Japanese sabellid polychaetes belonging to the genera *Megalomma* Johansson, 1925, *Notaulax* Tauber, 1879, *Parasabella* Bush, 1905 and *Sabella* Linnaeus, 1767, is in progress. In the course of this revision, several Japanese collections are being revised for specimens belonging to these genera. As a result, two specimens belonging to the same species showed radioles with sub-distal swellings, like those found in *Sabella discifera* Grube, 1874 and in *Bispira brunnea* (Treadwell, 1917), as reported by Tovar-Hernández

and Pineda-Vera (2008). These swellings can be pigmented, in which case they superficially resemble the compound eyes of *Megalomma* and *Stylomma* Knight-Jones, 1997. Other main features of the specimens include the long flanged radiolar lobes (similar to those in *Notaulax*, *Stylomma*, and *Anamobaea* Krøyer, 1856), and simple radiolar eyes (like those in *Notaulax*, *Anamobaea*, and *Hypsicomus* Grube, 1870). All these genera were revised or described by Rullier and Amoureux (1970), Perkins (1984), Knight-Jones (1997), Knight-Jones and Perkins (1998), Fitzhugh (2002) and Capa (2007). Further information on these genera can also be found in Fitzhugh (1989, 2003) and Capa et al. (2014).

The specimens collected at Okinawa and Ogasawara (south-western Japan) were studied using both light and scanning electron microscopy (SEM) for their external morphology, and through histological cross sections at different levels of the radioles for the internal anatomy of the radioles and their sub-distal swellings. As a result, the specimens were determined to belong to an unknown species of *Notaulax*, which is described below as a new taxon.

Material and methods

The specimens were collected together with the surrounding coral at shallow water by hand, using chisels to break pieces of the coral, and fixed in the laboratory with a 10% seawater-buffered formalin solution. Some parapodia were removed from the body and prepared for microscopy observations. For light microscopy observations the parapodia were placed on a microscope slide, covered with a cover slip, and gentle pressure was applied in order to observe the chaetae and uncini. Histological sections were made from radioles embedded in paraffin, cut on a microtome, and stained with Sudan Black B. For SEM observations, the parapodia were run through a series of increasing concentrations of ethanol (80, 90, 95, 99 and 100%), air-dried, coated with palladium and platinum, and viewed in a Hitachi S-800 SEM. The holotype and paratype were deposited in the Coastal Branch of Natural History Museum and Institute, Chiba at Katsuura, Chiba, Japan (catalogue code, CMNH-ZW). The terminology for the anatomical structures of *Notaulax* follows Fitzhugh (1989, 2002).

Systematics

Genus *Notaulax* Tauber, 1879

Notaulax yamasui sp. n.

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Figs 1–3, 4A–B, 5A–E

Material examined. Holotype: CMNH-ZW00217, complete specimen with fragment of tube, extracted from living coral mass of *Porites* sp., collected in the subtidal zone

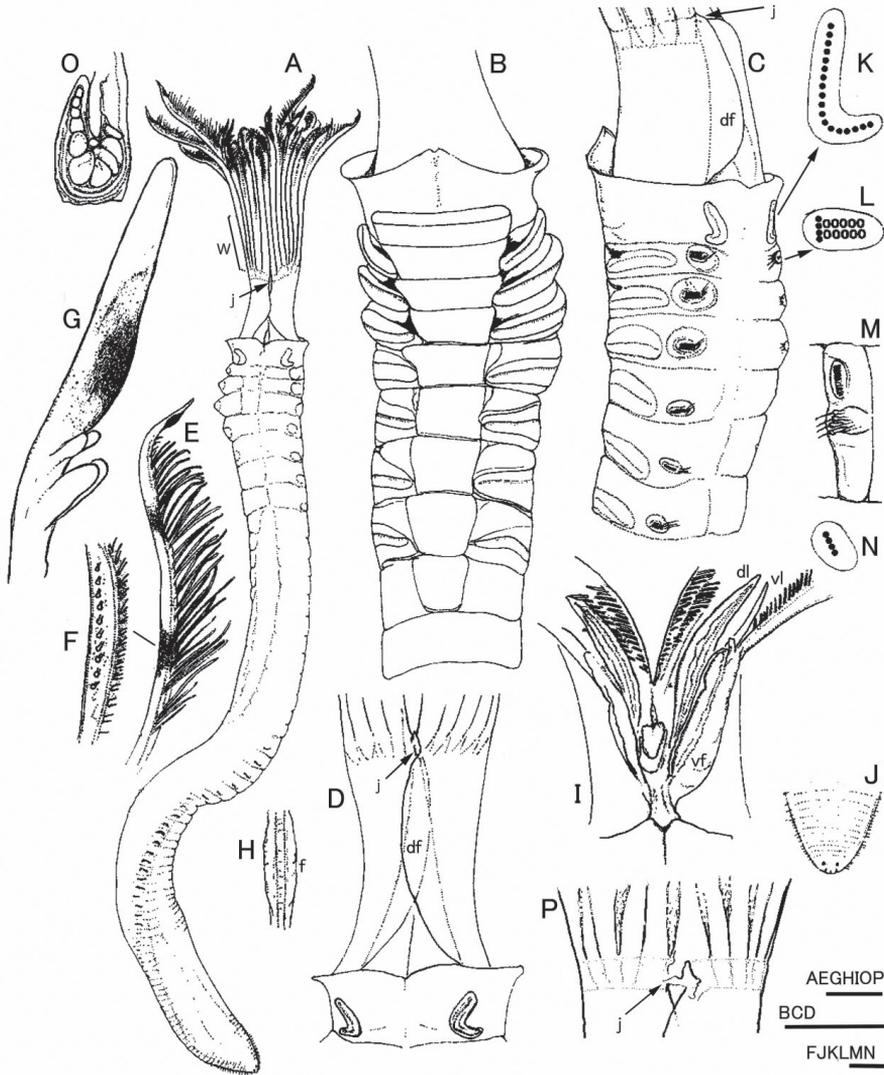


Figure 1. *Notaulax yamasui* sp. n.: **A** holotype, dorsal view **B** ventral view of thorax **C** latero-dorsal view of left side of thorax **D** dorsal view of first chaetiger and radiolar base **E** distal side view of radiole **F** middle region of radiole showing a row of simple radiolar eyes **G** lateral close up view of tip of radiole, with pigmented sub-distal swelling **H** basal part of radiole showing paired longitudinal flanges (f) **I** schematic ventral view of interior of crown showing dorsal lip (dl), ventral lip (vl), ventral flange of radiolar base margin (vf) **J** posterior abdomen and pygidium, showing eye-spots **K** schematic arrangement of collar chaetae, right side **L** schematic arrangement of thoracic chaetae from second chaetiger, black spots representing superior chaetae, white circles representing inferior chaetae **M** anterior abdominal segment, left side view **N** schematic arrangement of neuropodial abdominal chaetae **O** cross-section of radiole, middle region **P** base of radioles and inter-radiolar membrane. Abbreviations: df, dorsal basal flange; dl, dorsal lip; f, longitudinal flange; j, junction of dorsal basal flange; vf, ventral flange; vl, ventral lip; w, inter-radiolar membrane. Scale bars 1 mm (**A**, **B**, **C**), 0.5 mm (**D**, **J**), 0.25 mm (**E**, **F**, **H**, **K**, **P**), 0.1 mm (**G**, **I**, **L**, **M**, **N**, **O**).

(0–2 m) of a shallow coral reef area at Maeda-Misaki Cape, 26°26.716'N, 127°46.329'E, Okinawa Island, Ryukyu Archipelago, south-western Japan, Pacific Ocean, 13 February 1996, by hand, coll. by E. Nishi. Paratype: CMNH-ZW00220, incomplete specimen lacking posterior abdomen and tube, collected on a dead *Porites* sp. coral colony, at Kominato, Chichi-jima Island, Ogasawara Archipelago, south-east Japan, Pacific Ocean, 16 July 1999, coll. by Prec. Institute Co Ltd.

Comparative material. *Megalomma* sp., CMNH-ZW uncatalogued, Yoshio, Katsuura, Boso Peninsula, Japan, subtidal, coll. by E. Nishi.

Diagnosis. Pigmented sub-distal swelling on tips of crown radioles; collar chaetal row in L-shape orientation; dorsal basal flanges of radiolar lobes long and with a dorsal joint.

Description. *Tube* dark brown, thin and membranous. Body and radiolar crown pale in preserved specimens, except for light brown collar and for two (upper and lower) brown bands on distal free region of radioles (Fig. 1A, E).

Body of holotype 40 mm long (excluding crown) for 130 chaetigers (including thorax and abdomen); thorax 4 mm long and 2.0–2.5 mm wide, excluding chaetae; radiolar crown 6 mm long, radiolar lobes 1 mm long. Paratype similar in size, body 6 mm long (posterior portion of abdomen missing) for 32 chaetigers, thorax 3 mm long and 1.5 mm wide, excluding chaetae; radiolar crown 7 mm long, radiolar lobes 1.5 mm long.

Crown with 16 pairs of radioles, joined by inter-radiolar membrane (Fig. 1C, D, P), inter-radiolar membrane about 1/2 length of radiole length (Fig. 1A); radiolar lobes with narrow dorsal flanges (Fig. 1A, C), flanges closed at lower level of inter-radiolar membrane by dorsal joint (Fig. 1P), and free proximally (Fig. 1C, D); ventral margins of radiolar lobes also flanged, ventral flanges free (Fig. 1I); radioles with 4 or more skeletal cells in cross-section (Figs 1O, 5B, C, D, E), with paired longitudinal flanges on outer surface, more prominent at basal region near inter-radiolar membrane (Figs 1H, 4B, 5C), turning distally into flattened long tongue-shaped tips (Figs 1A, E, G, 4A, 5A); each radiole with one pigmented sub-distal swelling on inner side (not pigmented in paratype, showing same color to rest of body) (Figs 1A, E, G, 4A, 5A) and 8–12 pale brown simple radiolar eyes in single row on each side, at lateral margin of central region of radioles (within lower brown band) (Fig. 1E, F). Dorsal lips long, tapered to slender, with supporting mid-rib, joined to adjacent radiole (= radiolar appendage), but not to basal pinnule (Fig. 1I). Ventral lips tapered and small, merging proximally into parallel lamellae (Fig. 1I); ventral sacs absent.

Thorax with eight chaetigers; posterior peristomial ring collar entire, without dorsal or ventral slits, well separated from peristomium, with straight brown line above ventral glandular shield (Fig. 1B), mid-dorsal margin slightly embayed, lateral margin transverse to body axis and extending well above junction of radiolar crown with thorax, ventral margin raised in middle and incised ventrally with small notch on midline (Fig. 1B, C, D). First ventral glandular shield rectangular, divided transversally, with nearly straight anterior margin, slightly wider than shield of chaetiger 2 and about 2/3 longer (Fig. 1B). Other thoracic ventral glandular shields sub-trapezoidal (broader anteriorly), margins postero-laterally indented by tori. Abdomen with 122 (holotype) and 24 (paratype, posterior region missing) chaetigers. Pygidial eyespots present (Fig. 1A, J).

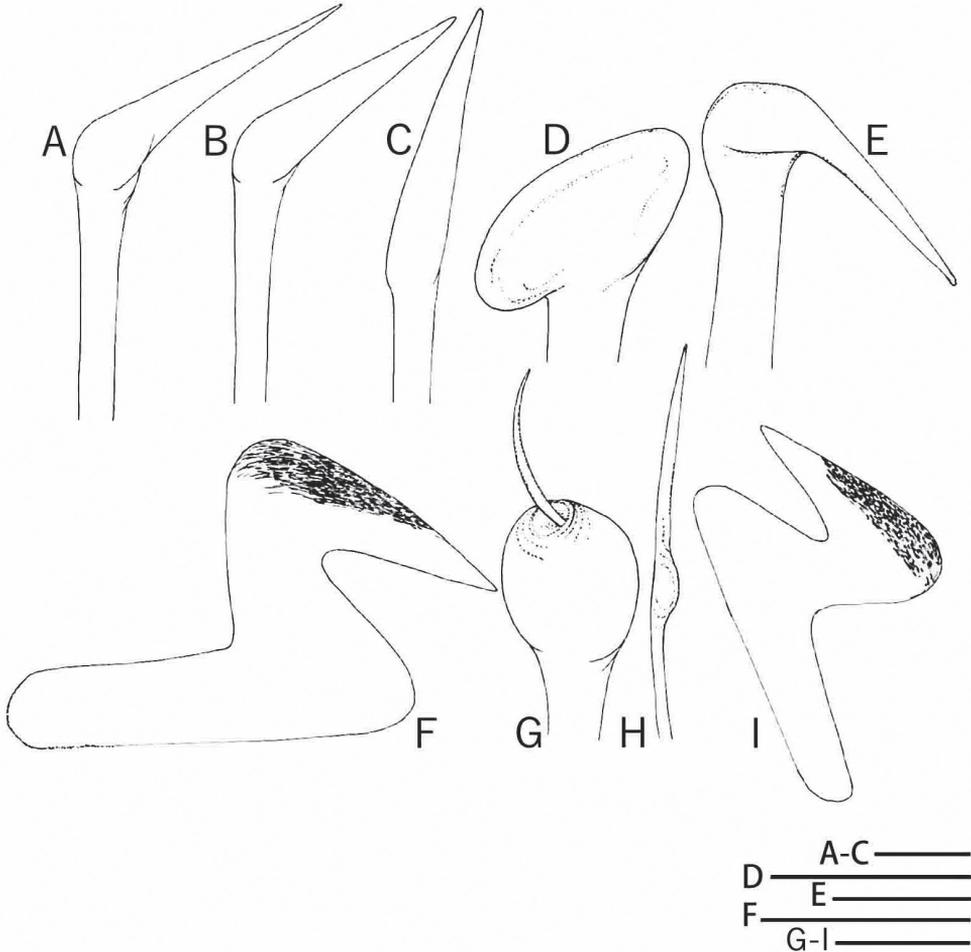


Figure 2. *Notaulax yamasui* sp. n. Chaetae of thorax (A–E) and abdomen (G, H) drawn from SEM micrographs, and uncini (F, I), drawn under a dissecting light microscope. A–B collar chaetae C superior thoracic chaeta D inferior thoracic chaeta E companion chaeta, dorsal view F thoracic uncini G inferior abdominal chaeta, anterior abdominal chaetiger H inferior abdominal chaeta, posterior abdominal chaetiger I abdominal uncini. Scale bars 20 μm (A–C), 50 μm (D), and 30 μm (E–I).

Collar chaetae spine-like, each with knee wider than shaft (Figs 2A, B, 3A), in longitudinal rows, curved outwards posteriorly (Fig. 1C, D, K). Superior chaetae of thoracic notopodial fascicles spine-like, similar to chaetae in chaetiger 1 (Figs 2C, 3B, C) and in short row (Fig. 1L), dorsal to paleate inferior thoracic notochaetae with hoods distally rounded (Figs 2D, 3B, C), arranged in two transverse rows (Fig. 1L). Thoracic neuropodial fascicles with avicular uncini, with several minute teeth above main fang, prominent breast and handle longer than distance between breast and main fang (Figs 2F, 3D). Companion neurochaetae in row parallel and anterior to uncini, with broad, thin teardrop-shaped blades at right angle to shafts, pointing anteriorly (Figs 2E, 3D).

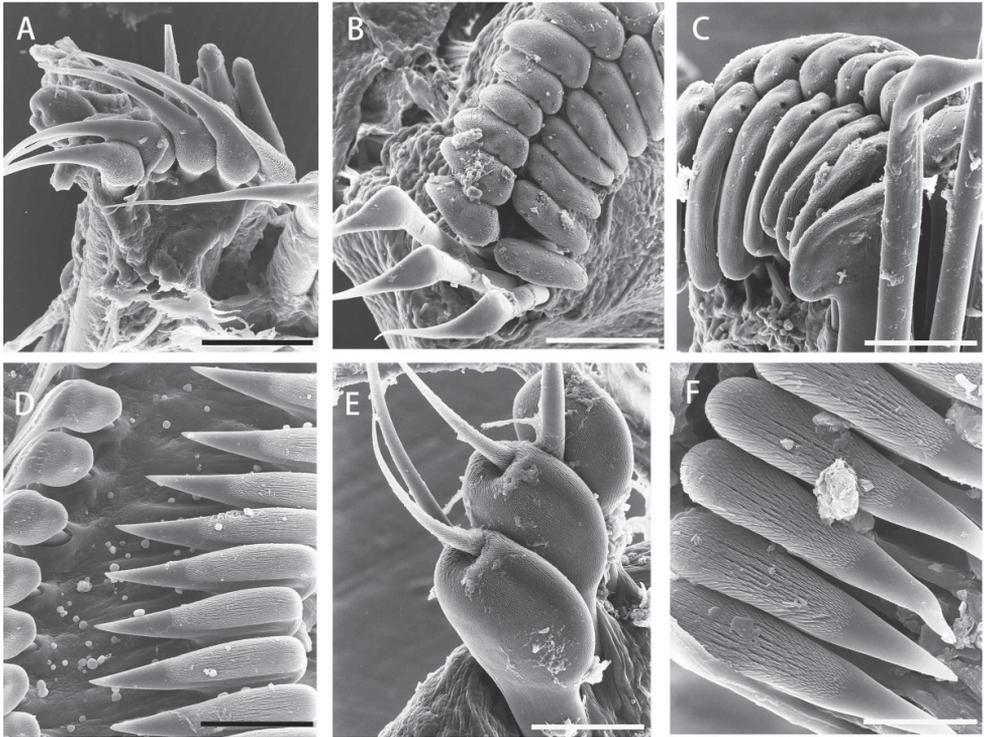


Figure 3. *Notaulax yamasui* sp. n. SEM micrographs of chaetae and uncini. **A** collar chaetae **B** 3rd left notopodial thoracic fascicle **C** detail of B, showing superior chaetae **D** uncini and companion chaetae, 3rd thoracic neuropodial torus **E** inferior abdominal spatulate chaetae showing distal mucros from 7th fascicle of abdomen, lateral view **F** abdominal uncini. Scale bars 30 μ m (**A**), 60 μ m (**B**), 40 μ m (**C**), 30 μ m (**D**, **E**), 12 μ m (**F**).

Abdominal neuropodia with neuropodial fascicles of paleate chaetae in short transverse rows (Fig. 1M, N); paleate neurochaetae with distal mucros shorter than hooded area in anterior abdominal segments (Figs 2G, 3E), mucros becoming longer than hooded area in posterior abdominal segments. Paleate neurochaetae numbering 4 per fascicle on most anterior abdominal segments (1st to 7th), 3 on median segments (8th to 20th), and one or two on posterior chaetigers. Superior neuropodial abdominal chaetae slender and straight, with or without sub-distal bulge (Fig. 2H), one per fascicle on anterior abdominal chaetigers (1st to 20th) and two to three in posterior ones. Abdominal notopodial avicular uncini similar to thoracic uncini (Figs 2I, 3F).

Habitat. *Notaulax yamasui* sp. n. is known to live in the subtidal zone, embedded in dead coral masses of *Porites* sp.

Etymology. The new species is named after Dr. Terufumi Yamasu, Emeritus Professor of the University of the Ryukyus, Japan, for his great contribution to the development of the Okinawan marine biology.

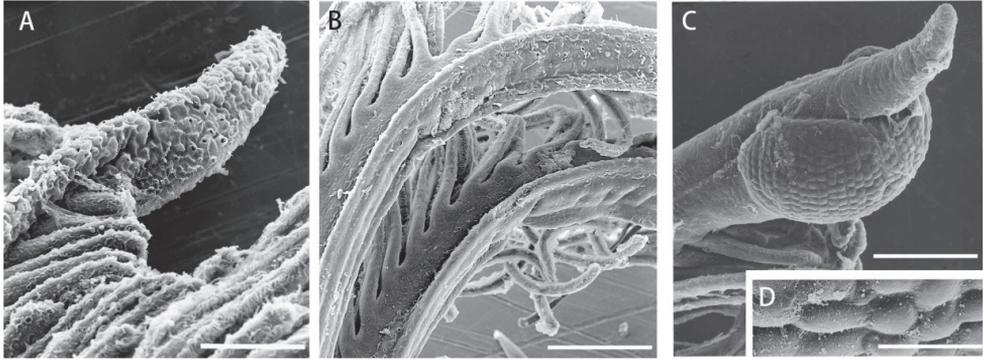


Figure 4. *Notaulax yamasui* sp. n. (**A, B**) and *Megalomma* sp. (**C, D**), SEM micrographs of anterior and middle parts of radiole and distal tip with a distal swelling in *N. yamasui* sp. n. and with a compound eye in *Megalomma* sp. **A** close-up view of a sub-distal radiolar swelling **B** middle part of radiole showing pinules and dorsal flange **C** compound eye on radiole **D** close-up view of surface of compound eye. Scale bars 75 μm (**A**), 200 μm (**B**), 300 μm (**C**), and 30 μm (**D**).

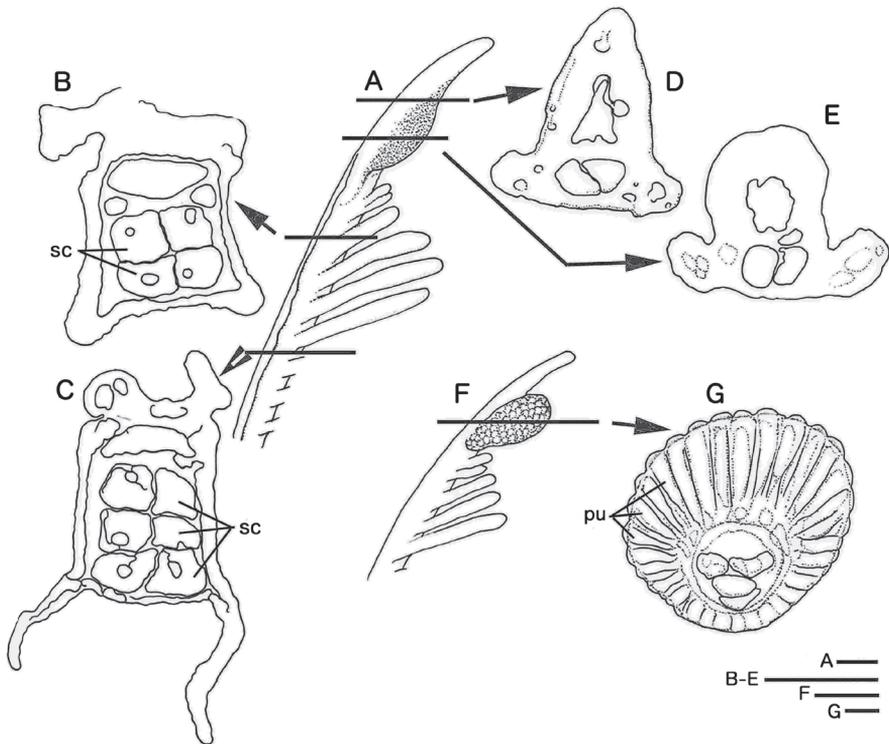


Figure 5. *Notaulax yamasui* sp. n. (**A–E**) and *Megalomma* sp. (**F, G**), internal structure of radiole. *Notaulax yamasui* sp. n. **A** radiole tip, lateral view **B, C** internal structure of proximal region of radiole **D, E**, internal structure of sub-distal swelling. *Megalomma* sp. **F, G** internal structure of compound eye **F** radiole with compound eye, lateral view **G** internal structure of compound eye, with many individual photoreceptor units (pu) **B–E** and **G** are drawn from sliced sections of eyes and radioles. Abbreviations: sc, skeletal cells; pu, photoreceptor unit. Scale bars 100 μm (**A**), 200 μm (**B–E**), 300 μm (**F**), 20 μm (**G**).

Discussion

Systematics

Under the stereo-microscope the radiolar sub-distal swellings of *Notaulax yamasui* sp. n., pigmented in the holotype, superficially resemble the typical radiolar compound eyes of the genera *Megalomma* and *Stylomma*, while other characters are typical of other sabellid genera lacking such eyes: the linear collar chaetae fascicles of *Notaulax*, *Panousea* Rullier and Amoureux, 1970, or *Panoumethus* Fitzhugh, 2002; the loosely aligned simple radiolar eyes of *Hypsicomus*, *Notaulax*, and *Anamobaea*; the long radiolar lobes of *Stylomma*, *Notaulax*, and *Anamobaea*. From these, *Panousea* and *Panoumethus* were ruled out from the beginning due to the presence of thoracic acicular uncini.

The fan-worm eyes and other photoreceptors are summarized in Bok and Nilsson (2016) and Bok et al. (2016). The compound eyes of *Stylomma* are stalked, which occurs neither in *Megalomma*, nor in the swellings of *N. yamasui* sp. n. The radiolar sub-distal swellings of the specimens of *N. yamasui* sp. n. were compared with the compound eyes of an unidentified *Megalomma* specimen collected at Katsuura, Chiba (Honshu, Japan). Scanning electron micrographs of *Megalomma* sp. eyes showed a surface structure analogous to the insect compound eyes, with many individual lenses arranged in a geometrical array (Fig. 4C, D). This does not occur in the sub-distal radiolar swellings of *N. yamasui* sp. n., where the surface of the swellings does not show any kind of special array (Fig. 4A). Moreover, while the former eyes have clearly defined edges, the latter have diffused edges around the swelling.

The internal morphology of both structures in *Megalomma* sp. and *N. yamasui* sp. n. compared through histological cross-sections showed ultrastructural differences: *Megalomma* sp. presents lenticular photoreceptor units (Fig. 5G), while the swellings of *N. yamasui* sp. n. are structurally similar to other regions of the radioles (Fig. 5B–E). These differences show that the new species lacks the compound eyes typical of *Megalomma* or *Stylomma*.

The remaining three genera (*Notaulax*, *Anamobaea*, and *Hypsicomus*) belong to a well-defined group inside the Sabellidae (Fitzhugh 1989: Clade IV in fig. 28; Nogueira et al. 2010: clade in figs 18–20, 22). These three genera share a number of features, including the presence of scattered simple radiolar eyes along the lateral margins of the radioles (Fig. 1E, F). However, *Hypsicomus* and *Anamobaea* can be easily separated from *Notaulax* and the new species by having the collar chaetae arranged in a bundle, instead of a long row. Besides, the spine-like shape of the superior thoracic notochaetae of the new species is typical of *Notaulax*, while in both *Hypsicomus* and *Anamobaea* thoracic notochaetae are elongated and narrowly hooded.

Finally, other characters typical for the genus *Notaulax* and also present in the new species, such as long flanged radiolar lobes, gave further support to its identification as a member of the genus. The genera *Hypsicomus* and *Notaulax* were partially revised by Perkins (1984) who, after examining the type species of *Hypsicomus*, the Adriatic *H. stichophthalmos* (Grube, 1863), redefined the genus and transferred to *Notaulax* all

but the type species previously included in *Hypsicomus*. This means that the literature records of coral-boring *Hypsicomus phaeotaenia sensu lato* or *Hypsicomus* ssp. would be referable to *Notaulax* species (see below).

Among the members of the genus *Notaulax* (see Perkins 1984, Capa and Murray 2015), *N. yamasui* sp. n. is unique in having radiolar sub-distal swellings and L-shaped distributed collar chaetae. Another remarkable character of *Notaulax yamasui* sp. n. is the structure of the dorsal basal flange, which is rounded and long (Fig. 1A, D), with bases closed dorsally by a dorsal joint (Fig. 1P). A similar structure was reported in *Stylomma palmatum* (Quatrefages, 1866) by Capa (2008). In Japanese waters, the only recorded *Notaulax* species is *N. lyra* (Moore and Bush, 1904). *Notaulax yamasui* sp. n. is differentiated from *N. lyra* by the presence of radiolar subdistal swellings, a much longer inter-radiolar membrane which is about half the length of the radioles (Fig. 1A), and the color pattern of radioles (two or three brown bands in the former species, and reddish brown eyes pots occupying the basal three-tenth of radiole in the latter species) (Imajima and Hartman 1964).

The entire posterior peristomial ring collar is also an uncommon feature among *Notaulax* species, being described only in two other species: *Notaulax pyrrhogaster* (Grube, 1878) from Philippine Islands, and *N. alticollis* (Grube, 1868) from the Red Sea. Like in these two species, *N. yamasui* sp. n. also shows the ventral margin of the collar more or less extended forward, forming a triangular lobe. However, neither of those two species has radiolar distal swellings, nor the collar chaetae in an L-shaped arrangement. Besides, *N. pyrrhogaster* does not show simple radiolar eyes (likely not faded by alcohol, as according to Wiktor (1980), the syntype has been preserved in formalin), and *N. alticollis* has the group of radiolar eyes positioned along two rows with less than 15 eyes in each, corresponding to about 7 pinnules in length. *Notaulax yamasui* sp. n. has the radiolar eyes in a group corresponding to about 11-12 pinnules in length, with 8–12 eyes in a single row. Capa and Murray (2015) recorded *Notaulax* sp., having radiolar eyes (noted as radiolar ocelli) arranged in a single row or in teardrop-shaped groups. Other types of radiolar eyes and further details about their structure can be found in Bok et al. (2016).

Ecology of *Notaulax*

The two types of *Notaulax yamasui* sp. n. were found living embedded in dead masses of coral *Porites* sp. Boring by worms in coral reefs is a common and very well-known phenomenon described as early as in 1902 by Gardiner (1902), and recently revised by Hutchings (2008). With the prevalent predation pressures at shallow coral reefs being high, the advantage of burrowing for protection into hard surfaces such as corals seems obvious, with positions submitted to currents and vertical surfaces being particularly favored by filter feeders to maximize feeding benefits and avoid sedimentation (Elias 1986, Hutchings 1986). Normally worms only bore into dead corals, or in the dead edges of living corals, avoiding contact with the soft parts. The recruitment by the worms is believed to be entirely *via* larvae or juveniles settling on the surface; as coral

polyps are carnivores, the successful recruitment and subsequent boring is restricted mainly to the coral areas where polyps are damaged or very scarce (Hutchings and Murray 1982, Hutchings 2008).

Boring by worms plays an important role in the bio-erosion of coral reefs, but much less so than grazing by echinoids and fish, with boring polychaete species belonging to several families (the most important being Eunicidae, Lumbrineridae, Dorvilleidae, Oeonidae, Spionidae, Cirratulidae, and Sabellidae) and also Sipuncula (Warne 1975, Hutchings 1986, Hutchings and Peyrot-Clausade 2002, Hutchings 2008). Boring mechanisms in polychaetes can include mechanical (Eunicida) or chemical methods (Spionidae, Sabellidae, and probably Cirratulidae) (Hutchings 2008), and normally tubes or holes made by boring organisms can be recognized by their nearly constant diameter, as they are bored continuously to accommodate the growth of the host corals (Nishi and Nishihira 1999).

Many (if not all) Sabellidae *sensu* Kupriyanova and Rouse, 2008 secrete mucus tubes by ventral sacs, general body walls, ventral gland shields, and parapodial glands, and at least in five genera (*Sabella*, *Myxicola* Koch in Renier, 1847, *Pseudopotamilla* Bush, 1905, *Perkinsiana* Knight-Jones, 1983, and *Sabellastarte* Krøyer, 1856) the tubes are made of acid mucopolysaccharide-protein complexes (Chungtai and Knight-Jones 1988, Hutchings 2008). Hartman (1954) already suggested that the penetrating effect of *Notaulax* sp. (as *Hypsicomus phaeotaenia*) could be a result of a chemical action on the coral surface (see below).

Similarly, larvae of *Notaulax* species settle on dead corals, probably benefiting from the rugose surface for protection, while burrowing holes into the dead coral mass. A transverse section of a *Notaulax* sp. burrow in a *Porites* sp. coral is represented in Nishi and Nishihira (1999).

Many sabellids are known to live in hard carbonate substrates and some of them have been described as having their tubes embedded into substrates such as rocks (*Sabellastarte magnifica* (Shaw, 1800); *Pseudopotamilla reniformis* (Bruguière, 1789); *Parasabella saxicola* (Grube, 1861), as *Demonax brachychona* (Claparède, 1870); *Potamethus mucronatus* (Moore, 1923)), concretions of coralline algae (*Demonax langerhansi* Knight-Jones, 1983), shells or limestone (*Perkinsiana rubra* (Langerhans, 1880)), abalone shells (*Terebrasabella heterouncinata* Fitzhugh and Rouse, 1999) or shells of freshwater mollusks (genus *Caobangia*) (Jones 1974, Chungtai and Knight-Jones 1988, Fitzhugh and Rouse 1999, Kuris and Culver 1999, Simon et al. 2005, Moreno et al. 2006).

At least seven species of *Notaulax* live embedded in dead corals (see below), and the same is true for one undescribed *Megalomma* species (Chughtai and Knight-Jones 1988), one undescribed species of Fabriciidae (Hutchings and Peyrot-Clausade 2002), *Potamilla ehlersi* Gravier, 1906, *Megalomma claparedii* (Gravier, 1906) (as *Branchiomma*), *M. circumspectum*, *Branchiomma* cf. *bairdi*, *Megalomma mushaense* (Gravier, 1906) (as *Branchiomma mushaensis*), *Megalomma miyukiae* Nishi, 1998, *Perkinsiana fonticula* (Hoagland, 1919) (as *Parasabella*), *Amphicorina schlenzae* Nogueira and Amaral, 2000, *A. bichaeta* Capa and López, 2004, *A. perkinsi* Capa and López, 2004, *Amphiglena jimenezii* Capa and López, 2004, *Pseudobranchiomma minima* Nogueira and Knight-Jones, 2002, *Bispira paraporifera* Tovar-Hernández & Salazar-Vallejo, 2006,

B. melanostigma (Schmarda, 1861), *Pseudopotamilla intermedia* Moore, 1905, or *Pseudopotamilla fitzhughii* Tovar-Hernández & Salazar-Vallejo, 2006 (Gravier 1906, Nishi 1998, Nogueira and Amaral 2000, Nogueira and Knight-Jones 2002, Capa and López 2004, Tovar-Hernández and Salazar-Vallejo 2006), but the list is probably much longer. In many cases, lack of ecological data on the described species hides the boring habitat of the worm, while in others it is not clear whether the worms were embedded in the hard carbonate substrates or just associated with them.

Scleractinian corals seem to constitute the preferred habitat of the genus *Notaulax*. From the 20 described species of *Notaulax* valid according to Perkins (1984), besides *N. yamasui* sp. n., six are known to bore into coral masses (*N. nudicollis* (Krøyer, 1856); *N. occidentalis* (Baird, 1865); *N. marenzelleri* (Gravier, 1906); *N. pigmentata* (Gravier, 1906); *N. midoculi* (Hoagland, 1919); and *N. bahamensis* Perkins, 1984), and one was found associated with a fossil reef (*N. longithoracalis* (Hartmann-Schröder, 1980)) (Gravier 1906, Perkins 1984, Capa and López 2004, Tovar-Hernández and Salazar-Vallejo 2006). Additionally, Capa and Murray (2015) reported *Notaulax* spp. 1, 2 and 3 from the coral reef of Lizard Island, Great Barrier Reef, Australia. The remainder of the species have been described with no information on the substrates where they were collected, but one indeterminate species (*Notaulax* sp., in Fitzhugh 2002) was found in muddy sand.

Giangrande and Licciano (2004: fig. 4g) reported species richness of the genus *Notaulax* along global latitudinal belts. It is clear that *Notaulax*, being absent from the polar regions, has a preferentially tropical distribution, with the most records occurring between 30°N and S, and a clear domain in the northern hemisphere. This asymmetrical distribution between the hemispheres is probably simply due to a 'concentration effect', a consequence of the higher number of specialists working in the northern hemisphere, where some of the most studied marine faunas of the world are also located (Giangrande and Licciano 2004).

The latitudinal distribution of *Notaulax* fits almost perfectly the global carbonate production, especially as aragonite (Buddemeier 1997: fig. 1; Wood 2001: fig. 1), and by extension, the location of the scleractinian coral reefs (composed mainly by aragonite), also up to about 30°N and S, beyond which coral reefs are usually absent. *Notaulax* species seem to be typically borers, mainly in corals, but also in other carbonate (apparently mainly in aragonite) substrates. Besides the above cited species, references to *Notaulax* specimens as coral borers are frequent in the literature on coral reef polychaetes, especially as unidentified *Hypsicomus* species (e.g., Hartman 1954, Marsden 1960, Peyrot-Clausade et al. 1992, Nishi 1997, Hutchings and Peyrot-Clausade 2002), as *H. elegans* (see Gibbs 1969), *H. phaeotaenia* (see Hutchings et al. 1992), or as *Notaulax* sp. (Nishi and Nishihira 1999, Capa and Murray 2015).

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A new species of terrestrial-breeding frog (Amphibia, Craugastoridae, *Pristimantis*) from high elevations of the Pui Pui Protected Forest in central Peru

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Abstract

We describe a new species of *Pristimantis* from upper montane forests and high Andean grasslands of the Pui Pui Protected Forest and its close surroundings, Región Junín, central Peru. The description of the new species is based on 34 specimens found at elevations between 3400 and 3936 m a.s.l. *Pristimantis attenboroughi* sp. n. is characterized by a snout–vent length of 14.6–19.2 mm in adult males (n = 21), 19.2–23.0 mm in adult females (n = 10), and is compared morphologically and genetically with other taxonomically and biogeographically relevant species of *Pristimantis*. The new species is characterized by having narrow digits that lack circumferential grooves, irregularly shaped, discontinuous dorsolateral folds, and absence of both tympanic membrane and tympanic annulus. The high similarity in morphology between *P. attenboroughi* sp. n. and members of the Andean genera *Phrynopus* and *Bryophryne* provides an example for convergent evolution, and highlights the importance of using molecular data to justify generic assignment. *Pristimantis attenboroughi* sp. n. is most similar to *Phrynopus chaparroi* from the Región Junín, suggesting that the generic placement of this species needs to be revised. Phylogenetically the new species belongs to the *Pristimantis danae* species Group, a clade that includes several *Pristimantis* species distributed in the montane forests of central Peru, including *P. albertus*, *P. aniptopalmaris*, *P. ornatus*, and *P. stictogaster*.

Keywords

Andes, DNA barcoding, frogs, molecular phylogeny, montane forest, *Pristimantis attenboroughi* new species, Puna

Introduction

The Pui Pui Protected Forest (Bosque de Protección Pui Pui, hereafter PPPF, Fig. 1) is located in the Selva Central of Peru and is one of twelve natural protected areas with different levels of legal protection such as national parks, national sanctuaries, and national reserves in the regions of Pasco and Junín (SERNANP 2010). The PPPF, located in the Región Junín, was established in 1985 and covers 60,000 hectares encompassing montane forest (30%) and high Andean grassland (Puna; 70%) habitats (SERNANP 2010). The area protects the upper watershed of several rivers and includes elevations between 1700 and 4500 m a.s.l. (SERNANP 2010).

In 2012–2014, we conducted herpetological surveys in montane forests and Puna of the PPPF to catalog the amphibian and reptile species and to evaluate their conservation status. As a result, we found several new species of frogs (Craugastoridae) as well as new species of lizards (Gymnophthalmidae). All new species were compared morphologically and genetically with other taxonomically and biogeographically relevant taxa mostly from Ecuador, Peru, and Bolivia. Herein we describe a new species of *Pristimantis* from upper montane and Puna habitats collected between 2012 and 2013.

Materials and methods

Fieldwork. Because of its remote location, the PPPF is difficult to reach and is only accessible through a few entrances located ca. 1–2 days of walking distance from the nearest villages. The upper montane forests and Puna of the PPPF were reached from Toldopampa (11°30'15.4"S, 74°55'32.7"W, 3670 m a.s.l., ca. 45 km SW from Satipo) with the help of local guides by walking in 1.5 days (ca. 11 km airline). In 2012 fieldwork was conducted between May 8 and 21 by EL and RvM, and in 2013 between June 21 and July 8 by EL, J. Moravec, and J.C. Cusi. Amphibians were preserved in 96% ethanol and stored in 70% ethanol. Deposited eggs were stored in 70% ethanol.

Morphological characters. The format for the description follows Lynch and Duellman (1997), except that the term dentigerous processes of vomers is used instead of vomerine odontophores (Duellman et al. 2006), and diagnostic characters are those of Duellman and Lehr (2009). Taxonomic classification follows Hedges et al. (2008), except that we followed Pyron and Wiens (2011) for family placement and Padiál et al. (2014) for names of *Pristimantis* species groups. Sex and maturity of specimens were identified by observing gonads through dissections. Specimens were considered juveniles when gonads were too small to distinguish between sexes. The tympanic region of two specimens (MUSM 31199, NMP6V 75534) was opened to see if a tympanic annulus is present under the skin. We measured the following variables to the nearest 0.1 mm with digital calipers under a stereomicroscope: snout–vent length (SVL, straight length distance from tip of snout to vent), tibia length (TL, distance from the knee to the distal end of the tibia), foot length (FL, distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), head length (HL, from angle of jaw to tip

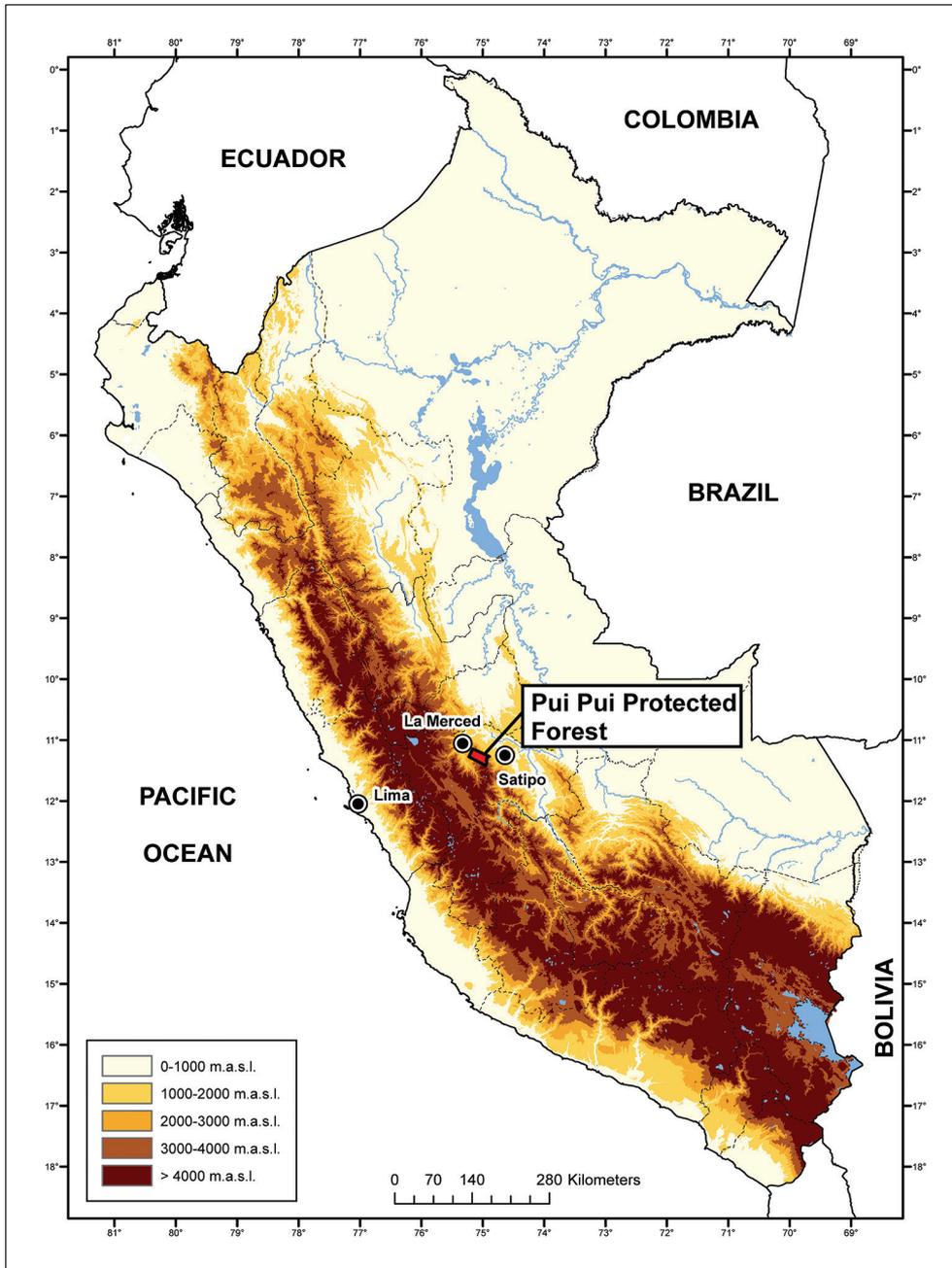


Figure 1. Map of Peru with the Pui Pui Protected Forest indicated in red.

of snout), head width (HW, at level of angle of jaw), horizontal eye diameter (ED), interorbital distance (IOD), upper eyelid width (EW), internarial distance (IND), eye–nostril distance (E–N, straight line distance between anterior corner of orbit and

posterior margin of narial opening), and egg diameter. Fingers and toes are numbered preaxially to postaxially from I–IV and I–V, respectively. We compared the lengths of toes III and V by adpressing both toes against Toe IV; lengths of fingers I and II were compared by adpressing the fingers against each other. All drawings were made by EL using a stereomicroscope and a camera lucida. Photographs taken by EL and RvM were used for descriptions of coloration in life. Comparisons of congeners focus on species in similar habitats from Ecuador and Peru and those with close phylogenetic relationships as recovered in our phylogenetic trees. Information on species for comparative diagnoses was obtained from Duellman and Lehr (2009) and from original species descriptions. For specimens examined see Appendix. Codes of collections are: MUSM = Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima, Peru; NMP6V = National Museum Prague, Prague, Czech Republic; UMMZ = University of Michigan Museum of Zoology, Ann Arbor, USA. Field number code is: IWU = Illinois Wesleyan University, Bloomington, USA. Conservation status was evaluated using the criteria in IUCN (2001). Maps were designed with ArcGIS 10.0 by J.C. Cusi.

Molecular phylogenetic analysis. The phylogenetic position of the new species with respect to other morphologically similar species was determined through analysis of DNA sequence data. This analysis included two mitochondrial genes, 16S rRNA (16S) and 12S rRNA (12S). We used tissue samples from specimens collected in central Peru (Región Junín) to obtain DNA sequences for the new species and several other *Pristimantis* species (Table 1). Additionally, we downloaded selected sequences of morphologically similar taxa (*Bryophyrne*, *Lynchius*, *Phrynopus*, *Oreobates*) distributed at high elevations (> 2000 m a.s.l.) from Genbank (Table 1). We included *Hamptophyrne boliviana*, *Ischnocnema guentheri*, and *Bufo melanostictus* as outgroup taxa (Padial et al. 2014).

Extraction, amplification, and sequencing of DNA followed protocols previously used for Neotropical terrestrial breeding frogs (Lehr et al. 2005, Hedges et al. 2008). We used the 16SA (forward) primer (5'-3' sequence: CGCCTGTTTATCAAAAACAT) and the 16SB (reverse) primer (5'-3' sequence: CCGGTCTGAACTCAGATCACGT) to amplify a fragment of the 16S gene (Palumbi et al. 1991), and we employed the following thermocycling conditions to amplify DNA using the polymerase chain reaction (PCR): 1 cycle of 96°C/3 min; 35 cycles of 95°C/30 s, 55°C/45 s, 72°C/1.5 min; 1 cycle 72°C/7 min. Additionally, we used the L25195 (forward) primer (5'-3' sequence: AACTGGGATTAGATACCCCACTA) and the H2916 (reverse) primer (5'-3' sequence: GAGGGTGACGGGCGGTGTGT) to amplify a fragment of the 12S gene (Palumbi et al. 1991, Vences et al. 2000), and we employed the following thermocycling conditions to amplify DNA using PCR: 1 cycle of 94°C/1.5 min; 35 cycles of 94°C/45 s, 50°C/1 min., 74°C/2 min; 1 cycle 72°C/10 min. We completed the cycle sequencing reactions by using the corresponding PCR primers and the Big-Dye Terminator 3.1 (Applied Biosystems), and obtained sequence data by running the purified reaction products in an ABI 3730 Sequence Analyzer (Applied Biosystems). The newly obtained sequences are deposited in GenBank (Table 1).

Table 1. GenBank accession numbers for taxa and genes sampled in this study.

Taxon	16S	12S	Voucher_Nbr	Reference
<i>Bryophryne bakersfield</i>	KT276289	na	MHNC5999	Chaparro et al. 2015
<i>Bryophryne bakersfield</i>	KT276287	KT276281	MHNC6022	Chaparro et al. 2015
<i>Bryophryne bakersfield</i>	KT276290	KT276282	MHNC6023	Chaparro et al. 2015
<i>Bryophryne bakersfield</i>	KT276291	KT276283	MHNC6007	Chaparro et al. 2015
<i>Bryophryne bakersfield</i>	KT276288	KT276284	MHNC6009	Chaparro et al. 2015
<i>Bryophryne bustamantei</i>	KT276293	KT276286	MHNC6019	Chaparro et al. 2015
<i>Bryophryne cophites</i>	EF493537	EF493537	KU173497	Heinicke et al. 2007
<i>Bufo melanostictus</i>	FJ882791	FJ882791	VUB 0052	Van Bocxlaer et al. 2009
<i>Hamptophryne boliviana</i>	DQ283438	DQ283438	na	Frost et al. 2006
<i>Ischnocnema guentheri</i>	EF493533	EF493533	na	Heinicke et al. 2007
<i>Lynchius flavomaculatus</i>	EU186667	EU186667	KU218210	Hedges et al. 2008
<i>Lynchius nebulanastes</i>	EU186704	EU186704	KU181408	Hedges et al. 2008
<i>Lynchius oblitus</i>	AM039640	AM039708	MUSM19914	Lehr et al. 2005, Motta et al. 2016
<i>Lynchius oblitus</i>	AM039639	AM039707	MTD45954	Lehr et al. 2005, Motta et al. 2016
<i>Lynchius parkeri</i>	EU186705	EU186705	KU181307	Hedges et al. 2008
<i>Lynchius simmonsii</i>	JF810004	JF809940	QZ41639	Padial et al. 2014
<i>Oreobates amarakaeri</i>	JF809996	JF809934	MHNC6975	Padial et al. 2014
<i>Oreobates ayacucho</i>	JF809970	JF809933	MNCN_IDIR5024	Padial et al. 2014
<i>Oreobates cruzalis</i>	EU186666	EU186666	KU215462	Hedges et al. 2008
<i>Oreobates gemcare</i>	JF809960	JF809930	MHNC6687	Padial et al. 2014
<i>Oreobates granulosis</i>	EU368897	JF809929	MHNC3396	Padial et al. 2014
<i>Phrynopus auriculatus</i>	EF493708	EF493708	KU291634	Heinicke et al. 2007
<i>Phrynopus barthlenae</i>	AM039653	AM039721	SMF81720	Lehr et al. 2005
<i>Phrynopus bracki</i>	EF493709	EF493709	USNM286919	Heinicke et al. 2007
<i>Phrynopus bufoides</i>	AM039645	AM039713	MUSM19860	Lehr et al. 2005
<i>Phrynopus heimorum</i>	AM039635	AM039703	MTD45621	Lehr et al. 2005
<i>Phrynopus heimorum</i>	AM039636	AM039704	MTD45622	Lehr et al. 2005
<i>Phrynopus horstpauli</i>	AM039651	AM039719	MTD44333	Lehr et al. 2005
<i>Phrynopus horstpauli</i>	AM039647	AM039715	MTD44334	Lehr et al. 2005
<i>Phrynopus kauneorum</i>	AM039650	AM039718	MTD44332	Lehr et al. 2005
<i>Phrynopus kauneorum</i>	AM039655	AM039723	MUSM20595	Lehr et al. 2005
<i>Phrynopus pesantesi</i>	AM039656	AM039724	MTD45072	Lehr et al. 2005
<i>Phrynopus tautzorom</i>	AM039652	AM039720	MUSM20613	Lehr et al. 2005
<i>Phrynopus tribulosus</i>	EU186725	EU186707	KU291630	Hedges et al. 2008
<i>Pristimantis acuminatus</i>	EU130579	na	QCAZ19664	Elmer et al. 2007
<i>Pristimantis albertus</i>	EU186695	EU186695	KU291675	Hedges et al. 2008
<i>Pristimantis albertus</i>	KY594749	na	RVM41_14	This study
<i>Pristimantis albertus</i>	KY594750	na	RVM42_14	This study
<i>Pristimantis albertus</i>	KY594751	na	RVM527	This study
<i>Pristimantis altamazonicus</i>	EF493670	EF493670	KU215460	Heinicke et al. 2007
<i>Pristimantis altamazonicus</i>	DQ195449	na	MC11717	Mahecha et al., unpublished
<i>Pristimantis aniptopalrnatus</i>	EF493390	EF493390	KU291627	Heinicke et al. 2007
<i>Pristimantis aniptopalrnatus</i>	EU186694	EU186694	KU291666	Padial et al. 2014

Taxon	16S	12S	Voucher_Nbr	Reference
<i>Pristimantis attenboroughi</i> sp. n.	KY594752	na	MUSM31186	This study
<i>Pristimantis attenboroughi</i> sp. n.	KY594753	KY594761	NMP6V75522	This study
<i>Pristimantis attenboroughi</i> sp. n.	KY594754	KY594762	NMP6V75524	This study
<i>Pristimantis attenboroughi</i> sp. n.	KY594755	KY594763	NMP6V75525	This study
<i>Pristimantis attenboroughi</i> sp. n.	KY594756	KY594764	NMP6V75528	This study
<i>Pristimantis attenboroughi</i> sp. n.	KY594757	na	NMP6V75529	This study
<i>Pristimantis aureoventris</i>	JQ742152	na	VUB3748	Kok et al. 2012
<i>Pristimantis bipunctatus</i>	EF493702	EF493702	KU291638	Heinicke et al. 2007
<i>Pristimantis bipunctatus</i>	KY594758	na	MUSM31179	This study
<i>Pristimantis</i> cf. <i>mendax</i>	KY628996	na	MUSM31157	This study
<i>Pristimantis</i> cf. <i>mendax</i>	EU186659	na	MTD45080	Hedges et al. 2008
<i>Pristimantis croceoinguinis</i>	KY594759	na	MUSM31154	This study
<i>Pristimantis cruciocularis</i>	EU186656	EU186656	KU291673	Hedges et al. 2008
<i>Pristimantis cruciocularis</i>	KY594760	na	NMP6V75535	This study
<i>Pristimantis danae</i>	EU192270	na	MNCN44234	Padial and De la Riva 2009
<i>Pristimantis diadematus</i>	EU186668	EU186668	KU221999	Hedges et al. 2008
<i>Pristimantis llojsintuta</i>	EU712641	na	MNCNDNA7314	Padial et al. 2009
<i>Pristimantis melanogaster</i>	EF493664	EF493826	na	Heinicke et al. 2007
<i>Pristimantis orestes</i>	EF493388	EF493388	KU218257	Heinicke et al. 2007
<i>Pristimantis ornatus</i>	EU186660	EU186660	MTD45073	Hedges et al. 2008
<i>Pristimantis petrobarbus</i>	EF493367	EF493825	KU212293	Heinicke et al. 2007
<i>Pristimantis platydactylus</i>	EU712653	na	MNCNDNA3943	Padial et al. 2009
<i>Pristimantis platydactylus</i>	EU712671	na	MNCNDNA4138	Padial et al. 2009
<i>Pristimantis platydactylus</i>	EU712718	na	MNCNDNA6377	Padial et al. 2009
<i>Pristimantis pluvialis</i>	KX155577	na	CORBIDI_11862	Shepack et al. 2016
<i>Pristimantis pluvialis</i>	KX155578	na	CORBIDI_16695	Shepack et al. 2016
<i>Pristimantis reichlei</i>	EF493707	EF493707	MUSM9267	Padial et al. 2014
<i>Pristimantis rhabdocnemus</i>	EU186706	EU186724	KU291651	Hedges et al. 2008
<i>Pristimantis rhabdolaemus</i>	EF493706	EF493706	KU173492	Heinicke et al. 2007
<i>Pristimantis sagittulus</i>	EF493705	EF493705	KU291635	Duellman and Hedges 2005
<i>Pristimantis schultei</i>	EF493681	na	KU212220	Heinicke et al. 2007
<i>Pristimantis simonbolivari</i>	EF493671	EF493671	KU218254	Heinicke et al. 2007
<i>Pristimantis simonsii</i>	EU186665	EU186665	KU212350	Hedges et al. 2008
<i>Pristimantis skydmainos</i>	EF493393	EF493393	MUSM10071	Heinicke et al. 2007
<i>Pristimantis</i> sp.	AM039658	na	MTD45201	Lehr et al. 2005
<i>Pristimantis stictogaster</i>	EF493704	EF493704	KU291659	Heinicke et al. 2007
<i>Pristimantis tofae</i>	EF493353	EF493353	KU215493	Heinicke et al. 2007
<i>Pristimantis tofae</i>	EU192294	na	MNCN43246	Padial and De la Riva 2009
<i>Pristimantis wiensi</i>	EF493668	EF493377	KU219796	Heinicke et al. 2007

Geneious R6, version 6.1.8 (Biomatters 2013; <http://www.geneious.com/>) was used to align the sequences. Within Geneious, we used the MAFFT, version 7.017 (Kato and Standley 2013) alignment program. Prior to conducting phylogenetic analysis, we used PartitionFinder, version 1.1.1 (Lanfear et al. 2012) to select the appropriate models of nucleotide evolution and used the Bayesian information criterion (BIC) to

determine the best partitioning scheme and substitution model for each gene. According to PartitionFinder, the best scheme included one partition combining both 12S and 16S and the best model of nucleotide substitution was GTR + I + Γ . Phylogenetic analysis was done using Maximum Likelihood (ML) approach using RaxML version 8.2.4 (Stamatakis 2006), where the “f-a” function was employed to conduct a bootstrap analysis and search for the optimal likelihood tree. Our analysis included 82 terminals and a 922 bp concatenated alignment that included the 16S and 12S dataset. The GTR + I + Γ model of nucleotide substitution was used to perform 200 trees searches; node support was assessed using 1000 bootstrap replicates. Additionally, we used the R package ‘APE’ (Paradis et al. 2004) to estimate uncorrected p-distances (i.e., the proportion of nucleotide sites at which any two sequences are different).

