

# Review of the fish parasitic genus *Elthusa* Schioedte & Meinert, 1884 (Crustacea, Isopoda, Cymothoidae) from South Africa, including the description of three new species

Serita van der Wal<sup>1,2</sup>, Nico J. Smit<sup>1</sup>, Kerry A. Hadfield<sup>1</sup>

**1** Water Research Group, Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom, 2520, South Africa **2** Zoomorphology group, Department of Biology II, Ludwig-Maximilians-University, Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany

Corresponding author: Kerry A. Hadfield ([kerry.malherbe@nwu.ac.za](mailto:kerry.malherbe@nwu.ac.za))

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## Abstract

The branchial-attaching cymothoid genus, *Elthusa* Schioedte & Meinert, 1884 is a genus with a world-wide distribution of 36 species, including the three species described here. *Elthusa raynaudii* (Milne Edwards, 1840) is the only species that has been described from southern Africa. All South African material held at the National Museum of Natural History, Paris, France (MNHN) and the Iziko South African Museum, Cape Town (SAMC) identified as, or appearing to belong to, *Elthusa* was examined. Four species were identified, *Elthusa raynaudii* and three species that proved to be undescribed. *Elthusa xena* **sp. n.** can be distinguished by an evenly rounded pereonite 1 anterior margin, a roughly rectangular pleotelson, and narrowly rounded uropod apices that extend to more than half the length of the pleotelson. *Elthusa acutinasa* **sp. n.** is identified by the produced and narrowly rounded cephalon anterior margin, acute uropods that are shorter than half the length of the pleotelson, and pereonite 1 anterior margin with medial projection. *Elthusa rotunda* **sp. n.** is characterised by the round body shape, broadly rounded uropod apices, and protrusions on the proximal and lateral margins of the merus and carpus of pereopod 7. A key to the South African *Elthusa* species is provided, together with a table summarising the hosts and localities of the 33 previously known species of *Elthusa*.

## Keywords

Alexander Bay, Atlantic Ocean, *Clinus superciliosus*, *Elthusa raynaudii*, fish parasites, Indian Ocean, taxonomy

## Introduction

*Elthusa* Schioedte & Meinert, 1884 is a branchial cavity-inhabiting cymothoid genus that was described as a monotypic genus for *Elthusa emarginata* (Bleeker, 1857). *Elthusa* was subsequently largely overlooked until Bruce (1990) provided a new diagnosis based on one of Bleeker's (1857) syntypes and the Australian species of the genus. Most species of *Elthusa* were originally described and placed within the genus *Livoneca* before their revision and redescription by Bruce (1990).

Currently, there are 33 known and accepted *Elthusa* species (Öktener et al. 2018a). *Elthusa* is one of the more speciose genera within the family Cymothoidae Leach, 1818, however many species of *Elthusa* still need to be studied and redescribed due to their original descriptions being inadequate, lacking morphological detail and illustrations. The high morphological intraspecific variability that exists within this genus (Hadfield et al. 2017) has also contributed, in some cases, to misidentifications and confusion regarding the placement of species.

Most species of *Elthusa* inhabit the branchial cavities of their fish hosts (Smit et al. 2014), with the exception of two species. *Elthusa neocyttta* (Avdeev, 1975) ovigerous females have been recorded from the buccal cavity of the spiky oreo, *Neocyttus rhomboidalis* Gilchrist, 1906 (see Stephenson 1987), and *Elthusa splendida* (Sadowsky & Moreira, 1981) has been described from the buccal cavity of the spiny dogfish *Squalus cubensis* Rivero, 1936 (see Sadowsky and Moreira 1981).

*Elthusa* is considered to be cosmopolitan, except for polar waters (Bruce 1990, Bruce et al. 2002, Rocha-Ramírez et al. 2005, Hadfield et al. 2017), and is predominantly recorded from the Indo-West Pacific (see Bruce 1990, Trilles and Justine 2006) with only occasional records of species from the Eastern Pacific (Brusca 1978, Espinosa-Pérez and Hendrickx 2001), the Atlantic (Kensley and Brusca 2001) and the Mediterranean (Trilles and Justine 2006, Öktener et al. 2018a). *Elthusa raynaudii* (Milne Edwards, 1840) is the only species of *Elthusa* that has been described from sub-Saharan Africa. The lack of species records is most likely due to the lack of studying cymothoid isopods from this region and is not a true representation of the biodiversity of this genus. This paper forms part of a detailed study on the cymothoids from sub-Saharan Africa and confirms this postulation with the identification of three new species from the region.

## Materials and methods

Twenty-seven specimens of *Elthusa* were examined. Material loaned from the National Museum of Natural History, Paris, France (MNHN) and the Iziko South African Museum, Cape Town (SAMC) was included in the examination. These specimens were collected as early as 1840 (MNHN) and 1960 (SAMC). Non-museum material was

collected during 1993 in the intertidal zone of Alexander Bay, as well as from deep-sea trawlers during January 1999 and April 2003 off the south coast (RV *Africana*), and during February 2010 off the west coast of South Africa (RV *Dr Fridtjof Nansen*).

Specimens were identified by illustrating all body parts and appendages using a Nikon SMZ1500 Stereo Microscope and a Nikon Eclipse80i Compound Microscope, both equipped with drawing tubes. The position of specimens and dissected parts were manipulated to obtain the most accurate direct and complete view in order to minimise errors in illustrated ratios of segments. Material loaned from national museums was not dissected. Species descriptions were made with the aid of the taxonomy software package DELTA (Descriptive Language for Taxonomy) (see Coleman et al. 2010), following a general Cymothoidae character data set originally developed by Hadfield et al. (2010) and recently updated for other genera (Hadfield et al. 2013, 2016b). Ratios and measurements for the descriptions were made using the maximum values at the middle of the specific measured segment, and all proportional measurements were rounded to one decimal place. Higher-level classification follows that of Brandt and Poore (2003). Host authorities are not included in the text or references; host nomenclature and distribution were sourced from FishBase (see Froese and Pauly 2018) and Catalog of Fishes (see Eschmeyer 2018).

#### Abbreviations:

<b>DELTA</b>	Descriptive Language for Taxonomy	<b>RV</b>	research vessel
<b>MNHN</b>	National Museum of Natural History, Paris, France	<b>SAMC</b>	Iziko South African Museum
<b>NWU</b>	North-West University, Potchefstroom Campus	<b>Syn</b>	synonym
<b>OH</b>	other hosts	<b>TH</b>	type host
<b>OL</b>	other localities	<b>TL</b>	total length
		<b>TLoc</b>	type locality
		<b>W</b>	width

## Taxonomy

### Suborder Cymothoidea Wägele, 1989

### Superfamily Cymothoidea Leach, 1814

### Family Cymothoidae Leach, 1814

### Genus *Elthusa* Schioedte & Meinert, 1884

*Elthusa*: Schioedte and Meinert 1884: 337; Bruce 1990: 254; Trilles and Randall 2011: 453; Hadfield et al. 2017: 3.

**Type species.** *Livoneca emarginata* Bleeker, 1857; by monotypy (Schioedte and Meinert 1884). The original number of type specimens that were available to Bleeker (1857) is unknown. A single female syntype, examined by Bleeker (1857), is deposited at the Naturalis Biodiversity Center (previously the Rijksmuseum von Natuurlijke Historie),

Leiden (RMNH.CRUS.I.66). Another type specimen from the latter museum has been lost. The specimen examined by Schioedte and Meinert (1884) is held at the Natural History Museum in Paris (MNHN241) (Trilles 1976).

**Remarks.** Species from *Elthusa* can be distinguished from other genera by having a weakly vaulted dorsum with a wide pleon; antennulae that are shorter than, or subequal in length to antennae, bases not in contact; a cephalon posterior margin that is not trilobed; and lamellar pleopods. Other diagnostic characters include a slender maxilliped palp article 3, with setae present; as well as pereopods with relatively short dactyli (see Bruce 1990 for a revised diagnosis of the genus).

Trilles and Randall (2011) redescribed the type species for the genus, *E. emarginata*. This redescription provided a more detailed description and more accurate drawings of the species that had previously not been possible due to the fragility of the syntype. It also allows for a diagnosis and description of the genus based on the type material. However, Trilles and Randall (2011) designated one of the examined specimens [material deposited by Schioedte and Meinert (1884) into the Natural History Museum in Paris, MNHN No. 241] as the lectotype for the species. This does not follow the ICZN rules (Article 74.1) for lectotype designation as there is extant type material (RMNH.CRUS.I.66). Furthermore, no figures were provided of the designated lectotype material to ensure recognition of the specimen designated (ICZN Article 74.7.2). As such this lectotype designation is invalid and set aside (ICZN Article 74.2).

The original description by Bleeker (1857) did not specify any host species, genus or even family (“the skin of various species of fish”) and Trilles and Randall’s (2011) redescription is not supported by or based on specimens being from the same host species or genus. Trilles and Randall (2011) did not examine Bleeker’s remaining syntype, and comparison of the two accounts suggest that there are some differences between the Bleeker (1857) figures and those of Trilles and Randall (2011); most notably being the shape of the cephalon, which is truncate or subtruncate in the syntype but anteriorly concave in Trilles and Randall’s redescription; and the pleotelson in the syntype is broadly rounded (“semi-circular”) while distally narrowed in Trilles and Randall’s redescription. Trilles and Randall (2011) made no direct reference to Bleeker’s (1857) description and did not comment on any perceived character difference. These differences suggest that direct comparison to Bleeker’s syntype is needed to confirm conspecificity of the specimens identified by Trilles and Randall (2011) as *E. emarginata*.

### Key to the species of *Elthusa* from southern Africa

- 1 Pleonite 5 lateral margins visible; uropods half the length of pleotelson or longer; pereonite 1 anterior margin without medial projections; pereonite 1 anterolateral margin extending to medial region of the eye ..... **2**
- Pleonite 5 lateral margins largely concealed by pleonite 4; uropods short, less than half the length of pleotelson; pereonite 1 anterior margin medially pointed; pereonite 1 anterolateral margin extending to posterior margin of the eye ..... ***Elthusa acutinasa* sp. n.**

- 2 Cephalon with rounded anterior margin; uropod rami apices broadly rounded; pleotelson evenly rounded.....**3**
- Cephalon anterior margin narrowly rounded; uropod rami apices narrowly rounded; pleotelson sub-quadrate ..... *Elthusa xena* sp. n.
- 3 Pereon 1.2–1.4 times as long as wide; cephalon anterior margin blunt; pereopod 7 without bulbous protrusions; uropods more than half the length of pleotelson; pleonites subequal in length ..... *Elthusa raynaudii*
- Pereon as long as wide; cephalon anterior margin concave; pereopod 7 merus and carpus with bulbous protrusions; uropods half the length of pleotelson; pleonite 5 longest..... *Elthusa rotunda* sp. n.

***Elthusa raynaudii* (Milne Edwards, 1840)**

Figures 1–3, Table 1

*Livoneca Raynaudii*: Milne Edwards 1840: 262; Krauss 1843: 66; Bleeker 1857: 30; Schioedte and Meinert 1884: 367, pl. 12, figs 9–13; Thielemann 1910: 42; Hale 1926: 215–217, figs 10a–j.

*Cymothoa Novae-Zealandia*: White 1847: 110 (nomen nudum).

*Lironeca novae-zealandia*: Miers 1874: 228; 1876: 106, pl. III, fig. 2; 1881: 64, 67.

*Lironeca laticauda*: Miers 1877: 677, pl. 69, fig. 5; Ellis 1981: 124.

*Livoneca Raynaudi*.–Gerstaecker 1882: 259.

*Livoneca Novae Zelandiae*.–Gerstaecker 1882: 263.

*Lironeca Stewarti*: Filhol 1885: 450, pl. 4, fig. 6.

*Lironeca neo-zelanica*.–Thomson and Chilton 1886: 154.

*Livoneca raynaudii*.–Whitelegge 1902: 236; Chilton 1909: 606; 1911: 309; 1912: 135; Stebbing 1910: 125; Young 1926: 283; Hale 1926: 215, fig. 10; 1929: 261, figs 253, 259; 1940: 303; Barnard 1940: 491; 1955: 6; Hurley 1961: 268; Hewitt and Hine 1972: 108; Sivertsen and Holthuis 1980: 34; Beumer et al. 1982: 33.

*Livoneca epimerias*: Richardson 1909: 88, fig. 13; Kussakin 1979: 301, figs 69, 170.

*Livoneca raynaudi*.–Nierstrasz 1915: 97; 1931: 145; Barnard 1920: 358; Pillai 1954: 16.

*Livoneca laticauda*.–Nierstrasz 1931: 143.

*Lironeca raynaudii*.–Brian and Dartevelle 1949: 176; Avdeev 1975: 250; 1978: 281; Trilles 1976: 778, pl. 1, fig. 4; Poore 1981: 341.

*Lironeca raynaudi*.–Menzies 1962: 115, fig. 36A–B; Kensley 1978: 80, fig. 33B; Moreira and Sadowsky 1978: 111.

*Lironeca magna*: Mañé-Garzón 1979: 18, figs 1–5.

*Elthusa raynaudii*.–Bruce 1990: 263; Bruce et al. 2002: 177; Williams et al. 2010: 99–101.

*Elthusa raynaudi*.–Ghani 2003: 218.

**Type material.** Type material held at the Museum national d’Histoire naturelle, Paris (syntypes MNHN-IU-2016-9885; MNHN-IU-2016-9884).

**Type locality.** Cape of Good Hope, South Africa.

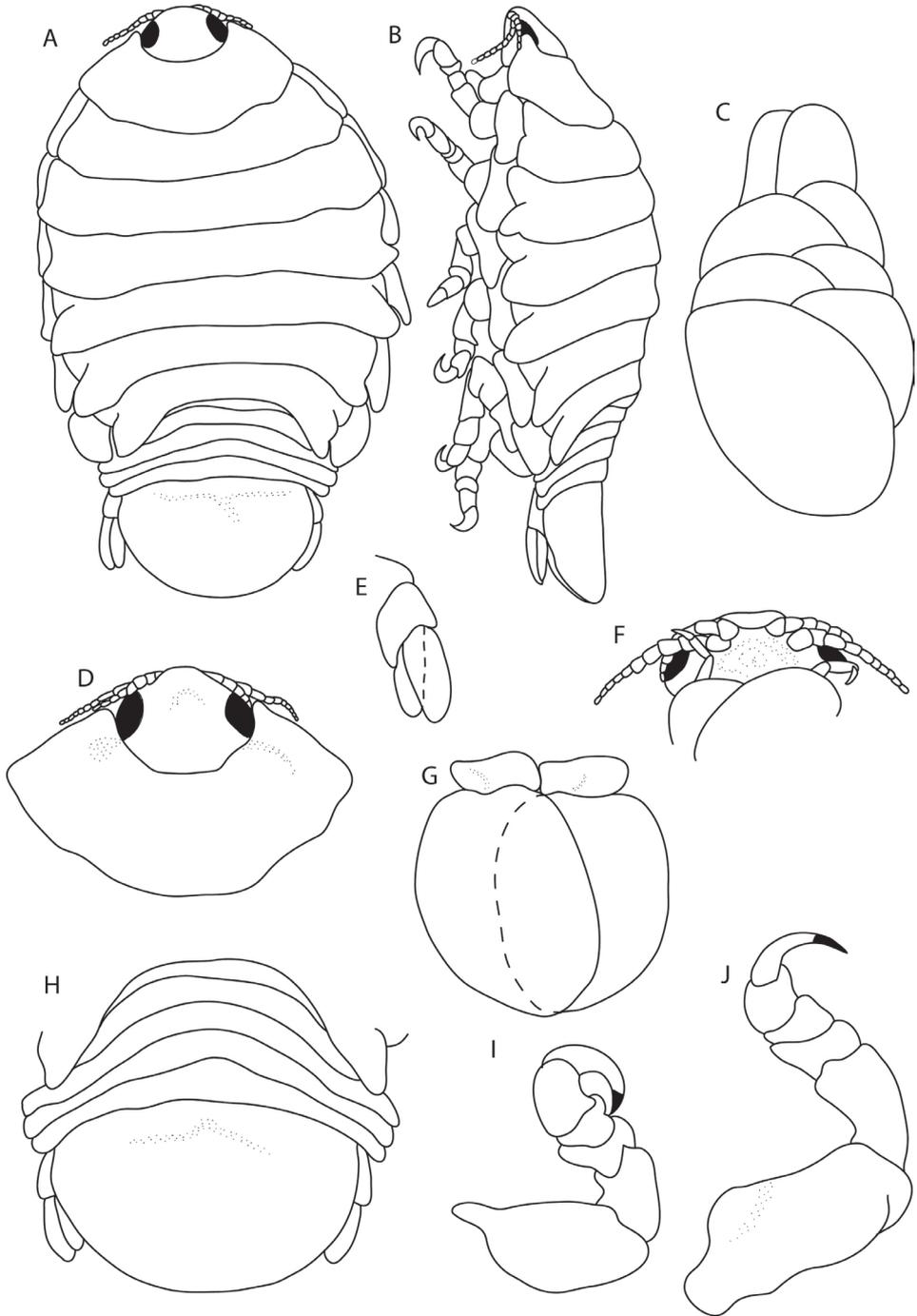
**Type host.** Unknown.

**Material examined** (all from South Africa). *Syntype*. SOUTH AFRICA • 1 ♀ (ovigerous, 26.7 mm TL, 14.1 mm W); south coast of South Africa, Cape of Good Hope; MNHN-IU-2016-9885. *Other material*. SOUTH AFRICA • 1 ♀ (ovigerous, 26.0 mm TL, 14.0 mm W); Indian Ocean, south coast of South Africa, RV Africana (fish sorting table); 34°38'S, 25°38'E; April 2003; coll. Nico J. Smit; dissected; in the collection of the authors at NWU • 1 ♀ (ovigerous, 26.0 mm TL, 15.0 mm W); Atlantic Ocean, RV Dr Fridtjof Nansen trawl (Station NAN401T062); January 2007; coll. L Atkinson; SAMC-A47881 • 1 ♀ (ovigerous, 20.0 mm TL, 12.0 mm W); Atlantic Ocean, RV Dr Fridtjof Nansen (fish sorting table); 32°17'S, 16°54'E; 269 m; February 2010; coll. KA Hadfield; dissected; SAMC-A089957.

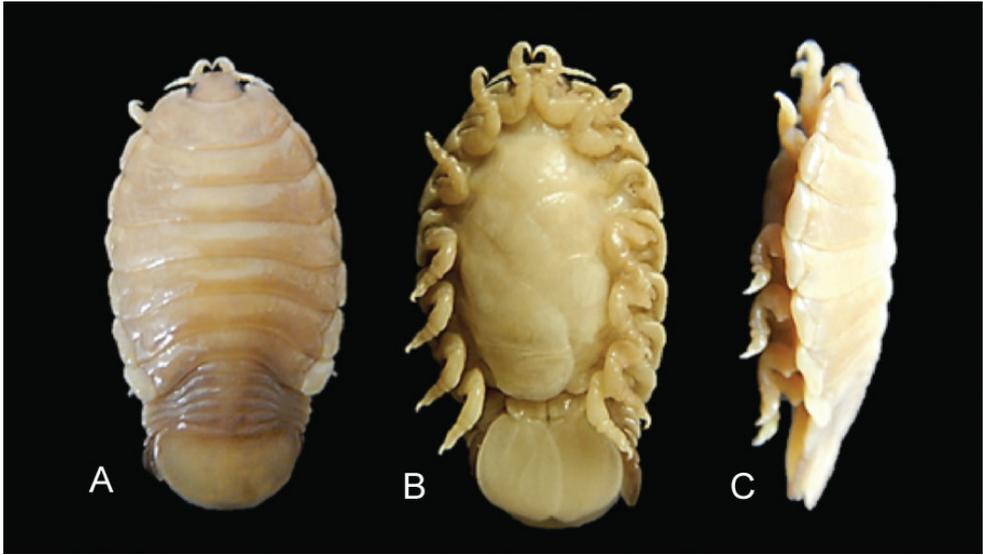
**Description** (ovigerous ♀). Figs 1–3. *Body* ovoid, slightly twisted to the left, 1.7 times as long as greatest width; dorsal surfaces smooth and polished in appearance, widest at pereonite 5, most narrow at pereonite 1; pereonite lateral margins mostly posteriorly ovate, medially indented. *Cephalon* 0.9 times longer than wide, visible in dorsal view, sub-truncate with blunt anterior margin. *Frontal margin* thickened, ventrally folded. *Eyes* oval with distinct margins; one eye 0.2 times width of cephalon, 0.4 times length of cephalon. *Pereonite 1* smooth; anterior border medially straight, curved laterally; anterolateral angle narrowly rounded, extending to the medial region of eyes. Posterior margins of pereonites smooth, slightly curved laterally. *Coxae* 2–3 wide, with posteroventral angles rounded; coxae 4–7 with rounded point, not extending past pereonite posterior margin. Pereonites 2–5 subequal, becoming more progressively rounded posteriorly; pereonites 6 and 7 slightly narrower. *Pleon* 0.4 times as long as total body length, with pleonite 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleonites posterior margin mostly concave. *Pleonite 2* partially overlapped by pereonite 7. Pleonites 3–5 similar in form to pleonite 2; pleonites subequal in length, with posterolateral angles narrowly rounded, posterior margin straight. *Pleotelson* 0.6 times as long as anterior width, dorsal surface smooth; lateral margins weakly convex; posterior margin evenly rounded.

*Antennula* shorter than antenna, consisting of eight articles; antennula peduncle articles I and II distinct and articulated, extending to anterior of pereonite 1. *Antenna* consists of eleven articles, extending to middle of pereonite 1.

*Pereopod 1* basis 1.6 times as long as greatest width; ischium 0.7 times as long as basis; merus proximal margin without bulbous protrusion; carpus with rounded proximal margin; propodus 1.4 times as long as wide; dactylus slender, 1.6 times as long as propodus, 2.9 times as long as basal width. All pereopods without robust or simple setae. *Pereopod 7* basis with carina, 2.5 times as long as greatest width; ischium without protrusions, 0.5 times as long as basis; merus 0.7 times as long as wide, 0.4 times as long as ischium; carpus without bulbous protrusion, 0.7 times as long as wide, 0.3 times as long as ischium; propodus 0.8 times as long as wide, 0.3 times as long as ischium; dactylus slender, 2.3 times as long as propodus, 3.5 times as long as basal width.



**Figure 1.** *Elthusa raynaudii* (Milne Edwards, 1840) ♀ (ovigerous, 20.0 mm TL, 12.0 mm W) (SAMC-A089957) from Dr Fridtjof Nansen research vessel **A** dorsal body **B** lateral body **C** oostegites **D** dorsal view of cephalon and pereonite 1 **E** uropod **F** ventral cephalon **G** pleopod 1 **H** dorsal view of pleonite 1 **I** pereopod 1 **J** pereopod 7.

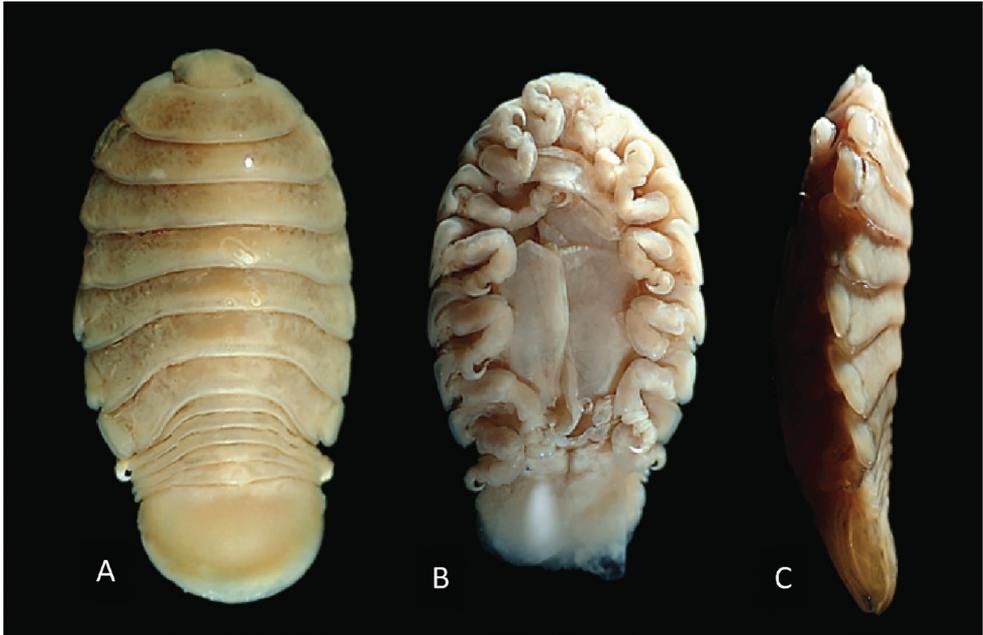


**Figure 2.** Photos of *Elthusa raynaudii* (Milne Edwards, 1840) ♀ (ovigerous, 26.0 mm TL, 15.0 mm W) (SAMC-A47881) from Dr Fridtjof Nansen research vessel **A** dorsal view **B** ventral view **C** lateral view.

*Pleopods* simple, exopod larger than endopod. *Pleopod 1* exopod 1.3 times as long as wide, lateral margin weakly convex, distally narrowly rounded, mesial margin straight; peduncle 2.3 times as wide as long.

*Uropod* more than half the length of pleotelson; peduncle 0.5 times longer than rami, lateral margin without setae; rami not extending beyond pleotelson, apices broadly rounded. *Endopod* apically rounded, 2.7 times as long as greatest width, terminating without setae. *Exopod* extending to end of endopod, 2.2 times as long as greatest width, apically rounded, terminating without setae.

*Variations.* Intra-specific variations can cause difficulty in identification and should be taken into consideration. One of the more obvious variations is the overall body shape of examined individuals, as seen from the dorsal view. While the syntype (MNHN-IU-2016-9885) has weakly convex, symmetrical lateral margins, specimen SAMC-A089957 is not as symmetrical, with the right margin being strongly convex and that of the left margin, weakly convex. The latter specimen therefore appears to be less symmetrical. Bruce (1990) mentioned this occasional asymmetrical body shape as an observed variation, as a result of slightly twisted individuals. The body shape of the South African specimen (SAMC-A089957) accords to the shape of individuals illustrated and described by Bruce (1990). In addition, the widest part of this species may vary between pereonite 4 and pereonite 5. This variation may also cause individual body shapes to appear dissimilar. The anterior margin of the cephalon of the syntype (MNHN-IU-2016-9885) appears to be rounded rather than subtruncate. The posterior margin of pleonite 5 can be roughly straight (AM G2181 from Bruce 1990), have a slight medial point, or be weakly concave (Bruce 1990, present study). Although



**Figure 3.** Photos of syntype material *Livoneca raynaudii* Milne Edwards, 1840 ♀ (ovigerous, 26.7 mm TL, 14.1 mm W) (MNHN-IU-2016-9885) **A** dorsal view **B** ventral view **C** lateral view.

Bruce (1990) described the uropods as being short, most measure more than half the length of the pleotelson.

**Size.** Ovigerous females 20.0–26.7 mm TL, 14.0–15.0 mm W. Other material: ovigerous females 22.0–67.0 mm TL (average 30.83 mm TL) (Bruce 1990).

**Distribution.** Records listed from west to east. North Pacific Ocean: Bering Sea (Kensley 1976). South America: Punta Quillaie (Menziés 1962) and Chile (Nierstrasz 1931); Uruguay (Mañé-Garzón 1979). South Atlantic Ocean: Saint Helena and Tristan da Cunha (Sivertsen and Holthuis 1980). South Africa: Table Bay (Barnard 1920); Cape of Good Hope (Milne Edwards 1840); Durban (Barnard 1955). India: Travancore (Pillai 1954). Southern Indian Ocean: Amsterdam Island (Kensley 1976). Australia: southern and south-eastern Australia (Schioedte and Meinert 1884, Hale 1926, Bruce 1990, Whitelegge 1901). Japan: Yokohama (Schioedte and Meinert 1884). New Zealand (Filhol 1885, Chilton 1909, Nierstrasz 1915, Hurley 1961, Bruce 1990).

**Hosts.** *Elthusa raynaudii* has been recorded from various fish hosts of multiple orders and families. These hosts are: *Chelidonichthys kumu* (Cuvier, 1829) (see Avdeev 1978); *Chorisochismus dentex* (Pallas, 1769) (see Barnard 1920); *Cyttus australis* (Richardson, 1843) (see Avdeev 1978, 1984, Bruce 1990); *Cyttus novaezelandiae* (Arthur, 1885) (see Avdeev 1978, 1984); *Cyttus traversi* Hutton, 1872, previously *Cyttoidops mccullochi* (Whitley, 1947) (see Avdeev 1984, Bruce 1990); *Genypterus blacodes* (Bloch and Schneider, 1801) (see Hewitt and Hine 1972); *Gnathanacanthus goetzeei* Bleeker, 1855 (see Bruce 1990); *Hyporhamphus intermedius* (Cantor, 1842) (see Powell 1959,

Stephenson 1969); *Latris lineata* (Forster, 1801) (see Kensley 1976); *Meuschenia freycineti* (Quoy and Gaimard, 1824) (see Bruce 1990); *Mustelus antarcticus* Günther, 1870 (see Hewitt and Hine 1972); *Nemadactylus monodactylus* (Carmichael, 1819), previously *Acantholatris monodactylus* (Carmichael, 1819) (see Sivertsen and Holthuis 1980); *Nematalosa nasus* (Bloch, 1795) (see Ghani 2003); *Notacanthus sexspinis* Richardson, 1846 (see Avdeev 1978, 1984); *Notothenia microlepidota* Hutton, 1875, previously *Notothenia colbecki* (see Chilton 1909, Hewitt and Hine 1972, Avdeev 1978, 1984); *Notolabrus tetricus* (Richardson, 1840), previously *Pseudolabrus tetricus* (see Bruce 1990); *Paranotothenia magellanica* (Forster, 1801), previously *Notothenia macrocephala* (see Avdeev 1978); *Ilisha melastoma* (Bloch and Schneider, 1801) previously *Pellona brachysoma* (see Pillai 1954); *Pelotretis flavilatus* Waite, 1911 (see Chilton 1911); *Pseudophycis bachus* (Forster, 1801), previously *Physiculus bachus* (see Hewitt and Hine 1972); *Physiculus* sp. (see Bruce 1990); *Pseudophycis barbata* Günther, 1863, previously *Physiculus barbatus* (Günther, 1863) (see Bruce 1990); *Pseudolabrus miles* (Schneider and Forster, 1801) (see Poore 1981, Bruce 1990); *Pseudophycis bachus* (Forster, 1801) (see Chilton 1911, Bruce 1990); *Rexea solandri* (Cuvier, 1832) (see Bruce 1990); *Rhombosolea* sp. (see Hewitt and Hine 1972); *Sardinops sagax* (Jenyns, 1842), previously *Clupea neopilchardus* Steindachner, 1879 (see Chilton 1911); *Scorpaena cardinalis* Solander and Richardson, 1842 (see Poore 1981); *Sebastes capensis* (Gmelin, 1789), previously *Sebastichthys capensis* (Gmelin, 1789) (see Sivertsen and Holthuis 1980); *Stolephorus commersonnii* Lacepède, 1803 (see Pillai 1954); *Thyrsites atun* (Euphrasen, 1791) (see Sivertsen and Holthuis 1980); *Zenopsis nebulosa* (Temminck and Schlegel, 1845), previously *Zenopsis nebulosus* (see Bruce 1990); *Zeus faber* Linnaeus, 1758 (see Hale 1926, Avdeev 1984). Unidentified by scientific names: banded perch (Serranidae), flathead (Platycephalidae) (see Bruce 1990).

**Remarks.** *Elthusa raynaudii* can be distinguished by the cephalon having a narrowly truncate rostrum; pereonite 1 with anterior margin straight; pleonites subequal in shape and width; and broadly rounded uropod apices that extend to more than half the length of the pleotelson.

Originally described in 1840, from the Cape of Good Hope in South Africa, from an unknown host, *Elthusa raynaudii* has been recorded numerous times from a wide range of localities within the Indo-Pacific region. It is the only species of *Elthusa* that has been described from sub-Saharan Africa. It has been recorded from an unknown host from the Cape of Good Hope (see Milne Edwards 1840); from the rocksucker, *Chorisochismus dentex* (Pallas, 1769) near Cape Town (Table Bay) (see Barnard 1920); from a wrasse in Durban (see Barnard 1955); as well as from the striped trumpeter, *Latris lineata* (Forster, 1801) (see Kensley 1976).

*Elthusa sigani* Bruce, 1990, which is only known from its type locality in Queensland, Australia, seems to be most similar to *E. raynaudii*. *Elthusa sigani* can be distinguished from *E. raynaudii* by having an evenly concave pereonite 1 anterior margin; a flat, straight cephalon anterior margin; and coxae 7 that extend past the posterior margin of pereonite 7. In addition, *E. sigani* is a much smaller species in overall body length range (9.0–13.0 mm), compared to *E. raynaudii* (20.0–26.7 mm).

***Elthusa xena* sp. n.**

<http://zoobank.org/338A44A2-746F-4D9B-B890-5372D1E45B4C>

Figures 4–7, Table 1

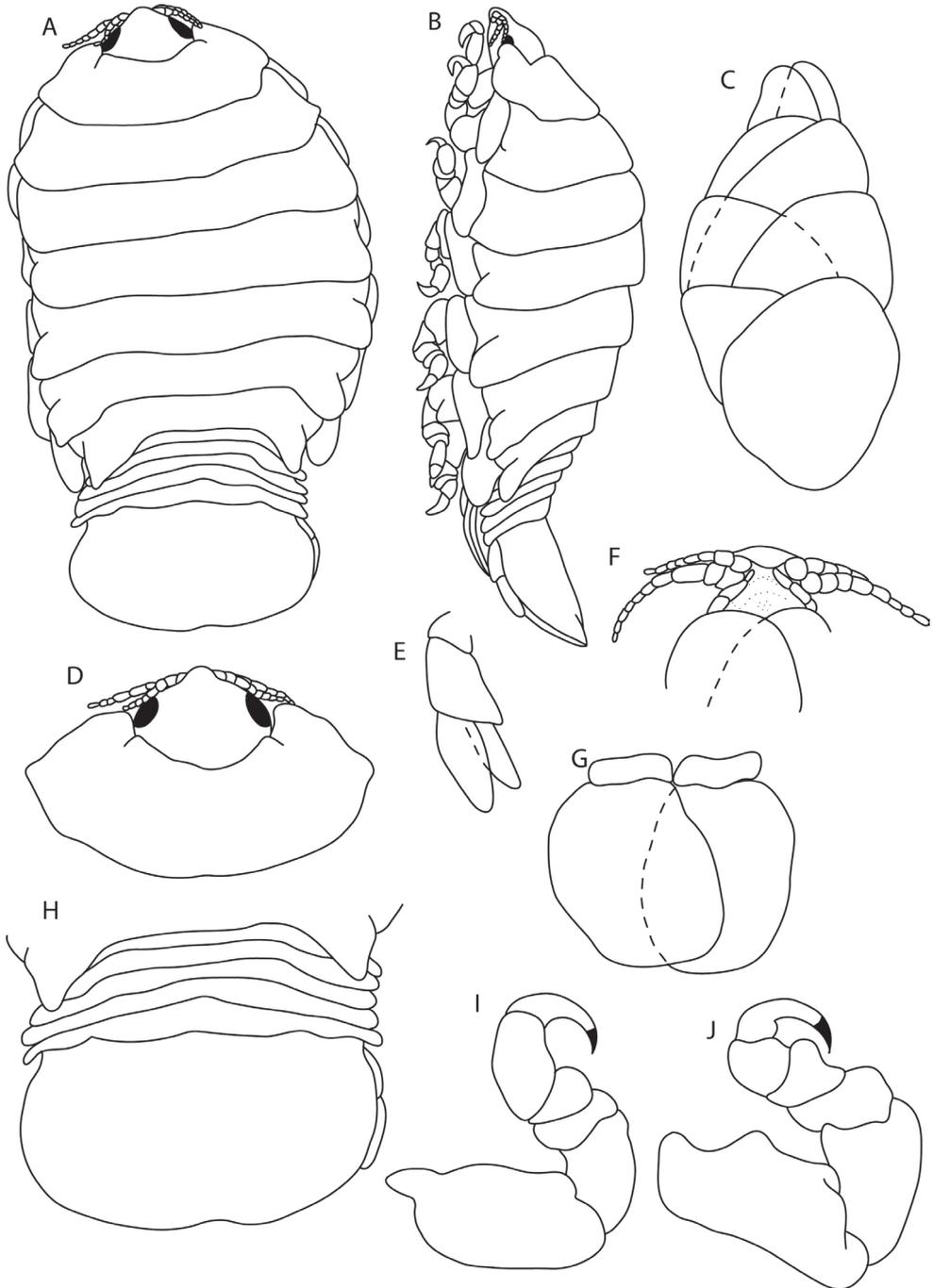
**Material examined.** *Holotype*. SOUTH AFRICA • 1 ♀ (ovigerous, 34.0 mm TL, 17.0 mm W); Alexander Bay, mouth of the Orange River; 28°38'S, 16°27'E; July 1993; coll. J Laubscher; from the super klipfish, *Clinus superciliosus* (Linnaeus, 1758); SAMC-A089958.

*Paratype*. SOUTH AFRICA • 1 ♂ (intermoult, 8.0 mm TL, 4.0 mm W); same data as holotype; SAMC-A089959.

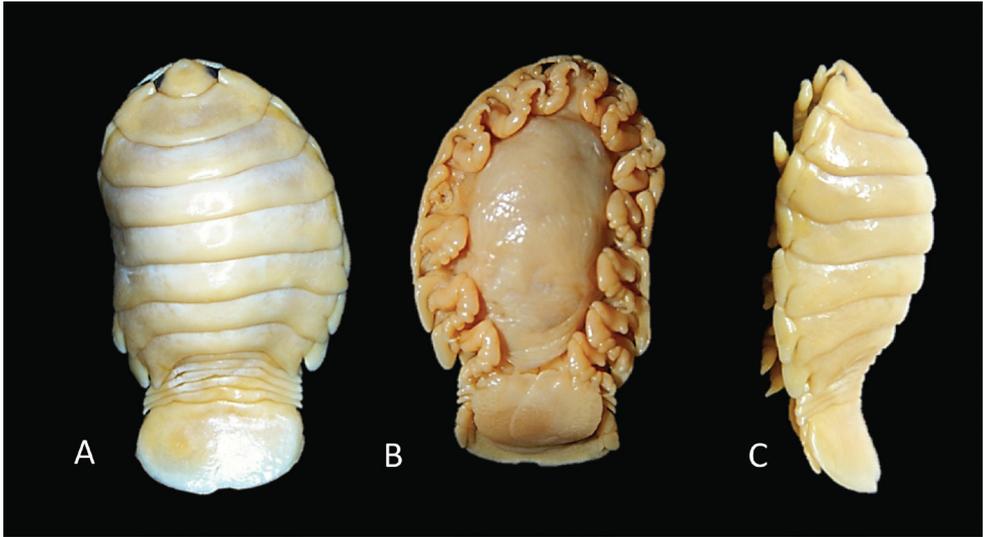
**Description** (ovigerous ♀). Figs 4–5. *Body* slightly twisted to the left, elongated ovoid, twice as long as greatest width; dorsal surfaces smooth and polished in appearance, widest at pereonite 5, most narrow at pereonite 1, pereonite lateral margins mostly rounded, medially indented. *Cephalon* 0.8 times longer than wide, visible from dorsal view, sub-triangular with blunt anterior point. *Frontal margin* thickened, ventrally folded. *Eyes* oval with distinct margins; one eye 0.1 times width of cephalon, 0.3 times length of cephalon. *Pereonite 1* smooth, anterior border slightly concave; anterolateral angle rounded, extending to the medial region of eyes. Posterior margins of pereonites smooth, slightly curved laterally. *Coxae 2–3* narrow with posteroventral angles narrowly rounded; coxae 4–7 with rounded point, not extending past pereonite margin. Pereonites 2–5 subequal, pereonites 6 and 7 slightly narrower. *Pleon* 0.4 times as long as total body length, with pleonite 1 same width as other pleonites, lateral margins concealed by pereonite 7, slightly visible in dorsal view; pleonites posterior margin smooth, slightly curved laterally. *Pleonite 2* partially overlapped by pereonite 7; posterolateral angles of pleonite 2 rounded. *Pleonites 3–5* similar in form to pleonite 2; pleonite 5 longest, free, not overlapped by lateral margins of pleonite 4, with posterolateral angles narrowly rounded, posterior margin with 3 indentations. *Pleotelson* 0.6 times as long as anterior width, dorsal surface smooth; lateral margins convex; posterior margin evenly rounded.