Results

Molecular phylogenetic analysis. The Maximum Likelihood (ML) tree (Fig. 2) was generally congruent with a previous molecular phylogeny (Padial et al. 2014) and supported the distinctiveness of the new species from other closely related taxa. Placement of *Pristimantis attenboroughi* sp. n. in the genus *Pristimantis* Jiménez de la Espada, 1871 was strongly supported and, based on the available data, the new species is most closely related to *P. albertus* Duellman and Hedges, 2007, *P. aniptopalmatum* (Duellman and Hedges, 2005), *P. ornatus* (Lehr, Lundberg, Aguilar, and von May, 2006), and *P. stictogaster* (Duellman and Hedges, 2005) (Fig. 2). Table 2 compares uncorrected p-distances of a 542 bp (including gaps) fragment of the 16S mitochondrial rRNA gene of *Pristimantis* species included in our analyses. The lowest distance occurs between the new species and *P. aniptopalmatum* (uncorrected p-distance 4.3 %) while the uncorrected p-distances between the new species and the other three species in the same clade of the *Pristimantis danae* species Group (*P. albertus*, *P. ornatus*, *P. reichlei* Padial and De la Riva, 2009, *P. rhabdolaemus* [Duellman, 1978a], *P. stictogaster* [Duellman and Hedges, 2005], *P. sagittulus* [Lehr, Aguilar, and Duellman, 2004], *P. toftae* [Duellman, 1978b]) vary between 5.2 to 11.8 %.

Pristimantis attenboroughi sp. n.

<http://zoobank.org/DCE88D49-0EB1-4DA4-A672-5341763B3236>

Common name. English: Attenborough’s Rubber Frog. Spanish: Rana cutín Attenborough.

Holotype. MUSM 31196 (IWU 178, Figs 3, 4), adult male from the Pui Pui Protected Forest, Provincia Satipo, Región Junín, Peru, Upper part of Quebrada Tarhuish, “Laguna Udrecocha”, Puna, open area on east side of Laguna Udrecocha, 11°23'24.1"S, 74°58'32.5"W, 3936 m a.s.l. (Fig. 8A), collected on 17 May 2012 by E. Lehr and R. von May.

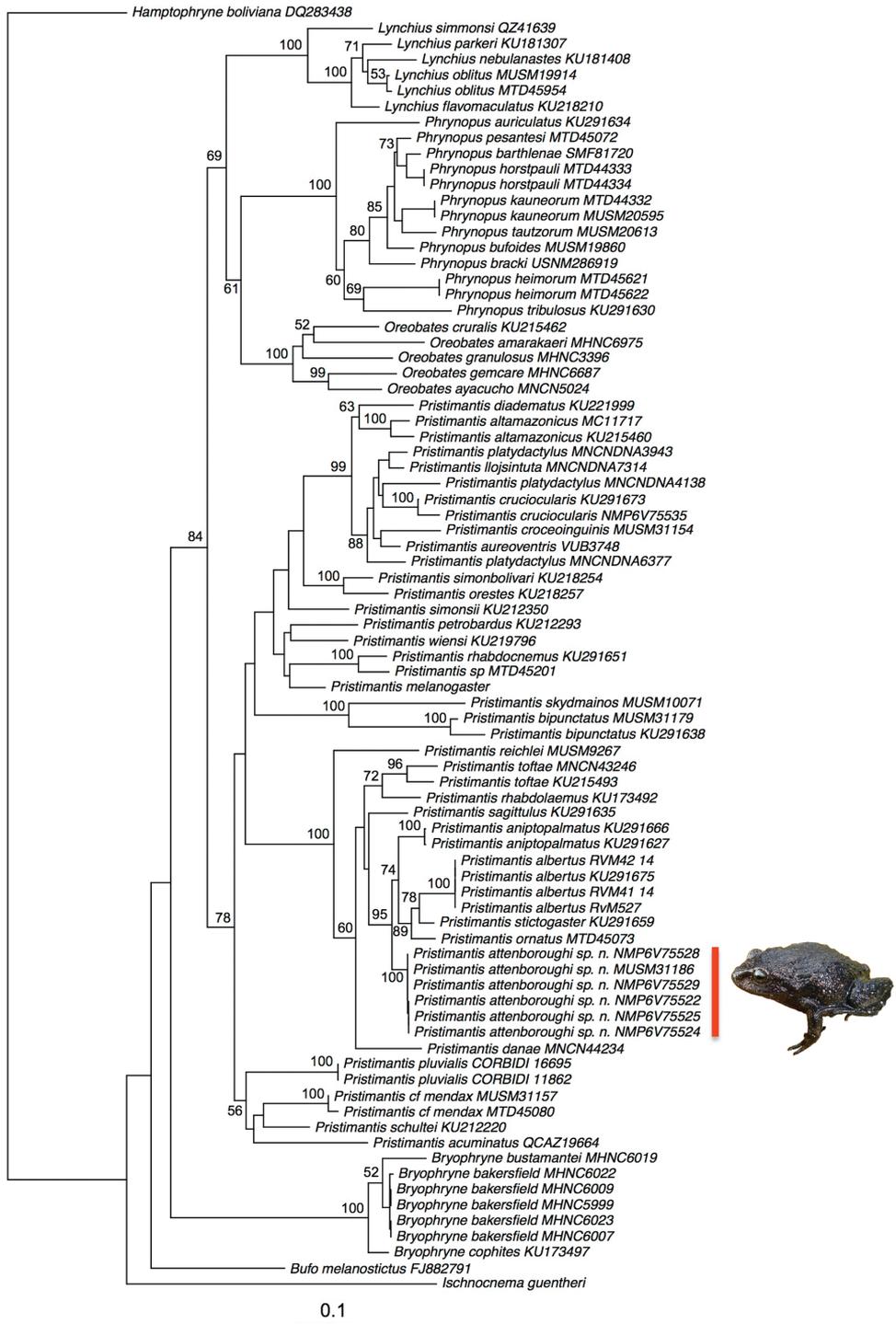


Figure 2. Maximum Likelihood (ML) phylogeny based on the combined 16S + 12S dataset (ML bootstrap values >50 are indicated at each node).

Table 2. Uncorrected p-distances of the 16s mitochondrial rRNA gene for six specimens of *Pristimantis attenboroughi* sp. n. (in bold) and other *Pristimantis* species from GenBank.

		1	2	3	4	5	6	7	8	9
1	<i>Pristimantis albertus</i> KU291675									
2	<i>Pristimantis albertus</i> RvM41_14	0.000								
3	<i>Pristimantis albertus</i> RvM42_14	0.000	0.000							
4	<i>Pristimantis albertus</i> RvM527	0.000	0.000	0.000						
5	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75522	0.062	0.065	0.062	0.066					
6	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75529	0.062	0.065	0.062	0.066	0.000				
7	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75524	0.062	0.065	0.062	0.066	0.000	0.000			
8	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75525	0.062	0.065	0.062	0.066	0.000	0.000	0.000		
9	<i>Pristimantis attenboroughi</i> sp. n. MUSM 31186	0.062	0.065	0.062	0.066	0.000	0.000	0.000	0.000	
10	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75528	0.062	0.065	0.062	0.066	0.000	0.000	0.000	0.000	0.000
11	<i>Pristimantis ornatus</i> MTD45073	0.056	0.059	0.056	0.059	0.052	0.052	0.052	0.052	0.052
12	<i>Pristimantis stictogaster</i> KU291659	0.041	0.043	0.041	0.043	0.049	0.049	0.049	0.049	0.049
13	<i>Pristimantis aniptopalmodus</i> KU291627	0.056	0.059	0.056	0.059	0.043	0.043	0.043	0.043	0.043
14	<i>Pristimantis aniptopalmodus</i> KU291666	0.056	0.059	0.056	0.059	0.043	0.043	0.043	0.043	0.043
15	<i>Pristimantis rhabdolaemus</i> KU173492	0.093	0.097	0.093	0.097	0.058	0.058	0.058	0.058	0.058
16	<i>Pristimantis toftae</i> KU215493	0.110	0.115	0.110	0.115	0.074	0.074	0.074	0.074	0.074
17	<i>Pristimantis toftae</i> MNCN43246	0.105	0.110	0.105	0.110	0.070	0.070	0.070	0.070	0.070
18	<i>Pristimantis sagittulus</i> KU291635	0.093	0.097	0.093	0.099	0.066	0.066	0.066	0.066	0.066
19	<i>Pristimantis danae</i> MNCN44234	0.116	0.121	0.116	0.122	0.094	0.094	0.094	0.094	0.094
20	<i>Pristimantis reichlei</i> MHNSM9267	0.132	0.135	0.132	0.136	0.118	0.118	0.118	0.118	0.118

Paratypes. A total of 33 (Figs 5–7, 8C), all from inside the PPPF (except for: MUSM 31199–31202, NMP6V 75526–29), Provincia Satipo, Región Junín: 10 adult females (MUSM 31977, 31980, 31987, 31201, NMP6V 75076, 75522 [GenBank accession numbers KY594753, KY594761], 75523, 75528 [GenBank accession numbers KY594756, KY594764], 75529 [GenBank accession number KY594757], 75534), 20 adult males (MUSM 31186 [GenBank accession number KY594752], 31195, 31199, 31202, 31975, 31979, 31988, 31989, 31992, 31993, NMP6V 75077–75079, 75524 [GenBank accession numbers KY594754, KY594762], 75525 [GenBank accession numbers KY594755, KY594763], 75526, 75527, 75533, UMMZ 244726, 244727), 3 juveniles (MUSM 31187, 31990, 31200).

MUSM 31186, MUSM 31187, NMP6V 75522, 75523: Quebrada Tarhuish, left bank of Antuyo River, “Shiusha”, upper montane forest, 11°22'3.9"S, 74°56'12.7"W, 3414 m a.s.l. collected on 12 May 2012 by E. Lehr and R. von May. MUSM 31195, NMP6V 75524, 75524: collected at the type locality along with the holotype. MUSM 31199, 31200, MUSM 31201, 31202, NMP6V

Table 2. Continued.

		10	11	12	13	14	15	16	17	18	19
1	<i>Pristimantis albertus</i> KU291675										
2	<i>Pristimantis albertus</i> RvM41_14										
3	<i>Pristimantis albertus</i> RvM42_14										
4	<i>Pristimantis albertus</i> RvM527										
5	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75522										
6	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75529										
7	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75524										
8	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75525										
9	<i>Pristimantis attenboroughi</i> sp. n. MUSM 31186										
10	<i>Pristimantis attenboroughi</i> sp. n. NMP6V 75528										
11	<i>Pristimantis ornatus</i> MTD45073	0.052									
12	<i>Pristimantis stictogaster</i> KU291659	0.049	0.037								
13	<i>Pristimantis aniptopalmatum</i> KU291627	0.043	0.048	0.049							
14	<i>Pristimantis aniptopalmatum</i> KU291666	0.043	0.048	0.049	0.000						
15	<i>Pristimantis rhabdolaemus</i> KU173492	0.058	0.082	0.076	0.074	0.074					
16	<i>Pristimantis toftiae</i> KU215493	0.074	0.091	0.091	0.083	0.083	0.070				
17	<i>Pristimantis toftiae</i> MNCN43246	0.070	0.099	0.088	0.082	0.082	0.074	0.055			
18	<i>Pristimantis sagittulum</i> KU291635	0.066	0.084	0.080	0.068	0.068	0.066	0.078	0.095		
19	<i>Pristimantis danae</i> MNCN44234	0.094	0.107	0.107	0.100	0.100	0.082	0.101	0.100	0.083	
20	<i>Pristimantis reichlei</i> MHNSM9267	0.118	0.124	0.113	0.117	0.117	0.103	0.126	0.114	0.117	0.113

75526, 75527: Upper part of Quebrada Tasta, “Laguna Luichococha”, Puna, 11°27'23.7"S, 74°55'10.6"W, 3708 m a.s.l. collected on 20 May 2012 by E. Lehr and R. von May. NMP6V 75528, 75529: near trail from Tasta to Tarhuish (first mountain peak), Polylepis forest patch, 11°26'8.6"S, 74°53'56.5"W, 3886 m a.s.l. collected on 20 May 2012 by E. Lehr and R. von May. MUSM 31975: Antuyo, 11°20'03.7"S, 74°59'49.1"W, 3700 m a.s.l. collected on 27 June 2013 by E. Lehr, J. Moravec, and J.C. Cusi. MUSM 31977, 31979, MUSM 31980, NMP6V 75076, UMMZ 244726: Hatunpata, 11°18'07.9"S, 75°01'35.0"W, 3710 m a.s.l. collected on 28 June 2013 by E. Lehr, J. Moravec, and J.C. Cusi. MUSM 31987–31990, NMP6V 75077, 75078, 75533, UMMZ 244727: Trancapampa, 11°17'49.2"S, 75°00'46.3"W, 3550 m a.s.l. collected on 2 July 2013 by E. Lehr, J. Moravec, and J.C. Cusi. MUSM 31992, 31993, NMP6V 75079, 75534: Antuyo Bajo, 11°18'53.4"S, 74°59'34.8"W, 3400 m a.s.l. collected on 4 July 2013 by E. Lehr, J. Moravec, and J.C. Cusi.



Figure 3. Life male holotype (MUSM 31196, SVL 18.9 mm) of *Pristimantis attenboroughi* sp. n. in dorsolateral view (A), dorsal view (B), flanks, groin, anterior surfaces of thighs (C), posterior surfaces of thighs (D), and ventral view (E). Photos by E. Lehr.

Generic placement. We assign this species to *Pristimantis* based on our molecular data (Fig. 2).

Diagnosis. A new species of *Pristimantis* assigned to the *danae* species Group having the following combination of characters: (1) Skin on dorsum shagreen with low scattered tubercles, skin on flanks tuberculate, skin on venter areolate; discoidal fold absent, thoracic fold present; irregularly shaped, discontinuous dorsolateral folds present; (2) tympanic membrane and tympanic annulus absent; (3) snout short, rounded in dorsal and in lateral views; (4) upper eyelid without enlarged conical tubercles; EW shorter

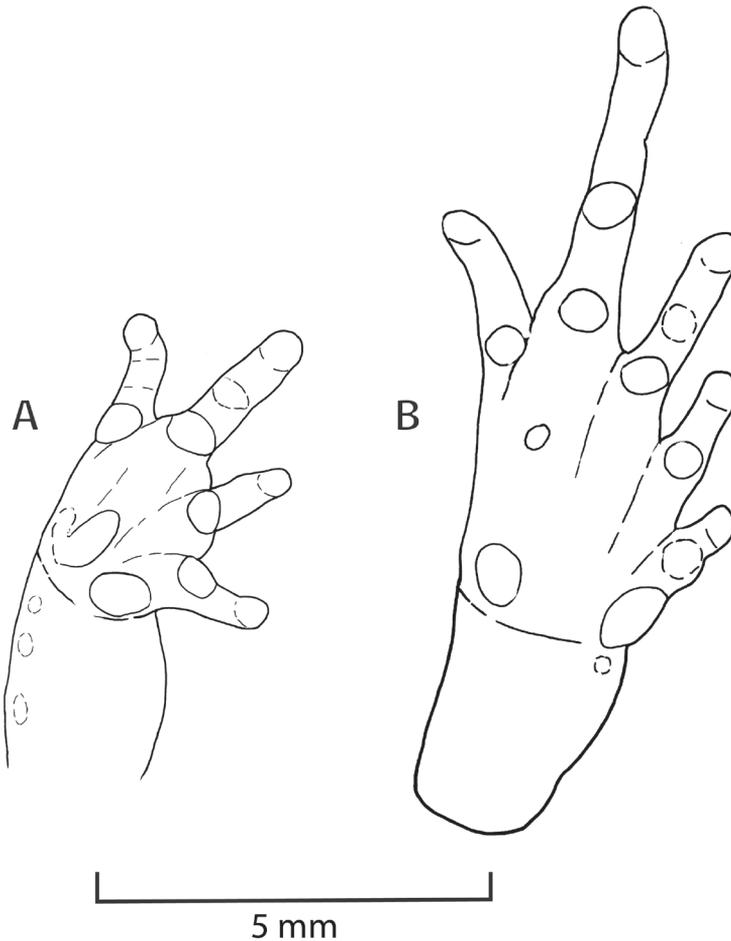


Figure 4. Ventral views of right hand (A) and right foot (B) of holotype of *Pristimantis attenboroughi* sp. n. (MUSM 31196). Drawings by E. Lehr.

than IOD; cranial crests absent; (5) dentigerous processes of vomers present; (6) males without vocal slits, nuptial pads absent; (7) Finger I shorter than Finger II; tips of digits narrow, rounded, lacking circumferential grooves; (8) fingers without lateral fringes; (9) small conical ulnar and tarsal tubercles present; (10) heel with a small conical tubercle; inner tarsal fold usually absent; (11) inner metatarsal tubercle ovoid, 1.5 times as large as outer; outer metatarsal tubercle small, rounded; via low supernumerary plantar tubercles; (12) toes without lateral fringes; basal toe webbing absent; Toe V longer than Toe III; tips of digits narrow, rounded, lacking circumferential grooves, toe tips slightly smaller than those on fingers; (13) in life, dorsal ground coloration pale or dark gray, reddish brown or brownish olive with dark gray scattered flecks, some with X-shaped mark on scapular and ill-defined diagonal bars on flanks; dark grayish-brown canthal and supratympanic stripes usually present; groin dark gray or pale reddish brown with a pale



Figure 5. Variation of male paratypes of *Pristimantis attenboroughi* sp. n. in dorsolateral, dorsal, and ventral views. **A–C** (MUSM 31186, SVL 18.6 mm) **D–F** (MUSM 31195, SVL 16.9 mm) **G–I** (MUSM 31992, SVL 15.9 mm). Photos by E. Lehr.

red to pink tint in some; venter dark gray, pale gray, grayish brown or pale grayish green and in some dark gray mottled; iris pale grayish green with fine black vermiculation and brownish-orange horizontal streak across pupil and lower half of iris; (14) SVL in adult males 14.6–19.2 mm ($n = 21$), in adult females 19.2–23.0 mm ($n = 10$).

Comparisons. *Pristimantis attenboroughi* is readily distinguished from its congeners in Ecuador (176 species, AmphibiaWeb 2016), Peru (128 species, AmphibiaWeb 2016), and Bolivia (17 species, AmphibiaWeb 2016) by having narrow digits without circumferential grooves, by lacking a tympanic annulus and tympanic membrane, and by having irregularly shaped, discontinuous dorsolateral folds. In Peru 18 species of *Pristimantis* lack a tympanum; these are *P. academicus* Lehr, Moravec, and Gagliardi Urrutia, 2010, *P. altamazonicus* (Barbour and Dunn, 1921), *P. ashaninka* Lehr and Moravec, 2017, *P. colodactylus* (Lynch, 1979), *P. coronatus* Lehr and Duellman, 2007a, *P. croceinguinis* (Lynch, 1968), *P. cruciocularis* (Lehr, Lundberg, Aguilar, and von May, 2006), *P. flavobracatus* (Lehr, Lundberg, Aguilar, and von May, 2006), *P. imitatrix* (Duellman, 1978b), *P. livellus* (Dwyer, 1995), *P. leucorrhinus* Boano, Mazzotti, and Sindaco, 2008, *P. martiae* (Lynch, 1974), *P. minutulus* Duellman and Hedges, 2007, *P. rhabdocnemus* (Duellman and Hedges, 2005), *P. simonsii* (Boulenger, 1900), *P. tantanti* (Lehr, Torres-Gastello,

and Suárez-Segovia, 2007), *P. ventrimarmoratus* (Boulenger, 1912), and *P. vilcabambae* Lehr, 2007. Of these, only *Pristimantis simonsii* from northern Peru has narrow digits without circumferential grooves. *Pristimantis attenboroughi* and *P. simonsii* lack circumferential grooves and a tympanum, and both have dorsolateral folds, but *P. attenboroughi* is smaller than *P. simonsii* (female SVL 26.2–33.3 mm in *P. simonsii*), and male *P. attenboroughi* lack nuptial pads which are present in *P. simonsii*.

Members of the *Pristimantis orestes* species Group are terrestrial and inhabit high elevations in southern Ecuador and in Peru (Duellman and Lehr, 2009) and have narrow digits, and only one of the 17 species (Guayasamin and Artega 2013) lacks circumferential grooves (*P. simonsii*), and only two (*P. seorsus*, *P. simonsii*) lack a tympanum. Furthermore *P. attenboroughi* is phylogenetically distant from members of this group which is considered to be not monophyletic (Duellman and Lehr 2009, Fig. 2).

Among the three other new species of *Pristimantis* from the upper montane forests and Puna of the PPPF, only *Pristimantis* sp. n. E lacks circumferential grooves and a tympanum. However, *P. attenboroughi* and *P. sp. n. E* both differ regarding other morphological traits, coloration, and genetically.

Pristimantis attenboroughi shares with *P. stipa* Venegas and Duellman, 2012 from the Puna of northern Peru (Venegas and Duellman 2012) narrow digits without circumferential grooves and dorsolateral folds. However, *P. attenboroughi* is smaller (female SVL 19.2–23.0 mm [$n = 10$] vs. 35.1 mm [$n = 1$]), lacks a tympanum (present in *P. stipa*), and has ulnar tubercles not coalesced into fold (coalesced into low fold in *P. stipa*), Venegas and Duellman (2012).

The new species shares narrow digits without circumferential grooves and the absence of a tympanic annulus and tympanic membrane with the Andean genera *Phrynopus* Peters, 1873 (except for *Phrynopus auriculatus* Duellman and Hedges, 2008, and *P. peruanus* Peters, 1873), 28 species from elevations between 2200 and 4400 m a.s.l. in central and northern Peru, Duellman and Lehr, 2009) and *Bryophryne* Hedges, Duellman, and Heinicke, 2008 (8 species from elevations between 2900 and 4120 m a.s.l. in southern Peru, Duellman and Lehr 2009), AmphibiaWeb (2016). *Pristimantis attenboroughi* is most similar with *Phrynopus chaparroi* Mamani and Malqui, 2014 which was described based on morphological characters and found at elevations between 4205 and 4490 m a.s.l. in southern Región Junín (Mamani and Malqui 2014). Both *Pristimantis attenboroughi* and *Phrynopus chaparroi* lack a tympanum and have narrow digits without circumferential grooves. However, *P. attenboroughi* is smaller than *P. chaparroi* (female SVL 19.2–23.0 mm [$n = 10$] vs. 30.0–32.2 [$n = 4$]), lacks protuberant subconical post-triangular tubercles (present in *P. chaparroi*), has dorsolateral folds (absent in *P. chaparroi*), dentigerous processes of vomers present (absent in *P. chaparroi*), and males lack nuptial pads (present in *P. chaparroi*). *Phrynopus chaparroi* might belong to *Pristimantis*, but molecular characters need to be applied to confirm our suspicion.

Description of the holotype. Head about as long as wide; head length 39.7% of SVL; head width 38.6% of SVL; cranial crests absent; snout short, rounded in dorsal view, rounded in lateral view (Fig. 3A, B); eye-nostril distance 70% of eye diameter; nostrils slightly protuberant, directed dorsolaterally; canthus rostralis short, rounded

in lateral view, weakly concave in dorsal view; loreal region concave; lips rounded; outer margin of upper eyelid each with few slightly enlarged conical tubercles; upper eyelid width 51.9% of IOD (see photo in life Fig. 3); supratympanic fold short and broad, extending from posterior margin of upper eyelid slightly curved to insertion of arm; tympanic membrane and annulus absent; distinct conical postrictal tubercles present bilaterally. Choanae small, ovoid, not concealed by palatal shelf of maxilla; dentigerous processes of vomers positioned posterior to level of choanae, oblique, narrowly separated; tongue long, oval, about three times as long as wide, not notched posteriorly, posterior half free.

Skin on dorsum shagreen with low scattered tubercles, skin on flanks tuberculate, irregularly shaped, discontinuous dorsolateral folds present extending from posterior level of tympanic area to level of hind limb insertion; skin on throat, chest, and belly areolate; discoidal fold absent, thoracic fold present; cloacal sheath short.

Outer ulnar surface each with a row of four minute low tubercles; palmar tubercle bifid; thenar tubercle ovoid; subarticular tubercles well defined, most prominent on base of fingers, round in ventral view, subconical in lateral view; supernumerary tubercles indistinct; fingers short and stout lacking lateral fringes, Finger I shorter than Finger II; tips of digits of fingers narrow, round, lacking circumferential grooves (Fig. 4A).

Hind limbs short, slender, tibia length 40.2% of SVL; foot length 41.3% of SVL; dorsal surfaces of hind limbs tuberculate; inner surface of thighs smooth, posterior surfaces of thighs tuberculate, ventral surfaces of thighs areolate; heels each with a small conical tubercle; outer surface of tarsus with few scattered minute low tubercles; inner tarsal fold absent, but small tubercle proximal to metatarsal tubercle; inner metatarsal tubercle ovoid, one and a half times the size of round outer metatarsal tubercle; subarticular tubercles well defined, round in ventral view, subconical in lateral view; few plantar supernumerary tubercles, about one third the size of subarticular tubercles; toes without lateral fringes; basal webbing absent; tips of digits narrow, round, less expanded than those on fingers, lacking circumferential grooves; relative length of toes: $1 < 2 < 5 < 3 < 4$; Toe V slightly longer than Toe III (tip of digit of Toe III and Toe V not reaching distal subarticular tubercle on Toe IV; Fig. 4B).

Measurements (in mm) of the holotype. SVL 18.9; tibia length 7.6; foot length 7.8; head length 7.5; head width 7.3; eye diameter 2.0; inter orbital distance 2.7; upper eyelid width 1.4; internarial distance 1.9; eye–nostril distance 1.4.

Coloration of the holotype in life (Fig. 3). The dorsal ground coloration is pale reddish brown with few dark brown flecks; narrow dark brown canthal and supratympanic stripes; flanks pale reddish brown with dark brown flecks forming irregularly shaped diagonal bars; groin and anterior surfaces of thighs reddish brown with dark brown flecks and pale reddish tint; chest, belly, and ventral surfaces of thighs dark grayish brown, throat pale reddish brown and pale gray mottled; palmar and plantar surfaces, and fingers and toes dark grayish brown; iris pale grayish green with fine black vermiculation and brownish-orange horizontal streak across pupil and lower half of iris.

Coloration of the holotype in preservative. The dorsal ground coloration is pale brown with few dark brown flecks; narrow dark brown canthal and supratympanic

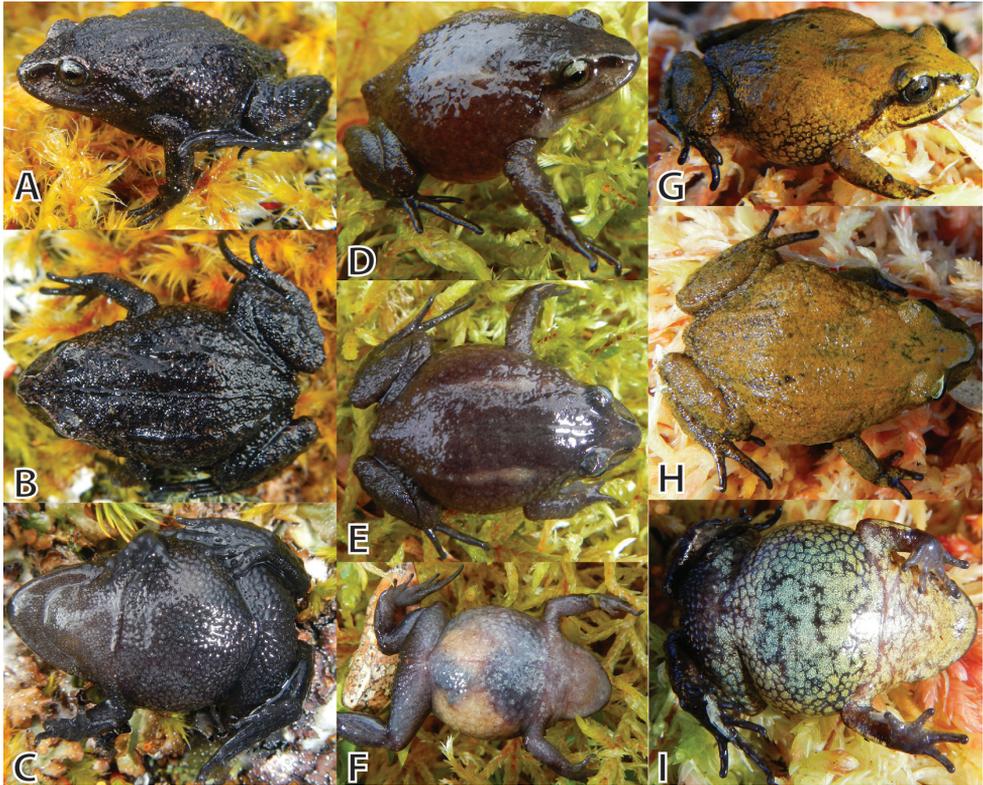


Figure 6. Variation of female paratypes of *Pristimantis attenboroughi* sp. n. in dorsolateral, dorsal, and ventral views. **A–C** (NMP6V 75522, SVL 19.2 mm) **D–F** (MUSM 31987, SVL 23.0 mm) **G–I** (MUSM 31977, SVL 21.9 mm). Photos by E. Lehr.

stripes; flanks pale brown with many dark brown flecks forming irregularly shaped diagonal bars; groin and anterior surfaces of thighs brown with dark brown flecks; chest, belly, and ventral surfaces of thighs dark brown, throat pale brown and pale gray mottled; palmar and plantar surfaces, and fingers and toes dark brown; iris pale gray.

Variation. All paratypes (Figs 5–7) are similar to the holotype regarding morphology and proportions (Tables 3, 4). Besides differences in SVL, notable morphological variation includes prominence of dorsolateral folds (e.g., prominent dorsolateral folds in MUSM 31192, 31195, Fig. 5D–F, G–I; weak dorsolateral folds in MUSM 31186, 31975, 31977, NMP6V 75522, 75528, 75529, Fig. 6G–I), and coarseness of tuberculate skin texture on flanks and hind limbs (skin coarsely tuberculate in MUSM 31186, 31192, 31195, NMP6V 75525, Fig. 5; skin weakly tubercular MUSM 31987, 31997, NMP6V 75528, 75529). Two specimens (NMP6V 75529, 75534) have a tubercle-like inner tarsal fold present. *Pristimantis attenboroughi* demonstrates a remarkable polymorphism in coloration (Figs 5–7).

The dorsal coloration ranges from pale gray (MUSM 31987, NMP6V 75533, Fig. 6D–F), dark gray (MSUM 31186, 3199, NMP6V 75522, 75523, 75528, 75529,



Figure 7. Variation of juvenile paratypes of *Pristimantis attenboroughi* sp. n. in dorsolateral, dorsal, and ventral views. **A–C** (MUSM 31990, SVL 14.0 mm) **D–F** (MUSM 31187, SVL 12.5 mm) **G–I** (MUSM 31200, SVL 14.0 mm). Photos by E. Lehr.

Fig. 6A–C), reddish brown (MUSM 31195, 31975, NMP6V 75525, Figs 5D–F) to brownish olive (MUSM 31992, 31997, Figs 5G–I, 6G–I) with dark gray scattered flecks. Some have an X-shaped mark on scapular (MUSM 31200, 31975, 31990), some ill-defined diagonal bars on the flanks (MUSM 31195). Dark grayish-brown canthal and supratympanic stripes are usually present except for dark gray specimens (MUSM 31186, 3199, NMP6V 75522, 75523, 75528, 75529). The groin is dark gray (MUSM 31186, 3199, NMP6V 75522, 75523, 75528, 75529) or pale reddish brown with a pale red to pink tint in some specimens (MUSM 31195, 31196). The venter is dark gray (NMP6V 75522, 75523, 75528, 75529, Fig. 6C), pale gray (MUSM 31987, Fig. 6F), grayish brown (MUSM 31186, 31195, NMP6V 75525, Fig. 5C, F) or pale grayish green and gray mottled (MUSM 31197, Fig. 6I) or dark gray and pale gray mottled (MUSM 31199, 31975, 31992, NMP6V 75533, Fig. 5I).

Juveniles (MUSM 31187, 31990, 31200, Fig. 7) have a paler coloration (yellowish to reddish brown) with contrasting dark brown flecks and distinct canthal and supratympanic stripes. All have the iris pale grayish green with fine black vermiculation and brownish-orange horizontal streak across pupil and lower half of iris, and usually a narrow vertical dark gray streak from pupil through middle of lower iris.

Table 3. Measurements (in mm) of selected adult type specimens of *Pristimantis attenboroughi* sp. n. M = male, F = female. For other abbreviations see methods.

Characters	MUSM 31988	MUSM 31992	MUSM 31186	UMMZ 244727	NMP6V 75523	MUSM 31980	MUSM 31977	NMP6V 75076	MUSM 31987
sex	M	M	M	M	F	F	F	F	F
SVL	14.6	15.9	18.6	19.2	20.1	21.5	21.9	22.9	23.0
TL	6.0	6.2	7.3	6.8	8.3	8.4	8.1	8.3	8.8
FL	5.8	6.1	7.7	7.3	9.4	8.8	8.8	9.2	10.2
HL	5.3	6.2	6.2	6.8	7.5	7.6	7.3	8.4	7.1
HW	5.0	5.7	6.3	6.6	7.4	7.8	7.8	7.9	7.9
ED	1.6	1.7	1.9	1.9	2.0	2.2	2.4	2.4	2.2
IOD	1.8	2.1	2.4	2.1	2.7	2.5	2.3	2.6	2.9
EW	0.9	1.4	1.2	1.3	1.6	1.6	1.6	1.6	1.3
IND	1.3	1.5	1.7	2.0	2.0	1.9	2.1	2.3	2.1
N-E	1.1	1.0	1.3	1.3	1.3	1.7	1.5	1.8	1.7

Table 4. Measurements (in mm) and proportions of adult male and adult female type specimens of *Pristimantis attenboroughi* sp. n.; ranges followed by means and one standard deviation in parentheses. For abbreviations see methods.

Characters	Males (n = 21)	Females (n = 10)
SVL	14.6–19.2 (17.1 ± 1.2)	19.2–23.0 (21.6 ± 1.1)
TL	5.8–7.6 (6.7 ± 0.5)	8.0–8.8 (8.4 ± 0.2)
FL	5.8–7.8 (7.0 ± 0.5)	8.8–10.2 (9.3 ± 0.4)
HL	5.3–7.3 (6.3 ± 0.5)	7.1–8.4 (7.6 ± 0.4)
HW	5.0–6.9 (6.0 ± 0.5)	7.3–8.3 (7.9 ± 0.3)
ED	1.6–2.1 (1.9 ± 0.2)	1.8–2.4 (2.1 ± 0.2)
IOD	1.8–2.5 (2.1 ± 0.1)	2.3–2.9 (2.7 ± 0.2)
EW	0.9–1.9 (1.3 ± 0.2)	1.3–1.7 (1.5 ± 0.1)
IND	1.3–2.1 (1.6 ± 0.2)	1.9–2.3 (2.1 ± 0.1)
E–N	0.8–1.4 (1.2 ± 0.1)	1.3–1.8 (1.5 ± 0.2)
TL/SVL	0.34–0.44	0.36–0.42
FL/SVL	0.35–0.46	0.40–0.47
HL/SVL	0.33–0.41	0.31–0.39
HW/SVL	0.31–0.38	0.34–0.39
HW/HL	0.84–1.02	0.94–1.11
E–N/ED	0.47–0.71	0.62–0.89
EW/IOD	0.45–0.70	0.45–0.70

Etymology. We dedicate this species to Sir David Frederick Attenborough in honor for his educational documentaries on wildlife, especially on amphibians (e.g., *Life in Cold Blood*, *Fabulous Frogs*), and for raising awareness about the importance of wildlife conservation. The specific epithet is used as noun in apposition.

Distribution, natural history, and conservation status. *Pristimantis attenboroughi* is known from six localities inside the PPPF (Puna of Quebrada Tarhuish at

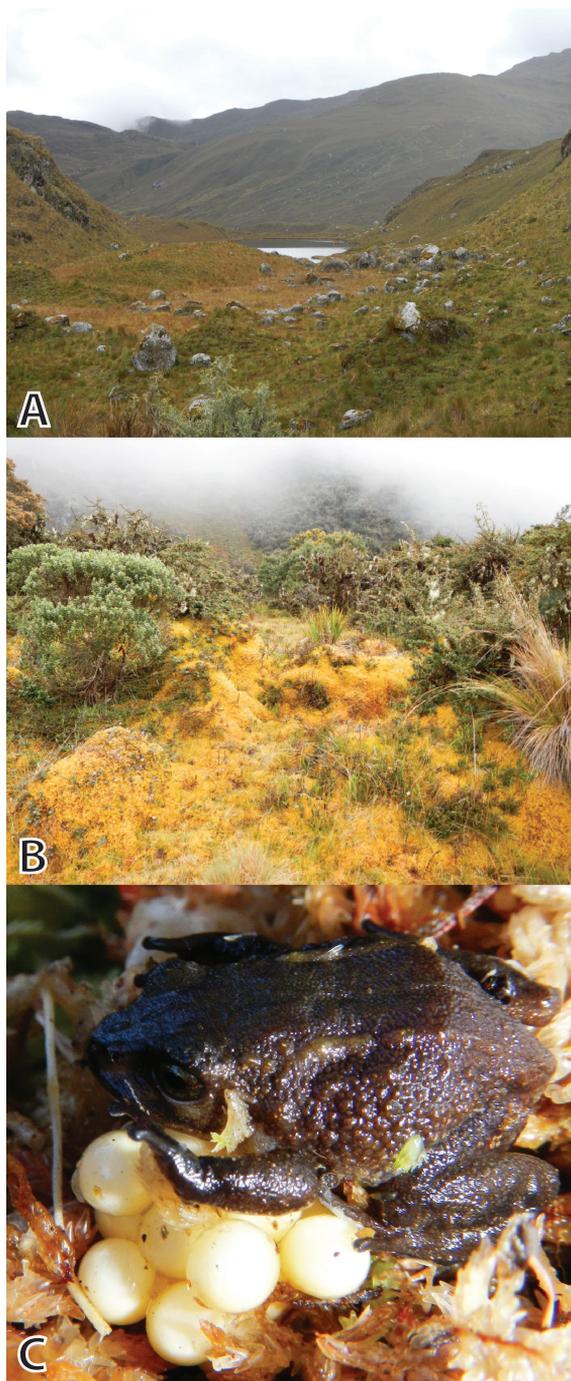


Figure 8. Habitats of *Pristimantis attenboroughi* sp. n. in the PPPF: **A** type locality in the upper Tarhuish valley at Laguna Udrecocha, Puna at 3936 m a.s.l., 17 May 2012 **B** upper montane forest at 3550 m a.s.l. where *P. attenboroughi* sp. n. was found in moss pads **C** female *P. attenboroughi* sp. n. (MUSM 31980, SVL 21.5 mm) guarding a clutch in a moss pad. Photos by E. Lehr.

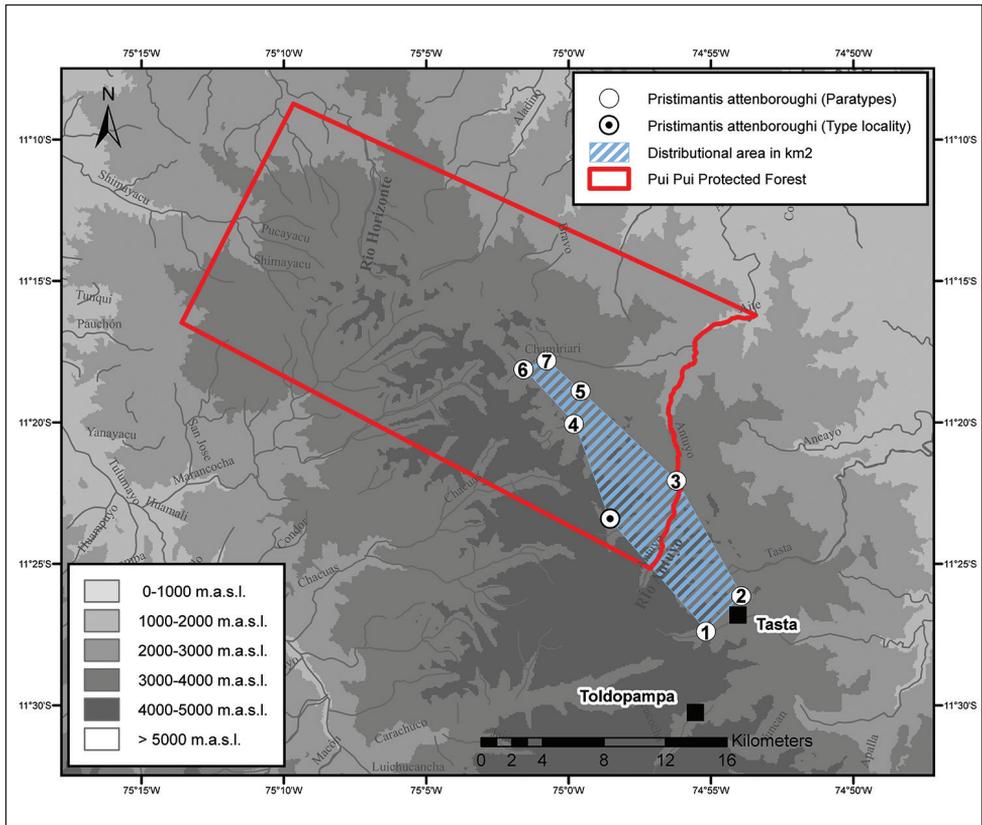


Figure 9. Distribution of *Pristimantis attenboroughi* sp. n. in the PPPF and its surroundings: type locality: Laguna Udrecocha, 3936 m a.s.l.; **1** Upper part of Quebrada Tasta, “Laguna Luichococha”, 3708 m a.s.l. **2** near trail from Tasta to Tarhuish (first mountain peak), *Polylepis* forest patch, 3886 m a.s.l. **3** Quebrada Tarhuish, left bank of Antuyo River, “Shiusha”, 3414 m a.s.l. **4** Antuyo, 3700 m a.s.l. **5** Antuyo Bajo, 3400 m a.s.l. **6** Hatunpata, 3710 m a.s.l. **7** Trancapampa, 3550 m a.s.l.

Laguna Udrecocha, Fig. 8A; upper montane forest of Quebrada Tarhuish on the left bank “Shiusha” of Antuyo River; Antuyo; Antuyo Bajo; Hatunpata, and Trancapampa, Figs 8B, 9) and from two outside the PPPF (upper part of Quebrada Tasta close to Laguna Luichococha; in *Polylepis* forest of first mountain peak next to trail from Tasta to Tarhuish), and is distributed at elevations between 3400 and 3936 m a.s.l., Fig. 9. The type locality (Figs 8A, 9), upper part of Quebrada Tarhuish, on the east side of Laguna Udrecocha at 3936 m a.s.l., belongs to the Puna ecoregion (Brack 1986). The vegetation consists of Peruvian feather grass (*Stipa ichu*), mosses, and small bushes. The holotype was found inside moss in the afternoon on 17 May 2012. No sympatric anurans were found at the type locality. At the upper montane forest of Quebrada Tarhuish on the left bank “Shiusha” of Antuyo River, *P. attenboroughi* was found deep inside large moss layers. Sympatric anurans are *Gastrotheca griswoldi* (MUSM 31193),

Pristimantis sp. n. C (MUSM 31190–92), *Pristimantis* sp. n. D (MUSM 31197–98), and *Phrynopis* sp. n. A (MUSM 31203).

A female *Pristimantis attenboroughi* (MUSM 31980, Fig. 8C) guarding 20 eggs was found at Hatunpata inside moss, 3710 m a.s.l., on 28 June 2013. The eggs were pale cream colored and had an average diameter of 3.5 ± 0.1 mm (3.3–3.6 mm, $n = 20$).

The IUCN Red List criteria (IUCN 2001) consider that if a species occurs in fewer than 10 threat-defined locations and the extent of occurrence (EOO) is $< 20,000$ km², it should be classified as Vulnerable or Endangered. *Pristimantis attenboroughi* is known from seven localities distributed in the PPPF and its buffer zone (Fig. 9), with an estimated EOO of 66.54 km². As such, this new species might be classified as Vulnerable if we take into account these criteria. However, given that the PPPF may host a greater number of locations and most of them are inside the protected area, we propose that *Pristimantis attenboroughi* should likely be categorized as Near Threatened (NT).

Given that the known distribution of *Pristimantis attenboroughi* overlaps with the PPPF, a substantial portion of the habitat of this species is formally protected. However, other factors such as fungal infections, climate change, pollution, and man-made fires (used to expand grazing areas for livestock) continue to be threats for many Andean amphibians even inside protected areas (Catenazzi and von May 2014).

Discussion

When we encountered the first specimen of *Pristimantis attenboroughi* in the field both of us were sure that we had found a new species of *Phrynopis* because of its overall morphological appearance: most species in the genus *Phrynopis* usually lack tympanum, have narrow digits without circumferential grooves and are distributed at high elevations. However, following an integrative taxonomy approach that included molecular and morphological data, we realized that *Pristimantis attenboroughi* is not a *Phrynopis* species. Our analysis also revealed that *Pristimantis attenboroughi* is not closely related to other *Pristimantis* species that have narrow digits (e.g., members of the *P. orestes* species group), an assumption that could have been made if only morphological data were available. In other words, *Pristimantis attenboroughi* displays convergence that easily could have led to an incorrect generic assignment. *Pristimantis attenboroughi* is morphologically most similar to *Phrynopis chaparroi* (Mamani and Malqui 2014) and we assume that the latter species might belong to *Pristimantis* and to the *danae* species group. Thus, molecular data are needed to determine whether the current generic placement of *Phrynopis chaparroi* is correct.

With *Pristimantis attenboroughi*, seven species of *Pristimantis* are known from the Puna (> 3000 m a.s.l.) of Peru. Of these, six occur in northern Peru (*P. atrabracus* [Duellman and Pramuk, 1999], 2963–3330 m a.s.l.; *P. bellator* Lehr, Aguilar, Siu-Ting, Jordán, 2007, 1900–3100 m a.s.l.; *P. cordovae* [Lehr and Duellman, 2007b], 3400–4100 m a.s.l.; *P. mariaelenae* Venegas and Duellman, 2012, 3596 m a.s.l.; *P. pinguis*

[Duellman and Pramuk, 1999], 3000–3916 m a.s.l.; *P. stipa* Venegas and Duellman, 2012, 3596 m a.s.l.), and only one species in central Peru (*P. attenboroughi*, 3400–3936 m a.s.l.), Duellman and Lehr 2009. Navarrete et al. (2016) pointed out the disparity in species richness of *Pristimantis* at high elevation between Ecuador (18 species of *Pristimantis*) and Peru (5 species of *Pristimantis*). Whilst the Páramo in Ecuador is more humid than the drier Puna in Peru, it is likely that, besides climatic differences between the two regions, the lower species richness of *Pristimantis* in the Puna of Peru is an artifact of lower survey effort and the presence of other high-elevation clades not present in Ecuador. Thus, we hypothesize that the occurrence of the genus *Phrynopus* at high elevations (28 species from elevations between 2200–4400 m a.s.l., AmphibiaWeb 2016, Duellman and Lehr 2009) in central Peru might restrict the number of niches available for *Pristimantis* at high elevations.

Additional new species of terrestrial-breeding frogs from montane forests and Puna of the PPPF will be described in the near future.

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Appendix

Comparative specimens examined

- Pristimantis mariaelena*: Peru: Lambayeque: Cañaris, 3406–3494 m: MUSM 26478.
- Pristimantis simonsii*: Peru: Cajamarca: 23.5 km NE Encanada, 3510 m: MUSM 1163–1179.
- Pristimantis stipa*: Peru: Peru: Lambayeque: Cañaris, 3406–3494 m: MUSM 26481, 26482.
- Phrynopus* sp. n. A: Peru: Junín: Pui Pui Protected Forest: near trail from Tasta to Tarhuish (first mountain peak), Polylepsis forest patch, 3886 m: MUSM 31203.
- Pristimantis* sp. n. C: Peru: Junín: Pui Pui Protected Forest: Quebrada Tarhuish on the left bank „Shiusha“ of Antuyo River, 3414 m: MUSM 31190–92.
- Pristimantis* sp. n. D: Peru: Junín: Pui Pui Protected Forest: Quebrada Tasta, Runda, 3463 m: MUSM 31197–98.
- Pristimantis* sp. n. E: Peru: Junín: Peru: Junín: Pui Pui Protected Forest: Laguna Sinchon, 3890 m: MUSM 31981–83.

Four new species of the millipede genus *Eutrichodesmus* Silvestri, 1910 from Laos, including two with reduced ozopores (Diplopoda, Polydesmida, Haplodesmidae)

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Abstract

Laos has large areas of primary forest with a largely unexplored fauna. This is evidenced by millipedes, class Diplopoda, with fewer than 60 species being recorded from the country. In the widespread Southeast Asian “Star Millipede” genus *Eutrichodesmus* Silvestri, 1910 (family Haplodesmidae), only two of 49 recorded species have been found in Laos. Four new species of Star Millipedes are here described from caves in Laos: *Eutrichodesmus steineri* Liu & Wesener, **sp. n.**, *E. deponatus* Liu & Wesener, **sp. n.**, *E. paraster* Liu & Wesener, **sp. n.** and *E. parvus* Liu & Wesener, **sp. n.**. A fifth species, for which only a female is available, remains unnamed. The defensive glands (ozopores) are found to be strongly or entirely suppressed in two of the new species, *E. deponatus* Liu & Wesener, **sp. n.** and *E. paraster* Liu & Wesener, **sp. n.**, both troglobionts, which is new to the family. All of the Star Millipedes were collected during Northern Lao-European Cave Project faunal surveys conducted by the Senckenberg Museum, Frankfurt. A key to the six species of *Eutrichodesmus* currently known to occur in Laos is provided.