*Antennula* shorter than antenna, consisting of eight articles; peduncle articles I and II distinct and articulated, extending to anterior of pereonite 1. *Antenna* consists of eleven articles, extending to past anterior margin of pereonite 1.

*Pereopod 1* basis 1.8 times as long as greatest width; ischium 0.7 times as long as basis; merus proximal margin without bulbous protrusion; carpus with rounded proximal margin; propodus 1.8 times as long as wide; dactylus slender, 0.8 times as long as propodus, 2.3 times as long as basal width. *Pereopods 2–3* similar to pereopod 1, all pereopods without robust or simple setae. *Pereopod 7* basis with carina, 1.5 times as long as greatest width; ischium without protrusions, 0.9 times as long as basis; merus proximal margin with slight bulbous protrusion, 0.6 times as long as wide, 0.3 times as long as ischium; carpus with bulbous protrusion, 0.9 times as long as wide, 0.5 times as long as ischium; propodus as long as wide, 0.4 times as long as ischium; dactylus slender, 1.9 times as long as propodus, 3.1 times as long as basal width.



**Figure 4.** *Elthusa xena* sp. n. holotype ♀ (ovigerous, 34.0 mm TL, 17.0 mm W) (SAMC-A089958) from Alexander Bay, South Africa **A** dorsal body **B** lateral body **C** oostegites **D** dorsal view of cephalon and pereonite 1 **E** uropod **F** ventral cephalon **G** pleopod 1 **H** dorsal view of pleon **I** pereopod 1 **J** pereopod 7.



**Figure 5.** Photos of *Elthusa xena* sp. n. holotype ♀ (ovigerous, 34.0 mm TL, 17.0 mm W) (SAMC-A089958) from Alexander Bay, South Africa **A** dorsal view **B** ventral view **C** lateral view.

*Pleopods* simple, exopod larger than endopod. *Pleopod 1* exopod 1.1 times as long as wide, lateral margin strongly convex, distally broadly rounded, mesial margin weakly convex; peduncle 2.8 times as wide as long.

*Uropod* more than half the length of pleotelson, peduncle 0.8 times longer than rami, peduncle lateral margin without setae; rami not extending beyond pleotelson, apices narrowly rounded. *Endopod* apically rounded, 2.5 times as long as greatest width, lateral margin weakly convex, mesial margin straight, terminating without setae. *Exopod* extending beyond end of endopod, twice as long as greatest width, apically rounded, lateral margin weakly convex, mesial margin straight, terminating without setae.

**Description** (paratype intermoult ♂). Figs 6, 7. Male similar to female but smaller. Specimen mid-moult. *Body* rectangular, not twisted, twice as long as greatest width. Pereonite lateral margins mostly subparallel. *Cephalon* 0.7 times longer than wide. *Frontal margin* rounded to form blunt rostrum. *Eyes* oval with distinct margins; one eye 0.2 times width of cephalon; 0.5 times length of cephalon. *Pereonite 1* smooth, anterior border concave, extending past base of cephalon. Posterior margins of pereonites smooth and straight, except pereonite 4 and 5. *Coxae* 2–3 wide, with posteroventral angles rounded; coxae 4–7 rounded. Pereonites 6 and 7 narrower, becoming more progressively rounded posteriorly. *Pleon* 0.3 times as long as total body length, with pleonite 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleonites 1–3 posterior margin posteriorly concave, smooth and slightly curved laterally. Pleonite 5 overlapped by lateral margins of pleonite 4, with posterolateral angles narrowly rounded, posterior margin straight. *Pleotelson* 0.8 times as long as anterior width, lateral margins straight or weakly convex, posterior margin broadly truncate.

*Antennula* shorter than antenna, consisting of eight articles. *Antenna* consists of ten articles, extending to middle of pereonite 1.

*Pereopod 1* basis twice as long as greatest width; ischium 0.6 times as long as basis; propodus 1.6 times as long as wide; dactylus 1.1 times as long as propodus, 3 times as long as basal width. *Pereopod 7* twice as long as greatest width; ischium 0.7 times as long as basis; merus proximal margin without bulbous protrusion, 0.7 times as long as wide, 0.4 times as long as ischium; carpus without bulbous protrusion, 0.7 times as long as wide, 0.4 times as long as ischium; propodus 1.3 times as long as wide, 0.6 as long as ischium; dactylus slender, 1.4 times as long as propodus, 2.7 times as long as basal width.

*Pleopod 1* exopod 1.2 times as long as wide, lateral margin weakly convex, distally broadly rounded, mesial margin straight; endopod 2.1 times as long as wide, lateral margin weakly convex, mesial margin straight, peduncle 2.2 times as wide as long. *Pleopod 2* appendix masculina with parallel margins, 1.1 times as long as endopod, distally narrowly rounded.

*Uropod* same length or slightly longer than the pleotelson, peduncle 0.4 times longer than rami, rami extending slightly beyond pleotelson, apices narrowly rounded. *Endopod* apically slightly pointed, 3 times as long as greatest width. *Exopod* 2.6 times as long as greatest width.

*Penes* medially adjacent; penial process 0.7 times as long as basal width.

**Etymology.** The epithet is constructed in a possessive form of a personal name. This species is named after Xena, the warrior princess, in reference to the strong nature of the female cymothoid isopod.

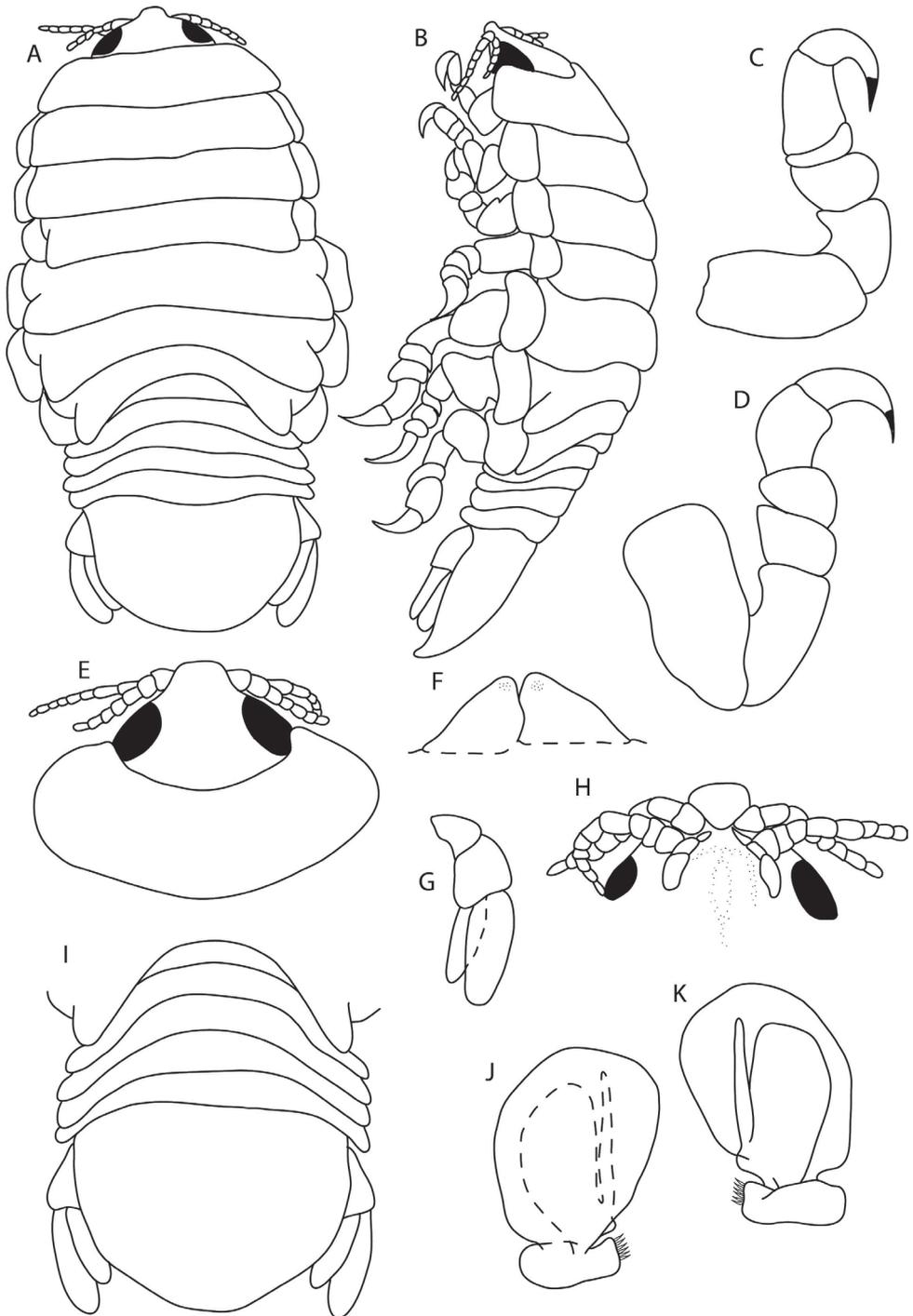
**Size.** Ovigerous female (34.0 mm TL, 17.0 mm W), male (8.0 mm TL, 4.0 mm W).

**Distribution.** Currently only known from the mouth of the Orange River, Alexander Bay, South Africa (Atlantic Ocean).

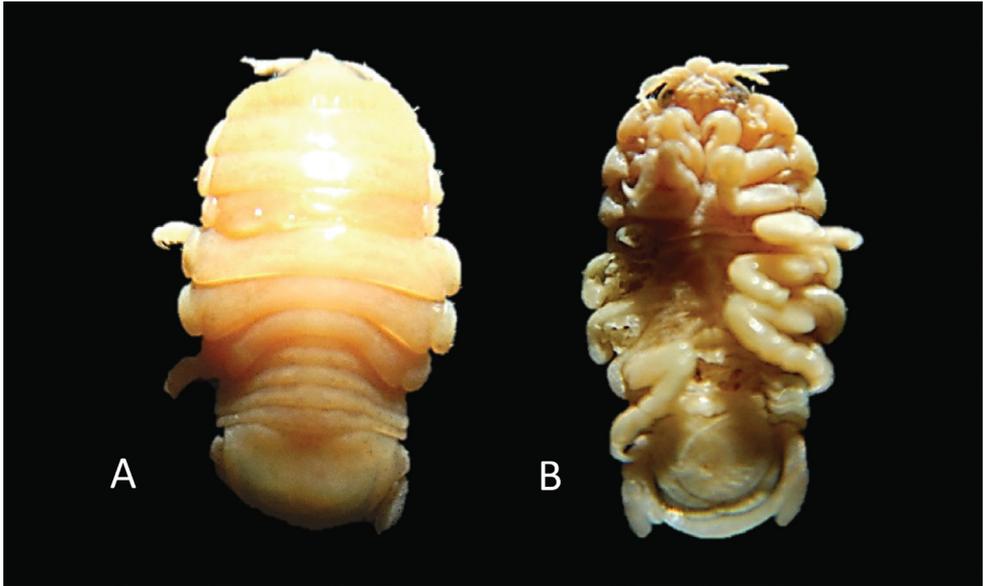
**Hosts.** *Clinus superciliosus* (Linnaeus, 1758). This is the first record of a klipfish (of the genus *Clinus* Cuvier, 1816), and of the intertidal super klipfish, *Clinus superciliosus*, as a fish host of a species of *Elthusa*. This host belongs to the fish order Perciformes, and is endemic to the Southeast Atlantic Ocean, from northern Namibia to the Kei River of South Africa (Smith and Heemstra 1986).

**Remarks.** *Elthusa xena* sp. n. female can be identified by the elongate, ovoid body shape; coxae 7 that do not extend past the posterior margin of pereonite 7; a bluntly pointed anterior margin of the cephalon; evenly rounded, slightly concave anterior margin of pereonite 1; uropod rami with apices narrowly rounded and more than half the length of pleotelson; pleonite 5 posterior margin with indentations; and the pleotelson is short, roughly quadrate, with margins that curl upward.

Two other *Elthusa* species have been recorded from related perciform fish hosts from the family Clinidae Swainson, 1839 (blennies). *Elthusa californica* (Schioedte & Meinert, 1884) was noted from the striped kelpfish *Gibbonsia metzi* Hubbs, 1927; and *Elthusa menziesi* (Brusca, 1981) from both the spotted kelpfish *Gibbonsia elegans* (Cooper, 1864) and the crevice kelpfish *Gibbonsia montereyensis* Hubbs, 1927. However, this is the first record of *Elthusa* collected from a *Clinus* sp.



**Figure 6.** *Elthusa xena* sp. n. paratype ♂ (intermolt) (8 mm TL, 4 mm W) (SAMC-A089959) from Alexander Bay, South Africa **A** dorsal body **B** lateral body **C** pereopod 1 **D** pereopod 7 **E** dorsal view of cephalon **F** penes **G** uropod **H** ventral cephalon **I** dorsal view of pleon **J** ventral pleopod 2 **K** dorsal pleopod 2.



**Figure 7.** Photos of *Elthusa xena* sp. n. paratype ♂ (intermoult) (8.0 mm TL, 4.0 mm W) (SAMC-A089959) from Alexander Bay, South Africa **A** dorsal view **B** ventral view.

*Elthusa xena* sp. n. can be distinguished from *E. raynaudii* by having a bluntly pointed cephalon anterior margin, compared to the narrowly truncate margin of *E. raynaudii*. Other differences include the shape of the pleotelson (which is quadrate, wide and short for *E. xena* sp. n., and evenly rounded for *E. raynaudii*); pleonite 1 is the same length as the other pleonites in *Elthusa xena* sp. n. but narrower in *E. raynaudii*; and the uropod apices of *E. xena* sp. n. are narrowly rounded compared to the broadly rounded apices of *E. raynaudii* uropods. See Table 1 for further morphological variation and comparisons.

***Elthusa acutinasa* sp. n.**

<http://zoobank.org/D5AFAEC4-F03D-400F-98A0-8D86631E495E>

Figures 8–11, Table 1

**Material examined.** *Holotype.* SOUTH AFRICA • 1 ♀ (ovigerous, 39.0 mm TL, 19.0 mm W); Indian Ocean, south coast of South Africa, RV Africana (fish sorting table); 34°38'S, 25°38'E; April 2003; coll. Nico J Smit; SAMC-A089960.

*Paratypes.* SOUTH AFRICA • 3 ♀♀ (ovigerous, 28.0–30.0 mm TL, 15.0–17.0 mm W); same data as holotype; SAMC-A089961.

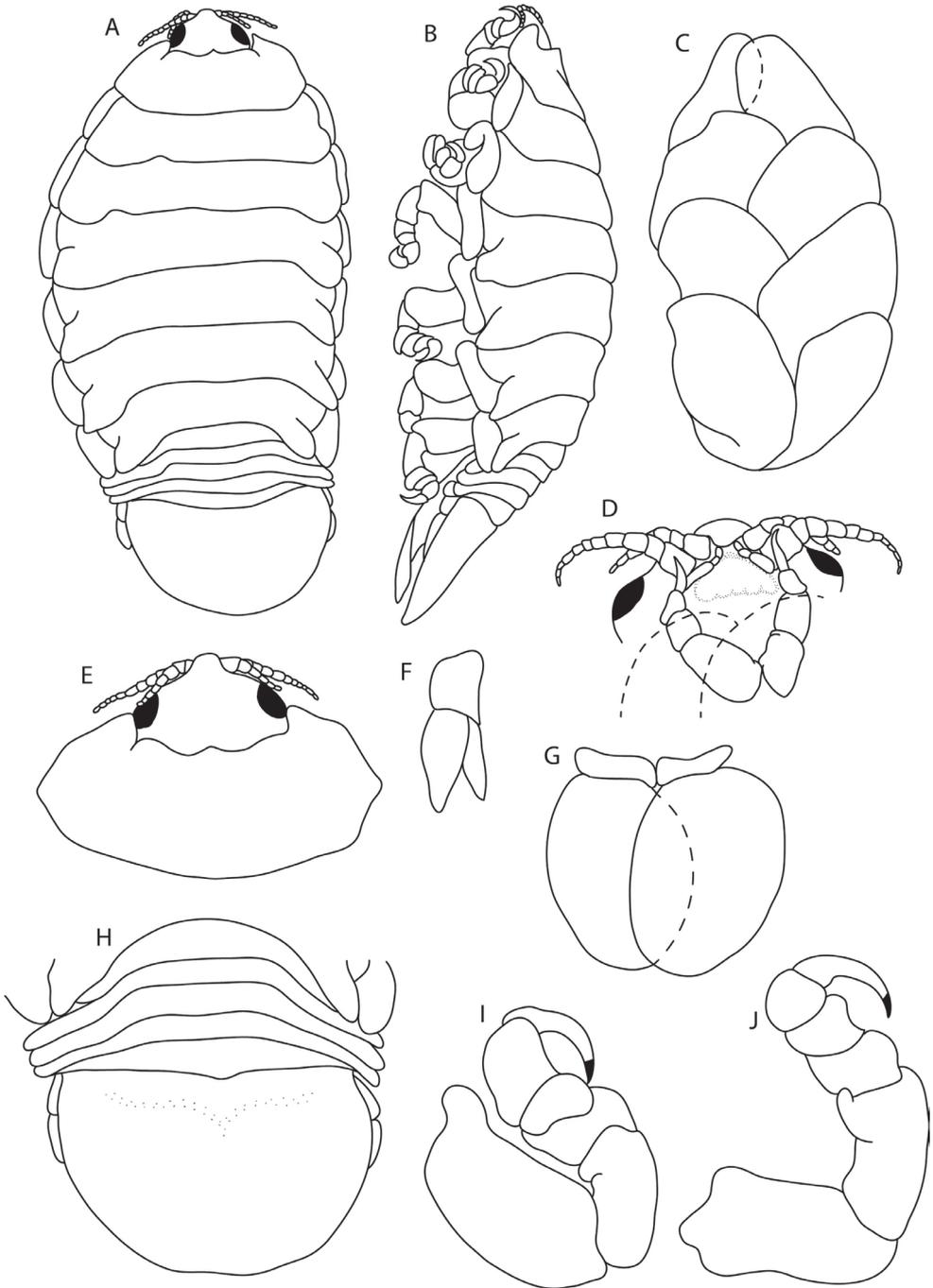
*Other material.* SOUTH AFRICA • 1 ♀ (ovigerous, 29.0 mm TL, 17.0 mm W); same data as holotype; dissected; in the collection of the authors at NWU • 4 ♀♀ (non-ovigerous, 19.0–24.0 mm TL, 10.0–14.0 mm W); same data as holotype; in the col-

lection of the authors at NWU • 9 ♀♀ (three ovigerous, six non-ovigerous, 15.0–40.0 mm TL, 8.0–19.0 mm W); Indian Ocean, south coast of South Africa, RV Africana (fish sorting table); 30°29'S, 16°0'E; 213 m depth; January 1999; SAMC-A091307 • 1 ♀ (ovigerous, 40.0 mm TL, 19.0 mm W); same data as preceding; 30°25'S, 16°9'E; 259 m depth; SAMC-A091308 • 1 ♀ (ovigerous, 30.0 mm TL, 15.0 mm W); same data as preceding; 31°8'S, 15°20'E; 234 m depth; SAMC-A091309.

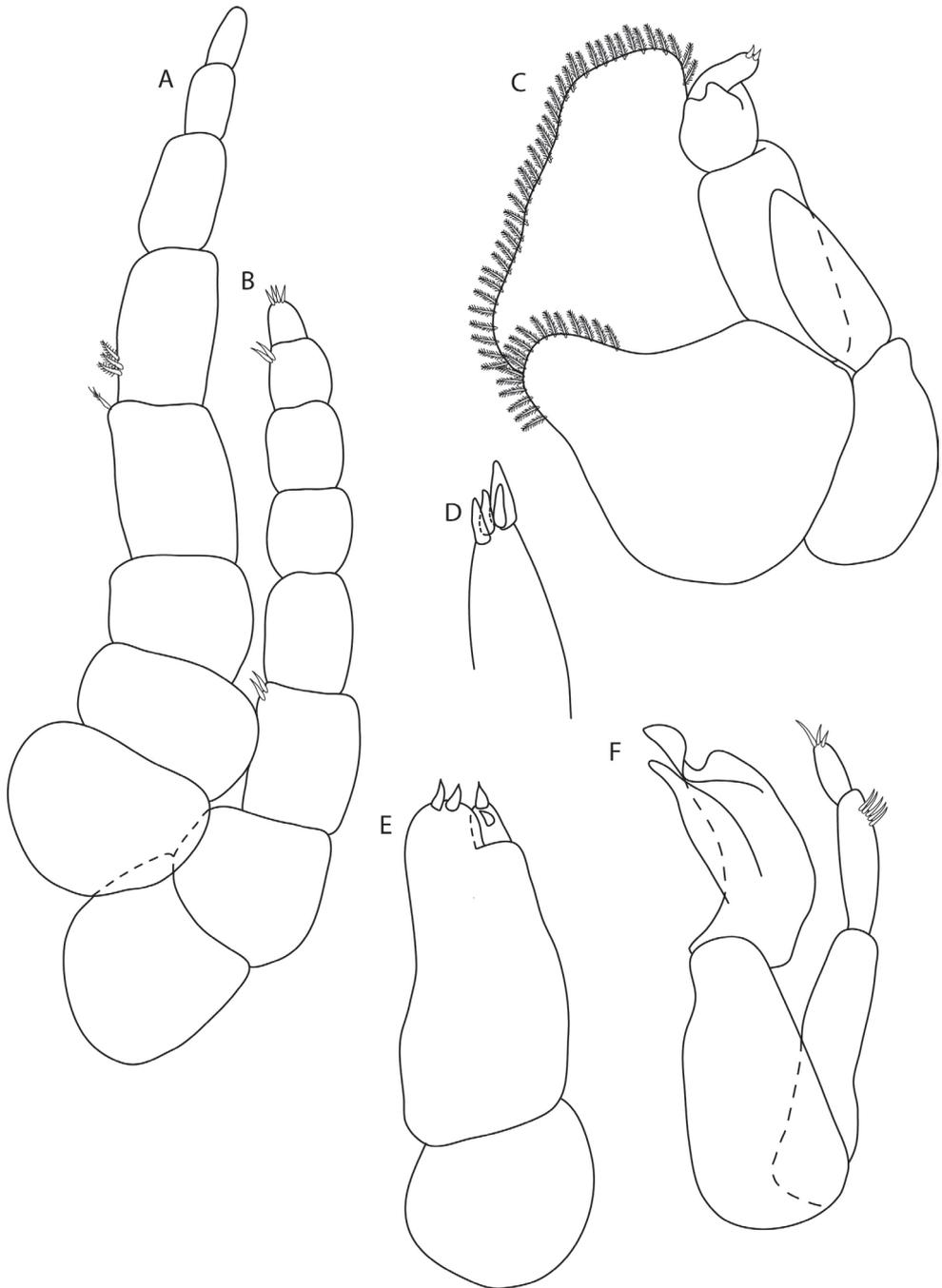
**Description** (ovigerous ♀). Figs 8–11. *Body* slightly twisted to the right, elongated ovoid, 2.1 times as long as greatest width. Body dorsal surfaces smooth and polished in appearance, widest at pereonite 4, most narrow at pereonite 1, pereonite lateral margins mostly posteriorly ovate, medially indented. *Cephalon* 0.4 times longer than wide, visible from dorsal view, sub-triangular with narrowly rounded anterior point. *Frontal margin* thickened, ventrally folded. *Eyes* oval with distinct margins; one eye 0.2 times width of cephalon, 0.4 times length of cephalon. *Pereonite 1* smooth, anterior border with medially produced point, with two indentations; anterolateral angle rounded, extending to posterior margin of eyes. Posterior margins of pereonites smooth and slightly curved laterally. *Coxae 2–3* wide; with posteroventral angles rounded; 4–7 with rounded point. *Coxae 7* extending slightly past pereonite posterior margin. *Pereonites 2–5* subequal, becoming more progressively rounded posteriorly. *Pleon* 0.4 times as long as total body length, with pleonite 1 longest, lateral margins concealed by pereonite 7, visible in dorsal view; pleonites posterior margin smooth and slightly curved laterally. *Pleonite 2* partially overlapped by pereonite 7; posterolateral angles of pleonite 2 rounded. *Pleonites 3–5* similar in form to pleonite 2; pleonite 5 overlapped by lateral margins of pleonite 4, posterior margin straight, with slight medial point. *Pleotelson* 0.7 times as long as anterior width, dorsal surface smooth; lateral margins weakly convex; posterior margin rounded, with slight medial indent.

*Antennula* shorter than antenna, consisting of eight articles; antennula peduncle articles I and II distinct and articulated; article II 0.9 times as long as article 1; article III 1.4 times as long as wide, 0.5 times as long as combined lengths of articles I and II; antennula flagellum with five articles, extending to middle of eye, with tufts of setae on articles I–III and article VIII. *Antenna* consists of twelve articles. *Antenna* peduncle article III 1.3 times as long as article II; article IV 1.3 times as long as wide, 1.2 times as long as article III; article V 1.5 times as long as wide, 1.1 times as long as article IV. *Antenna* flagellum with six articles, terminal article terminating in 1–5 short simple setae, extending to past anterior margin of pereonite 1. *Mandible palp* article II with five distolateral setae, and article III with three simple setae. *Maxillula* simple with four terminal robust setae. *Maxilla* mesial lobe not fused to lateral lobe; lateral lobe without simple setae, two recurved robust setae; mesial lobe without simple setae, and two large recurved robust setae. *Maxilliped* consists of III articles, with lamellar oostegite lobe or second, smaller oostegite lobe on basal part of article, palp article II without simple setae, article III with three recurved robust setae. Oostegites margin covered in numerous plumose setae.

*Pereopod 1* basis 1.9 times as long as greatest width; ischium 0.7 times as long as basis; merus proximal margin with slight bulbous protrusion; carpus with rounded



**Figure 8.** *Elthusa acutinasa* sp. n. holotype ♀ (ovigerous, 39.0 mm TL, 19.0 mm W) (SAMC-A089960) from Africana research vessel **A** dorsal body **B** lateral body **C** oostegites **D** ventral cephalon **E** dorsal view of cephalon and pereonite 1 **F** uropod **G** pleopod 1 **H** dorsal view of pleon **I** pereopod 1 **J** pereopod 7.



**Figure 9.** *Elthusa acutinasa* sp. n. paratype ♀ (ovigerous, 33.0 mm TL, 16.0 mm W) (SAMC-A089961) from Africana research vessel **A** antennula **B** antenna **C** maxilliped **D** tip of maxillula **E** maxilla **F** mandible.

proximal margin; propodus 1.1 times as long as wide; dactylus slender, 1.3 times as long as propodus, 3 times as long as basal width. *Pereopod 3* similar to pereopod 2, all pereopods without robust or simple setae. *Pereopod 7* basis 1.9 times as long as greatest width; ischium with slight bulbous protrusion on distal margin, 0.9 times as long as basis; merus proximal margin with slight bulbous protrusion, 0.6 times as long as wide, 0.3 times as long as ischium; carpus with bulbous protrusion, 0.7 times as long as wide, 0.3 times as long as ischium; propodus 1 times as long as wide, 0.3 times as long as ischium; dactylus slender, 1.9 times as long as propodus, 3.3 times as long as basal width.

*Pleopods* simple; exopod larger than endopod, with 4–7 simple setae on peduncle of pleopods 2–5. *Pleopod 1* exopod 1.3 times as long as wide, lateral margin weakly convex, distally broadly rounded, mesial margin straight; peduncle 3 times as wide as long. *Endopod* 1.6 times as long as wide, lateral margin convex, distally narrowly rounded, mesial margin straight, peduncle 2.4 times as wide as long. *Pleopods 2–5* similar to pleopod 1, mesial margins becoming more strongly produced, peduncle lobes absent.

*Uropod* less than half the length of the pleotelson, peduncle 0.7 times longer than rami, peduncle lateral margin without setae, marginal setae absent, apices narrowly rounded. *Endopod* apically slightly pointed, 3.4 times as long as greatest width, lateral margin weakly convex, mesial margin straight, terminating without setae. *Exopod* extending to end of endopod, 2.3 times as long as greatest width, apically rounded, lateral margin distally convex, mesial margin straight, terminating without setae.

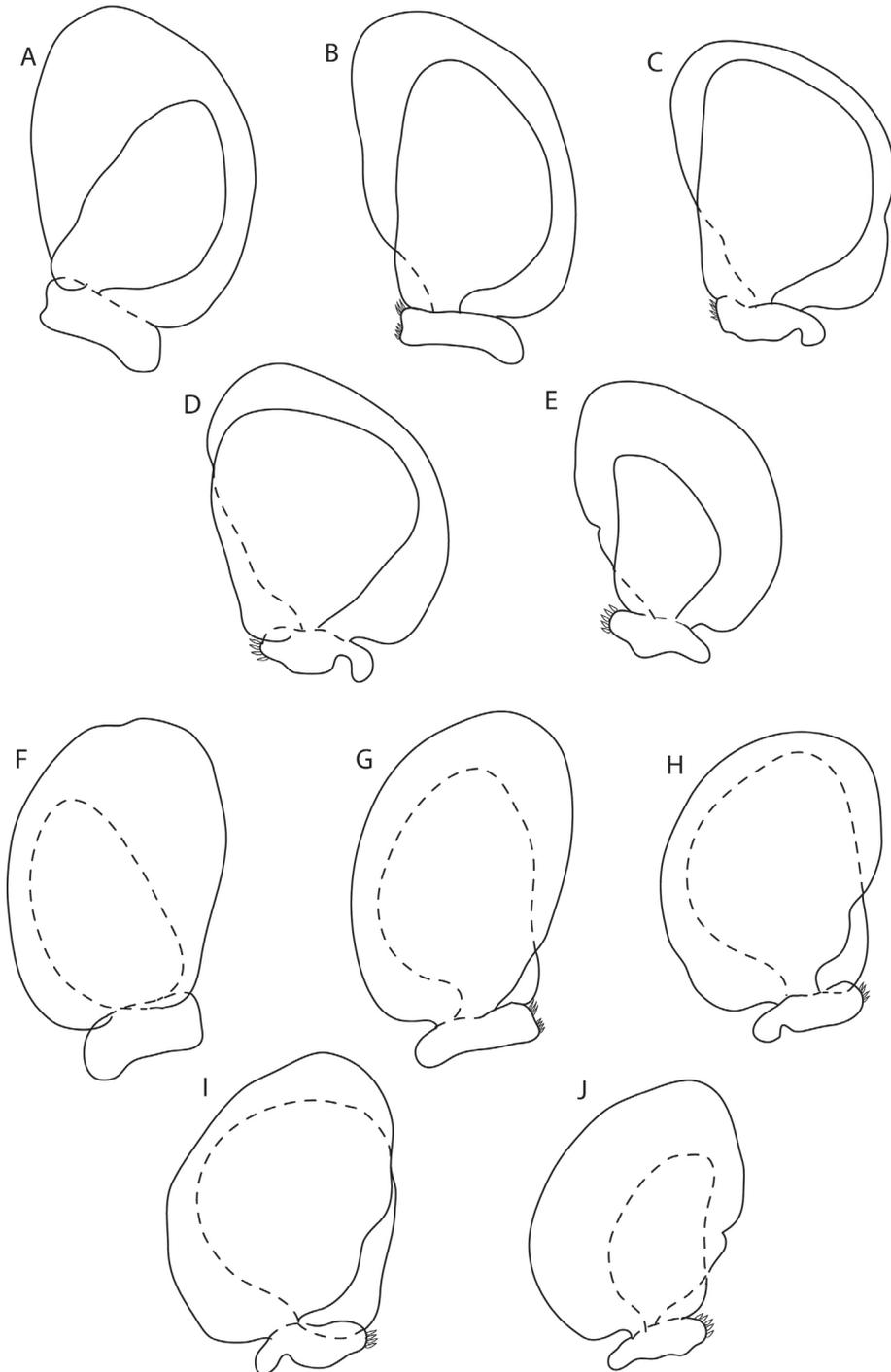
*Variations.* Intra-specific variation was observed among the examined specimens of *Elthusa acutinasa* sp. n. The size of the medial point formed at the anterior margin of pereonite 1 may vary. Some specimens portrayed an obvious, sharp medial point, while others only had a weak medial projection of the anterior margin of pereonite 1. Variation in the length of the uropods are slight, but one specimen had uropod rami extending to half the length of the pleotelson, while all the others specimens' uropods were remarkably short. The overlapping of pleonite 5 lateral margins by pleonite 4 was consistent, except with one of the other examined paratype females, where pleonite 5 lateral margins were slightly visible. Some variation was also noted in the width of pleonite 1.

**Etymology.** The epithet is a noun in the genitive singular. The species name *acutinasa* was derived by the son of one of us (NJS) from a combination of the two Latin words *acute* and *nasus*. The word *acute* translates to a feature that is pointy or ends with a sharp point; while *nasus* translates to nose. The combined word, *acutinasa*, therefore means pointy nose, and appropriately describes one of the characters of this species, which is its pointed anterior margin of the rostrum.

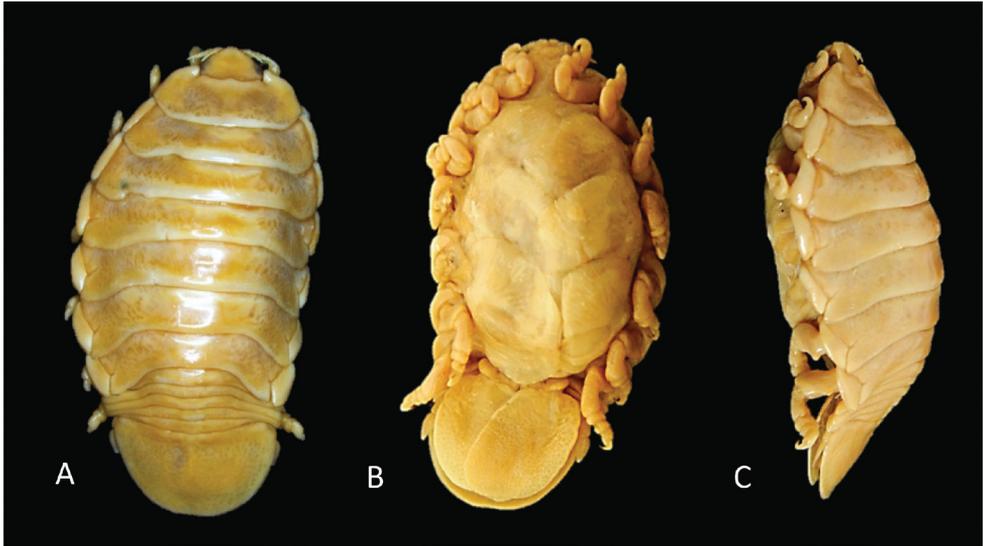
**Size.** Ovigerous females (28.0–40.0 mm TL, 15.0–19.0 mm W), non-ovigerous females (19.0–24.0 mm TL, 10.0–14.0 mm W).

**Distribution.** Known from the Indian Ocean, off the south coast of South Africa.

**Hosts.** Not known (type material was collected from the fish sorting table following a trawl and not from a specific fish species).



**Figure 10.** *Elthusa acutinasas* sp. n. paratype ♀ (ovigerous, 33.0 mm TL, 16.0 mm W) (SAMC-A089961) from Africana research vessel **A–E** dorsal view of pleopods 1–5 respectively **F–J** ventral view of pleopods 1–5 respectively.



**Figure 11.** Photos of *Elthusa acutinasa* sp. n. holotype ♀ (ovigerous, 39.0 mm TL, 19.0 mm W) (SAMC-A089960) from Africana research vessel **A** dorsal view **B** ventral view **C** lateral view.

**Remarks.** *Elthusa acutinasa* sp. n. can be identified by its elongate, ovoid body shape; pointed anterior margin of the cephalon; anterior margin of pereonite 1 with short medial point; short, apically pointed uropod rami, which extend to less than half of the length of the pleotelson; coxae 7 that extends past the posterior margin of pereonite 7; pleonite 5 lateral margins that are largely concealed by pleonite 4; pleonite 5 posterior margin with a slight medial point; pleonite 1 the longest of the pleonites; and pleopod 5 endopod approximately half the size of the exopod.

Several characters differentiate between *E. acutinasa* sp. n. from *E. raynaudii* (see Table 1). *Elthusa acutinasa* sp. n. has a prominent, pointed cephalon anterior margin with a medially pointed pereonite 1 anterior margin compared to the straight anterior margin of *E. raynaudii* cephalon and pereonite 1. Pleon differences include the longer pleotelson of *E. acutinasa* sp. n. with pleonite 1 widest and pleonite 5 lateral margins concealed by those of pleonite 4 (not seen in *E. raynaudii*). *Elthusa acutinasa* sp. n. also has short uropods that do not extend to the half of the pleotelson length, whereas those of *E. raynaudii* reach to, or extend past, the half of the pleotelson length.

*Elthusa acutinasa* sp. n. can also be distinguished from *E. xena* sp. n. by its short uropods and coxae 7 that extend past the posterior margin of pereonite 7. Further differences are found within pleon morphology, where *E. acutinasa* sp. n. pleonite 5 lateral margins are largely concealed by pleonite 4, whereas those of *E. xena* sp. n. are visible. Pleonite 1 in *E. xena* sp. n. is as wide as the other pleonites, whereas pleonite 1 in *E. acutinasa* sp. n. is narrower than the other pleonites. The pleotelson shape of *E. acutinasa* sp. n. is evenly rounded, compared to the roughly quadrate pleotelson of *E. xena* sp. n. (see Table 1).

***Elthusa rotunda* sp. n.**

<http://zoobank.org/138FBF0D-2E4B-4561-86C8-F209B78A33E0>

Figures 12–13, Table 1

**Material examined.** *Holotype*. SOUTH AFRICA • 1 ♀ (ovigerous, 29.0 mm TL; 20.0 mm W); Cape Town, Sea Point; 33°55'S, 18°23'E; January 1960; coll. G Branch; SAMC A11001.