Keywords

Millipede, reduced ozopores, biodiversity, taxonomy, cave adaptation, Laos

Introduction

The documenting of biodiversity and the subsequent taxonomic descriptions of undescribed species have been highlighted as one of the most urgent research programmes of our planet, as indicated by the declaration of the “United Nations Decade on Biodiversity”, as well as the signing of the UN “Convention on Biological Diversity” by numerous countries (e.g., Wheeler 2008; Padial et al. 2010; Popescu 2015). Laos, a landlocked, largely montane, tropical country in Southeast Asia, is one of the highly biodiverse Great Mekong countries, which together have yielded more than 2200 new species since 1997 (WWF 2016). Furthermore, in contrast to its neighbours China, Vietnam and Thailand, the forests in Laos still remain relatively intact (STEA 2000). However, this might change in the near future as illegal logging and timber smuggling to Vietnam are being conducted on a large scale (EIA 2011; Smirnov 2015; Gan et al. 2016). The very large amount of still undescribed biodiversity in Laos is especially evident in arthropods, including the large, ecologically important, mostly sylvicolous and mesophilous millipedes, class Diplopoda. Most diplopods are detritivores whose primary habitat is forest litter and topsoil, but many species live in caves, dead wood, suspended soil or even tree canopies (e.g., Golovatch and Kime 2009). Diplopoda are an ancient, diverse and widespread group, with fossils dating back to the Silurian (Edgecombe 2015) and with about 12,000 described species in >3,000 recognized genera, >150 families and 16 orders (Minelli 2015). Since the bulk of global millipede diversity is confined to tropical forest, which is a rapidly shrinking biome, and because diplopods are poor dispersers that are largely confined to forests and woodlands, and are prone to strongly localized endemism (e.g. Wesener 2009; Car and Harvey 2014; Enghoff 2015), the problem of documenting millipede faunas is increasingly acute (Golovatch and Kime 2009). These localized occurrences make millipede species important subjects for biogeographic studies (Stoer and Enghoff 2003; Wesener et al. 2010; Wesener et al. 2011), but also put them at risk of local extinction from human activities such as forest destruction or large-scale mining operations (Wesener and Wägele 2007; Iniesta et al. 2012). This holds especially true for Laos where the pace of forest destruction is alarmingly high (Gan et al. 2016).

Fortunately, fresh collections of Laotian millipedes have encouraged recent taxonomic studies, and since the latest checklist for the country which listed 34 species (Likhitrakarn et al. 2014a), another 23 have been added (Likhitrakarn et al. 2014a, 2014b, 2014c, 2015a, 2015b, 2016a, 2016b; Golovatch 2016a, 2016b; Golovatch et al. 2016a, 2016b). Still, the achievement is modest, as the faunas of the adjacent Vietnam, Thailand and southern China comprise from >100 to a few hundred millipede species each (e.g., Enghoff et al. 2004; Enghoff 2005; Golovatch 2015). In addition, only seven of the 16 orders of Diplopoda have been recorded so far in Laos, the most species-rich being the Polydesmida.

Within the Polydesmida, the tiny species of “Star Millipedes”, genus *Eutrichodesmus* Silvestri, 1910 (family Haplodesmidae), with their often conspicuous dorsal projections

(e.g., Fig. 1), together with the larger “Dragon Millipedes”, genus *Desmoxytes* Chamberlin, 1923 (family Paradoxosomatidae, see Liu et al. 2014, 2016), are among the most remarkable diplopods in Southeast Asia. *Eutrichodesmus* is one of the most speciose genera of SE Asian millipedes, presently containing 49 described species (Golovatch et al. 2015, 2016a). The genus is distributed from southern Japan in the north, through southern China and Indochina, to Vanuatu, Melanesia in the south. Most species are strongly localized country endemics, this being especially true of the rather numerous cavernicoles. Laos is situated more or less north-centrally within the distribution range of the genus, but only two Laotian species have been named so far: *E. multilobatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, and *E. nadan* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2016. Both are highly localized endemics found in caves and are presumed troglobites (Golovatch et al. 2009a, 2016a).

Below we describe four new species and provide a key to all six members of *Eutrichodesmus* currently known to occur in Laos. In addition, for the first time in the family we report strongly or completely suppressed ozopores, which is unusual because all previously described *Eutrichodesmus* seem to show normal pore formulae: 5, 7, 9, 10, 12, 13, 15–19.

Material and methods

Specimens were collected for the Northern Lao-European Cave Project, and kept in 70% ethanol. The holotypes and a number of paratypes are deposited in the zoological collection of the Senckenberg Research Institute and Natural History Museum (SMF), with some material also to be housed in the Zoological Research Museum A. Koenig (ZFMK).

Observation and dissections were performed using an Olympus SZ51 stereo microscope. The line drawings were prepared with the help of an Olympus BX51 microscope and an attached camera for the scope. SEM micrographs were taken using a ZEISS Sigma 300VP scanning electron microscope (based at the ZFMK). Dry SEM material was coated with gold, removed after study from stubs and returned to alcohol. The photographs were taken with Canon EOS 7D cameras and further processed using Adobe Photoshop CS6 software.

The terminology used here follows that of Golovatch et al. (2009a, 2009b).

Abbreviations used

- SMF** Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany
SEM Scanning electron microscopy
ZFMK Zoological Research Museum Alexander Koenig, Bonn, Germany

Taxonomy

A key to species of *Eutrichodesmus* in Laos

- 1 Habitus in lateral view resembling a star: metaterga 5–19 each with a very high, mid-dorsal projection (Fig. 1A–C).....**2**
- Habitus non-asteriform: metaterga 5–19 devoid of mid-dorsal projections (Fig. 1D)**4**
- 2 Metatergum 4 with a high mid-dorsal projection (Figs 1C, 8E). Gonopod with a large, lateral, denticulate, distofemoral process (**dp**); acropodite with a very small mesal tooth (**t**) subapically (Fig. 10) ***E. paraster* sp. n.**
- Metatergum 4 devoid of a high mid-dorsal projection. Gonopod with a prominent, digitiform, distofemoral process (**dp**); acropodite with a micro-papillate process (**pp**) near midway or at base (Figs 4, 7).....**3**
- 3 Body larger, about 9.5–10.0 mm long, grey-brown in colour. Ozopores distinct (Figs 2E, 3H), pore formula normal. Seminal groove on gonopod terminating at a mesal lobule (**lo**) subapically (Figs 3N, 4).....***E. steineri* sp. n.**
- Body smaller, about 7.5–8.0 mm long, uniformly pallid. Ozopores strongly reduced, only visible on paraterga 17 (Fig. 6C, G). Gonopod acropodite subapically with a slightly bifid, dorsolateral tooth (**t1**); seminal groove terminating at a small triangular tooth (**t2**) subapically (Fig. 7)....***E. deporatus* sp. n.**
- 4 Paraterga 5-lobulated laterally. Gonopod very simple, acropodite devoid of any tooth or lobe.....
-***E. multilobatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009**
- Paraterga 2- or 3-lobulated laterally. Gonopod relatively complex, acropodite with a tooth or lobe subapically**5**
- 5 Body conglobation complete, with laterally bilobate paraterga. Tip of gonopod acropodite subunciform, with a small, mesal, subapical lobule; seminal groove terminating in an evident accessory seminal chamber, with a distinct hairpad proximal to it.....***E. nadan* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2016**
- Body conglobation incomplete, with laterally mostly trilobate paraterga. Gonopod acropodite with a small tooth (**t**) dorsally and an evident, digitiform lobe (**lo**) ventrally; seminal groove terminating without hairpad (Fig. 13).....
-***E. parvus* sp. n.**

***Eutrichodesmus steineri* Liu & Wesener, sp. n.**

<http://zoobank.org/C94274F9-16D8-41E0-8B38-C8DC6C7A6678>

Figs 1A, 2–4

Material examined. Holotype male (SMF), Laos, Luang Prabang Province, Phou Khoun District, Cave Tham Deu (E 48-013-005), N19°26'4.3", E102°29'16.6", 6.I.2007, coll. L. Price (205/07-).

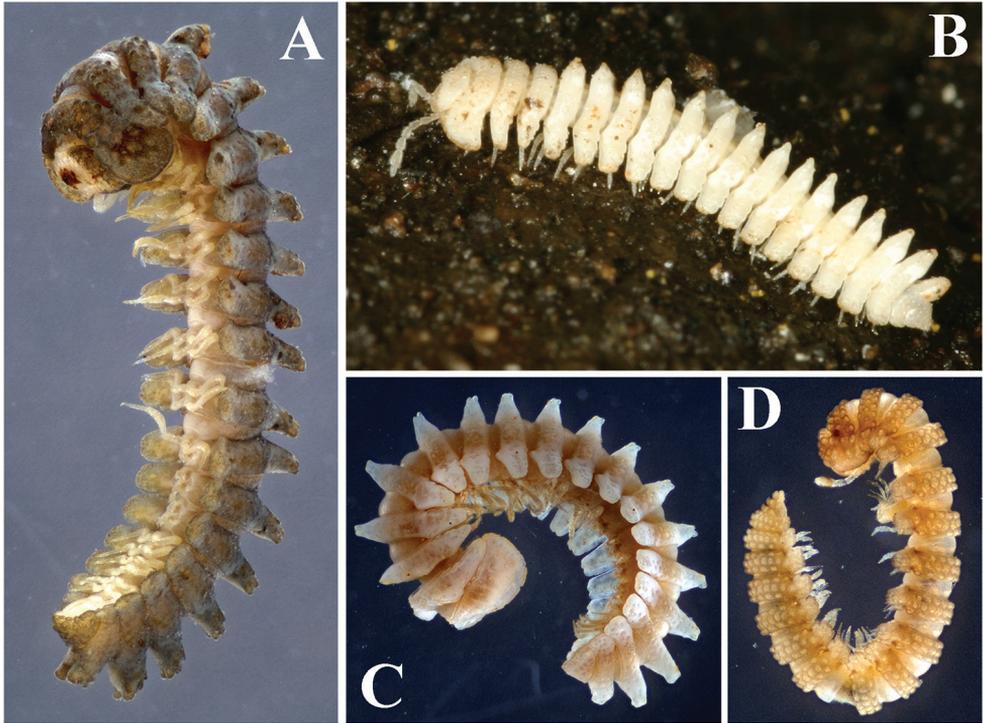


Figure 1. Habitus photographs. **A** *E. steineri* sp. n., male paratype (SMF) from Cave Tham Dout, ventrolateral view **B** *E. deparatus* sp. n., a male ecological photo from Cave Tham Pathok, sublateral view **C** *E. paraster* sp. n., male holotype (SMF) from Cave Tham Long Puang, lateral view **D** *E. parvus* sp. n., male paratype (ZFMK) from Cave Tham Nam Long, lateral view.

Paratypes. 1 male (ZFMK MYR6130), 2 juveniles (ZFMK MYR6126), same data as holotype; 1 male, 5 females, 7 juveniles (SMF), same locality (E 48-013-005), 5.I.2007, coll. H. Steiner (210/07-); 1 female (ZFMK MYR6133), same data as above; 1 male, 1 female, 1 juvenile (SMF), same district, Cave Tham Dout (E 48-013-004), 5.I.2007, coll. L. Price (139/07-).

Etymology. Honours Mr. H. Steiner, one of the collectors; noun.

Diagnosis. Differs from other species of the genus in showing laterally 3-lobulated paraterga and the extremely high mid-dorsal projections on metaterga 5–19, the latter character very similar to that observed in *E. macclurei* Hoffman, 1977, from western Malaysia (Hoffman 1977). However, *E. steineri* sp. n. is distinct from *E. macclurei* in the gonopod, which has a long, digitiform, distofemoral process, *vs.* a short spiniform process in the counterpart. See also Key above.

Description. Length of adults of both sexes ca. 9.5–10.0 mm, width 0.8–1.0 mm and 2.0–2.2 mm on midbody pro- and metazona, respectively.

Coloration uniformly grey-brown with pallid antennae (Fig. 1A).

Adults with 20 segments (Fig. 1A), body subcylindrical, conglobation complete.

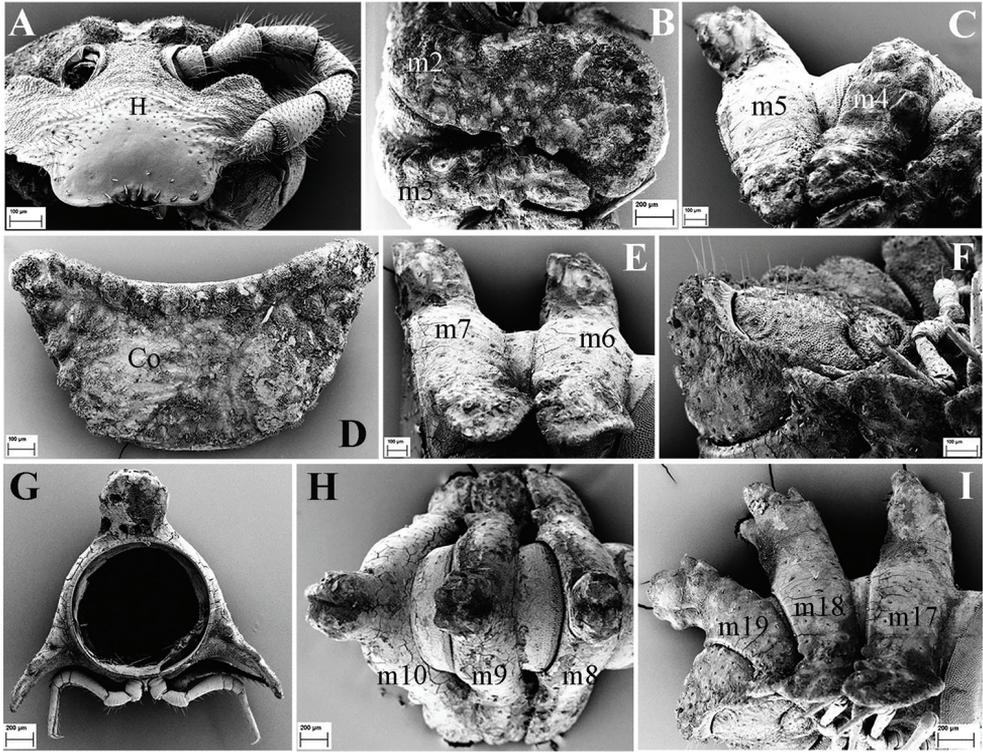


Figure 2. *E. steineri* sp. n., SEM, male paratype from Cave Tham Deu. **A** head (H) and left antenna, frontal view **B** segments 2 and 3, lateral view **C**, segments 4 and 5, lateral view (m2–m5 = metaterga 2–5) **D** collum (Co), dorsal view **E** segments 6 and 7, lateral view (m6–m7 = metaterga 6, 7) **F** telson, subventral view **G** cross-section of segment 11, caudal view **H** segments 8–10, dorsal view **I** segments 17–19 and telson, lateral view (m8–m10, m17–m19 = metaterga 8–10, 17–19).

Head slightly transverse, frons densely pilose, microgranular except for clypeus, with a paramedian pair of rounded, paramedian, microvillose knobs above antennal sockets (Fig. 2A). Epicranial suture conspicuous.

Antennae densely pilose, short, but slender, only slightly clavate (Figs 2A, 3A). In length, antennomere $6 > 3 > 2 > 4 = 5 > 7 > 1$. Antennomeres 5 and 6 each with an evident group of minute bacilliform sensilla dorso-apically; disc with four sensory cones apically (Figs 2A, 3A).

Labrum usually with three, rarely five teeth, lateral ones smaller (Fig. 2A).

Gnathochilarium (Fig. 3B) with a long bacilliform sensillum apically on each lamella lingualis (**ll**); mentum (**m**) triangular.

Mandible with a movable external tooth (**et**), an internal tooth (**it**) with four cusps; six pectinate lamellae (**pl**) consisting of long, smooth teeth; intermediate area (**ia**) covered with small cuticular scales; a large, stairs-like molar plate (**mp**) close to anterior fringe with pin-like structures (Fig. 3C).

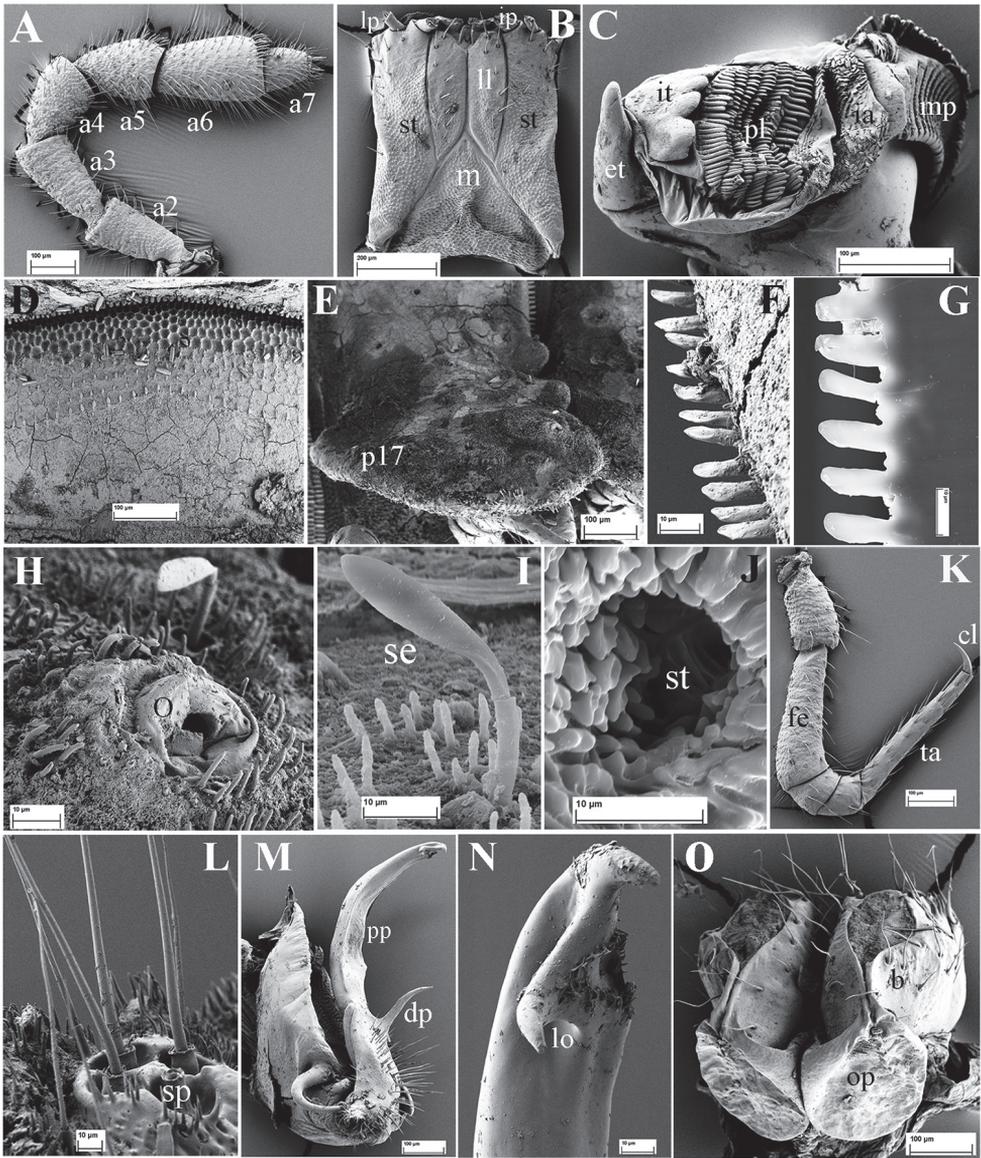


Figure 3. *E. steineri* sp. n., SEM, male paratype from Cave Tham Deu. **A** right antenna, lateral view (a2–a7 = antennomeres 2–7) **B** gnathochilarium, ventral view (lp = lateral palpus; ip = inner palpus; st = stipites; ll = lamellae linguae; m = mentum) **C** right mandible, general view (et = external tooth; it = internal tooth; pl = pectinate lamellae; ia = intermediate area; mp = molar plate) **D** prozonum 8, dorsal view **E** paratergum 17 (p17), lateral view **F** limbus of metatergum 5, lateral view **G** endotergum 7 **H** ozopore (o) and a seta of paratergum 17, general view **I** a seta (se) **J** stigmata (st) on segment 6, ventral view **K** midbody leg, frontal view (fe = femur; ta = tarsus; cl = claw) **L** spinnerets (sp), subventral view **M** left gonopod, mesal view (dp = distofemoral process; pp = papillate process) **N** tip of left gonopod, mesal view (lo = lobule) **O** female paratype, vulvae, general view (op = operculum; b = bursa).

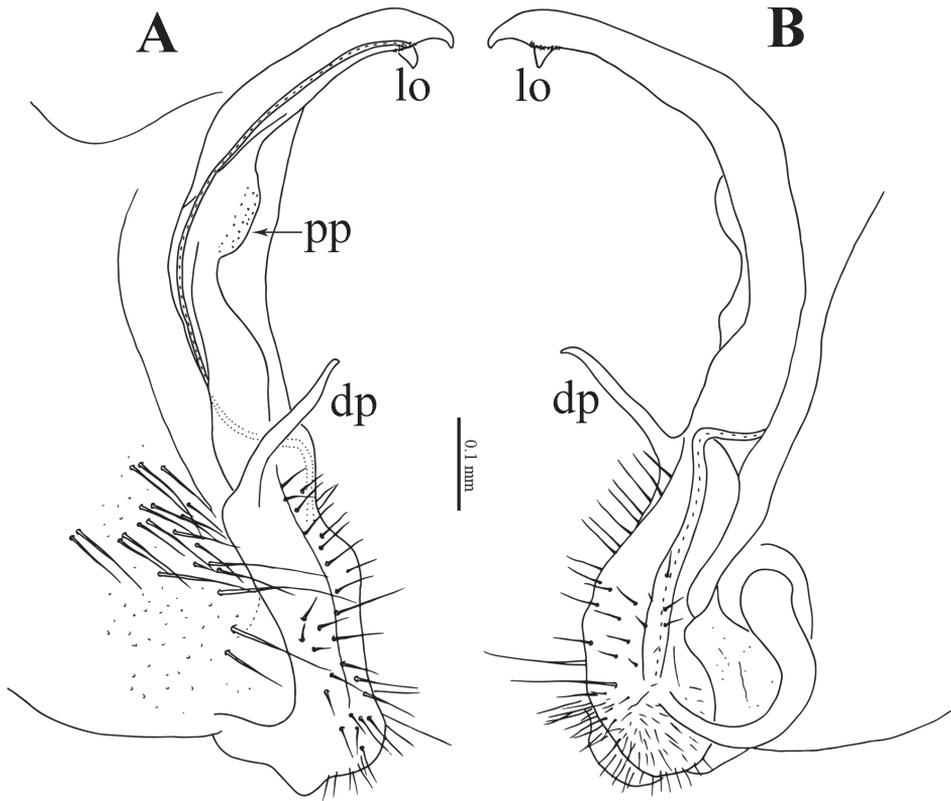


Figure 4. *E. steineri* sp. n., male paratype from Cave Tham Deu. **A–B** right gonopod, sublateral and mesal views, respectively. Abbreviations: dp = distofemoral process; pp = papillate process; lo = lobule.

Collum subtrapeziform (Fig. 2D), slightly broader than head, not covering the latter from above; dorsal surface with six transverse rows of round microvillose tubercles, flattened medially (Fig. 2D); each tubercle crowned by a 2-segmented seta, these setae being mostly abraded. Frontal margin slightly elevated (Fig. 2D).

Prozona very finely alveolate; stricture between pro- and metazona broad, shallow and smooth (Fig. 3D). Limbus regularly crenulate (Fig. 3F–G). Endotergum smooth (Fig. 3G).

Metaterga 2–4 each with three transverse mixostictic rows of similar small tubercles extending onto paraterga (Fig. 2B–C), 7(8) + 7(8) per row. Three transverse rows of very small, shallow, microvillose tuberculations on metaterga 5–19 (Fig. 2C, E, H–I), while metaterga 5–19 with a very high, large, mid-dorsal projection bifid on each side (Figs 1A, 2C, E, G–I). Projections 5–17 directed upright, then inclined slightly caudad on metaterga 18 and 19 (Fig. 2I). Metatergal setae 2-segmented, often abraded (Fig. 3H–I).

Paraterga with evident shoulders anteriorly, strongly declivous, broad and usually trilobate laterally (Figs 2H–I, 3E), evidently extending down below level of venter (Fig. 2G); caudolaterally at base with two distinct lobulations (Figs 2H–I, 3E). Para-

terga 2 strongly enlarged, a lateral lobulation indistinct, but two caudolateral lobulations evident (Fig. 2B); paraterga 3 and 4 slightly shorter than others, bilobate laterally (Fig. 2B).

Pore formula normal (5, 7, 9, 10, 12, 13, 15–19), ozopores distinct, each located near top of caudolateral lobulation (Figs 2E, 3E, H).

Pre-anal ring short, with four transverse rows of very small and flat tuberculations (Fig. 2F, I). Epiproct apically with four spinnerets (Fig. 3L). Paraprocts and hypoproct densely microvillose; paraprocts with two pairs of long setae, hypoproct subtrapeziform, with two long setae (Fig. 2F).

Pleurosternal keels absent. Sterna very narrow (Fig. 2G), but much broader only between male coxae 6–7 and 9. Stigmata clearly visible (Fig. 3J). Gonopod aperture suboval.

Legs long and slender, nearly reaching tips of paraterga (Fig. 2G); tarsus longer than femur; claw simple, curved ventrad (Fig. 3K).

Gonopods (Figs 3M–N, 4) simple. Coxae large, abundantly micropapillate and setose ventrolaterally. Telopodite slightly longer than coxite, slender throughout, subfalcate, distinctly curved ventrad, setose in its basal part, with a prominent, digitiform, lateral, distofemoral process (**dp**) at about basal one-third. Acropodite with a micropapillate process (**pp**) at midway; seminal groove long, terminating in a hairpad at a small, triangular, mesal lobule (**lo**) subapically.

Vulvae lying inside a membranous sac, each vulva consisting of a large horseshoe-shaped operculum (**op**) and a bursa (**b**) with several long setae (Fig. 3O).

***Eutrichodesmus deporatus* Liu & Wesener, sp. n.**

<http://zoobank.org/F01FD071-6226-4A7F-A3AB-45FCFF7FFA1E>

Figs 1B, 5–7

Material examined. Holotype male (SMF), Laos, Luang Prabang Prov., NE Luang Prabang, Nam Ou, Nong Khiao, Cave Tham Pathok, hand collected, N20°33.082', E102°37.925', 373 m, 11.III.2006, coll. P. Jäger & J. Altmann.

Paratypes. 1 male, 1 female (ZFMK MYR6128 & 6129), same data as holotype; 2 females, 3 juveniles (SMF), same data as holotype; 1 male (SMF), same locality, 29.II.2008, coll. P. Jäger.

Etymology. To emphasize the ozopores in this species being mostly reduced; adjective.

Diagnosis. Differs from all other species of the genus in the ozopores retained only on body segment 17, coupled with the gonopod acropodite showing a slightly bifid dorsolateral tooth subapically. See also Key above.

Description. Length of adults of both sexes ca. 7.5–8.0 mm, width 0.6–0.8 mm and 1.6–1.8 mm on midbody pro- and metazona, respectively.

Coloration uniformly pallid (Fig. 1B).

Adults with 20 segments (Fig. 1B), body conglobation complete.

Antennae short, but slender (Figs 1B, 5A); in length, antennomere $6 > 3 = 2 > 4 = 5 > 7 > 1$.

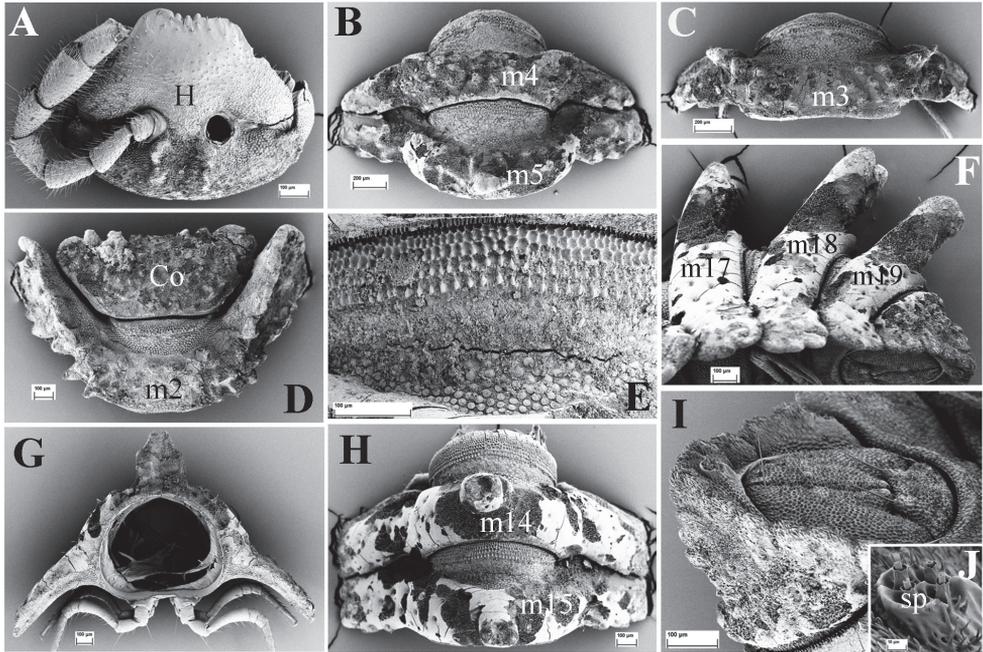


Figure 5. *E. deporatus* sp. n., SEM, male paratype from Cave Tham Pathok. **A** head (H) and left antenna, frontal view **B** segments 4 and 5, dorsal view **C** segment 3, dorsal view (m3–m5 = metaterga 3–5) **D** collum (Co) and segment 2 (m2 = metatergum 2), dorsal view **E** prozonum 15, dorsal view **F** segments 17–19 and telson, lateral view (m17–m19 = metaterga 17–19) **G** cross-section of segment 6, caudal view **H** segments 14 and 15, dorsal view (m14–m15 = metaterga 14–15) **I** telson, subventral view **J** spinnerets (sp), subventral view.

Labrum with three teeth (Fig. 5A).

Head (Fig. 5A), bacilliform sensilla on antennae (Fig. 6A), gnathochilarium (Fig. 6D), mandibles (Fig. 6B), prozona (Fig. 5E), endoterga, metatergal setae (Fig. 6H), sterna (Fig. 6E), pleurosternal keels, stigmata (Fig. 6I–J), legs (Fig. 6K), gonopod aperture, telson (Fig. 5I–J), and vulvae (Fig. 6K) all similar to *E. steineri* sp. n.

Collum subtrapeziform, with five transverse rows of round microvillose tubercles, flattened medially (Fig. 5D). Fore margin with two distinct tubercles on each side (Fig. 5D).

Stricture between pro- and metazona broad and shallow, finely microgranulate (Fig. 5E). Limbus with relatively long crenulations and nearby abundant microvilli (Fig. 6F).

Metaterga 2–5 with three transverse mixostictic rows of similarly microvillose tubercles, flattened medially, about 7 + 7 per row (Fig. 5B–D). Three transverse rows of rather small, flat tuberculations on metaterga 6–19 (Fig. 5F–H). Metaterga 5–19 each with a very high, large, bifid, mid-dorsal projection (Fig. 5B, F–H). Projections 5–17 upright, then directed slightly caudad on metaterga 18 and 19 (Fig. 5F).

Front margin of paraterga 2–4 strongly elevated (Fig. 5B–D). Paraterga 2 strongly enlarged, vaguely trilobate laterally, with four frontal and three caudal evident lobulations (Fig. 5D); paraterga 3 and 4 slightly shorter than others, bilobate laterally (Fig.

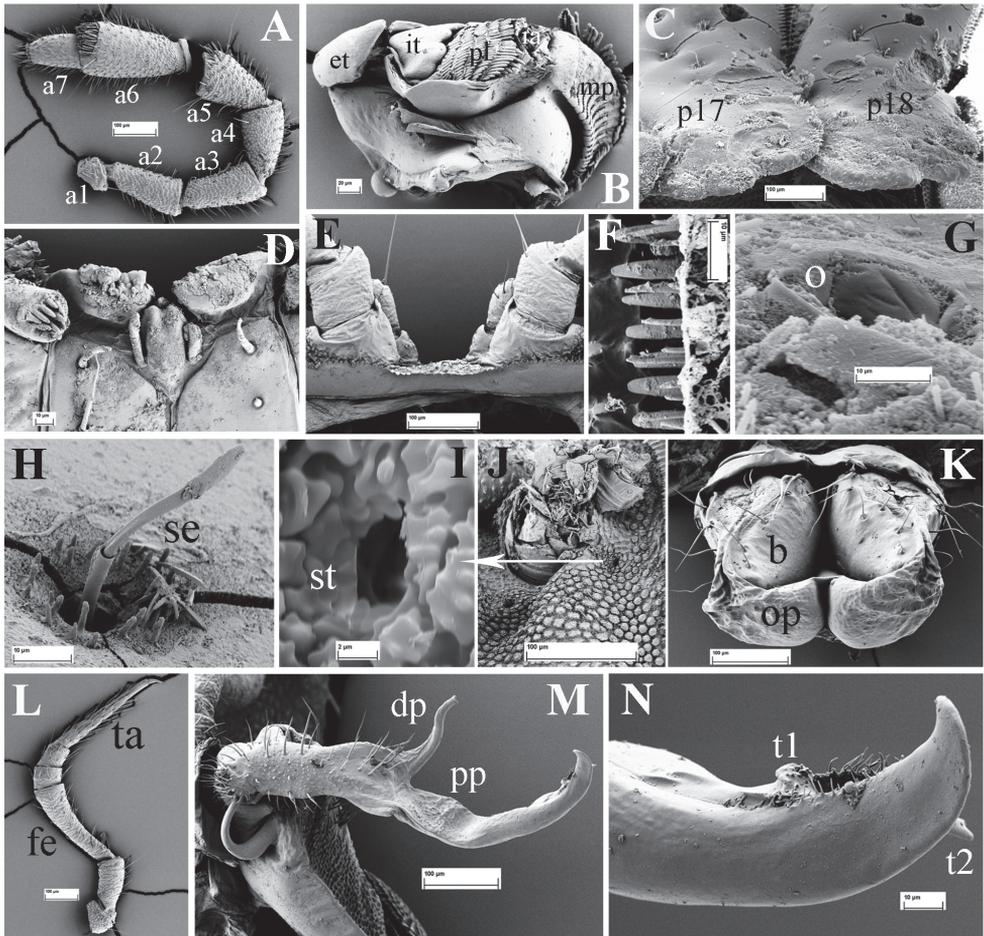


Figure 6. *E. deparatus* sp. n., SEM, male paratype from Cave Tham Pathok. **A** right antenna, lateral view (a1–a7 = antennomeres 1–7) **B** right mandible, general view (et = external tooth; it = internal tooth; pl = pectinate lamellae; ia = intermediate area; mp = molar plate) **C** paratergum 17 (p17) and 18 (p18), dorsal view **D** tip of gnathochilarium, ventral view **E** sternum 6, caudal view **F** limbus of metatergum 14, dorsal view **G** ozopore (o) on paratergum 17 **H** a seta (se) on metatergum 14, general view **I** stigmata (st), detail **J** stigmata of segment 17, subventral view **K** female paratype, vulvae, general view (op = operculum; b = bursa) **L** midbody leg, frontal view (fe = femur; ta = tarsus) **M** right gonopod, mesal view (dp = distofemoral process; pp = papillate process) **N** tip of right gonopod, mesal view (t1–2 = teeth 1–2).

5B–C); following paraterga laterally 3- or 4-lobulated, caudolaterally at base with two distinct lobulations (Figs 5F, H, 6C).

Ozopores mostly reduced, only visible on paraterga 17 (Fig. 6G).

Gonopods (Figs 6M–N, 7) simple. Coxae abundantly micropapillate and sparsely setose ventrolaterally, with an apicolateral lobe (cl). Telopodite longer than coxite, slender throughout, setose in basal half, with a prominent, digitiform, lateral, distofemoral process (dp) at about midway. Acropodite with a micropapillate process (pp)

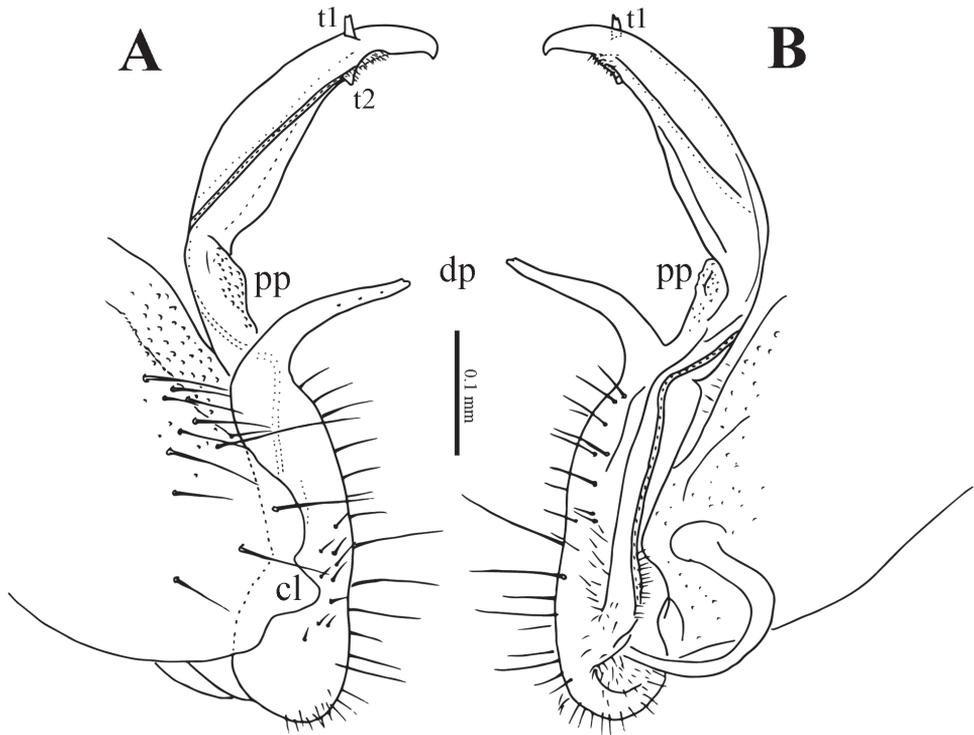


Figure 7. *E. deporatus* sp. n., ♂ paratype from Cave Tham Pathok. **A–B** right gonopod, lateral and mesal views, respectively. Abbreviations: cl = coxal lobe; dp = distofemoral process; pp = papillae process; t1–2 = teeth 1–2.

at base and a dorsolateral tooth (**t1**) subapically, tip slightly bifid; seminal groove terminating in a hairpad at a small triangular tooth (**t2**) subapically.

Remarks. The specimens come from the Cave Tham Pathok which is about 100 meters long, and the temperature inside is about 15 °C. The animals were found living at a small waterfall at a distance of 20 meters from the entrance. In addition, *Heteropoda* spp. (Arachnida) and *Glyphiulus* sp. (Diplopoda, Cambalopsidae) were found in the cave (Steinmetz 2007).

The pallid body and long legs suggest that *E. deporatus* sp. n. is most likely a troglobite.

***Eutrichodesmus paraster* Liu & Wesener, sp. n.**

<http://zoobank.org/7EC7CE3B-1990-49E5-953C-B0B8D5B46DEB>

Figs 1C, 8–10

Material examined. Holotype male (SEM), (SMF), Laos, Huaphan Prov., Xop, Cave Tham Long Puang (F 48-123-001), N20°28'25.7", E103°21'44.4", 16.I.2009, coll. H. Steiner (101/09-).

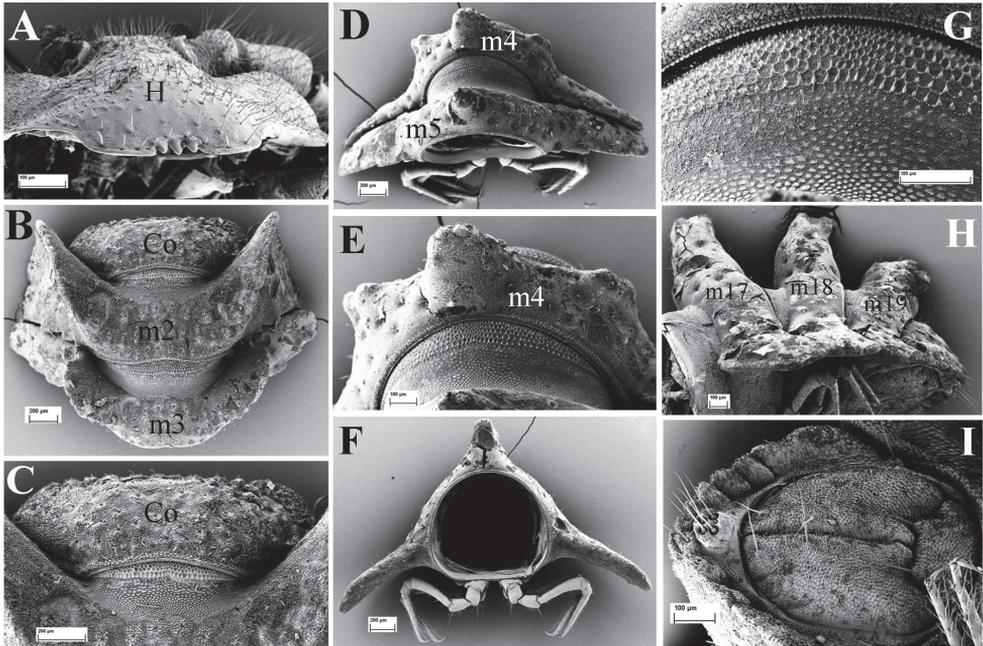


Figure 8. *E. paraster* sp. n., SEM, male holotype from Cave Tham Long Puang. **A** head (H), subfrontal view **B** collum (Co) and segments 2–3 (m2–m3 = metaterga 2, 3), dorsal view **C** collum (Co), dorsal view **D** segments 4 and 5 (m4–m5 = metaterga 4, 5), dorsal view **E** segment 4 (m4 = metatergum 4), dorsal view **F** cross-section of segment 6, caudal view **G** prozonum 5, dorsal view **H** segments 17–19 and telson, lateral view (m17–m19 = metaterga 17–19) **I** telson, ventral view.

Paratypes. 1 female (SMF), same data as holotype; 1 juvenile (ZFMK MYR6131), same data.

Etymology. To emphasize the similarity to *E. aster* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009; adjective.

Diagnosis. Differs from other species of the genus primarily by the completely reduced ozopores. Superficially very similar to *E. aster*, but distinguished from the latter through the smaller body, laterally 3-lobulated paraterga, and the relatively complex gonopod showing a large, laterally denticulate, distofemoral process; the acropodite subapically has a very small mesal tooth and an evident, digitiform, dorsal lobule. See also Key above.

Description. Length of adults ca. 8.0 mm (holotype) or 9.0 mm (paratype), width 1.0 mm and 2.5 mm on midbody pro- and metazona, respectively.

Coloration uniformly pallid (Fig. 1C).

Adults with 20 segments (Fig. 1C), body conglobation complete.

Antennae short, but slender; in length, antennomere 6 = 3 > 2 > 4 = 5 > 7 > 1 (Fig. 9A).

Labrum with three teeth (Fig. 8A).

Head (Fig. 8A), bacilliform sensilla on antennae (Fig. 9A), gnathochilarium (Fig. 9B), mandibles (Fig. 9D), prozona (Fig. 8G), endoterga (Fig. 9J), metatergal setae

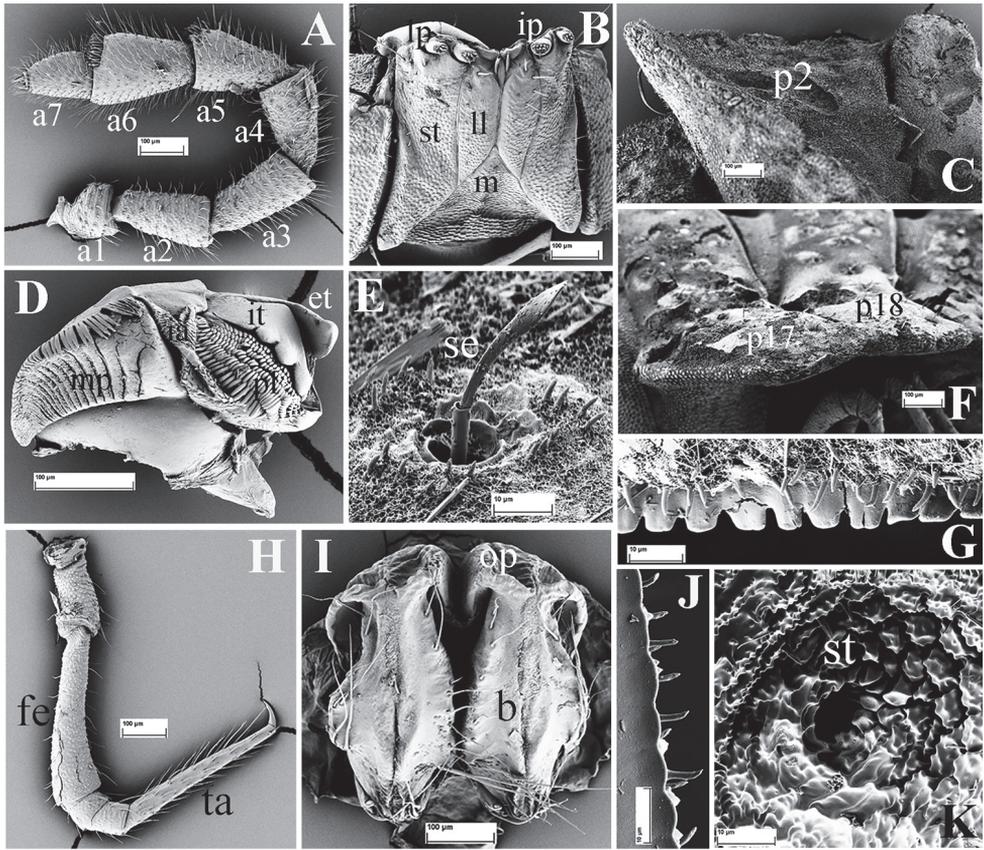


Figure 9. *E. paraster* sp. n., SEM, male holotype from Cave Tham Long Puang. **A** right antenna, lateral view (a1–a7 = antennomeres 2–7) **B** gnathochilarium, ventral view (lp = lateral palpus; ip = inner palpus; st = stipites; ll = lamellae linguales; m = mentum) **C** paratergum 2 (p2), dorsal view **D** right mandible, general view (et = external tooth; it = internal tooth; pl = pectinate lamellae; ia = intermediate area; mp = molar plate) **E** a seta (se) on metatergum 18 **F** paraterga 17 (p17) and 18 (p18), lateral view **G** limbus of metatergum 5, dorsal view **H** midbody leg, frontal view (fe = femur; ta = tarsus) **I** female paratype, vulvae, general view (op = operculum; b = bursa) **J** endotergum 5 **K** stigmata (st), ventral view.

(Fig. 9E), sterna (Fig. 8F), pleurosternal keels, stigmata (Fig. 9K), legs (Fig. 9H), gonopod aperture, telson (Fig. 8I) and vulvae (Fig. 9I) all similar to those in *E. steineri* sp. n.

Collum subtrapeziform, with six transverse rows of round microvillose tubercles (Fig. 8B–C).

Stricture between pro- and metazona broad and shallow, more finely alveolate-microgranulate than prozona (Fig. 8G). Limbus regularly microcrenulate (Fig. 9G).

Front margin of metaterga 2–4 strongly elevated, each latter with three transverse mixostictic rows of similar tubercles (Fig. 8B, D–E). Following metaterga with three transverse rows of small, flattened, microvillose tuberculations (Figs 8D, 9E). Metaterga 4–19 each with a very high mid-dorsal projection, slightly smaller on metatergum 4 (Fig. 8D–F, H); tip of projections usually bilobed, always bilobed on each side on

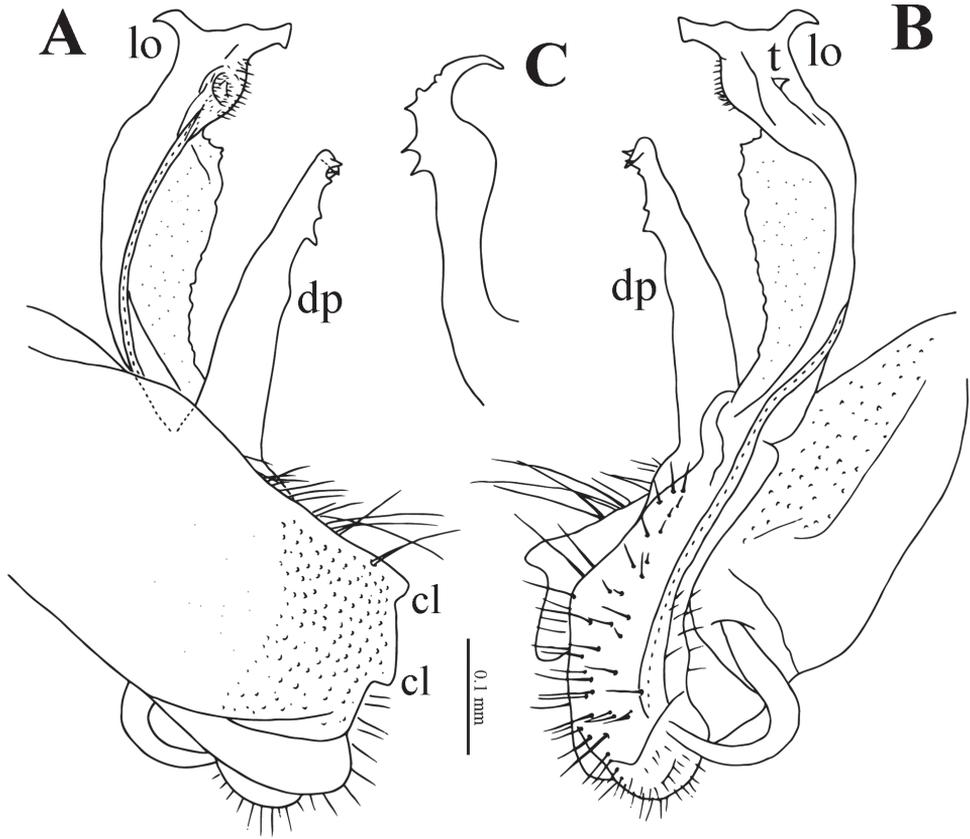


Figure 10. *E. paraster* sp. n., male holotype from Cave Tham Long Puang. **A–B** right gonopod, lateral and mesal views, respectively **C** distofemoral process, subventral view. Abbreviations: cl = coxal lobe; dp = distofemoral process; lo = lobule; t = tooth.

metaterga 5 and 6 (Fig. 8D). Projections upright, directed slightly caudad only on metatergum 19 (Fig. 8H).

Paraterga 2 strongly enlarged, vaguely 4-lobulated laterally (Fig. 9C). Following paraterga bi- or trilobate laterally in anterior and posterior parts of body, respectively, each with two small caudal lobulations (Figs 1C, 9F).

Ozopores absent.

Gonopods (Fig. 10) relatively complex. Coxae large, micropapillate and sparsely setose ventrolaterally, with two small apicolateral lobes (**cl**). Telopodite slightly longer than coxite, slender throughout, setose in basal half, with a prominent, laterally denticulate, distofemoral process (**dp**) at about midway. Acropodite twisted, subapically with a very small mesal tooth (**t**) and an evident digitiform lobule (**lo**) dorsally; seminal groove terminating subapically in a hairpad.

Remarks. As this species was collected in a cave, and has a pallid body it appears to be a real troglobite. The absence of ozopores is unique for the family Haplodesmidae.

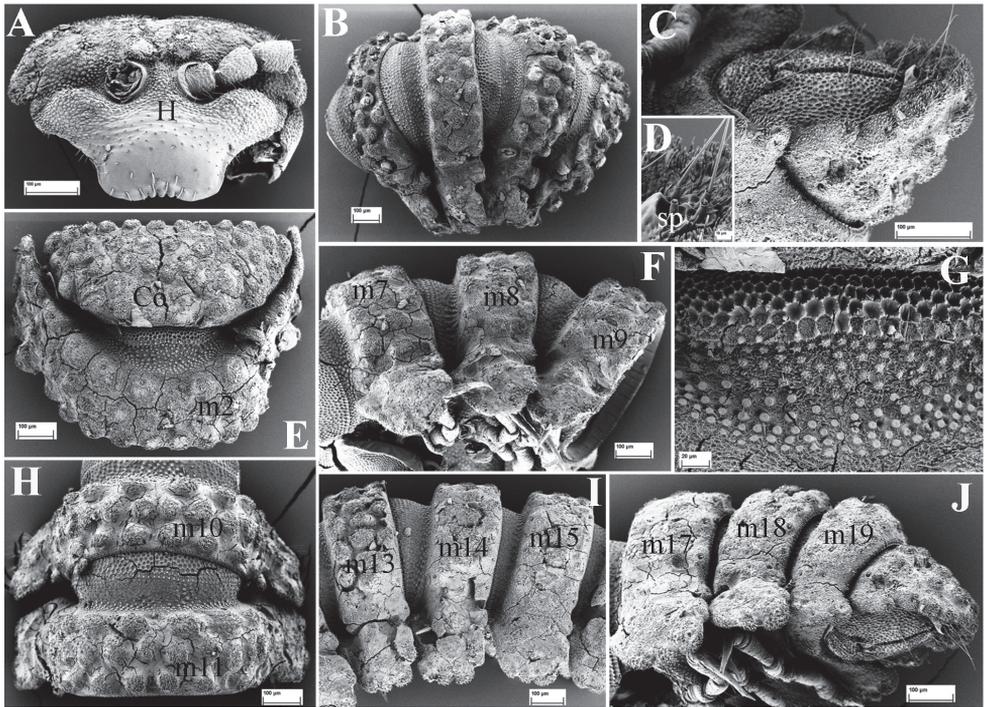


Figure 11. *E. parvus* sp. n., SEM, male paratype from Cave Tham Nam Long. **A** head (H), frontal view **B** segments 3–6, subdorsal view **C** telson, subventral view **D** spinneret (sp), detail **E** collum (Co) and segment 2 (m2 = metatergum 2), dorsal view **F** segments 7–9, lateral view (m7–m9 = metaterga 7–9) **G** prozonum 2, dorsal view **H** segments 10–11, dorsal view **I** segments 13–15, dorsal view **J** segments 17–19 and telson, lateral view (m10–11, 13–15, 17–19 = metaterga 10, 11, 13–15, 17–19).

***Eutrichodesmus parvus* Liu & Wesener, sp. n.**

<http://zoobank.org/09C6E621-12C0-4837-A231-99A692E135C2>

Figs 1D, 11–13

Material examined. Holotype male (SMF), Laos, Huaphan Prov., Cave Tham Nam Long (F 48-125-007), N20°27'50.3", E104°9'10.7", 10.I.2008, coll. H. Steiner (133/08-).

Paratypes. 1 male (SEM), (ZFMK MYR6132), 1 female (ZFMK MYR6128), same data as holotype; 2 females (SMF), same data.

Etymology. To emphasize the very small body of this species; adjective.

Diagnosis. Differs from other species of the genus in the very small body (4.0–5.0 mm long), three regular transverse rows of round microvillose tubercles on metaterga, short paraterga, as well as the relatively complex gonopod with a large, laterally denticulate, distofemoral process; the acropodite subapically has a small dorsal tooth and an evident, digitiform, ventral lobe; the seminal groove is devoid of a hairpad near the place of its termination. See also Key above.

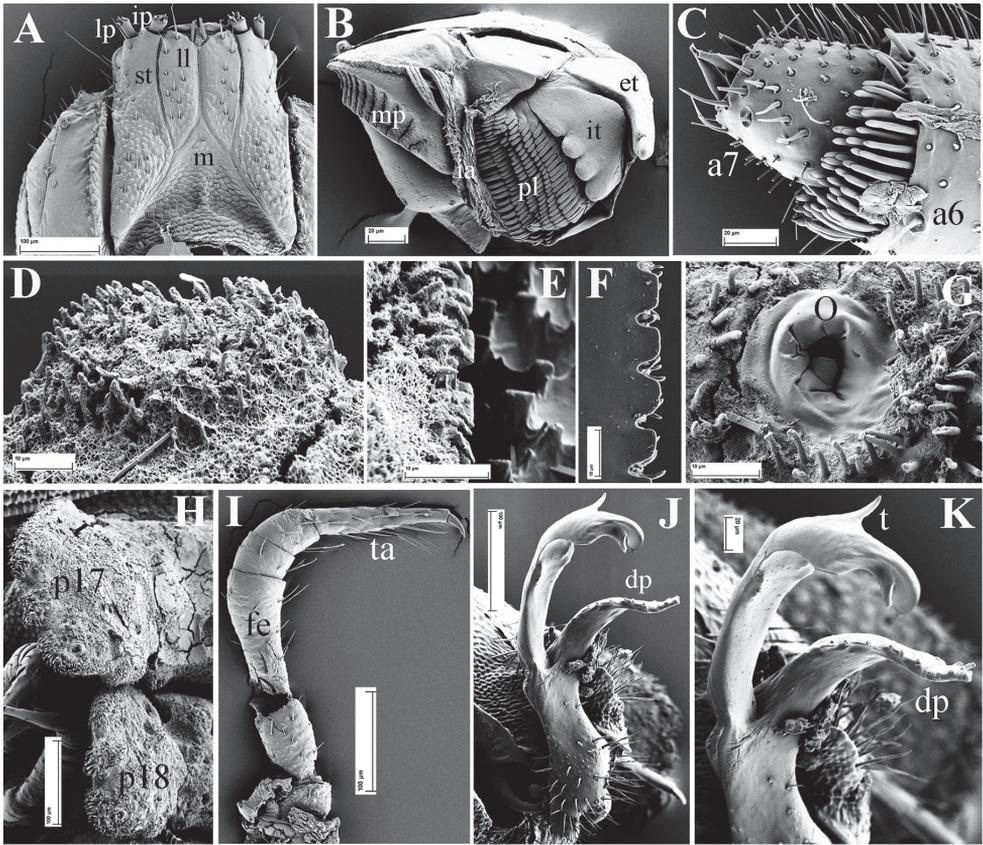


Figure 12. *E. parvus* sp. n., SEM, male paratype from Cave Tham Nam Long. **A** gnathochilarium, ventral view (lp = lateral palpus; ip = inner palpus; st = stipites; ll = lamellae linguales; m = mentum) **B** right mandible, general view (et = external tooth; it = internal tooth; pl = pectinate lamellae; ia = intermediate area; mp = molar plate) **C** tip of antenna, laterodorsal view (a6–a7 = antennomeres 6, 7) **D** a tubercle at fore margin of collum, dorsal view **E** limbus of metatergum 10, dorsal view **F** endotergum 9 **G** ozopore (o) on paratergum 17, general view **H** paratergum 17 (p17) and 18 (p18), lateral view **I** midbody leg, frontal view (fe = femur; ta = tarsus; cl = claw) **J** left gonopod, submesal view **K** half of left gonopod, detail (dp = distofemoral process; t = tooth).

Description. Length of adults of both sexes ca .4.0–5.0 mm, width 0.3–0.4 mm and 0.6–0.8 mm on midbody pro- and metazona, respectively.

Coloration uniformly light yellow-brown with pallid antennae (Fig. 1D).

Adults with 20 segments (Fig. 1D), body subcylindrical, conglobation incomplete. Antennae short (Fig. 1D); in length, antennomere 6 > 5 > 2 > 3 = 4 > 7 > 1.

Labrum with three teeth (Fig. 11A).

Head (Fig. 11A), bacilliform sensilla of antenna (Fig. 12C), gnathochilarium (Fig. 12A), mandible (Fig. 12B), prozona (Fig. 11G), endoterga (Fig. 12F), sterna, pleurosternal keels, gonopod aperture (Fig. 11F), telson (Fig. 11C–D) and vulvae all similar to those in *E. steineri* sp. n.

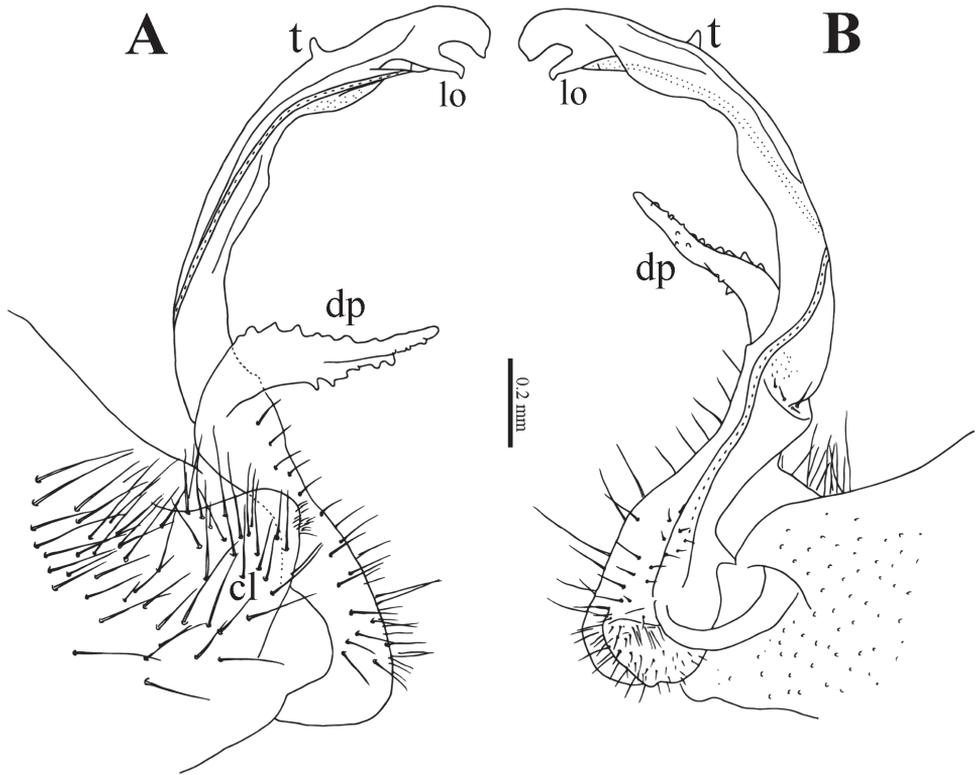


Figure 13. *E. parvus* sp. n., male paratype from Cave Tham Nam Long. **A–B** right gonopod, lateral and mesal views. Abbreviations: cl = coxal lobe; dp = distofemoral process; lo = lobe; t = tooth.

Collum semi-circular, with five transverse rows of round, small, microvillose tubercles (Fig. 11E). First row with 12 round tubercles (Fig. 11E).

Stricture between pro- and metazona broad and shallow, more finely alveolate-microgranular than prozona (Fig. 11G). Limbus regularly microcrenulate (Fig. 12E).

Metaterga 2 to pre-anal segment each with three transverse rows of high, round, regular, microvillose tubercles, usually about 5 + 5 per row (Figs 11–12). Metatergal setae inconspicuous, mostly abraded.

Paraterga short, slightly extending down below level of venter, especially paraterga 18 and 19 being shorter with previous one (Figs 11J, 12H); usually trilobate laterally and with two caudal lobulations (Figs 11F, I, J, 12H).

Pore formula normal, ozopores distinct, located near top of caudolateral lobulation (Fig. 12G–H).

Legs long and slender, femur somewhat longer than tarsus (Fig. 12I).

Gonopods (Figs 12J–K, 13) relatively complex. Coxae large, micropapillate and setose ventrolaterally, with a large apicolateral lobe (cl). Telopodite slightly longer than coxite, slender throughout, setose in basal half, with a large, prominent, denticulate,

lateral, distofemoral process (**dp**) at about midway. Acropodite subapically with a small tooth (**t**) dorsally and an evident digitiform lobe (**lo**) ventrally; seminal groove terminating without hairpad.

Eutrichodesmus sp.

Material examined. 1 female, 2 juveniles (SMF), Laos, Cave Tham Mokfek, N20°48'34.7", E101°47'14.5", 28.I.2010, coll. H. Steiner (155/10-).

Remarks. These specimens do not fit any of the six *Eutrichodesmus* described from Laos, base on somatic characters alone. As only one adult female is available, we refrain from naming this species.

Discussion

All attempts to extract the DNA from some of the specimens using the DNeasy Blood & Tissue kit from Qiagen were unsuccessful. One reason might be the specimens had been preserved in low-concentration ethanol for nearly ten years. In addition, it was not at all easy to get enough tissue from legs of these tiny specimens for DNA extractions.

In our study, two new species were found, *E. deporatus* sp. n. and *E. paraster* sp. n., both from caves, and unsurprisingly less pigmented, that show strongly or completely reduced ozopores. The function of the defensive glands and their ozopores is known to lie in the production of defence fluids, as a protection against predators (Shear 2015). From the recent paper concerning the adaptation in the cave millipedes to the cave environment (Liu et al. 2017) it remains unclear whether or not the suppression may be related to cavernicolity. We are rather inclined to think it is not. Firstly, about half of the known species of *Eutrichodesmus* are cave-dwellers, but their pore formulae are normal: 5, 7, 9, 10, 12, 13, 15–19 (Golovatch et al. 2009a, 2009b, 2015, 2016a; Liu and Tian 2013). Secondly, within the family Haplodesmidae the normal pore formulae dominate, but there are several genera or species with increased formulae as well: *Helodesmus* Cook, 1896 and *Koponenius* Golovatch & VandenSpiegel, 2014, both showing 5, 7–17(18) formulae, and culminating in *Prosopodesmus panporus* Blower & Rundle, 1980 with its unique 5–17(18) formula (Golovatch et al. 2009a, Mesibov 2012; Golovatch and VandenSpiegel 2014). The occasional loss of ozopores in haplodesmids seems to be surprising, but not unthinkable. After all, some species of Sphaeriodesmidae have also been noted to lack ozopores. In addition, ozopores are often very difficult to observe in those *Eutrichodesmus* species which lack porosteles and where the small ozopores open flush with a surface beset with tubercles, grains, setiferous fossae and microvilli.

All material of *Eutrichodesmus* from Laos treated here was collected opportunistically by a research group focusing on Arachnida, headed by Peter Jäger (SMF). Because

Eutrichodesmus species hide in the soil and are small and often coiled, it is possible they were missed during searches focused on Arachnida. It can only be hoped that more efforts to investigate and describe the highly unique and diverse diplopod fauna of Laos will be undertaken in the future, before the utilization of natural resources leads to the loss of the existing natural forests, something that has already happened in the last decades in neighbouring nations (Sodhi et al. 2010).

Acknowledgements

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Checklist of American sand flies (Diptera, Psychodidae, Phlebotominae): genera, species, and their distribution

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Abstract

Phlebotomine sand flies are dipteran insects of medical importance because many species are involved in the transmission of pathogens between human and non-human animals. A total of 530 American species of sand flies is presented in an updated checklist, along with their author(s) and year of publication using the classification by Galati (1995, 2003). Distribution by country is also provided.

Keywords

Distribution, Nearctic, Neotropical, Psychodomorpha, sand fly, taxonomy

Introduction

Phlebotomine sand flies (Diptera, Psychodidae, Phlebotominae) are medically important insects involved in the transmission of arboviruses, bacteria and protozoan parasites among human and non-human animals (Rangel and Lainson 2009).

There are approximately 1,000 valid described species of sand flies in the world of which 530 are known to occur in the Americas. Historically, the systematics of sand flies has been based on the division of species into few genera (Fairchild 1955, Theodor 1965, Lewis et al. 1977, Young and Duncan 1994). Based on an extensive comparative analysis of characters, Theodor (1965) made an attempt to define groups of American sand flies, but preferred not to give nomenclatorial rank to them, suggesting these groupings might change taxonomic status with future studies. Lewis et al. (1977) considered the Atlantic Ocean as the main cause of differentiation between sand flies from the “Old World” (Palearctic, Afrotropical, Oriental and Australasian regions) and the “New World” (Nearctic and Neotropical regions), and maintained five genera of which two, *Phlebotomus* Rondani & Berté, 1840 and *Sergentomyia* França & Parrot, 1920, occur in the “Old World” and three, *Brumptomyia* França & Parrot, 1921, *Warileya* Hertig, 1948 and *Lutzomyia* França, 1924, are present in the “New World”. Later, Young and Duncan (1994) amended the classification of Lewis et al. (1977), becoming the most widely adopted by those working with sand flies.

Artemiev (1991) attempted to establish a phylogenetic classification for sand flies. He divided sand fly species into two tribes (Idiophlebotomini Artemiev, 1991 and Phlebotomini Rondani, 1840), seven sub-tribes (Idiophlebotomina Artemiev, 1991; Hertigiina Abonnenc & Léger, 1976; Phlebotomina Rondani, 1840; Spelaeomyiina Artemiev, 1991; Sergentomyiina Artemiev, 1991; Australophlebotomina Artemiev, 1991; Brumptomyiina Artemiev, 1991), and 24 genera. However, no explicit method was used to group the sand flies, and his classification was not accepted among researchers of this group of insects.

A proposal for the classification of Phlebotominae was presented by Galati (1995, 2003) who used the cladistic method in her study of American sand flies. In her classification, the tribe Idiophlebotomini Artemiev, 1991 was synonymized with Hertigiina Abonnenc & Léger, 1976, while the tribe Phlebotomini Rondani, 1840 was maintained. Six subtribes from Artemiev (1991) were kept (Idiophlebotomina, Hertigiina, Phlebotomina, Sergentomyiina, Australophlebotomina, and Brumptomyiina) and an additional subtribe was created (Psychodopygina Galati, 1995). In addition, one subtribe previously considered synonymous was reinstated (*Lutzomyiina* Abonnenc & Léger, 1976). Galati reclassified “New World” sand flies into 22 genera. Later, *Edentomyia* Galati, Andrade-Filho, Silva & Falcão, 2003 was proposed as another Neotropical genus in the tribe Phlebotomini; however, this genus was not included in any subtribe (Galati et al. 2003).

The aim of this work is to provide a checklist of valid Phlebotominae species of the Neotropical and Nearctic regions, together with their distribution by country,

highlighting their type-locality. This work updates the list of American sand flies and provides currently accepted names for use by taxonomists, students, researchers and health workers.

Material and methods

The list contains information updated until December, 2016, and data was collated from our own work with sand fly taxonomy, literature surveys, and studies of sand flies deposited in different entomological collections: (i) Coleção de Flebotomíneos (FIOCRUZ/ COLFLEB); (ii) Museu de Zoologia da Universidade de São Paulo (MZUSP); (iii) Coleção de Referência da Faculdade de Saúde Pública (FSP–USP); (iv) Coleção Entomológica do Laboratório de Entomologia em Saúde Pública (FSP–USP–LESP–Phlebotominae); (v) Coleção da Seção de Parasitologia do Instituto Butantan (IBut); (vi) Coleção de Flebotomíneos do Instituto Evandro Chagas (COLFleIEC); (vii) Natural History Museum, London (NHM).

To be considered valid, and therefore included in this checklist, a species name has to meet the criteria of publication in Articles 8 and 9 of International Code of Zoological Nomenclature (ICZN) (1999, 2011).

The checklist presents genera arranged according to the classification of Galati (2003), and subgenera, species groups/series and species are listed alphabetically within each genus. Countries are listed alphabetically and the country of the type locality is marked with asterisk (*). Fossil species are indicated by the symbol †. We intend to add information about synonymies and full references for distributional records in a later, more comprehensive, catalogue.

Results

This checklist includes 530 species of the Phlebotominae, distributed among 23 genera, occurring in 28 countries.

There are seven “informal” taxa that comprise unavailable names since they do not meet the requirements of the ICZN, and two other names are available but are found to denote more than one taxon (availability of name is not affected according to provisions of the ICZN, Articles 17.2 and 23.8). Here, we report one *nomem dubium* for *Nyssomyia singularis* and one *species inquirerenda* for *Bichromomyia inornata*.

Despite the great amount of data on American sand flies and the increased interest in the study of these insects, there has been slow progress in the understanding of taxonomy and systematics of this subfamily. The checklist presented herein aims to give an updated account of which valid species have been recorded in the Neotropical and Nearctic regions, as well as provide information on the geographical range of these species by country.

Systematics

Phylum Arthropoda von Siebold, 1848

Subphylum Hexapoda Latreille, 1825

Class Insecta Linnaeus, 1758

Order Diptera Linnaeus, 1758

Sub-order Psychodomorpha Hennig, 1968

Family Psychodidae Newman, 1834

Subfamily Phlebotominae Rondani, 1840

Tribe Hertigiini Abonnenc & Léger, 1976

Subtribe HERTIGIINA Abonnenc & Léger, 1976

Genus *Hertigia* Fairchild, 1949

Hertigia hertigi Fairchild, 1949

Distribution. Costa Rica, Panama*.

Genus *Warileya* Hertig, 1948

Warileya euniceae Fernández, Carbajal, Astete & Wooster, 1998

Distribution. Peru*.

Warileya fourgassiensis Le Pont & Desjeux, 1984

Distribution. French Guiana*.

Warileya leponti Galati & Cáceres, 1999

Distribution. Peru*.

Warileya lumbrerasi Ogosuku, Perez, Davies & Villaseca, 1996

Distribution. Peru*.

Warileya nigrosaccula Fairchild & Hertig, 1951

Distribution. Colombia, Panama*.

Warileya phlebotomanica Hertig, 1948

Distribution. Ecuador, Peru*.

Warileya rotundipennis Fairchild & Hertig, 1951

Distribution. Bolivia, Colombia, Costa Rica, Panama*, Peru.

Warileya yungasi Velasco & Trapido, 1974

Distribution. Bolivia*.

Tribe Phlebotomini Rondani, 1840

Subtribe BRUMPTOMYIINA Artemiev, 1991

Genus *Brumptomyia* França and Parrot, 1921

Brumptomyia angelae Galati, Santos & Silva, 2007

Distribution. Brazil*.

***Brumptomyia avellari* (Costa Lima, 1932)**

Distribution. Argentina, Bolivia, Brazil*, Colombia, Panama, Paraguay, Peru, Venezuela.

***Brumptomyia beaupertuyi* (Ortiz, 1954)**

Distribution. Colombia, Venezuela*.

***Brumptomyia bragai* Mangabeira & Sherlock, 1961**

Distribution. Brazil*.

***Brumptomyia brumpti* (Larrousse, 1920)**

Distribution. Argentina, Bolivia, Brazil*.

***Brumptomyia cardosoi* (Barretto & Coutinho, 1941)**

Distribution. Brazil*.

***Brumptomyia carvalhoi* Shimabukuro, Marassá & Galati, 2007**

Distribution. Brazil*.

***Brumptomyia cunhai* (Mangabeira, 1942)**

Distribution. Brazil*, Honduras.

***Brumptomyia devenanzii* (Ortiz & Scorza, 1963)**

Distribution. Venezuela*.

***Brumptomyia figueireidoi* Mangabeira & Sherlock, 1961**

Distribution. Brazil*.

***Brumptomyia galindoi* (Fairchild & Hertig, 1947)**

Distribution. Brazil, Panama*.

***Brumptomyia guimaraesi* (Coutinho & Barretto, 1941)**

Distribution. Argentina, Brazil*, Paraguay.

***Brumptomyia hamata* (Fairchild & Hertig, 1947)**

Distribution. Belize, Colombia, Ecuador, Mexico, Panama*, Peru.

***Brumptomyia leopoldoi* (Rodriguez, 1953)**

Distribution. Belize, Colombia, Ecuador*, Panama.

***Brumptomyia mangabeirai* (Barretto & Coutinho, 1941)**

Distribution. Brazil*.

***Brumptomyia mesai* Sherlock, 1962**

Distribution. Belize, Colombia*, Honduras, Mexico.

***Brumptomyia nitzulescui* (Costa Lima, 1932)**

Distribution. Brazil*.

***Brumptomyia orlando* Fraiha, Shaw & Lainson, 1970**

Distribution. Brazil*.

***Brumptomyia ortizi* Martins, Silva & Falcão, 1971**

Distribution. Brazil*.

***Brumptomyia pentacantha* (Barretto, 1947)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, Peru.

***Brumptomyia pinto* (Costa Lima, 1932)**

Distribution. Argentina, Bolivia, Brazil*, French Guiana, Surinam, Venezuela.

***Brumptomyia quimper* Galati & Cáceres, 1999**

Distribution. Peru*.

Brumptomyia spinosipes* (Floch & Abonnenc, 1943)*Distribution.** Brazil, French Guiana*, Panama.***Brumptomyia travassosi* (Mangabeira, 1942)****Distribution.** Brazil*, French Guiana, Panama, Surinam.***Brumptomyia troglodytes* (Lutz, 1922)****Distribution.** Brazil*, Peru.***Brumptomyia virgens* Mangabeira & Sherlock, 1961****Distribution.** Brazil*.**Genus *Oligodontomyia* Galati, 1995*****Oligodontomyia isopsi* (Léger & Ferte, 1996)****Distribution.** Chile*.***Oligodontomyia oligodonta* (Young, Pérez & Romero, 1985)****Distribution.** Peru*.***Oligodontomyia toroensis* (Le Pont, Torrez-Espejo & Dujardin, 1997)****Distribution.** Bolivia*.**Subtribe SERGENTOMYIINA Artemiev, 1991****Genus *Deanemyia* Galati, 1995*****Deanemyia appendiculata* (Martins, Falcão & Silva, 1961)****Distribution.** Brazil*.***Deanemyia derelicta* (Freitas & Barrett, 1999)****Distribution.** Brazil*.***Deanemyia maruaga* (Alves, Freitas & Barrett, 2008)****Distribution.** Brazil*.***Deanemyia ramirezi* (Martins, Falcão, Silva & Miranda-Filho, 1982)****Distribution.** Bolivia, Brazil*.**Note.** The record for Bolivia is based on specimens collected in Aguas Calientes Department of Santa Cruz and donated by François Le Pont to one of us (EABG).***Deanemyia samueli* (Deane, 1955)****Distribution.** Brazil*.**Genus *Micropygomyia* Barretto, 1962****Subgenus (*Coquilletimyia*) Galati, 1995****Series *chiapanensis* Theodor, 1965*****Micropygomyia* (*Coquilletimyia*) *californica* (Fairchild & Hertig, 1957)****Distribution.** United States of America*.

Micropygomyia (Coquillettomyia) chiapanensis* (Dampf, 1947)*Distribution.** Costa Rica, El Salvador, Honduras, Mexico*, Nicaragua, Panama.***Micropygomyia (Coquillettomyia) stewarti* (Mangabeira & Galindo, 1944)****Distribution.** Mexico, United States of America*.**Series vexator Fairchild, 1955*****Micropygomyia (Coquillettomyia) apache* (Young & Perkins, 1984)****Distribution.** United States of America*.***Micropygomyia (Coquillettomyia) oppidana* (Dampf, 1944)****Distribution.** Canada, Mexico*, United States of America.***Micropygomyia (Coquillettomyia) vexator* (Coquillett, 1907)****Distribution.** Canada, Mexico, United States of America*.***Micropygomyia (Coquillettomyia) vindicator* (Dampf, 1944)****Distribution.** Mexico*.**Subgenus (*Micropygomyia*) Barretto, 1962****Series cayennensis Fairchild, 1955*****Micropygomyia (Micropygomyia) absonodonta* (Felicangeli, 1995)****Distribution.** Peru, Venezuela*.***Micropygomyia (Micropygomyia) ancashensis* Galati & Cáceres, 2007****Distribution.** Peru*.***Micropygomyia (Micropygomyia) cayennensis cayennensis* (Floch & Abonnenc, 1941)****Distribution.** Belize, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana*, Honduras, Mexico, Nicaragua, Panama, Peru, Trinidad and Tobago, Venezuela.***Micropygomyia (Micropygomyia) cayennensis braci* (Lewis, 1967)****Distribution.** Cayman Islands*.***Micropygomyia (Micropygomyia) cayennensis cruzi* (González & García, 1981)****Distribution.** Cuba*.***Micropygomyia (Micropygomyia) cayennensis hispaniolae* (Fairchild & Trapido, 1950)****Distribution.** Dominican Republic*, Haiti.***Micropygomyia (Micropygomyia) cayennensis jamaicensis* (Fairchild & Trapido, 1950)****Distribution.** Jamaica*.***Micropygomyia (Micropygomyia) cayennensis maciasi* (Fairchild & Hertig, 1948)****Distribution.** Belize, Guatemala, Mexico*.***Micropygomyia (Micropygomyia) cayennensis puertoricensis* (Fairchild & Hertig, 1948)****Distribution.** Puerto Rico*.***Micropygomyia (Micropygomyia) cayennensis viequesensis* (Fairchild & Hertig, 1948)****Distribution.** Puerto Rico*, Virgin Islands.

Micropygomyia (Micropygomyia) ctenidophora (Fairchild & Hertig, 1948)

Distribution. Mexico*.

Micropygomyia (Micropygomyia) cubensis (Fairchild & Trapido, 1950)

Distribution. Cuba*, United States of America.

Micropygomyia (Micropygomyia) duppyorum (Fairchild & Trapido, 1950)

Distribution. Jamaica*.

Micropygomyia (Micropygomyia) durani (Vargas & Diaz-Nájera, 1952)

Distribution. El Salvador, Honduras, Mexico*.

Micropygomyia (Micropygomyia) lewisi (Feliciangeli, Ordoñez & Fernández, 1984)

Distribution. Venezuela*.

Micropygomyia (Micropygomyia) micropyga (Mangabeira, 1942)

Distribution. Bolivia, Brazil*, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Peru, Trinidad and Tobago, Venezuela.

Micropygomyia (Micropygomyia) schreiberi (Martins, Falcão & Silva, 1975)

Distribution. Brazil*.

Micropygomyia (Micropygomyia) yencanensis (Ortiz, 1965)

Distribution. Colombia, Venezuela*.

Series pilosa Theodor, 1965

Micropygomyia (Micropygomyia) chassigneti (Floch & Abonnenc, 1944)

Distribution. Brazil, Colombia, French Guiana*, Surinam.

Micropygomyia (Micropygomyia) mangabeirana (Martins, Falcão & Silva, 1963)

Distribution. Brazil*.

Micropygomyia (Micropygomyia) pilosa (Damasceno & Causey, 1944)

Distribution. Brazil*, Colombia, Costa Rica, French Guiana, Grenada, Panama, Trinidad and Tobago, Venezuela.

Subgenus (*Sauromyia*) Artemiev, 1991

Series atroclavata Fairchild, 1955

Micropygomyia (Sauromyia) atroclavata (Knab, 1913)

Distribution. Colombia, Costa Rica, Guadeloupe, Martinica, Panama, Trinidad and Tobago*, Venezuela, Virgin Islands.

Micropygomyia (Sauromyia) venezuelensis (Floch & Abonnenc, 1948)

Distribution. Colombia, Venezuela*.

Series osvaldoi Barretto, 1962

Micropygomyia (Sauromyia) capixaba (Dias, Falcão, Silva & Martins, 1987)

Distribution. Brazil*.

Micropygomyia (Sauromyia) dereuri (Le Pont, Matias, Martinez & Dujardin, 2004)

Distribution. Bolivia*.

†*Micropygomyia (Sauromyia) dorafeliciangeli* Andrade-Filho, Galati & Brazil, 2009

Distribution. Dominican amber*.

Micropygomyia (Sauromyia) ferreirana (Barretto, Martins & Pellegrino, 1956)

Distribution. Brazil*.

Micropygomyia (Sauromyia) huacalquensis (Le Pont, Matias, Martinez & Dujardin, 2004)

Distribution. Bolivia*.

Micropygomyia (Sauromyia) longipennis (Barretto, 1946)

Distribution. Brazil*, Peru.

Micropygomyia (Sauromyia) machupicchu (Martins, Llanos & Silva, 1975)

Distribution. Peru*.

Micropygomyia (Sauromyia) oswaldoi (Mangabeira, 1942)

Distribution. Argentina, Bolivia, Brazil*.

†*Micropygomyia (Sauromyia) paterna* (Quate, 1963)

Distribution. Mexican amber*.

Micropygomyia (Sauromyia) peresi (Mangabeira, 1942)

Distribution. Argentina, Bolivia, Brazil*, French Guiana.

Micropygomyia (Sauromyia) petari Galati, Marassá & Gonçalves-Andrade, 2003

Distribution. Brazil*.

Micropygomyia (Sauromyia) pratti (Vargas & Diaz-Nájera, 1951)

Distribution. Mexico*.

Micropygomyia (Sauromyia) pusilla (Dias, Martins, Falcão & Silva, 1986)

Distribution. Brazil*, French Guiana.

Micropygomyia (Sauromyia) quechua (Martins, Llanos & Silva, 1975)

Distribution. Peru*.

Micropygomyia (Sauromyia) quinquefer (Dyar, 1929)

Distribution. Argentina*, Bolivia, Brazil.

Micropygomyia (Sauromyia) rorotaensis (Floch & Abonnenc, 1944)

Distribution. Brazil, Colombia, French Guiana*, Peru, Surinam, Panama, Venezuela.

Micropygomyia (Sauromyia) saccai (Feliciangeli, Ramírez Pérez & Ramírez, 1989)

Distribution. Venezuela*.

Micropygomyia (Sauromyia) trinidadensis (Newstead, 1922)

Distribution. Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Peru, Panama, Surinam, Trinidad and Tobago*, Venezuela.

Micropygomyia (Sauromyia) vellelai (Mangabeira, 1942)

Distribution. Brazil*.

Micropygomyia (Sauromyia) vonatzingeni Galati, 2007

Distribution. Brazil*.

Micropygomyia (Sauromyia) zikani (Barretto, 1950)

Distribution. Brazil*.

Subgenus (*Silvamyia*) Galati, 1995

Micropygomyia (*Silvamyia*) *acanthopharynx* (Martins, Falcão & Silva, 1962)

Distribution. Brazil*.

Micropygomyia (*Silvamyia*) *echinatopharynx* Andrade-Filho, Galati, Andrade & Falcão, 2004

Distribution. Brazil*.

Micropygomyia incertae sedis

†*Micropygomyia brandaoi* Andrade-Filho, Galati, Falcão & Brazil, 2008

Distribution. Dominican amber*.

Micropygomyia xerophila (Young, Brener & Wargo, 1983)

Distribution. United States of America*.

Subtribe LUTZOMYIINA Abonnenc and Léger, 1976

Genus *Sciopemyia* Barretto, 1962

Sciopemyia fluviatilis (Floch & Abonnenc, 1944)

Distribution. Brazil, French Guiana*.

Sciopemyia microps (Mangabeira, 1942)

Distribution. Brazil*.

Sciopemyia nematoducta (Young & Arias, 1984)

Distribution. Brazil*, Colombia.

Sciopemyia pennyi (Arias & Freitas, 1981)

Distribution. Brazil*.

Sciopemyia preclara (Young & Arias, 1984)

Distribution. Bolivia, Brazil, Colombia*, Peru.

Sciopemyia servulolimai (Damasceno & Causey, 1945)

Distribution. Bolivia, Brazil*, Colombia, Peru.

Sciopemyia sordellii (Shannon & Del Ponte, 1927)

Distribution. Argentina*, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Peru, Trinidad and Tobago, Venezuela.

Sciopemyia vattierae (Le Pont & Desjeux, 1992)

Distribution. Bolivia*, Colombia, Peru.

Genus *Lutzomyia* França, 1924

Subgenus (*Castromyia*) Mangabeira, 1942

Lutzomyia (*Castromyia*) *amarali* (Barretto & Coutinho, 1940)

Distribution. Brazil*.

Lutzomyia (Castromyia) caligata Martins, Falcão & Silva, 1965

Distribution. Brazil*.

Lutzomyia (Castromyia) castroi (Barretto & Coutinho, 1941)

Distribution. Brazil*.

Subgenus (*Helcocyrtomyia*) Barretto, 1962

Series *osornoi* Galati & Cáceres, 1994

Lutzomyia (Helcocyrtomyia) caballeroi Blancas, Cáceres & Galati, 1989

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) castanea Galati & Cáceres, 1994

Distribution. Ecuador, Peru*.

Lutzomyia (Helcocyrtomyia) ceferinoi (Ortiz & Alvarez, 1963)

Distribution. Colombia, Venezuela*.

Lutzomyia (Helcocyrtomyia) erwindonaldi (Ortiz, 1978)

Distribution. Colombia, Venezuela*.

Lutzomyia (Helcocyrtomyia) herreri Galati & Cáceres, 2003

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) imperatrix (Alexander, 1944)

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) larensis Arredondo, 1987

Distribution. Venezuela*.

Lutzomyia (Helcocyrtomyia) munaypata Ogusuku, Chevarria, Porras & Pérez, 1999

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) osornoi (Ristorcelli & Van Ty, 1941)

Distribution. Bolivia, Colombia*, Ecuador, Peru.

Lutzomyia (Helcocyrtomyia) quillabamba Ogusuku, Chevarria, Porras & Pérez, 1999

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) rispaili Torrez-Espejo, Cáceres & Le Pont, 1995

Distribution. Bolivia*, Peru.

Lutzomyia (Helcocyrtomyia) strictivilla Young, 1979

Distribution. Colombia*, Ecuador, Venezuela.

Lutzomyia (Helcocyrtomyia) watsi Fernández, Carbajal, Astete & Wooster, 1998

Distribution. Peru*.

Series *peruensis* Barretto, 1962

Lutzomyia (Helcocyrtomyia) ayacuchensis Cáceres & Galati, 1988

Distribution. Ecuador, Peru*.

Lutzomyia (Helcocyrtomyia) blancasi Galati & Cáceres, 1990

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) chavinensis Pérez & Ogusuku, 1999

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) galatae Le Pont, Martínez, Torrez-Espejo & Dujardin, 1998

Distribution. Bolivia*.

Lutzomyia (Helcocyrtomyia) noguchii (Shannon, 1929)

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) pallidithorax Galati & Cáceres, 1994

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) peruensis (Shannon, 1929)

Distribution. Bolivia, Peru*.

Lutzomyia (Helcocyrtomyia) pescei (Hertig, 1943)

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) tejadai Galati & Cáceres, 1990

Distribution. Peru*.

Series sanguinaria Barretto, 1962

Lutzomyia (Helcocyrtomyia) adamsi Fernández, Galati, Carbajal, Wooster & Watts, 1998

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) botella (Fairchild & Hertig, 1961)

Distribution. Panama*.

Lutzomyia (Helcocyrtomyia) caceresi Le Pont, Matías, Martínez & Dujardin, 2004

Distribution. Bolivia*.

Lutzomyia (Helcocyrtomyia) cirrita Young & Porter, 1974

Distribution. Colombia*.

Lutzomyia (Helcocyrtomyia) gonzaloi Ogusuku, Canales & Pérez, 1997

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) guderiani Torrez-Espejo, Cáceres & Le Pont, 1995

Distribution. Bolivia*, Peru.

Lutzomyia (Helcocyrtomyia) hartmanni (Fairchild & Hertig, 1957)

Distribution. Colombia, Costa Rica, Ecuador, Mexico, Panama*, Peru.

Lutzomyia (Helcocyrtomyia) kirigetiensis Galati & Cáceres, 1992

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) monzonensis Ogusuku, Canales & Pérez, 1997

Distribution. Peru*.

Lutzomyia (Helcocyrtomyia) sanguinaria (Fairchild & Hertig, 1957)

Distribution. Colombia, Costa Rica, Ecuador, Honduras, Nicaragua, Panama*, Peru.

Lutzomyia (Helcocyrtomyia) scorzai (Ortiz, 1965)

Distribution. Colombia*, Peru, Venezuela.

Lutzomyia (Helcocyrtomyia) tolimensis Carrasquilla, Munstermann, Marín, Ocampo & Ferro, 2012

Distribution. Colombia*.

Lutzomyia (Helcocyrtomyia) tortura* Young & Rogers, 1984*Distribution.** Bolivia, Colombia, Ecuador*.***Lutzomyia (Helcocyrtomyia) vezei* Bejarano, Vivero & Uribe, 2010****Distribution.** Colombia*.**Subgenus (*Lutzomyia*) França, 1924*****Lutzomyia (Lutzomyia) alencari* Martins, Souza & Falcão, 1962****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) almerioi* Galati & Nunes, 1999****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) battistinii* (Hertig, 1943)****Distribution.** Brazil, Peru*.***Lutzomyia (Lutzomyia) bicornuta* (Blancas & Herrer, 1960)****Distribution.** Peru*.***Lutzomyia (Lutzomyia) bifoliata* Osorno-Mesa, Morales, Osorno & Hoyos, 1970****Distribution.** Colombia*.***Lutzomyia (Lutzomyia) cavernicola* (Costa Lima, 1932)****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) cruzi* (Mangabeira, 1938)****Distribution.** Bolivia, Brazil*.***Lutzomyia (Lutzomyia) dispar* Martins & Silva, 1963****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) elizabethrangela* Vilela, Azevedo & Godoy, 2015****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) falquetoi* Pinto & Santos, 2007****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) fonsecai* (Costa Lima, 1932)****Distribution.** Bolivia*.

Note. Placement in *Lutzomyia* based on the study by one of us (EABG) of specimens collected in several caves close to the type-locality of *Lu. fonsecai* in the Chiquitano seasonally dry forest of Serrania Santiago (Calvario of the Robore municipality and Aguas Calientes near Robore, Santa Cruz Department).

Lutzomyia (Lutzomyia) forattinii* Galati, Rego, Nunes & Teruya, 1985*Distribution.** Bolivia, Brazil*.***Lutzomyia (Lutzomyia) gaminarai* (Cordero, Vogelsang & Cossio, 1928)****Distribution.** Brazil, Uruguay*.***Lutzomyia (Lutzomyia) ischnacantha* Martins, Souza & Falcão, 1962****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) ischyraantha* Martins, Falcão & Silva, 1962****Distribution.** Brazil*.***Lutzomyia (Lutzomyia) lichyi* (Floch & Abonnenc, 1950)****Distribution.** Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Peru, Trinidad and Tobago, Venezuela*.

***Lutzomyia (Lutzomyia) longipalpis* (Lutz & Neiva, 1912)**

Distribution. Argentina, Bolivia, Brazil*, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Uruguay, Venezuela.

***Lutzomyia (Lutzomyia) matiasi* Le Pont & Mollinedo, 2009**

Distribution. Bolivia*.

***Lutzomyia (Lutzomyia) pseudolongipalpis* Arrivillaga & Feliciangeli, 2001**

Distribution. Venezuela*.

***Lutzomyia (Lutzomyia) renei* (Martins, Falcão & Silva, 1957)**

Distribution. Brazil*.

***Lutzomyia (Lutzomyia) souzalopesi* Martins, Silva & Falcão, 1970**

Distribution. Brazil*.

Subgenus (*Tricholateralis*) Galati, 1995***Lutzomyia (Tricholateralis) araracuarensis* Morales & Minter, 1981**

Distribution. Brazil, Colombia*.

***Lutzomyia (Tricholateralis) carvalhoi* (Damasceno, Causey & Arouck, 1945)**

Distribution. Brazil*, French Guiana.

***Lutzomyia (Tricholateralis) cruciata* (Coquillett, 1907)**

Distribution. Belize, Brazil, Costa Rica, El Salvador, Guatemala*, Honduras, Mexico, Nicaragua, Panama, United States of America.

***Lutzomyia (Tricholateralis) cultellata* Freitas & Albuquerque, 1996**

Distribution. Brazil*, Peru.

Note. Placement in his subgenus was possible due to the study of specimens provided to us (EABG and PHFS) by Mr. Rui Freitas (Instituto Nacional de Pesquisas da Amazônia). We concluded it belongs to the subgenus *Tricholateralis* because among other characters this species presents the ventro-cervical sensillae, setae in the abdominal pleura and lacks the ascoids with posterior spurs.

***Lutzomyia (Tricholateralis) diabolica* (Hall, 1936)**

Distribution. Mexico, United States of America*.

***Lutzomyia (Tricholateralis) evangelistai* Martins & Fraiha, 1971**

Distribution. Bolivia, Brazil*, Colombia, Peru.

***Lutzomyia (Tricholateralis) falcata* Young, Morales & Ferro, 1994**

Distribution. Brazil, Colombia*, Ecuador.

***Lutzomyia (Tricholateralis) flabellata* Martins & Silva, 1964**

Distribution. Bolivia, Brazil*.

***Lutzomyia (Tricholateralis) gomezi* (Nitzulescu, 1931)**

Distribution. Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Honduras, Mexico, Nicaragua, Panama, Peru, Trinidad and Tobago, Venezuela*.

***Lutzomyia (Tricholateralis) legerae* Le Pont, Gantier, Hue & Valle, 1995**

Distribution. Nicaragua*.

Lutzomyia (Tricholateralis) maesi* Le Pont, Ibáñez-Bernal & Fuentes, 2011*Distribution.** Nicaragua*.***Lutzomyia (Tricholateralis) marinkellei* Young, 1979****Distribution.** Brazil*, Colombia.***Lutzomyia (Tricholateralis) sherlocki* Martins, Silva & Falcão, 1971****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, Peru.***Lutzomyia (Tricholateralis) spathotrichia* Martins, Falcão & Silva, 1963****Distribution.** Bolivia, Brazil*, Ecuador, French Guiana.***Lutzomyia incertae sedis******Lutzomyia chotensis* Galati, Cáceres & Zorilla, 2003****Distribution.** Peru*.***Lutzomyia ignacioi* (Young, 1972)****Distribution.** Colombia, Venezuela*.

Note. Galati (2003) placed this species in *Psathryromyia* as *incertae sedis*. However, Sábio, PB (pers. comm.) examined the type material deposited in the Entomological Collection - Smithsonian Institution / Walter Reed Biosystematic Unit, Suitland, MD - USA) and observed the presence of the ventro-cervical sensillae and the papilla in F3, the setae in the anterior region of the katapisternum is absent, ascoids present reduced posterior spurs and spermathecae are ringed. These characters are synapomorphies shared by some species of *Lutzomyia* (*Castromyia*, *Tricholateralis* and *Lutzomyia*), but this species also lacks characters to place it with confidence in any of these three subgenera.

Lutzomyia infusca* Porter & Young, 1999*Distribution.** Guatemala*.***Lutzomyia manciola* Ibáñez-Bernal, 2001****Distribution.** Belize*.

Note. The insertion of this species in *Lutzomyia* is provisional. There were no female characters to be observed that could lead to more accurate placement in any genus, nor was the male known. The inclusion of *L. manciola* in *Sciopemyia* was suggested by Ibáñez-Bernal (2001). However, *L. manciola* do not present the head and labrum-epipharynx shorter than the sum of flagellomeres FI + FII, which are diagnostic characters for *Sciopemyia*.

Lutzomyia ponsi* (Perruollo, 1984)*Distribution.** Venezuela*.

Note. The description of this species does not provide sufficient information to place it in any genus; and the similarity of their spermathecae with those of *L. ignacioi* led us to include it together with this species in the genus *Lutzomyia*.

Lutzomyia tanyopsis* Young & Perkins, 1984*Distribution.** United States of America*.***Lutzomyia vargasi* (Fairchild & Hertig, 1961)****Distribution.** Mexico*.

Genus *Migonemyia* Galati, 1995**Subgenus (*Blancasmyia*) Galati, 1995*****Migonemyia (Blancasmyia) bursiformis* (Floch & Abonnenc, 1944)**

Distribution. Brazil, Colombia, Ecuador, French Guiana*, Venezuela.

***Migonemyia (Blancasmyia) cerqueirai* (Causey & Damasceno, 1945)**

Distribution. Brazil*, Colombia, Peru.

***Migonemyia (Blancasmyia) gorbitzi* (Blancas, 1960)**

Distribution. Colombia, Costa Rica, Ecuador, Panama, Peru*.

***Migonemyia (Blancasmyia) moucheti* (Pajot & Le Pont, 1978)**

Distribution. Brazil, French Guiana*, Peru.

Subgenus (*Migonemyia*) Galati, 1995***Migonemyia (Migonemyia) migonei* (França, 1920)**

Distribution. Argentina, Bolivia, Brazil, Colombia, Paraguay*, Peru, Trinidad and Tobago, Venezuela.

***Migonemyia (Migonemyia) rabelloi* (Galati & Gomes, 1992)**

Distribution. Brazil*.

***Migonemyia (Migonemyia) vaniae* Galati, Fonseca & Marassá, 2007**

Distribution. Brazil*.

Genus *Pintomyia* Costa Lima, 1932**Subgenus (*Pifanomyia*) Ortiz and Scorza, 1963****Series *evansi* Galati, 1995*****Pintomyia (Pifanomyia) evansi* (Nuñez-Tovar, 1924)**

Distribution. Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Peru, Venezuela*.

***Pintomyia (Pifanomyia) maranonensis* (Galati, Cáceres & Le Pont, 1995)**

Distribution. Ecuador, Peru*.

***Pintomyia (Pifanomyia) nevesi* (Damasceno & Arouck, 1956)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, Peru.

***Pintomyia (Pifanomyia) ovallesi* (Ortiz, 1952)**

Distribution. Belize, Colombia, Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama, Trinidad and Tobago, Venezuela*.

Series *monticola* Artemiev, 1991***Pintomyia (Pifanomyia) misionensis* (Castro, 1959)**

Distribution. Argentina*, Brazil, Paraguay.

Pintomyia (Pifanomyia) monticola* (Costa Lima, 1932)*Distribution.** Argentina, Brazil*, Paraguay, Peru.**Series pacaе Galati, 1995*****Pintomyia (Pifanomyia) gruta* (Ryan, 1986)****Distribution.** Brazil*.***Pintomyia (Pifanomyia) pacaе* (Floch & Abonnenc, 1943)****Distribution.** Brazil, French Guiana*, Surinam.**Series pia Galati, 1995*****Pintomyia (Pifanomyia) emberai* (Bejarano, Duque & Vélez, 2004)****Distribution.** Colombia*.***Pintomyia (Pifanomyia) limafalcaoae* Wolff & Galati, 2002****Distribution.** Colombia*.***Pintomyia (Pifanomyia) pia* (Fairchild & Hertig, 1961)****Distribution.** Bolivia, Colombia, Costa Rica, Panama*, Peru, Venezuela.***Pintomyia (Pifanomyia) reclusa* (Fernández & Rogers, 1991)****Distribution.** Peru*.***Pintomyia (Pifanomyia) suapiensis* (Le Pont, Torrez-Espejo & Dujardin, 1997)****Distribution.** Bolivia*, Peru.***Pintomyia (Pifanomyia) tihuiliensis* (Le Pont, Torrez-Espejo & Dujardin, 1997)****Distribution.** Bolivia*, Colombia, Peru.***Pintomyia (Pifanomyia) tocaniensis* (Le Pont, Torrez-Espejo & Dujardin, 1997)****Distribution.** Bolivia*, Peru.***Pintomyia (Pifanomyia) torrealbai* (Martins, Fernandez & Falcão, 1979)****Distribution.** Venezuela*.***Pintomyia (Pifanomyia) valderramai* (Cazorla, 1988)****Distribution.** Venezuela*.**Series serrana Barretto, 1962*****Pintomyia (Pifanomyia) boliviana* (Velasco & Trapido, 1974)****Distribution.** Bolivia*.***Pintomyia (Pifanomyia) christophei* (Fairchild & Trapido, 1950)****Distribution.** Dominican Republic*, Haiti.***Pintomyia (Pifanomyia) diazi* (Gonzales & Garcia, 1981)****Distribution.** Cuba*.***Pintomyia (Pifanomyia) guilvardae* (Le Pont, Martinez, Torrez-Espejo & Dujardin, 1998)****Distribution.** Bolivia*.***Pintomyia (Pifanomyia) novoae* (Gonzales & Garcia, 1981)****Distribution.** Cuba*.

***Pintomyia (Pifanomyia) odax* (Fairchild & Hertig, 1961)**

Distribution. Brazil, Costa Rica, French Guiana, Guatemala, Honduras, Nicaragua, Panama*, Venezuela.

***Pintomyia (Pifanomyia) oresbia* (Fairchild & Hertig, 1961)**

Distribution. Costa Rica, Panama*.

***Pintomyia (Pifanomyia) orestes* (Fairchild & Trapido, 1950)**

Distribution. Brazil, Cayman Islands, Cuba*.

***Pintomyia (Pifanomyia) ottolinai* (Ortiz & Scorza, 1963)**

Distribution. Venezuela*.

***Pintomyia (Pifanomyia) piedraferroi* (León, 1971)**

Distribution. Guatemala*.

***Pintomyia (Pifanomyia) robusta* (Galati, Cáceres & Le Pont, 1995)**

Distribution. Ecuador, Peru*.

***Pintomyia (Pifanomyia) serrana* (Damasceno & Arouck, 1949)**

Distribution. Belize, Bolivia, Brazil*, Colombia, Costa Rica, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela.

***Pintomyia (Pifanomyia) torresi* (Le Pont & Desjeux, 1991)**

Distribution. Argentina, Bolivia*.

Series townsendi Galati, 1995***Pintomyia (Pifanomyia) amilcari* (Arredondo, 1984)**

Distribution. Venezuela*.

***Pintomyia (Pifanomyia) longiflocosa* (Osorno-Mesa, Morales, Osorno & Hoyos, 1970)**

Distribution. Colombia*.

***Pintomyia (Pifanomyia) nadiae* (Feliciangeli, Arredondo & Ward, 1992)**

Distribution. Venezuela*.

†*Pintomyia (Pifanomyia) paleotownsendi* Andrade-Filho, Falcão, Galati & Brazil, 2006

Distribution. Dominican amber*.

†*Pintomyia (Pifanomyia) paloetrichia* Andrade-Filho, Brazil, Falcão & Galati, 2007

Distribution. Dominican amber*.

***Pintomyia (Pifanomyia) quasitownsendi* (Osorno, Osorno-Mesa & Morales, 1972)**

Distribution. Colombia*.

***Pintomyia (Pifanomyia) sauroida* (Osorno-Mesa, Morales & Osorno, 1972)**

Distribution. Colombia*, Venezuela.

***Pintomyia (Pifanomyia) spinicrassa* (Morales, Osorno-Mesa, Osorno & Hoyos, 1969)**

Distribution. Colombia*, Venezuela.

***Pintomyia (Pifanomyia) torvida* (Young, Morales & Ferro, 1994)**

Distribution. Colombia*.

***Pintomyia (Pifanomyia) townsendi* (Ortiz, 1959)**

Distribution. Colombia, Venezuela*.

***Pintomyia (Pifanomyia) youngi* (Feliciangeli & Murillo, 1985)**

Distribution. Colombia, Costa Rica, Venezuela*.