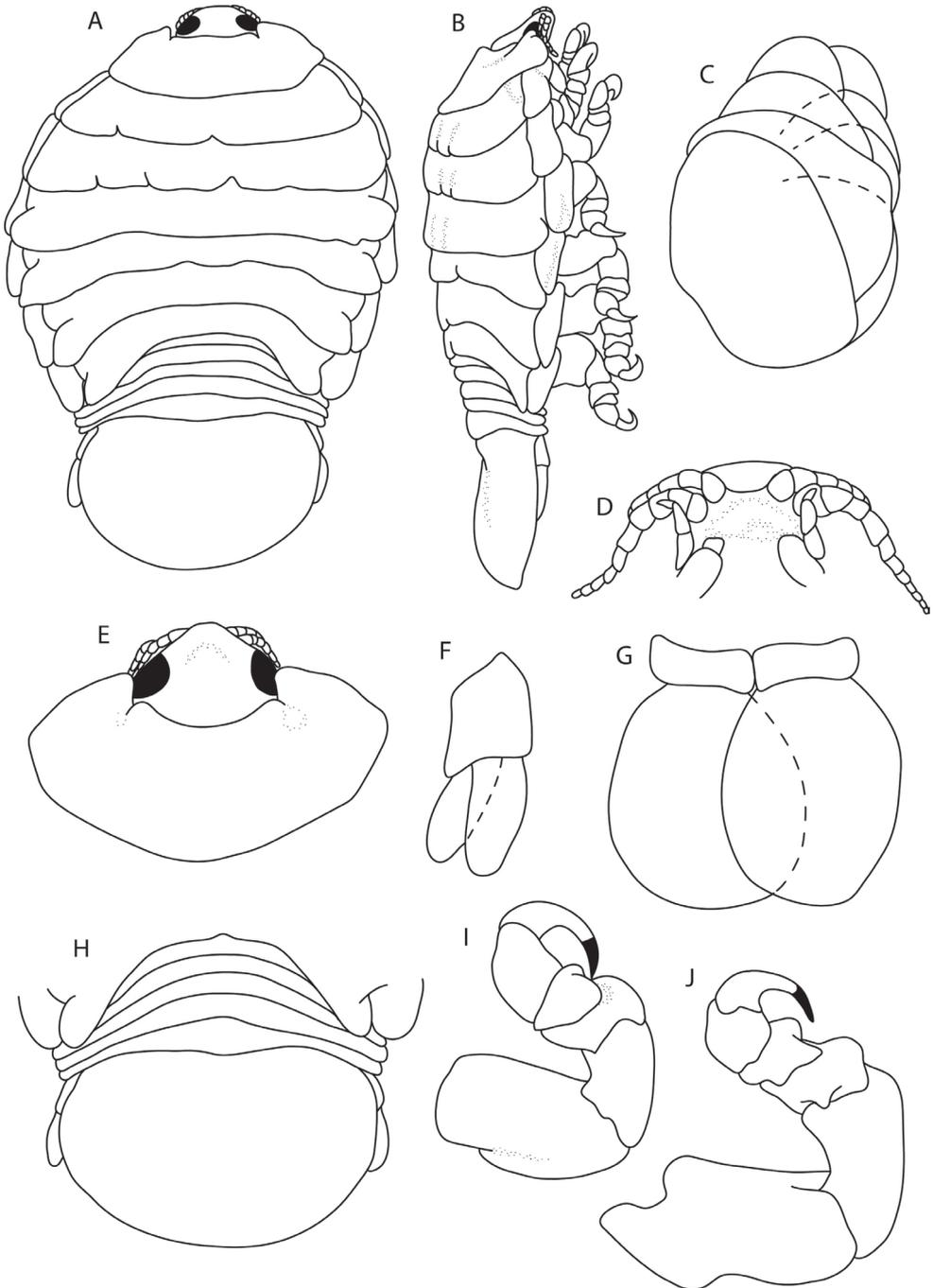
**Description** (ovigerous ♀). Figs 12–13. *Body* round, not twisted, 1.4 times as long as greatest width; dorsal surfaces smooth and polished in appearance, widest at pereonite 4, most narrow at pereonite 1; pereonite lateral margins mostly posteriorly ovate, medially indented. *Cephalon* 0.4 times longer than wide, visible from dorsal view, sub-triangular with blunt anterior point. *Frontal margin* thickened, ventrally folded. *Eyes* oval with distinct margins; one eye 0.2 times width of cephalon; 0.5 times length of cephalon. *Pereonite 1* smooth, anterior border evenly concave; anterolateral angles rounded, extending to the medial region of eyes. Posterior margins of pereonites smooth, slightly curved laterally, posterior margins of pereonites 2–3 uneven. Coxae 2–3 wide; with posteroventral angles rounded; coxae 4–7 with rounded point, not extending past pereonite posterior margin. Pereonites becoming more progressively rounded posteriorly; pereonite 5 most narrow. *Pleon* 0.4 times as long as total body length; pleonite 1 largely concealed by pereonite 7, slightly visible in dorsal view; pleonites posterior margin slightly concave, smooth, slightly curved laterally. Pleonite 2 lateral margins overlapped by pereonite 7. Pleonites 3–4 similar in form to pleonite 2; pleonite 5 longest, overlapped by lateral margins of pleonite 4, posterior margin medially convex. *Pleotelson* broadly rounded, 0.7 times as long as anterior width, dorsal surface smooth; lateral margins convex; posterior margin evenly rounded.

*Antennula* shorter than antenna, consisting of eight articles; peduncle articles I and II distinct and articulated; extending to middle of eye. *Antenna* consists of ten articles, extending to past anterior margin of pereonite 1.

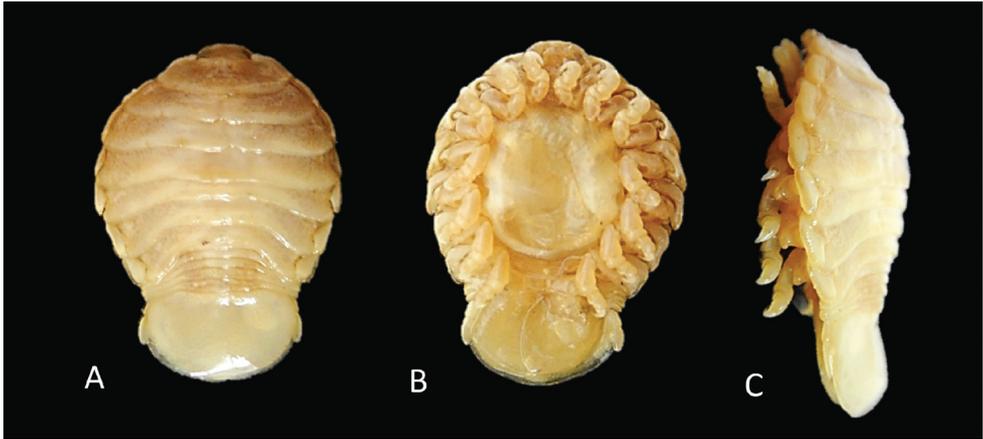
*Pereopod 1* basis 1.7 times as long as greatest width; ischium 0.7 times as long as basis; merus proximal margin without bulbous protrusion; propodus 1.4 times as long as wide; dactylus slender, 1.3 times as long as propodus, 2.9 times as long as basal width. All pereopods without robust or simple setae. *Pereopod 7* basis with carina, 2.1 times as long as greatest width; ischium with slight bulbous protrusion, 0.8 times as long as basis; merus proximal margin with bulbous protrusion, 0.6 times as long as wide, 0.3 times as long as ischium; carpus with bulbous protrusion, 0.7 times as long as wide, 0.3 times as long as ischium; propodus 1.2 times as long as wide, 0.9 times as long as ischium; dactylus slender, 1.7 times as long as propodus, 2.5 times as long as basal width.

*Pleopods* simple, exopod larger than endopod. *Pleopod 1* exopod 1.3 times as long as wide, lateral margin weakly convex, distally broadly rounded, mesial margin weakly convex; peduncle 2.5 times as wide as long.

*Uropod* half the length of pleotelson, peduncle 0.9 times longer than rami, peduncle lateral margin without setae; rami not extending beyond pleotelson, marginal setae absent, apices broadly rounded. *Endopod* apically rounded, 2.6 times as long as greatest width, lateral margin weakly convex, mesial margin weakly convex. *Exopod* extending



**Figure 12.** *Elthusa rotunda* sp. n. holotype ♀ (ovigerous, 28 mm TL, 19 mm W) (SAMC-A11001) from Sea Point, South Africa **A** dorsal body **B** lateral body **C** oostegites **D** ventral cephalon **E** dorsal view of cephalon and pereonite 1 **F** uropod **G** pleopod **H** dorsal view of pleon **I** pereopod 1 **J** pereopod 7.



**Figure 13.** Photos of *Elthusa rotunda* sp. n. holotype ♀ (ovigerous, 28 mm TL, 19 mm W) (SAMC-A11001) from Sea Point, South Africa **A** dorsal view **B** ventral view **C** lateral view.

to end of endopod, 2.2 times as long as greatest width, apically rounded, lateral margin weakly convex, mesial margin straight.

**Size.** Ovigerous female (29.0 mm TL, 20.0 mm W).

**Etymology.** The epithet is a noun in the nominative singular. It is named after its most distinct, defining character, which is the rounded shape of the body. The Latin word for round is *rotundus*.

**Distribution.** Currently only known from Sea Point, Cape Town, South Africa.

**Hosts.** Not known.

**Remarks.** The diagnostic characters of *E. rotunda* sp. n. include its circular body shape; a sub-triangular cephalon with blunt anterior margin; pereopod 7 merus and carpus with protrusions on the proximal and lateral margins; pereonite 7 lateral margins that extend to pleonite 4; pleonite 5 longest and medially convex; a broadly rounded pleotelson posterior margin; and uropod rami that are sub-equal in length to the peduncle.

When comparing *E. rotunda* sp. n. to the rest of the identified *Elthusa* species, its closest resemblance is to that of *E. raynaudii*. This is especially in regards to the shape of the uropods, pleon, and cephalon anterior margin. It can be distinguished from *E. raynaudii* in having a more rounded body shape compared to the ovoid body shape of *E. raynaudii*; triangular cephalon as opposed to the narrowly truncate cephalon of *E. raynaudii*; the broadly rounded pereonite 1 anterolateral margins of *E. rotunda* sp. n. compared to the narrowly rounded to pointed anterolateral margins of *E. raynaudii* pereonite 1; as well as the uropod rami and peduncles that are subequal in length, as opposed to the longer rami of *E. raynaudii* (see Table 1).

*Elthusa rotunda* sp. n. can be distinguished from *E. xena* sp. n. by the cephalon anterior margin which is more pointed in *E. xena* sp. n. and more rounded in *E. rotunda* sp. n.; broadly rounded uropod apices compared to the narrowly rounded ones from *E. xena* sp. n.; the shape of the pleotelson, which is broadly rounded for *E. rotunda* sp. n. and roughly quadrate for *E. xena* sp. n.; as well as the prominent presence of pereopod 7 protrusions on the merus and carpus of *E. rotunda* sp. n., that are less bulbous on *E. xena* sp. n.

The main differentiating characters between *E. rotunda* sp. n. and *E. acutinasas* sp. n. include the shape of the cephalon anterior margin (bluntly rounded versus produced point); and the uropod morphology, with *E. rotunda* sp. n. having broadly rounded, longer uropodal rami in comparison to the short, pointed uropodal rami of *E. acutinasas* sp. n. *Elthusa rotunda* sp. n. pleonite 5 is the longest, whereas *E. acutinasas* sp. n. pleonite 1 is the longest; the presence of pereopod 7 protrusions on *E. rotunda* sp. n. is more prominent and bulbous than those of *E. acutinasas* sp. n. pereopod 7 (see Table 1).

## Conclusions

From previous collections across South Africa, four *Elthusa* species were recognised. *Elthusa raynaudii*, the only known *Elthusa* species from South Africa, was identified along with three new species from this genus. These new species, *E. xena* sp. n., *E. acutinasas* sp. n., and *E. rotunda* sp. n., more than double the known records of *Elthusa* from this region. Descriptions were provided for the three new *Elthusa* species along with an identification key with diagnostic characters to distinguish between the sub-Saharan *Elthusa* species (Table 1). A summative table was provided with currently known information on all species from the genus *Elthusa*, including host and location records of each (Table 2).

**Table 1.** Interspecific character states between *Elthusa raynaudii* (Milne Edwards, 1840), *Elthusa xena* sp. n., *Elthusa acutinasas* sp. n., and *Elthusa rotunda* sp. n. from sub-Saharan African marine waters.

Morphological feature	<i>Elthusa raynaudii</i> (Milne Edwards, 1840)	<i>Elthusa xena</i> sp. n.	<i>Elthusa acutinasas</i> sp. n.	<i>Elthusa rotunda</i> sp. n.
<b>Body shape</b>	Ovoid	Elongate ovoid	Elongate ovoid	Round
<b>Shape of cephalon and anterior margin</b>	Sub-truncate, blunt anterior margin	Sub-triangular, bluntly pointed anterior margin	Sub-triangular, pointed anterior margin	Sub-triangular, blunt anterior margin
<b>Pleonite 1 anterior margin</b>	Straight	Medially indented	Medial projection	Concave
<b>Coxae 7 posterior margin</b>	Not extending past posterior margin of pleonite 7	Not extending past posterior margin of pleonite 7	Extending past posterior margin of pleonite 7	Not extending past posterior margin of pleonite 7
<b>Pereopod 7 protrusions</b>	Absent	Absent	Absent	Present on merus and carpus
<b>Pleonite length</b>	Pleonites 1–5 sub-equal	Pleonite 5 longest and indented	Pleonite 1 longest	Pleonite 5 longest, medially convex
<b>Pleonite 1 width</b>	Narrower than other pleonites	As long as other pleonites	As wide as pleotelson	Narrower than other pleonites
<b>Pleonite 5 lateral margins</b>	Visible	Visible	Largely concealed by pleonite 4	Slightly concealed by pleonite 4
<b>Pleotelson shape</b>	Evenly rounded	Roughly quadrate and curved upwards	Rounded	Broadly rounded
<b>Pleopod 5 endopod</b>	Slightly smaller than exopod	Smaller than exopod (not dissected)	Half the size of exopod	Smaller than exopod (not dissected)
<b>Uropods</b>	Broadly rounded, more than half the length of pleotelson	Apices narrowly rounded, more than half the length of pleotelson	Short, pointed, less than half the length of pleotelson	Broadly rounded, half the length of pleotelson

**Table 2.** Summary of the hosts, distribution, and attachment sites of all 33 species from the genus *Elthusa* Schioedte & Meinert, 1884, as well as the references for each record.

Species	Distribution	Hosts	References
<i>Elthusa alvaradoensis</i> ; Rocha-Ramírez, Chávez-López & Bruce, 2005	<b>TLoc:</b> Alvarado, Veracruz, Mexico.	<b>TH:</b> <i>Synodus foetens</i> (Linnaeus, 1766)	Rocha-Ramírez et al. (2005)
<i>Elthusa arnogglossi</i> Trilles & Justine, 2006	<b>TLoc:</b> Chesterfield Islands, New Caledonia.	<b>TH:</b> <i>Arnogglossus</i> sp.	Trilles and Justine (2006)
<i>Elthusa atlantimiroi</i> (Kononenko, 1988)	<b>TLoc:</b> Bay of Biscay, northeast Atlantic Ocean	<b>TH:</b> <i>Cepola macrophthalma</i> (Linnaeus, 1758)	Kononenko (1988)
<i>Elthusa californica</i> (Schioedte & Meinert, 1884) <b>Syn:</b> <i>Livoneca californica</i> Schioedte & Meinert, 1884	<b>TLoc:</b> California, near San Francisco <b>OL:</b> Pacific coast from Alaska to Peru; Canada; USA; Mexico	<b>TH:</b> <i>Holconoti</i> sp. <b>OH:</b> Species from the families: Atherinidae; Aulohynchidae; Clinidae; Clupeidae; Coriidae; Embiotocidae; Fundulidae; Gasterosteidae; Gobiidae; Hexagrammidae; Moronidae; Mugilidae; Pholidae; Osmeridae; Paralichthyidae; Pholidae; Pleuronectidae; Sebastidae	Schioedte and Meinert (1884); Keys (1928); Harch (1947); Olson (1972); Iverson (1974); Miller (1975); Waugh et al. (1989); Bennett (1993); Brusca (1981); Brusca et al. (2001); Gamble et al. (2013)
<i>Elthusa caudata</i> (Schioedte & Meinert, 1884) <b>Syn:</b> <i>Livoneca caudata</i> Schioedte & Meinert, 1884	<b>TLoc:</b> Laponica islands, Japan <b>OL:</b> New Zealand	<b>TH:</b> Unknown <b>Other hosts:</b> <i>Gempiterus blacodes</i> (Forster, 1801)	Schioedte and Meinert (1884); Avdeev (1978)
<i>Elthusa emarginata</i> (Bleeker, 1857) <b>Syn:</b> <i>Livoneca emarginata</i> Bleeker, 1857	<b>TLoc:</b> Java, Indonesia <b>OL:</b> East India; Malaysia; Indonesia	<b>TH:</b> Unknown <b>OH:</b> Species from the family Mullidae	Bleeker (1857); Miers (1881); Schioedte and Meinert (1884); Nierstrasz (1915); Trilles and Randall (2011)
<i>Elthusa epinepheli</i> Trilles & Justine, 2010	<b>TLoc:</b> Off Nouméa, New Caledonia	<b>TH:</b> <i>Epinephelus boulandi</i> (Günther, 1873)	Trilles and Justine (2010)
<i>Elthusa foveolata</i> (Hansen, 1897) <b>Syn:</b> <i>Irona foveolata</i> Hansen, 1897	<b>TLoc:</b> Sri Lanka	<b>TH:</b> Unknown	Hansen (1897)
<i>Elthusa frontalis</i> (Richardson, 1910) <b>Syn:</b> <i>Livoneca frontalis</i> Richardson, 1910	<b>TLoc:</b> Sablayan, Philippines	<b>TH:</b> <i>Balistes</i> sp.	Richardson (1910)
<i>Elthusa menziesi</i> (Brusca, 1981) <b>Syn:</b> <i>Livoneca menziesi</i> Brusca, 1981	<b>TLoc:</b> San Quintin Bays, Baja California, Mexico <b>OL:</b> Mexico and Western Baja California	<b>TH:</b> <i>Clinocottus analis</i> (Cuvier, 1858) <b>OH:</b> Species from the families of Atherinidae; Blenniidae; Clinidae; Coriidae; Gobiocidae; Kyphosidae; Labrisomidae; Lessoniaceae	Brusca (1981); Ruiz-Campos (1986); Wézer et al. (1991); Espinosa-Pérez and Hendrickx (2001)
<i>Elthusa methepia</i> (Schioedte & Meinert, 1884)	<b>TLoc:</b> Rio de Janeiro, Brazil	<b>TH:</b> <i>Achirus</i> sp.	Schioedte and Meinert (1884)

Species	Distribution	Hosts	References
<i>Ethusa moritakii</i> Saito & Yamauchi, 2016	<b>TLoc:</b> Honshu and east China Sea coast of Kyushu, Japan	<b>TH:</b> <i>Ereunias grillator</i> Jordan & Snyder, 1901	Saito and Yamauchi (2016)
<i>Ethusa myrpiristae</i> Bruce, 1990	<b>TLoc:</b> Escape Reef, outer Barrier Reef, Australia	<b>TH:</b> <i>Myrpiristis violacea</i> Bleeker, 1851	Bruce (1990)
<i>Ethusa nanoidea</i> (Stebbing, 1905) <b>Syn:</b> <i>Irona nanoidea</i> Stebbing, 1905	<b>TLoc:</b> Galle, Sri Lanka (old Ceylon) <b>OL:</b> Gulf of Suez, Red Sea	<b>TH:</b> Unknown <b>OH:</b> Species from the families Holothuridae; Leiognathidae; Moliidae; Plotosidae; Scorpaenidae; Sparidae	Stebbing (1905); Monod (1923); Trilles (1976)
<i>Ethusa neocyta</i> (Avdeev, 1975) <b>Syn:</b> <i>Lironeca neocyta</i> Avdeev, 1975	<b>TLoc:</b> New Zealand <b>OL:</b> Tasmania and south-east New Zealand	<b>TH:</b> <i>Neocyttus rhomboidalis</i> Gilchrist, 1906 <b>OH:</b> species from the families Cytridae; Oreosomatidae; Scombridae; Zeidae	Avdeev (1975, 1984); Stephenson (1987); Bruce (1990)
<i>Ethusa nierstraszii</i> Hadfield, Bruce & Smit, 2016 <b>Syn:</b> <i>Lironeca parva</i> Nierstrasz, 1915.	<b>TLoc:</b> Kisar Island, Moluccas, Indonesia	<b>TH:</b> <i>Ereunias grillator</i> Jordan & Snyder, 1901	Nierstrasz (1915); Avdeev (1984); Hadfield et al. (2016a)
<i>Ethusa ochotensis</i> (Kussakin, 1979) <b>Syn:</b> <i>Lironeca ochotensis</i> Kussakin, 1979	<b>TLoc:</b> Sea of Ochosk (near the city of Ayan), western Pacific Ocean	<b>TH:</b> Unknown	Kussakin (1979)
<i>Ethusa parabothi</i> Trilles & Justine, 2004	<b>TLoc:</b> New Caledonia, off Coëtlogon Bank	<b>TH:</b> <i>Parabothus tiensis</i> (Tanaka, 1918)	Trilles and Justine (2004)
<i>Ethusa parva</i> (Richardson, 1910) <b>Syn:</b> <i>Ceratothoa parva</i> (Richardson, 1910)	<b>TLoc:</b> Opol, Mindanao, Philippines	<b>TH:</b> Unknown	Richardson (1910); Hadfield et al. (2016b)
<i>Ethusa philippinensis</i> (Richardson, 1910) <b>Syn:</b> <i>Lironeca philippinensis</i> Richardson, 1910	<b>TLoc:</b> Jolo Light, Philippines	<b>TH:</b> Unknown	Richardson (1910)
<i>Ethusa poutasouensis</i> (Penso, 1939) <b>Syn:</b> <i>Ceratothoa poutasouensis</i> (Penso, 1939)	<b>TLoc:</b> Babakale Port, Aegean Sea Coasts, Turkey <b>OL:</b> Genova Gulf, Italy	<b>TH:</b> <i>Micromesistius poutasou</i> (Risso, 1827)	Brian (1939); Penso (1939); Ökrenet et al. (2018b)
<i>Ethusa propinqua</i> (Richardson, 1904) <b>Syn:</b> <i>Lironeca propinqua</i> Richardson, 1904	<b>TLoc:</b> Port Heda, Japan <b>OL:</b> Arabian Sea; Laccadive Islands; India; Maldives; Myanmar; Japan; Philippines; Australia	<b>TH:</b> Unknown <b>OH:</b> “ <i>chalinura</i> ”; “ <i>macrura</i> ”; “ <i>Macrurus</i> ”; <i>Ventrifossa</i> cf. <i>nigrodorsalis</i>	Richardson (1904, 1910); Barnard (1936); Bruce (1990)
<i>Ethusa raynaudii</i> (Milne Edwards, 1840) <b>Syn:</b> <i>Lironeca raynaudii</i> Milne Edwards, 1840	<b>TLoc:</b> Cape of Good Hope, South Africa <b>OL:</b> See text	<b>TH:</b> Unknown <b>OH:</b> See text	See in text.
<i>Ethusa sacciger</i> (Richardson, 1909) <b>Syn:</b> <i>Lironeca sacciger</i> Richardson, 1909	<b>TLoc:</b> Bungo Channel; Japan <b>OL:</b> North-western Pacific; Australia; Japan and Pacific coast	<b>TH:</b> <i>Synaphobranchus</i> sp. <b>OH:</b> Species from the families Synaphobranchidae; Sebastidae	Avdeev (1984); Bruce (1990); Hata et al. (2017); Richardson (1909); Shiino (1951); Yamauchi (2009)

Species	Distribution	Hosts	References
<i>Elthusa samariscii</i> (Shiino, 1951) <b>Syn:</b> <i>Lironeca samariscii</i> Shiino, 1951	<b>TLoc:</b> Japan	<b>TH:</b> <i>Samariscus japonicus</i> Kamohara, 1936	Shiino (1951); Biju Kumar and Bruce (1997)
	<b>OL:</b> Kerala coast, India	<b>Other hosts:</b> <i>Samaris cristatus</i> Gray, 1831	
<i>Elthusa samoensis</i> (Schioedte & Meinert, 1884) <b>Syn:</b> <i>Lironeca samoensis</i> Schioedte & Meinert, 1884	<b>TLoc:</b> Samoa Islands (Samoenses islands)	<b>TH:</b> Unknown	Schioedte and Meinert (1884)
	<b>TLoc:</b> North Stradbroke Island, Moreton Bay, southeastern Queensland, Australia	<b>TH:</b> <i>Siganus spinus</i> (Linnaeus, 1758)	
<i>Elthusa sinuata</i> (Koelbel, 1879) <b>Syn:</b> <i>Lironeca sinuata</i> Koelbel, 1879	<b>TLoc:</b> Mediterranean coast	<b>TH:</b> <i>Cepola macrophthalmus</i> (Linnaeus, 1758)	Koelbel (1879); Schioedte and Meinert (1884); Carus (1885); Gourret (1891); Gerstaecker (1901); Galati-Mosella (1920); Brian (1921); Monod (1924); Trilles (1968, 1977, 2008); Trilles and Raibaut (1973); Dollfus and Trilles (1976); Rokicki (1984, 1985); Trilles et al. (1989); Bello and Marinello (1998); Trilles and Ökterer (2004); Ökterer et al. (2009, 2018a)
	<b>OL:</b> North-West Africa; United Kingdom; Mediterranean; Adriatic Sea; Spain; France; Algeria; Tunisia; Italy; Yugoslavia; Montenegro; Turkey	<b>OH:</b> Species from the families Argentinidae; Bramidae; Cepolidae; Gobiidae; Loliiginidae; Pleuronectidae; Rajidae; Sepioliidae; Sparidae; Trichiuridae	
<i>Elthusa splendida</i> (Sadowsky & Moreira, 1981) <b>Syn:</b> <i>Lironeca splendida</i> Sadowsky & Moreira, 1981	<b>TLoc:</b> South Western Atlantic Ocean	<b>TH:</b> <i>Squalus cubensis</i> Howell Rivero, 1936	Sadowsky and Moreira (1981)
<i>Elthusa tropicalis</i> (Menzies & Kruczynski, 1983) <b>Syn:</b> <i>Lironeca tropicalis</i> Menzies & Kruczynski, 1983	<b>TLoc:</b> off Egmont Key, Florida, USA	<b>TH:</b> <i>Ogcocephalus parvus</i> Longley & Hildebrand, 1940	Menzies and Kruczynski (1983)
	<b>TLoc:</b> Western Australia	<b>TH:</b> Unknown	
<i>Elthusa turgidula</i> (Hale, 1926) <b>Syn:</b> <i>Lironeca turgidula</i> Hale, 1926	<b>OL:</b> One Tree Island, Great Barrier Reef	<b>OH:</b> Species from the families Scaridae; Scaridae	Hale (1926); Bruce (1990)
	<b>TLoc:</b> San Francisco Bay; Tomales Bay; Monterey	<b>TH:</b> Unknown	
<i>Elthusa vulgaris</i> (Simpson, 1857) <b>Syn:</b> <i>Lironeca vulgaris</i> Simpson, 1857	<b>OL:</b> Pacific Ocean including the western coast of USA, Mexico and Colombia	<b>OH:</b> Species from the families Carangidae; Chaenopsidae; Cottidae; Cynoglossidae; Embiotocidae; Engraulidae; Gobiidae; Hexagrammidae; Moronidae; Paralichthyidae; Pleuronectidae; Scorpaenidae; Serranidae; Synodontidae. Also "rock cod", "flounder", "lingcod"	Simpson (1857); Richardson (1904); Turner et al. (1969); Hobson (1971); Brusca (1978, 1981); Bennett (1993); Espinosa-Pérez and Hendricks (2001); Gamble et al. (2013)
	<b>TLoc:</b> Hawaii	<b>TH:</b> <i>Ctenochaetus strigosus</i> (Bennett, 1828); <i>Acanthurus nigroris</i> Valenciennes, 1835	
<i>Elthusa winstonii</i> Hadfield, Turtle & Smit, 2017			Hadfield et al. (2017)

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# The study of hidden habitats sheds light on poorly known taxa: spiders of the Mesovoid Shallow Substratum

Enrique Ledesma<sup>1</sup>, Alberto Jiménez-Valverde<sup>1</sup>, Alberto de Castro<sup>2</sup>,  
Pablo Aguado-Aranda<sup>1</sup>, Vicente M. Ortuño<sup>1</sup>

**1** *Research Team on Soil Biology and Subterranean Ecosystems, Department of Life Science, Faculty of Science, University of Alcalá, Alcalá de Henares, Madrid, Spain* **2** *Entomology Department, Aranzadi Science Society, Donostia - San Sebastián, Gipuzkoa, Spain*

Corresponding author: *Enrique Ledesma* ([kike.ledesma3553@gmail.es](mailto:kike.ledesma3553@gmail.es));  
*Alberto Jiménez-Valverde* ([alberto.jimenezv@uah.es](mailto:alberto.jimenezv@uah.es))

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## Abstract

The scarce and biased knowledge about the diversity and distribution of Araneae species in the Iberian Peninsula is accentuated in poorly known habitats such as the Mesovoid Shallow Substratum (MSS). The aim of this study was to characterize the spiders inventory of the colluvial MSS of the Sierra de Guadarrama National Park, and to assess the importance of this habitat for the conservation of the taxon.

Thirty-three localities were selected across the high peaks of the Guadarrama mountain range and they were sampled for a year using subterranean traps specially designed to capture arthropods in the MSS. Species accumulation curves were built both for the observed species richness and for the non-parametric richness estimators. The literature was reviewed in order to update the distributional maps of the rarest species.

Forty-two species were collected, of which four were species new to science. More than half were represented by one or two individuals which caused the accumulation curves to rise slowly and to end without reaching an asymptote. Almost half of the species showed significant increases in their Iberian distribution ranges. Two species were recorded for the first time in the Iberian Peninsula and 32 species were new additions to the spider checklist of the Sierra de Guadarrama National Park.

## Keywords

Araneae, Iberian Peninsula, inventory completeness, species distributions, stone debris

## Introduction

The Mesovoid Shallow Substratum (MSS) is a subterranean habitat originally described by Juberthie et al. (1980, 1981) and Uéno (1980, 1981) as the network of voids and interstices found just above the deep subterranean domain and immediately beneath the soil (if soil exists). The structure of the MSS is a direct consequence of the action of different lithological processes in diverse substrates; accordingly, various types of MSS have been categorised, including colluvial, alluvial, volcanic, and bedrock (see Mammola et al. 2016). The absence of light, the usually high and constant relative humidity and the cushioned temperature fluctuations throughout the year are common abiotic conditions for any MSS (Mammola et al. 2016; Giachino and Vailati 2010; Pipan et al. 2011; Mammola et al. 2017a). The shallow condition of the MSS typically results in a significant flow of material and energy from the upper layers (Gers 1998).

The phylum Arthropoda dominates in the MSS (Mammola et al. 2017a; Nitzu et al. 2010, 2014; Ortuño et al. 2013; Langourov et al. 2014; Jiménez-Valverde et al. 2015). In general, the MSS assemblages are very rich and diverse and are formed both by hypogean species with different degrees of adaptation to the subterranean environment and by a notable contingent of epigean and endogean species which transit between the surface and the hypogean environment (Gers 1998; Pipan et al. 2011; Pipan and Culver 2012; Nitzu et al. 2014; Jiménez-Valverde et al. 2015; Rendoš et al. 2016; Mammola et al. 2017a). The MSS, by virtue of its biophysical characteristics, plays a fundamental ecological role as an ecotone between the surface and the deep subterranean environment (Moseley 2010), as well as serving as a biogeographic corridor and climatic refuge (Ortuño et al. 2013; Moseley 2010; Růžička 1993; Hernando et al. 1999; Růžička et al. 2012). All of these roles have obvious important implications in conservation.

The study of the MSS is limited by logistical difficulties and requires substantial research effort. Consequently, knowledge about MSS biodiversity is scarce and tends to be geographically biased (Jiménez-Valverde et al. 2015; Mammola et al. 2016). However, when the sampling difficulties can be overcome, exploration of the MSS usually reveals taxonomic novelties and interesting species records (see Mammola et al. 2016, for an extensive list of references). In the Iberian Peninsula, for example, new species from different arthropod orders have been described from the MSS, including the Orthoptera (Barranco et al. 2013), Coleoptera (Toribio and Rodríguez 1997; Carabajal et al. 1999; Faille et al. 2012; Ortuño et al. 2014), Collembola (Baquero et al. 2017), Diplura (Sendra et al. 2017), and Diplopoda (Gilgado et al. 2015a, 2015b, 2017; Akkari et al. 2018). Therefore, the MSS is a habitat that hosts many rare and poorly known species (see, for instance, Ortuño 1996, 2002, 2004; Ortuño and Toribio 1994; Ortuño and Martínez-Pérez 2011; Ortuño et al. 2014; Gilgado et al. 2015a, 2015b, 2015c; Jiménez-Valverde et al. 2015). However, the significance of the potential of the MSS to enhance our knowledge of biodiversity is not easy to evaluate because of the minimal number of comprehensive studies that have covered a broad spatial, temporal, and taxonomic scale.

Araneae is a hyperdiverse taxon that includes more than 47200 accepted species distributed in 116 families and in more than 4000 genera (World Spider Catalog 2018). Approximately 1000 spider species across 48 families occur in subterranean ecosystems (Mammola and Isaia 2017). Nevertheless, the taxonomic and chorologic knowledge on spiders is generally scarce and geographically biased, despite their high abundance and richness in almost all ecosystems, their key role in ecological networks, and their potential as biological indicators (New 1999). The Iberian-Balearic region harbours around 1382 species (Morano et al. 2014), although the true number is estimated to lie between 1500 and 2000 species (Melic et al. 2015). Given the current state of knowledge, around 19% of the species are considered Iberian endemics (Melic 2001).

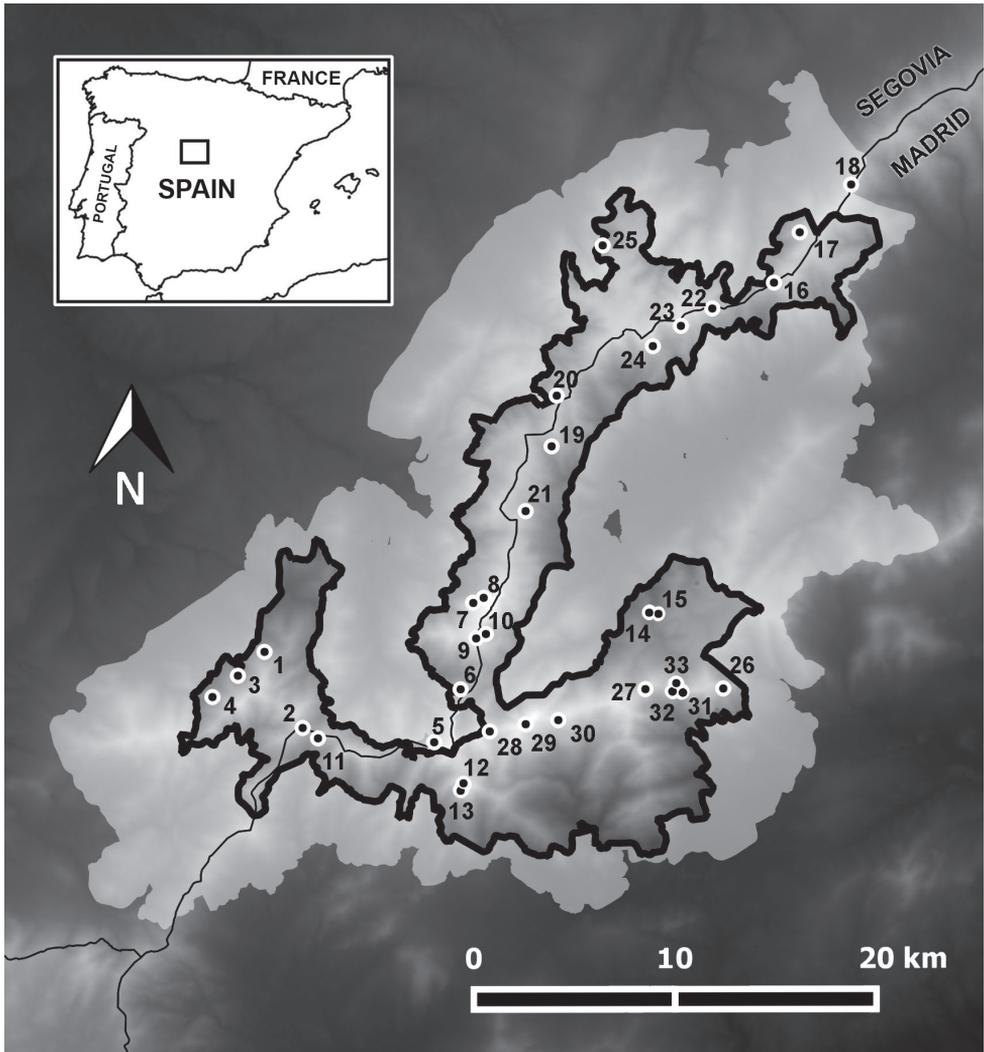
The paucity of knowledge about Iberian spiders is illustrated by the fact that 20% of the species are known from just a single record and 50% of the species from fewer than 5 records (Cardoso and Morano 2010). The accumulated records also show a strong geographical bias, as illustrated by the fact that some provinces have fewer than 30 recorded species (Morano et al. 2014). Approximately one hundred of the Iberian Peninsula spider species are considered troglobiont or troglophile (*sensu* Sket 2008, Mammola et al. 2017b) and most of this knowledge comes from captures made inside caves in karstic areas (Cardoso 2012), i.e., from natural subterranean spaces in the underground that are accessible to humans. However, the MSS is an important subterranean habitat for spiders, and its study has the potential to reveal new and interesting catches, as the extensive work by the arachnologist Vlastimil Růžička in colluvial MSS (scree slopes) from the Czech Republic has shown (see Růžička 1990; Růžička and Dolanský 2016, and references therein), as well as other studies in different European regions (see, for instance, Nae 2008; Deltshv et al. 2011; Nae and Ilie 2004).

The Sierra de Guadarrama National Park, located in the Central System of the Iberian Peninsula, was recently established in order to protect the high-elevation areas and summits of the Guadarrama Mountains (BOE 2013). This mountain range has traditionally received considerable attention from scientists and naturalists, but only a few recent studies have focused on its shallow subterranean environment (see Baquero et al. 2017; Gilgado et al. 2017). The aim of the present study was to characterise, across an entire year, the diversity of spider species inhabiting the colluvial MSS present throughout the National Park and to evaluate the importance of this habitat for the conservation of rare and poorly known species.

## **Materials and methods**

### **Study area**

Sierra de Guadarrama National Park is located in the Central System of the Iberian Peninsula, between the two provinces of Madrid and Segovia (Figure 1). It covers an expanse of 33960 hectares (BOE 2013) and is surrounded by a peripheral buffering



**Figure 1.** Location of the 33 scree slopes that were sampled in the Sierra de Guadarrama National Park. Each point corresponds to one subterranean sampling device (SSD). The innermost area of the map delimited by the thick black line delimits the National Park and the surrounding light gray area corresponds to the buffering zone (peripheral protection area).

zone of 62687 hectares (MAPAMA no year). The altitudinal gradient ranges from 1200 to 2428 m a.s.l.; consequently, the climate and vegetation show the expected variability associated with this type of gradient. Globally, the climate of Sierra de Guadarrama National Park can be categorised as cold continental Mediterranean: it has a short, dry, and chilly summer season and a long cold winter (PNSG no year). Precipitation in the highest elevations occurs mostly in the form of snow, forming a layer that lasts all winter and part of the spring season (Salazar Rincón and Vía García 2003).

The orthogneiss, rocks of metamorphic quartz-feldspathic origin, are the predominant rocks of the Park (Viallette et al. 1987). The fragmentation of these rocks, mainly as a direct consequence of past (pre)glacial events, is the origin of the typical moraines and colluvial deposits (Sanz 1986), the so-called scree slopes. Baquero et al. (2017) provide more details on the different bioclimatic levels present in Guadarrama and an extensive description of the study area.

## **Sampling**

After evaluating the amount of effort that could be spent in the time available for field work, 33 scree slopes were selected across the Sierra de Guadarrama National Park with the intention of covering most of the geographic area of the Park, while taking into account access possibilities (Figure 1). Of these, 31 sampling localities were placed in the National Park and the other 2 were located in the peripheral cushioning area. A subterranean sampling device (SSD) was installed on each scree slope; a full description of these traps, which are designed to collect species inhabiting the MSS, can be found in Baquero et al. (2017). Briefly, each SSD is made up of a PVC cylinder one meter long and 11 cm in diameter that has numerous perforations (8 mm in diameter) from the middle to its base (50–90 cm). The cylinder is inserted vertically into an excavated hole, a pitfall baited with very smelly cheese and filled with 1,2-propanediol is placed at the bottom and the SSD is covered and made flush with the ground surface. The sampling period was from 20-V-2015 to 13-VII-2016. Sampling permits for the corresponding National Park were obtained from the following appropriate authorities: Ismael Hernández Fernández, Deputy Directorate General of Management and Planning of Protected Areas (2015) and José Lara Zabía, Head of Conservation Area of Flora and Fauna (2016) at the General Directorate of Environment of the Community of Madrid, and José Ignacio Quintanilla Rubio (2015), and Montserrat de Andrés Boal (2016), General Director of the Natural Environment by delegation of the Head of the Territorial Service of the Environment of the Junta de Castilla y León. Samples were taken to the laboratory and the spider specimens were separated from the rest of the material and stored in glass vials filled with 70% ethanol. All the samples were deposited in the collection of the University of Alcalá. Adult specimens were identified to the species level using the keys and the compilation of identification work available in Nentwig et al. (2018). Species nomenclature in this study follows that of the World Spider Catalog (2018).