Series verrucarum Fairchild, 1955

- Pintomyia (Pifanomyia) andina* (Osorno, Osorno-Mesa & Morales, 1972)
Distribution. Colombia*.
- Pintomyia (Pifanomyia) antioquiensis* Wolff & Galati, 2002
Distribution. Colombia*.
- Pintomyia (Pifanomyia) aulari* (Feliciangeli, Ordoñez & Manzanilla, 1984)
Distribution. Venezuela*.
- Pintomyia (Pifanomyia) cajamarcensis* (Galati, Cáceres & Le Pont, 1995)
Distribution. Peru*.
- Pintomyia (Pifanomyia) columbiana* (Ristorcelli & Van Ty, 1941)
Distribution. Colombia*.
- Pintomyia (Pifanomyia) deorsa* (Pérez, Ogusuku, Monje & Young, 1991)
Distribution. Peru*.
- Pintomyia (Pifanomyia) disjuncta* (Morales, Osorno & Osorno-Mesa, 1974)
Distribution. Colombia*.
- Pintomyia (Pifanomyia) itza* Ibáñez-Bernal, May-UC & Rebollar-Tellez, 2010
Distribution. Mexico*.
- Pintomyia (Pifanomyia) moralesi* (Young, 1979)
Distribution. Colombia*.
- Pintomyia (Pifanomyia) verrucarum* (Townsend, 1913)
Distribution. Peru*.

Subgenus (*Pintomyia*) Costa Lima, 1932

- Pintomyia (Pintomyia) bianchigalatae* (Andrade-Filho, Aguiar, Dias & Falcão, 1999)
Distribution. Argentina, Brazil*.
- Pintomyia (Pintomyia) christenseni* (Young & Duncan, 1994)
Distribution. Brazil, Colombia, Panama*, Trinidad and Tobago, Venezuela.
- Pintomyia (Pintomyia) damascenoi* (Mangabeira, 1941)
Distribution. Brazil*, Colombia, French Guiana, Surinam.
- Pintomyia (Pintomyia) fischeri* (Pinto, 1926)
Distribution. Argentina, Bolivia, Brazil*, Paraguay, Peru, Venezuela.
- Pintomyia (Pintomyia) gibsoni* (Pifano & Ortiz, 1972)
Distribution. Venezuela*.
- Pintomyia (Pintomyia) kuscheli* (Le Pont, Martinez, Torrez-Espejo & Dujardin, 1998)
Distribution. Bolivia*, Brazil.
- Pintomyia (Pintomyia) mamedei* (Oliveira, Afonso, Dias & Brazil, 1994)
Distribution. Brazil*.
- Pintomyia (Pintomyia) pessoai* (Coutinho & Barretto, 1940)
Distribution. Argentina, Brazil*, Paraguay.

Pintomyia incertae sedis†*Pintomyia adiketis* Poinar, 2008

Distribution. Dominican amber*.

†*Pintomyia bolontikui* Ibáñez-Bernal, Kraemer, Stebner & Wagner, 2013

Distribution. Mexican amber*.

†*Pintomyia brazilorum* Andrade-Filho, Galati & Falcão, 2006

Distribution. Dominican amber*

Pintomyia diamantinensis (Barata, Serra e Meira & Carvalho, 2012)

Distribution. Brazil*.

†*Pintomyia dissimilis* Andrade-Filho, Serra e Meira, Sanguinette & Brazil, 2009

Distribution. Dominican amber*

†*Pintomyia dominicana* Andrade-Filho, Galati & Brazil, 2009

Distribution. Dominican amber*

†*Pintomyia falcaorum* Brazil & Andrade-Filho, 2002

Distribution. Dominican amber*

†*Pintomyia filipalpis* (Peñalver & Grimaldi, 2005)

Distribution. Dominican amber*

†*Pintomyia killickorum* Andrade-Filho & Brazil, 2004

Distribution. Dominican amber*

Pintomyia maracayensis (Nuñez-Tovar, 1924)

Distribution. Venezuela*.

†*Pintomyia miocena* (Peñalver & Grimaldi, 2005)

Distribution. Dominican amber*

Pintomyia naiffi (Freitas & Oliveira, 2013)

Distribution. Brazil*.

Pintomyia nuneztovari (Ortiz, 1954)

Distribution. Venezuela*.

†*Pintomyia paleopestis* (Peñalver & Grimaldi, 2005)

Distribution. Dominican Republic*.

Pintomyia rangeliana (Ortiz, 1953)

Distribution. Colombia, Panama, Trinidad and Tobago, Venezuela*.

†*Pintomyia succini* (Peñalver & Grimaldi, 2005)

Distribution. Dominican amber*

Genus *Dampfomyia* Addis, 1945Subgenus (*Coromyia*) Barretto, 1962*Dampfomyia* (*Coromyia*) *aquilonia* (Fairchild & Harwood, 1961)

Distribution. Canada, United States of America*.

Dampfomyia (*Coromyia*) *beltrani* (Vargas & Díaz-Nájera, 1951)

Distribution. Honduras, Mexico*.

Dampfomyia (Coromyia) deleoni* (Fairchild & Hertig, 1947)*Distribution.** Belize, Costa Rica, El Salvador, Guatemala*, Honduras, Mexico.***Dampfomyia (Coromyia) disneyi* (Williams, 1987)****Distribution.** Belize*, Guatemala, Mexico.***Dampfomyia (Coromyia) isovespertilionis* (Fairchild & Hertig, 1958)****Distribution.** Colombia, Costa Rica, Panama*.***Dampfomyia (Coromyia) steatopyga* (Fairchild & Hertig, 1958)****Distribution.** Mexico*.***Dampfomyia (Coromyia) vesicifera* (Fairchild & Hertig, 1947)****Distribution.** Costa Rica, Nicaragua, Panama*.***Dampfomyia (Coromyia) vespertilionis* (Fairchild & Hertig, 1947)****Distribution.** Colombia, Costa Rica, Ecuador, Nicaragua, Panama*.***Dampfomyia (Coromyia) viriosa* (Fairchild & Hertig, 1958)****Distribution.** Costa Rica, Panama*.***Dampfomyia (Coromyia) zeledoni* (Young & Murillo, 1984)****Distribution.** Costa Rica*, Honduras, Nicaragua.**Subgenus (*Dampfomyia*) Addis, 1945*****Dampfomyia (Dampfomyia) anthophora* (Addis, 1945)****Distribution.** Mexico, Nicaragua, United States of America*.***Dampfomyia (Dampfomyia) atulapai* (León, 1971)****Distribution.** El Salvador, Guatemala*, Mexico.***Dampfomyia (Dampfomyia) dodgei* (Vargas & Díaz-Nájera, 1953)****Distribution.** El Salvador, Mexico*.***Dampfomyia (Dampfomyia) insolita* (Fairchild & Hertig, 1956)****Distribution.** Costa Rica, Panama*.***Dampfomyia (Dampfomyia) leohidalgoi* (Ibáñez-Bernal, Hernández-Xoliot & Mendoza, 2006)****Distribution.** Mexico*.***Dampfomyia (Dampfomyia) permira* (Fairchild & Hertig, 1956)****Distribution.** Belize, Guatemala, Mexico*.***Dampfomyia (Dampfomyia) rosabali* (Fairchild & Hertig, 1956)****Distribution.** Colombia, Costa Rica, Panama*.**Group *delpozoi* Young & Fairchild, 1974*****Dampfomyia delpozoi* (Vargas & Díaz-Nájera, 1953)****Distribution.** Belize, Guatemala, Mexico*.***Dampfomyia inusitata* (Fairchild & Hertig, 1961)****Distribution.** Mexico*.**Note.** The *Dampfomyia delpozoi* group shows characters of both the subgenus *Coromyia* and *Dampfomyia s.str.* and are therefore listed separately.

*Dampfomyia incertae sedis**Dampfomyia caminoi* (Young & Duncan, 1994)

Distribution. Mexico*.

Genus *Expapillata* Galati, 1995*Expapillata cerradincola* (Galati, Nunes, Oshiro & Dorval, 1995)

Distribution. Brazil*.

Expapillata firmatoi (Barretto, Martins & Pellegrino, 1956)

Distribution. Argentina, Brazil*.

Genus *Pressatia* Mangabeira, 1942*Pressatia calcarata* (Martins & Silva, 1964)

Distribution. Bolivia, Brazil*, Peru, Venezuela.

Pressatia camposi (Rodríguez, 1950)

Distribution. Colombia, Costa Rica, Ecuador*, Nicaragua, Panama.

Pressatia choti (Floch & Abonnenc, 1941)

Distribution. Bolivia, Brazil, Colombia, Ecuador, French Guiana*, Peru, Surinam.

Pressatia duncanae (Le Pont, Martinez, Torrez-Espejo & Durjardin, 1998)

Distribution. Bolivia*, Colombia, Peru.

Note. The record of this species for Peru is from the illustrations published by Velasco 1973: 88 (*Lutzomyia* sp. D) and Young & Morales 1987: 662 (*Lutzomyia* sp. 1).

Pressatia dysponeta (Fairchild & Hertig, 1952)

Distribution. Brazil, Colombia, Costa Rica, Ecuador, Panama*, Venezuela.

Pressatia equatorialis (Mangabeira, 1942)

Distribution. Brazil*, French Guiana.

Pressatia triacantha (Mangabeira, 1942)

Distribution. Brazil*, Colombia, Ecuador, French Guiana, Peru, Venezuela.

Pressatia trispinosa (Mangabeira, 1942)

Distribution. Brazil*, French Guiana, Peru.

Genus *Trichopygomyia* Barretto, 1962*Trichopygomyia conviti* (Ramírez-Pérez, Martins & Ramírez, 1976)

Distribution. Brazil, Colombia, Venezuela*.

Trichopygomyia dasypodogeton (Castro, 1939)

Distribution. Bolivia, Brazil*.

Trichopygomyia depaquitii (Gantier, Gaborit & Rabarison, 2006)

Distribution. Brazil, French Guiana*.

Trichopygomyia elegans (Martins, Llanos & Silva, 1976)

Distribution. Brazil, Peru*.

***Trichopygomyia ferroae* (Young & Morales, 1987)**

Distribution. Colombia*.

***Trichopygomyia gantieri* (Le Pont & Desjeux, 1987)**

Distribution. Bolivia*.

***Trichopygomyia longispina* (Mangabeira, 1942)**

Distribution. Brazil*, Colombia, French Guiana, Venezuela.

***Trichopygomyia martinezi* (Young & Morales, 1987)**

Distribution. Colombia*.

***Trichopygomyia pinna* (Felicangeli, Ramírez-Pérez & Ramírez, 1989)**

Distribution. Brazil, Venezuela*.

***Trichopygomyia ratcliffei* (Arias, Ready & Freitas, 1983)**

Distribution. Brazil*.

***Trichopygomyia rondonienseis* (Martins, Falcão & Silva, 1965)**

Distribution. Bolivia, Brazil*.

***Trichopygomyia trichopyga* (Floch & Abonnenc, 1945)**

Distribution. Brazil, French Guiana*, Surinam.

***Trichopygomyia triramula* (Fairchild & Hertig, 1952)**

Distribution. Belize, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama*.

***Trichopygomyia turelli* (Fernández, Galati, Carbajal & Watts, 1998)**

Distribution. Peru*.

***Trichopygomyia wagleyi* (Causey & Damasceno, 1945)**

Distribution. Bolivia, Brazil*, Colombia, Venezuela.

***Trichopygomyia witoto* (Young & Morales, 1987)**

Distribution. Colombia*, Ecuador.

Genus *Evandromyia* Mangabeira, 1941**Subgenus (*Aldamyia*) Galati, 1995*****Evandromyia* (*Aldamyia*) *aldafalcaoae* (Santos, Andrade-Filho & Honer, 2001)**

Distribution. Brazil*.

***Evandromyia* (*Aldamyia*) *andersoni* (Le Pont & Desjeux, 1988)**

Distribution. Bolivia*, Brazil.

***Evandromyia* (*Aldamyia*) *apurinan* Shimabukuro, Figueira & Silva, 2013**

Distribution. Brazil*.

***Evandromyia* (*Aldamyia*) *bacula* (Martins, Falcão & Silva, 1965)**

Distribution. Bolivia, Brazil*.

***Evandromyia* (*Aldamyia*) *carmelinoi* (Ryan, Fraiha, Lainson & Shaw, 1986)**

Distribution. Brazil*.

***Evandromyia* (*Aldamyia*) *dubitans* (Sherlock, 1962)**

Distribution. Brazil, Colombia*, Costa Rica, Panama, Trinidad and Tobago, Venezuela.

***Evandromyia* (*Aldamyia*) *evandroi* (Costa Lima & Antunes, 1936)**

Distribution. Argentina, Brazil*.

Evandromyia (Aldamyia) hashiguchii* León, Teran, Neira & Le Pont, 2009*Distribution.** Ecuador*.***Evandromyia (Aldamyia) lenti* (Mangabeira, 1938)****Distribution.** Bolivia, Brazil*, Surinam.***Evandromyia (Aldamyia) orcyi* Oliveira, Sanguinette, Almeida & Andrade-Filho, 2015****Distribution.** Brazil*.***Evandromyia (Aldamyia) sericea* (Floch & Abonnenc, 1944)****Distribution.** Brazil, Colombia, Ecuador, French Guiana*, Surinam, Venezuela.***Evandromyia (Aldamyia) termitophila* (Martins, Falcão & Silva, 1964)****Distribution.** Bolivia, Brazil*.***Evandromyia (Aldamyia) walkeri* (Newstead, 1914)****Distribution.** Bolivia*, Brazil*, Colombia, Ecuador, French Guiana, Panama, Peru, Trinidad and Tobago, Venezuela.**Note.** The type locality of *E. walkeri* is along the Abuña river, which forms part of the border between Bolivia and Brazil, however it is not clear in which of the countries the exact type locality is located.***Evandromyia (Aldamyia) williamsi* (Damasceno, Causey & Arouck, 1945)****Distribution.** Brazil*, Peru, Venezuela.**Subgenus (*Barrettomyia*) Martins and Silva, 1968****Series *cortelezzii* Galati, 1995*****Evandromyia (Barrettomyia) cortelezzii* (Brèthes, 1923)****Distribution.** Argentina*, Bolivia, Brazil, Paraguay, Peru, Uruguay.***Evandromyia (Barrettomyia) corumbaensis* (Galati, Nunes, Oshiro & Rego, 1989)****Distribution.** Bolivia, Brazil*.***Evandromyia (Barrettomyia) sallesi* (Galvão & Coutinho, 1939)****Distribution.** Argentina, Bolivia, Brazil*, Ecuador, Paraguay, Peru.***Evandromyia (Barrettomyia) spelunca* Carvalho, Brazil, Sanguinette & Andrade-Filho, 2011****Distribution.** Brazil*.**Series *monstruosa* Lewis, Young & Minter, 1977*****Evandromyia (Barrettomyia) monstruosa* (Floch & Abonnenc, 1944)****Distribution.** Brazil, Colombia, French Guiana*, Surinam, Venezuela.***Evandromyia (Barrettomyia) teratodes* (Martins, Falcão & Silva, 1964)****Distribution.** Brazil*, Paraguay.**Series *tupynambai* Martins & Silva, 1968*****Evandromyia (Barrettomyia) bahiensis* (Mangabeira & Sherlock, 1961)****Distribution.** Brazil*.

Evandromyia (Barrettomyia) callipyga (Martins & Silva, 1965)

Distribution. Brazil*.

Evandromyia (Barrettomyia) costalimai (Mangabeira, 1942)

Distribution. Brazil*.

Evandromyia (Barrettomyia) petropolitana (Martins & Silva, 1968)

Distribution. Brazil*.

Evandromyia (Barrettomyia) tupyngambai (Mangabeira, 1942)

Distribution. Brazil*.

Subgenus (*Evandromyia*) Mangabeira, 1941

Series *infraspinosa* Young & Arias, 1977

Evandromyia (Evandromyia) begonae (Ortiz & Torrez, 1975)

Distribution. Brazil, Colombia, Venezuela*.

Evandromyia (Evandromyia) bourrouli (Barretto & Coutinho, 1941)

Distribution. Bolivia, Brazil*.

Evandromyia (Evandromyia) brachyphalla (Mangabeira, 1941)

Distribution. Brazil*, French Guiana.

Evandromyia (Evandromyia) georgii (Freitas & Barrett, 2002)

Distribution. Brazil*.

Evandromyia (Evandromyia) infraspinosa (Mangabeira, 1941)

Distribution. Bolivia, Brazil*, Colombia, French Guiana, Peru, Surinam, Venezuela.

Evandromyia (Evandromyia) inpai (Young & Arias, 1977)

Distribution. Brazil*, Venezuela.

Evandromyia (Evandromyia) ledezmaae León, Teran, Neira & Le Pont, 2009

Distribution. Ecuador*.

Evandromyia (Evandromyia) pinottii (Damasceno & Arouck, 1956)

Distribution. Brazil*, French Guiana, Venezuela.

Evandromyia (Evandromyia) sipani (Fernández, Carbajal, Alexander & Need, 1994)

Distribution. Brazil, Colombia, Peru*.

Evandromyia (Evandromyia) tarapacaensis (Le Pont, Torrez-Espejo & Galati, 1997)

Distribution. Bolivia*, Brazil.

Series *rupicola* Young & Fairchild, 1974

Evandromyia (Evandromyia) correalimai (Martins, Coutinho & Luz, 1970)

Distribution. Brazil*.

Evandromyia (Evandromyia) gaucha Andrade-Filho, Souza & Falcão, 2007

Distribution. Brazil*.

Evandromyia (Evandromyia) grimaldii Andrade-Filho, Pinto, Santos & Carvalho, 2009

Distribution. Brazil*.

Evandromyia (Evandromyia) rupicola* (Martins, Godoy & Silva, 1962)*Distribution.** Brazil*.***Evandromyia (Evandromyia) tylophalla* Andrade & Galati, 2012****Distribution.** Brazil*.**Series saulensis Lewis, Young & Minter, 1977*****Evandromyia (Evandromyia) saulensis* (Floch & Abonnenc, 1944)****Distribution.** Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana*, Panama, Peru, Venezuela.***Evandromyia (Evandromyia) wilsoni* (Damasceno & Causey, 1945)****Distribution.** Brazil*.***Evandromyia incertae sedis******Evandromyia edwardsi* (Mangabeira, 1941)****Distribution.** Brazil*.**Subtribe Psychodopygina Galati, 1995****Genus *Psathyromyia* Barretto, 1962****Subgenus (*Forattiniella*) Vargas, 1978*****Psathyromyia (Forattiniella) abunaensis* (Martins, Falcão & Silva, 1965)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, Peru.***Psathyromyia (Forattiniella) antezanai* (Le Pont, Dujardin, Mouchet & Desjeux, 1990)****Distribution.** Bolivia*.***Psathyromyia (Forattiniella) aragaoi* (Costa Lima, 1932)****Distribution.** Bolivia, Brazil*, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Paraguay, Peru, Trinidad and Tobago, Venezuela.***Psathyromyia (Forattiniella) barrettoi barrettoi* (Mangabeira, 1942)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Trinidad and Tobago.***Psathyromyia (Forattiniella) barrettoi majuscula* (Young, 1979)****Distribution.** Colombia, Costa Rica, Ecuador, El Salvador, Honduras, Nicaragua, Panama*.***Psathyromyia (Forattiniella) brasiliensis* (Costa Lima, 1932)****Distribution.** Brazil*, French Guiana, Peru.***Psathyromyia (Forattiniella) campograndensis* (Oliveira, Andrade-Filho, Falcão & Brazil, 2001)****Distribution.** Brazil*, French Guiana.***Psathyromyia (Forattiniella) carpenteri* (Fairchild & Hertig, 1953)****Distribution.** Belize, Colombia, Costa Rica, Mexico, Panama*.

Psathyromyia (Forattiniella) castilloi* (León, Mollinedo & Le Pont, 2009)*Distribution.** Bolivia, Ecuador*, French Guiana.***Psathyromyia (Forattiniella) coutinhoi* (Mangabeira, 1942)****Distribution.** Bolivia, Brazil*, Peru.***Psathyromyia (Forattiniella) elizabethdorvalae* Brillhante, Sábio & Galati, 2016****Distribution.** Brazil*.***Psathyromyia (Forattiniella) inflata* (Floch & Abonnenc, 1944)****Distribution.** Bolivia, Brazil, French Guiana*.***Psathyromyia (Forattiniella) lutziana* (Costa Lima, 1932)****Distribution.** Bolivia, Brazil*, Colombia, French Guiana, Peru, Surinam, Venezuela.***Psathyromyia (Forattiniella) naftalekatzi* (Falcão, Andrade-Filho, Almeida & Brandão-Filho, 2000)****Distribution.** Brazil*.***Psathyromyia (Forattiniella) pascalei* (Coutinho & Barretto, 1940)****Distribution.** Brazil*.***Psathyromyia (Forattiniella) pradobarrientosi* (Le Pont, Matias, Martinez & Dujardin, 2004)****Distribution.** Bolivia*, Brazil.**Note.** This species has been collected in Brazil in Amapá (PHFS) and in Distrito Federal (AJA).***Psathyromyia (Forattiniella) runoides* (Faichild & Hertig, 1953)****Distribution.** Brazil, Colombia, Costa Rica, Ecuador, Panama*, Peru.**†*Psathyromyia (Forattiniella) schleei* (Peñalver & Grimaldi, 2005)****Distribution.** Dominican amber****Psathyromyia (Forattiniella) texana* (Dampf, 1938)****Distribution.** Mexico*, United States of America.**Subgenus (*Psathyromyia*) Barretto, 1962****Series *lanei* Theodor, 1965*****Psathyromyia (Psathyromyia) digitata* (Damasceno & Arouck, 1950)****Distribution.** Brazil*.***Psathyromyia (Psathyromyia) lanei* (Barretto & Coutinho, 1941)****Distribution.** Argentina, Brazil*, Paraguay.***Psathyromyia (Psathyromyia) pelli* (Sherlock & Alencar, 1959)****Distribution.** Brazil*.**Series *shannoni* Fairchild, 1955*****Psathyromyia (Psathyromyia) abbonenci* (Floch & Chassignet, 1947)****Distribution.** Bolivia, Brazil, Colombia, Ecuador, French Guiana*, Panama, Peru, Surinam, Venezuela.

Psathyromyia (Psathyromyia) baratai* Sábio, Andrade & Galati, 2015*Distribution.** Brazil*.***Psathyromyia (Psathyromyia) barretti* Alves & Freitas, 2016****Distribution.** Brazil*.***Psathyromyia (Psathyromyia) bigeniculata* (Floch & Abonnenc, 1941)****Distribution.** Brazil, French Guiana*.***Psathyromyia (Psathyromyia) campbelli* (Damasceno, Causey & Arouck, 1945)****Distribution.** Bolivia, Brazil*, Colombia, French Guiana, Peru, Venezuela.***Psathyromyia (Psathyromyia) cratifer* (Fairchild & Hertig, 1961)****Distribution.** Belize, Costa Rica, Honduras, Mexico*, Panama.***Psathyromyia (Psathyromyia) dasymera* (Fairchild & Hertig, 1961)****Distribution.** Belize, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Nicaragua, Panama*, Venezuela.***Psathyromyia (Psathyromyia) dendrophyla* (Mangabeira, 1942)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Venezuela.***Psathyromyia (Psathyromyia) guatemalensis* (Porter & Young, 1986)****Distribution.** Guatemala*.***Psathyromyia (Psathyromyia) lerayi* (Le Pont, Martinez, Torrez-Espejo & Dujardin, 1998)****Distribution.** Bolivia*, Colombia.***Psathyromyia (Psathyromyia) limai* (Fonseca, 1935)****Distribution.** Brazil*.***Psathyromyia (Psathyromyia) pifanoi* (Ortiz, 1972)****Distribution.** Brazil, Colombia, Peru*.***Psathyromyia (Psathyromyia) punctigeniculata* (Floch & Abonnenc, 1944)****Distribution.** Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana*, Panama, Peru, Surinam, Venezuela.***Psathyromyia (Psathyromyia) ribeirensis* Sábio, Andrade & Galati, 2014****Distribution.** Brazil*.***Psathyromyia (Psathyromyia) scaffi* (Damasceno & Arouck, 1956)****Distribution.** Bolivia, Brazil*, Colombia, French Guiana, Peru, Surinam.***Psathyromyia (Psathyromyia) shannoni* (Dyar, 1929)****Distribution.** Belize, Bolivia, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama*, Peru, Surinam, Trinidad and Tobago, United States of America, Venezuela.***Psathyromyia (Psathyromyia) soccula* (Fairchild & Hertig, 1961)****Distribution.** Costa Rica, Panama*.***Psathyromyia (Psathyromyia) souzacaastroi* (Damasceno & Causey, 1944)****Distribution.** Brazil*.***Psathyromyia (Psathyromyia) undulata* (Fairchild & Hertig, 1950)****Distribution.** Belize, Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana*, Guatemala, Honduras, Mexico, Panama.

Psathyromyia (Psathyromyia) volcanensis* (Fairchild & Hertig, 1950)*Distribution.** Bolivia, Costa Rica, Panama*.**Subgenus (*Xiphopsathyromyia*) Ibáñez-Bernal & Marina, 2015*****Psathyromyia (Xiphopsathyromyia) aclydifera* (Fairchild & Hertig, 1952)****Distribution.** Belize, Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama*.***Psathyromyia (Xiphopsathyromyia) dreisbachi* (Causey & Damasceno, 1945)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Venezuela.***Psathyromyia (Xiphopsathyromyia) hermanlenti* (Martins, Silva & Falcão, 1970)****Distribution.** Brazil*.***Psathyromyia (Xiphopsathyromyia) rugarupa* (Martins, Llanos & Silva, 1976)****Distribution.** Bolivia, Peru*.***Psathyromyia incertae sedis******Psathyromyia maya* Ibáñez-Bernal, May-UC & Rebollar-Tellez, 2010****Distribution.** Mexico*.**Genus *Viannamyia* Mangabeira, 1941*****Viannamyia caprina* (Osorno-Mesa, Morales & Osorno, 1972)****Distribution.** Colombia*, Costa Rica, Honduras, Panama, Peru, Nicaragua.***Viannamyia fariasi* (Damasceno, Causey & Arouck, 1945)****Distribution.** Brazil*, French Guiana.***Viannamyia furcata* (Mangabeira, 1941)****Distribution.** Bolivia, Brazil*, Colombia, Costa Rica, Ecuador, French Guiana, Peru, Venezuela.***Viannamyia tuberculata* (Mangabeira, 1941)****Distribution.** Bolivia, Brazil*, Colombia, French Guiana, Panama, Peru, Surinam, Venezuela.**Genus *Martinsmyia* Galati, 1995****Group *alphabetica* Fairchild, 1955*****Martinsmyia alphabetica* (Fonseca, 1936)****Distribution.** Argentina, Brazil*, Paraguay.***Martinsmyia brisolai* (Le Pont & Desjeux, 1987)****Distribution.** Bolivia*, Brazil.

Martinsmyia minasensis* (Mangabeira, 1942)*Distribution.** Brazil*.***Martinsmyia mollinedoi* (Le Pont & Desjeux, 1991)****Distribution.** Bolivia*.***Martinsmyia oliveirai* (Martins, Silva & Falcão, 1970)****Distribution.** Brazil*.***Martinsmyia pisuquia* (Ogusuku, Guevara, Revilla, Inga & Pérez, 2001)****Distribution.** Peru*.***Martinsmyia quadrispinosa* (Floch & Chassignet, 1947)****Distribution.** French Guiana*.***Martinsmyia reginae* Carvalho, Brazil, Sanguinette & Andrade-Filho, 2010****Distribution.** Brazil*.***Martinsmyia waltoni* (Arias, Freitas & Barrett, 1984)****Distribution.** Brazil*.**Group gasparviannai Young & Fairchild, 1974*****Martinsmyia cipoensis* (Martins, Falcão & Silva, 1964)****Distribution.** Brazil*.***Martinsmyia gasparviannai* (Martins, Godoy & Silva, 1962)****Distribution.** Brazil*.**Genus *Bichromomyia* Artemiev, 1991*****Bichromomyia flaviscutellata* (Mangabeira, 1942)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Trinidad and Tobago, Venezuela.***Bichromomyia inornata* (Martins, Falcão & Silva, 1965)****Distribution.** Bolivia, Brazil*.**Note.** Several authors (Young and Arias 1982, Young and Duncan 1994, Carvalho et al. 2015) have mentioned the possibility that *B. inornata* is conspecific with *B. flaviscutellata*. According to the description of *B. inornata*, its scutellum is dark, which would distinguish this species from all other species in the genus *Bichromomyia*. However, at FIOCRUZ/COLFLEB, we have checked the holotype (slide number 39.581) plus three males from Maranhão (slide numbers NE 1139.63, No. 32203; NE 930.62, No. 28734; NE 933.62, No. 28761) that were identified as *B. inornata* by the authors of the species, and all specimens have pale rather than dark scutellum, making this species indistinguishable from *B. flaviscutellata*.***Bichromomyia olmeca bicolor* (Fairchild & Theodor, 1971)****Distribution.** Brazil, Colombia, Costa Rica, Ecuador, Panama*, Peru, Venezuela.***Bichromomyia olmeca nociva* (Young & Arias, 1982)****Distribution.** Brazil*, Peru.

Bichromomyia olmeca olmeca* (Vargas & Díaz-Nájera, 1959)*Distribution.** Belize, Costa Rica, Guatemala, Honduras, Mexico*, Nicaragua.***Bichromomyia reducta* (Felicíangeli, Ramírez-Pérez & Ramírez, 1988)****Distribution.** Brazil, Colombia, Peru, Venezuela*.**Genus *Psychodopygus* Mangabeira, 1941****Series *arthuri* Barretto, 1962*****Psychodopygus arthuri* (Fonseca, 1936)****Distribution.** Brazil*.***Psychodopygus lloydi* (Antunes, 1937)****Distribution.** Brazil*.***Psychodopygus matosi* (Barretto & Zago, 1956)****Distribution.** Brazil*.**Series *chagasi* Barretto, 1962*****Psychodopygus bernali* (Osorno-Mesa, Morales & Osorno, 1967)****Distribution.** Bolivia, Brazil, Colombia*, Venezuela.***Psychodopygus chagasi* (Costa Lima, 1941)****Distribution.** Brazil*, Colombia, Peru, Venezuela.***Psychodopygus complexus* (Mangabeira, 1941)****Distribution.** Bolivia, Brazil*.***Psychodopygus douradoi* (Fé, Freitas & Barrett, 1998)****Distribution.** Brazil*.***Psychodopygus fairtigi* (Martins, 1970)****Distribution.** Colombia*.***Psychodopygus killicki* (Felicíangeli, Ramírez-Pérez & Ramírez, 1988)****Distribution.** Venezuela*.***Psychodopygus leonidasdeanei* Fraiha, Ryan, Ward, Lainson & Shaw, 1986****Distribution.** Brazil*.***Psychodopygus squamiventris maripaensis* (Floch & Abonnenc, 1946)****Distribution.** Brazil, French Guiana*, Surinam.***Psychodopygus squamiventris squamiventris* (Lutz & Neiva, 1912)****Distribution.** Brazil*, French Guiana, Peru, Venezuela.***Psychodopygus wellcomei* Fraiha, Shaw & Lainson, 1971****Distribution.** Brazil*, Venezuela.**Series *davisi* Barretto, 1962*****Psychodopygus amazonensis* (Root, 1934)****Distribution.** Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru*, Surinam, Trinidad and Tobago, Venezuela.

***Psychodopygus clautrei* (Abonnenc, Léger & Fauran, 1979)**

Distribution. Bolivia, Brazil, Colombia, French Guiana*, Peru, Surinam, Venezuela.

***Psychodopygus davisii* (Root, 1934)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Venezuela.

***Psychodopygus parimaensis* (Ortiz & Álvarez, 1972)**

Distribution. Venezuela*.

Series *guyanensis* Barretto, 1962***Psychodopygus corossoniensis* (Le Pont & Pajot, 1978)**

Distribution. Brazil, Costa Rica, French Guiana*, Mexico, Panama, Surinam.

***Psychodopygus dorelinsis* (Le Pont & Desjeux, 1982)**

Distribution. French Guiana*.

***Psychodopygus francoisleponti* Zapata, Depaquit & León, 2012**

Distribution. Ecuador*.

***Psychodopygus geniculatus* (Mangabeira, 1941)**

Distribution. Belize, Bolivia, Brazil*, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Panama, Peru, Nicaragua, Venezuela.

***Psychodopygus guyanensis* (Floch & Abonnenc, 1941)**

Distribution. Belize, Colombia, Ecuador, French Guiana*, Peru, Surinam.

***Psychodopygus lainsoni* (Fraiha & Ward, 1974)**

Distribution. Bolivia, Brazil*, Peru.

***Psychodopygus luisleoni* León, Mollinedo & Le Pont, 2009**

Distribution. Ecuador*.

Series *panamensis* Young & Fairchild, 1974***Psychodopygus ayrozai* (Barretto & Coutinho, 1940)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Panama, Peru, Trinidad and Tobago, Venezuela.

***Psychodopygus carrerai* (Barretto, 1946)**

Distribution. Bolivia, Brazil, Colombia*, Ecuador, Peru, Venezuela.

***Psychodopygus fairchildi* (Barretto, 1966)**

Distribution. Brazil*.

***Psychodopygus hirsutus* (Mangabeira, 1942)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam.

***Psychodopygus joliveti* Le Pont, León, Galati & Dujardin, 2009**

Distribution. French Guiana*.

***Psychodopygus llanosmartinsi* Fraiha & Ward, 1980**

Distribution. Bolivia, Brazil, Peru*.

***Psychodopygus nicaraguensis* (Fairchild & Hertig, 1961)**

Distribution. Brazil, Panama, Nicaragua*.

***Psychodopygus nocticolus* (Young, 1973)**

Distribution. Bolivia, Colombia*, Ecuador, French Guiana, Mexico, Panama, Peru.

***Psychodopygus panamensis* (Shannon, 1926)**

Distribution. Belize, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama*, Peru, Surinam, Venezuela.

***Psychodopygus paraensis* (Costa Lima, 1941)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Venezuela.

***Psychodopygus recurvus* (Young, 1973)**

Distribution. Colombia*, Panama.

***Psychodopygus thula* (Young, 1979)**

Distribution. Colombia, Costa Rica, Ecuador, Honduras, Panama*.

***Psychodopygus yasuniensis* León, Neira & Le Pont, 2009**

Distribution. Ecuador*.

***Psychodopygus yucumensis* (Le Pont, Caillard, Tibayrenc & Desjeux, 1986)**

Distribution. Bolivia*, Brazil, Peru.

Psychodopygus incertae sedis***Psychodopygus bispinosus* (Fairchild & Hertig, 1951)**

Distribution. Belize, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama*, Surinam.

Genus *Nyssomyia* Barretto, 1962***Nyssomyia anduzei* (Rozeboom, 1942)**

Distribution. Brazil, Costa Rica, French Guiana, Panama, Peru, Venezuela*.

***Nyssomyia antunesi* (Coutinho, 1939)**

Distribution. Bolivia, Brazil*, Colombia, French Guiana, Peru, Surinam, Trinidad and Tobago, Venezuela.

***Nyssomyia bibinae* (Léger & Abonnenc, 1988)**

Distribution. French Guiana*.

***Nyssomyia delsonatali* Galati & Galvis, 2012**

Distribution. Brazil*.

***Nyssomyia edentula* (León, 1971)**

Distribution. Costa Rica, Guatemala*, Honduras, Panama.

***Nyssomyia elongata* (Floch & Abonnenc, 1945)**

Distribution. French Guiana*.

***Nyssomyia fraihai* (Martins, Falcão & Silva, 1979)**

Distribution. Bolivia, Brazil*, Peru.

***Nyssomyia hernandezii* (Ortiz, 1965)**

Distribution. Colombia, Venezuela*.

***Nyssomyia intermedia* (Lutz & Neiva, 1912)**

Distribution. Brazil*.

***Nyssomyia neivai* (Pinto, 1926)**

Distribution. Argentina, Bolivia, Brazil*, Paraguay.

***Nyssomyia pajoti* (Abonnenc, Léger & Fauran, 1979)**

Distribution. Brazil, Colombia, French Guiana*, Peru, Surinam.

***Nyssomyia richardwardi* (Ready & Fraiha, 1981)**

Distribution. Bolivia, Brazil*, Colombia, Ecuador, Peru.

***Nyssomyia shawi* (Fraiha, Ward & Ready, 1981)**

Distribution. Bolivia, Brazil*, Colombia, Peru.

***Nyssomyia sylvicola* (Floch & Abonnenc, 1945)**

Distribution. Brazil, French Guiana*.

***Nyssomyia trapidoi* (Fairchild & Hertig, 1952)**

Distribution. Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Nicaragua, Panama*.

***Nyssomyia umbratilis* (Ward & Fraiha, 1977)**

Distribution. Bolivia, Brazil*, Colombia, French Guiana, Peru, Surinam, Venezuela.

***Nyssomyia urbinatti* Galati & Galvis, 2012**

Distribution. Brazil*.

***Nyssomyia whitmani* (Antunes & Coutinho, 1939)**

Distribution. Argentina, Bolivia, Brazil*, French Guiana, Paraguay, Peru, Surinam.

***Nyssomyia ylephiletor* (Fairchild & Hertig, 1952)**

Distribution. Belize, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama*.

***Nyssomyia yuilli* (Young & Porter, 1972)**

Distribution. Bolivia, Brazil, Colombia*, Ecuador, Peru, Venezuela.

Genus *Trichophoromyia* Barretto, 1962***Trichophoromyia acostai* (Llanos, 1966)**

Distribution. Peru*.

***Trichophoromyia adelsonsouzai* Santos, Silva, Barata, Andrade & Galati, 2013**

Distribution. Brazil*.

***Trichophoromyia arevaloi* Galati & Cáceres, 1999**

Distribution. Peru*.

***Trichophoromyia auraensis* (Mangabeira, 1942)**

Distribution. Bolivia, Brazil*, Colombia, Peru, Surinam, Venezuela.

***Trichophoromyia beniensis* (Le Pont & Desjeux, 1987)**

Distribution. Bolivia*.

***Trichophoromyia bettinii* (Felicangeli, Ramírez-Pérez & Ramírez, 1988)**

Distribution. Colombia, Venezuela*.

***Trichophoromyia brachipyga* (Mangabeira, 1942)**

Distribution. Brazil*, French Guiana.

- Trichophoromyia castanheirai* (Damasceno, Causey & Arouck, 1945)
Distribution. Brazil*.
- Trichophoromyia cellulana* (Young, 1979)
Distribution. Colombia*, Ecuador.
- Trichophoromyia clitella* (Young & Pérez, 1994)
Distribution. Brazil, Peru*.
- Trichophoromyia dunhami* (Causey & Damasceno, 1945)
Distribution. Brazil*.
- Trichophoromyia eurypyga* (Martins, Falcão & Silva, 1963)
Distribution. Brazil*, Venezuela.
- Trichophoromyia flochi* (Abonnenc & Chassignet, 1948)
Distribution. Brazil, French Guiana*.
- Trichophoromyia gibba* (Young & Arias, 1994)
Distribution. Brazil*.
- Trichophoromyia howardi* (Young, 1979)
Distribution. Brazil, Colombia*, Peru.
- Trichophoromyia incasica* (Llanos, 1966)
Distribution. Peru*.
- Trichophoromyia ininii* (Floch & Abonnenc, 1943)
Distribution. Brazil, French Guiana*, Surinam.
- Trichophoromyia lopesi* (Damasceno, Causey & Arouck, 1945)
Distribution. Brazil*.
- Trichophoromyia loretonensis* (Llanos, 1964)
Distribution. Brazil, Peru*.
- Trichophoromyia meirai* (Causey & Damasceno, 1945)
Distribution. Brazil*.
- Trichophoromyia melloi* (Causey & Damasceno, 1945)
Distribution. Brazil*, Surinam.
- Trichophoromyia napoensis* (Young & Rogers, 1984)
Distribution. Ecuador*.
- Trichophoromyia nautaensis* (Fernández, Lopez, Cardenas & Requena, 2015)
Distribution. Peru*.
- Trichophoromyia nemorosa* (Young & Pérez, 1994)
Distribution. Peru*.
- Trichophoromyia octavioi* (Vargas, 1949)
Distribution. Bolivia, Brazil*, Peru.
- Trichophoromyia omagua* (Martins, Llanos & Silva, 1976)
Distribution. Peru*.
- Trichophoromyia pabloi* (Barreto, Burbano & Young, 2002)
Distribution. Colombia*, Ecuador.
- Trichophoromyia pastazaensis* (Fernández, Carbajal, Alexander & Need, 1993)
Distribution. Peru*.

Trichophoromyia readyi* (Ryan, 1986)*Distribution.** Brazil*.***Trichophoromyia reburra* (Fairchild & Hertig, 1961)****Distribution.** Colombia, Costa Rica, Ecuador, Panama*.***Trichophoromyia reinerti* (Young & Duncan, 1994)****Distribution.** Brazil*.***Trichophoromyia rostrans* (Summers, 1912)****Distribution.** Brazil*.***Trichophoromyia ruifreitasi* Oliveira, Teles, Medeiros, Camargo & Pessoa, 2015****Distribution.** Brazil*.***Trichophoromyia ruii* (Arias & Young, 1982)****Distribution.** Brazil*, Colombia.***Trichophoromyia saltuosa* (Young, 1979)****Distribution.** Colombia*.***Trichophoromyia sinuosa* (Young & Duncan, 1994)****Distribution.** Peru*.***Trichophoromyia ubiquitalis* (Mangabeira, 1942)****Distribution.** Bolivia, Brazil*, Colombia, Ecuador, French Guiana, Peru, Surinam, Venezuela.***Trichophoromyia uniniensis* Ladeia-Andrade, Fé, Sanguinette & Andrade-Filho, 2014****Distribution.** Brazil*.***Trichophoromyia velascoi* (Le Pont & Desjeux, 1992)****Distribution.** Bolivia*.***Trichophoromyia viannamartinsi* (Sherlock & Guitton, 1970)****Distribution.** Brazil*.***Trichophoromyia wilkersoni* (Young & Rogers, 1984)****Distribution.** Ecuador*.**Unplaced genera of Phlebotomini****Genus *Edentomyia* Galati, Andrade-Filho, Silva & Falcão, 2003*****Edentomyia piauiensis* Galati, Andrade-Filho, Silva & Falcão, 2003****Distribution.** Brazil*.***Nomina dubia* in New World Phlebotominae*****Nyssomyia singularis* (Costa Lima, 1932)****Distribution.** Brazil*.**Note.** This species is only known from the type specimen mounted in Canada Balsam medium. The specimen “cotype” is deposited in the Coleção Entomológica

do Instituto Oswaldo Cruz (FIOCRUZ/CEIOC) (number of the slides: 1436–1439). The specimen was collected in 08-VIII-1902 by Adolpho Lutz in Juqueri (currently Mairiporã municipality) state of São Paulo, Brazil. One of us (AJA) studied the type and observed that the thorax is damaged, but it is possible to observe the colour of the paratergite and scutum, which is similar to species in the genus *Nyssomyia*. The spermathecae was dissected, but was not observed in any of the slides, so it is likely the spermathecae has oxidized over time. The original description is insufficient for a positive identification, however the spermathecae as illustrated show the same number of rings as *Nyssomyia neivai*. In the absence of evidence positively linking the two species, however, we prefer to consider *Nyssomyia singularis* as a *nomen dubium*.

Available names but found to denote more than one taxon (availability of the name is not affected according to provisions of the ICZN, Articles 17.2 and 23.8)

***Phlebotomus breviductus* Barretto, 1950**

Note. Only known from the holotype and five females collected by Rangel et al. (1985). Andrade et al. (2013) examined the holotype and concluded that the head and wing of this specimen belong to a *Trichopygomyia* sp. specimen, whereas the thorax and abdomen belong to an anomalous specimen of *Nyssomyia umbratilis*.

***Phlebotomus oliverioi* Barretto & Coutinho, 1941**

Note. Andrade et al. (2014) examined the holotype and concluded that the head of this specimen belongs to a specimen of *Psychodopygus* while the wings, thorax and abdomen belong to another specimen, of the genus *Psathyromyia*.

Unavailable names not meeting the requirements of the ICZN

***Micropygomyia (Sauromyia)* sp. 2 of Araracuara (Morales & Minter, 1981)**

Distribution. Colombia*.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described from both males and females, but the authors decided not to name it.

***Lutzomyia (Helcocyrtomyia)* sp. of Pichinde Young, 1979**

Distribution. Colombia*.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described from both males and females. Young (1979) and Young and Duncan (1994) stated that this species was closely related to *L. (H.) hartmanni* and *L. (H.) scorzai*, but noted that further studies were necessary before formally naming this species.

***Pintomyia* sp. of Anchicaya (Young, 1979)**

Distribution. Colombia*.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described from a single male, but Young and Duncan (1994) stated that they were waiting for the collection of the female before formally naming this species.

***Dampfomyia* sp. of Suchitepequez (Young & Duncan, 1994)**

Distribution. Guatemala*.

Note. This species appears as an illustration in Young and Duncan (1994: 247), who stated it was the holotype of *Lutzomyia piedraferroi*. However, Galati (2003) interpreted their illustration as a different species, which differs markedly in the number and shape of the spines in the gonostyle from the original description by León (1971); she referred to the species as *Dampfomyia* sp. of Suchitepequez, and it awaits formal description.

***Pressatia* #1 Mangabeira, 1942**

Distribution. Bolivia*, Colombia.

Note. Unavailable according to article 11.4 of the ICZN. This species is listed by Young and Duncan (1994), and reported as being described from a single male by Velasco (unpublished). However, Young and Duncan (1994) stated that the latter was waiting for the collection of the female before formally naming this species.

***Evandromyia* (*Aldamyia*) sp. of Baduel (Floch & Abonnenc, 1945)**

Distribution. Brazil, Colombia, French Guiana*, Surinam.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described from both males and females. Although this species has been recorded in different publications, no attempt has been made so far to formally describe it.

***Psychodopygus* sp. of Três Esquinas (Young, 1979)**

Distribution. Colombia*.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described only from females. Because females of the series *guyanensis* are indistinguishable in morphology, it is not possible to know if this species has been previously described from a male.

***Trichophoromyia* sp. 1 of Araracuara (Morales & Minter, 1981)**

Distribution. Colombia*.

Note. Unavailable according to article 11.4 of the ICZN. This species has been described from both males and females. However, the authors were not sure if it was a variant of *T. howardi* Young, 1979, and hence decided not to name it.

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Ten new genera of Agathidini (Hymenoptera, Braconidae, Agathidinae) from Southeast Asia

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Abstract

The Agathidini (Braconidae: Agathidinae) genera of Southeast Asia are revised based on a phylogenetic analysis of COI and 28S. Ten new genera are proposed, i.e., *Agathigma*, *Asperagathis*, *Chimaeragathis*, *Cymagathis*, *Liragathis*, *Leuroagathis*, *Scabagathis*, *Trochantagathis*, *Xanthagathis*, and *Zosteragathis*. An illustrated key to the Southeast Asian genera of this tribe is presented. Species from Thailand are keyed and described for all genera of Agathidini except *Bassus* and *Zosteragathis* which have too many species for this publication and will be dealt with separately. The phylogenetic analyses indicate that *Bassus s.s.* is polyphyletic. However, there are no morphological characters to support this and we have retained the current concept of *Bassus*, which is basically those Agathidini with simple tarsal claws. Numerous new combinations are proposed based on species that are moved to the newly erected genera.

Keywords

Taxonomy, systematics, *Agathigma*, *Asperagathis*, *Chimaeragathis*, *Cymagathis*, *Liragathis*, *Leuroagathis*, *Scabagathis*, *Trochantagathis*, *Xanthagathis*, *Zosteragathis*

Introduction

Agathidinae is a moderately diverse subfamily of Braconidae with about 1,200 described species (Yu et al. 2012) and many times that number are yet to be named. Larvae are parasitoids of lepidopteran caterpillars of a multitude of families. Most agathidine genera, and probably all of the genera treated here, attack an early instar caterpillar and are quiescent until the host has reached the final instar and is ready to spin a cocoon. At this point in time the parasitoid larva becomes active and quickly consumes the host, i.e., they are koinobiont endoparasitoids.

This is the sixth publication on the Agathidine fauna with a concentration on Thailand. Sharkey et al. (2009) revised the Oriental genera of Agathidinae. Sharkey and Clutts (2011) revised the Thai agathidine genera with one or a few species and updated the generic key to the Oriental genera. Sharkey and Stoelb (2012, 2013) revised the Thai species of *Zelodia* van Achterberg and *Agathacrista* Sharkey. Lastly, van Achterberg et al. (2014) revised the Thai species of *Euagathis*. It is the aim of this paper to revise the genera of Agathidini that have not been treated and to describe the Thai species of these that are not overly species-rich.

The recent redefinition of *Bassus* (Sharkey et al. 2009) to refer only to those species of Old World agathidines with simple claws, necessitated the erection or resurrection of numerous genera to house species formerly contained in the broader, polyphyletic concept of *Bassus* (Sharkey et al. 2015; Sharkey and Chapman 2015; Sharkey and Stoelb 2013; Sharkey et al. 2016; Achterberg and Long 2010). The previously published genera of this nature are: *Gelastagathis* Sharkey, 2015; *Aphelagathis* Sharkey, 2015; *Pneumagathis* Sharkey, 2015; *Agathacrista* Sharkey, 2013; *Neothlipsis* Sharkey, 2011; *Gyrageathis* Achterberg & Long, 2010; *Aerophilus* Szépligeti, 1902; and *Therophilus* Wesmael, 1837. Most of the aforementioned genera, including *Bassus* s.s., are small and restricted to the Old or New world. The two exceptions are *Aerophilus*, and *Therophilus*. These are both species-rich and cosmopolitan. Unfortunately, but perhaps necessarily, *Therophilus* has become the new dumping ground for unplaced members of Agathidini (Stevens et al. 2010, 2011; Achterberg and Long 2010). This is all the worse because most of the species recently placed in *Therophilus* are not closely related to it. *Therophilus* is sister to the clade *Mesocoelus* + *Aneurobracon* and has a number of unique features as outlined in Sharkey and Stoelb (2012). It is the purpose of this paper to erect new Old World genera to avoid the further debasement of *Therophilus*. The revision is primarily based on material collected in Thailand. New species from Thailand are keyed and described for all genera of Agathidini except *Bassus* and *Zosteragathis* which have too many species for this publication and will be dealt with separately.

Methods

All specimens except for some duplicates are deposited in the Entomological Museum of The Queen Sirikit Botanic Gardens, Chaing Mai, Thailand.

Diagnoses

Diagnoses are rather comprehensive however an abbreviated diagnosis for each genus is given in bold font within each diagnosis.

Morphological terms

Morphological terms are from Sharkey and Wharton (1997) and are matched to the Hymenoptera Anatomy Ontology (HAO; Yoder et al. 2010; <http://portal.hymao.org/projects/32/public/ontology/>). Identifiers (URIs) in the format http://purl.obolibrary.org/obo/HAO_XXXXXXX represent anatomical concepts in HAO version <http://purl.obolibrary.org/obo/ha0/2011-05-18/ha0.owl>. They are provided to enable readers to confirm their understanding of the anatomical structures being referenced. To find out more about a given structure, including images, references and other metadata, use the identifier as a web-link, or use the HAO:XXXXXXX (note colon replaces underscore) as a search term at <http://glossary.hymao.org>. In this paper, terms are linked to the ontology in the results section, each couplet of the key, and in the first description of a taxon (genus *Aphelagathis*). From this point forward, only terms that do not appear in these areas are hyperlinked.

DNA extraction, PCR and sequencing

DNA was extracted from individual legs with the QIAGEN DNeasy Blood and Tissue Kit using the animal tissue protocol (QIAGEN Inc., Chatsworth, California, USA). The nuclear 28S, regions D2-D3 (~600 bp), rDNA and mitochondrial COI (~650 bp) genes were amplified with the 28S primer pairs 28SD2F (Belshaw and Quicke 1997) and D3R (Harry et al. 1996) and the COI primer pairs LepF1 and LepR1 (Hebert et al. 2004). For COI, PCR was conducted using Takara reagents, with each reaction consisting of 1X buffer, 0.3 mM nucleotides, 0.4 µM of each primer, 0.625 U Takara Ex Taq, ddH₂O, and 1–3 µL template DNA in a total reaction volume of 25 µL. The thermal cycling protocol had an initial denaturation period at 95 °C for 2.5 min, followed by 40 cycling steps which denatured at 95 °C for 30 s, annealed at 44 °C for 30 s and extended at 68 °C for 45 s, with a final extension step of 72 °C for 7 min. For 28S, PCR consisted of Qiagen 1X buffer, 4 mM MgSO₄, 0.3 mM dNTP, 0.4 µM of each primer, 1.0 U Qiagen Taq, ddH₂O, and 1–3 µL template DNA with a total reaction volume of 25 µL. Thermal cycling was as above except annealing at 53 °C, extending for 70 s, and a total of 35 cycles. To determine reaction success, PCR products were electrophoresed in 1% agarose stained with ethidium bromide. PCR products were outsourced for Sanger sequencing either by the Advanced Genetic Technologies Center (University of Kentucky, Lexington, KY) or Beckman Coulter Genomics (Danvers, MA, USA) using labelled dideoxynucleotides with ABI 3730, Big-Dye Terminator mix v. 3.0 or with ABI PRISM 3730xl, BigDye Terminator mix v. 3.1 (Applied Biosystems, Foster City, California, USA).

DNA assembly and phylogenetic analysis

Bi-directional sequences were aligned and edited using Geneious Pro (v. 6.1.5; Drummond et al. 2009) and multiple alignments were assembled using MAFFT (v. 5; Katoh et al. 2006) using the default settings and refined by eye. Maximum likelihood (ML) phylogenetic analyses were conducted on a concatenated (using MacClade v. 4.08; Maddison and Maddison 2000) 1,313-character total evidence data set (COI = 723 bp, 28S = 590 bp) using Garli (v. 2.01; Zwickl 2006). The data were partitioned by gene region and codon position (COI: 3 partitions; 28S: unpartitioned, total of 4 partitions). We applied the most complex model available (GTR+I+G; Rodriguez et al. 1990) to each partition as per recommendations of Huelsenbeck and Rannala (2004). We conducted a 20-replicate ML search for the tree of highest log-likelihood and a 500-replicate ML bootstrap analysis (Felsenstein 1985). Both analyses used the default settings. The data sets analyzed herein are available from the authors upon request.