## **Assessment of inventory completeness**

The accumulation of new species as a function of sampling effort was assessed by building a sample-based species accumulation curve by randomising the order of entrance of each SSD (sample) 100 times and calculating the mean species richness for each level of sampling effort (number of SSDs; Gotelli and Colwell 2001). The following

non-parametric species richness estimators were calculated: Chao1, Chao2, first-order Jackknife (Jack1), second-order Jackknife (Jack2), ICE, and ACE (Colwell and Coddington 1994). The numbers of singletons (species with one specimen), doubletons (species with two specimens), unique species (those appearing in one SSD) and duplicates (species that appear in two SSDs) were also determined. The expected number of species (Sest) for each level of sampling effort was calculated and extrapolated up to 66 samples (double the sampling effort) using the analytical approach based on the Bernoulli product moment proposed by Colwell et al. (2012). All calculations were done using EstimateS version 9.1.0 software (Colwell 2013).

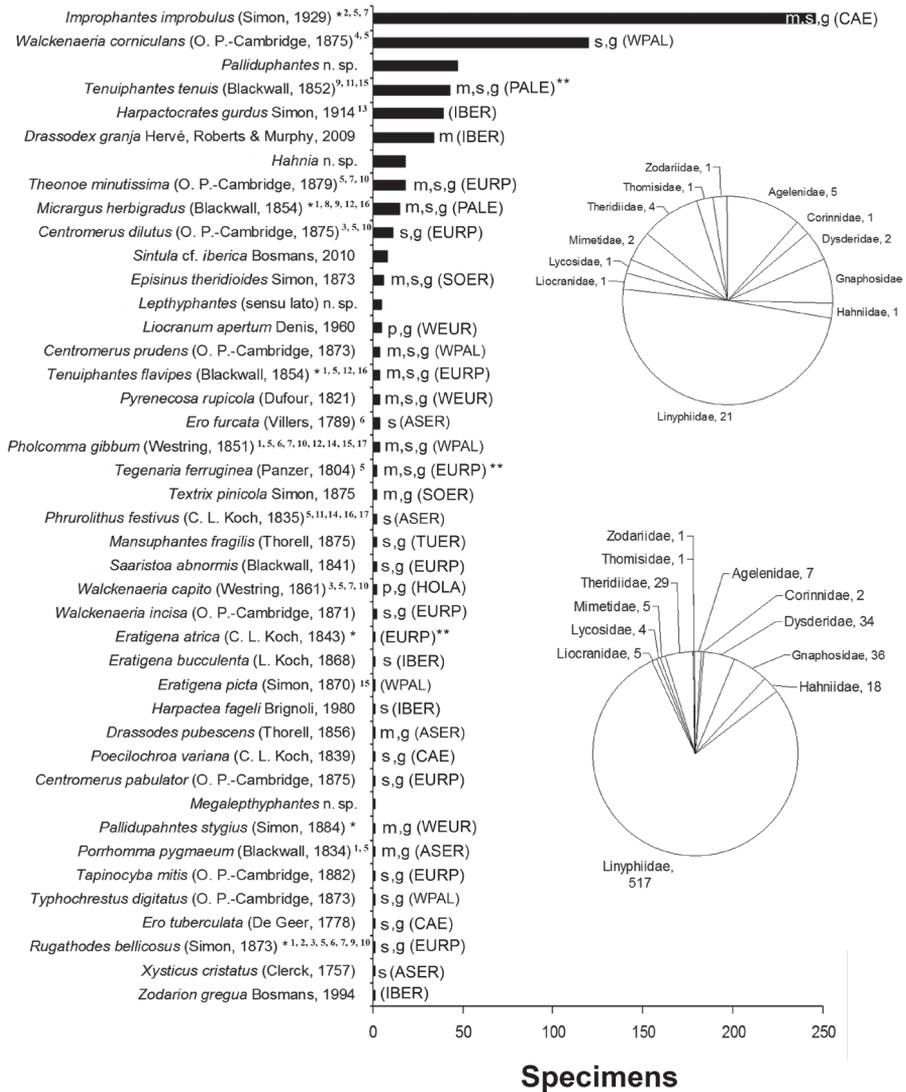
### Distribution and ecotype characterisation of the species

The chorotype classification proposed by Vigna Taglianti et al. (1992) was used to classify each species following the information of the World Spider Catalog (2018) and Nentwig et al. (2018). The Iberian Spider Catalogue (Morano et al. 2014) was used as a primary consulting source, and after a thorough search of the literature up to 2018, each species was evaluated as a possible new record for either the Segovia or Madrid provinces, for the Sierra de Guadarrama National Park or for the Iberian Peninsula. Except for the most common and widespread species (see Results), the presence records in the Iberian Peninsula for each species were compiled from the literature up to 2018. All records were referred to a 10 × 10 km UTM grid; only a few records were discarded because the provided place name was insufficiently precise to be ascribed to a unique 10 × 10 km UTM cell. Distribution maps were built with QGIS version 2.16.3 software (Quantum GIS Development Team 2016).

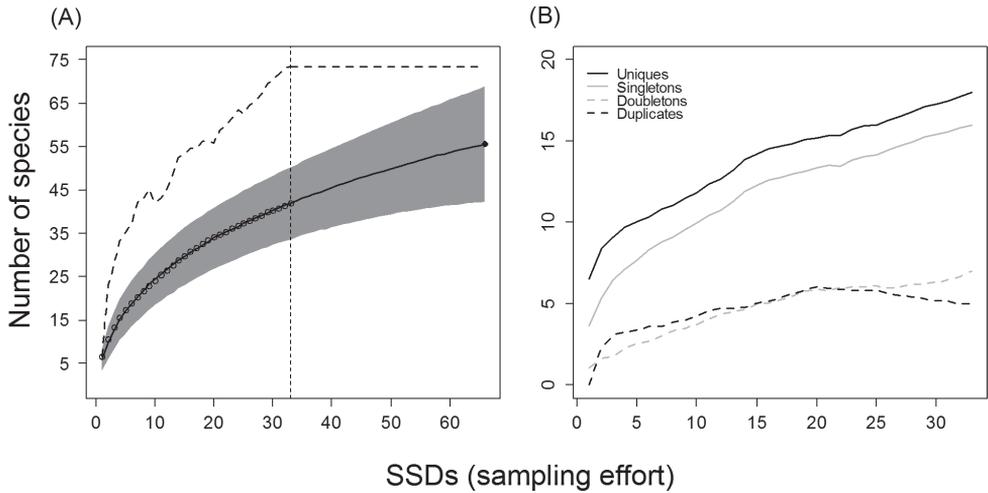
Troglobiont or troglophile species were classified as such, following Mammola et al. (2017b). Each species was characterised as newly or previously recorded from the MSS after a literature review.

### Results

In total, 1388 spiders were collected, although only 665 specimens, belonging to 42 species and 12 families, were adults (Figure 2 and Suppl. material 1: Table S1). The Linyphiidae was the most important family both in terms of species and specimens numbers. This was followed by the Theridiidae, Gnaphosidae, Dysderidae and Ageleidae (Figure 2). The accumulation curve ended while still rising (Figure 3A), as did the curves of most of the non-parametric estimators (Figure 3A and Suppl. material 2: Figure S1). The only exception was Chao1, whose curve started to stabilise at around 27 SSDs (Suppl. material 2: Figure S1). The number of singletons, doubletons, and unique species continued to increase at the end of the inventory; only the number of duplicates started to decrease (Figure 3B). Overall, 23 of 42 species (54.8%) were represented by just one or two specimens (singletons = 16, doubletons = 7) or appeared in only one or two samples (uniques = 18, duplicates = 5). The estimated degree of



**Figure 2.** Number of specimens for each spider species. Pie charts represent the distribution of species (up) and specimens (down) into spider families in the inventory. Abbreviations: m = new species record for Madrid province; s = new species record for Segovia province; p = new species record for the Iberian Peninsula; g = new species record for the Sierra de Guadarrama National Park. Chorotypes based on the criteria proposed by Vigna Taglianti et al. (1992): (HOLA) = Holarctic; (PALE) = Palearctic; (WPAL) = West-Palearctic; (ASER) = Asiatic-European; (CAE) = Centralasiatic-European; (TUER) = Turanian-European; (EURP) = European; (SOER) = South-European; (WEUR) = West-European. The chorotype Iberian Endemism (IBER) follows the criteria of Novoa (1975) and Serrano et al. (2003). \* = troglophile species (sensu Mammola et al. (2017b)); \*\* = species introduced in other regions beyond its original range (following Nentwig et al. 2018). Records for species previously listed in the MSS are given in: <sup>1</sup>Růžička (1989); <sup>2</sup>Růžička (1990); <sup>3</sup>Růžička and Zacharda (1994); <sup>4</sup>Růžička et al. (1995); <sup>5</sup>Růžička and Hajer (1996); <sup>6</sup>Růžička and Thaler (2002); <sup>7</sup>Růžička and Klimeš (2005); <sup>8</sup>Nitzu, et al. (2006); <sup>9</sup>Nitzu, et al. (2010); <sup>10</sup>Růžička and Zacharda (2010); <sup>11</sup>Deltshev et al. (2011); <sup>12</sup>Laška et al. (2011); <sup>13</sup>Barranco et al. (2013); <sup>14</sup>Langourov et al. (2014); <sup>15</sup>Jiménez-Valverde et al. (2015); <sup>16</sup>Růžička and Dolanský (2016); <sup>17</sup>Mammola et al. (2017a).

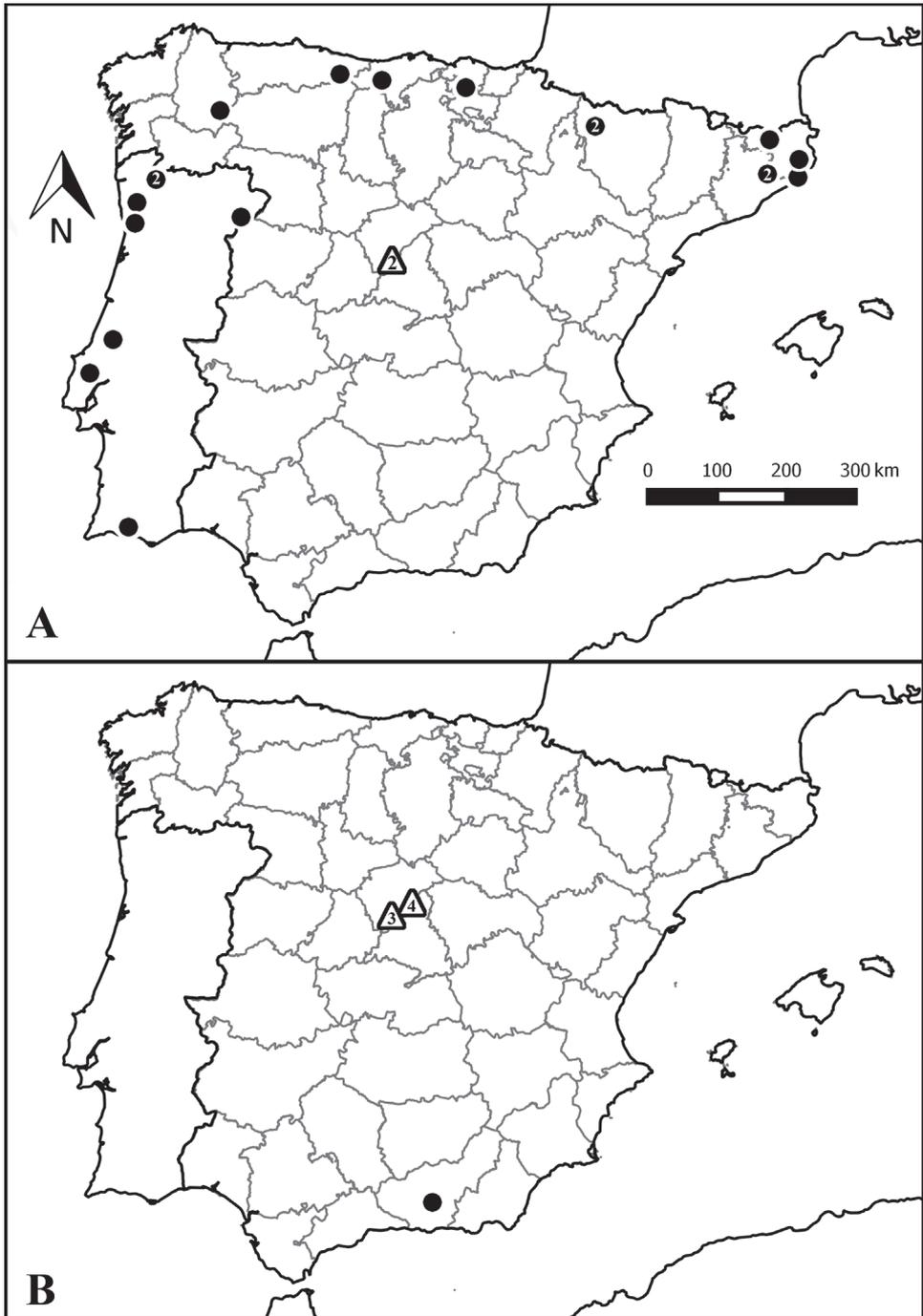


**Figure 3.** Species accumulation curves for the complete inventory of the Sierra de Guadarrama National Park. **A** Sample-based species accumulation curve using subterranean sampling devices (SSDs) as effort units (empty circles); extrapolation curve for a sampling effort of 66 SSDs (thick black line); 95% confidence interval as grey bands, and Chao2 curve (stripped line). Vertical line marks the realized sampling effort (33 SSDs) **B** Species accumulation curves of singleton, doubleton, unique and duplicate species.

completeness of the inventory ranged from 57.2% to 70.6% (estimated number of species [mean  $\pm$  SD]: Chao2 =  $73.42 \pm 21.17$ , Jack2 =  $71.81 \pm 0.00$ , ICE =  $68.19 \pm 0.03$ , ACE =  $61.27 \pm 0.00$ , Chao1 =  $60.26 \pm 12.22$ , Jack1 =  $59.45 \pm 4.42$ ). Doubling the sampling effort (66 SSDs) predicted the addition of 14 species to the inventory (55.61 species; Figure 3A).

Four species represent previously undescribed species, five species were Iberian endemics, and the remainder of the species had wider ranges of distribution (Figure 2). Almost half of the spider species captured in this study (19 out of 42) showed moderate to dramatic increases in their Iberian distribution ranges. Figure 4 illustrates two typical patterns. The first case corresponds to *Centromerus dilutus* (O. P.-Cambridge, 1875), a species of Linyphiidae that was previously only known as a restricted species in the northern and western strips of the Iberian Peninsula (Cantabrian Mountains, extending through the Pyrenees and to the west and south of Portugal; Figure 4A). The second example corresponds to *Improphantes improbulus* (Simon, 1929), another Linyphiidae species that was only known from a locality in southern Spain (Figure 4B). The other 19 species followed similar patterns (see Suppl. material 3: Figure S2). Without considering *Sintula* cf. *iberica* and the four new species, a total of 15 species are new records for the province of Madrid, 26 species are new records for Segovia, two species are recorded for the first time in the Iberian Peninsula, and 27 species are new additions to the spider checklist of the Sierra de Guadarrama National Park (Figure 2).

One noteworthy observation is that some of the most common species in this inventory were poorly known until now. For instance, *I. improbulus* was the most



**Figure 4.** Species distribution maps. (A) *Centromerus dilutus* and (B) *Improphantes improbulus*. Black circles represent records from the literature; triangles represent records from the present study. In cases where the symbol includes several  $10 \times 10$  km UTM cells, and to improve legibility, their number is indicated (note that one  $10 \times 10$  km UTM cell usually contains several sampling locations, see Suppl. material 1: Table S1).

numerous species (246 specimens; Figure 2) and was widely distributed across the surveyed area (24 out of 33 SSDs; Suppl. material 1: Table S1), although it was previously only known from a record published in 1957 (Janetscheck 1957) (Figure 4B). *Drassodex granja* Hervé, Roberts & Murphy, 2009, with 34 specimens and also widely distributed across the surveyed area (15 out of 33 SSDs; Suppl. material 1: Table S1), was only known from a record dating back to 1914 (Simon 1914; Suppl. material 3: Figure S2). Two of the new species for science had 47 (*Palliduphantes* sp. nov.) and 18 (*Hahnina* sp. nov.) specimens.

Only six of 42 species were categorised as troglophile species; one of them, *I. improbulus*, was the most abundant species of the inventory (Figure 2). Four of these species plus another 12 species from the whole species list had been previously reported in other MSS studies (Figure 2).

## Discussion

The order Araneae is one of the dominant taxa in the MSS (Mammola et al. 2016), especially when the number of species is considered. On the contrary, when the number of specimens is taken into account the relevance of the taxon decreases (e.g., Jiménez-Valverde et al. 2015). This occurs because spider assemblages in the MSS tend to be very uneven and are mostly represented by only a few abundant species and a high number of extremely rare species. This pattern is confirmed in the present study, where more than half the species are represented by one or two specimens (38.1% and 16.7%, respectively). Although making comparisons is difficult due to methodological differences among studies, this number of rare species is similar to those reported in other studies across Europe; for instance, 48.6% and 11.4% in Růžička (1989), 39.1% and 13% in Růžička and Zacharda (1994), 20.8% and 14.6% in Laška et al. (1995), 46.4% and 14.3% in Růžička et al. (1995), 34.2% and 31.6% in Růžička (1996), 25.9% and 16.7% in Růžička and Hajer (1996), 52% and 12% in Růžička and Thaler (2002), 51.9% and 13.5% in Růžička and Zacharda (2010), 55% and 5% in Jiménez-Valverde et al. (2015), 42.4% and 9.1% in Růžička and Dolanský (2016) and 50% and 5.6% in Mammola et al. (2017a) (the percentage values correspond to singletons and doubletons, respectively, calculated from the data provided in the tables by the aforementioned authors).

This high component of rare species makes each sample very different from the others in terms of species composition (high percentages of uniques and duplicates; Jiménez-Valverde et al. 2015); therefore, the addition of species to the inventory is slow and constant, as the species accumulation curve of the present study shows. The species accumulation curve ends while it is still rising, as do the curves of almost all the non-parametric estimators (Fig. 3 Suppl. material 2: Figure S1), indicating that still more species are expected to be found in the colluvial MSS of the Sierra de Guadarrama National Park. If these curves are far from stabilising, then caution is mandatory when interpreting richness estimations (Melo and Froehlich 2001; Thompson et al. 2003;

Thompson and Thompson 2007; Gotelli and Colwell 2001). Thus, as a conservative score, at least 18 more spider species could be expected to be found in this area. Fourteen species could be added to the inventory by doubling the number of sampled scree slopes, which would imply a significant increase in terms of monetary and work effort.

A low degree of inventory completeness is typical of hyperdiverse taxa such as spiders (Colwell and Coddington 1994; Coddington et al. 1996; Dobyns 1997; Toti et al. 2000; Sørensen et al. 2002; Scharff et al. 2003; Cardoso et al. 2008), and is even magnified in a habitat like the MSS, as the current study and other studies (e.g., Jiménez-Valverde et al. 2015) have shown. In fact, the proportion of singletons in this and other MSS studies is comparable to the percentages frequently found in spider inventories from tropical forests (see Coddington et al. 2009). As Coddington et al. (2009) suggested for tropical arthropod surveys, undersampling is probably the main cause of the high number of species represented by just one specimen in the MSS, and this is further exacerbated by the generally low densities attained in the subterranean realm (Růžička and Hajer 1996; Růžička and Klimeš 2005; Mammola et al. 2016). However, a second factor may provide an equally important explanation for the presence of low-prevalence species in the MSS. As already pointed out by Jiménez-Valverde et al. (2015), delimiting the sampling universe is extremely challenging due to the closeness to the surface and because of the ecotone role of the MSS (Moseley 2010). Thus, an unknown proportion of the rare species encountered in the present study is likely to represent simply occasional visitors, such as *Xysticus cristatus* (Clerck, 1757), *Zodarion gregua* (Bosmans, 1994) or *Pyrenecosa rupicola* (Dufour, 1821). These are, however, important elements (or they are at least as important as other equally rare troglophile/troglobiont species) of the interaction network in the MSS (Gers 1998; Pipan et al. 2011; Nitzu et al. 2014), and this is a good reason to consider them as part of the inventory. The high proportion of low-prevalence species in the MSS makes obtaining complete and reliable arthropod inventories a challenge, which, in turn, hampers the understanding of biodiversity and ecological patterns in the MSS (Jiménez-Valverde et al. 2015).

The presence of an important number of exogenous species in the MSS is the rule rather than the exception, and this presence will depend on the characteristics of the MSS and on the depth at which the traps are placed (Medina and Oromí 1990; Mammola et al. 2016). However, this number is difficult to estimate due to the lack of basic autecological knowledge for most of the species (the Hutchinsonian shortfall; see (Cardoso et al. 2011; Hortal et al. 2015)). Following the classification proposed by Mammola et al. (2017b), which is mostly based on morphological traits, only 14.3% of the species collected in the present study can be considered troglophiles, and no troglobite species were captured. However, 28.6% of the species have been reported previously from the MSS in other studies but have not been classified as troglophiles by Mammola et al. (2017b), so their ecological preferences should probably be re-evaluated and some of them be classified as troglophiles as well. The original description of *D. granja* did not comment on any aspect of its biology and did not highlight any morphological adaptation to the subterranean environment (Simon 1914). However, the density and the extent of its occurrence in Guadarrama reported in the present study suggest a substantial affinity for

the underground realm, which leads us to consider *D. granja* to be a troglophile species. The four new species also need to be classified as troglophiles. Adaptation to the subterranean environment can take many forms besides morphology (Sket 2008), and the study of the MSS will increase the knowledge about the ecological preferences of many species and will help in establishing a better ecotype classification for many of them.

Four species collected in this study were new to science. The Linnaean shortfall (i.e., the discrepancy between the number of already described species and the number of species that actually exist) manifests particularly in poorly studied habitats (Lomolino 2004; Hortal et al. 2015), as is the case for the MSS (Jiménez-Valverde et al. 2015; Mammola et al. 2016). Three of these four new species were Linyphiidae, which is the dominant spider family in subterranean habitats (Bellés 1987; Růžička 1989; Ribera and Juberthie 1994; Mammola et al. 2017a) and one of the most poorly known families (Melic et al. 2015), probably due to its small size, high diversity and difficult taxonomy.

*Liocranum apertum* Denis, 1960 and *Walckenaeria capito* (Westring, 1861) are new species for the Iberian Peninsula. Whereas the first one has only been recorded in France, the second has a West-Palaearctic distribution (World Spider Catalog 2018). More than half of the species (31 out of 42 species, 73.8%) are new records for the province of Segovia, Madrid or for both. Many of these species have wide distribution ranges (Figure 2). For instance, *I. improbulus*, with 246 specimens collected in this study, is found from Spain to China (World Spider Catalog 2018), although the single record from Spain dates back more than half a century (Janetscheck 1957). The records of most of all these species imply not only new provincial records but also significant increases in their extent of occurrence (sensu IUCN 2001) in the Iberian Peninsula. All these results evidence the scarce arachnological knowledge in the Iberian Peninsula (Melic 2001; Morano 2004; Cardoso and Morano 2010), and this significant lack of chorological information hinders not only the accurate delimitation of distributional ranges but also the accurate prediction of ranges through statistical techniques such as species distribution models (Lobo 2008). Moreover, the impossibility to precisely estimate the distribution of the species (the Wallacean shortfall; see Lomolino 2004; Hortal et al. 2015) hampers the proper application of certain criteria that are used to categorize species into different grades of vulnerability (IUCN 2001).

Usually, protected natural areas, especially those easily accessible and close to big urban areas, are highly attractive for recorders (Dennis et al. 1999; Boakes et al. 2010). Yet, the general lack of spider records for Iberian protected natural areas has been repeatedly recognized (Barriga et al. 2006; Pérez Sánchez and Méndez Iglesias 2013; Morano 2018). When it comes to National Parks, the maximum protection status, the scenario is still disheartening; despite the existence of 12 National Parks in the Iberian Peninsula, only three of them have been submitted to a relatively intense sampling effort: the Picos de Europa National Park (Méndez 1998; Pérez Sánchez and Méndez Iglesias 2013; Mardomingo Vargas et al. 2016; Jiménez Segura et al. 2017), the Cabañeros National Park (Barriga et al. 2006, 2010) and the Tablas de Daimiel National Park (Morano 2018). In the case of the Sierra de Guadarrama National Park,

there is no published catalog for the area and the citations of spider species are scattered through the literature. The literature survey provided a preliminary checklist of the Park spider species and revealed that 32 (27 plus the four new species plus *S. cf. iberica*) out of the 42 species were new additions, which increased the list of species from 120 to 153 species. This lack of information about spiders in protected natural spaces necessarily excludes these organisms from their protection plans (Skerl and Gilliespie 1999).

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## Supplementary material I

### Table S1. Araneae species captured and their distribution in the MSS of the Sierra de Guadarrama National Park

Authors: Enrique Ledesma, Alberto Jiménez-Valverde, Alberto de Castro, Pablo Aguado-Aranda, Vicente M. Ortuño

Data type: species data

Explanation note: UTM 1 × 1 km cells are provided and the corresponding SSD numbers (see Fig 1) are indicated into parentheses. Note that some SSDs lay in the same UTM cell.

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Link: <https://doi.org/10.3897/zookeys.841.33271.suppl1>

## Supplementary material 2

### Figure S1. Non-parametric species richness estimators

Authors: Enrique Ledesma, Alberto Jiménez-Valverde, Alberto de Castro, Pablo Agudo-Aranda, Vicente M. Ortuño

Data type: statistical data

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## Supplementary material 3

### Figure S2. Species distribution maps

Authors: Enrique Ledesma, Alberto Jiménez-Valverde, Alberto de Castro, Pablo Agudo-Aranda, Vicente M. Ortuño

Data type: occurrence

Explanation note: Black circles represent records from the literature; triangles represent records from the present study. In cases where the symbol includes several 10 × 10 km UTM cells, and to improve legibility, their number is indicated (note that one 10 × 10 km UTM cell usually contain several sampling locations, see Table S1). A) *Centromerus pabulator*; B) *Drassodes pubescens*; C) *Episinus theridioides*; D) *Ero tuberculata*; E) *Mansuphantes fragilis*; F) *Micrargus herbigradus*; G) *Pholcomma gibbum*; H) *Poecilochroa variana*; I) *Pyrenecosa rupicola*; J) *Rugathodes bellicosus*; K) *Saaristoa abnormis*; L) *Tapinocyba mitis*; M) *Tegenaria ferruginea*; N) *Tenuiphantes flavipes*; O) *Theonoe minutissima*; P) *Typhochrestus digitatus*; Q) *Walckenaeria incisa*.

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Link: <https://doi.org/10.3897/zookeys.841.33271.suppl3>



# A new species of *Wesmaelius* Krüger from Mexico, with a key to the New World species of the subgenus *Kimminsia* Killington (Neuroptera, Hemerobiidae)

Yesenia Marquez-López<sup>1</sup>, Atilano Contreras-Ramos<sup>2</sup>

<sup>1</sup> *Maestría en Biología, Universidad Autónoma Metropolitana-Iztapalapa, Departamento de Biología, 09340 Ciudad de México, Mexico* <sup>2</sup> *Instituto de Biología-UNAM, Departamento de Zoología, Ciudad Universitaria, 04510 Ciudad de México, Mexico*

Corresponding author: *Atilano Contreras-Ramos* ([acontreras@ib.unam.mx](mailto:acontreras@ib.unam.mx))

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## Abstract

*Wesmaelius* (*Kimminsia*) *nanacamilpa* Marquez & Contreras, **sp. n.**, a brown lacewing from Tlaxcala state, Mexico is described and illustrated. This is the second recorded species of *Wesmaelius* from Mexico, and the third from Middle America. Males of the new species may be identified by parameres separate apically, styliform sclerites directed basally, as well as a rounded gonarcus with a short entoprocessus. Females may be distinguished from closely related species by a subgenital plate with the central plate broadly incised basally. There are now 16 species of *Wesmaelius* known from the New World.

## Keywords

Brown lacewings, taxonomy, Tlaxcala, Transmexican Volcanic Belt

## Introduction

*Wesmaelius* Krüger is a mostly Holarctic brown lacewing genus, with highest diversity in temperate regions of Eurasia and North America (Yang 1980, Oswald 1993). It includes 65 valid species worldwide (Zhao et al. 2017, Oswald 2018). Thirteen species are known from the United States and Canada, with one more from the south-western

United States and Mexico and one from Guatemala, the latter with the southernmost distribution for the genus in the New World (Makarkin 1996, Monserrat 1998, Oswald 2018). *Wesmaelius* (*Kimminsia*) *longipennis* (Banks) is known from western (California) and south-western (Texas) United States (Klimaszewski and Kevan 1987a, Oswald 2018), as well as from the Mexican states of Chihuahua, Durango, and Morelos (Oswald et al. 2002), and is the only previously known species in Mexico. The New World species were treated more recently by Klimaszewski and Kevan (1987a, b), who revised the species from Alaska and Canada, and diagnosed the two subgenera proposed by Aspöck et al. (1980), *Kimminsia* Killington and *Wesmaelius* Krüger. This subdivision was questioned by Oswald (1993), on the grounds that *Kimminsia* may be paraphyletic, a position followed by Zhao et al. (2017), however there is no conclusive evidence yet to settle the validity of the subgenera. In this work, we describe a new species of *Wesmaelius* from Tlaxcala state, central Mexico, which belongs to the Transmexican Volcanic Belt biogeographic province (Morrone 2014). Following the classification scheme with subgenera (Aspöck et al. 1980; Klimaszewski and Kevan 1987a; Makarkin 1995, 1996), the new species agrees well with the subgenus *Kimminsia*, particularly because the elongate, narrowly rectangular male ectoproct, and the short female gonapophyses laterales. A key for the identification of the 15 currently known species of *Wesmaelius* (*Kimminsia*) from the New World is included; the only currently known species of *Wesmaelius* (*W.*) from the New World, the Nearctic *Wesmaelius* (*W.*) *longifrons* (Walker), may be identified with Klimaszewski and Kevan (1987b).

## Material and methods

The last four abdominal segments of both sexes were separated from the thorax and cleared in 10% potassium hydroxide (KOH) for 10 minutes at 60 °C. Structures were rinsed in distilled water with the aid of a 1 ml insulin syringe, placed in a glass microvial with glycerine, and then included with the specimen within a larger vial containing 96% ethanol. The terminology for wing and genitalia morphology follows Klimaszewski and Kevan (1987a). Observations were made under a Carl Zeiss Discovery V8 stereomicroscope and photographs were taken under a Carl Zeiss AxioZoom V16 stereomicroscope and a Leica Z16APO-A stereomicroscope with a camera Leica DFC490, both with automontage system. The collecting site, Municipality of Nanacamilpa, Tlaxcala State, has a temperate mesic climate with summer rains, with a mean annual temperature of 14.8 °C, and mean annual precipitation of 1729 mm (INEGI 2014). The holotype and one female paratype, both dissected, are deposited at the Colección Nacional de Insectos (CNIN) of the Instituto de Biología, UNAM, Mexico City; one male (undissected) and one female (dissected) paratype will be deposited at the National Museum of Natural History, Smithsonian Institution (NMNH), Washington, D.C. The Neuropterida species of the World platform (Oswald 2018) was helpful to track down all known *Wesmaelius* species, whose descriptions were compared in order to rule

out synonymy. The key was constructed based on Klimaszewski and Kevan (1987a) and descriptions of other *Wesmaelius* (*Kimminsia*) species in the New World: *Wesmaelius* (*K.*) *longipennis* (Banks) from Mexico (Banks 1920, Carpenter 1940), and *Wesmaelius* (*K.*) *magnus* (Kimmins) from Guatemala (Kimmins 1928, Monserrat 1998). In the key, “fig.” refers to figures from literature, while “Fig.” refers to original figures.

## Taxonomy

### *Wesmaelius* (*Kimminsia*) *nanacamilpa* Marquez & Contreras, sp. n.

<http://zoobank.org/A877B409-F953-42B2-8BCE-901FB464FB84>

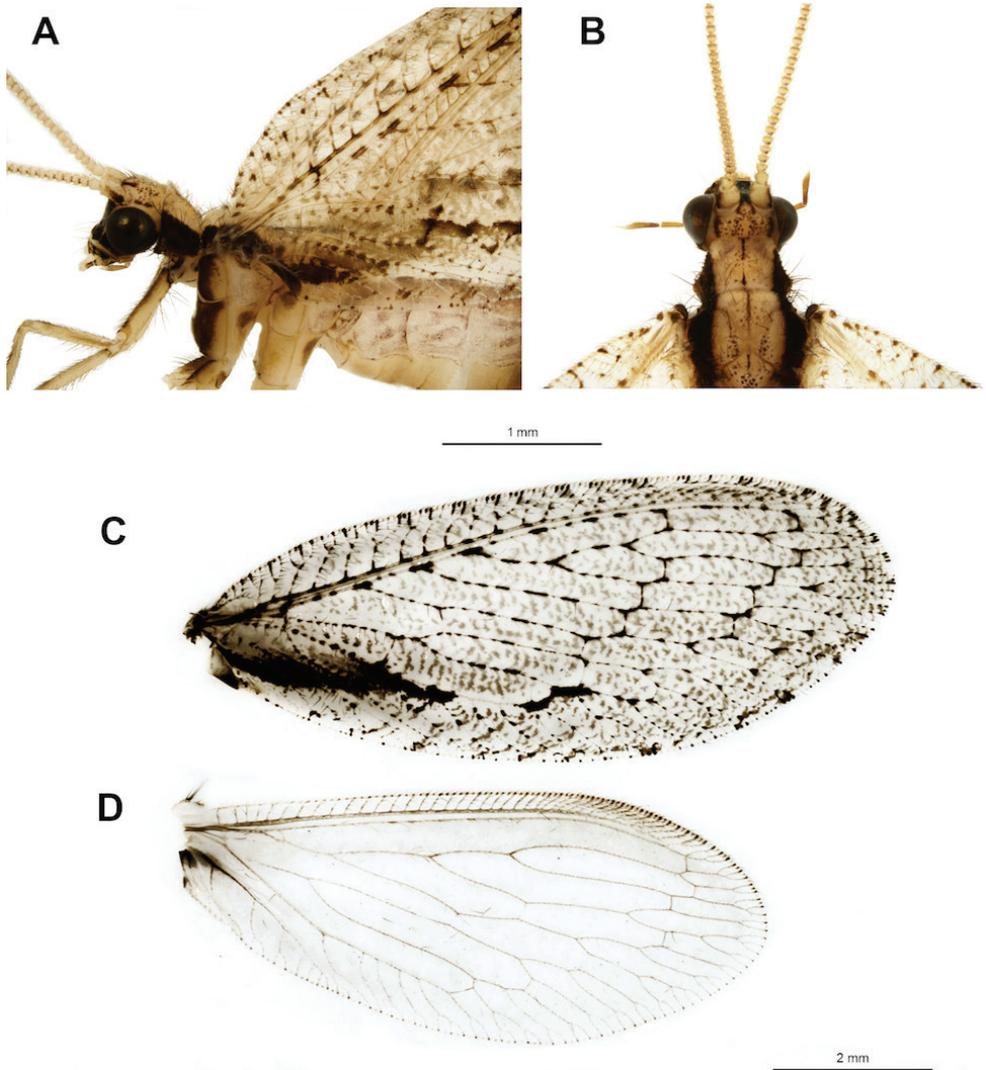
Figs 1, 2

**Material examined.** Holotype: Male; MEXICO: Tlaxcala, Nanacamilpa de Mariano Arista, Comunidad San Felipe Hidalgo, Bosque Mágico de Piedra Canteada, Santuario de la Luciérnaga, 19°27'22.3"N, 98°36'02.0"W, 2839 m, 03.vi.2016, Marquez, Contreras, Ramírez, Mayorga, Luna, luz blanca, bosque de *Abies* [alcohol, genitalia dissected] (CNIN). Paratypes: same data as holotype, 1 female [alcohol, genitalia dissected] (CNIN), 1 female [alcohol, dissected] (NMNH); same data as holotype but 2855 m, 02.vi.2017, Marquez, Contreras, Ramírez, Luna, mercury vapor light, 1 male [alcohol, undissected] (NMNH).

**Diagnosis.** Head mostly dark brown (Fig. 1A), vertex yellowish with small brown spots (Fig. 1B); outer side of scape brown (Fig. 1A); colour pattern of pronotum a mid-longitudinal discontinuous line with adjacent small irregular spots (Fig. 1B); dark brown band running laterally along pronotum, mesothorax and extending towards the basal third of forewing (Fig. 1A, C). Male ectoproct with pecten strongly sclerotized (Fig. 2A, B); parameres diverging, distally with a narrow V-shape, styliform sclerites directed basally (Fig. 2E); gonarcus with short entoprocessus (Fig. 2C, D), lateral lobe broad (Fig. 2D); female lateral gonapophyses separate from ectoproct and ovoid (Fig. 2G), subgenital plate with large lateral lobe and central plate with broad basal incision (Fig. 2H), spermathecal duct moderately coiled (Fig. 2G).

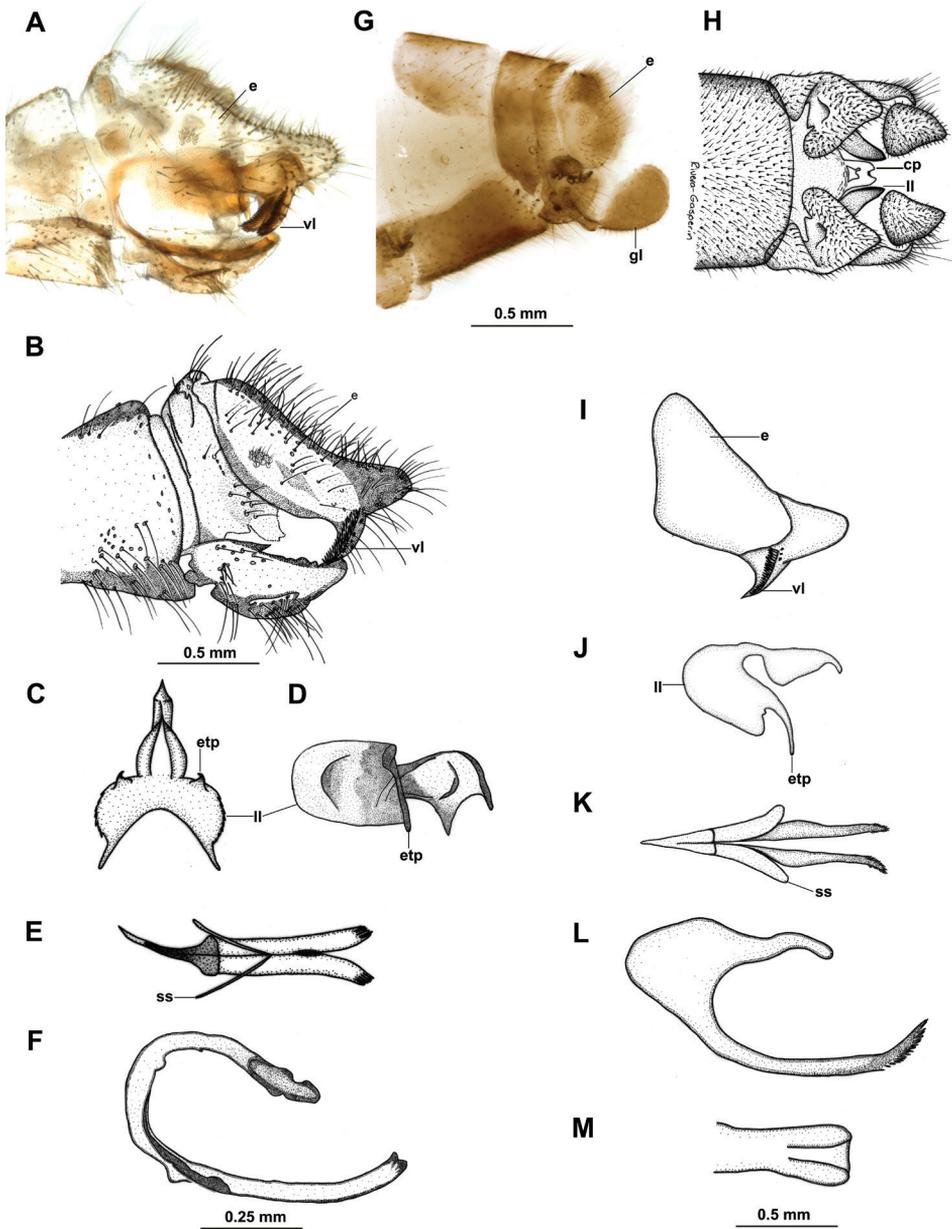
**Description.** *Dimensions.* Forewing length 9.2–9.5 mm, width 3.5–3.6 mm male (n = 2), length 9.6 mm, width 4.0 mm female (n = 2). *Body colour pattern.* Yellowish brown, with portions of head and thorax dark brown; wings patterned; abdomen yellowish, dark brown beyond fourth segment.

*Head.* Mostly dark brown. Vertex pale yellow with dark brown spots, two pale brown lines between antennae and two pale brown lines behind eyes (Fig. 1B); frons dark brown nearly black, clypeus reddish brown with transverse row of conspicuous setae on posterior margin (Fig. 1A); labrum reddish brown, gena and postorbital region dark brown, nearly black; male antennae 73–75-segmented (n = 2), female 73-segmented (n = 1), scape yellowish, laterally brown, pedicel yellowish, flagellomeres yellowish with narrow brown ring at base (Fig. 1A); eyes black with metallic luster (Fig. 1A).



**Figure 1.** *Wesmaelius (Kimminsia) nanacamilpa*, sp. n., habitus and wings: **A** Head and thorax, lateral **B** Head and thorax, dorsal **C** Forewing **D** Hind wing. Scale bars: 1 mm (**A**, **B**), 2 mm (**C**, **D**).

*Thorax.* Contrasting yellowish brown with dark brown. Pronotum yellowish with two discontinuous mid-longitudinal lines with adjacent small irregular spots (Fig. 1B); dark brown band running along pronotum, mesothorax and extending towards the basal third of forewing (Fig. 1A, C); mesonotum yellowish, small dark brown spots forming a pattern (Fig. 1B); frontal side of mesothorax blackish brown (Fig. 1A). Legs mostly yellowish brown, anterior side of forefemur and midcoxa brown, hind legs mostly yellowish.



**Figure 2.** *Wesmaelius (Kimminsia) nanacamilpa*, sp. n., genitalia: **A, B** Male genitalia, lateral **C** Male gonarcus, dorsal **D** Male gonarcus, lateral **E** Male parameres, dorsal **F** Male parameres, lateral **G** Female genitalia, lateral **H** Female genitalia, ventral. *Wesmaelius (Kimminsia) magnus* (Kimmins): **I** Male ectoproct, lateral **J** male gonarcus, lateral **K** Male parameres, dorsal **L** Male parameres, lateral **M** Female subgenital plate, ventral. Abbreviations: cp, central plate; e, ectoproct; etp, entoprocessus; gl, gonapophyses laterales; ll, lateral lobe; ss, styliform sclerites; vl, ventral lobe. Scale bars: 0.5 mm (**A, B, G, H**), 0.25 mm (**C-F**), 0.5 mm (**I-M**); **I-M** redrawn from Monserrat (1998).

**Wings.** Forewing narrowly oval; patterned with pale brown maculation; pterostigma pinkish, undefined; costal area narrow, wider at basal third; gradate series equally distanced; dark brown, nearly black irregular band along anal and cubital proximal third of wing; irregular elongate maculation at medial-cubital area in middle of wing (Fig. 1C). Hind wing broadly oval, mostly hyaline, without maculation except portions of costal and anal areas; patch of setae at base, before costal vein (Fig. 1D).

**Abdomen.** Mostly pale brown, dark brown beyond fourth segment, particularly dorsally.

**Male genitalia.** Ninth tergum narrow dorsally, broad basally, concave at upper posterior margin in lateral view (Fig. 2A, B); ectoproct subrectangular, with a prominent posterodorsal lobe, ventral lobe short with sclerotized teeth, 12 or 13 trichobothria (Fig. 2A, B). Gonarcus rounded, with mediuncus sharp, spine-like in dorsal view, short in lateral view (Fig. 2C, D); arcus with anterior projection subtriangular; lateral lobes convex in dorsal view (Fig. 2C), amply subquadrate in lateral view (Fig. 2D), proximal corners sharp (Fig. 2C); entoprocessus short, far from mediuncus (Fig. 2C, D). Parameres bar-like, diverging distally with a narrow V-shape, tips sclerotized with small teeth, base slender, strongly sclerotized, styliform sclerites directed basally (Fig. 2E, F).

**Female genitalia.** Gonapophyses laterales separate from ectoproct, ovoid, less sclerotized at proximal side; ectoproct short, subrectangular, bearing 12–14 trichobothria (Fig. 2G); subgenital plate with central plate incised apically, conspicuously incised at base, internal margins of basal incision serrate; lateral lobes narrowly lanceolate, longer than central plate (Fig. 2H); spermatheca with sclerotized duct moderately coiled (Fig. 2G).

**Variation.** Females were slightly larger than males, also females had a stronger colour pattern than males.

**Etymology.** Named after Nanacamilpa, the municipality of Tlaxcala State where the specimens were collected, meaning ‘field of mushrooms’ in Nahuatl.

**Ecology.** Specimens were attracted to white light (domestic light bulb) and mercury vapour light in an *Abies religiosa* (Sacred Fir) forest, during the rainy season (early June). Specimens of *Wesmaelius* are generally captured in conifer forests, maintaining their activity at low temperatures with small population sizes (Klimaszewski and Kevan 1987b; Monserrat 1998, 2015).

## Discussion

The new species is similar to *Wesmaelius (Kimminsia) magnus* (Kimmins) in wing colour pattern, including a pinkish pterostigma and a dark spot at the MP-CuA inner gradates, however *W. (K.) magnus* lacks the conspicuous dark band at the base of forewing (Kimmins 1928, Monserrat 1998); both have the head vertex with dark brown punctuations, less dense in *W. (K.) magnus* (Monserrat 1998). *Wesmaelius (K.) longipennis* (Banks) appears to have a similar colour pattern, but the face has numerous red specks (Carpenter 1940). Regarding external genitalia, the new species is similar to

*W. (K.) longipennis*, *W. (K.) magnus*, *W. (K.) involutus* (Carpenter), *W. (K.) brunneus* (Banks), *W. (K.) yuconensis* Klimaszewski and Kevan, and *W. (K.) pretiosus* (Banks) in the shape of the ectoproct, however considering the morphology of the parameres and gonarcus, the new species is distinct from the other known species. At present, it would be difficult to propose a possible sister species. In general, the anterior projection of the gonarcus is similar in dorsal view between *W. (K.) magnus* from Guatemala and the new species, yet in detail there are marked differences. The gonarcus is broader in the new species (Fig. 2C, D), entoprocessus is shorter (Fig. C, D), and the parameres are bar-like, with uniform width in the new species (Fig. 2E, F), while slightly curvy and widened at the base in *W. (K.) magnus* (Fig. 2K, L). Females of the new species might be characteristic based on the shape of the subgenital plate, with a marked basal incision with an internal irregular margin (Fig. 2H), however not clearly comparable with *W. (K.) magnus* at present (Fig. 2M); the sclerotized spermathecal duct is less coiled and shorter in the new species (Fig. 2G), as compared with *W. (K.) magnus* (Monserrat 1998, fig. 17). A study focused on the brown lacewings of cold mountainous habitats in Mexico, may increase the number of recorded *Wesmaelius* species in the country.

**Key to New World species of *Wesmaelius (Kimminsia)* Killington (males)**

- 1 First fork of anterior cubitus (CuA) at or extremely close to mediocubital inner gradate cross-vein (m+cuig) (Klimaszewski and Kevan 1987a: figs 157A, 158A, 165A)..... **2**
- First fork of anterior cubitus (CuA) distal to mediocubital inner gradate cross-vein (m+cuig) (Klimaszewski and Kevan 1987a: figs 159A, 160A-163A, 164A, 166A, 167A) ..... **6**
- 2 Forewing apparently immaculate or little maculate, veins unicolorous without variegation (Klimaszewski and Kevan 1987a: fig. 165A) ..... ***W. brunneus* (Banks)**
- Forewing with distinct maculation pattern, veins variegated pale and dark (Klimaszewski and Kevan 1987a: figs 157A, 158A) ..... **3**
- 3 Forewing with apex and ventral (posterior) margin broadly rounded, costal area gradually narrowed at base (Fig. 1C)..... **4**
- Forewing with apex and ventral (posterior) margin slightly rounded, costal area abruptly narrowed at base (Klimaszewski and Kevan 1987a: figs 157A, 158A) ..... **5**
- 4 Vertex with scarce punctuation (Monserrat 1998: fig. 11); parameres deeply divided, with apex amply denticulate, styliform sclerites directed apically (Fig. 2K, L)..... ***W. magnus* (Kimmins)**
- Vertex with dense punctuation (Fig. 1B); parameres divided distally, with apex narrowly denticulate, styliform sclerites directed basally (Fig. 2E, F) ..... ***W. nanacamilpa* Marquez & Contreras, sp. n.**

- 5 Ectoproct with large ventral lobes, gonarcus with arcus and mediuncus close in lateral and dorsal views, parameres with styliform sclerites large-convex (Klimaszewski and Kevan 1987a: figs 64–68) ..... *W. coloradensis* (Banks)
- Ectoproct with short ventral lobes, gonarcus with arcus and mediuncus distal in lateral and dorsal views, parameres with styliform sclerites small, triangular (Klimaszewski and Kevan 1987a: figs 24, 25, 27–30)..... *W. involutus* (Carpenter)
- 6 Ectoproct with long ventral lobe (Klimaszewski and Kevan 1987a: figs 45, 46, 74, 75).....7
- Ectoproct with short ventral lobe (Klimaszewski and Kevan 1987a: figs 8, 9, 56, 57)..... **10**
- 7 Ectoproct with ventral lobe twisted, directed first inwards and then caudad, exceptionally long (Klimaszewski and Kevan 1987a: figs 45, 74) ..... **8**
- Ectoproct with ventral lobe curved, long, directed only once inwards (Klimaszewski and Kevan 1987a: figs 8, 56) ..... **9**
- 8 Ectoproct strongly narrowing apically, with twisted ventral lobe (Klimaszewski and Kevan 1987a: figs 74, 75)..... *W. furcatus* (Banks)
- Ectoproct elongate, subquadrate, with ventral lobe strongly curved inwards (Klimaszewski and Kevan 1987a: figs 45, 46) ..... *W. subnebulosus* (Banks)
- 9 Ectoproct with ventral lobe elongate, subquadrate, gonarcus with mediuncus and entoprocessus close, compact and broad (Klimaszewski and Kevan 1987a: figs 56, 57, 60) ..... *W. posticatus* (Banks)
- Ectoproct with ventral lobe elongate-narrow, gonarcus with mediuncus and entoprocessus distal and extended, separate and slim (Klimaszewski and Kevan 1987a: figs 8, 14)..... *W. nervosus* (Fabricius)
- 10 Body and wings marked with red specks; gonarcus with elongate arcus (Carpenter 1940: fig. 20C) ..... *W. longipennis* (Banks)
- Body and wings differently marked, without red specks; gonarcus with short arcus (Klimaszewski and Kevan 1987a: fig. 11) ..... **11**
- 11 Gonarcus with two lateral emarginations in lateral view (Klimaszewski and Kevan 1987a: fig. 111)..... *W. constrictus* (Parfin)
- Gonarcus without lateral emarginations (Klimaszewski and Kevan 1987a: fig. 104)..... **12**
- 12 Parameres continuous (Klimaszewski and Kevan 1987a: fig. 101) ..... *W. yuconensis* (Klimaszewski & Kevan)
- Parameres apparently subdivided (Klimaszewski and Kevan 1987a: fig. 118) ..... **13**
- 13 Arcus curved in lateral view, triangular in dorsal view (Klimaszewski and Kevan 1987a: figs 103, 104)..... *W. fumatus* (Carpenter)
- Arcus straight in lateral view, subtriangular in dorsal view (Klimaszewski and Kevan 1987a: figs 107, 116) ..... **14**
- 14 Frons dark brown to almost black. Arcus with small tooth at base in lateral view (Klimaszewski and Kevan 1987a: fig. 107)..... *W. schwarzi* (Banks)
- Frons yellow to yellowish-brown. Arcus with protuberance at base in lateral view (Klimaszewski and Kevan 1987a: fig. 116)..... *W. pretiosus* (Banks)

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# Taxonomic status of *Apostolepis barrioi* Lema, 1978, with comments on the taxonomic instability of *Apostolepis* Cope, 1862 (Serpentes, Dipsadidae)

Omar Machado Entiauspe-Neto<sup>1</sup>, Arthur de Sena<sup>2</sup>,  
Arthur Tiutenko<sup>3</sup>, Daniel Loebmann<sup>1</sup>

**1** Universidade Federal do Rio Grande, Instituto de Ciências Biológicas, Laboratório de Vertebrados, Av. Itália Km 8, CEP: 96203-900, Vila Carreiros, Rio Grande, Rio Grande do Sul, Brazil **2** Universidade do Estado de Mato Grosso, Departamento de Biologia. CEP: 78690-000, Nova Xavantina, Mato Grosso, Brazil **3** University of Erlangen-Nuremberg, Schlossplatz 6, D-91054 Erlangen, Germany

Corresponding author: Omar Machado Entiauspe-Neto ([omarentiauspe@hotmail.com](mailto:omarentiauspe@hotmail.com))

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## Abstract

*Apostolepis* is a diverse neotropical snake genus, which has been historically subjected to poor taxonomic descriptions, largely based on either a small type series or subjective diagnoses. We evaluate the case of *Apostolepis barrioi* Lema, 1978 and its intricate taxonomic history, suggesting its synonymization with *Apostolepis dimidiata* (Jan, 1862), and providing brief commentary on the taxonomic instability that has been plaguing the genus.

## Keywords

Elapomorphini, Neotropical, synonymy, taxonomy

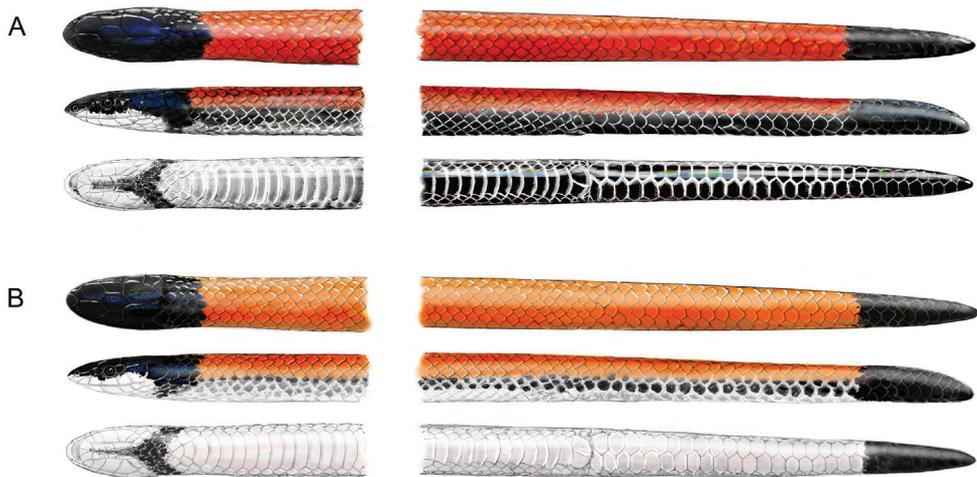
## Introduction

The Neotropical dipsadid snake genus *Apostolepis* Cope, 1862 comprises over 30 species, with an even broader synonym list, being marked by a systemic proliferation of “poorly defined” taxa, described based on single or few individuals with poor documentation of

variation (Vanzolini 1986; Ferrarezzi 1993; Harvey 1999; Ferrarezzi et al. 2005; Nogueira et al. 2012). *Apostolepis dimidiata* (Jan, 1862) is a small-sized fossorial snake that occurs in the Cerrado, Chaco and Atlantic Forests at Argentina, Brazil and Paraguay (Ceia 1993; Giraudo and Scrocchi 1998; Harvey 1999). Jan (1862) described *Elapomorphus dimidiatus* based on a specimen from “Brazil”, and allocated it to the subgenus *Elapomojus* Jan, 1862. Later, Peters (1880) described *Elapomorphus erythronotus* based on a specimen from “São Paulo” in southeastern Brazil. Cope (1887) presented two brief taxon descriptions, *Apostolepis erythronotus lineatus* and *Rhynchonyx ambiniger vittatus*, both from Chapada dos Guimarães, Mato Grosso, in central-western Brazil. Boulenger (1896) elevated both of Cope’s subspecies to species level and placed *Elapomorphus erythronotus* in *Apostolepis*. Werner (1897) described *Apostolepis nigriceps* based on two specimens, of which only one has a known locality given as “São Paulo”, in southeastern Brazil. Lema (1978) described three new species for Paraguay: *Apostolepis barrioi* from the Ypané River, Cororo, Concepción Province; *Apostolepis ventrimaculatus* from “Paraguay”; and *Apostolepis villaricae* from Villa Rica, Concepción Province. Later, Lema (1986) would synonymize *A. erythronota*, *A. nigriceps* and *A. ventrimaculatus* with *A. dimidiata*, while also revalidating *A. lineata*. Lema (1993) presented a review on the morphological variation of *A. dimidiata*, while also allocating the species he previously described, *A. barrioi* and *A. ventrimaculatus*, as synonyms of the former.

## Taxonomy

Recently, Cabral et al. (2017) presented a revalidation of *A. barrioi*, diagnosing it from all congeners based on an immaculate white venter, narrow dorsolateral stripes not in contact with the ventrals, and a terminal black shield. There is also a wide overlap between the meristic variation of *A. barrioi* and *A. dimidiata*, such as in the number of ventral scales (222–256 in *A. barrioi*; 214–264 in *A. dimidiata*) and subcaudal scales (23–55 in *A. barrioi*; 22–39 in *A. dimidiata*), in its morphometric variation (given in mm), in snout-vent length (188–542 in *A. barrioi*; 180–676 in *A. dimidiata*) and tail length (16–45 in *A. barrioi*; 16–60 in *A. dimidiata*), and geographic variation, since both species are sympatric along their whole distribution, as reported by the authors (Cabral et al. 2017: 246). Furthermore, the authors present a comparative table of *Apostolepis* species in which *A. barrioi* is stated as having an immaculate venter and *A. dimidiata*, a venter heavily pigmented with black, having only the edge of the ventrals white. This is in clear conflict with the original description, considering that the holotype of *A. dimidiata* presented an immaculate yellow venter according to the original description “[...] *parte inferiore del corpo é giallastra, meno la testa che inferiormente ha del nero sugli inframascellari e sulle squame che stanno in vicinanzi ai sottolabiali*” (En: lower part of the body is yellowish, except for the head, that has black inferiorly, in the inframaxillary (region) and in the scales near the infralabials) (Jan 1862: 48). Unfortunately, this specimen (holotype of *A. dimidiata*) could not be examined, since it was destroyed during the Second World War. It is also relevant that Lema (1993: 47)



**Figure 1.** Dorsal, lateral and ventral illustrations of previously recognized taxa, *Apostolepis dimidiata* (A) and *A. barrioi* (B), according to the diagnoses of Cabral et al. (2017). However, these represent merely phenotypic variations of *A. dimidiata* and, according to the descriptions of Jan (1862) and Lema (1978), both holotypes of *A. barrioi* and *A. dimidiata* present the bottom coloration.

presents a plate that encompasses all known ventral pattern variation for *A. dimidiata*, with a gradual change from immaculate yellow to black ventral patterns.

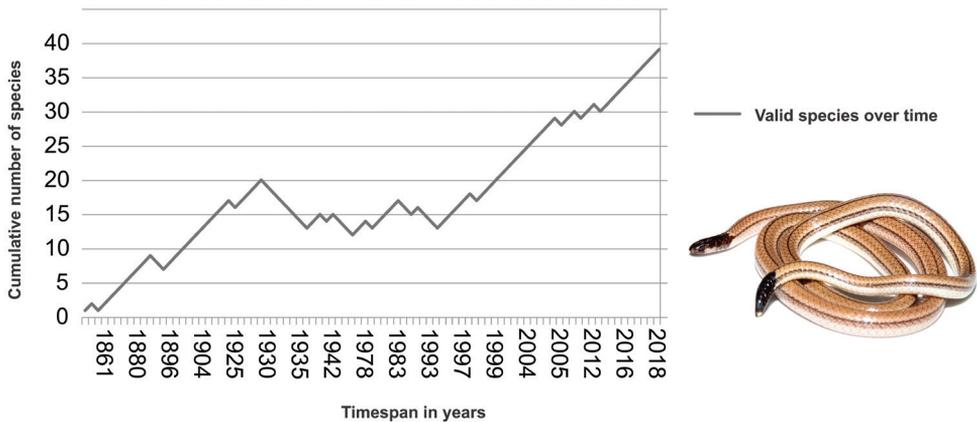
Considering that *Apostolepis barrioi* and *A. dimidiata* share the same morphological features and variation (Fig. 1), present virtually identical geographic distribution, and both descriptions are based on specimens that have the same ventral coloration, which was erroneously cited as “diagnostic” at the time, we argue that *A. barrioi* Lema, 1978 should be relegated as a junior synonym of *A. dimidiata* (Jan, 1862). The work of Cabral et al. (2017) seems to follow a recent, genus-wide trend, in which several species have been described based on poorly supported diagnoses (e.g. *Apostolepis mariae* Borges-Nojosa et al. 2017 (2016); *A. roncadori* Lema, 2016; *A. thalesdelemai* Borges-Nojosa et al. 2016 (2017); *A. underwoodi* Lema & Campbell, 2017). None of these studies presented descriptions of osteology or hemipenes, nor do they include molecular support for their proposed species, relying exclusively upon highly variable morphological characters such as coloration and body shape. It is also noteworthy that, *A. barrioi* was described, synonymized, and then revalidated by the same author over a timespan of almost 40 years.

## Final remarks

Unfortunately, several interest conflicts among researchers in the past decades have caused strong instability in *Apostolepis*, as well as most Elapomorphini taxa (Fig. 2). Here we present an overview of the currently recognized species of *Apostolepis* as well as their known specimens and diagnoses. It is noteworthy that poor diagnoses and small type series are usually associated with previous synonymizations (Table 1). We urge our fellow authors

**Table I.** Valid species of *Apostolepis* Cope, 1862 up to date. Characters present on diagnosis: Coloration (CO), Meristic (ME), Morphometric (MO), Subjective character states related to external morphology (SU), Molecular Data (MD), Internal Morphology (IM). References: <sup>1</sup>França et al. 2018; <sup>2</sup>Lema 2002b; <sup>3</sup>Peters 1869; <sup>4</sup>Ferrarezzi et al. 2005; <sup>5</sup>Rodrigues 1993; <sup>6</sup>Reinhardt 1861; <sup>7</sup>Peracca 1904; <sup>8</sup>Harvey et al. 2001; <sup>9</sup>Gomes 1915; <sup>10</sup>Lema 2003; <sup>11</sup>Lema 2002; <sup>12</sup>Jan 1862; <sup>13</sup>Schlegel 1837; <sup>14</sup>Duméril et al. 1854; <sup>15</sup>Prado 1942; <sup>16</sup>Koslowsky 1898; <sup>17</sup>Santos et al. 2018; <sup>18</sup>Cope 1887; <sup>19</sup>Gomes in Amaral 1921; <sup>20</sup>Borges-Nojosa et al. 2017; <sup>21</sup>Harvey 1999; <sup>22</sup>Lema and Renner 2004; <sup>23</sup>Amaral 1935; <sup>24</sup>Peters 1869; <sup>25</sup>Boulenger 1896; <sup>26</sup>Amaral 1922; <sup>27</sup>Boulenger 1903; <sup>28</sup>Giraud and Scrocchi 1998; <sup>29</sup>Lema and Renner 2006; <sup>30</sup>Lema 2004a; <sup>31</sup>Ruthven 1927; <sup>32</sup>Lema 2004b; <sup>33</sup>Lema 2016; <sup>34</sup>Lema and Campbell 2017.

Taxon	Year of description	Individuals in type series	Previously synonymized?	CO	ME	MO	SU	MD	IM
<i>Apostolepis adhara</i> <sup>1</sup>	2018	2	No	+	+	+	-	-	+
<i>Apostolepis albicollaris</i> <sup>2</sup>	2002	28	No	+	+	+	+	-	-
<i>Apostolepis ambinigra</i> <sup>3</sup>	1869	1	No	+	+	+	-	-	-
<i>Apostolepis ammodites</i> <sup>4</sup>	2005	25	No	+	+	+	+	-	+
<i>Apostolepis arenaria</i> <sup>5</sup>	1993	4	No	+	+	+	-	-	-
<i>Apostolepis assimilis</i> <sup>6</sup>	1861	1 (≥)	No	+	+	-	-	-	-
<i>Apostolepis borelli</i> <sup>7</sup>	1904	1	Yes	+	+	+	-	-	-
<i>Apostolepis breviceps</i> <sup>8</sup>	2001	4	No	+	+	+	+	-	-
<i>Apostolepis cearensis</i> <sup>9</sup>	1915	7	No	+	+	+	-	-	-
<i>Apostolepis cerradoensis</i> <sup>10</sup>	2003	1	No	+	+	+	+	-	-
<i>Apostolepis christinae</i> <sup>11</sup>	2002	1	No	+	+	+	+	-	-
<i>Apostolepis dimidiata</i> <sup>12</sup>	1862	1	Yes	+	+	-	+	-	-
<i>Apostolepis dorbignyi</i> <sup>13</sup>	1837	1	No	+	+	+	-	-	-
<i>Apostolepis flavotorquata</i> <sup>14</sup>	1854	1	Yes	+	+	+	-	-	-
<i>Apostolepis gabori</i> <sup>5</sup>	1993	1	No	+	+	+	-	-	-
<i>Apostolepis goiasensis</i> <sup>15</sup>	1942	1	Yes	+	+	+	+	-	-
<i>Apostolepis intermedia</i> <sup>16</sup>	1898	1	No	+	+	+	-	-	-
<i>Apostolepis kikoi</i> <sup>17</sup>	2018	5	No	+	+	+	-	-	+
<i>Apostolepis lineata</i> <sup>18</sup>	1887	1	Yes	+	-	-	-	-	-
<i>Apostolepis longicaudata</i> <sup>19</sup>	1921	1	No	+	+	+	+	-	-
<i>Apostolepis mariae</i> <sup>20</sup>	2017	22	No	+	+	+	+	-	-
<i>Apostolepis multicincta</i> <sup>21</sup>	1999	3	No	+	+	+	-	-	-
<i>Apostolepis nelsonjorgei</i> <sup>22</sup>	2004	7	No	+	+	+	+	-	-
<i>Apostolepis niceforoi</i> <sup>23</sup>	1935	1	No	+	+	+	+	-	-
<i>Apostolepis nigrolineata</i> <sup>24</sup>	1869	1	Yes	+	+	+	-	-	-
<i>Apostolepis nigroterminata</i> <sup>25</sup>	1896	1	No	+	+	+	-	-	-
<i>Apostolepis phillipsi</i> <sup>21</sup>	1999	1	No	+	+	+	-	-	-
<i>Apostolepis polylepisi</i> <sup>26</sup>	1922	4	No	+	+	+	+	-	-
<i>Apostolepis pymi</i> <sup>27</sup>	1903	1	Yes	+	+	+	-	-	-
<i>Apostolepis quinquelineata</i> <sup>25</sup>	1896	1	Yes	+	+	+	-	-	-
<i>Apostolepis quirogai</i> <sup>28</sup>	1998	2	No	+	+	+	-	-	-
<i>Apostolepis serrana</i> <sup>29</sup>	2006	1	No	+	+	+	+	-	-
<i>Apostolepis striata</i> <sup>30</sup>	2004a	1	No	+	+	+	+	-	-
<i>Apostolepis tenuis</i> <sup>31</sup>	1927	1	Yes	+	+	+	-	-	-
<i>Apostolepis tertulianoibeui</i> <sup>32</sup>	2004b	1	No	+	+	+	+	-	-
<i>Apostolepis thalesdelemai</i> <sup>20</sup>	2017	15	No	+	+	+	+	-	-
<i>Apostolepis roncadori</i> <sup>33</sup>	2016	1	No	+	+	+	+	-	-
<i>Apostolepis underwoodi</i> <sup>34</sup>	2017	3	No	+	+	+	+	-	-
<i>Apostolepis vittata</i> <sup>18</sup>	1887	1	Yes	+	-	-	-	-	-



**Figure 2.** The impact of the taxonomic history of *Apostolepis* Cope, 1862 species. The line refers to the cumulative number of species considered as valid during the time span, suffering either reductions from synonymies or additions from descriptions and revalidations. Inset picture: *Apostolepis* sp. from Serra do Cachimbo, Pará, Brazil.

not to commit taxonomic malpractice and to carefully generate, rethink and analyze their data, providing compelling evidence for their claims. The careless proliferation and splitting of taxa may present deleterious consequences not only to the field of taxonomy but also to directing conservation efforts. An integrative revision, preferably incorporating aspects of external and internal morphology, along with molecular data, is largely warranted in order to mitigate and reevaluate the taxonomy of *Apostolepis* as a whole.

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# Dwarfs under dinosaur legs: a new millipede of the order Callipodida (Diplopoda) from Cretaceous amber of Burma

Pavel Stoev<sup>1,2</sup>, Leif Moritz<sup>3</sup>, Thomas Wesener<sup>3</sup>

**1** National Museum of Natural History, Sofia, Tsar Osvoboditel Blvd. 1, Sofia 1000, Bulgaria **2** Pensoft Publishers, Sofia, Bulgaria **3** Zoological Research Museum Alexander Koenig (ZFMK), Leibniz Institute for Animal Biodiversity, Adenauerallee 160, D-53113, Bonn, Germany

Corresponding author: *Pavel Stoev* ([projects@pensoft.net](mailto:projects@pensoft.net))

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## Abstract

The entire Mesozoic Era is rather poor in millipede (class Diplopoda) fossils, with less than a dozen species being taxonomically described. Here, we describe the first fossil millipede of the order Callipodida, *Burmanopetalum inexpectatum* **gen. nov. et sp. nov.**, found in early Cenomanian amber of Burma, 98.79±0.62 Mya. The species possesses a number of morphological traits that exclude it from all extant suborders, and Burmanopetalidea suborder nov. and Burmanopetalidae fam. nov. are here erected to accommodate it. The new suborder can be recognized by the following unique characters: pleurotergal setae absent; telson with a specific spatulate shape twice the size of the penultimate body ring; hypoproct devoid of setae; and eyes composed of five well-separated ommatidia. While the callipodidan habitus seems to have remained generally unchanged for at least 99 million years, pleurotergal and hypoproctal setation, as well as the complexity of eyes in ground-dwelling forms may have evolved recently in the order. As *B. inexpectatum* **gen. nov. et sp. nov.** is the first true callipodidan in the fossil record, the minimum age of Callipodida is thus at least 99 Mya.

## Keywords

Burmanopetalidea suborder nov., Burmanopetalidae fam. nov., *Burmanopetalum inexpectatum* gen. nov. et sp. nov., Cenomanian, Mesozoic.

## Introduction

Millipedes (Diplopoda) are a highly diverse but also a largely understudied group of arthropods with >11,000 described species (Enghoff et al. 2015). The actual number of species is estimated to be between 15,000–20,000 (Brewer et al. 2012) or 50,000–80,000 (Minelli and Golovatch 2013). The earliest fossil records of millipedes come from the Middle Silurian or Lower Devonian of Scotland about 420 Mya, where three archipolypod species were found (Wilson and Anderson 2004; Shear and Edgecombe 2010; Wolfe et al. 2016; Suarez et al. 2017). Being the first animals to conquer land (Wilson and Anderson 2004), millipedes play a significant ecological role as major destruents in the terrestrial ecosystems probably since the Silurian (Kime and Golovatch 2000; Golovatch and Kime 2009).

Callipodida is a small order of spinneret-carrying millipedes of the superorder Nematophora (Blanke and Wesener 2014; Enghoff et al. 2015). The exact relationship with the other two nematophoran orders, Stemmiulida and Chordeumatida, is not yet clarified. Callipodida are considered a sister-group either to Stemmiulida (Blanke and Wesener 2014) or to Chordeumatida (Brewer and Bond 2013). Some callipodidans are among the handful of known carnivorous species of the Diplopoda (Hoffman and Payne 1969). In addition, several species of Callipodida are unusually fetid due to their defense secretions containing *p*-cresol (Makarov et al. 2011), and can be smelled several meters away (author observations).

Callipodida show a disjunct distribution in the Northern Hemisphere, with three major centers of diversification – the North Mediterranean region, Central and South East Asia, and North America. The order is absent from South America, Africa, the Pacific Islands, Australia, and the northern parts of Eurasia (Shear et al. 2003; Shelley and Golovatch 2011). The group is also remarkably absent from the Indian subcontinent (Golovatch and Wesener 2016), with just one species, *Bollmania kohalana* (Attems, 1936), from the region of Kashmir, between Pakistan and India (Stoev et al. 2008). Despite their interesting distribution pattern, the phylogenetic relationships within Callipodida are largely unresolved, which also holds true for all but five millipede orders (Simonsen 1990; Enghoff 1991; Wesener and VandenSpiegel 2009; Pitz and Sierwald 2010; Oeyen and Wesener 2018). The order is moderately rich, with around 140 known extant species (Stoev et al. 2008) grouped into three suborders, eight families, and 36 genera or subgenera (Enghoff et al. 2015).

While the known Paleozoic millipedes significantly differ from extant forms and the Cenozoic fossils can be placed in extant families and genera, the fossil record of millipedes in the entire Mesozoic Era was considered extremely poor (see Shear 1998; Shear and Edgecombe 2010; Edgecombe 2015) until recent discoveries in Burmese amber (Liu et al. 2017a; Wesener and Moritz 2018; Jiang et al. 2019).

Cockerell (1917) was the first to describe a millipede from Burmese amber, *Polyxenus burmiticus* Cockerell, 1917, a species which was later transferred to the extant genus *Phryssonotus* Scudder, 1885 (Rasnitsyn and Golovatch 2004; Zhang 2017). Just recently, two species of Siphoniulida (Liu et al. 2017a) and one species of Siphonophorida (Jiang et al. 2019), all belonging to extant genera, have been added to the list. So far there is no described non-amber fossil which can be definitely placed in the order Callipodida, but Shear et al. (2009) hypothesized that *Hannibaliulus wilsonae*

Shear, Selden & Gall, 2009 from the Triassic of France could be a representative of Callipodida, although clear apomorphies of the order were not observable.

Burmese amber from the Hukawng Valley in Kachin State, northern Myanmar (formerly Burma), is precisely dated to the Cretaceous Cenomanian  $98.79 \pm 0.62$  Mya (Shi et al. 2012) and has a long history of exploitation. For a review of its history and geology see Zherikhin and Ross (2000), Grimaldi et al. (2002), and Cruickshank and Ko (2003). Burmese amber has proven to be an important source of arthropod fossils, containing no less than 849 described species of arthropods (Ross et al. 2010; Ross 2018). Recently, the great importance of Burmese amber for the understanding of the Myriapoda fossil record and historical biogeography was demonstrated with the discovery of two species of the enigmatic order Siphoniulida (Liu et al. 2017a), a species of the order Siphonophorida (Jiang et al. 2019), and the first known fossil representative of the Symphyla family Scolopendrellidae (Moritz and Wesener 2018). A recent investigation of 460 newly discovered Diplopoda inclusions in Burmese amber included specimens belonging to 13 of the 16 extant orders, as well as the oldest known fossil representatives for eight extant orders (Wesener and Moritz 2018). Among the 529 millipede specimens hitherto known from Burmese amber (Wesener and Moritz 2018; Jiang et al. 2019), a single female specimen belongs to the order Callipodida, and its description is the purpose of this paper.

## **Material and methods**

### **Material and data deposition**

The single female specimen (ZFMK-MYR07366) came into our possession from the private collection of Mr Patrick Müller and is deposited in the Zoological Research Museum A. Koenig (ZFMK, Bonn, Germany). The authenticity of the amber was checked under UV light, producing a characteristic pale blue colour when photographed (Xing et al. 2016). All legal exportation permits were obtained and are available upon request.  $\mu$ CT-data are deposited in MorphoBank (O'Leary and Kaufman 2012) under project number 3360 (<http://morphobank.org/permalink/?P3360>).

### **Light microscopy and photography**

Morphological characters were investigated with a Discovery.V12 stereo-microscope (Zeiss) and a BX51 light microscope (Olympus). Photographs were taken with a Canon EOS 7D camera equipped with magnifier lenses.

### **Micro-computer tomography ( $\mu$ CT) and visualization**

$\mu$ CT-Scans were acquired with a SKYSCAN 1272 (Bruker microCT, Kontich, Belgium) at the Zoological Research Museum Alexander Koenig. For the parameters, see

the media information in MorphoBank (<http://morphobank.org/permalink/?P3360>). Thermal-drift correction, ring artefact reduction and digital section reconstruction was done with NRecon 1.7 (Bruker microCT, Kontich, Belgium). Volume rendering and measurements were performed in Drishti version 2.6.3 (Limaye 2012).

## Terminology

We use ‘body ring’ when pleurotergites and sterna are referred to collectively. Callipodida do not have fused rings as in some other millipede orders (eg. Julida) because the sterna are free.

## Results

### Systematic palaeontology

**Class Diplopoda de Blainville in Gervais, 1844**

**Subclass Chilognatha Latreille, 1802/1803**

**Infraclass Helminthomorpha Pocock, 1887**

**Superorder Nematophora Verhoeff, 1913**

**Order Callipodida Pocock, 1894**

**Suborder †Burmanopetalidea suborder nov.**

**Diagnosis.** Body less than 10 mm, composed of 35 body rings (including collum and two apodous body rings) and telson. Eyes composed of five ommatidia situated in two rows (3+2). Body rings cylindrical, with fused tergites and pleurites and free sternites. Pleurotergites composed of smooth prozonites and carinate metazonites, latter being greater in diameter than prozonites. Pleurotergal crests most pronounced from 3<sup>rd</sup> to 8<sup>th</sup> pleurotergite. Pleurotergal setae absent; telson spatulate, twice the size of the penultimate body ring; hypoproct tripartite, devoid of setae.

The suborder comprises one family: †Burmanopetalidae fam. nov.

**Family †Burmanopetalidae fam. nov.**

<http://zoobank.org/37E00121-783A-4842-961D-5DB98ADA1BDD>

**Diagnosis.** As for the suborder.

**Type genus.** †*Burmanopetalum* gen. nov.

**Genus †*Burmanopetalum* gen. nov.**

<http://zoobank.org/DB4A75E7-8626-4B8B-B172-43E2D7D51D71>

**Type species.** †*Burmanopetalum inexpectatum* sp. nov.

**Etymology.** From “Burma”, the country of origin, and “-petalum” a frequent generic termination in Callipodida. Gender: neuter.

**Diagnosis.** Differs from all extant genera of Callipodida by its minute size (less than 1 cm in length), lack of pleurotergal setae, and its spatulate telson being twice the size of the penultimate body ring. Eyes composed of five ommatidia.