Results

Phylogenetic considerations

Here we treat a number of species from Thailand and propose 10 new genera. Most of these are demonstratively monophyletic and morphologically distinct; however, some compromises are made due to poor resolution in the phylogenetic analysis. The tree of highest log-likelihood is presented in Figure 1, with the ML bootstrap values plotted on nodes with $\geq 50\%$ bootstrap support.

In the case of the Thai fauna treated here, there were a number of options in terms of the number of genera that could be proposed. The criteria that I (MJS) used in making decisions on generic limits were: to recognize those monophyletic clades with high (usually $> 90\%$) ML bootstrap support values (Fig. 1), which are also clearly diagnosed by morphological character states, and the recognition of which would not render other genera paraphyletic. A secondary criterion was to rely solely on potential morphological synapomorphies when they were not contradicted by molecular evidence, as in the case of *Bassus* (see below). Most of the genera are well-supported by molecular evidence as demonstrated in Figure 1 and by morphological synapomorphies; e.g., *Agathacrista*, *Asperagathis*, *Camptothlipsis*, *Chimaeragathis*, *Liragathis*, *Neothlipsis*, and *Trochantagathis*. However, *Bassus* was polyphyletic forming two clades. The members of clades are not distinct morphologically, and they share the character state of lacking a lobe at the base of the tarsal claws. Rather than dividing *Bassus* into two indistinguishable genera, we prefer to continue to recognize the current concept. *Agathigma*, *Cymagathis*, *Gyragathis*, *Leuroagathis*, *Scabagathis*, and *Xanthagathis* are each represented by only one species; therefore there are no nodes from which to obtain bootstrap values. However, all are on relatively long branches on the total evidence tree, all have distinct autapomorphies, and none renders another taxon paraphyletic (Fig. 1). *Zosteragathis*



Figure 1. Tree of highest log-likelihood from 20 ML search reps of the combined COI+28S data set with bootstrap values $\geq 50\%$ plotted at the nodes.

is most likely a paraphyletic genus. Although members have similarities, there is not a morphological or molecular autapomorphy for the group. The ML bootstrap values (plotted on Fig. 1) support multiple monophyletic clades of *Zosteragathis*, but none of these have an obvious morphological autapomorphy. Rather than propose a number of vague genera, I (MJS) thought it best to propose a conservative hypothesis in the interest of stability.

Discussions of each genus are presented below in alphabetical order

***Agathacrista* Sharkey, 2013:** The genus was described and revised by Sharkey and Stoelb (2013). The thin interantennal crest is an autapomorphy for the genus, though convergently found in *Chimaeragathis* and in a few species of a few other genera; e.g., *Therophilus*.

***Agathigma* Sharkey, new genus:** *Agathigma templei* is the sole species. Morphological autapomorphies are the squared temples (Fig. 2) and the labial palpus reduced to 2 segments. The former character state is rarely found in other agathidine genera such as *Gyragathis* and convergently in a few New World *Therophilus* and *Aerophilus*. In the tree in Figure 1 it appears as sister to the clade *Leuroagathis* + *Xanthagathis*; however there is no bootstrap support for this relationship. The branch leading to the terminus *A. templei* is the longest of all branches, a fact that further erodes confidence in its placement.

***Asperagathis* Sharkey, new genus:** This genus is sister to one of the *Zosteragathis* clades in the total evidence tree (Fig. 1). The rugose sculpture of the mesosoma is a proposed autapomorphy; however, even rougher sculpture occurs in Southeast Asian specimens that author MJS has viewed which may not be congeneric.

***Bassus* Fabricius, 1804:** *Bassus*, the strict definition of which was proposed by Sharkey et al. (2009), is restricted to those Old World agathidines with simple tarsal claws. This autapomorphy is convergently found in all *Sesioctonus*, a Neotropical genus, and in a few species of other genera such as *Neothlipsis*. *Bassus* is polyphyletic in the ML tree (Fig. 1); and the polyphyly is not resolved in the ML bootstrap tree (not shown). Interestingly, both COI and 28S gene-trees (analyzed as above; not shown) are completely congruent with the tree in Figure 1 regarding *Bassus*, showing the same species membership in the 2 clades. Because there are no obvious morphological character states to distinguish either of the two clades of *Bassus*, we choose to retain the genus as it is until more data confirm that it is not monophyletic.

***Camptothlipsis* Enderlein, 1920:** This is an Old World genus, primarily tropical, that is sister to the New World genus *Neothlipsis* in Figure 1 (but see Fig. 1 in Sharkey and Chapman 2015). Both lack strong sculpture on the metasomal median tergites and possess granulate sculpture on metasomal median tergites 1–3.

***Chimaeragathis* Sharkey, new genus:** An interantennal crest is shared convergently with members of *Agathacrista*. Another autapomorphy is the relatively dense pilosity on the scutellar triangle and the lateral areas of the propodeum. The total

evidence tree (Fig. 1) shows a sister-group relationship with ((*Gyragathis* + *Cymagathis*) *Liragathis*) but this relationship lacks bootstrap support.

***Cymagathis* Sharkey, new genus:** An autapomorphy for the genus is that the second median tergite is covered with strong smooth striae that end evenly at the apex of the tergite with the striae forming a semicircular pattern anteromedially. This is convergently found in some species of *Trochantagathis*. It is sister to *Gyragathis* on the total evidence tree (Fig. 1), supported with a bootstrap value of 90.

***Gyragathis* Achterberg & Long, 2010:** An autapomorphy for the genus is that the antennal sockets are margined with carinae. Other possible autapomorphies include the interantennal space with a longitudinal depression and the squared temples, the latter of which is shared convergently with *Agathigma*. Possession of margined antennal sockets is a character state shared by several distantly related New World Agathidini genera, e.g., *Alabagrus* and *Trachagathis*, as well as some genera of Cremnoptini and Disophrini. *Gyragathis* is sister to *Cymagathis* on the total evidence tree (Fig. 1), supported with a bootstrap value of 90.

***Leuroagathis* Sharkey, new genus:** This genus possesses two autapomorphic character states: notauli absent, and median tergite 1 smooth, lacking sculpture. It is sister to *Xanthagathis* in the total evidence tree but the relationship lacks bootstrap support (Fig. 1). Many agathidines from Australia share these two autapomorphies. The one Australian specimen with these characteristics for which we obtained 28S and COI data does not fall within the clade examined herein (unpublished).

***Liragathis* Sharkey, new genus:** An autapomorphy is the median carina of the first median tergite which is as strong as, or stronger than, the lateral carinae. It is sister to *Gyragathis* + *Cymagathis* but this relationship lacks bootstrap support (Fig. 1).

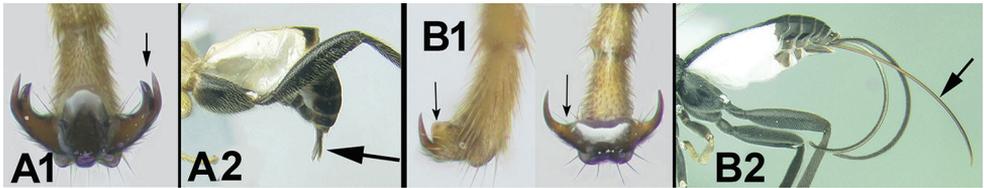
***Scabagathis* Sharkey, new genus:** There are two autapomorphic character states. The vertex has rough sculpture and the labial palpus, normally 4-segmented, is 3-segmented, with the third palpomere lacking. The total evidence tree (Fig. 1) shows this genus arising early in the evolution of this group and is sister to a clade containing all genera except *Aerophilus*, *Alabagrus*, and *Braunsia*.

***Xanthagathis* Sharkey, new genus:** It is sister to *Leuroagathis* in the total evidence tree, but the relationship has a low bootstrap support (Fig. 1; bootstrap value = 64). The pale coloration (particularly the yellow head) is autapomorphic. Other potential autapomorphic states are the hyaline wings and the smooth second median tergite.

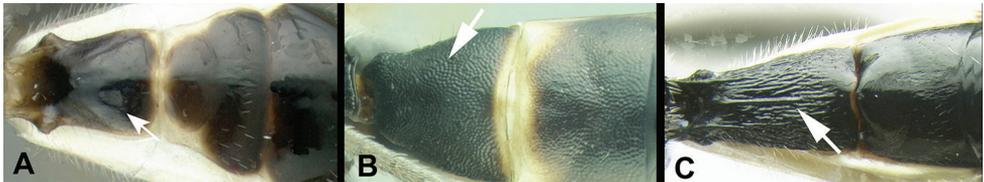
***Zosteragathis* Sharkey, new genus:** There are no obvious morphological synapomorphies for *Zosteragathis* and its monophyly is not supported (Fig. 1). Most species have fine longitudinal striations on the second metasomal median tergite and most have a white transverse band on the same tergite. Neither of these is universal and the striations are found in other genera. Members of *Zosteragathis* are recovered in five separate clades in the total evidence tree (Fig. 1). Monophyly of the genus is not falsified in the total evidence bootstrap tree (not shown) where seven *Zosteragathis* clades fall into a large polytomy that includes all genera in the tree except *Aerophilus*, *Alabagrus*, and *Braunsia*. Although monophyly of *Zosteragathis* is dubious, it seems preferable to the alternative of erecting new genera for weakly supported clades that have little or no morphological or sequence support.

Key to Thai genera of Agathidini

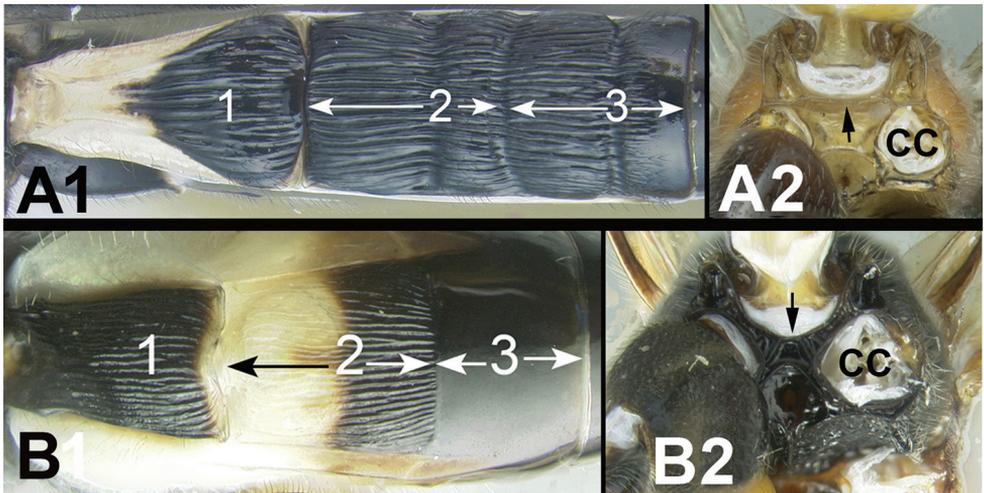
- 1 **A1.** Fore and mid claws cleft. **A2.** Ovipositor variable, often barely exerted or shorter than 1/2 length of metasoma, rarely longer. **Disophrini** and **Cremnoptini**
- **B1.** Fore and mid claws simple with or without a basal lobe. **B2.** Ovipositor longer than 1/2 length of metasoma 2



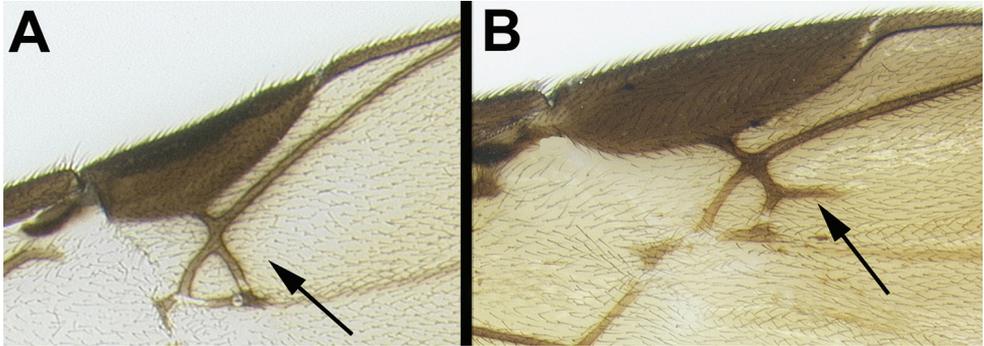
- 2 **A.** Median tergite 1 entirely smooth..... 20
- **B.** Median tergite 1 mostly granulate or coriarius..... 21
- **C.** Median tergite 1 with other sculpture, usually striate 3



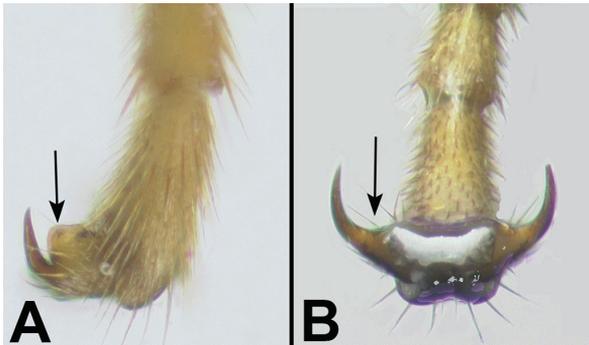
- 3(2) **A1.** Median tergite 3 usually extensively striate in anterior half or more. **A2.** Straight carina situated above hind coxal cavities (CC) 4
- **B1.** Median tergite 3 not extensively striate, usually smooth, or rarely, weakly coriarius. **B2.** If carina exists between hind coxal cavities (CC) then it is curved and dipping below dorsal margin of coxal cavities. 5



- 4(3) A. Adventitious vein (2RS) on r-m crossvein of fore wing absent or indicated only by slight swelling.....*Aerophilus* Szépligeti
 – B. Adventitious vein (2RS) on r-m crossvein of fore wing present & distinct
*Braunsia* Kriechbaumer



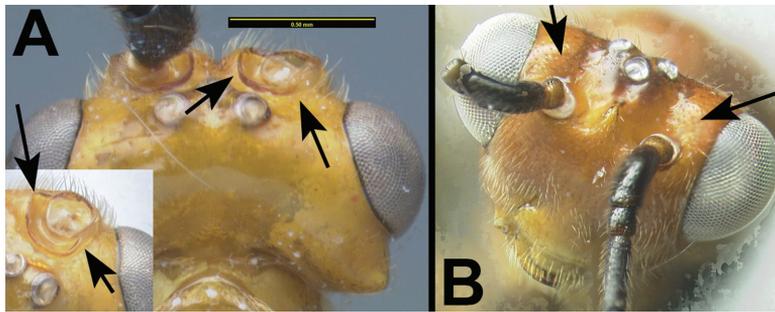
- 5(3) A. Fore and mid tarsal claws with a basal lobe..... 6
 – B. Fore and mid tarsal claws simple *Bassus* Fabricius



- 6(5) A. Mouthparts long, galea significantly longer than wide; gena often elongate.....*Agathis* Latreille
 – B. Mouthparts short (normal), galea not longer than wide; gena not especially elongate 7



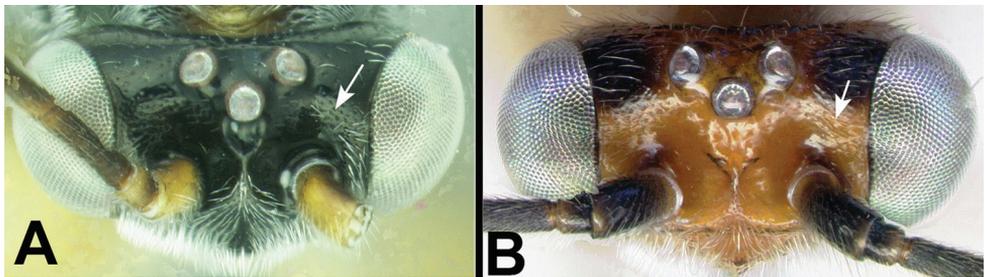
- 7(6) A. With carina partly or completely surrounding antennal socket *Gyragathis* Achterberg & Long
- B. Lacking carina partly or completely surrounding antennal socket 8



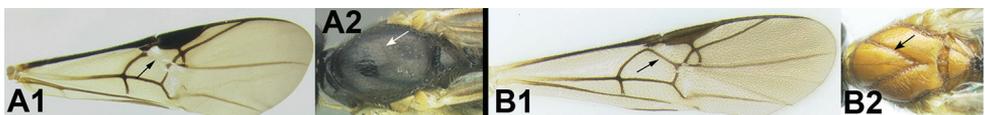
- 8(7) A. Hind trochantellus with ventral longitudinal carinae *Trochantagathis* gen. n.
- B. Hind trochantellus lacking ventral longitudinal carinae 9



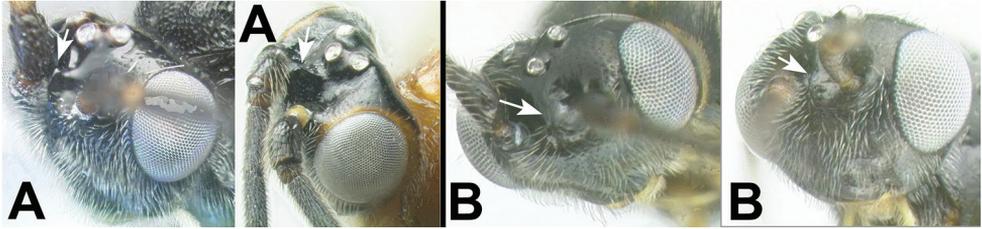
- 9(8) A. Vertex of head smooth, with weak punctures 10
- B. Vertex of head rugosopunctate *Scabagathis* gen. n.



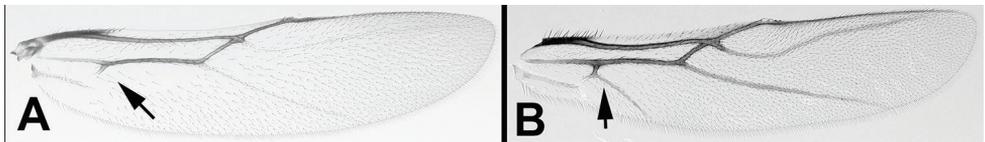
- 10(9) A1. RS+M vein of fore wing mostly or entirely absent. A2. Notauli present ... 11
- B1. RS+M vein of fore wing present and complete. B2. Notauli absent *Earinus* Wesmael



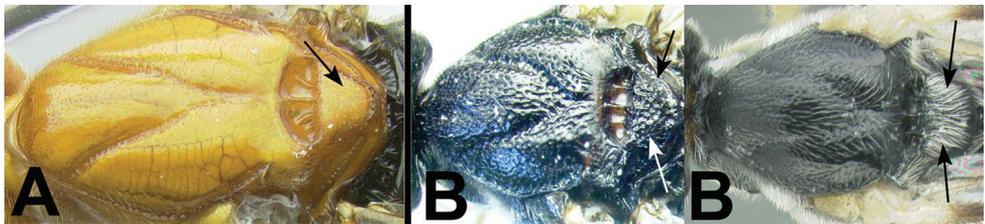
- 11(10) A. Sharply declivous crest in interantennal space present..... 12
 – B. Sharply declivous crest in interantennal space absent..... 14



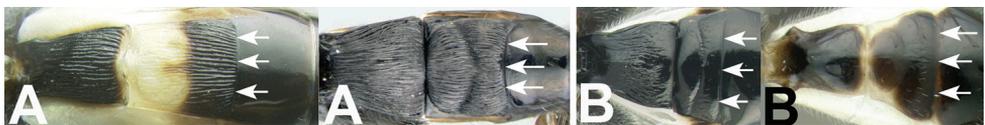
- 12(11) A. Cub vein of hind wing absent, or if present, clear and weak, not tubular, and not contiguous with cu-a (base) 13
 – B. Cub vein of hind wing present, tubular and pigmented.....
 *Therophilus anuchati* Sharkey



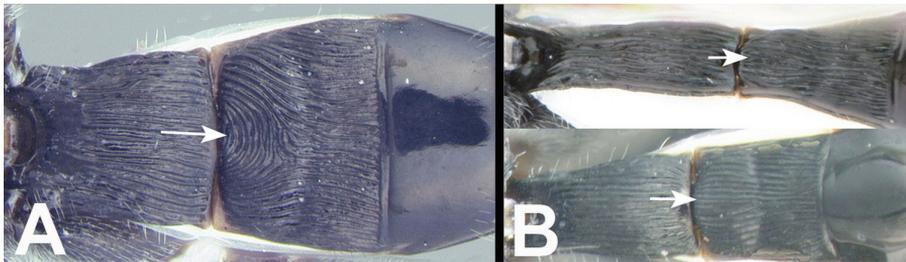
- 13(12) A. Scutellar triangle smooth with punctures and sparse setae
 *Agathacrista* Sharkey
 – B. Scutellar triangle rugose or with dense aciculations, sometimes obscured
 with dense setae *Chimaeragathis* gen. n.



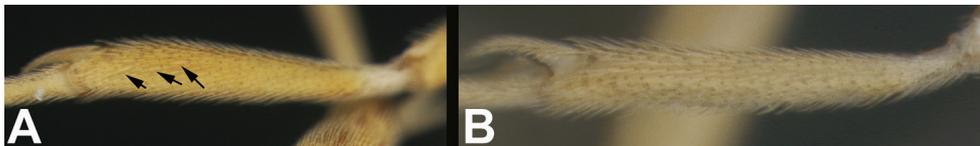
- 14(11) A. Median tergite 2 mostly striate with striae coming to an abrupt and uni-
 form end at or near apex of tergite 15
 – B. Median tergite 2 striate or not; if striate, striae not coming to an abrupt
 and uniform end at apex of tergite 17



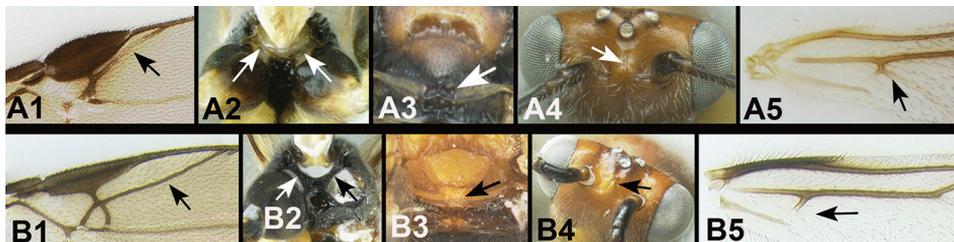
- 15(14) **A.** Semicircular striae at base of median tergite 2 present.....*Cymagathis* gen. n.
- **B.** Semicircular striae at base of median tergite 2 not present 16



- 16(15) **A.** Pegs of fore tibia present (concolorous with tibia therefore difficult to see).....*Asperagathis* gen. n.
- **B.** Pegs of fore tibia absent *Zosteragathis* gen. n.

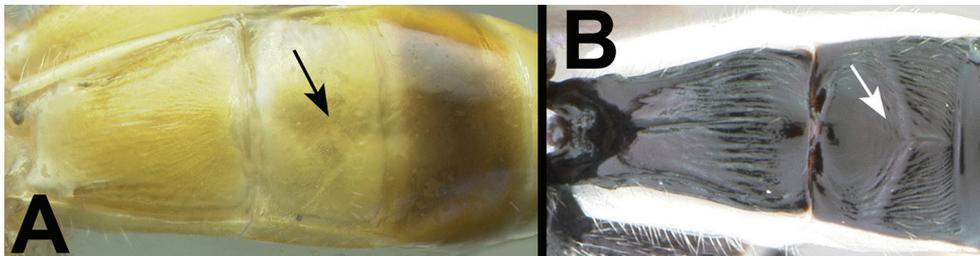


- 17(14) With two or more of the following characters: **A1.** Rs vein of fore wing weak medially and bent: **A2.** Sclerite separating hind coxal cavities from metasomal foramen narrow or absent. **A3.** Apex of scutellum (at border with metanotum) with a distinct, often semicircular, depression. **A4.** Interantennal space often with two small protrusions separated by a depression (use frontal view). **A5.** Cub vein of hind wing pigmented and tubular where it is attached to subbasal cell and causing an angle in the distal margin of the cell where it is attached. Note: often (70%) small and pale in coloration..... *Therophilus* Wesmael
- With none or at most one of the above character states. Rather the following character states apply: **B1.** Rs vein of fore wing evenly sclerotized and straight. **B2.** Sclerite separating hind coxal cavities from metasomal foramen relatively wide. **B3.** Apex of scutellum (at border with metanotum) smooth or sculptured but lacking deep depression(s). **B4.** Interantennal space without two small protrusions separated by a depression (use frontal view), rather smooth, or with a median keel that may or may not be pronounced. **B5.** Cub vein of hind wing absent, OR not attached to basal cell, OR not pigmented, and subbasal cell not angled at point of intersection. Note: often (70%) small and pale in coloration Note: body usually mostly melanic 18

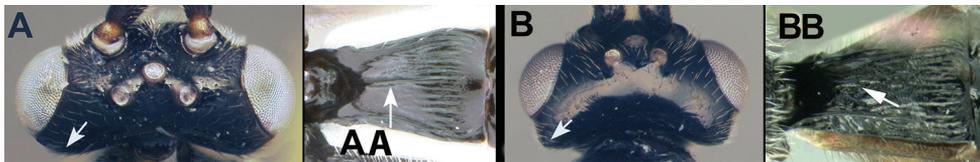


Key I Figure 18. lorem ipsum

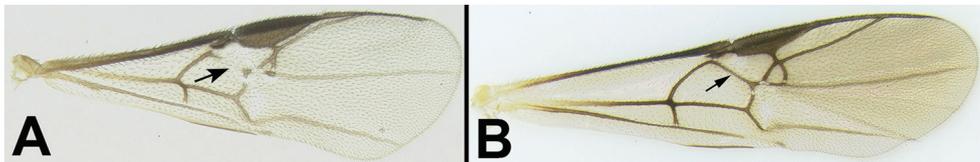
- 18(17) **A.** Median tergite 2 partly or entirely white, ivory, or pale yellow.....
 *Xanthagathis* gen. n.
 – **B.** Median tergite 2 entirely melanic 19



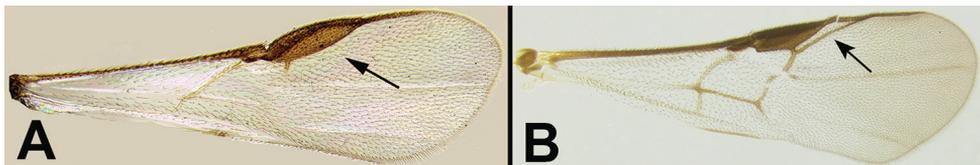
- 19(18) **A.** Temples rounded. **AA.** Median longitudinal ridge of first median tergite present..... *Liragathis* gen. n.
 – **B.** Temples squared. **BB.** Median longitudinal ridge of first median tergite absent *Agathigma* gen. n.



- 20(2) **A.** RS+M vein of fore wing mostly or entirely absent ... *Leuroagathis* gen. n.
 – **B.** RS+M vein of fore wing present and complete *Earinus* Wesmael



- 21(2) **A.** RS vein of fore wing completely absent *Aneurobracon* Brues
 – **B.** RS vein of fore wing present, though sometimes interrupted at midlength *Camptothlipsis* Enderlein



Descriptions

Note: The text in bold font in the diagnoses below show a minimum set of character states to distinguish the taxon. The numbers preceded with the letter H are unique identifiers associated with each specimen.

Agathigma Sharkey, gen. n.

<http://zoobank.org/BF65FFF9-3E72-4294-ABB1-F20BD2027EE5>

Type species. *Agathigma templei* Sharkey, sp. n.

Etymology. *Aga* (from *Agathis*); *thigma* is Greek for touch, here used as a reference to the reduced 2-segmented palpi. Feminine.

Diagnosis. Body except for fore and mid legs black, hind leg entirely black. Fore wing slightly infusate in distal half. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly approaching the median ocellus. **Temple squared in dorsal view. Labial palpus reduced to 2 segments; presumably palpomere 3 is one of the two lost palpomeres.** Notauli depressed and partly or entirely pitted. Scutellar triangle smooth with weak sparse punctures. Ventral margin of hind coxal cavities situated below dorsal margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae. **Second submarginal cell of fore wing minute, cell about the same diameter as wing veins.** First median tergite almost entirely irregularly striate, lateral longitudinal carina prominent. Second median tergite slightly wider than long and entirely smooth with hints of short striae and some very weak coriarius microsculpture.

Distribution and diversity. Known only from the type specimen collected in Mae Wong National Park, Thailand.

***Agathigma templei* Sharkey, sp. n.**

<http://zoobank.org/983A6820-7326-4051-9683-5A35EDD0BE93>

Etymology. Named after Jimmy Temple, childhood friend of the first author; the fact that the temples are squared may be coincidental.

Diagnosis. Body length 4.7 mm. Ovipositor length/body length ratio = 1.0. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly approaching the median ocellus. Antenna with 30 flagellomeres. Labial palp reduced, 2-segmented. Notauli pitted anteriorly, smooth posteriorly where they converge. Scutellar triangle and its posterior surface unusually smooth. Scutellar groove with 1 longitudinal ridge. Fore tibia lacking spines or pegs; mid tibia with 3 pegs; hind tibia with 5 pegs. Basal lobe of tarsal claws large and right-angled, claw only extending slightly beyond apex of lobe. RS vein of fore wing slightly sinuate. Second submarginal cell minute. Hind tibial spurs melanic. Hind tibia entirely melanic. Cu-a crossvein of hind wing bent at point where it is intersected by vein Cub.

Specimens examined. Holotype 2♀♀ (H415): THAILAND, Kamphaeng Phet, Mae Wong NP Chong Yen, 16°5.212'N, 99°6.576'E, 1306 m, Malaise trap, 20–27. viii.2007, Piluek C. & Inpuang A. leg.

Distribution. Known only from the type specimen collected in Mae Wong National Park, Thailand. For a distribution map go to: <http://bit.ly/22WV8JD>

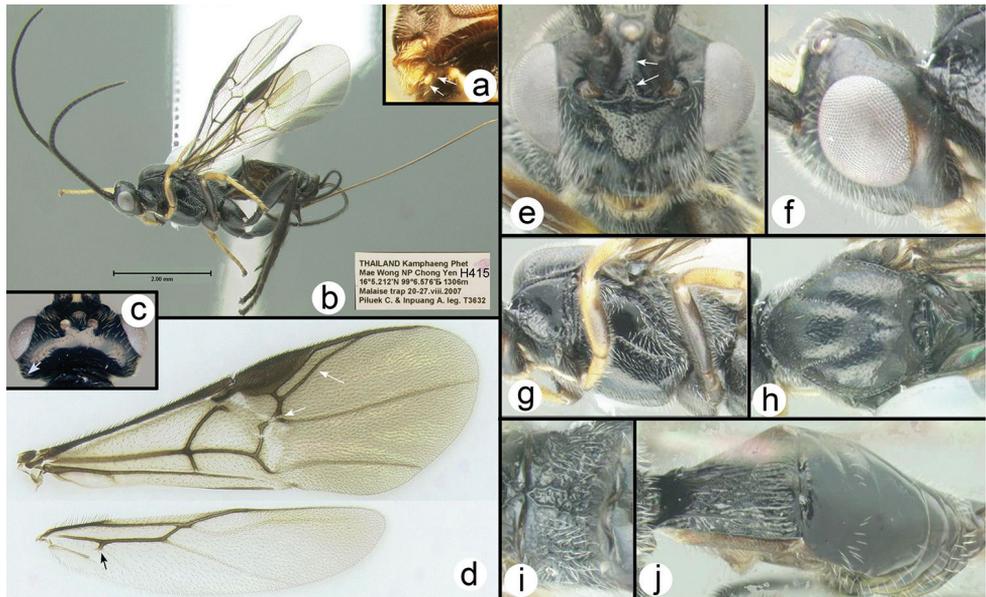


Figure 2. *Agathigma templei* holotype female: **a** labial palpus, arrows indicate the two palpomeres **b** lateral habitus **c** dorsal head **d** wings; arrows from top to bottom indicate: RS vein; minute second submarginal cell; angle in cu-a crossvein of hind wing **e** anterodorsal head, arrows indicate ridge between antennae **f** lateral head **g** lateral mesosoma **h** dorsal mesonotum **i** dorsal propodeum **j** dorsal metasoma.

Asperagathis Sharkey, gen. n.

<http://zoobank.org/DF7D4C7E-A82A-4F34-8226-6B850C3F07EC>

Type species. *Asperagathis xesta* Sharkey, sp. n.

Etymology. *Asper* is Latin for rough; here it is in reference to the rugose sculpture on the thoracic pleura of members of the genus. Feminine.

Diagnosis. Body predominantly black; head including orbits of eyes black; dorsal apex of pronotum pale yellow or yellowish brown; metasomal terga all black. Fore wing slightly infusate in apical half or entirely clear/hyaline. Antennal sockets not margined with carinae. Interantennal space with a shallow crest; between the crest and the median ocellus there is a triangular depression flanked by weak smooth carinae. Temple rounded in dorsal view. Third labial palpomere not greatly reduced, about 1/2 as long as apical palpomere. Notauli depressed and entirely sculptured. **Mesoscutum with more rough sculpture than most genera, especially posteriorly near junction of notauli.** Scutellar triangle rugose or with deep sparse punctures. **Sternaulus completely sculptured to epicnemium, metapleuron covered in rough sculpture.** Ventral margin of hind coxal cavities situated below dorsal margin of metasomal foramen. Spines or pegs on anterior surface of fore tibia present or absent. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing varying from minute, cell about the same diameter as wing veins, to petiolate with petiole slightly longer than cell diameter. First median tergite mostly to about 1/2 irregularly striate, lateral longitudinal carina prominent. Second median tergite slightly wider than

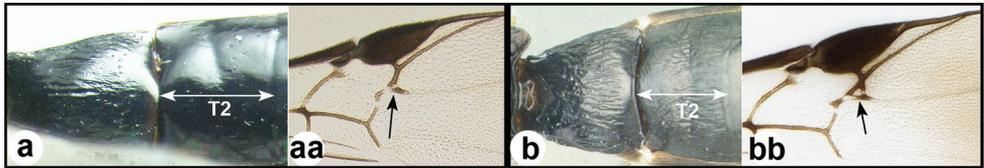
long and entirely smooth with some very weak coriarius microsculpture, varying to almost entirely irregularly longitudinally striate, with striae terminating evenly near apex of tergite.

Distribution and diversity. Thailand, but undoubtedly more widespread.

Biology. Unknown.

Key to the Thai species of *Asperagathis*

- 1 a. Metasomal median tergite 2 mostly or entirely smooth. aa. Second submarginal cell minute, diameter about equal to thickness of surrounding wing veins *Asperagathis xesta* Sharkey, sp. n.
 – b. Metasomal median tergite 2 mostly rugosostriate. bb. Second submarginal cell normal (wider than below), diameter much wider than thickness of surrounding wing vein..... *Asperagathis aspera* Sharkey, sp. n.



Asperagathis aspera Sharkey, sp. n.

<http://zoobank.org/898E350A-2A6F-4901-913F-7C04054FC4BB>

Etymology. *Asper* is Latin for rough and refers to the sculpture of the second metasomal median tergite.

Diagnosis. Body length 7.6 mm; ovipositor length/body length ratio = 1.0. Inter-antennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short carinae that diverge to either side of the median ocellus. Antenna with 38 flagellomeres. 3rd labial (penultimate) palpomere long, about ½ as long as apical palpomere. Scutellar groove with 3-4 longitudinal ridges. Fore tibia with about 9 thickened spines concolorous with normal setae; mid tibia with 7 pegs; hind tibia with 8 pegs.

Specimens examined. Holotype ♀ (H274): THAILAND, Phetchabun, Thung Salaeng Luang NP, Pine forest; Gang Wang Nam Yen, 16°35.789'N, 100°52.769'E, 732 m, Malaise trap, 15–22.vi.2007, Pongpitak & Sathit leg.

Distribution. Known only from the type specimen collected in Thung Salaeng Luang National Park, Thailand. For a distribution map go to: <http://bit.ly/1T5FqXj>

Asperagathis xesta Sharkey, sp. n.

<http://zoobank.org/A2028B25-6FEF-45D6-980E-A1375A966D5F>

Etymology. *Xestos* is Greek for smooth and refers to the smooth second metasomal median tergite.

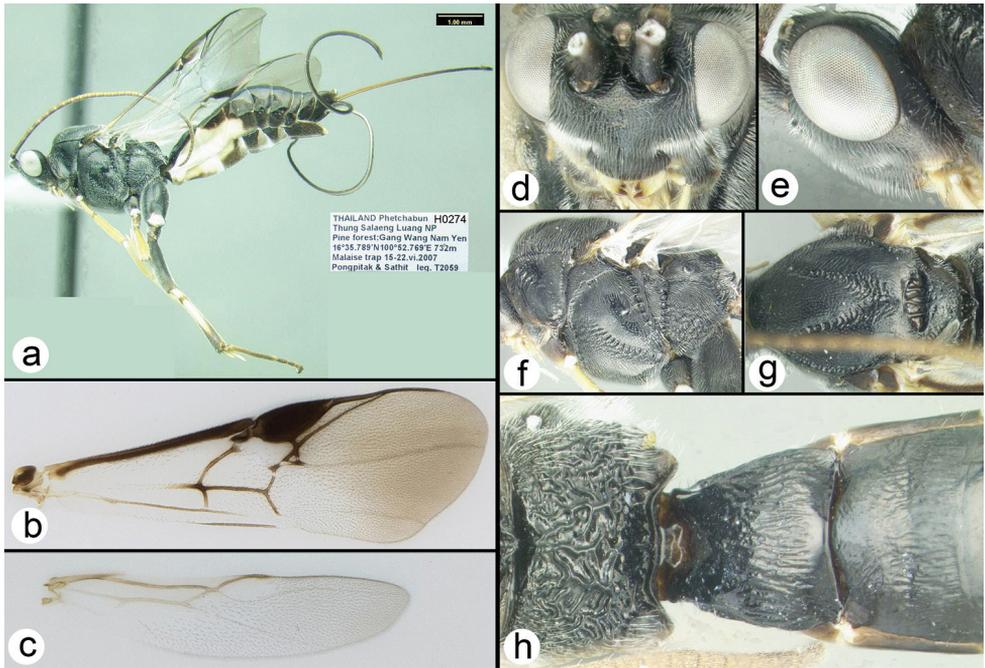


Figure 3. *Asperagathis aspera*, holotype female: **a** lateral habitus **b** fore wing **c** hind wing **d** dorsal head **e** lateral head **f** lateral mesosoma **g** dorsal thorax **h** propodeum and metasomal terga 1-2.

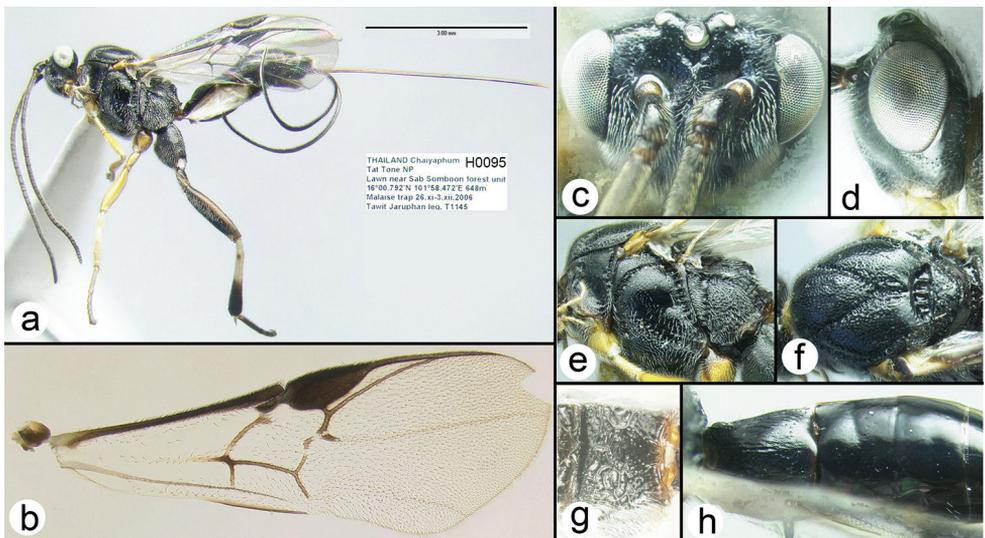


Figure 4. *Asperagathis xesta* Holotype female: **a** lateral habitus **b** fore wing **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1-3.

Diagnosis. Body length 4.5 mm; ovipositor length/body length ratio = 1.1. Inter-antennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short carinae that diverge to either side of the median ocellus.

Antenna with 32 flagellomeres. 3rd labial (penultimate) palpomere long, more than ½ as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking thickened spines; mid tibia with 6 pegs; hind tibia with 10 pegs.

Specimens examined. **Holotype** ♀ (H095): THAILAND, Chaiyaphum, Tat Tone NP, Lawn near Sab Somboon forest unit, 16°0.792'N, 101°58.472'E, 648m, Malaise trap, 26.xi–3.xii.2006, Tawit Jaruphan leg. **Paratype** ♀ (H1682): Same data as holotype.

Distribution. Known only from the type specimens collected in Tat Tone National Park, Thailand. For a distribution map go to: <http://bit.ly/1VPL5H8>

***Chimaeragathis* Sharkey, gen. n.**

<http://zoobank.org/19BD7E73-FE7C-4947-B3B2-4B2F5C32E41C>

Type species. *Chimaeragathis eurysoma* Sharkey, sp. n.

Etymology. Chimaera is a mythological Greek monster with a goat's body, lion's head, and serpent's tail. In this case, the name is a reference to the many diagnostic characters of the genus which are a combination of features each of which diagnoses other agathidine genera, e.g., crest between antennae, fore tibia with thickened spines. Feminine.

Diagnosis. Metapleuron, scutellum, and all but median cell of propodeum thickly setose. Head, including orbits of eye, black; mesosoma black; metasoma variable. Fore wing slightly infuscate in apical half or entirely clear/hyaline. Antennal sockets not margined with carinae. Interantennal space with a high crest that is sharply declivous posteriorly; between the crest and the median ocellus there is a triangular depression flanked by weak smooth carinae. Temple rounded in dorsal view. Third labial palpomere small, less than 1/3 length of apical palpomere. Notauli depressed and partly or entirely pitted. **Scutellar triangle rugose.** Ventral margin of hind coxal cavities situated below dorsal margin of metasomal foramen. Pegs on anterior surface of fore tibia present. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing varying from minute, cell about the same diameter as wing veins, to petiolate with petiole longer than cell diameter. First median tergite partly or mostly irregularly striate to rugosostriate, otherwise smooth; lateral carina present, sometimes weak; median carina present, sometimes weak. Second median tergite wider than long and smooth or mostly smooth with some irregular striae.

Distribution and diversity. Undescribed species are found in other Southeast Asian countries.

Biology. Unknown.

Key to Thai species of *Chimaeragathis*

- 1 **a.** Hind femur yellow; hind tibia mostly yellow
 *Chimaeragathis lohmani* Sharkey, sp. n.

- b. Hind femur yellow laterally at mid length, black basally and apically, hind tibia black. *Chimaeragathis chrysona* Sharkey, sp. n.
- c. Hind femur black; hind tibia mostly black with pale patches basally
..... *Chimaeragathis eurysoma* Sharkey, sp. n.



Chimaeragathis chrysona Sharkey, sp. n.

<http://zoobank.org/46EB8961-A3DE-4951-B077-459C9F7481F5>

Etymology. *Chrysona* is Greek for an object made of gold and is a reference to the gold colored setae on the mesosoma.

Diagnosis. Body length 6.9 mm; ovipositor length/body length ratio = 0.8. Antenna with 42 flagellomeres. Third labial (penultimate) palpomere about 1/3 as long as apical palpomere. Propleuron convex, lacking distinct bump. Scutellar groove with 3 longitudinal ridges. Fore tibia with 2 pegs; mid tibia with 5 pegs; hind tibia with 4 pegs. Basal lobe of tarsal claws large, right-angled; claw extending slightly beyond apex of lobe.

Specimens examined. Holotype ♀ (H710): THAILAND, Petchaburi, Kaeng Krachan NP km33/helipad, 12°50.177'N, 99°20.688'E, 735 m, Malaise trap, 18-25.v.2009, Sirichai leg.

Distribution. Known only from the type specimen collected in Kaeng Krachan National Park, Thailand. For a distribution map go to: <http://bit.ly/29nOQIL>

Chimaeragathis eurysoma Sharkey, sp. n.

<http://zoobank.org/664E801F-8A72-40E1-99A6-48FC848F974B>

Etymology. *Eurys* is Greek for wide; *soma* is Greek for body. The species name refers to the wide metasoma of this species.

Diagnosis. Body length 4.8 mm; ovipositor length/body length ratio = 0.7. Antenna with 34 flagellomeres. Third labial (penultimate) palpomere about 1/3 as long as apical palpomere. Propleuron convex, lacking distinct bump. Scutellar groove with 3 longitudinal ridges. Fore tibia with 3 pegs; mid tibia with 4 pegs; hind tibia with 3 pegs. Basal lobe of tarsal claws large, right-angled; claw extending slightly beyond apex of lobe.

Specimens examined. Holotype ♀ (H925): THAILAND, Petchaburi, Kaeng Krachan NP, km33/helipad, 12°50.177'N, 99°20.688'E, 735 m, Malaise trap, 25.i-4.

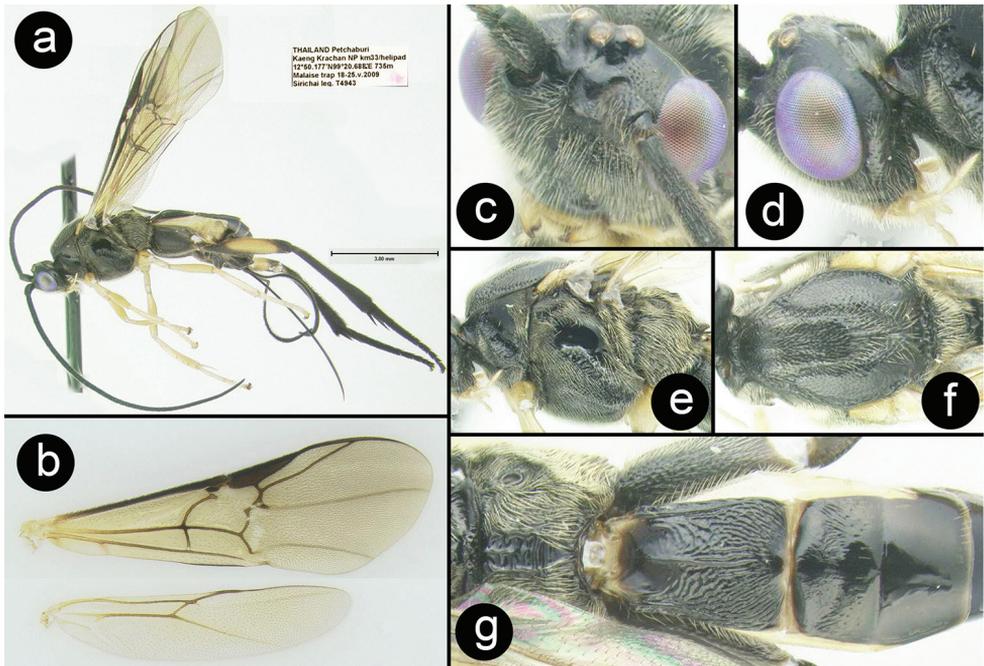


Figure 5. *Chimaeragathis chrysuma* holotype female: **a** lateral habitus **b** wings **c** anterolateral head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum and metasomal terga 1-3.

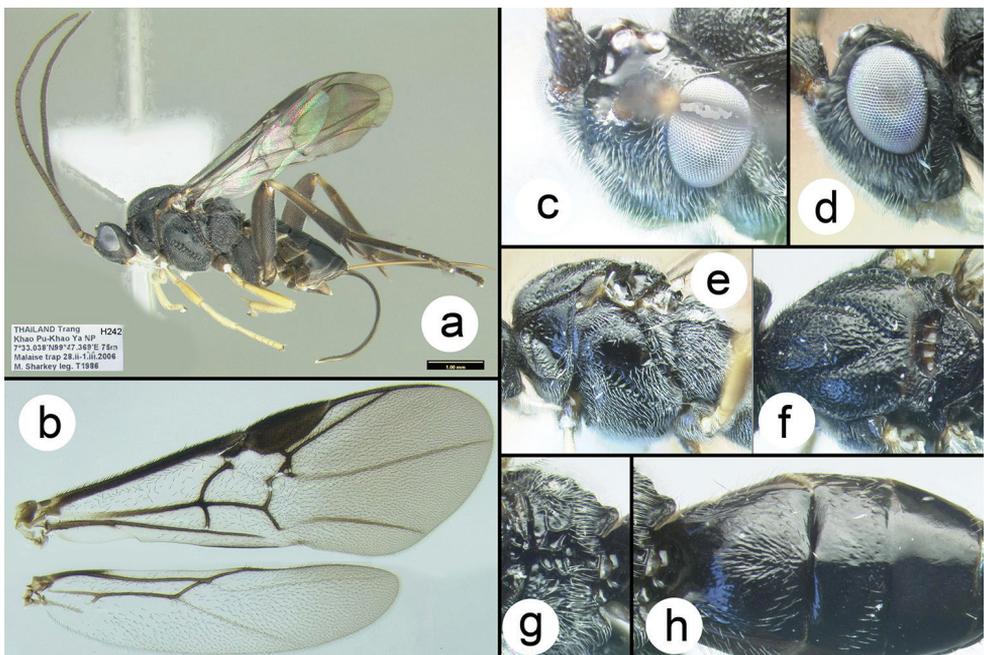


Figure 6. *Chimaeragathis eurysuma*, female paratypes: **a** lateral habitus **b** wings **c** anterolateral head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1-3.

ii.2009, Sirichai leg. **Paratypes:** THAILAND: ♀ (H321), Prachuab Khiri Khan, Khao Sam Roi Yot NP Khao Look Glang 12°6.414'N, 99°57.292'E, Malaise trap, 28.ix–5.x.2008, Yai Amnad leg. ♀ (H242), Trang, Khao Pu-Khao Ya NP, 7°33.038'N, 99°47.369'E, 75 m, Malaise trap, 28.ii–1.iii.2006 M Sharkey leg. ♀ (H649), Chanthaburi, Khao Khitchakut NP, nature trail/fern, 12°50.55'N, 102°7.3'E, 50 m, Malaise trap, 1–8.v.2009, Suthida Charoenchai leg. ♀ (H335), Chanthaburi, Khao Khitchakut NP, nature trail/Banyan tree, 12°50.54'N, 102°7.31'E, 90 m, Malaise trap, 1–8.v.2009, Suthida Charoenchai leg. ♀ (H045), Trang, nr. nam Tok Ton Prew Kae Chong, MT, 140 m, 7°33.15'N, 99°47.38'E, 28.i–3.ii.2005 D Lohman. ♀ (H069), Trang, nr. nam Tok Ton Prew Kae Chong, MT, 140 m, 7°33.15'N, 99°47.38'E, 4–11.ii.2005 D Lohman.

Distribution. Known only from the type specimens collected in Thailand. For a distribution map go to: <http://bit.ly/1WNrlTX>

***Chimaeragathis lohmani* Sharkey, sp. n.**

<http://zoobank.org/54EB7934-9C28-47C5-924C-ECD9A8425A41>

Etymology. Named after David Lohman, who collected one of the specimens in the type series and who serviced Malaise traps in Trang Province for many months.

Diagnosis. Body length 6.2 mm; ovipositor length/body length ratio = 0.8. Antenna with 39 flagellomeres. Third labial (penultimate) palpomere about 1/3–1/2 as long as apical palpomere. Propleuron convex, lacking distinct bump. Scutellar groove with 3 longitudinal ridges. Fore tibia with 1 peg; mid tibia with 3 pegs; hind tibia with 4 pegs. Basal lobe of tarsal claws large, right-angled; claw extending slightly beyond apex of lobe.

Specimens examined. Holotype ♀ (H072), THAILAND, Trang, Ampuh Nayong Khaochong, 7°33.038'N, 99°47.369'E, 75 m, 14–16.ii.2005, Mal. trap D Lohman. **Paratypes:** THAILAND: ♀ (H077), Trang, Khaochong, 7°33.038'N, 99°47.369'E, 75 m, 13.vi.2005, Mal. trap. ♀ (H412), Surat Thani, Khao Sok NP Klong Morg Unit, 8°53.725'N, 98°39.025'E, 87 m, Malaise trap, 10–17.ii.2009, Pongphan leg. Malaysia: 2♀♀ (H5932, H5935), Perlis, Wang Kelian, 6°40'40.94"N, 100°11'23.94"E, 2008, Sharkey and Norliyana.

Distribution. Known only from the type specimens collected in northern Malaysia and southern Thailand. For a distribution map go to: <http://bit.ly/1r7TE3x>

***Cymagathis* Sharkey, gen. n.**

<http://zoobank.org/5B95835D-D202-428C-BFAF-C3D8564B55B1>

Type species. *Cymagathis krikoma* Sharkey, sp. n.

Etymology. *Cymato* is Greek for wave; here it is a reference for the uniform, large, wave-like striae on metasomal median tergite 2. Feminine.