**†*Burmanopetalum inexpectatum* sp. nov.**

<http://zoobank.org/DC6B3267-B386-4C1B-9D0A-7404AF469D32>

Figures 1A–H, 2A–G, 3

**Previous records.** Callipodida, family undetermined: Wesener and Moritz 2018: 1135–1136, fig. 2C.

**Material examined.** Holotype (ZFMK-MYR07366), from the collection of Mr Patrick Müller (transferred to ZFMK), adult female, Myanmar, Kachin State, Hukawng Valley, Noije Bum amber mine, 26°15'N, 96°34'E.

**Diagnosis.** As for the suborder, family and genus. Species further characterized by antennomeres III–V strongly conical (infundibular), VI and VII subrectangular; metazonites with 28 more or less well-developed narrow, subparallel crests, well-separated from one another, poriferous crests missing.

**Etymology.** “inexpectatum” in Latin means “unexpected” referring to the stunning discovery of just a single specimen among the 529 millipede specimens so far found in Burmese amber. The species epithet is an adjective.

**Locality and horizon.** Burmese amber, early Cenomanian, 98.79±0.62 Mya (Shi et al. 2012) from the Noije Bum amber mine, Hukawng Valley, Kachin State, northern Myanmar.

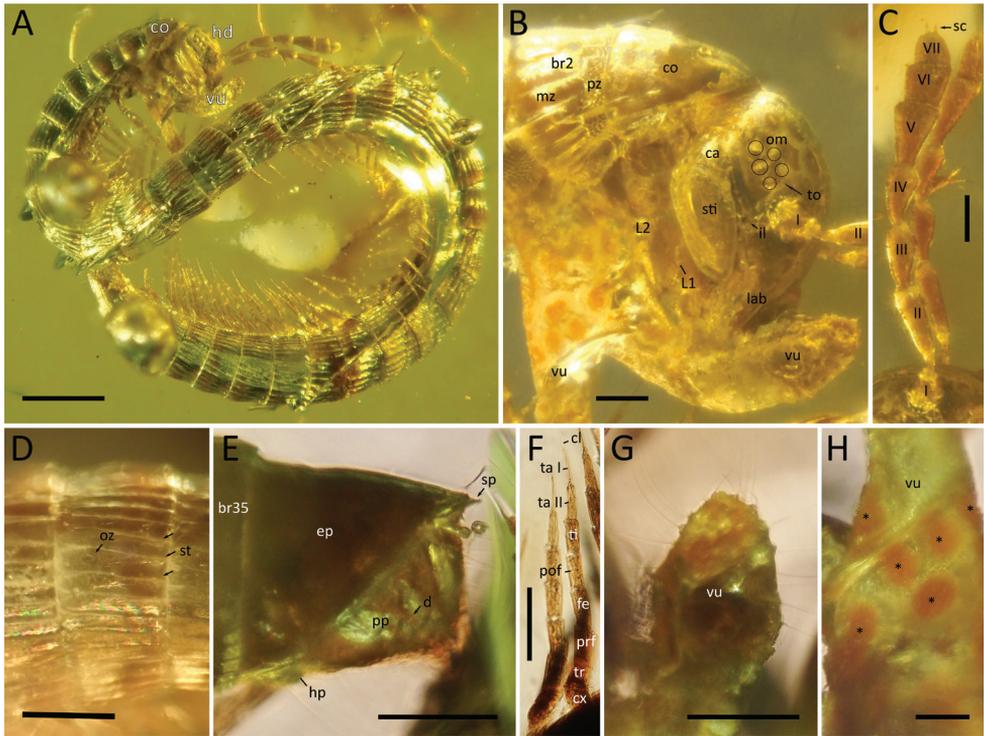
**Taphonomic features.** *Amber:* Cut and polished. Piece rectangular, upper surface slightly convex, 14.1 mm × 6.3 mm × 2.5 mm. Colour: light yellow transparent.

**Specimen:** Close to surface, body coiled in S-shape, vulvae extended.

**Syninclusions:** Ensifera (Insecta: Orthoptera), Stellate hairs, large grayish spherical structure (Sporangia?).

**Description.** Body length: 8.2 mm (measured from the CT scan); width of largest body ring 14: 0.4 mm. Body composed of 35 body rings and telson (Figs 1A, 2A, 3).

**Head** elliptical, longer than wide, covered by long setae (Figs 1B, 2B,C). Labrum with 3 teeth. Eyes composed of 5 ommatidia situated in 2 rows (3+2). Incisura lateralis present, extending from mandible stipes to antennal base. Antennae (Fig. 1C) long and slender reaching to, or slightly extending beyond posterior margin of body ring 4 when folded backwards. Antennae 0.9 mm long, relative antennomere lengths

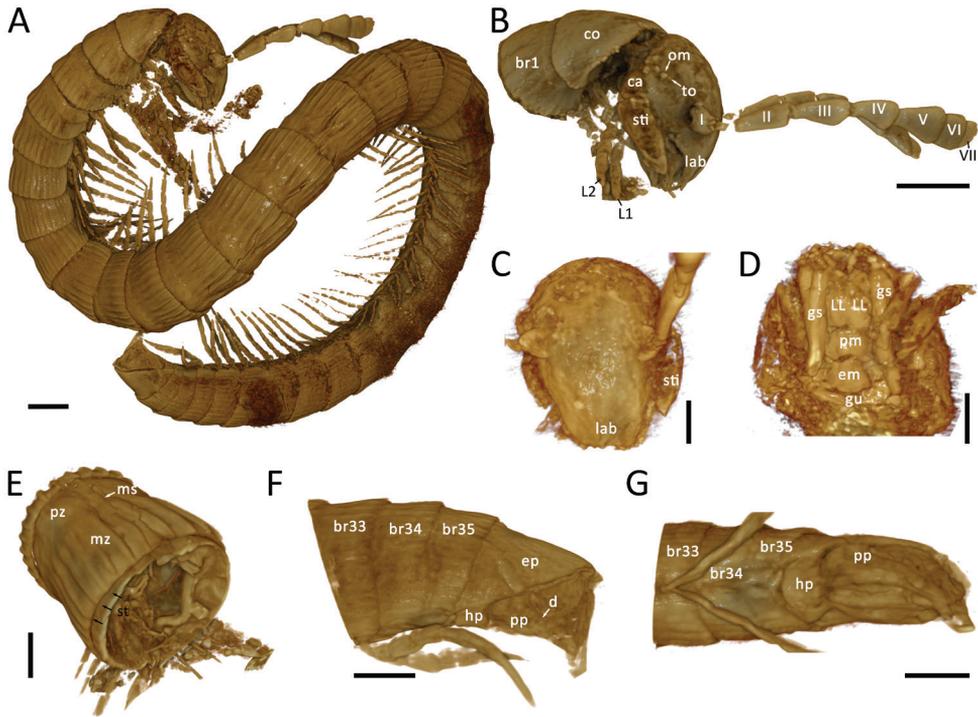


**Figure 1.** *Burmanopetalum inexpectatum* gen. nov. et sp. nov., female holotype (ZFMK-MYR07366) **A** habitus **B** head, anterior-most body rings and vulvae, anterior view **C** antennae, lateral view **D** pleurotergal crests ornamentation, lateral view **E** telson, lateral view **F** legs, dorsolateral view **G** apical part of vulva, lateral view **H** basal part of vulva, lateral view. Abbreviations: I–VII = antennomeres I–VII; br# = body ring number #; ca = mandibular cardo; cl = claw; co = collum; cx = coxa; d = division of paraproct; ep = epiproct; fe = femur; hd = head; hp = hypoproct; il = incisura lateralis; L# = leg number #; lab = labrum; mz = metazonite; om = ommatidia; oz = ozopore; pof = postfemur; pp = paraproct; prf = prefemur; pz = prozonite; sc = sensory cones; sp = spinnerets; st = stria; sti = mandibular stipes; ta I = tarsus I, ta II = tarsus II; ti = tibia; to = Tömösváry organ; tr = trochanter; vu = vulva; \* = reddish circles of the basal part of vulvae. Scale bars: 500 µm (**A**), 100 µm (**B–G**).

II>V>III>IV>VI>VII=I, antennomere II more than twice the length of VI, antennomeres III–V strongly conical (infundibular), VI and VII subrectangular, ultimate disc with 4 apical cones. Tömösváry organ small, located between antennal base and ommatidia, nearly touching the foremost ommatidium. Mandible cardo small (Fig. 1B), stipes ca 3× as long as cardo. Gnathochilarium (Fig. 2D) consisting of a larger eumentum and a smaller promentum, lamellae linguales and long stipites; stipites 2× as long as lamellae linguales and slightly swollen.

**Collum** not concealing head from above, nearly as wide as head, anteriorly smooth, only posterior third with poorly developed crests (Figs 1B, 2B).

**Body** cylindrical, with tergites and pleurites fused, sternites free (Fig. 2E). Body rings half as long as wide, 3 penultimate body rings shorter, ca 1/3 as long as wide. Pleurotergites with an inconspicuous median suture, composed of smooth prozonites and



**Figure 2.** *Burmanopetalum inexpectatum* gen. nov. et sp. nov., female holotype (ZFMK-MYR07366), volume rendering **A** habitus **B** head, collum and pleurotergite 2, lateral view **C** head, anterior view **D** Gnathochilarium, ventral view **E** midbody body ring, dorsoposterior view **F** telson, and the last 3 pleurotergites, lateral view **G** same, ventral view. Abbreviation: I–VII = antennomere; br# = body ring number #; ca = mandibular cardo; co = collum; d = division of paraproct; em = eumentum; ep = epiproct; gs = gnathochilarium stipes; gu = gula; hp = hypoproct; lab = labrum; LL = lamella lingualis; L# = leg number #; ms = median suture; mz = metazonite; om = ommatidia; pm = promentum; pp = paraproct; pz = prozonite; sti = mandibular stipes; to = Tömösváry organ. Scale bars: 200  $\mu$ m (**A**), 100  $\mu$ m (**B–F**).

carinate metazonites, latter being greater in diameter than prozonites. Prozonites void of crests, with minute scale-like ornamentation (Fig. 1B), metazonites with 28 more or less well-developed longitudinal, narrow, subparallel crests, well-separated from one another, extending over whole body ring, gradually reduced in size laterally and ventrally (Fig. 1D). Crests most pronounced on pleurotergites 3–8. Anterior 4 body rings narrower than following body rings, with less conspicuous crests. Ozopores inconspicuous, an ozopore-like opening visible on body ring 8 (Fig. 1D) and also possibly on body ring 4, situated between the crests, poriferous crests missing. Pleurotergal setae absent.

**Telson** enlarged, spatulate, 2 $\times$  the size of the last body ring, dorsal side slightly concave anteriorly (Figs 1E, 2F). Epiproct with inconspicuous crests and 2 spinnerets. Hypoproct divided into a single median plate and 2 lateral plates, all devoid of macrosetae. Paraprocts (anal valves) projecting posteriorly, divided transversally (Fig. 2G).

**Legs** Anterior leg of body ring 14 0.35 mm long, legs composed of 8 podomeres, relative lengths coxa = trochanter < tarsus 1 = tarsus 2 < femur < tibia = postfemur =



**Figure 3.** *Burmanopetalum inexpectatum* gen. nov. et sp. nov., female holotype (ZFMK-MYR07366), 3D model, volume rendering.

prefemur (Fig. 1F). Tarsus 2 with a short claw. Leg 1 and 2 not visibly modified. Some midbody legs with coxal vesicles.

**Male sexual characters** unknown.

**Female sexual characters** a pair of long, tubular, apically club-like vulvae behind leg 2 (Fig. 1G); vulvae 0.9 mm long when extruded, apically with long setae. Basal part of vulvae covered by reddish circles (ca 80  $\mu\text{m}$  in diameter) (Fig. 1H). Third pleurotergite slightly enlarged as is typical for adult female callipodidans.

**Taxonomic remarks.** Several important characters used in the current systematics of Callipodida are unknown in the described specimen, such as the distribution of coxal vesicles on legs in both sexes, as well as male-specific traits such as the shape of gonopods, the presence/absence of modifications on the head and the anterior part of legs and sternites.

## Discussion

### Taxonomic position

*Burmanopetalum inexpectatum* gen. nov. et sp. nov. is the first fossil callipodidan which shows the typical body plan of the order. The presence of 35 body rings, free sternites, pleurotergites with subparallel crests, well-separated from one another, a dorsal midline

suture, a telson bearing spinnerets, a tripartite hypoproct and a pair of long retractable vulvae, allow the species to be unequivocally assigned to the order Callipodida. Fossil Callipodida could be confused with the nowadays much more common Cambalidea (Spirostreptida), which are known from 20 specimens in Burmese amber (Wesener and Moritz 2018), but cambalideans have neither a middorsal tergal suture nor spinnerets, both of which are clearly visible in *Burmanopetalum inexpectatum* gen. nov. et sp. nov. Fossil Callipodida might also be confused with species of Stemmiulida, which are known from eight specimens in Burmese amber, both orders showing similar habitus and tergite ornamentation. However, Stemmiulida can be ruled out by the higher number of ommatidia (five vs only two or three in all members of the order), the presence of a long, tubular, vulva attached to coxa 2 (vulvae in Stemmiulida are located between legs 2 and 3, a unique position within Diplopoda, see Silvestri 1916; Enghoff et al. 2015), the clear separation into prozonite and metazonite (absent in Stemmiulida, Hoffman 1982), presence of coxal vesicles, as well as by the divided hypoproct (Enghoff et al. 2015).

The absence of pleurotergal and hypoproctal setae and the presence of an enlarged spatulate telson are characters not observed in any of the extant suborders and families (Table 1) of Callipodida. Therefore, a new suborder and family, Burmanopetalidea suborder nov. and Burmanopetalidae fam. nov., respectively, have been here proposed to accommodate the new species.

### Size and number of body rings

Extant Callipodida species vary in length from approximately 12 to 100 mm (Enghoff et al. 2015). The species of the East Mediterranean genus *Eurygyrus* C.L. Koch, 1847 (e.g. *E. bilselli* (Verhoeff, 1940) and *E. ochraceus* C.L. Koch, 1847), reach almost 10 cm and are among the largest members of the order. On the other hand, members of the Anatolian and Balkan genera *Euxinopetalum* Hoffman, 1972, *Dorypetalum* Verhoeff, 1900, and *Schizopetalum* Verhoeff, 1900, as well as some North American Tynommatidae, are between 15–20 mm in size. Small size seems to be correlated with a low number of body rings. Callipodida usually develop through teloanamorphosis which means that the addition of body rings stops at a certain stage which is always the same for a given sex of a given species. In some callipodidans, however, it is possible that other types of anamorphosis occur (e.g. hemianamorphosis) (Enghoff et al. 1993). The number of body rings in the order varies between 35 and 88, with the lowest numbers observed in *Schizopetalum koelbeli* (Verhoeff, 1895) (35–38) and *Euxinopetalum dobatorem* Hoffman, 1973 (38). Both species are also among the smallest members of the order with adults having a length of 15–17.5 mm.

*Burmanopetalum inexpectatum* gen. nov. et sp. nov. is remarkable with a body size in an apparently mature female of just 8.2 mm, which is an extreme case of miniaturization for the order. At the same time the number of body rings is highly reduced. The presence of a pair of long vulvae demonstrates that the specimen is a mature female which most likely reached its last stadium and full body length.

**Table 1.** Main differential characters between Burmanopetalidae fam. nov. and the extant families of Callipodida. *Hannibalulus wilsonae* Shear, Selden & Gall, 2009 from the Triassic of France is also included in the table, although clear apomorphies of the order are not known.

	Burmanopetalidae fam. nov.	<i>Hannibalulus wilsonae</i>	Sinocallipodidae	Callipodidae	Abacionidae	Caspiopetalidae	Dorypetalidae	Schizopetalidae	Paracortinidae	Tynnomatidae
Length	8.2 mm	53–56 mm	40–70 mm	50–70 mm	19–59	28–45 mm	12–50 mm	12–100 mm	32–60 mm	13–50 mm
Number of PTs	35	39–43	55–72	55–65	46–61	53–66	43–54	35–56	50–85	43–88
Antennae	Antennal articles III–V strongly conical (infundibular); 6–7 <sup>th</sup> subrectangular	Unknown	antennal articles generally long; in <i>S. thazi</i> article VI short and infundibular	Only VI <sup>th</sup> article infundibular; 7 <sup>th</sup> article conical	Only VI <sup>th</sup> article infundibular; 7 <sup>th</sup> article conical	V–VI <sup>th</sup> articles infundibular; 7 <sup>th</sup> article conical	Generally short, article V–VI infundibular (fig. 5 Stoev and Enghoff 2006; Reboleira & Enghoff, 2015–Lusitanipus)	Only V <sup>th</sup> article infundibular; VI <sup>th</sup> article conical	Only V <sup>th</sup> article infundibular; VI <sup>th</sup> article conical	V–VI <sup>th</sup> articles infundibular?; VII <sup>th</sup> article conical
Ommatidia	5, well-separated, arranged in two rows	Numerous (at least 10) arranged in subtriangular patch	5–11, arranged in 2–3 rows, in oval shape in others; reduced in some cave species	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch	Numerous, arranged in subtriangular patch; reduced in some cave species
Collum	Smooth, some crests posteriorly	Unknown	Smooth	Smooth	With crests posteriorly	With crests	Smooth or with moderate crests	With crests or smooth	With crests	With crests
Pleurotergal crests	Moderately to poorly developed; narrow, subparallel.	Metazonites of the pleurotergites smooth, with a distinct transverse depression and ventrolateral rebordered flange	Moderately to poorly developed; narrow, subparallel	Missing, instead of crests there are grooves	Well developed; poriferous crests much larger	Well developed; poriferous crests much larger	Moderately to poorly developed	Moderately developed to lacking	Well developed; poriferous crests much larger	Well-developed, poriferous crests more pronounced



Miniaturisation in fossil Chelicerata has been suggested to be due to the utilization of new ecological niches which larger chelicerates were not able to colonise (Dunlop 2019), which might also be the case here. Simplified eyes and the lack of setation of *B. inexpectatum* gen. nov. et sp. nov. might also be correlated with the general miniaturization of its body and a simplification of the sensory system, rather than with a subterranean manner of living (Dunlop 2019). Furthermore, *B. inexpectatum* gen. nov. et sp. nov. does not show any of the general cave adaptations observable in the Diplopoda (Liu et al. 2017b). Nevertheless, given that the sister order Chordeumatida mostly consists of minute to small species, it is equally possible that the small size of the new species is an ancestral trait.

### **Pleurotergal setae**

Burmanopetalidae fam. nov. is well characterized by the lack of any pleurotergal setae. Pleurotergal setae are traditionally used as a family- and even subordinal-level character in the classification of Callipodida (Hoffman 1982; Enghoff et al. 2015). In the suborder Callipodidea Pocock, 1894 they are present in a posterior position on all pleurotergites, while in the suborder Sinocallipodidea Shear, 2000 they emerge from the anterior end of the pleurotergites. In the largest callipodidan suborder Schizopetalidea, setae are in an anterior position in the anteriormost pleurotergites, migrating completely to a caudal position usually by the 8<sup>th</sup> or 9<sup>th</sup> one (Hoffman 1982). Thus, having a species completely devoid of pleurotergal setae is a unique state, which coupled with several other morphological characters fully justifies the creation of both a new suborder and a new family. We exclude the possibility that the lack of body pilosity is due to taphonomic reasons, as setae seem to preserve generally well in Burmese amber, even in much smaller, 5 mm-long Siphoniulida (Liu et al. 2017a). In addition, the setae on the vulvae are well-preserved in the specimen.

### **Telson**

The shape of the telson in Callipodida is subtriangular and rather uniform. In most species it is almost equal in size or smaller to the last body ring. In small species up to 15 mm long, i.e. *Dorypetalum*, some Tynnomatidae, it is proportionally reduced. In *B. inexpectatum* gen. nov. et sp. nov., however, the telson is highly enlarged, twice the size of the penultimate body ring and with a spatulate shape. To the best of our knowledge, such a shape is not known in any extant callipodidan. Furthermore, although the hypoproct is subdivided into three plates as in most extant callipodidans, it lacks macrosetae, which are normally present in all extant species in the combination 1+2+1.

### **Eyes**

The majority of adult callipodidans have eyes composed of at least 30 ommatidia grouped in a subtriangular eye patch (Enghoff et al. 1993). The only exceptions are

observed in some cave-dwellers such as species of the North American genus *Tetracion* Hoffman, 1956, as well as the two highly specialized Asian species *Sinocallipus simplipodicus* Zhang, 1993 and *S. jaegeri* Stoev & Enghoff, 2011 (Stoev and Enghoff 2011). However, even in the most cave-adapted taxa, the number of ommatidia in adults is more than 10, while in the surface-dwelling species *B. inexpectatum* gen. nov. et sp. nov., we witness an extreme reduction to only five ommatidia situated in two rows. Juvenile callipodidans usually hatch from eggs with only one ommatidium. Stadium II would have three (1+2), stadium III would have at most six (1+2+3) ommatidia, thus the adult number of five would have been reached at third larval stadium earliest. Some callipodidans (e.g. *Callipus foetidissimus* (Savi, 1819)) do not add any ommatidia between stadia I and II (Enghoff et al. 1993). Nevertheless, the fully developed cyphopods leave no doubt that the holotype is a fully mature specimen.

### Abundance and distribution

Callipodida is the rarest among all millipede orders preserved in Burmese amber, with only a single specimen out of 529 specimens hitherto known (Wesener and Moritz 2018; Jiang et al. 2019). Even nowadays Callipodida are far less common compared than Julida, Polydesmida, Spirostreptida, Chordeumatida, and Spirobolida, which prevail in temperate and tropical forests. In most cases, being habitat specialists, mostly petrophilic and associated with limestone, callipodidans are usually represented by only a few individuals in the collecting sites (Stoev et al. 2008).

Callipodidans have not previously been recorded from Myanmar (Likhitrakarn et al. 2017), and thus, the finding of *B. inexpectatum* gen. nov. et sp. nov. extends the historical range of the order in Southeast Asia. Of all contemporary families of Callipodida, Burmanopetalidae fam. nov. is geographically closest to Sinocallipodidae Zhang, 1993, which is known from China, Thailand, Laos, and Vietnam (Stoev and Enghoff 2011), Paracortinidae Wang & Zhang, 1993 from China and Vietnam (Stoev and Geoffroy 2004; Liu and Tian 2015), and Caspiopetalidae Lohmander, 1931 from China and Central Asia (Stoev and Enghoff 2005).

### The fossil record

*Burmanopetalum inexpectatum* gen. nov. et sp. nov. can be readily distinguished from *Hannibaliulus wilsonae* Shear et al. 2009, a possibly nematophoran callipodid-like millipede of early Triassic (Anisian) age (ca 243 Mya) by having 'normal' undivided metazonites (vs divided by a wide, shallow transverse depression into anterior and posterior parts, with ventral margins strongly rebordered) and eyes composed of only five ommatidia (vs eyepatches with numerous ommatidia). Furthermore, the Triassic fossil is known to have a body composed of 40–44 body rings and a much longer length (ca 55 mm). Ozopores, pleurotergal setae and spinnerets have not been detected in *H. wilsonae* (Shear et al. 2009).

Enghoff (1990) provided a reconstruction of the ground-plan of the chilognathan millipede based on a cladistic analysis. He argued that the hypothetical ancestor should be regarded as a few-segmented, small animal, lacking trichobothria, with eyes, 8-segmented antennae, defense glands, middorsal suture, segments composed of free sternites and pleurotergites, and a simple telson. *Burmanopetalum inexpectatum* gen. nov. et sp. nov., shows remarkable similarity to the chilognathan ground-plan, especially in the minute size, reduced segmentation, the presence of eyes, a middorsal suture, and ozopores.

Until now, all myriapods known from Burmese amber have been assigned to Recent families and even genera. The monotypic genus *Kachinophilus* Bonato et al., 2014 was recognized as a member of the currently widespread family Geophilidae Leach, 1815 (Bonato et al. 2014). Likewise, the only species of class Symphyla described from Burmese amber, *Symphylella patrickmuelleri* Moritz & Wesener, 2018, is referred to a genus with more than 40 extant species (Moritz and Wesener 2018). In Diplopoda, the only penicillatan millipede *Polyxenus burmiticus* was assigned to the extant genus *Phryssonotus* in the family Synxenidae (Rasnitsyn and Golovatch 2004). Specimens of Polyxenida recently found in Burmese amber (Wesener and Moritz 2018) were assigned to Polyxenidae and Synxenidae, as well as to an uncertain family. Likewise, the subclass Helminthomorpha Pocock, 1887 was hitherto represented in the fossil record by three species (Liu et al. 2017a; Jiang et al. 2019), all assigned to the contemporary genera *Siphoniulus* Pocock, 1894 and *Siphonophora* Brandt, 1837. In their checklist of the Myriapoda found in Burmese amber Wesener and Moritz (2018) reported only very few taxa that possibly belong to extinct, yet undescribed families. For instance, a number of specimens of the suborder Cambalidea Cook, 1895 were found to possess frontal setae on their head, a character which is not present in recent Spirostreptida. In other terrestrial arthropods with similar habits and evolutionary patterns, numerous specimens from Burmese amber are assigned to families that are no longer extant (for a complete list see Ross 2018). In scorpions alone, there are five families known only as fossils: †Palaeoescorpiidae, †Palaeotrilineatidae, †Sucinolourencoidae, †Chaeirilobuthidae, and †Palaeoburmesebuthidae, and in the order Ricinulei, all fossil taxa have been assigned to extinct families – †Hirsutisomidae, †Poliocheridae, and †Primoricinuleidae (Ross 2018).

With this detailed description of the first fossil Callipodida from the Mesozoic, we lay down the foundation for further research on the classification and phylogeny of the group. Furthermore, the minimum age of order Callipodida is now known to be at least 99 Mya.

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# First description of the male of *Volesus nigripennis* Champion, 1899, with new records from Ecuador and Panama, taxonomical notes, and an updated key to the genera of Sphaeridopinae (Hemiptera, Reduviidae)

Hélcio R. Gil-Santana<sup>1</sup>, Jader Oliveira<sup>2</sup>

**1** Laboratório de Díptera, Instituto Oswaldo Cruz, Av. Brasil, 4365, 21040-360, Rio de Janeiro, RJ, Brazil

**2** Laboratório de Parasitologia, Universidade Estadual Paulista “Julio de Mesquita Filho”, Faculdade de Ciências Farmacêuticas UNESP/FCFAR, Rodovia Araraquara Jaú, KM 1, 14801-902, Araraquara, SP, Brazil

Corresponding author: Hélcio R. Gil-Santana ([helciogil@uol.com.br](mailto:helciogil@uol.com.br); [helciogil@ioc.fiocruz.br](mailto:helciogil@ioc.fiocruz.br))

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## Abstract

The genus *Volesus* Champion, 1899 is redescribed and the male of *V. nigripennis* Champion, 1899 is described for the first time and found to be similar to the female in both structure and coloration. The genus and the species are recorded from Ecuador and Panama for the first time. Notes on the taxonomic history of Sphaeridopinae and an updated key to the genera are provided.

## Keywords

Heteroptera, male genitalia, Neotropics, Salyavatinae, *Sphaeridops*, *Veseris*

## Introduction

Recent papers have documented new records of reduviid genera and species for several Neotropical countries (e.g. Forero 2006, Gil-Santana 2007, 2008, Melo 2008, Inés and Coscarón 2009, Dellapé et al. 2010).

Froeschner (1981, 1999) provided catalogs of Heteroptera, including Reduviidae, recorded from Ecuador and Panama, respectively. Further records of Reduviidae from Ecuador and Panama were provided by Maldonado (1990) and in papers describing or reviewing different taxa of this family (e.g. Dougherty 1995, Martin-Park et al. 2012, Zhang et al. 2016).

The cladistic analysis of Weirauch (2008) showed that Salyavatinae and Sphaeridopinae are a monophyletic group, while studies by Weirauch (2008) and Gordon and Weirauch (2016) provided evidence that Salyavatinae is paraphyletic and Sphaeridopinae is a sister group to the genus *Salyavata* Amyot & Serville, 1843 (Salyavatinae). Here we are considering Salyavatinae and Sphaeridopinae as separate subfamilies (following e.g. Weirauch et al. 2014, Gil-Santana et al. 2015).

Sphaeridopinae includes *Sphaeridops* Amyot & Serville, 1843 with three species, *Veseris* Stål, 1865 with two species and *Volesus* Champion, 1899 monotypic with *V. nigripennis* Champion, 1899 (Gil-Santana et al. 2000, Gil-Santana and Alencar 2001, Forero 2004, Gil-Santana et al. 2015).

A summary of the scant data on biology of Sphaeridopinae was provided by Gil-Santana et al. (2015).

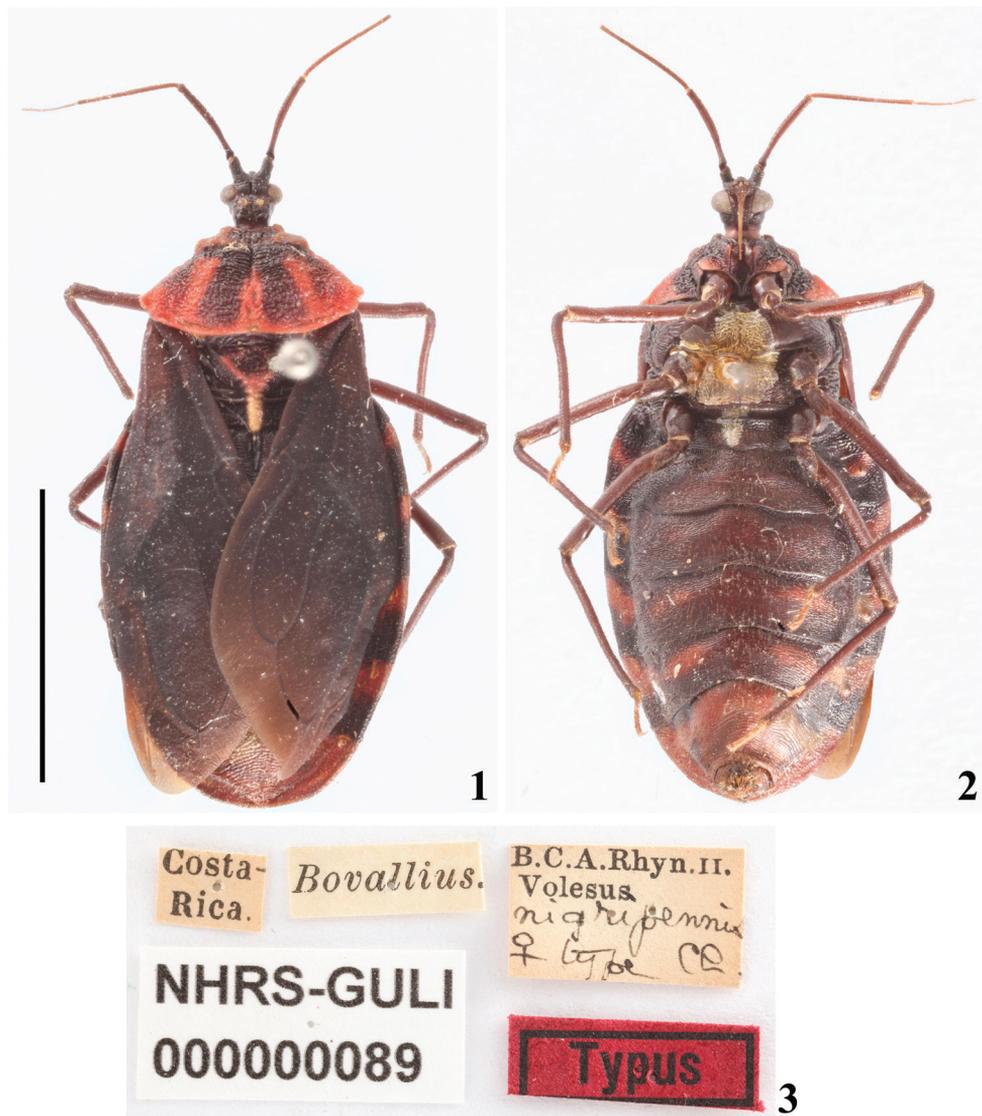
In the present paper, notes on the taxonomical history of Sphaeridopinae are provided, clarifying some inconsistencies regarding nomenclature and taxonomical changes. *Volesus* is redescribed and the male of *V. nigripennis* is described for the first time. The genus and the species are recorded from Ecuador and Panama for the first time. Based on the results obtained here, an updated key to the genera of Sphaeridopinae is presented.

## Material and methods

Photographs of the holotype of *Volesus nigripennis* Champion, 1899 (Figs 1–3), which is deposited at the Swedish Museum of Natural History (NRM), Stockholm, Sweden, were kindly provided by Dr Gunvi Lindberg (NRM).

Data on a female of *V. nigripennis* from Panama and deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC, USA, were kindly provided by Dr Silvia A. Justi (The Walter Reed Biosystematics Unit, WRBU, Smithsonian Institution, Museum Support Center), with the support of Dr Thomas Henry and James N. Zahniser (NMNH).

Scanning electron microscopy images (Figs 7–8, 12–13, 15, 17–19, 21–23, 29–34, 36–40, 46) were obtained by the second author (JO). A male of *V. nigripennis* and its external genitalia were cleaned in an ultrasound machine. Subsequently, the samples were dehydrated in alcohol, dried in an incubator at 45 °C for 20 min, and fixed in small aluminum cylinders with transparent glaze. Sputtering metallization was then performed on the samples for 2 minutes at 10 mA in an Edwards sputter coater. After this process, the samples were studied and photographed using a high-resolution field emission gun scanning electron microscope (FEG-SEM; JEOL, JSM-7500F), as described by Rosa et al. (2010, 2014).



**Figures 1–3.** *Volesus nigripennis*, female, holotype deposited in NRM, catalog number NHRS-GULI000000089, photographed by Gunvi Lindberg, © 2018 Naturhistoriska riksmuseet. Made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0, <https://creativecommons.org/licenses/by/4.0/legalcode>. **1** dorsal view **2** ventral view **3** labels. Scale bar: 10 mm (**1**).

All remaining figures were produced by the first author (HRG-S). The fixed adults, microscopic preparations and genitalia were photographed using digital cameras (Nikon D5200 with a Nikon Macro Lens 105 mm, Sony DSC-W830). Drawings were made using a camera lucida. Images were edited using Adobe Photoshop CS6.

Observations were made using a stereoscope microscope (Zeiss Stemi) and a compound microscope (Leica CME). Measurements were made using a micrometer eyepiece. The total length of the head was measured excluding the neck, for better uniformity of this measurement. Dissections of the male genitalia were made by first removing the pygophore from the abdomen with a pair of forceps and then clearing it in 20% NaOH solution for 24 hours. Following this procedure, the phallus was recorded without inflation (Figs 48–50). The endosoma was then everted (Figs 51, 52) by carefully pulling on the endosoma wall, using a pair of fine forceps. The dissected structures were studied and photographed in glycerol.

General morphological terminology mainly follows Schuh and Slater (1995). The terminology of the genitalia structures follows Lent and Wygodzinsky (1979). However, the “vesica”, as recognized by the latter authors, has been considered as absent in reduviids. The assumed equivalent structure in reduviids is a somewhat sclerotized appendage of endosoma (Forero and Weirauch 2012) but not the homologous vesica of other heteropterans, such as Pentatomomorpha (Rédei and Tsai 2011). Thus, this term is not used here. Yet, we adopted the denomination of paired membranous lobes on the endosoma, lateral to the dorsal phallosomal sclerite, from Weirauch (2008), to the flat paired expansions of the endosoma wall (Fig. 50). On the other hand, in order to maintain uniformity with the general terminology followed here, the basal plate bridge is named as such and not as ponticulus basilaris as in Weirauch (2008).

The specimens described here will be deposited in the Entomological Collection of the Oswaldo Cruz Institute (“Coleção Entomológica do Instituto Oswaldo Cruz”), Rio de Janeiro (CEIOC) and in the Dr Jose Maria Soares Barata Triatominae Collection (CTJMSB) of the São Paulo State University Julio de Mesquita Filho, School of Pharmaceutical Sciences, Araraquara, São Paulo, Brazil.

When citing the text on the labels of a pinned specimen, a slash (/) separates the lines and a double slash (//) different labels. All measurements are in millimeters (mm).

## Results

### Taxonomy

#### Subfamily Sphaeridopinae Amyot & Serville, 1843

Amyot and Serville (1843) created the “Groupe” “Sphéridopides” in the “tribu” “Brevicipites” to include only *Sphaeridops* described by them to accommodate the species *Reduvius amoenus* Lepeletier & Serville, 1825. Walker (1873a) recorded Sphaeridopidae with only *Sphaeridops* included in it. Interestingly, in the same volume this genus is further keyed out with *Veseris* Stål, 1865 as belonging to the subfamily “Acanthaspida”. The characteristics mentioned by Walker (1873a) to separate these genera were the same mentioned by Stål (1865, 1872). Walker (1873b) recognized the family “Sphaeridopidae, Serv.”, clearly referring to page 381 in which it was established by Amyot and Serville (1843).

*Sphaeridops* was regarded as belonging to Acanthaspidinae (e.g. Stål 1872, Lethier and Severin 1896), in which *Veseris* and *Volesus* Champion, 1899 were also included when described (Stål 1865, Champion 1899).

Pinto (1927) established Sphaeridopidae as a new family, containing *Sphaeridops* and *Limaia* Pinto, 1927, described in the same paper. Interestingly, Pinto (1927) argued that he was adopting the opinion of Amyot and Serville (1843) that *Sphaeridops* should be part of a separate family sensu “Brevicipites”, without mentioning the similarity between the etymology of Sphaeridopidae and “Sphéridopides”, neither the references of Walker (1873a, b) to it. Pinto (1927) also claimed that the name “Brevicipites” could not prevail according to nomenclatural rules, because it was not based on a genus name, and instead included it as a synonym of the new family Sphaeridopidae. The group has been subsequently considered as a subfamily and most authors credited its authorship to Pinto (1927) (e.g. Costa Lima 1940, Wygodzinsky 1949, Maldonado 1990, Forero 2004), but Putshkov and Putshkov (1985) attributed the authorship of Sphaeridopinae to Amyot and Serville (1843) (referring to “Sphaeridopides”). Costa Lima (1940) in a general book on Brazilian Heteroptera, stated the synonym between *Limaia ruber* Pinto, 1927 under *Veseris rugosicollis* (Stål, 1862), without giving any reasons for the proposed synonym. In order to review this synonymy, a search for the male type of *L. ruber* in the Entomological Collection of Oswaldo Cruz Institute, Rio de Janeiro, where it should be deposited (Pinto 1927) was performed (Gil-Santana et al. 1999), but it was not located. Nevertheless, although Maldonado (1990) had credited to Wygodzinsky (1949) the above-mentioned synonymy, it was undoubtedly firstly stated by Costa Lima (1940).

On the other hand, the synonym between *Limaia* and *Veseris* Stål, 1865 was in fact first recorded by Wygodzinsky (1949).

Similarly, Costa Lima (1940) was the first to record *Sphaeridops pallescens* (Walker, 1873) (described as *Reduvius pallescens*) as a junior synonym of *S. amoenus* and not Wygodzinsky (1949) as recorded by Maldonado (1990).

It is noteworthy that *Eurylochus bellator* Torre-Bueno, 1914 and *Volesus nigripennis* Champion, 1899 were first mentioned as belonging to Sphaeridopinae by Costa Lima (1940). *Eurylochus* Torre-Bueno, 1914 was considered a junior synonym of *Veseris* by Gil-Santana and Alencar (2001).

Therefore, Sphaeridopinae currently includes three exclusively Neotropical genera: *Sphaeridops*, *Veseris* and *Volesus* (Gil-Santana et al. 2015).

Pinto (1927) provided the following diagnosis for Sphaeridopidae: a short head, without an antecular portion; large antenniferous tubercles, clearly exceeding the anterior border of the head; eyes large, salient, almost touching each other on the ventral portion of the head; and the labium straight, with three [visible] segments.