Diagnosis. Body predominantly black, mesosoma all black, metasomal terga all black, head black except posterior orbit of eyes partly orange. Fore wing slightly infusate in apical

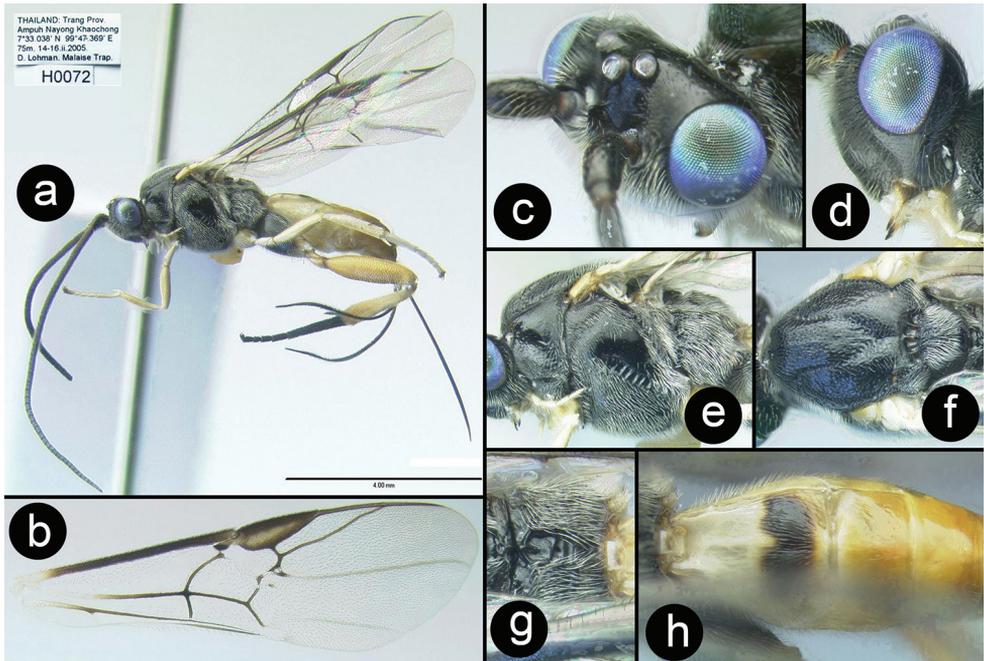


Figure 7. *Chimaeragathis lohmani*. **a** and **c–h** Holotype female **b** fore wing of paratype H412 **c** antero-lateral head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1–3.

half. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly approaching the median ocellus. Temple rounded in dorsal view. Third labial palpomere not greatly reduced, more than 1/2 as long as apical palpomere. Notauli depressed and partly or entirely pitted. Scutellar triangle with dense punctures or aciculations. Ventral margin of hind coxal cavities situated below dorsal margin of metasomal foramen. Pegs on anterior surface of fore tibia present. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing minute, cell about the same diameter as wing veins. First median tergite evenly and completely covered in strong striae, lateral carinae strong but partly obscured by sculpture. Second median tergite wider than long. **Second median tergite entirely covered with strong striae that end evenly at apex of tergite; striae forming semicircular pattern anteromedially.**

Distribution and diversity. Known only from the type species in Thailand but probably widespread throughout Southeast Asia.

Biology. Unknown

***Cymagathis krikoma* Sharkey, sp. n.**

<http://zoobank.org/78E27E64-BCA3-42D8-B0A9-AF01715ED249>

Etymology. *Krikoma* is Greek for ring and refers to the half ring-shaped carina on median tergite two.

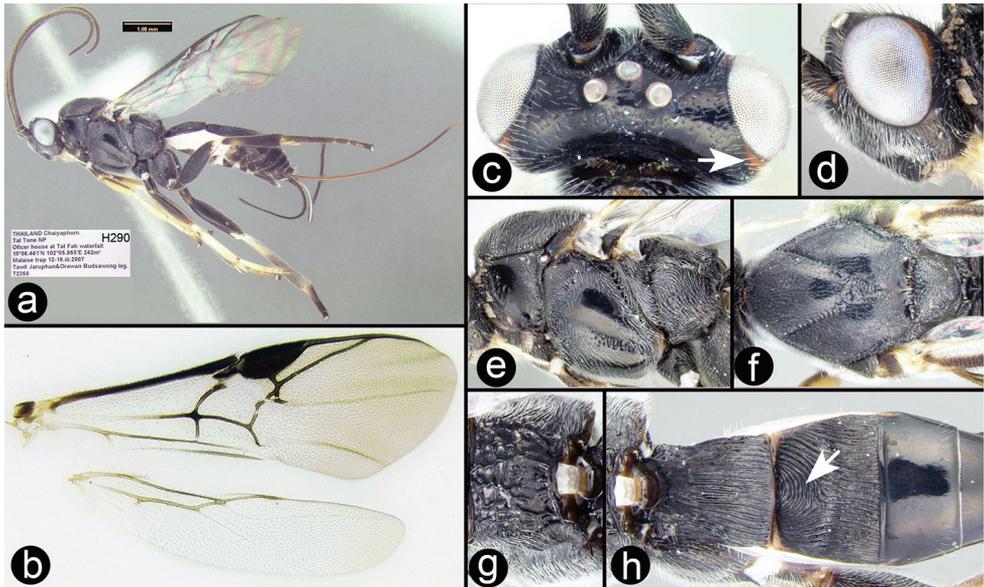


Figure 8. *Cymagathis krikoma* paratype female: **a** lateral habitus **b** wings **c** dorsal head, arrow indicating orange posterior orbit **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1-3, arrow indicating semicircular carina on median tergite 2.

Diagnosis. Body length 6.0 mm; ovipositor length/body length ratio = 0.9. Scutellar groove with 3 longitudinal ridges. Fore tibia with 4 thickened melanic spines; mid tibia with 3 pegs; hind tibia with 4 pegs. Flagellomeres rather pale colored. Posterior orbit of eye orange. Sternaulus deeply sculptured and long. Metapleuron rugose over most of surface.

Specimens examined. **Holotype** ♀ (H276), THAILAND, Chaiphaphum, Tat Tone NP, Water tank at Tat Fah waterfall, 15°56.468'N, 102°5.855'E, 245 m, Malaise trap, 19–26.iii.2007, Tawit Jaruphan & Orawan Budsawong leg. **Paratypes:** THAILAND: ♀ (H290), Chaiphaphum, Tat Tone NP, Officer house at Tat Fah waterfall, 15°56.461'N, 102°5.955'E, 242 m, Malaise trap, 12–19.iii.2007, Tawit Jaruphan & Orawan Budsawong leg. ♀ (H5924), Chaiphaphum, Tat Tone NP, Forest fire Protection station, 16°0.809'N, 102°1.335'E, 195 m, Malaise trap, 3–9. vi.2006, Tawit Jaruphan & Orawan Budsawong leg. ♀ (H2401), Phetchabun, Nam Nao NP Check point, 16°43.695'N, 101°33.797'E, 921 m, Malaise trap, 5–12.v.2007, Leng Janteab leg. ♀ (H483), Mae Hong Son, Namtok Mae Surin NP, Haad Saen, 19°20.857'N, 97°59.123'E, Malaise trap, 27.iv–4.v.2008, Na-maadkam, leg.

Distribution. Known only from the specimens collected in Thailand but *Bassus transtriatus* (Bhat and Gupta) from Philippines may belong here. For a distribution map go to: <http://bit.ly/1SWUYfQ>

Gyragathis Achterberg & Long, 2010

Diagnosis. Antennal sockets margined, completely or at least laterally and medially, with carinae. Interantennal space with a longitudinal depression bordered by carinae. **Temples squared in dorsal view.** Third labial palpomere minute, barely visible, much smaller than apical palpomere. Notauli depressed and partly or entirely pitted. Scutellar triangle smooth or **rugose.** Ventral margin of hind coxal cavities situated below or in line with dorsal margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae

Distribution and diversity. There are four species, all of which are restricted to the Oriental region (Taiwan, Philippines, and Viet Nam, Thailand). The three previously described species may be distinguished most easily from *G. leucosoma* sp. n. by the extensive pale color (yellow to orange) on their mesonota. Achterberg and Long (2010), described the genus *Gyragathis* and the new species *G. guyi* from Viet Nam. They also transferred three species to the new genus, viz. *G. angulosa* (Bhat & Gupta, 1977) *G. parallela* (Chou & Sharkey, 1989) and *G. daanyuanensis* (Chen & Yang, 2006). The species described here *G. leucosoma*, is strikingly different from other members of the genus in aspects of sculpture, dimensions, and color, and may belong in its own genus. Molecular data for the described species are lacking to confirm or refute this suspicion.

New combinations. *Gyragathis sabahensis* (Bhat and Gupta), comb. n., from *Agathis*. Contrary to Achterberg and Long (2010) *B. daanyuanensis* (Chen & Yang, 2006) is a member of *Therophilus*, *Therophilus daanyuanensis* comb. n.

Biology. Unknown.

Gyragathis leucosoma Sharkey, sp. n.

<http://zoobank.org/FECBAA53-5CAD-4F8D-9394-6B6A531A5265>

Etymology. *Leucosoma* is Greek for white body. The species name refers to the dense white setae on the metapleuron.

Diagnosis. Body length 6.1 mm; ovipositor length/body length ratio = 0.9. Antenna missing after 28th flagellomere. Third labial (penultimate) palpomere about 1/3 as long as apical palpomere. Propleuron with distinct bump near ventral margin. Scutellar groove with 5 longitudinal ridges. Fore tibia without pegs or thickened spines; mid tibia with 6 pegs; hind tibia with 13 pegs.

Biology. Unknown.

Specimens examined. Holotype ♀ (H275), THAILAND, Nakhon Nayok, Khao Yai NP, Lum Ta Kong View Point, 14°25.762'N, 101°23.527'E, 732 m, Malaise trap, 12–19.iv.2007, Wirat Sukho leg.

Distribution. Known only from the type specimen collected in Khao Yai National Park, Thailand. For a distribution map go to: <http://bit.ly/1SWVgDh>

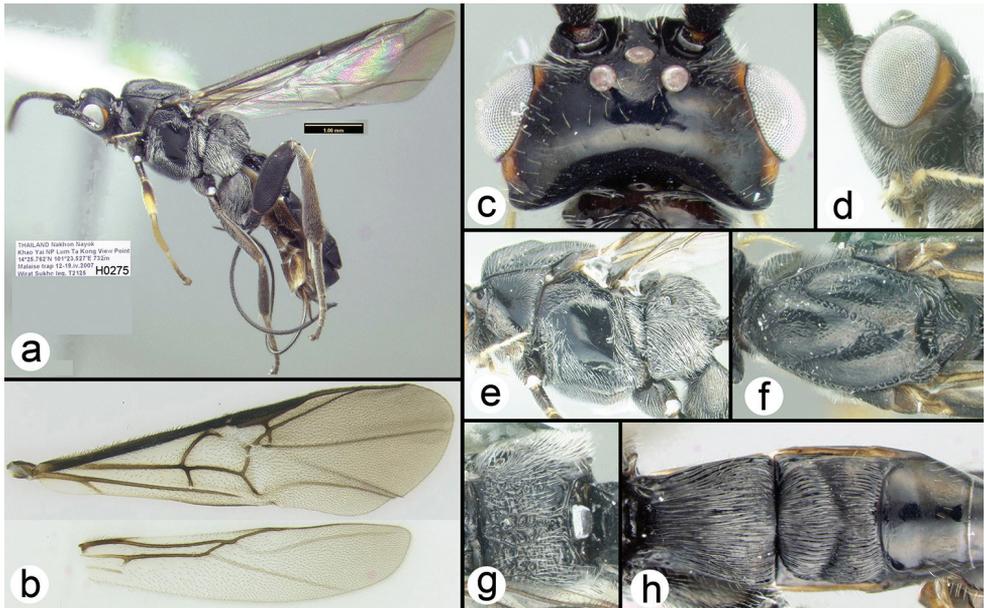


Figure 9. *Gyragathis leucosoma*, female holotype. **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1-3.

***Leuroagathis* Sharkey, gen. n.**

<http://zoobank.org/9B9284AB-0B40-4B80-8A81-851E04E8C174>

Type species. *Leuroagathis paulbakeri* Sharkey, sp. n.

Etymology. *Leuros* is Greek for smooth, level, polished and refers to the lack of notauli and smooth metasomal terga. Feminine.

Diagnosis. Head and mesosoma orange and black (head with black in ocellar triangle only); metasomal terga predominantly black with some white. Fore wing slightly infusate in apical half. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short indistinct carinae that approach the median ocellus. Temple rounded in dorsal view. Third labial palpomere small, less than 1/3 length of apical palpomere. **Notauli completely absent.** Scutellar triangle smooth with weak sparse punctures. Ventral margin of hind coxal cavities situated below dorsal margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing minute, cell about the same diameter as wing veins. First median tergite **smooth, lacking microsculpture and carina.** Second median tergite wider than long. Second median tergite smooth.

Distribution and diversity. Known only from the type species from Thailand. The few Australian Agathidini for which we have COI data do not belong here.

Biology. Unknown.

***Leurogathis paulbakeri* Sharkey, sp. n.**

<http://zoobank.org/5AEB324A-084A-48DF-9FC1-FBDEA27D954A>

Etymology. Named in honor of Mr. Paul Baker who obtained the highest mark (100%) in the written exam of Ent. 770 in the fall of 2015.

Diagnosis. Body length 4.5 mm; ovipositor length/body length ratio = 0.8. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short carinae that approach the median ocellus. Antenna with 29 flagellomeres. Third labial (penultimate) palpomere small but easily visible, much smaller than apical palpomere. Scutellar groove with 6 longitudinal ridges. Fore tibia with 7–8 thickened spines; mid tibia with 9 pegs; hind tibia with 12 pegs. First median tergite produced laterally around spiracles. Second median tergite widened apically.

Specimens examined. Holotype ♀ (H369), THAILAND, Prachuab Khiri Khan, Khao Sam Roi Yot NP, foot of Khao Taen, 12°8.75'N, 99°57.988'E, 1 m, Malaise trap, 17–24.v.2009, Yai Amnad leg.

Distribution. Known only from the type specimen collected in Khao Sam Roi Yot National Park, Thailand. For a distribution map go to: <http://bit.ly/29hEQ95>

***Liragathis* Sharkey, gen. n.**

<http://zoobank.org/70594E06-7AC3-4C4F-96EA-6E95B3F5FE3C>

Type species. *Liragathis baonai* Sharkey, sp. n.

Etymology. *Lira* is Latin for ridge, as in the ridge made by a plow in the earth; it is a reference to the median longitudinal ridge on the first metasomal median tergite. Feminine.

Diagnosis. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly approaching the median ocellus. Temple rounded in dorsal view. Third labial palpomere, about 1/2 length of apical palpomere. Notauli depressed and partly or entirely pitted. Scutellar triangle smooth or rugose. Dorsal margin of hind coxal cavities situated above ventral-most margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing varying from minute, cell about the same diameter as wing veins, to petiolate with petiole longer than cell diameter. **First median tergite** mostly with irregular striae, lateral and **median carinae strong**. Second median tergite wider than long. Second median tergite from mostly smooth with weak striae restricted to transverse depression, to almost completely striate; in the two species the mostly smooth anteromedial area has transverse or semicircular rugosities, much weaker but otherwise similar to those of *Cymagathis*.

Distribution and diversity. Known from India, Indonesia (Java) and Thailand.

Biology. *L. javana* has been reared from *Etiella zinckenella* (Pyralidae).

New combinations. *Liragathis relativa* (Bhat and Gupta), comb. n. from *Baeognatha*. *Liragathis javana* (Bhat and Gupta), comb. n. from *Baeognatha*.

***Liragathis baonai* Sharkey, sp. n.**

<http://zoobank.org/71A70AB7-C1EB-457B-BD59-579A07AD192E>

Etymology. *Bao* is Thai for light and *nai* is Thai for eye. The name refers to the pale color of the superior orbit of the eye.

Diagnosis. Body length 6.0 mm; ovipositor length/body length ratio = 1.0. Antenna with 35 flagellomeres. Third labial (penultimate) palpomere about ½ as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Propodeum rugose and mostly glabrous. Superior orbit of eye orange, posterior orbit also orange. Mesoscutum mostly punctate.

Specimens examined. Holotype ♀ (H360), THAILAND, Nakhon Si Thammarat, Namtok Yong NP, behind campground lavatory, 8°10.434'N, 99°44.508'E, 80 m, Malaise trap, 9–16.ix.2008, U-prai leg. **Paratypes:** ♀ (H282) THAILAND, Trang, Khao Pu-Khao Ya NP, 7°32.534'N, 99°47.856'E, 145 m, Malaise trap, 2–9.xii.2005 M Sharkey leg. MALAYSIA: 2♀ (H5928, H16987), Pahang, Kuala Lompat, 1.ix.1999, 3°41'44.27"N, 102°13'25.42"E, Nor Zaneedarwaty leg. ♀ (H16988), Selangor, Kuala Sawit, 3°11'N, 101°37'E, 22.xi.1999, Nor Zaneedarwaty leg.

Distribution. Known only from the specimens collected in Thailand. For a distribution map go to: <http://bit.ly/23QN2Ik>

***Liragathis damnai* Sharkey, sp. n.**

<http://zoobank.org/DC404004-2052-4A4C-8180-6D012BF3CFE9>

Etymology. *Dam* is Thai for black and *nai* is Thai for eye. The name refers to the black color of the superior orbit of the eye.

Diagnosis. Body length 5.3 mm; ovipositor length/body length ratio = 0.7. Antenna with 33 flagellomeres. Third labial (penultimate) palpomere about ½ as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking pegs; mid tibia with 3 pegs; hind tibia with 6 pegs. Fore tibia lacking pegs; mid tibia with 3 pegs; hind tibia with 6–8 pegs. Propodeum rugose but with discernible large areolae as in some *Lytopylus* species. Superior orbit of eye black, posterior orbit orange. Mesoscutum mostly rugose.

Specimens examined. Holotype ♀ (H468), THAILAND Chiang Mai, Doi Chiang Dao WS, Pha Tang unit, 19°24.978'N, 98°54.886'E, 526 m, Malaise trap, 24–31.iii.2008, Songkran & Apichart leg. **Paratypes:** THAILAND: ♀ (H999), Lampang Chae Son NP, Youthcamp/meeting hall, 18°49.866'N, 99°28.209'E, 476 m, Malaise trap, 15–22.iii.2008 B Kwannui & A. Sukpeng leg. ♀ (H2416), Lampang Chae Son NP Youthcamp, 18°49.826'N, 99°28.256'E, 455 m, Malaise trap, 1–7.iv.2008 B Kwannui & A. Sukpeng leg. ♀ (H397), Chiang Mai, Queen Sirikit Botanic Garden, 18°52'57.5"N, 98°51'35.5"E, 17–24.ii.2009, MT K Kaewjanta & R. Sawkord leg.

Distribution. Known only from the specimens collected in Thailand. For a distribution map go to: <http://bit.ly/22WZjoH>

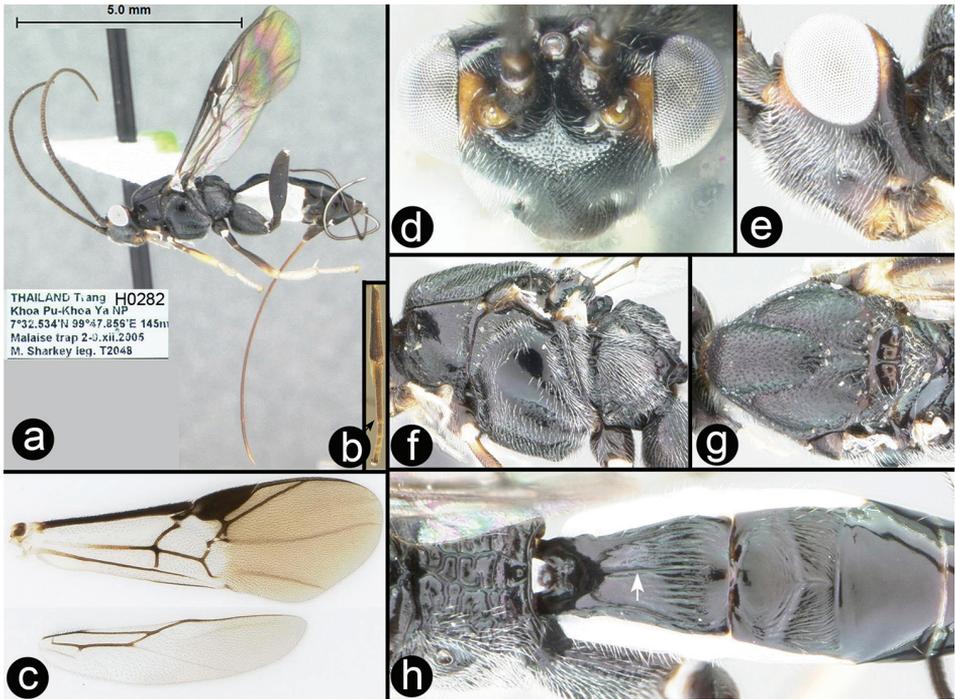


Figure 11. *Liragathis baonai* paratype female: **a** lateral habitus **b** hind tibia and tarsus **c** wings **d** dorsal head **e** lateral head **f** lateral mesosoma **g** dorsal thorax **h** propodeum and metasomal terga 1-3.

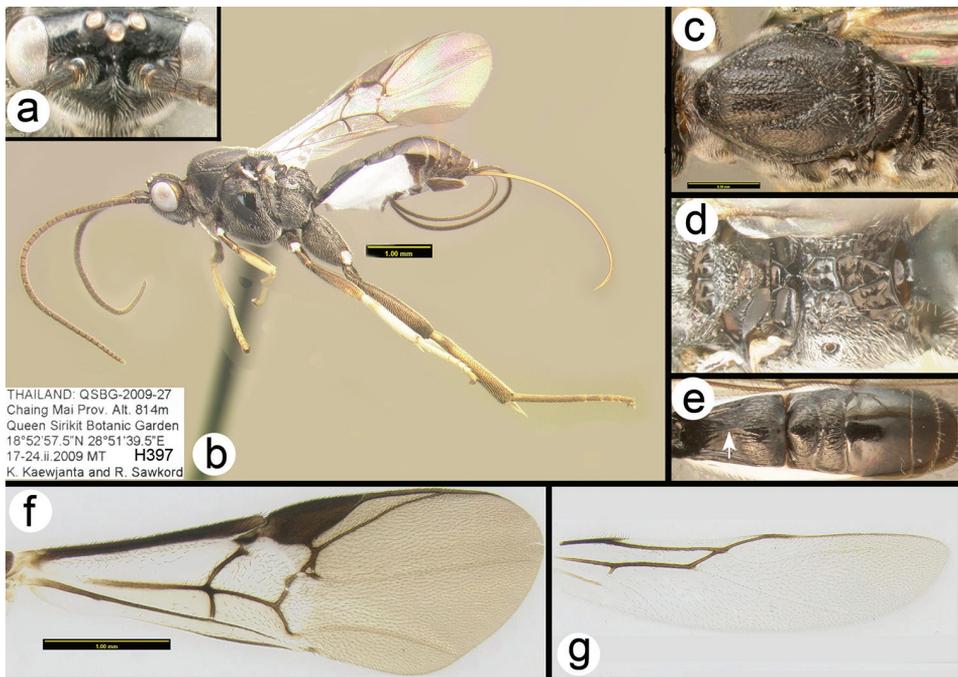


Figure 12. *Liragathis damnai* paratype female: **a** dorsal head **b** lateral habitus **b** hind tibia and tarsus **c** dorsal thorax **d** scutellum and propodeum **e** metasomal terga 1-3 **f** fore wing **g** hind wing.

Liragathis javana* (Bhat and Gupta)Baeognatha javana* Bhat & Gupta, 1977.

Diagnosis. Body length 6.0 mm; ovipositor length/body length ratio = 0.8. Antenna with 33 flagellomeres. Third labial (penultimate) palpomere about ½ as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking pegs; mid tibia with 4 pegs; hind tibia with 5 pegs. Posterior orbit of eye orange. Mesoscutum, scutellum, pronotum and part of mesopleuron orange. Second median tergite wide, about two times wider than long. Similar to *L. relativa* (Bhat and Gupta). Second sub-marginal cell of *L. javana* much larger.

Specimens examined. Holotype ♀, Indonesia, Java, Bogor (=Buitenzorg), 15.ix.1956, ex. *Etiella zinckenella* M Satarchi, USNM, examined). **Other:** Indonesia: 5♀♀, 2♂♂ (H16989 - H16992), Central Java, Tepus, 6°49'S, 110°53'E, 7.v.1990, host *Etiella* sp. [Pyrilidae], coll. G.C. Luther (EMEC). Thailand: ♀ (H628), Phetchabun, Nam Nao NP check point, 16°43.687'N, 101°33.754'E, 924 m, Malaise trap, 5–12.v.2007, Noopean Hongyothi leg. ♀ (H458), Phetchabun, Nam Nao NP check point, 16°43.695'N, 101°33.797'E, 921 m, Malaise trap, 28.iv–5.v.2007, Leng Janteab leg. ♀ (H2406), Phetchabun, Nam Nao NP check point 16°43.695'N, 101°33.797'E, 921 m, Malaise trap, 5–12.v.2007, Leng Janteab leg. ♀ (H419), Kanchanaburi, Khuean Srinagarindra NP, Tha Thung-na/Chong Kraborg, 14°29.972'N, 98°53.035'E, 210 m, Malaise trap, 19–26.iii.2009, Boonnam & Phumarin leg. ♀ (H366), Kanchanaburi, Khuean Srinagarindra NP, Tha Thung-na/Chong Kraborg, 14°29.972'N, 98°53.035'E, 210 m, Malaise trap, 26.iii–2.iv.2009, Boonnam & Phumarin leg.

Distribution. Known only from the specimens collected in Thailand and Indonesia. For a distribution map go to: <http://bit.ly/2ajVCca>

***Scabagathis* Sharkey, gen. n.**<http://zoobank.org/AF5DB06A-7A3F-466D-85A0-ABA92D2D2F85>

Type species. *Scabagathis emilynadeauae* Sharkey, sp. n.

Etymology. *Scaber* is Latin for rough, scabby, mangy; here it refers to the rough (rugose) sculpture on the vertex of the head. Feminine.

Diagnosis. Vertex of head with rugose sculpture. Head and mesosoma both black and orange; metasomal terga mostly black; base of first median tergite whitish; basal half of second median tergite whitish yellow. Fore wing **hyaline, not more infuscate in distal half**. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly. Temple rounded in dorsal view. **Third labial palpomere absent, palpus 3-segmented.** Notauli depressed and partly or entirely pitted. Scutellar triangle **rugose**. Dorsal margin of hind coxal cavities situated above ventral-most margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae.

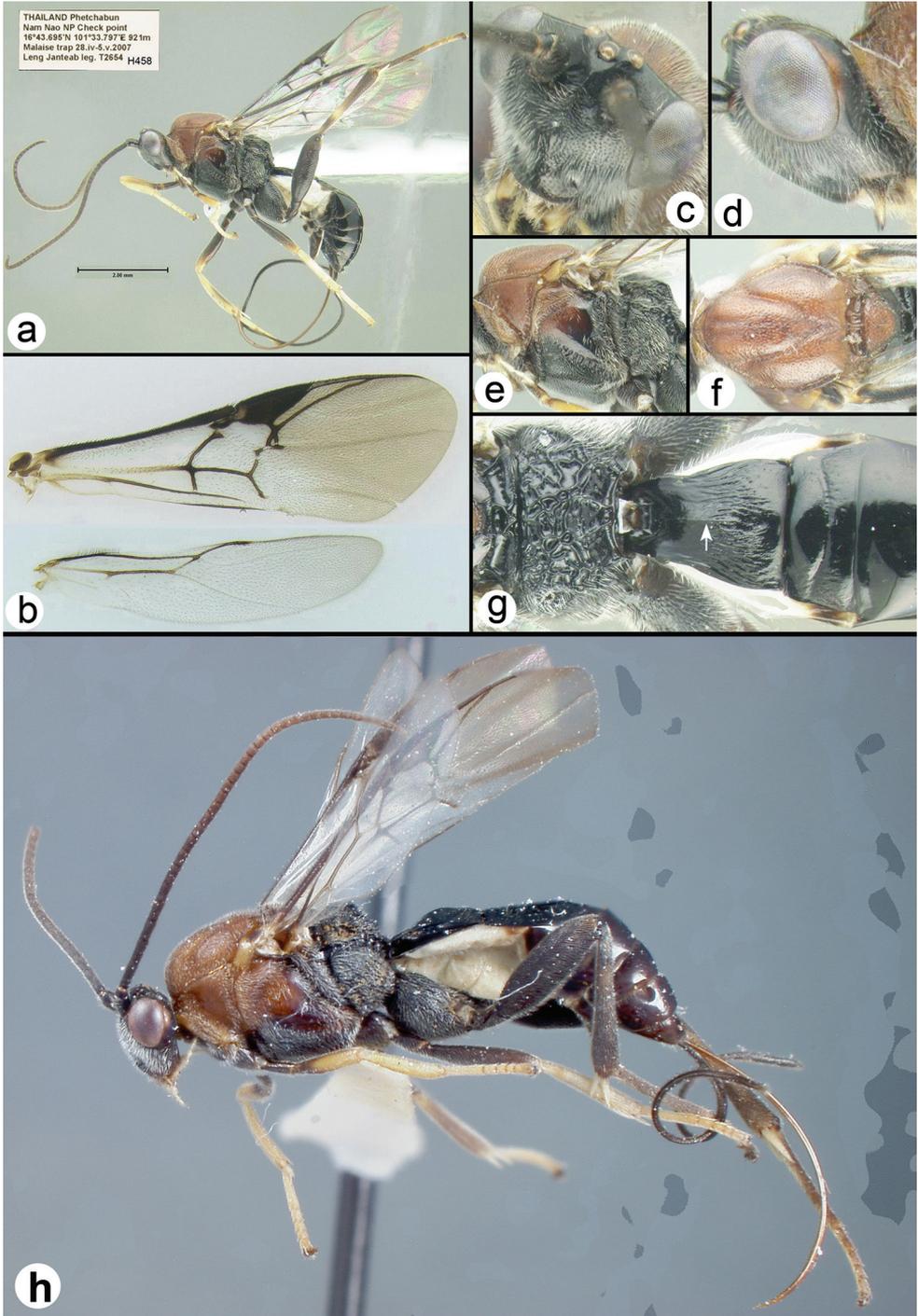


Figure 13. *Liragathis javana* female: **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum and metasomal terga 1-3 **h** holotype lateral habitus.

Second submarginal cell of fore wing minute, cell about the same diameter as wing veins. First median tergite entirely, finely, irregularly striate; lateral carina weak. Second median tergite **longer than wide**. Second median tergite entirely, finely, irregularly striate, with striae ending evenly near apex of tergite.

Distribution and diversity. Known only from the type species from Thailand.

Biology. Unknown.

***Scabagathis emilynadeauae* Sharkey, sp. n.**

<http://zoobank.org/61C5A34B-8C38-4DEA-ADC5-016B42790918>

Etymology. Named in honor of Ms. Emily Nadeau who obtained the highest mark in the weekly quizzes of Ent. 770 in the fall of 2015.

Diagnosis. Body length 5.1 mm; ovipositor length/body length ratio = 0.6. Antenna with 31 flagellomeres. Scutellar groove with 3 longitudinal ridges. Fore tibia without thickened spines or pegs; mid tibia with 2 pegs; hind tibia missing. First median tergite whitish at extreme base. Second median tergite whitish in basal half.

Specimens examined. Holotype ♀ (H033), Thailand, Trang, Nayong, Khao-chong, 24–27.vi.2005, 7°33.038'N, 99°47.369'E, 75 m, Malaise trap.

Distribution. Known only from the type specimen collected in Thailand. For a distribution map go to: <http://bit.ly/29kPFrZ>

***Trochantagathis* Sharkey, gen. n.**

<http://zoobank.org/0F3C1E89-8BBF-4E66-BEAC-352EDA3AF1BB>

Type species. *Baeognatha marshi* Bhat & Gupta, 1977

Etymology. *Trochanter* comes from the Greek *trochalos* meaning running; here it is a reference the pair of ridges on the hind trochantellus which are diagnostic for the genus. Feminine.

Diagnosis. Head (including posterior orbit of eye) and mesosoma black; metasomal tergites black or black and pale yellow. Fore wing hyaline, not infuscate in distal half. Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation that narrows to a short ridge posteriorly and then divides into two short indistinct carinae that approach the lateral margins of the median ocellus. Temple rounded in dorsal view. 3rd labial palpomere minute, barely visible, much smaller than apical palpomere. Notauli depressed and partly or entirely pitted. Scutellar triangle **rugose**. Dorsal margin of hind coxal cavities situated above ventral-most margin of metasomal foramen. Pegs on anterior surface of fore tibia present. **Hind trochantellus with pair of longitudinal carinae.** Second submarginal cell of fore wing varying from about the same diameter as vein Rs about 3x that diameter. First median tergite usually entirely striate, sometimes partly smooth, especially basally; lateral and medial carinae strong. Second median tergite wider than long and varying from completely

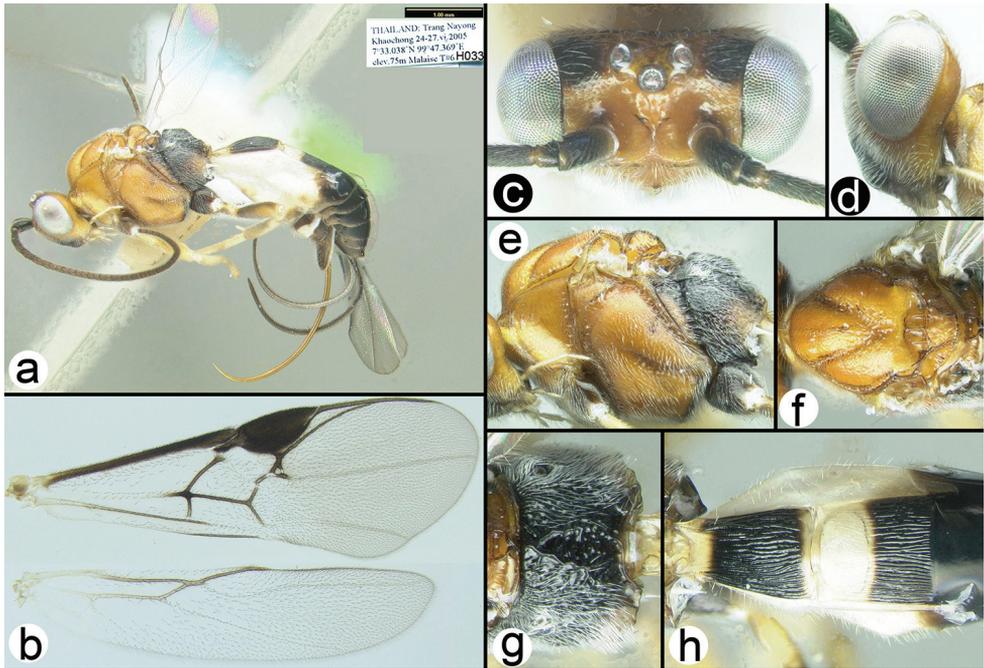


Figure 14. *Scabagathis emilynadeauae* holotype female: **a** lateral habitus **b** wings **c** dorsal head **d** lateral head **e** lateral mesosoma **f** dorsal thorax **g** propodeum **h** metasomal terga 1-3.

and smoothly striate, to mostly smooth with weak smooth striae; semicircular pattern of striae usually present anteromedially.

Distribution and diversity. Known from Vietnam, Thailand and Malaysia, but undoubtedly more widespread in the Oriental Region. Based on the analysis of sequence data presented in Figure 1 there are three species of *Trochantagathis* from Thailand. The females of these species are very similar whereas the males appear to be quite different from one another. Males of the more melanic species are almost entirely melanic whereas the males of the other species are only slightly more melanic than their female conspecifics. With the limited molecular data at hand, the sexual dimorphism, and the similarity of the females of the three putative species, it is not possible to tell with confidence which species, if any, corresponds with the type of *T. marshi*. Therefore, we choose not to describe the two or three new species at this time. The specimens from Vietnam placed in *Therophilus marshi* by Achterberg and Long (2010) need verification. They match well with the type except for minor color differences, but so too do the three Thai species. The images of Figure 17 are of a congeneric (and perhaps conspecific) male and female (specimens H799 and H965). These images present better illustrations of the generic characters discussed above as well as the color sexual dimorphism.

Biology. Unknown.

New combinations. *Trochantagathis marshi* (Bhat and Gupta), comb. n., from *Baeognatha*.

***Trochantagathis marshi* (Bhat and Gupta), comb. n.**

Baeognatha marshi Bhat & Gupta, 1977

Therophilus marshi, Achterberg and Long 2010

Diagnosis. Body length 5.6 mm; ovipositor length/body length ratio = 0.7. Antennae broken (37–38 flagellomeres in Thai congenetics). Third labial (penultimate) palpomere about 1/5 as long as apical palpomere. Scutellar groove with 3 longitudinal ridges. Fore tibia with 2 pegs; mid tibia with 5 pegs; hind tibia with 5 pegs.

Specimens examined. **Holotype** ♀, Malaysia, Sabah, Bettotan nr. Sandakan, 15.viii.1927 (FSCA).

Distribution. Malaysia, Vietnam and Thailand. For a distribution map of the Thai specimens go to: <http://bit.ly/1VK7I0a>

***Xanthagathis* Sharkey, gen. n.**

<http://zoobank.org/0F3C1E89-8BBF-4E66-BEAC-352EDA3AF1BB>

Type species. *Therophilus mellisoma* Achterberg & Long, 2010.

Etymology. *Xantho* is Greek for yellow and is a reference to the predominantly yellow color of the known species. Feminine.

Diagnosis. **Head yellow, mesosoma and metasoma predominantly yellow, with or without melanic areas. Fore wing hyaline.** Antennal sockets not margined with carinae. Interantennal space with a flat triangular elevation, with a weak shallow ridge posteriorly not as elevated as the triangular elevation. Temple rounded in dorsal view. Third labial palpomere minute, barely visible, much smaller than apical palpomere. Notauli depressed and partly or entirely pitted. Scutellar triangle smooth with weak sparse punctures. Dorsal margin of hind coxal cavities situated above ventral-most margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing minute, cell about the same diameter as wing veins. First median tergite entirely, finely, irregularly striate; lateral carina weak. Second median tergite wider than long. **Second median tergite smooth.**

Distribution and diversity. Viet Nam and Thailand. See below for the distribution of the Thai specimens.

Biology. Unknown.

***Xanthagathis mellisoma* (Achterberg and Long), comb. n.**

Therophilus mellisoma Achterberg & Long, 2010

Diagnosis. Body length 3.7 mm; ovipositor length/body length ratio = 0.64. Interantennal space with a flat triangular elevation, with a weak shallow ridge posteriorly not as elevated as the triangular elevation. Antenna with 27 flagellomeres. Third labial

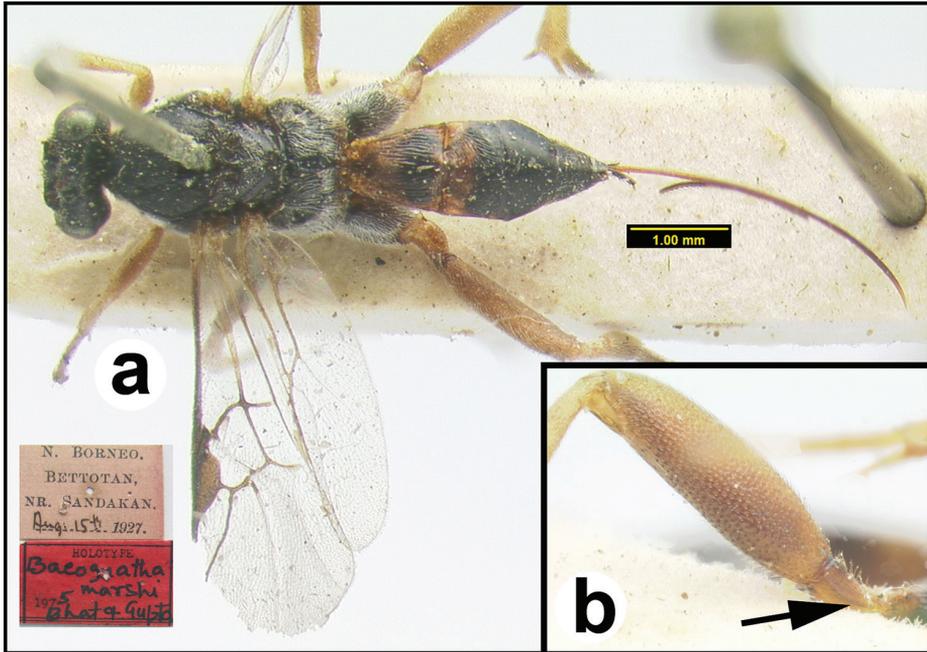


Figure 15. *Trochantagathis marshi* holotype female: **a** dorsal habitus **b** hind femur showing one of the two ridges on the trochantellus.

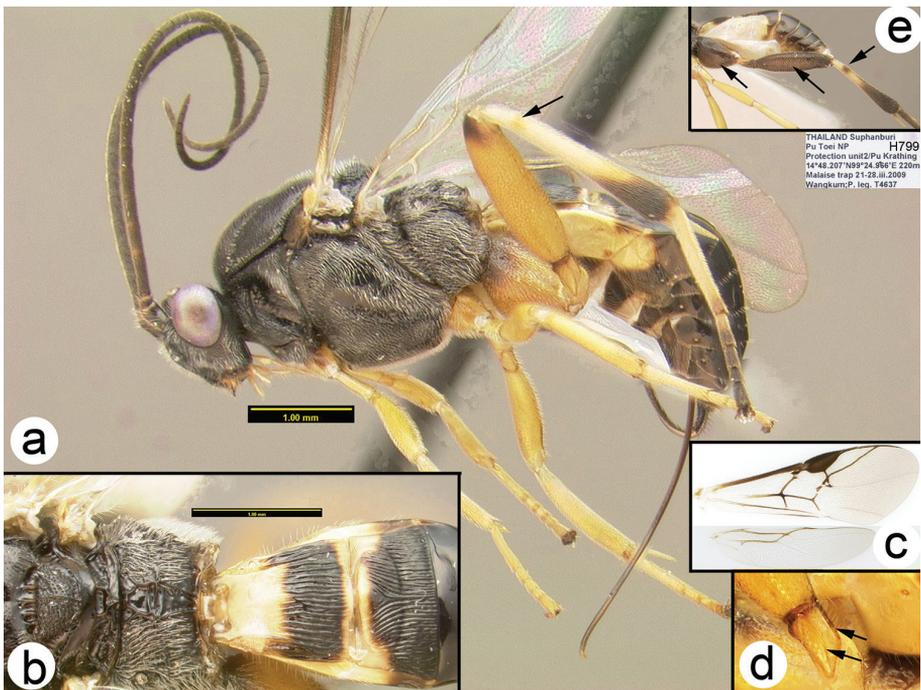


Figure 16. *Trochantagathis marshi?* female: **a** lateral habitus **b** propodeum and metasomal terga 1-2 **c** fore wing **d** detail of ridges on trochantellus of hind leg **e** lateral view of hind leg and metasoma of male (H965); note melanic color of hind coxa and femur.

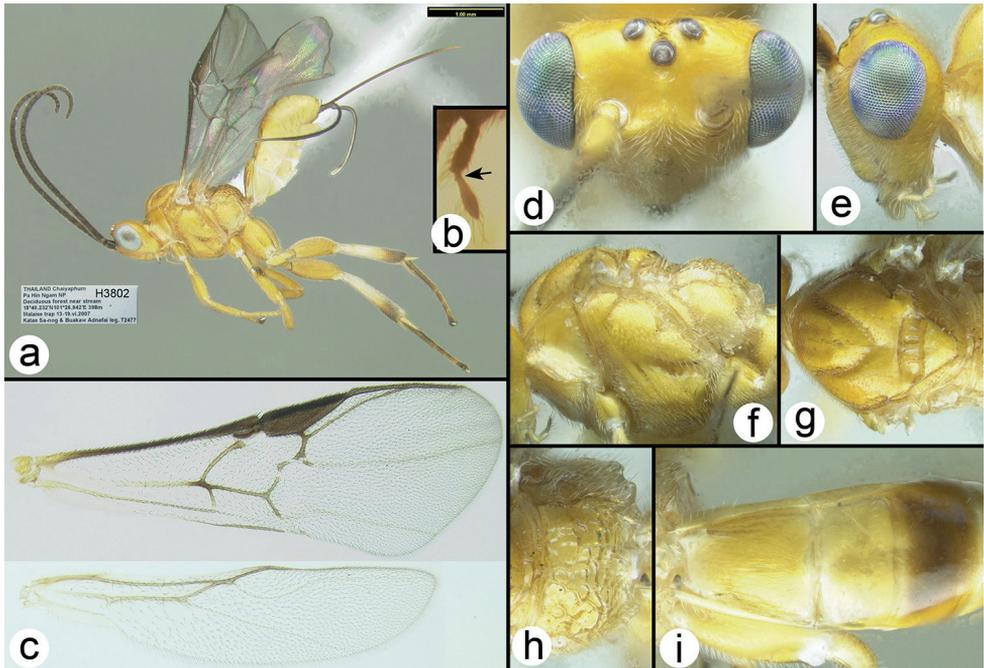


Figure 17. *Xanthagathis mellisoma*, female: **a** lateral habitus **b** labial palp, arrow indicates minute third palpomere **c** wings **d** dorsal head **e** lateral head **f** lateral mesosoma **g** dorsal thorax **h** propodeum **i** metasomal terga 1-3.

palpomere reduced, barely visible, much smaller than apical palpomere. Notauli pitted throughout. Scutellar groove with 3 longitudinal ridges. Fore tibia lacking spines; mid tibia with 6 pegs; hind tibia with 5 pegs. The Thai specimen in Figure 17 differs from the holotype in the lack of a melanic patch distally on hind femur.

Variation. Color usually entirely xanthic (yellow) except for brown as follows: most wing veins including stigma, antenna, hind tarsus and apex of hind tibia. Some specimens are more melanic with brown color extending to propodeum, most of hind leg and parts of most terga.

Distribution. For a distribution map of the Thai specimens go to: <http://bit.ly/1SWVASF>

Zosteragathis Sharkey, gen. n.

<http://zoobank.org/89E3D8D8-60B7-419A-8129-9D49A0D21EAD>

Type species. *Zosteragathis samensis* Sharkey, sp. n.

Etymology. *Zoster* is Greek for belt; here it is a reference to the white band present on the second metasomal median tergite of most species. Feminine.

Diagnosis. Fore wing hyaline, not infusate in distal half. Antennal sockets not margined with carinae. Temple rounded in dorsal view. Notauli depressed and partly

or entirely pitted. Dorsal margin of hind coxal cavities situated above ventral-most margin of metasomal foramen. Pegs on anterior surface of fore tibia absent. Hind trochantellus lacking longitudinal carinae. Second submarginal cell of fore wing petiolate, small to minute. First median tergite entirely, finely, irregularly striate; lateral carina weak. Second median tergite more than 2x longer than wide. **Second median tergite usually entirely, finely, irregularly, striate with striae ending evenly near apex of tergite, rarely striae partly absent. Some species have reduced striae on second median tergite and are recognized by the lack of apomorphic structures that distinguish other closely related genera, e.g., claws not simple, interantennal space without a sharply declivous keel, first median tergite without prominent lateral carina or medial carina, fore tarsus without spines or pegs.**

Distribution and diversity. Australian, Ethiopian, Oceania, Oriental, and eastern Palearctic regions.

Biology. Hosts are unknown for all Thai species; however, there are records for three extra-Thai species. These appear to suggest that the host range is wide. The records are: *Zosteragathis coryphe* was reared from *Phycodes radiata* (Sesioidea: Brachodidae) (Nixon 1950). *Zosteragathis robusta* (Achterberg and Long) from Vietnam was reared from “*Omiodes indicata* (Lepidoptera: Pyralidae: Pyraustinae) on soybean (*Glycine max* (Linnaeus)), according to the label data”, (Achterberg and Long 2010). *Zosteragathis festiva* (Muesebeck) was reared from *Grapholitha molesta*, the oriental fruit moth, (Tortricoidea: Tortricidae). Many other Lepidoptera from a wide range of families are listed by Yu et al. (2012) as hosts of *Z. festiva*, e.g., Blastobasidae, Carposinidae, Gelechiidae, Noctuidae, and Pyralidae.

New species combinations

Below is a list of all new combinations that I am aware of. Since the limits, and even the monophyly, of *Zosteragathis* are uncertain the list will undoubtedly change in the future.

Zosteragathis annulus (Chou & Sharkey, 1989), **comb. n.** from *Bassus*
Zosteragathis asper (Chou & Sharkey, 1989), **comb. n.** from *Bassus*
Zosteragathis conformis (Bhat & Gupta, 1977), **comb. n.** from *Agathis*
Zosteragathis contrasta (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis coryphe (Nixon, 1950), **comb. n.** from *Agathis*
Zosteragathis depressa (Chou & Sharkey, 1989), **comb. n.** from *Bassus*
Zosteragathis dravida (Bhat & Gupta, 1977), **comb. n.** from *Agathis*
Zosteragathis elongator (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis festiva (Muesebeck, 1953), **comb. n.** from *Agathis*
Zosteragathis festivooides (Sharkey, 1996), **comb. n.** from *Bassus*
Zosteragathis fujianicus (Chen & Yang, 2006), **comb. n.** from *Bassus*
Zosteragathis gracilis (Bhat & Gupta, 1977), **comb. n.** from *Agathis*
Zosteragathis lienhuachihensis (Chou & Sharkey, 1989), **comb. n.** from *Bassus*

Zosteragathis lini (Chou & Sharkey, 1989), **comb. n.** from *Bassus*
Zosteragathis masoni (Bhat & Gupta, 1977), **comb. n.** from *Agathis*
Zosteragathis nigrolineatus (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis nuichuaensis (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis oranae (Watanabe, 1970), (syn. of *Z. festiva*, syn. by Sharkey, 1996), **comb. n.** from *Agathis*
Zosteragathis parasper (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis punctiscutum (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis robusta (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis scutellatus (Achterberg & Long, 2010), **comb. n.** from *Therophilus*
Zosteragathis sungkangensis (Chou & Sharkey, 1989), **comb. n.** from *Bassus*
Zosteragathis tanycoleosus (Chen & Yang, 2006), **comb. n.** from *Bassus*

***Zosteragathis samensis* Sharkey, sp. n.**

<http://zoobank.org/36F4AC69-A720-4648-9159-13AF0ECDDE89>

Etymology. Named after the type locality Khao Sam Roi Yot National Park.

Diagnosis. Fore coxa yellow. Hind femur black. Second median tergite mostly pale in anterior half and mostly melanic in posterior half. Scutellum sculpture smooth with punctures. Second median tergite dimensions as wide as long or wider.

Description. Body length 5.4 mm. Ovipositor length 3.3 mm. Ovipositor $0.6 \times$ body length. Number of flagellomeres 31. Notauli sculpture not significantly wider posteriorly. Scutellum smooth with punctures. Mid tibia with 3 apical and 2 preapical spines. Hind tibia with 8 spines/pegs. Second submarginal cell diameter small, smaller than pedicel length, but larger than pedicel width

Wing hyaline with an infuscate patch posterior to stigma. Second median tergite $0.9 \times$ longer than wide. Second median tergite entirely striate, striae weak anteromedially where they converge medially. **Color:** head black except gena yellow; mesosoma black; fore and mid coxa yellow; posterior margin of first median tergite yellow; anterior half of second median tergite yellow.

Material examined. Holotype: ♀ (H2418): THAILAND, Prachuab Khiri Khan, Khao Sam Roi Yot NP, Khao Look Glang, 12.107°N, 99.955°E, Malaise trap, 8-15.iii.2009 (H2418), Yai Amnad. **Paratypes:** All ♀: THAILAND, Prachuab Khiri Khan, Khao Sam Roi Yot NP, foot of Khao Taen, 12.146°N, 99.966°E, 1 m elev., Malaise trap, 3–10.v.2009 (H638, H968), Yai Amnad; Prachuab Khiri Khan, Khao Sam Roi Yot NP, 30 m, N/protection unit4, 12.268°N, 99.944°E, 1 m elev., Malaise trap, 3–10.v.2009 (H973, T4824) 24-31.v.2009 (H490), Yai Amnad; Lampang, Chae Son NP, Youthcamp, 18.83°N, 99.471°E, 455 m elev., Malaise trap, 1–7.iv.2008 (H901) B Kwannui & A. Sukpeng; Mae Hong Son, Namtok Mae Surin NP, Haad Saen, 19.348°N, 97.985°E, Malaise trap, 27.iv–4.v.2008 (H481), Na-maadkam, M; Prachuab Khiri Khan, Khao Sam Roi Yot NP, Saline wetland/Pa Gwad/N, 12.153°N, 99.972°E, Malaise trap, 15–22.iii.2009 (H670), Yai Amnad.

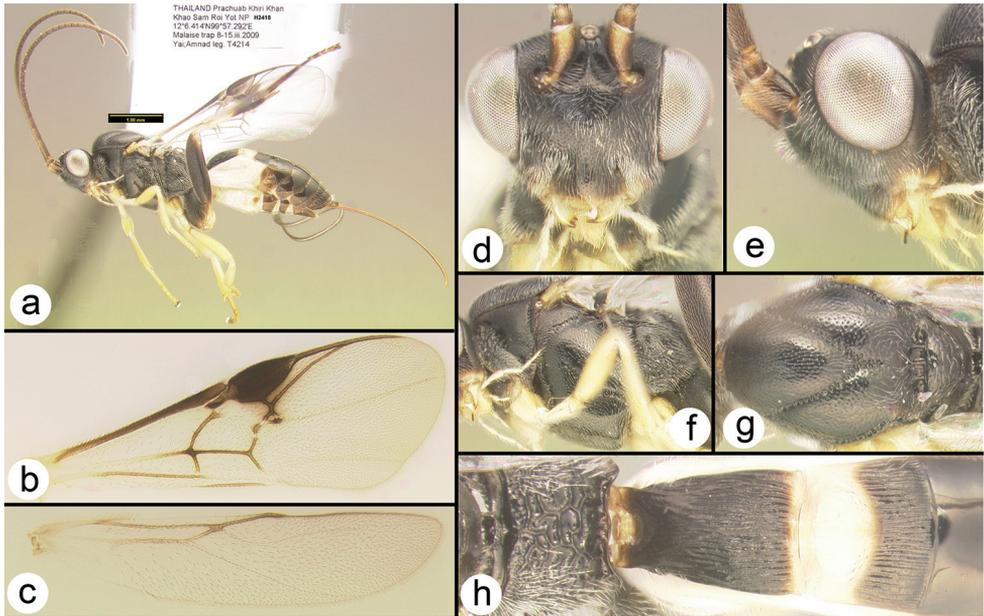


Figure 18. *Z. samensis*: **a** lateral habitus **b** fore wing **c** hind wing **d** anterior head **e** lateral head **f** lateral mesosoma **g** dorsal mesoscutum **h** propodeum and median tergites 1-3.

Distribution. Known only from the specimens collected in Thailand. For a distribution map go to: <http://bit.ly/1MPRTqu>

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Appendix I

Specimens used in the phylogenetic analyses, including specimen numbers, GenBank and BOLD accession numbers and rough geographical information.

Taxon name	Specimen number	Country: Region	Type status	COI	28S
<i>Aerophilus abdominalis</i>	H1313	USA: KY		ATRMK294-11	KP943685
<i>Aerophilus malus</i>	H1484	USA: WV	holotype	ATRMK309-11	KP943693
<i>Aerophilus rayfisheri</i>	H1212	USA: KY	holotype	ATRMK278-11	KP943675
<i>Agathacrista depressifera</i>	H002	Thailand: Phetchabun		KP943596	KC556782
<i>Agathacrista krataei</i>	H268	Thailand: Kalasin	holotype	KP943614	KC556781
<i>Agathacrista sailomi</i>	H013	Thailand: Chiang Mai	holotype	KX431796	KC556780
<i>Agathacrista winloni</i>	H502	Thailand: Phetchabun	holotype	ATRMK218-11	KC771135
<i>Agathigna templei</i>	H415	Thailand: Kamphaeng	holotype	ATRMK211-11	KX431753
<i>Alabagrus maculipes</i>	H6020	Mexico: Jalisco		ATRMK370-11	KP943698
<i>Asperagathis aspera</i>	H274	Thailand: Phetchabun	holotype	KX431797	KX431706
<i>Asperagathis xesta</i>	H095	Thailand: Chaiyaphum	holotype	KX431798	KX431707
<i>Bassus albifasciatus</i>	H014	Thailand: Sakon Nakhon		-----	KX431714
<i>Bassus albifasciatus</i>	H027	Thailand: Trang		KX431800	KX431716
<i>Bassus albifasciatus</i>	H032	Thailand: Trang		KX431799	KX431715
<i>Bassus albifasciatus</i>	H085	Thailand: Trang		KX431801	KX431719
<i>Bassus albifasciatus</i>	H343	Thailand: Chiang Mai		-----	KX431718
<i>Bassus albifasciatus</i>	H377	Thailand: Nakhon Si Thammarat		-----	KX431717
<i>Bassus alboapicalis</i>	H021	Thailand: Trang	paratype	KX431821	KX431767
<i>Bassus alboapicalis</i>	H022	Thailand: Trang	paratype	KX431819	KX431764
<i>Bassus alboapicalis</i>	H081	Thailand: Trang	paratype	KX431817	KX431762
<i>Bassus alboapicalis</i>	H269	Thailand: Trang	holotype	KX431820	KX431766
<i>Bassus alboapicalis</i>	H270	Thailand: Trang	paratype	KX431818	KX431763
<i>Bassus alboapicalis</i>	H307	Thailand: Surat Thani	paratype	ATRMK195-11	KX431765
<i>Bassus alboapicalis</i>	H410	Thailand: Nakhon Si Thammarat	paratype	-----	KX431761
<i>Bassus albobasalis</i>	H003	Thailand: Phetchabun		KX431802	KX431721
<i>Bassus albobasalis</i>	H092	Thailand: Trang		-----	KX431720
<i>Bassus albobasalis</i>	H328	Thailand: Phetchabun		JQ763436	KX431722
<i>Bassus alboocylus</i>	H308	Thailand: Phetchabun	paratype	-----	KX431724
<i>Bassus alboocylus</i>	H349	Thailand: Chiang Mai	paratype	-----	KX431725
<i>Bassus alboocylus</i>	H636	Thailand: Suphan Buri	holotype	ATRMK230-11	KX431723
<i>Bassus calculator</i>	H8008	Sweden: Stockholms län		-----	KX431712
<i>Bassus mediatratus</i>	H015	Thailand: Chiang Mai	holotype	KX431816	KX431760
<i>Bassus nopachoni</i>	H577	Thailand: Kamphaeng	holotype	ATRMK223-11	KX431713
<i>Bassus pallidus</i>	H055	Thailand: Chanthaburi	holotype	-----	KX431710
<i>Bassus</i> sp.	H376	Thailand: Phetchaburi		ATRMK204-11	KX431711
<i>Braunsia smithii</i>	H906	Thailand: Chiang Mai		ATRMK261-11	HQ667949
<i>Camptorhripsis lingualongis</i>	H1887	South Africa: Western Cape	paratype	ATRMK334-11	JN564494
<i>Camptorhripsis nigra</i>	H433	Thailand: Prachuap Khiri Khan		ATRMK430-11	HQ667951

Taxon name	Specimen number	Country: Region	Type status	COI	28S
<i>Camptothlipsis sheilae</i>	H664	Thailand: Kanchanaburi	holotype	ATRMK235-11	HQ667954
<i>Camptothlipsis</i> sp.	H162	Uganda: Homa Bay		-----	KX431699
<i>Camptothlipsis</i> sp.	H2299	Congo: Pool		-----	KX431698
<i>Chimaeragathis chrysoma</i>	H710	Thailand: Phetchaburi	holotype	ATRMK240-11	KX431738
<i>Chimaeragathis eurysona</i>	H045	Thailand: Trang	paratype	KX431805	KX431736
<i>Chimaeragathis eurysona</i>	H069	Thailand: Trang	paratype	KX431806	KX431737
<i>Chimaeragathis eurysona</i>	H925	Thailand: Phetchaburi	holotype	ATRMK265-11	KX431735
<i>Chimaeragathis lohmani</i>	H072	Thailand: Trang	holotype	KX431807	KX431739
<i>Chimaeragathis lohmani</i>	H077	Thailand: Trang	paratype	KX431808	KX431740
<i>Cymagathis krikoma</i>	H290	Thailand: Chaiyaphum	paratype	ATRMK192-11	KX431701
<i>Gyragathis leucosoma</i>	H275	Thailand: Nakhon Ratchasima	holotype	KX431794	KX431700
<i>Leuroagathis paulbakerei</i>	H369	Thailand: Prachuap Khiri Khan	holotype	-----	KX431709
<i>Liragathis baonai</i>	H360	Thailand: Nakhon Si Thammarat	holotype	ATRMK200-11	KX431705
<i>Liragathis damnai</i>	H397	Thailand: Chiang Mai	paratype	ATRMK210-11	KX431704
<i>Liragathis javana</i>	H283	Thailand: Trang		KX431795	KX431702
<i>Liragathis javana</i>	H628	Thailand: Phetchabun		ATRMK228-11	KX431703
<i>Neothlipsis parysae</i>	H4428	USA: KY	paratype	ATRMK364-11	KX431696
<i>Neothlipsis</i> sp.	H195	Thailand: Surat Thani		KP943607	KP943660
<i>Neothlipsis</i> sp.	H198	USA: KY		KX431793	KX431697
<i>Neothlipsis</i> sp.	H7618	Mexico: Yucatan		ATRMK403-11	KP943709
<i>Scabagathis emilynadeauae</i>	H033	Thailand: Trang	holotype	KX431792	KX431695
<i>Trochantagathis marshi</i>	H067	Thailand: Trang		KX431809	KX431742
<i>Trochantagathis marshi</i>	H089	Thailand: Trang		KX431811	KX431745
<i>Trochantagathis marshi</i>	H1851	Thailand: Trang		-----	KX431744
<i>Trochantagathis marshi</i>	H281	Thailand: Trang		KX431810	KX431743
<i>Trochantagathis marshi</i>	H765	Thailand: Ubon Ratchathani		ATRMK242-11	KX431741
<i>Trochantagathis marshi</i>	H799	Thailand: Suphan Buri		-----	KX431746
<i>Trochantagathis marshi</i>	H965	Thailand: Nakhon Si Thammarat		ATRMK266-11	KX431747
<i>Xanthagathis mellisoma</i>	H060	Thailand: Trang		KX431812	KX431749
<i>Xanthagathis mellisoma</i>	H145	Thailand: Phetchabun		-----	KX431748
<i>Xanthagathis mellisoma</i>	H286	Thailand: Chaiyaphum		ATRMK191-11	KX431751
<i>Xanthagathis mellisoma</i>	H348	Thailand: Chiang Mai		ATRMK199-11	KX431750
<i>Xanthagathis mellisoma</i>	H662	Thailand: Phetchaburi		ATRMK234-11	KX431752
<i>Zostenagathis contrastus</i>	H017	Thailand: Chiang Mai		KX431828	KX431783
<i>Zostenagathis contrastus</i>	H056	Thailand: Trang		KX431834	KX431790
<i>Zostenagathis contrastus</i>	H094	Thailand: Chiang Mai		KX431833	KX431789
<i>Zostenagathis contrastus</i>	H100	Thailand: Chaiyaphum		KX431832	KX431787
<i>Zostenagathis contrastus</i>	H101	Thailand: Loei		KX431827	KX431781
<i>Zostenagathis contrastus</i>	H104	Thailand: Loei		-----	KX431782
<i>Zostenagathis contrastus</i>	H142	Thailand: Nakhon Ratchasima		-----	KX431779

Taxon name	Specimen number	Country: Region	Type status	COI	28S
<i>Zosteragathis contrastus</i>	H143	Thailand: Phetchabun		KX431829	KX431784
<i>Zosteragathis contrastus</i>	H144	Thailand: Phetchabun		KX431830	KX431785
<i>Zosteragathis contrastus</i>	H146	Thailand: Phetchabun		KX431831	KX431786
<i>Zosteragathis contrastus</i>	H149	Thailand: Phetchabun		KX431826	KX431780
<i>Zosteragathis contrastus</i>	H1855	Thailand: Chaiyaphum		ATRMK501-11	-----
<i>Zosteragathis contrastus</i>	H603	Thailand: Surat Thani		ATRMK226-11	KX431791
<i>Zosteragathis contrastus</i>	H677	Thailand: Suphan Buri		-----	KX431788
<i>Zosteragathis contrastus</i>	H985	Thailand: Kanchanaburi		-----	KX431778
<i>Zosteragathis samensis</i>	H2418	Thailand: Prachuap Khiri Khan	holotype	ATRMK475-11	KX431775
<i>Zosteragathis samensis</i>	H973	Thailand: Prachuap Khiri Khan	paratype	ATRMK269-11	KX431774
<i>Zosteragathis</i> sp.	H065	Thailand: Trang		KX431803	KX431733
<i>Zosteragathis</i> sp.	H083	Thailand: Trang		KX431804	KX431734
<i>Zosteragathis</i> sp.	H091	Thailand: Sakon Nakhon		KX443589	KX431726
<i>Zosteragathis</i> sp.	H1859	Thailand: Phitsanulok		ATRMK329-11	KX431729
<i>Zosteragathis</i> sp.	H1860	Thailand: Surat Thani		ATRMK330-11	KX431731
<i>Zosteragathis</i> sp.	H239	Thailand: Trang		-----	KX431732
<i>Zosteragathis</i> sp.	H492	Thailand: Phetchaburi		ATRMK217-11	KX431728
<i>Zosteragathis</i> sp.	H660	Thailand: Mae Hong Son		ATRMK233-11	KX431727
<i>Zosteragathis</i> sp.	H687	Thailand: Nakhon Si Thammarat		-----	KX431730
<i>Zosteragathis</i> sp.	H016	Thailand: Chaiyaphum		KX431825	KX431776
<i>Zosteragathis</i> sp.	H080	Thailand: Chiang Mai		KX431814	KX431757
<i>Zosteragathis</i> sp.	H121	Thailand: Nong Bua Lam Phu		KX431822	KX431771
<i>Zosteragathis</i> sp.	H122	Thailand: Nong Bua Lam Phu		KX431823	KX431772
<i>Zosteragathis</i> sp.	H1625	Thailand: Chaiyaphum		ATRMK323-11	KX431754
<i>Zosteragathis</i> sp.	H1636	Thailand: Ubon Ratchathani		ATRMK325-11	KX431770
<i>Zosteragathis</i> sp.	H1858	Thailand: Chiang Mai		ATRMK328-11	KX431777
<i>Zosteragathis</i> sp.	H236	Thailand: Chiang Mai		KX431813	KX431756
<i>Zosteragathis</i> sp.	H237	Thailand: Lampang		KX431815	KX431758
<i>Zosteragathis</i> sp.	H279	Thailand: Ubon Ratchathani		KX431824	KX431773
<i>Zosteragathis</i> sp.	H473	Thailand: Phetchaburi		ATRMK216-11	KX431708
<i>Zosteragathis</i> sp.	H598	Thailand: Mae Hong Son		ATRMK225-11	KX431768
<i>Zosteragathis</i> sp.	H650	Thailand: Phetchabun		ATRMK232-11	KX431769
<i>Zosteragathis</i> sp.	H689	Thailand: Suphan Buri		ATRMK238-11	KX431755
<i>Zosteragathis</i> sp.	H989	Thailand: Phetchaburi		ATRMK271-11	KX431759

Cherax warsamsonicus, a new species of crayfish from the Kepala Burung (Vogelkop) peninsula in West Papua, Indonesia (Crustacea, Decapoda, Parastacidae)

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Abstract

A new species, *Cherax warsamsonicus* **sp. n.**, endemic to the Warsamson River drainage, in the western part of the Kepala Burung (Vogelkop) peninsula, West Papua, Indonesia, is described, figured and compared with its closely related species, *Cherax misolicus* Holthuis, 1949. The new species may be easily distinguished from *C. misolicus* by the shape of the rostrum, absence of setae on the rostrum, the shape of the chelae, the presence of 3–4 cervical spines and by using sequence divergence, which is substantial for considering *C. warsamsonicus* **sp. n.** to be a new species. The new species is collected and exported for ornamental purposes and its commercial name in the pet trade is *Cherax* “irian jaya”, *Cherax* “pink coral”, or *Cherax* “hoa creek”. Due to similar colouration it is often confused with the recently described *Cherax pulcher* Lukhaup, 2015.

Keywords

Cherax, Crustacea, Decapoda, morphology, New Guinea, Parastacidae, pet trade, taxonomy, Warsamson River

Introduction

The crayfishes of the island of New Guinea were extensively studied by Holthuis (1949, 1956, 1958, 1982, 1986, 1996), with additions by Lukhaup and Pekny (2006, 2008a), Lukhaup and Herbert (2008), Lukhaup (2015), Lukhaup et al. (2015) and Patoka et al. (2015). Nevertheless, over the last decade, there has been an increasing number of colourful crayfish, presumed to be a further undescribed species, sold from New Guinea in the ornamental fish trade in Europe and Asia under the names *Cherax* “irian jaya” and *Cherax* “hoa creek” (Lukhaup and Pekny 2014). These have been exported to some countries in Europe, East Asia and North America. While they are clearly species of *Cherax*, a large genus of freshwater crayfish occurring in Indonesia (West Papua), Papua New Guinea and Australia, their exact provenances could not be ascertained, with dealers claiming they came from Ajamaru (West Papua) and other places in the area that could not be confirmed. Also species have been mixed at the places of exporters in Sorong and Jakarta. Therefore in January 2016 we visited the Sorong Regency and South Sorong Regency to clarify the distribution of some of the species present in the pet trade. In the present contribution, this species is described as new to science and establish that it is in fact native to the Warsamson River Drainage, Sorong Regency of the Kepala Burung (Vogelkop) Peninsula West Papua, Indonesia. *Cherax warsamsonicus* sp. n., is genetically and morphologically most similar to *Cherax misolicus* Holthuis, 1949 endemic to the Island of Misool, one of four major islands in the Raja Ampat Islands in West Papua, Indonesia and two other undescribed species from Sorong and South Sorong Recency.

Cherax misolicus and *Cherax warsamsonicus* sp. n. may be easily distinguished using sequence divergence, by colouration and pattern of live individuals, by the shape of the chelae, the shape of rostrum, and presence of dense setae on the rostrum in *C. misolicus* which is absent in the new species.

Materials and methods

Samples of *Cherax warsamsonicus* sp. n. as well as three other species were collected from streams in the southwestern part of the Kepala Burung peninsula in February 2016. In addition, sequence from seven species of *Cherax* and from two other parastacid genera used as outgroup were downloaded from GenBank (see Table 1). Holotype and allotype were photographed and kept alive in indoor tanks until samples were obtained for DNA analysis. After this procedure animals were preserved in 70 % ethanol. Morphometric parameters of all individuals were taken using an electronic digital calliper with an accuracy of 0.1 mm.

DNA was purified from 2 mm³ of muscle tissue with a Qiagen BioSprint 96 using the manufacturer’s protocol. Polymerase chain reaction (PCR) was used to amplify two mitochondrial gene fragments, a ~535 bp region of the 16S ribosomal RNA gene (16S) using primers 1471 and 1472 (Crandall & Fitzpatrick 1996) and a 710 bp fragment of

Table 1. Material studied with GenBank accession numbers.

Species/sample	Location	GenBank acc. nos		Source
		COI	16S	
<i>Cherax albertisii</i>	Bensbach River, Papua New Guinea (Queensland Museum)	–	KJ920770	Eprilurahman et al., unpubl.
<i>C. boesemani</i>	Ajamaru Lake, Papua Barat; 1°17'19.97"S, 132°14'49.14"E; January 23, 2016	# #	# #	this study
<i>C. holtbuisi</i>	Papua Barat	KU821419	KU821433	Blaha et al. 2016
<i>C. misolicus</i>	Misool Island, South of Papua Barat (Leiden Museum)	–	KJ920813	Eprilurahman et al., unpubl.
<i>C. monticola</i>	Baliem River, Wamena, Papua	KF649851 –	KF649851 KJ920818	Gan et al. 2014
<i>C. paniaicus</i>	Lake Tage, Papua (Field collection)	KJ950528	KJ920830	Eprilurahman et al., unpubl.
<i>C. pekenyi</i>	Pet Shop	KU821422	KU821435	Blaha et al. 2016
<i>C. pulcher</i>	Hoa Creek (Teminabuan), Papua Barat; 1°28'32.73"S 132° 3'54.94"E; January 23, 2016	#	#	this study
<i>C. pulcher</i> ⁴	Papua Barat (Pet Shop)	KU821424	KU821438	Blaha et al. 2016
		KU821426	KU821437	Blaha et al. 2016
<i>C. rhynchotus</i>	Lake Wicheura, Cape York, Queensland (Queensland Museum)	–	KJ920765	Eprilurahman et al., unpubl.
<i>C. snowden</i>	Oinsok (Ainsok River Drainage), Papua Barat; 1°11'40.07"S 131°50'1.14"E; January 24, 2016	#	#	this study
<i>C. warsamsonicus</i>	Small tributary to Warsamson River Collection Date : January 20 ,2016 0°49'16.62"S, 131°23'3.34"E	#	#	this study
<i>Engaeus strictifrons</i>	Crawford River, Victoria, Australia	AF493633	AF492812	Munasinghe et al. 2003
<i>Euastacus bispinosus</i>	Crawford River, Victoria, Australia	AF493634	AF492813	Munasinghe et al. 2003

= No. pending, will be entered during revision process.

the Cytochrome Oxidase subunit I gene (COI) using primers LCO1490 and HCO2198 (Folmer et al. 1994).

PCR was performed in 25 µl volumes containing 1x Taq buffer, 1.5 mM MgCl₂, 200 µM each dNTP, 1 U Taq polymerase, ca. 50-100 ng DNA and ddH₂O. After an initial denaturation step of 3 min at 94 °C, cycling conditions were 35 cycles at 94 °C for 35 s, 45 °C (COI) or 50 °C (16S) for 60 s, and 72 °C for 1 min (COI) or 90 s (16S), with a final elongation step of 5 min at 72 °C. The same primers were used in PCR and sequencing. PCR products were sent to Macrogen Europe for purification and cycle sequencing of both strands of each gene.

Sequences were aligned by eye (COI) and with MAFFT (16S) using the G-INS-i strategy suitable for thorough alignments of sequences with global homology (Katho et al. 2002). The resulting alignments had a length of 658 bp (COI) and 543 bp (16S), respectively. To determine the best substitution model for Bayesian inference analyses (see below), hierarchical likelihood ratio tests were carried out with jModelTest (Posada 2008) on both

sequence sets (24 models tested). Based on the Akaike Information Criterion and the Bayesian Inference Criterion, the GTR + I + G (COI) and the GTR + G (16S) models were chosen. The two sequence datasets were subsequently analysed both separately and combined.

Phylogenetic trees were reconstructed by maximum parsimony (MP) using the heuristic search algorithm as implemented in PAUP* (Swofford 2002), with gaps treated as fifth base. Support for nodes was estimated by bootstrap analysis (1,000 bootstrap replicates with 10 random addition sequence replicates each). Maximum Likelihood (ML) analyses were conducted with RAxML (Stamatakis et al. 2008; RAxML BlackBox; 100 bootstrap replicates) under the GTR + (I) + G model of sequence evolution. In addition, Bayesian inference (BI) was employed to infer phylogeny by using MrBayes 3.2.2 (Ronquist and Huelsenbeck 2003). The MCMCMC-algorithm was run with four independent chains for 5,000,000 generations, samplefreq = 250, and burnin = 10,001) using the models specified above.

The combined dataset was subjected to a partitioned analysis (ML and BI) using the different models for the two genes in the BI analyses. All new sequences have been deposited in GenBank, see Table 1).

Systematics

Parastacidae Huxley, 1879

Genus *Cherax* Erichson, 1846

Cherax warsamsonicus sp. n.

<http://zoobank.org/4A8CC447-7082-4105-A676-BDB4B6092D95>

Figs 1–5

Material examined. Holotype: male (MZB Cru 4529), among roots along banks of a unnamed creek draining into Warsamson River, north of Sorong City, 0°49'16.62"S 131°23'3.34"E, West Papua, Indonesia. coll. Chris Lukhaup, Irianto Wahid and unnamed local guide January 20 2016. **Allotype:** female (MZB Cru 4530), same data as holotype. **Paratypes:** (MZB Cru 4531), same data as holotype.

Diagnosis. Carapace surface smooth with four small spiniform tubercles posterior to cervical groove on lateral carapace. Eyes large, pigmented. Cornea slightly broader than eyestalk. Rostrum lanceolate in shape with excavated margins. Rostral margins with three prominent teeth. Rostral carinae prominent. Postorbital ridges prominent with one acute tubercle at anterior terminus. Uncalcified patch on lateral margin of chelae of adult male white, translucent. Propodal cutting edge with row of small granules and one large tubercle. Chelipeds blue and white with white joints. Fingers blue in distal third black with hooked tips. Other walking legs blue-gray. Pleon black with pinkish-red pattern. Lateral pleura lighter becoming greyish green.

Description of male holotype (Figs 2–5). *Body* and eyes pigmented. Eyes not reduced. Body subovate, slightly compressed laterally. Pleon narrower than cepha-



Figure 1. *Cherax warsamsonicus* sp. n. **A** holotype male (MZB Cru 4529) from the Warsamson River, South Sorong Regency **B** idem, side view.

lothorax (width 16.7 mm and 17.5 mm respectively). Rostrum (Fig. 3A) broad in shape, reaching nearly to end of ultimate antennular peduncle and one third longer than wide (width 5 mm at base, length 13.6 mm). Upper surface smooth, slightly



Figure 2. *Cherax warsamsonicus* sp. n. holotype male (MZB Cru 4529). Scale bar: 10 mm.

scattered. Margins slightly elevated continuing in rostral carinae on carapace, almost straight in basal part, distally rather moderately tapering towards apex. Lateral rostral margin bearing three prominent teeth in distal half, pointing upwards at angle of approximately 45° . Few short hairs present on distal half of outer margins. Acumen with anteriorly orientated spine.

Rostral carinae extending as slight elevation posteriorly on carapace terminating at ending of postorbital ridges. Postorbital ridges well developed, terminating in spiniform tubercle anteriorly, fading at two-thirds of occipital carapace length, posteriorly. Dorsal surface of carapace smooth, slightly pitted, cervical and branchiocardiac grooves distinct, non-setose, one prominent corneous spine and three tubercles present at middle part behind cervical groove on lateral sides of carapace.

Areola length 13.7 mm, narrowest width 7.4 mm. Length of areola 31.8% of total length of carapace (43 mm).

Ventrolateral parts smooth with scattered pits; anterior margin strongly produced, rounded upper margin directed inward.

Scaphocerite (Fig. 3B) broadest at midlength, convex in distal part becoming narrower in basal part; thickened lateral margin terminating in large corneous spine, almost reaching distal margin of ultimate segment of antennular peduncle. Right scaphocerite 11 mm long and 4 mm wide. Proximal margins setose. Antennulae and antennae typical for genus. Antennae similarly long as body. Antennular peduncle reaching slightly behind acumen, antennal peduncle reaching slightly behind apex of scaphocerite. Antennal protopodite with spine anteriorly; basicerite with one lateral and one ventral spine.

Mouthparts typical for the genus. Epistome with subcordiform cephalic lobe anteriorly bearing lanceolate cephalomedian projection constricted at base. Lateral margins of lobe not thickened; each lateral margin with two groups of 8–9 tubercles separated by a smooth place. Central part smooth, not pitted, excavate. Eyes rather large; cornea globular, darkly pigmented, nearly as long as eyestalk; eyestalk slightly narrower than cornea.

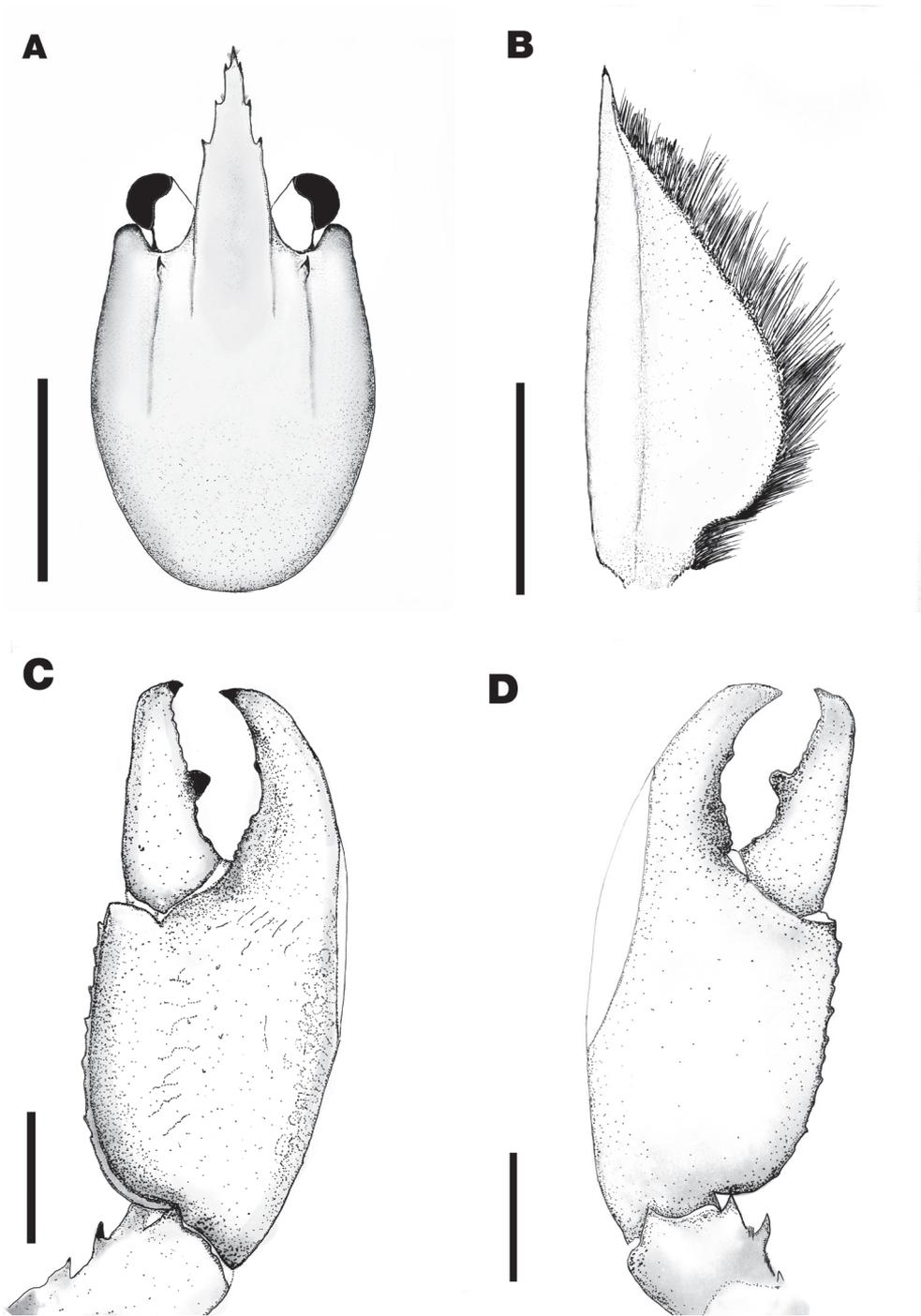


Figure 3. *Cherax warsamsonicus* sp. n. holotype male (MZB Cru 4529). **A** dorsal view of carapace **B** scaphocerite **C** dorsal view of right chelae **D** ventral view of left chelae. Scale bars: **A, C, D** 10 mm, **B** 5mm.

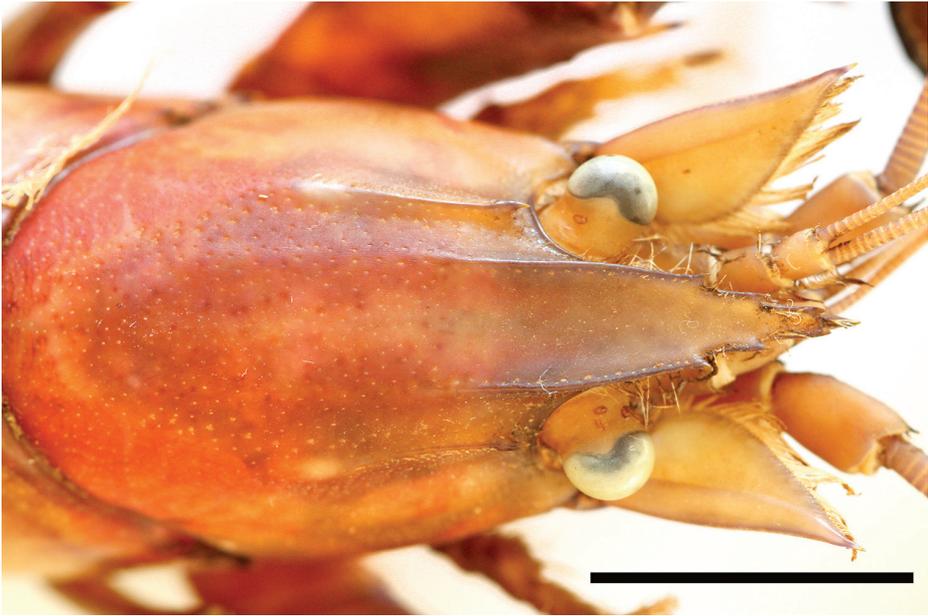


Figure 4. *Cherax warsamsonicus* sp. n. holotype male (MZB Cru 4529), dorsal view of cephalothorax. Scale bar: 10 mm.

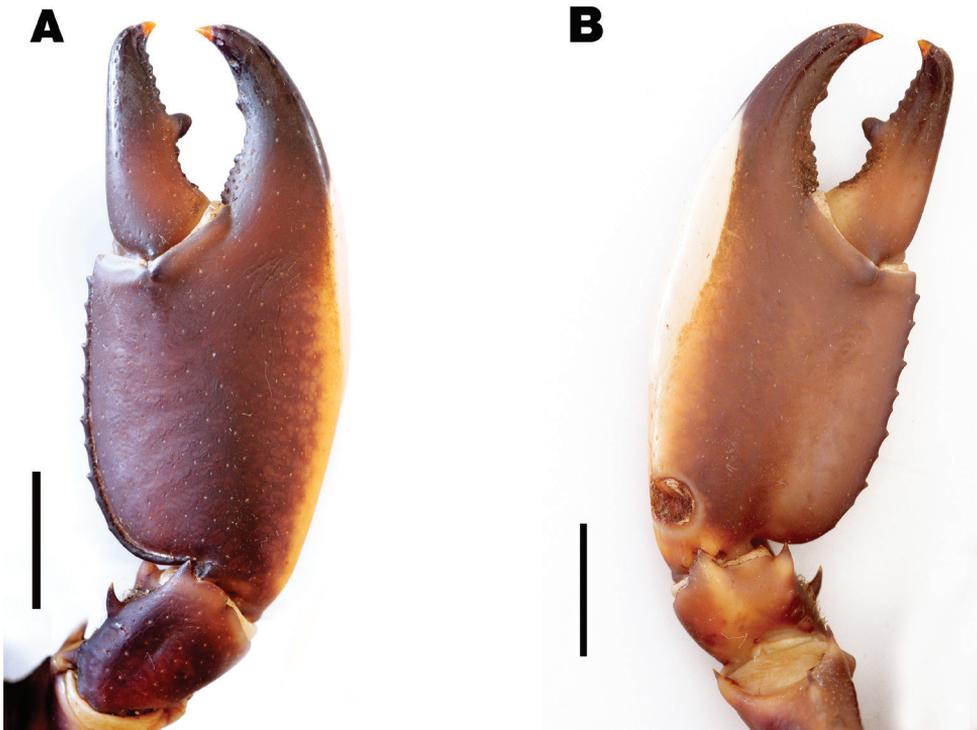


Figure 5. *Cherax warsamsonicus* sp. n. holotype male (MZB Cru 4529). **A** right first chela, dorsal aspect **B** right first chela, ventral aspect. Scale bars: 10 mm.

First pereopod equal in form, chela slightly gaping, equal in size, right cheliped (39 mm long, 8.2 mm high, 16.5 mm wide). Left chelae (Fig. 3C–D) 38.3 mm long and 8.2 mm high, 16.5 mm wide, strongly compressed. Fingers shorter than palm (dactylus 15.3 mm long). Dactylus broad at base (7 mm), tapering slightly towards tip.

Tip with sharp, corneous, hooked tooth pointing outwards at an angle of 45°. Cutting edge of dactyl with continuous row of rather small granular teeth and one prominent larger tooth at middle of cutting edge. Ventral and dorsal surface of movable finger with scattered punctuation. Posterior half of cutting edge with slightly rounded gap. Fixed finger triangular, merging gradually into palm, ending in sharp, corneous, hooked tooth, standing almost perpendicular to axis of finger. Tips of fingers slightly crossing when fingers clasp. Upper surface of palm practically smooth, slightly pitted, more densely pitted at margins. Fixed finger with approximately same width as dactyl at base (7.3 mm). Few scattered short setae present in posterior ventral part of fixed finger. Cutting edge of fixed finger with row of rather small granular teeth at posterior half and one at middle of anterior part.

Dorsal surface of carpus (11.77 mm) smooth and pitted, with slight excavation in middle part and with well-developed acute and hooked spiniform tubercle in middle of dorsolateral inner margin. Ventral carpal surface margins slightly elevated, non-setose and with fovea; inner margin with one acute spiniform tubercle oriented in angle of approx. 45°; outer margin smooth with one spiniform tubercle oriented almost anteriorly.

Merus (19.2 mm) laterally depressed in basal part; surface slightly pitted; one prominent spine at anterior part at dorsal surface. Row of 12–13 small granules on inner ventrolateral margin, four prominent spines, one at midlength other in middle of anterior part, third on distal ventrolateral outer margin, fourth on distal ventrolateral inner margin.

Ischium (10.8 mm) smooth with small spine and three granules at midlength of ventrolateral inner margin.

Second pereopod reaching anteriorly to approximately middle of scaphocerite. Finger as long as palm (5.6 mm), of same height. Short setae present on dactyl and fixed finger, getting denser anteriorly. Cutting edge of fixed finger and carpus with row of short setae. Carpus, smooth, not pitted, slightly longer than palm. *Merus* (12.7 mm) 1.7 times longer than carpus (7.2 mm). Ischium (6.2 mm) half as long as merus.

Third pereopod overreaching second by almost length of finger of second pereopods. Fingers shorter than palm. Fourth pereopod reaching distal margin of scaphocerite. Dactylus with corneous tip. Short scattered setae present. Propodus more than twice as long as dactylus, nearly 1.5 times as long as carpus; somewhat flattened, carrying many stiff setae on lower margin. *Merus* just slightly longer than propodus.

Fifth pereopod similar to fourth, slightly shorter.

Dorsal surface of pleon smooth, with scattered pits; abdominal segments with short setae present on caudal margins.

Telson with posterolateral spines, dense short setae present in posterior third. Posterior margins setose. Uropodal protopod with distal spine on mesial lobe. Exopod of uropod with transverse row of posteriorly directed diminutive spines ending in one



Figure 6. *Cherax warsamsonicus* sp. n., allotype female (MZB Cru 4530).

more prominent spine, posteriorly directed on outer margin of mesial lobe. Terminal half of exopod with small tubercles and short hairs, slightly corrugated. Endopod of uropod smooth. Short scattered hairs present on posterior third of dorsal exopod. Postrolateral spine on outer margin present. Second spine on medial dorsal surface present, directed posteriorly.

Description of allotype female (Fig. 6). Chela of first pereopods equal, 2.5 times as long as broad (24.5 mm and 9 mm respectively). Mesial margin of palm slightly elevated, forming slender serrated ridge with row of 9 small granular teeth. Cutting edge of dactylus with 8–9 rather small granular teeth. Cutting edge of fixed finger with 8–9 small granules. Small scattered short setae visible along ventral cutting edge of chelae, more dense and long in ventral posterior area. Tips of fingers slightly crossing when fingers clasp, not gaping. Cervical groove distinct, non-setose. Pleon just slightly narrower than cephalothorax (widths 12 mm and 12.5 mm respectively). Same colour pattern as in males, less intense.

Size. The biggest male examined has a carapace length of 48.7 mm, and a total length of 109 mm ($n = 4$), the holotype male has a total length of 92.8 mm the other males have a total length of 73 mm and 96 mm; the female has a carapace length of 31.8 mm and a total length of 73 mm ($n = 1$).

Colour. The living animals (Fig. 1A, B) are coloured as follows. Male: Chelae dark blue with white margins and white patch. Anterior part usually dark blue. Corneous tooth on tip of fingers orange. Cephalothorax greenish black, with small slightly darker spots laterally, fading ventrally to grey-green. Pink to pinkish red patch on dorsolateral side of the carapace between rostral carinae and cervical groove. Segments of pleon with pinkish red band anteriorly becoming black in posterior part. Lateral pleura slightly lighter becoming greyish green. Walking legs blue to dark bluish grey. Distal margin of tail-fan creamy orange to orange. Females: usually greyish green to bluish grey with bluish chelae and a white margin.

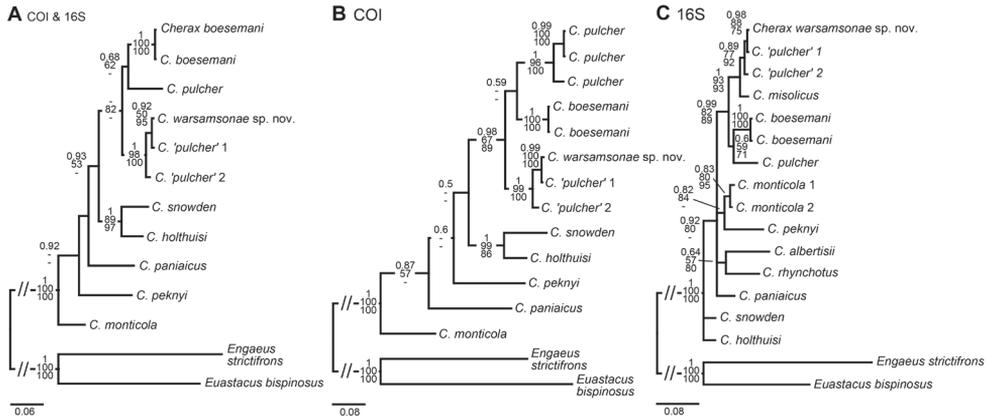


Figure 7. Phylogenetic position of *Cherax warsamsonicus* sp. n. within closely related New Guinean *Cherax* species, reconstructed by BI analyses of two mitochondrial gene fragments. Number on branches show, from top, Bayesian posterior probabilities and ML/MP bootstrap values. The scale bar indicates the substitution rate. See Table 1 for information on the sequenced specimens. **A** Topology based on concatenated COI and 16S dataset **B** Topology based on COI dataset **C** Topology based on 16S dataset.

Molecular phylogenetic results. *Cherax warsamsonicus* sp. n. clusters with two sequences retrieved from GenBank as *C. pulcher* and the entire cluster forms a well-supported clade with *Cherax misolicus* (16S only, Fig. 7C). The *C. 'pulcher'* sequences from GenBank almost certainly belong to *C. warsamsonicus* sp. n., as the included verified sequence of *C. pulcher* from a topotypical specimen is shown to be quite distinct and one of the two GenBank derived sequences is identical to the *C. warsamsonicus* sequence generated in this study. *C. warsamsonicus* sp. n. is well isolated from *C. misolicus* with a sequence divergence (p-distance, 16S) of 1.9-2.1 %, respectively, supporting the morphology-based description of *C. warsamsonicus* as a new species.

Deposition of types. The holotype (MZB Cru 4529), allotype (MZB Cru 4530) and paratypes (MZB Cru 4531) are deposited at the Museum Zoologicum Bogoriense (= Bidang Zoologi) Research Centre for Biology (=Pusat Penelitian Biologi), Indonesian Institute of Sciences (= LIPI), Jalan Raya Jakarta-Bogor Km 46 Cibinong 16911, Indonesia.

Systematic position. Holthuis (1949) in his publication on the New Guinea *Cherax* considered species should be placed into two groups. One with the rostral and median carinae absent or weakly developed and referred to as the *Cherax* group following the characteristics of the type species, *C. preissii* (Erichson) from southwest Australia. The other group contains species that have the rostral and sometimes the median carina well developed and referred to as the *Astaconephrops* group with Nobili's (1899) *Astaconephrops albertisii* as the type. Newly described species have been placed into one or the other of the two subgenera (Lukhaup and Pekny 2006; Lukhaup and Pekny 2008; Lukhaup and Herbert 2008; Lukhaup 2015, Lukhaup et al. 2015; Patoka, Blaha and Kouba 2015). Munasinghe et al. (2004a, b), Austin (1996); and Austin et al. (1996) however, identified three geographically-based lineages within *Cherax* based on

molecular genetics and phylogenetic studies. These consist of a southwestern group, an eastern group and a northern group. Support for the latter group however was based on only very limited sampling (e.g. single samples of *C. quadricarinatus*, *C. rhynchotus* and *C. peknyi* in Munasinghe et al. study). Munasinghe et al. (2004b) indicate that the division of *Cherax* into two subgenera, as conceived by Holthuis and subsequent authors dealing with New Guinea crayfish has to be reconsidered. Based on Munasinghe et al. (2004), Austin (1996), and Austin et al. (1996a). *Cherax warsamsonicus* sp. n. belongs to the northern species group lineage consisting of 22 species:

- C. albertisii* (Nobili, 1899)
- C. boesemani* Lukhaup & Pekny, 2008
- C. boschmai* Holthuis, 1949
- C. buitendijkae* Holthuis, 1949
- C. communis* Holthuis, 1949
- C. divergens* Holthuis, 1950
- C. gherardii* Patoka, Bláha & Kouba, 2015
- C. holthuisi* Lukhaup & Pekny, 2006
- C. lorentzi aruanus* (Roux, 1911)
- C. lorentzi lorentzi* (Roux, 1911)
- C. longipes* Holthuis, 1949
- C. misolicus* Holthuis, 1949
- C. murido* Holthuis, 1949
- C. monticola* Holthuis, 1950
- C. minor* Holthuis, 1996
- C. peknyi* Lukhaup & Herbert, 2008
- C. pallidus* Holthuis, 1949
- C. papuanus* Holthuis, 1949
- C. paniaicus* Holthuis, 1949
- C. pulcher* Lukhaup, 2015
- C. solus* Holthuis, 1949
- C. snowden* Lukhaup, Panteleit & Schrimpf, 2015

In comparison to all species of the northern group the new species, *C. warsamsonicus*, is most similar to *C. misolicus*, a species that is endemic to Misool Island, one of four major islands in the Raja Ampat Islands in West Papua, Indonesia.

Cherax warsamsonicus sp. n. differs from *C. misolicus* in the following characters: shape of the chelae, (Fig. 8C, D), shape of the rostrum, the presence of setae on the rostrum and in colouration. *Cherax misolicus* has two rostral teeth on each margin of the rostrum while *Cherax warsamsonicus* sp. n. bears 3–4 prominent teeth on each margin. The rostrum of *Cherax misolicus* is rather straight, triangular shaped, while the rostrum of *Cherax warsamsonicus* sp. n. is clearly bent outwards at middle part (Fig. 8A, B). *C. warsamsonicus* sp. n. has one prominent corneous spine and three tubercles present at middle part behind cervical groove on lateral sides of carapace while

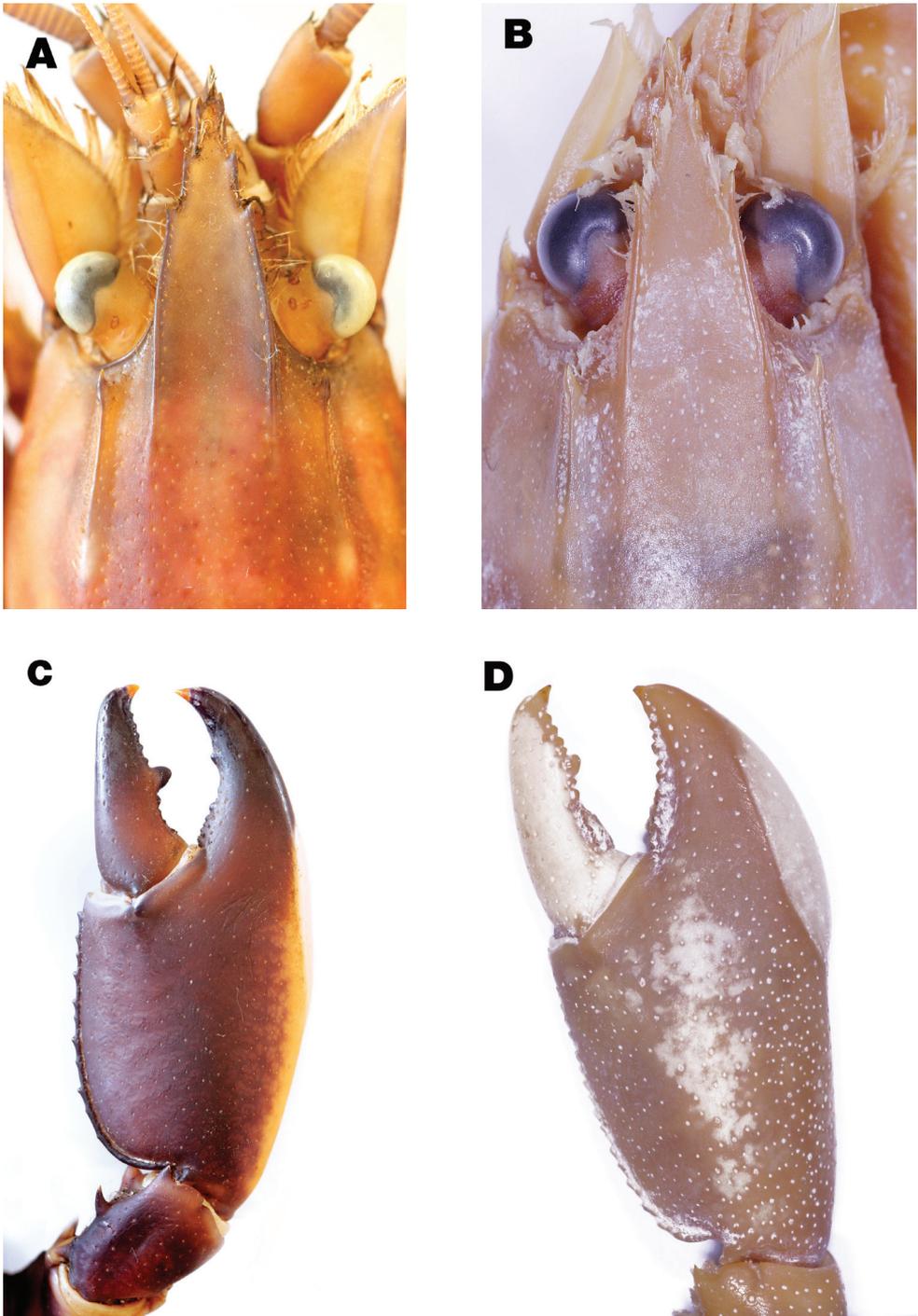


Figure 8. Rostrum dorsal view **A** *Cherax warsamsonicus* sp. n., holotype male, (MZB Cru 4529) **B** *Cherax misolicus* (NMB 956a) **C** *Cherax warsamsonicus* sp. n right first chela, dorsal aspect **D** *Cherax misolicus* right first chela, dorsal aspect.

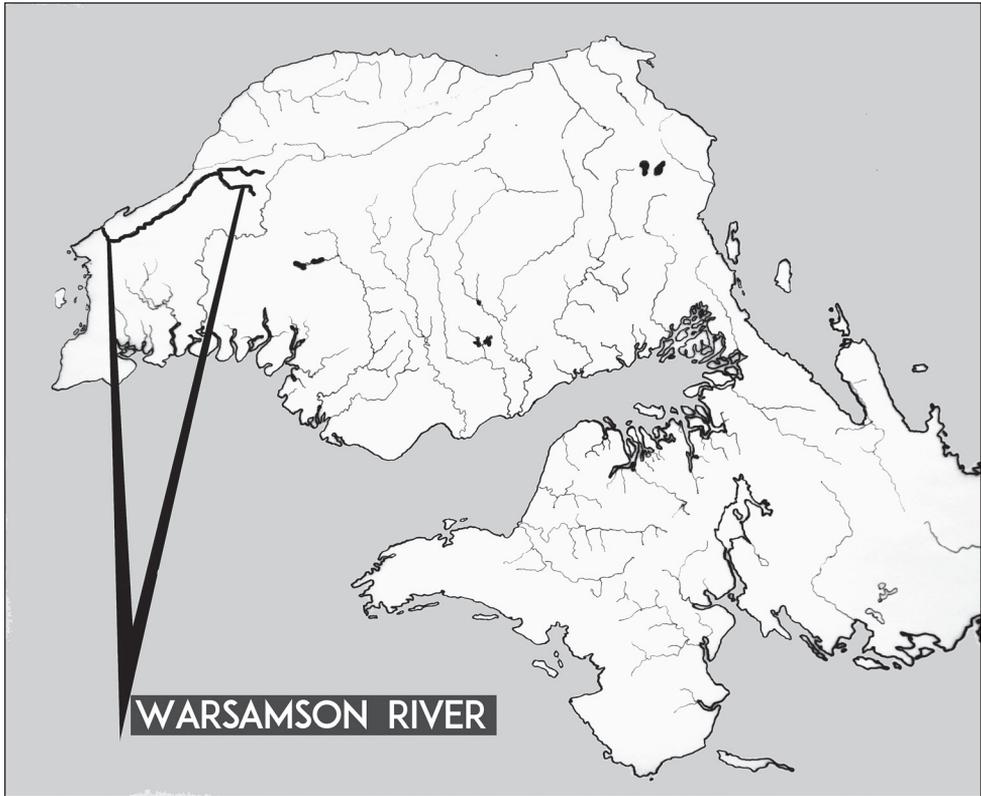


Figure 9. The Bird's Head Peninsula, West Papua, Indonesia with the type locality, Warsamson River, indicated.

C. misolicus has 6–7 small tubercles present there. *Cherax warsamsonicus* sp. n. usually has bluish or dark blue chelae with a white coloured lateral margin and a white patch. Body colour is greenish grey with some pink or red patches on the dorsal carapace right behind the rostral carinae. Pleon is greenish grey with a red to pink pattern dorsally. Legs are usually blue, grey blue or grey. *Cherax misolicus* has light blue chelae, the body is olive green with orange bluish legs and a dark blue pleon with orange on the lateral pleon.

Cherax warsamsonicus sp. n. is endemic in the Warsamson River and Warsamson tributaries in West Papua while *C. misolicus* is endemic in creeks and rivers of Misool Island.

Etymology. *Cherax warsamsonicus* sp. n. is named after the Warsamson River in West Papua where it seems to be endemic (Fig. 9).

Ecology. Known only from the Warsamson River and its tributaries, South Sorong Regency in the central part of the Kepala Burung (Vogelkop) peninsula. The creeks from where these crayfish have been collected are shallow (20–60 cm) with a moderate flow, the water is clear, and have a pH of approximately 6.5. In most of the parts no water plants are present. The substrate of the creek is gravel or sand and soil



Figure 10. Tributary to the Warsamson River, habitat of the new species.

mostly covered with silt and detritus, stones and larger rocks (Fig. 10). Crayfish hide in short borrows in the riverbank, under larger rocks or in detritus that gathers in slower flowing parts of the creek or river. To improve the knowledge of the distribution of the species more field trips will be necessary.

Common name. The common name of the new species in the pet trade is *Cherax* “irian jaya”, *Cherax* “pink coral”, and sometimes it is sold also as *Cherax pulcher*. Therefore we propose the name Warsamson River Crayfish as a common name for the new species.

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