Maldonado and Santiago-Blay (1992) considered that Sphaeridopinae are characterized by two unique characters: the head mostly occupied by the very large eyes, and the antennifers raised on the vertex, close together, between the eyes. These authors were the first to argue that the Sphaeridopinae have a few other unusual characters: presence of sensory organs on the fore lobe of the pronotum (unknown function) and the fact that the dorsal and ventral components of connexivum are well separated by a vertical

sclerite; these characteristics were recorded in *Sphaeridops eulus* Maldonado & Santiago-Blay, 1992. Maldonado and Santiago-Blay (1992) assumed that the smooth areas on the fore lobe of pronotum were sensory organs derived from SEM images of them. These authors also commented that they had observed “corresponding organs” in other two genera, without stating which ones. Gil-Santana et al. (1999) and Gil-Santana and Alencar (2001) recorded sensory organs on fore lobe of pronotum in both species currently included in *Veseris*. However, these latter authors based their conclusions only on the macroscopic aspect of similar smooth structures of fore lobe, without using SEM imaging.

Schuh and Slater (1995) diagnosed Sphaeridopinae by the following set of characters: head projecting only slightly beyond the anterior margin of eyes; eyes large, nearly contiguous ventrally; antennae inserted on anteriorly projecting tubercles; rostrum straight; all tarsi three-segmented. Weirauch et al. (2014) considered that Sphaeridopinae are characterized by a large, robust body; large eyes almost covering the entire head; and a short, straight, thin labium. The keys to the genera provided by Gil-Santana and Alencar (2001), Forero (2004) and Gil-Santana et al. (2015) included a different set of characteristics.

### ***Volesus* Champion, 1899**

*Volesus* Champion, 1899: 296 [description, comments on systematic relationship with other genera]; Wygodzinsky 1949: 65 [catalog]; Putshkov and Putshkov 1985: 99 [catalog]; Maldonado 1990: 490 [catalog]; Schuh and Slater 1995: 158 [citation]; Gil-Santana et al. 1999: 2 [citation]; Gil-Santana and Alencar 2001: 96, 100 [citation, key]; Forero 2004: 164 [diagnosis], 189 [key]; Forero 2006: 36 [citation]; Weirauch et al. 2014: 101 [citation]; Gil-Santana et al. 2015: 336 [citation], 337 [key].

**Type species.** *Volesus nigripennis* Champion, 1899, by monotypy.

**Diagnosis.** *Volesus* can be separated from other genera of Sphaeridopinae by the combination of characters presented in the key below, and additionally by the following characteristics: eyes medium-sized, not covering the head; interocular distance larger than the width of eye, dorsally, and approximately equivalent to it, ventrally; labium with only two visible segments.

**Redescription.** Body integument shiny, generally diffusely rugose, with linear irregular impressions more intensively and coarsely in thorax, except on lateral portions of mesosternum and median portions of some sternites, in which it is mostly smooth. *Head* subrectangular in dorsal view, moderately elongate in lateral view; transverse sulcus straight, moderately impressed meeting eyes at inner posterior angle; a midlongitudinal well-marked sulcus running from transverse sulcus to approximately level of anterior margin of eyes; antenniferous stout, cylindrical, diverging forward, straight apically; anteocular region curved downwards, not, or barely, visible in dorsal view; eyes medium-sized, interocular distance in dorsal view larger than width of an eye; labium with only two visible segments; first visible labial segment short, enlarged; sec-

ond visible segment long, thin, straight. *Thorax*: pronotum trapezoidal; fore lobe much shorter and narrower than hind lobe of pronotum; transverse (interlobar) sulcus indistinct; median longitudinal sulcus ill defined, short, running on approximately basal fourth of hind lobe and separated from the median transverse depression of fore lobe by an irregular, curved carina. Prosternum somewhat depressed, with a pair of acute short, lateral processes, directed forward, median portion mostly occupied by stridulitrum, shortly prolonged posteriorly on midline, not surpassing the level of posterior margin of fore coxae and continuous with adjacent sclerite; meso- and metasternum flattened; fore coxae close, separate by a distance smaller than width of each coxa; middle and hind coxae separated from each other by a distance approximately equivalent to slightly more than twice width of each of them. Femora, tibia and tarsi slender, segments with similar width in all three pairs of legs; femora with a small ventral subapical protuberance; a small spongy fossa on apices of fore and mid tibiae. Tarsi three segmented. *Abdomen* enlarged at about middle portion; small scars of dorsal abdominal glands openings (dag) on medial anterior margins of tergites IV–VI; a vertical sclerite separating dorsal and ventral components of connexivum. Sternites with canaliculae (carinulate) on anterior margin of some segments.

**Distribution.** Colombia, Costa Rica, Ecuador (**new record**), Panama (**new record**).

### ***Volesus nigripennis* Champion, 1899**

Figs 1–57

*Volesus nigripennis* Champion, 1899: 296 [description], Tab. XVIII [Figure 14]; Costa Lima 1940: 207 [citation], Wygodzinsky 1949: 65 [catalog]; Maldonado 1990: 490 [catalog]; Gil-Santana et al. 1999: 2 [citation]; Forero 2004: 164 [citation from Colombia], Figures 5.25, 5.103; Forero 2006: 36 [new record from Colombia], Figures 56–57; Gil-Santana et al. 2015: 336 [citation].

**Notes.** *Volesus nigripennis* was described based on a female from Costa Rica (Champion 1899). The female holotype is deposited at the Swedish Museum of Natural History (NRM), Stockholm, Sweden, and its photos are available on their website (Figs 1–3).

Forero (2004, 2006) recorded this species from Colombia, based on a unique female. These two females have been the only specimens of *V. nigripennis* known so far. Forero (2004) argued that the knowledge of the male of the species would be useful to a definition in relation to other members of Sphaeridopinae.

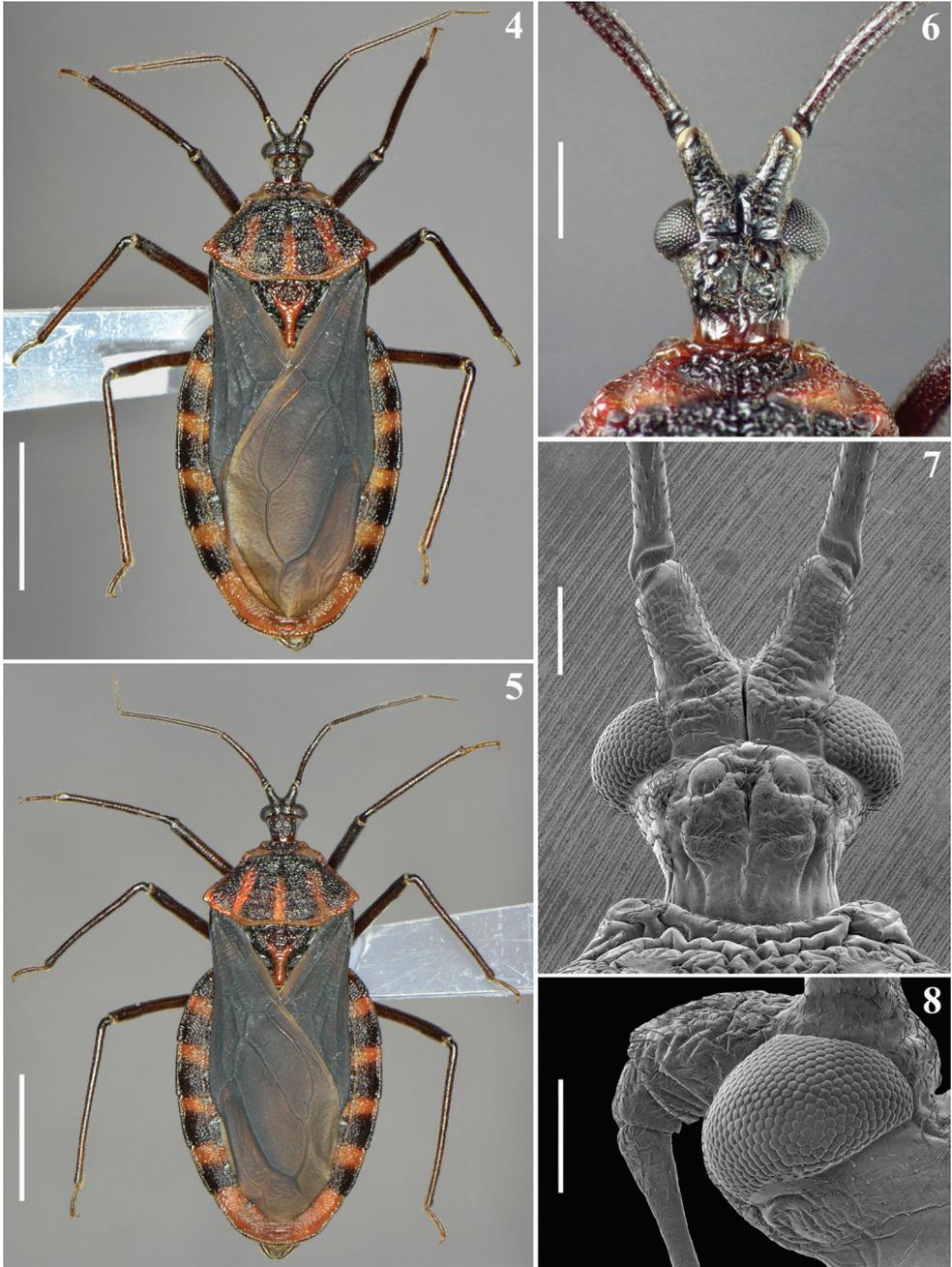
Additionally, a female specimen of *V. nigripennis* from Panama was located in the collection of the NMNH. Upon our request, Dr Silvia A. Justi (WRBU) examined the specimen, sent us photos of it and provided the data on the labels, which are transcribed below. The specimen was identified by the Late P. Wygodzinsky. Although it had been previously coated with metal for electronic microscopy, the identification of the specimen is still possible and represents a new record of this species for Panama.

**Material examined.** *Volesus nigripennis*. **ECUADOR, Esmeraldas**, Tundaloma Lodge, near Calderón, 01.18277N, 078.75259W (01°10'57"N 78°45'09"W), 55m a.s.l., 8–9.ii.2014, A. Kury & A. Giupponi *leg.*, 1 male (CEIOC), 1 male (CTJMSB).

**Additional specimen.** *Volesus nigripennis*. **PANAMA:** Escobal Road / Atl. Canal Zone / 24 VI [19]74 [handwritten] / Col: D. Engleman // Drake Colln. ex / J. Maldonado C. / Coll 1996 [characters partially cut off at the bottom of the label] // *Volesus* [handwritten] / *nigripennis* [handwritten] / Champion [handwritten] / Wygodzinsky [det.], 1 female (NMNH).

**Description. Male.** (Figs 4–57). Measurements: total length to tip of abdomen: 16.9–17.3; to tip of forewings: 16.1–16.5; head (excluding neck, measured in lateral view) length: 2.2; length of antecular portion (measured in lateral view): 0.5; length of postocular portion (measured in lateral view): 0.7; width across eyes: 1.8; interocular distance, dorsal view: 0.9, ventral view: 0.5–0.6; width of eye, dorsal view: 0.5; ventral view: 0.6; length of eye: 0.6–0.7; distance between external margin of ocelli: 0.7–0.8; distance between ocelli: 0.25; maximum width of ocellus: 0.2–0.25; length of antennifer: 0.7; lengths of antennal segments: I: 2.5; II: 3.8; III: 1.5; IV: 0.9; lengths of labial segments, first visible: 0.3; second visible: 1.7–1.8. Thorax: pronotum: fore lobe, length: 0.8; maximum width: 3.2; hind lobe: length 3.0; maximum width: 5.9; scutellum, length: 2.3; width: 2.7; length of process: 1.1–1.2; length of hemelytra: 12.5. Fore legs: length of femur: 3.8; length of tibia: 4.8–4.7; length of spongy fossa: 0.25; length of tarsus: 1.2–1.3; middle legs, length of femur: 4.5–4.6; length of tibia: 4.8–5.1; length of spongy fossa: 0.25; length of tarsus: 1.2–1.3; hind legs: length of femur: 5.2–5.3; length of tibia: 6.3–6.7; length of tarsus: 1.3. Abdomen, length: 12.5; maximum width: 7.7–7.8.

**Coloration:** general coloration blackish with reddish markings (Figs 4–5, 14, 20, 26, 28, 35). Head generally blackish; neck mostly reddish; apices of antenniferous tubercles pale; antennal segment II brownish black; antennal segments III–IV brownish; labium brownish (Figs 4–6, 9–11, 14, 20). Thorax blackish, brownish black on meso- and metasternum, with the following reddish thoracic markings: on anterior collar and their projections; on lateral and posterior margins of pronotum; on most of fore lobe of pronotum, except its median portion; on hind lobe of pronotum, a median and a pair of lateral converging bands, which are continuous with reddish posterior margin, ending approximately at mid and anterior thirds of hind lobe, respectively; and on postero-superior portion (approximately) of propleura and process of scutellum (Figs 4–6, 14, 16, 20, 26, 28). Legs generally blackish; spongy fossa on fore and mid tibiae somewhat paler (Figs 4–5, 20, 24–25). Hemelytra black, somewhat paler, brownish, on approximately distal half of clavus, medially and about distal half of the membrane, except veins and area just surrounding them (Figs 4–5, 26). Hind wing generally brownish, with veins darkened (Fig. 27). Abdomen blackish to blackish brown; tergite VI with a median reddish spot just below anterior margin; tergite VII almost completely reddish, blackish on and just below anterior margin and with a pair of rounded blackish spots on mid-lateral portion (Fig. 28). Connexivum reddish on: extreme base of segment II, approximately basal third of segments III–V, and somewhat less than basal half of segment VI; connexival portion of segment VII almost entirely reddish

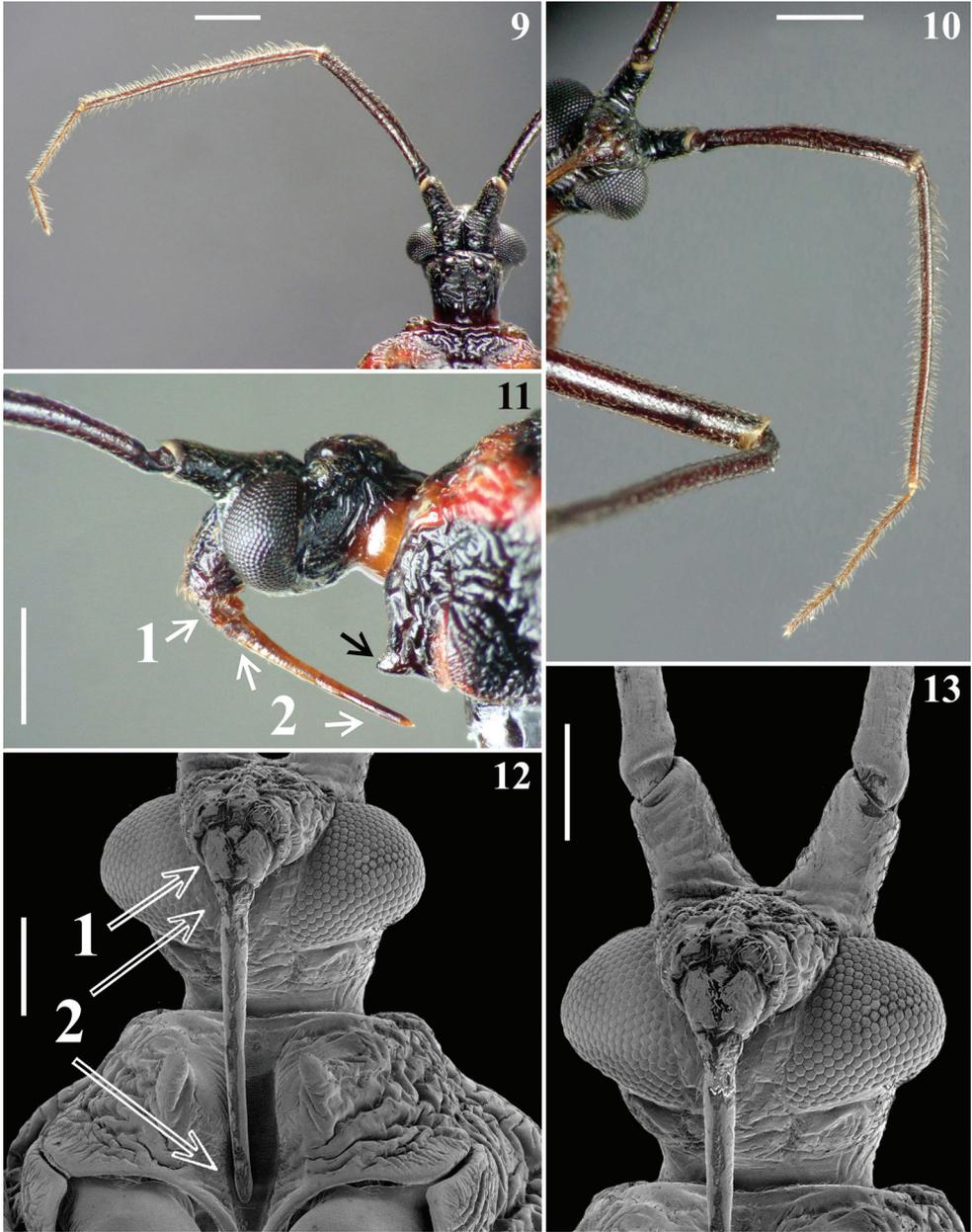


**Figures 4–8.** *Volesus nigripennis*, male 4–5 dorsal view 6–8 head 6–7 dorsal view 8 except distal half of second visible labial segment, lateral view. Scale bars: 5.0 mm (4–5); 1.0 mm (6); 0.5 mm (7–8).

with only posterior border of approximately distal half darkened; ventrally, marking on segment II is a small spot on external margin; on segments III–VI connexival reddish markings are prolonged dorsally to a short distance on lateral portion of respective tergite as a subtriangular marking, and ventrally, as a somewhat curved lateral marking, directed backwards, reaching spiracles, which are surrounded by reddish posterior margin; sternite II with anterior margin and median portion, on approximately distal half reddish to reddish brown; transverse median bands, on sternites III–VII, progressively larger, reddish brown in one specimen and pale brownish in other, joining lateral reddish markings described above in sternites V–VII, the latter almost completely reddish, with dark coloration restricted to anterior margin and adjacent to genital capsule (Figs 4–5, 26, 28, 35). Exposed portion of pygophore and parameres blackish (Fig. 35).

*Vestiture:* body generally covered by sparse short, somewhat curved, adpressed, thin, golden to brownish setae. Head: eyes, ocelli and neck glabrous; region adjacent to insertion of labium with more numerous and somewhat longer setae; ventral surface of first visible labial segment and basal portion of second visible labial segment moderately setose, dorsal surface of correspondent portions with fewer setae; additionally, some sparse setae scattered on the proximal third of second visible segment, remainder glabrous. Antenna: segment I sparsely covered with setae similar to those of general vestiture but slightly longer, more numerous at apex; segments II–IV densely setose, covered with scattered longer, somewhat curved, brownish setae and much more numerous shorter, thinner, whitish setae (Figs 9, 10). Thorax. Some longer straight thin setae on posterior margin of pronotum adjacent to lateral portion of scutellar base; setae are sparser on ventral surface; smooth lateral areas of mesosternum glabrous. Hemelytra: small adpressed setae sparsely scattered on corium, more numerous at its apex; apical two thirds of clavus, respective adjacent area of corium and membrane glabrous. Legs generally with similar vestiture of the body; setae longer and thicker on tibiae, becoming more numerous towards apex; tarsi with stiff, pale, yellowish to golden-yellowish, oblique to curved setae, with variable lengths. Abdomen: tergites I–V almost completely glabrous, with some scattered small darkened or pale setae, almost imperceptible; tergite VI with some more numerous pale setae; tergite VII with scattered longer golden setae. Connexivum: lateral margins with numerous adpressed short curved darkened setae, forming a few irregular rows; these setae become somewhat longer and paler on distal margin of segment VII; segments II–VI dorsally glabrous; some sparse setae on dorsal surface of distal third of segment VII. Sternites generally covered with sparse thin golden to pale setae; somewhat longer and more numerous setae on median portion of segments VI–VII and on pygophore, except its middle portion.

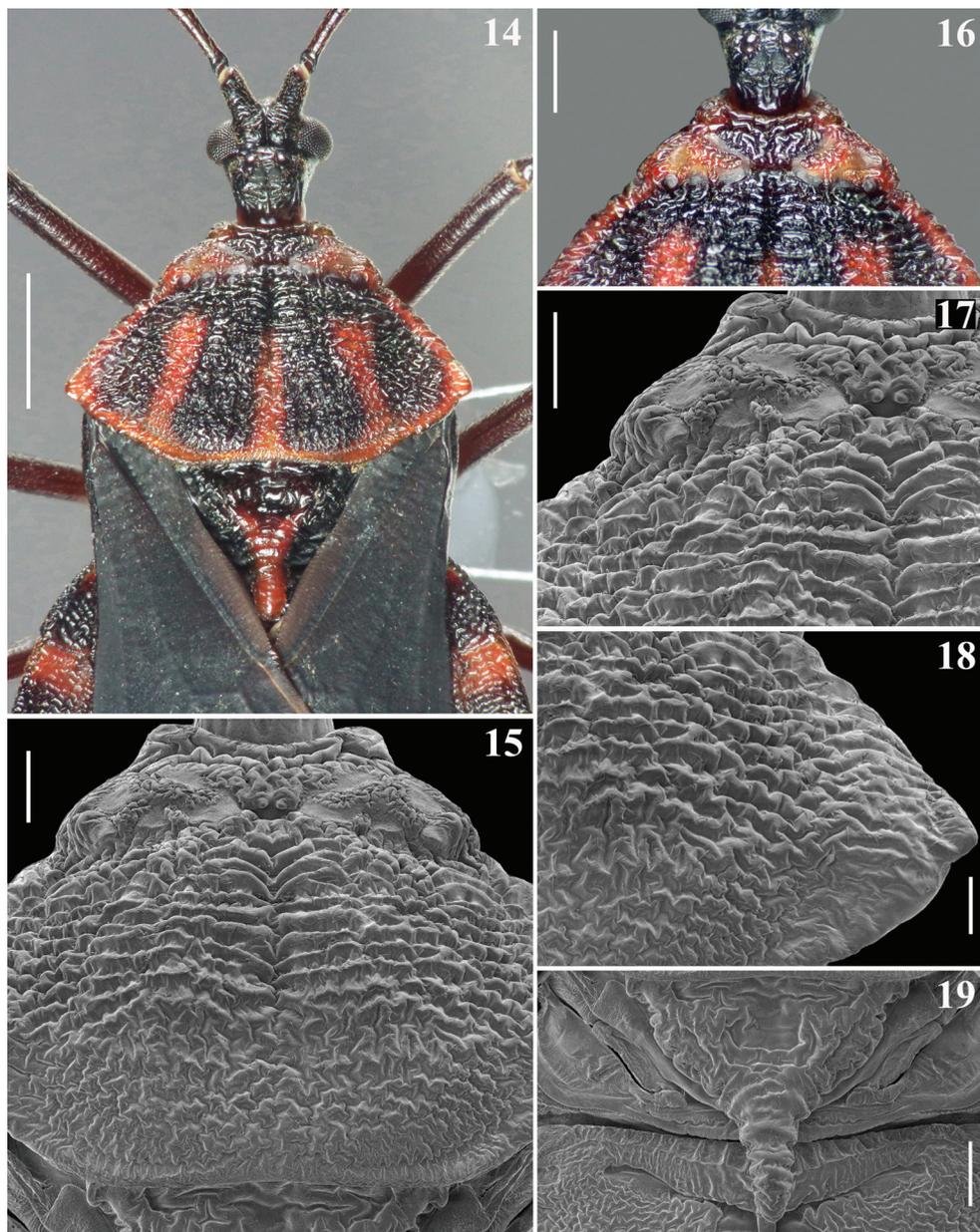
*Structure:* Head. Anteocular portion slightly shorter than postocular portion (in lateral view); ocelli separated by a distance slightly larger than transverse width of each ocellus, positioned medially to level of inner posterior angle of eyes and close to transverse sulcus; antenniferous large; first antennal segment slightly longer than head, stout, somewhat curved, its approximately basal fourth slightly thinner; remaining



**Figures 9–13.** *Volesus nigripennis*, male **9** head and left antenna, dorsal view **10** left antenna, ventral view **11** head and fore lobe of pronotum, lateral view (black arrow points to prosternal process; first and second visible labial segments indicated by white arrows) **12, 13** ventral view **12** head, except antenniferous, and most part of prosternum (arrows point to first and second visible labial segments) **13** head, except distal half of second visible labial segment. (**1** first **2** second visible labial segments). Scale bars: 1.0 mm (**9–11**); 0.5 mm (**12, 13**).

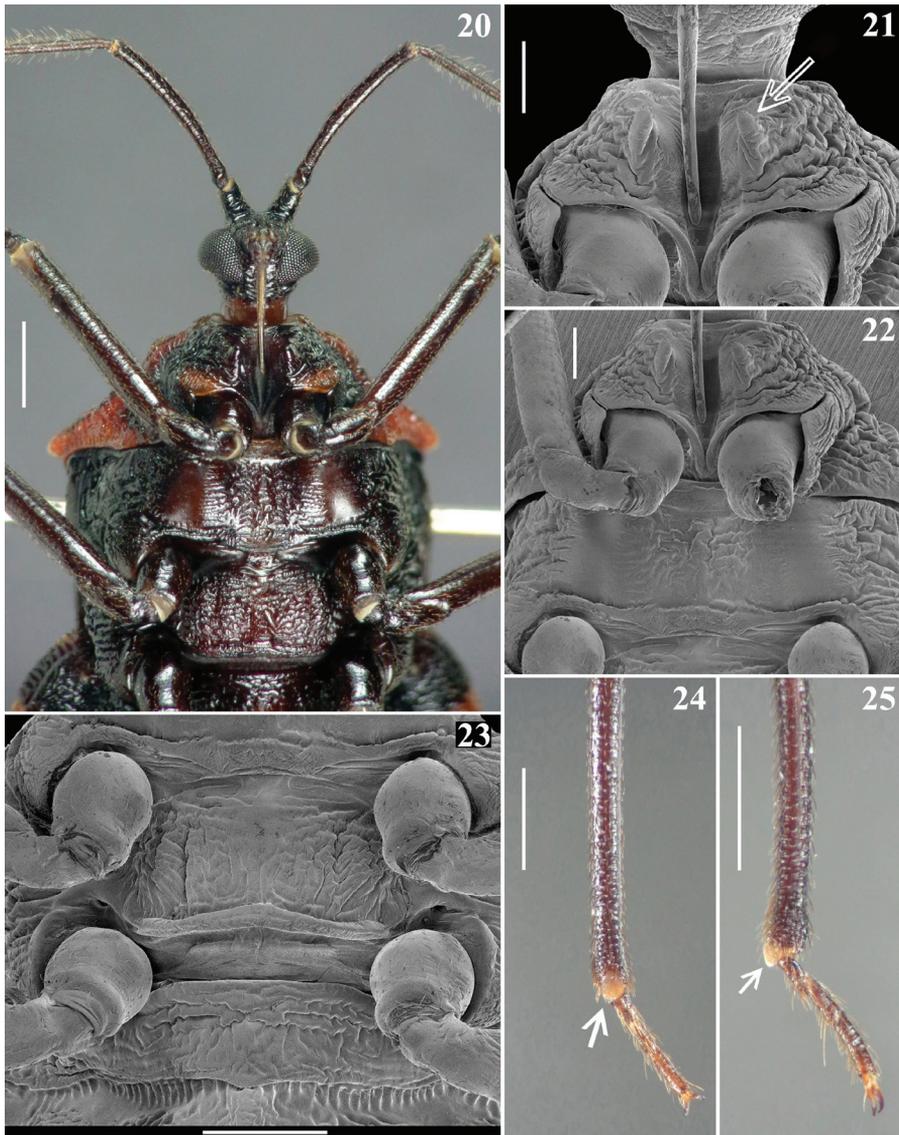
antennal segments progressively thinner, cylindrical; labium reaching or surpassing the mid third of stridulitrum (Figs 6–14, 20–22). Thorax. Anterior collar inconspicuous; anterolateral angles rounded and small (Figs 15, 16); fore lobe with irregular areas with smooth and whitish integument; a median transverse depression on fore lobe present between medial margins of longer curved smooth areas (Figs 14–17); humeral angles acute, slightly prominent (Figs 14, 18); posterior margin of hind lobe slightly curved on middle third (Figs 14, 15). Scutellum sculptured, median depression shallow, process stout, horizontal, apex rounded (Figs 14, 19). Distance between acute prosternal processes: 0.7. Hemelytra generally dull; on extreme base of dorsal surface, laterally, and on lateral portion, basally, moderately shiny; not reaching tip of abdomen, ending somewhat apically to level of the mid third of seventh tergite (Figs 4–5, 26); in one specimen, the membrane has a small additional cell at approximately apical fourth of cubital vein (Fig. 26). Abdomen. Integument generally also rugose (Figs 28–34), except on median portions of sternites IV–VII, in which it is mostly smooth (Figs 34–38). Connexivum largely exposed, laterally to hemelytra (Figs 4–5); anterior margin of tergite I carinulate (Figs 29–31); tergite II with a mid-longitudinal keel and median third of posterior margin curved backwards (Figs 28–31). Sternites carinulate on anterior margin of segments III–V in one specimen and also on segment VI in the other; on sternite III, canaliculae are somewhat larger and extend more towards lateral portion, occupying approximately two thirds of anterior margin, except midline; on following segments canaliculae become progressively slightly smaller and occupy approximately median third of anterior margin, except midline; a median shallow keel on distal two thirds of segment II and somewhat more elevated in sternites III–VI (Figs 35–38). Segment VIII not visible externally, sclerotized on ventral portion, which becomes somewhat wider towards posterior margin; latter almost straight and with a few short setae; dorsal portion membranous and narrower; spiracles on dorsal margin of ventral portion (Figs 39–41).

*Male genitalia* (Figs 35, 39–40, 42–57): genital capsule, in ventral and lateral views: exposed portion of pygophore hemispherical, posterior margin (**pm**) flattened, integument rugose and setose; non-exposed portion of pygophore less pigmented and less sclerotized, integument smooth and glabrous (Figs 39, 42–44); in dorsal view: between anterior and posterior genital openings, a very well-sclerotized dorsal (transverse) somewhat curved bridge; socket of insertion of paramere (**sp**) approximately in mid portion of pygophore, with a conspicuous medial prolongation obliquely directed posteriorly (**psp**); numerous, somewhat long, erect setae inserted on inner surface of basal portion of this prolongation; membranous areas of genital opening smooth; proctiger (**pct**) somewhat enlarged toward apex, with numerous long setae on distal half; posterior dorsal margin of pygophore (**pdm**) large, forming a horizontal extension of pygophore wall, with some scattered setae on inner margin and more numerous and somewhat shorter elements on median portion (Fig. 40). Median process of pygophore (**mpp**) only visible in dorsal and lateral views of pygophore, directed upwards, situated some distance from posterior margin, somewhat enlarged, almost straight and sub-squared in dorsal and anterior views, respectively (Figs 40, 42–43, 47). Paramere apices in contact in resting position (Fig. 35); parameres (**pa**) (Figs 40, 42–43) symmetrical,



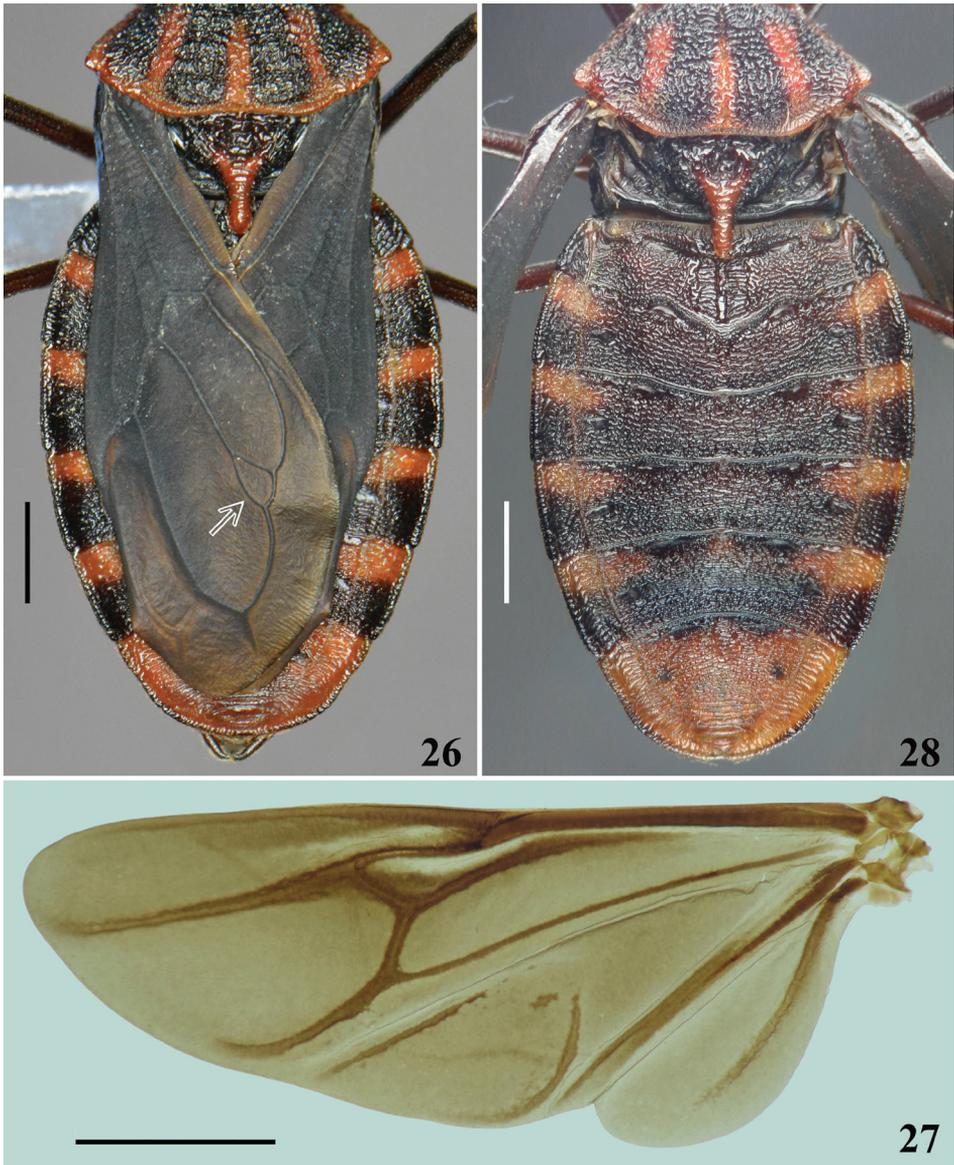
**Figures 14–19.** *Volesus nigripennis*, male, dorsal view **14** head, pronotum, scutellum and basal portions of hemelytra and connexivum **15–18** pronotum **15** median portion **16–17** fore lobe and basal portion of hind lobe **17** left side and midline **18** lateral right portion, including humeral angle **19** scutellum. Scale bars: 2.0 mm (**14**); 0.5 mm (**15–17, 19**); 0.3 mm (**18**).

elongated, with a lateral rounded enlargement just above inserted portion, moderately and strongly curved inwards at mid and apical portions, respectively, narrowing towards tip, which is somewhat rounded (Fig. 45) to acute (Fig. 46); with straight to moderately curved setae, more numerous towards apical portion; setae absent on



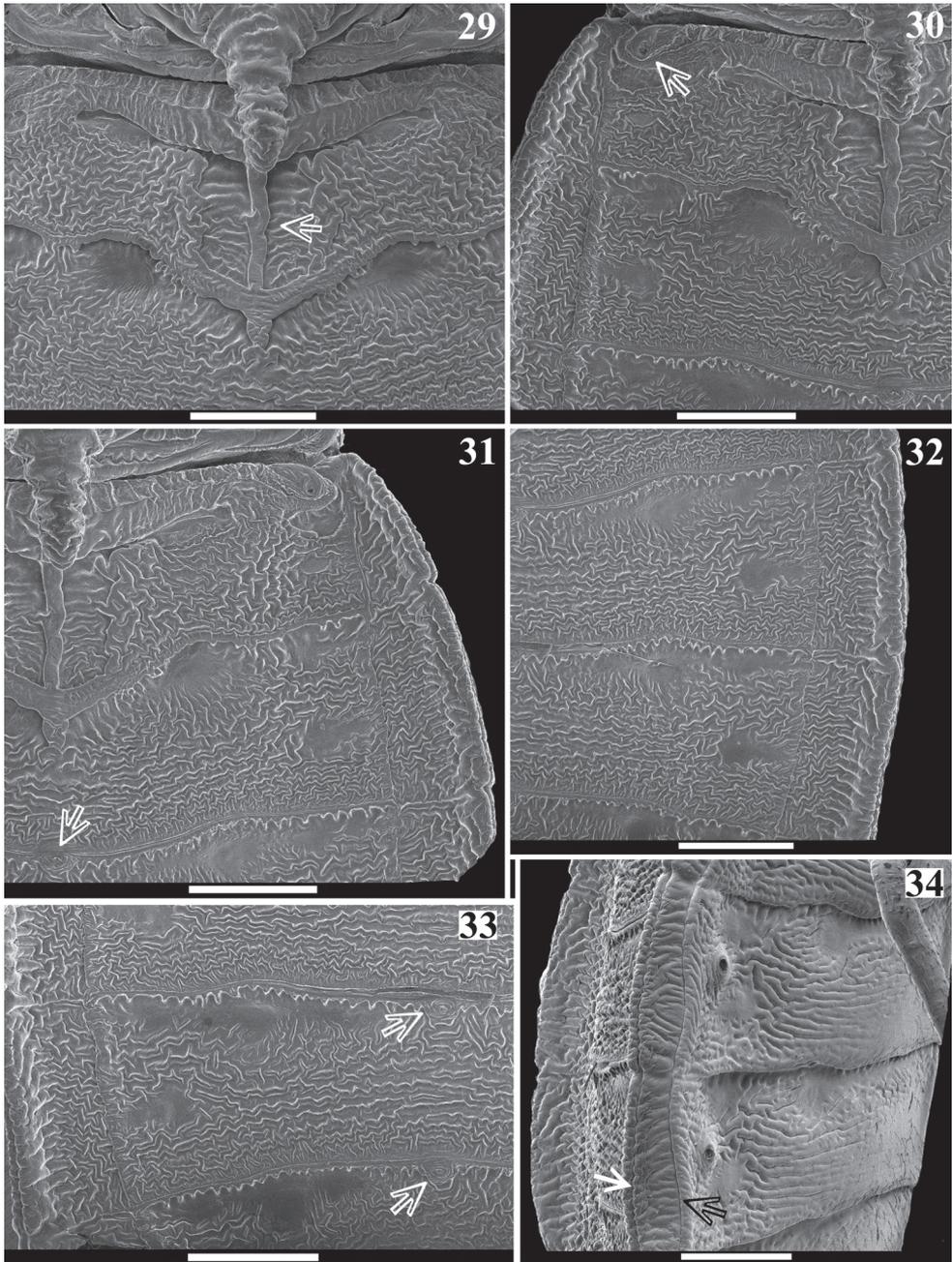
**Figures 20–25.** *Volesus nigripennis*, male **20–23** ventral view **20** head and thorax **21** prothorax, arrow points to prosternal process **22** prothorax and mesosternum **23** metasternum, middle and hind coxae, and median portion of base of abdomen **24, 25** apices of tibiae, arrow points to spongy fossa **24** fore tibia, ventral view **24** middle tibia, lateral view. Scale bars: 1.0 mm (**20, 23–25**) 0.5 mm (**21, 22**).

basal (inserted) portion and on inner surface of approximately basal fourth of the not inserted portion (Figs 40, 43, 45–46). Articular apparatus with moderately short basal plate arms (**bpa**); basal arms and basal plate bridge (**bpb**) forming a subtriangular set (Fig. 50); basal plate bridge (**bpb**) slightly bent ventrally (Fig. 50); pedicel (**pd**) elongated, somewhat enlarged at midportion, curved in lateral view (Figs 48, 49, 51, 52). Before inflation of the endosoma, a lateral oval area (**loa**) somewhat more

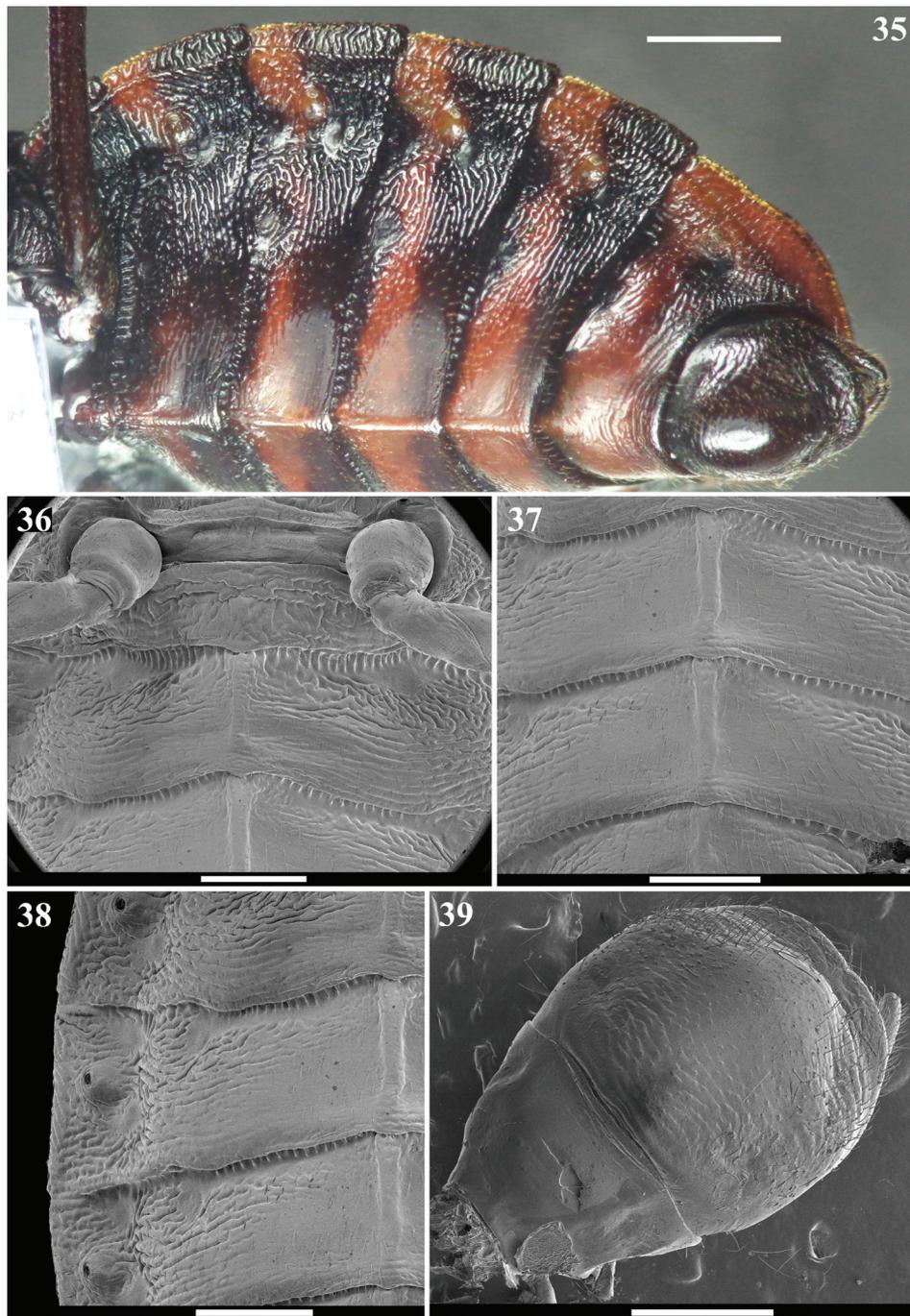


**Figures 26–28.** *Volesus nigripennis*, male, dorsal view **26** distal portion of pronotum, scutellum, hemelytra and connexivum, arrow points to a small additional cell at approximately apical fourth of the cubital vein **27** left hind wing **28** distal portion of thorax and abdomen (wings moved away). Scale bar: 2.0 mm.

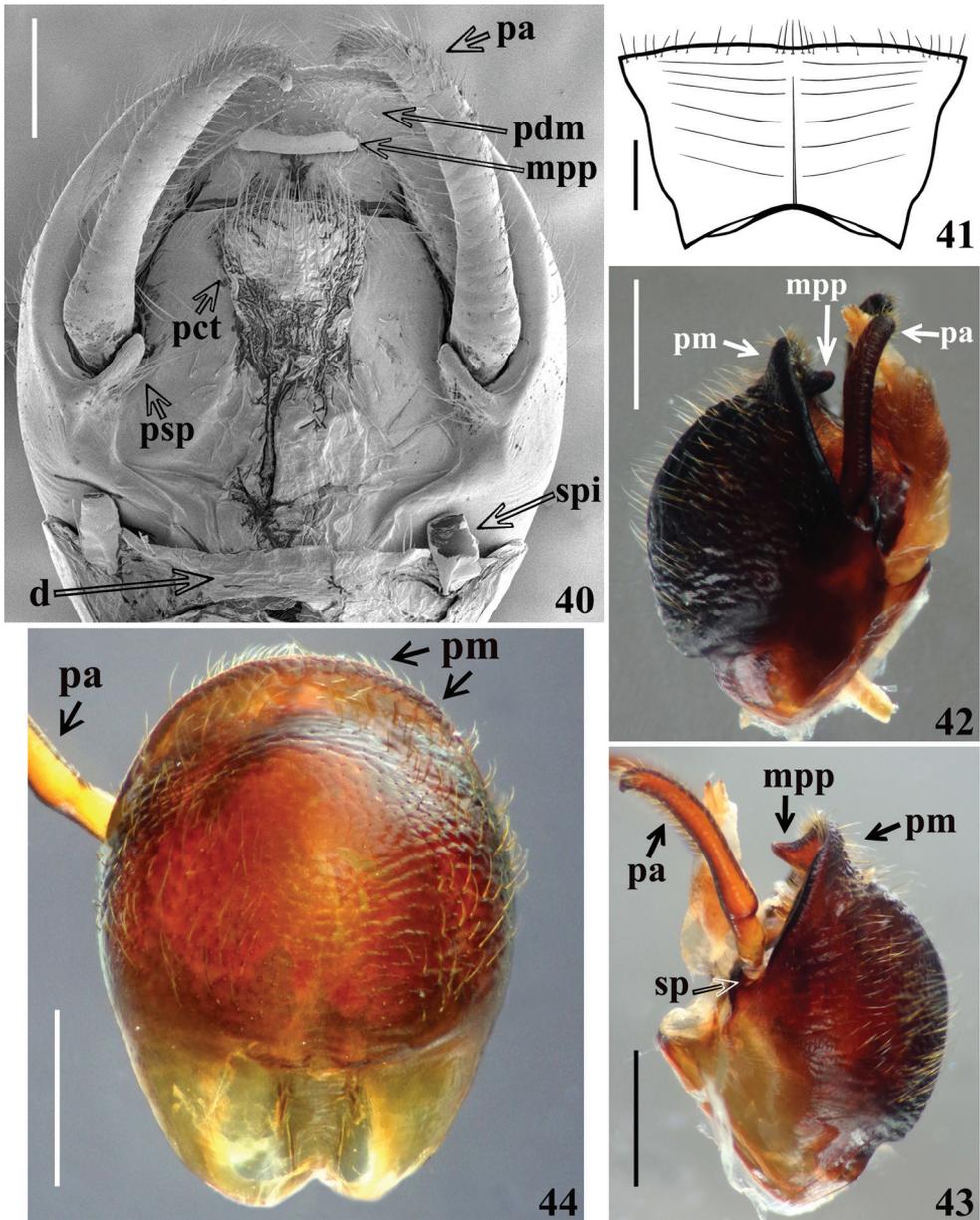
sclerotized on endosoma wall is evident (Figs 48–50) as well as a conspicuous dorsal pair of membranous lobes on endosoma (**mle**), united at their basal median portion which is inserted just above apex of dorsal phallothecal sclerite (**dps**) (Fig. 50). Each membranous lobe on endosoma (**mle**) is flattened, elongated, apex rounded, directed outwards, laterally to dorsal phallothecal sclerite (Figs 48, 50–52, 55). Dorsal phallothecal sclerite (**dps**) elongated, thrice curved in lateral view (Figs 51, 54); in dorsal



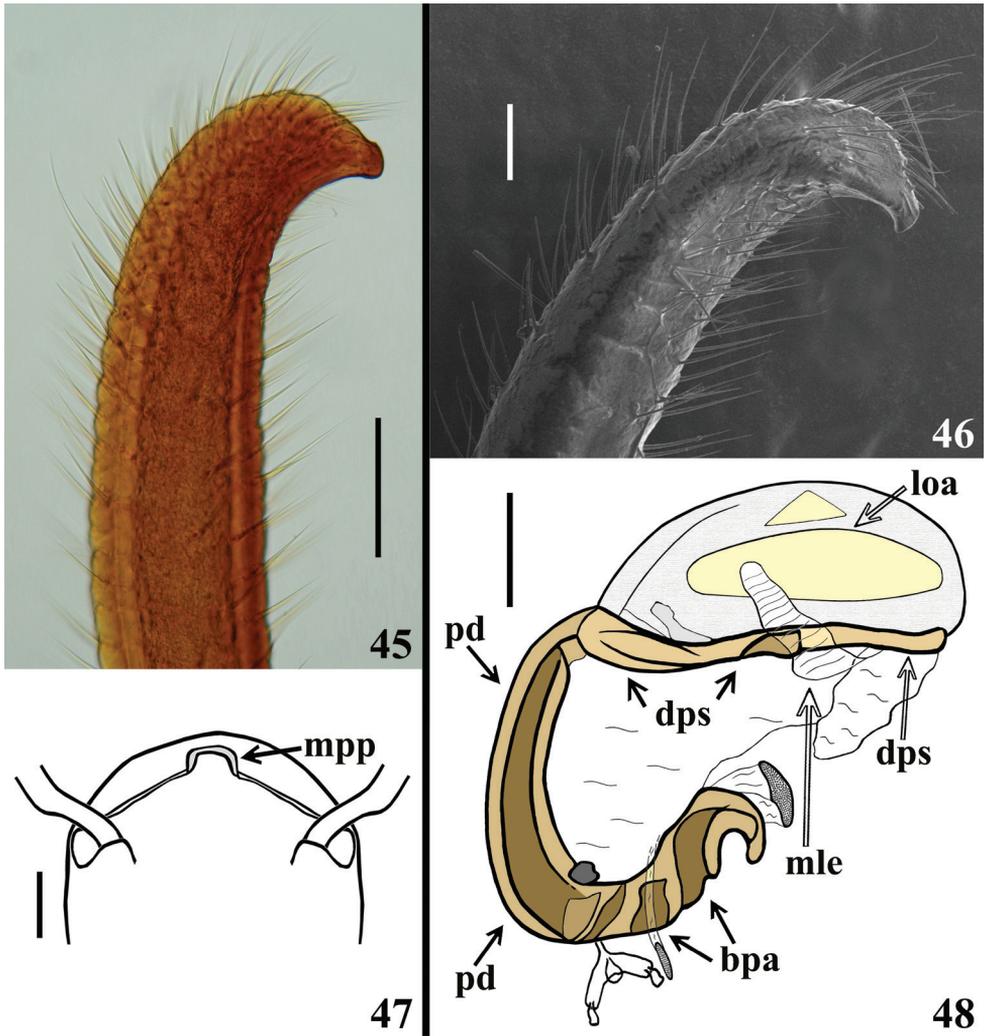
**Figures 29–34.** *Volesus nigripennis*, male **29–33** dorsal view **29** process of scutellum, median portions of tergites I–II and basal half of tergite III, arrow points to midlongitudinal keel of tergite II **30–31** mediolateral portions of tergites I–III **30** arrow points to first (dorsal) abdominal spiracle **31** arrow points to the **dag** on tergite IV **32** lateral portions of tergites III (distal part), IV–V **33** mediolateral portions of distal part of tergite IV, tergite V and basal part of tergite VI, arrows point to the **dag** on tergites V and VI **34** abdominal segments III–IV, lateral view, arrows point to the vertical sclerite of connexivum. (**dag** scar of dorsal abdominal gland opening). Scale bar: 1.0 mm.



**Figures 35–39.** *Volesus nigripennis*, male **35** abdomen, lateroventral view **36–39** ventral view **36** hind coxa, median portions of sternites II–III and basal portion of sternite IV **37** median portion of distal margin of sternite III, sternites IV–V and anterior margin of sternite VI **38** mediolateral portions of distal half of sternite III and sternites IV–V, except lateroposterior angle of the latter **39** segment VIII and genital capsule detached from abdomen. Scale bars: 2.0 mm (**35**); 1.0 mm (**36–39**).



**Figures 40–44.** *Volesus nigripennis*, male **40** distal half of segment VIII and genital capsule, dorsal view (**d** dorsal portion of segment VIII; **pct** proctiger; **pdm** posterior dorsal margin of pygophore; **psp** medial prolongation of the socket of the insertion of the paramere; **spi** spiracle of segment VIII) **41** segment VIII, ventral view **42, 43** genital capsule, lateral view **44** pygophore, ventral view. (**mpp** median process of pygophore; **pa** paramere; **pm** posterior margin of pygophore; **sp** socket of the insertion of the paramere. Scale bars: 0.5 mm (**40, 41**); 1.0 mm (**42–44**).



**Figures 45–48.** *Volesus nigripennis*, male genitalia **45, 46** apical portion of paramere, lateral view **47** apical portion of pygophore, anterior view (setae omitted). (**mpp** median process of pygophore) **48** phallus not inflated, lateral view. (**bpa** basal plate arm; **dps** dorsal phallothecal sclerite; **loa** lateral oval area; **mle** membranous lobe on endosoma; **pd** pedicel). Scale bars: 0.2 mm (**45**); 0.1 mm (**46**); 0.5 mm (**47, 48**).

view, it is narrower at approximately midportion and towards apical portion (Fig. 53); apical margin almost straight (Figs 50, 52, 53, 56); at its subapical enlarged portion there is a pair of symmetrical rounded flat lateral expansions (**fle**) (Figs 50, 52, 53). After inflation of endosoma, endosoma wall is smooth to longitudinally and transversely finely striated at approximately basal two thirds and coarsely rugose at distal third, with some areas in which the rugosities are more sclerotized (**ars**) (Figs 56, 57); endosoma wall forming three apical expansions: a median subrounded flat expansion (**mfe**) and a pair of lateral tubular short expansions (**lte**), each of the latter with a more sclerotized

thin longitudinal line along its length (**lsl**) (Figs 52, 57). Endosoma with the following processes: a pair of flat, somewhat sclerotized, asymmetrical and striated processes (**stp**) between apex of dorsal phallothecal sclerite and subapical process (**sbp**) (Fig. 56). The subapical process (**sbp**) provided with a pair of sclerotized arms, in which basal halves are shorter, diverge more and are formed by stronger sclerotizations of rugosities of wall, while distal half is somewhat longer, less diverging and formed by linear and aggregate thickenings (Figs 51, 52, 56, 57).

**Distribution.** Colombia, Costa Rica, Ecuador (**new record**), Panama (**new record**).

**Comments.** *Volesus nigripennis* is the first Sphaeridopinae recorded for Ecuador and Panama (Froeschner 1981, 1999, Maldonado 1990).

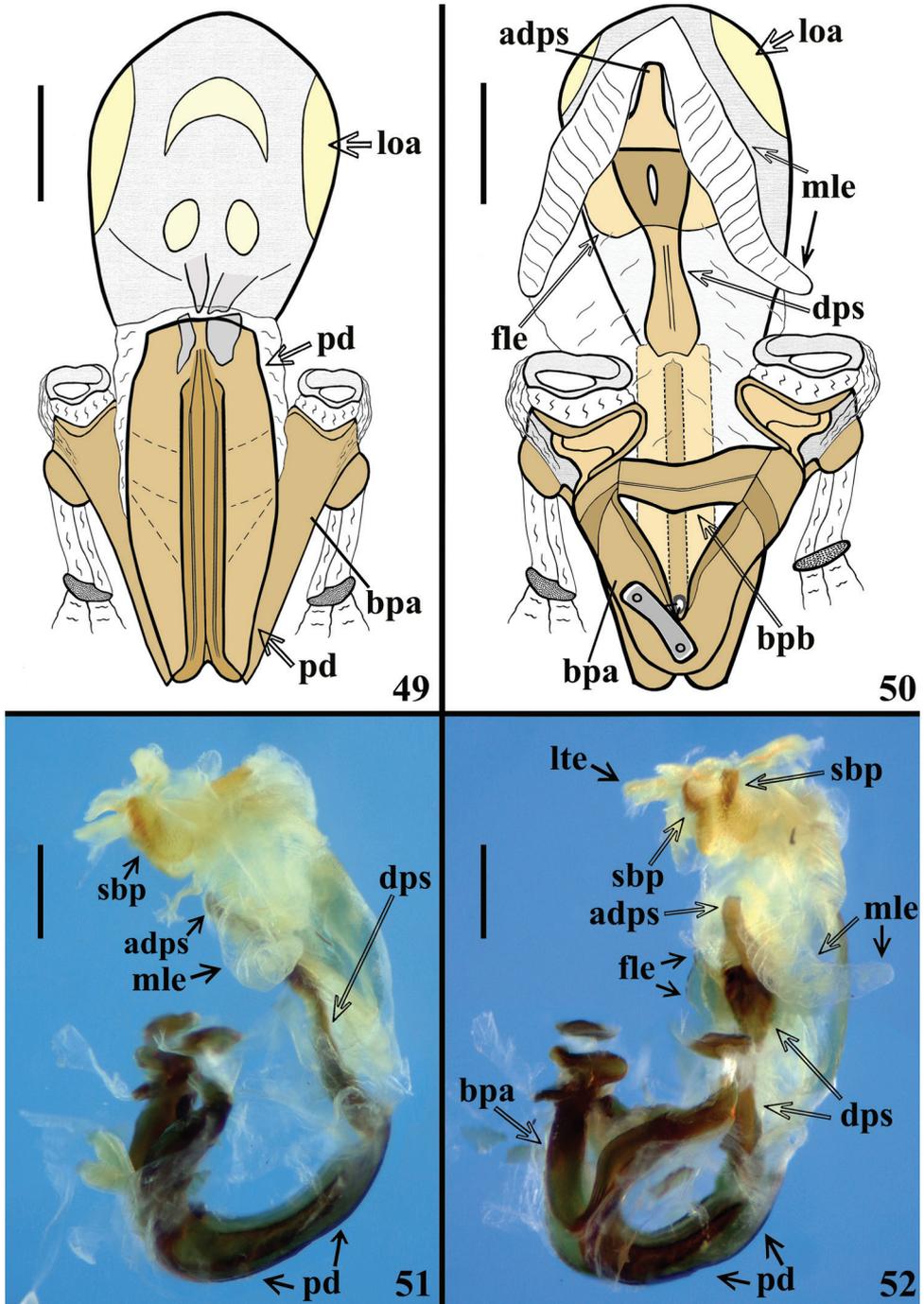
The male specimens (Figs 4, 5, 20, 35) described here seem to be generally similar to the female of the species in structure and coloration (Champion 1899, Forero 2006; Figs 1, 2). However, only the examination of more specimens of *V. nigripennis* will make it possible to ascertain whether there is sexual dimorphism.

Smooth areas on the fore lobe of pronotum were recorded here in *V. nigripennis* (Figs 6, 15–17) but it was not possible to distinguish a paired sensory organ similar to that described in *Sphaeridops eulus* by Maldonado and Santiago-Blay (1992: figs 13, 14). These authors emphasized that the nature of the sensory organ of these areas could be seen in their SEM images. However, judging by the SEM images obtained in the present study (Figs 15, 17), it is possible that the supposed sensory organ, also mentioned as present in both species of *Veseris* (Gil-Santana et al. 1999, Gil-Santana and Alencar 2001) may be in fact a portion of these smooth areas. Only future studies, preferably employing histological techniques will allow the evaluation of the existence and/or possible sensory functions of such portions in these species.

Although Champion (1899) had described that the labium would have the second and third visible labial segments equal in length, our studies, including the SEM images, made it clear that the labium is formed by only two visible segments, with the first visible segment short and enlarged and the other long, thin and straight (Figs 11, 12). It is opportune to mention that, according to our request, Dr Dimitri Forero kindly reexamined the female recorded by him from Colombia, sent us photos and confirmed these same features on the labial segments. Similarly, Dr Silvia A. Justi, when examining the female specimen from Panama, also verified that it had only two visible labial segments, with the same characteristics.

Some of the portions of the male genitalia of *V. nigripennis*, such as the parameres and articulatory apparatus, including a basal plate bridge bent ventrally (Figs 40, 45, 46, 50) seem similar to those recorded for species of *Veseris* (Gil-Santana et al. 1999, Gil-Santana and Alencar 2001).

Weirauch (2008) recorded the presence of the basal plate bridge (=ponticulus basilaris) bent ventrad and a pair of membranous lobes on endosoma, lateral to the dorsal phallothecal sclerite in *Sphaeridops amoenus* and *Salyavata nigrofasciata* Costa Lima, 1935 (Salyavatinae). Judging by her drawings, these lobes are smaller in *S. amoenus* and somewhat larger but shorter in *S. nigrofasciata*, respectively, than those recorded here in *V. nigripennis* (Figs 50–52). It is noteworthy that Weirauch (2008) considered both



**Figures 49–52.** *Volesus nigripennis*, male genitalia, phallus **49, 50** not inflated **49** ventral view **50** dorsal view **51, 52** inflated **51** lateral view **52** laterodorsal view. (**adps** apex of dorsal phallothecal sclerite; **bpa** basal plate arm; **bpb** basal plate bridge; **dps** dorsal phallothecal sclerite; **fle** flat lateral expansion; **loa** lateral oval area; **lte** lateral tubular short expansion; **mle** membranous lobe on endosoma; **pd** pedicel; **sbp** subapical process). Scale bar: 0.5 mm.



characteristics (a basal bridge bent ventrad and the pair of membranous lobes on the endosoma) as synapomorphies of the clade Salyavatinae + Sphaeridopinae obtained in her cladistic analysis.

On the other hand, because all other structures, such as those of phallus and endosoma, were not adequately recorded by the above-mentioned authors, nor by others who included just partial or incomplete descriptions of the male genitalia of species of *Sphaeridops* (e.g. Maldonado and Santiago-Blay 1992, Gil-Santana et al. 2000), only future comprehensive studies of these structures among Sphaeridopinae will allow useful comparisons with the results obtained here.

## Discussion

Based on historical evidence and contrary to several authors (e.g. Costa Lima 1940, Wygodzinsky 1949, Maldonado 1990, Forero 2004), we have followed Putshkov and Putshkov (1985) and attributed the authorship of Sphaeridopinae to Amyot and Serville (1843).

The presence of smooth areas on fore lobe of pronotum in between a rugose integument was also recorded in Triatominae, in which its integument “varies from smooth to granular; in many cases, smooth and granular sections occur side by side, forming a characteristic pattern” (Lent and Wygodzinsky 1979). These smooth areas may seem more prominent in Sphaeridopinae, because the surrounding integument is generally much more coarsely rugose.

An unusual characteristic of the group according to Maldonado and Santiago-Blay (1992), the dorsal and ventral components of connexivum well separated by a vertical sclerite, was also recorded to *Volesus nigripennis* (Fig. 34).

However, as commented above, the other alleged unusual characteristic of Sphaeridopinae (Maldonado and Santiago-Blay 1992), i.e., sensory organs on fore lobe of the pronotum, were not seen here in *V. nigripennis*; therefore, the presence of this feature needs more comprehensive studies among species of this group.

On the other hand, although the eyes of Sphaeridopinae have been considered large, almost covering the entire head, nearly contiguous ventrally (Pinto 1927, Maldonado and Santiago-Blay, 1992, Schuh and Slater 1995, Weirauch et al. 2014), this is not the case in *Volesus*. In the latter, the eyes are medium-sized, not covering the head and distant from each other ventrally (Figs 1, 2, 4–14, 20). In fact, the interocular distance is larger than the width of eye, dorsally, and approximately the same of it, ventrally.

Yet, although in the Sphaeridopinae the head had been considered without an anteoctular portion (Pinto 1927) or projecting only slightly beyond the anterior margin of eyes (Schuh and Slater 1995), the anteoctular portion in *Volesus* is longer, visibly projecting beyond the anterior margin of eyes for almost the same distance as the length of the eye (Figs 8, 11). Lastly, the presence of only two visible labial segments in *Volesus* (Figs 11, 12) is striking.

These dissimilarities between *Volesus* and other genera of Sphaeridopinae suggest that future studies including other species and more specimens, preferably with a phylogenetic approach, should be done in order to ascertain the set of features diagnostic of Sphaeridopinae.

In this case, it is worth mentioning that none of the phylogenetic studies which suggested that Sphaeridopinae would be a sister group to the genus *Salyavata* (Salyavatinae) (Weirauch 2008, Gordon and Weirauch 2016) had included *Volesus* in their analysis.

Therefore, possible future taxonomic changes involving these subfamilies, besides being based on cladistics studies, should also include specimens of *Volesus* to clarify its systematic position within Reduviidae.

In any case, the study of the male of *Volesus nigripennis* allowed for a better definition of the diagnostic characteristics to separate the genera currently considered as valid in Sphaeridopinae. Thus, a revised key to the genera of Sphaeridopinae is presented below.

### Key to the genera of Sphaeridopinae based on Stål (1865, 1872), Gil-Santana and Alencar (2001), Forero (2004) and Gil-Santana et al. (2015)

- 1 Length of second visible labial segment equal or subequal to first visible segment; prosternum with a large, rounded to subrounded median excavation. .... **Veseris Stål, 1865**
- Second visible labial segment approximately four to six times longer than first visible segment; prosternum without a rounded to subrounded excavation, but forming a median prolongation or process directed posteriorly for a variable extension between fore coxa..... **2**
- 2 Antenniferous straight apically; labium with only two visible segments; prosternum posteriorly shortly prolonged at midline, not surpassing level of posterior margin of fore coxae and continuous with adjacent sclerite..... **Volesus Champion, 1899**
- Antenniferous bifurcated apically; labium with three visible segments; prosternum variably prolonged posteriorly, forming a cylindrical median process which surpasses level of posterior margin of fore coxae for a variable extent, distinctly obliquely directed downwards and separated from adjacent sclerite..... **Sphaeridops Amyot & Serville, 1843**

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# Four new species of *Philoplitis* Nixon (Braconidae, Microgastrinae) with an updated key and illustrations of all described species

A.P. Ranjith<sup>1</sup>, J. Fernandez-Triana<sup>2</sup>, T. Veena<sup>3</sup>, D.R. Priyadarsanan<sup>4</sup>, M. Nasser<sup>1</sup>

**1** *Insect Ecology and Ethology Laboratory, Department of Zoology, University of Calicut, Kerala, Pin: 673635, India* **2** *Canadian National Collection of Insects, 960 Carling Ave., Ottawa, ON K1A 0C6, Canada* **3** *Department of Zoology, Malabar Christian College, Kozhikode (Affiliated to University of Calicut), 673001, Kerala, India* **4** *Ashoka Trust for Research in Ecology and the Environment, Bangalore, Karnataka, Pin: 560 064, India*

Corresponding author: *Jose Fernandez-Triana* ([jose.fernandez@canada.ca](mailto:jose.fernandez@canada.ca))

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## Abstract

The Microgastrinae genus *Philoplitis* Nixon is revised and four new species are described: *P. keralensis* **sp. n.** and *P. trifoveatus* **sp. n.** authored by Ranjith & Fernandez-Triana, and *P. dzangasangha* **sp. n.** and *P. margalla* **sp. n.** authored by Fernandez-Triana & Ranjith. A key to all nine known species is provided. *Philoplitis adustipalpus* Ahmad is redescribed and illustrated. Additional specimen records are presented, and the diagnostic value of some morphological characters previously used is discussed. Based on the very few specimens available for study in collections, *Philoplitis* seems to be restricted to the Old World tropics (Afrotropical and Oriental regions), with most known species found in the Oriental region. The first DNA barcodes for the genus are presented. No host data is currently available, but for one species a mass of five wasp cocoons was found and is illustrated for the first time.

## Keywords

Afrotropical, Oriental, Microgastrinae, *Philoplitis*, taxonomic revision

## Introduction

Microgastrinae is one of the most diverse and globally ubiquitous subfamilies of braconid parasitoid wasps, commonly encountered as pupae or prepupae encased in white silk cocoons on or near the dead or dying bodies of their host caterpillars. Species are the koinobiont endo-larval parasitoids of Lepidoptera (Quicke 2015). More than 100 species in this group have been used or investigated worldwide in the biological control of lepidopteran pests, and this total is likely to raise (Wharton et al. 1997).

Mason (1981) estimated that worldwide Microgastrinae comprises between 5,000 and 10,000 species; at present Microgastrinae contains 81 extant genera and 2,700+ extant species (Yu et al. 2016, Fernandez-Triana and Boudreault 2018). Rodriguez et al. (2013) estimated the species richness of microgastrines to be 8–10 times that of the ~2,000 species described at that time. The microgastrine fauna of India contains 231 species recorded within 21 genera so far (Gupta and Fernandez-Triana 2014). Recent studies show that there are many new distribution records like *Alloplitis* Nixon (Ranjith, unpublished) and many more species in both diverse and rare genera (Veena et al. 2014, Ranjith et al. 2015).

The genus *Philoplitis* Nixon was erected by Nixon (1965) and the species can be easily diagnosed by the large scutellum, which is prolonged posteriorly above the propodeum (Mason 1981). Fernandez-Triana and Goulet (2009) revised the genera, described three new species, and provided a key to all known species. The distribution of *Philoplitis* seems to be restricted to the Afrotropical and Oriental regions (Fernandez-Triana and Goulet 2009, current study). The hosts of *Philoplitis* species are still unknown.

Here we describe four new species from the Old World tropics, redescribe *Philoplitis adustipalpus* Ahmad, present additional records for some species, and discuss the diagnostic value of some morphological characters previously used.

## Materials and methods

We examined the specimens from various type repositories including the Centre for Biodiversity Genomics, University of Guelph, Canada (**BIOUG**), the Canadian National Collection of insects, Canada (**CNC**), the National Museum of Natural History, USA (**NMNH**), and the collection of the Zoology Department, Aligarh Muslim University, Uttar Pradesh, India (**ZDAMU**). Morphological terms and wing venation designations follow Huber and Sharkey (1993), Sharkey and Wharton (1997), Karlsson and Ronquist (2012), and Fernandez-Triana et al. (2014). The abbreviations F2 and F15 refer to antennal flagellomeres 2 and 15; T1, T2, and T3 are used for metasomal mediotergites 1, 2 and 3; and L and W refer to length and width, respectively. Calculation of wing vein ratios follows Fernandez-Triana and Goulet (2009). The terms for integument sculpture follow Harris (1979). Primary types are deposited in Department of Zoology, University of Calicut, Kerala, India (**DZUC**) and the CNC.

Indian specimens studied by the first author were treated with Hexamethyldisilazane (HMDS) in order to prevent collapsing during mounting. Specimens were imaged using an Leica M205A microscope with automated multiple image capture at preset focal levels using an Leica DFC 500 camera, and image combination using the Leica Application Suite (V4.7) image processing system. All images were edited using Photoshop CS8 (Version 6.1) (Adobe Inc.) for the removal of image artifacts and standardizing the background colour.

All specimens studied from BIOUG and CNC material (African and Oriental regions) were critical point dried, and imaged with a Keyence VHX-1000 Digital Microscope, using lens with a range of 10–130 $\times$ . Multiple images were taken of a structure through the focal plane and then combined to produce a single in-focus image using the software associated with the Keyence System. Images were corrected using Adobe Photoshop CS4, and plates were prepared using Microsoft PowerPoint 2010 and later saved as .tiff files.

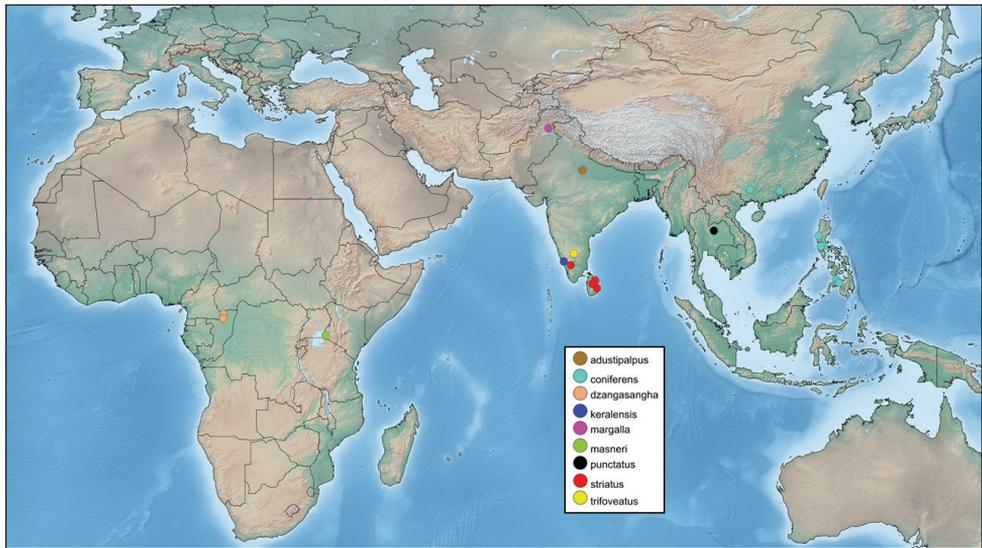
A distribution map of all known species of *Philoplitis* was made using Simplemappr (<https://www.simplemappr.net>).

## Results

With the four new species described below, the total number of known *Philoplitis* almost doubles, from five (Fernandez-Triana and Goulet 2009) to nine in this paper. It is likely that a few more species are found in the future, especially when the fauna of the Afrotropical and Oriental regions is more comprehensively collected and studied. Still, this genus is not likely to be very specious, and the specimens seem to be very rarely collected. Indeed, most of the species are known from one or very few specimens in collections (Table 1), despite of hundreds of microgastrinae specimens collected in some of the localities where *Philoplitis* specimens have been found so far.

**Table 1.** Described species of *Philoplitis* with their known geographical distribution (by biogeographical region and country), and the number of specimens in collections. Data from Nixon (1965), Mason (1981), He (1983), Ahmad et al. (2005), Fernandez-Triana and Goulet (2009), and present paper.

<i>Philoplitis</i> species	Known distribution as Biogeographical region: Countries	Number of known specimens
<i>P. adustipalpus</i> Ahmad, 2005	Oriental: India	2 female
<i>P. coniferens</i> Nixon, 1965	Oriental: Philippines, China	12+ female and male
<i>P. dzangasangha</i> Fernandez-Triana & Ranjith, sp. n.	Afrotropical: Central African Republic, Republic of Congo	5 male, 1 female
<i>P. keralensis</i> Ranjith & Fernandez-Triana, sp. n.	Oriental: India	1 female, 1 male
<i>P. margalla</i> Fernandez-Triana & Ranjith, sp. n.	Oriental: Pakistan	2 female, 1 male
<i>P. masneri</i> Fernandez-Triana & Goulet, 2009	Afrotropical: Kenya	1 male
<i>P. punctatus</i> Fernandez-Triana & Goulet, 2009	Oriental: Thailand	1 female, 4 male
<i>P. striatus</i> Fernandez-Triana & Goulet, 2009	Oriental: India, Sri Lanka	4 female, 3 male
<i>P. trifoveatus</i> Ranjith & Fernandez-Triana, sp. n.	Oriental: India	1 female



**Figure 1.** Distribution of known species of *Philoplitis*.

Based on current data, the genus seems to be restricted to the Old World tropics, with the majority of the species being found in the Oriental region and two species in the Afrotropics (Fig. 1). No host data is known at present but for one species, *P. keralensis* Ranjith & Fernandez-Triana, sp. n., a mass of five wasp cocoons was found associated with an unidentified lepidopteran larvae and is here illustrated for the first time (Fig. 8). We suspect other species of *Philoplitis* may be gregarious as well.

Seven sequences (DNA barcodes) are available in the Barcode of Life Data System (BOLD), representing three of the nine described species (Suppl. material 1, Supplementary Appendix 1). Those sequences are grouped in four Barcode Index Numbers (for details on the BIN system see Ratnasingham and Hebert 2013). The current BINs representing *Philoplitis* are: BOLD:AAW0954, BOLD:AAZ9051, BOLD:ACA6591, and BOLD:ACP5254 ([http://www.boldsystems.org/index.php/Public\\_BINSearch?query=Philoplitis&searchBIN=Search+BINs](http://www.boldsystems.org/index.php/Public_BINSearch?query=Philoplitis&searchBIN=Search+BINs)). The DNA barcodes of *Philoplitis* are very distinct, and cluster fairly separated from 35,000+ sequences of other microgastrines available in BOLD.

Future work should focus on better morphological characterization of the species, as the majority have been described from and/or are currently known from very few specimens (Table 1). Fernandez-Triana and Goulet (2009) put too much emphasis on the relative proportions of the fore wing veins near the areolet, but those proportions may be found to vary when more specimens become available. We have found that color of palpi and metatibia spurs, sculpture of head near occipital carina, and metafemur L/W ratio seem to have more diagnostic value than vein proportions in the fore wing. But we also caution that if/when more specimens become available, the value of those characters may also need to be reassessed.

**Key to *Philoplitis* species**

- 1 Metatibial spurs dark brown to black in both male and female specimens (Fig. 11A); scutellar disc (Figs 11D–F) comparatively shorter (length 1.00–1.10 × its width at anterior margin); fore wing with vein r from slightly less to about same length than vein r-m (Fig. 11C) [Thailand] ..... ***Philoplitis punctatus* Fernandez-Triana & Goulet, 2009**
- Metatibial spurs white, yellow or yellowish-brown in female specimens (and males of all species but one) (Figs 2A, 3D, 5A, 5B, 6A, 9A, 10A, 12A, 13A, 14A); scutellar disc comparatively longer (length at least 1.20 × its width) (Figs 2D, 4A, 5F, 6D, 9G, 10B, 12G, 13B, 14D, 15B); fore wing with vein r much longer than vein r-m (Figs 5B, 7B, 12A, 12C, 13A, 14A) ..... **2**
- 2 Anteromesoscutum with coarse punctures along anterior and lateral margins (Fig. 9G); male specimens with metatibial spurs dark brown to black [Pakistan] ..... ***Philoplitis margalla* Fernandez-Triana & Ranjith, sp. n.**
- Anteromesoscutum without coarse punctures along anterior and lateral margins, but sometimes with impressed sculpture postero-laterally (Figs 2D, 3B, 4A, 5F, 6D, 7A, 10B, 14D); male specimens with metatibial spurs white or yellow ..... **3**
- 3 Maxillary and labial palpi entirely yellow (Fig. 5E); pro- and mesocoxae yellow (Figs 5B, 5E); antennal flagellomeres yellow-brown (Fig. 5A); T2 with raised, median, polished field (Fig. 5D); impressed area behind posterior ocelli (Fig. 5F) mostly smooth and relatively very wide, as wide as distance between two posterior ocelli [Central African Republic] ..... ***Philoplitis dzangasangha* Fernandez-Triana & Ranjith, sp. n.**
- Maxillary and labial palpi partially (Figs 10D, 12B) to entirely reddish-brown to dark brown (Figs 2B, 2C, 3A, 6B, 6C, 14B, 15A, 15B); all coxae either reddish, dark brown or black (Figs 2F, 3A, 3D, 6A, 6C, 10A, 12A, 14A, 15A); antennal flagellomeres dark brown to black; T2 without raised median field (Figs 3C, 4B, 6F, 10C, 15C), if (rarely) median field is visible, then it is striated (Fig. 13D); impressed area behind posterior ocelli partially to entirely striate and relatively less wide, narrower than distance between two posterior ocelli (Figs 10E, 12G, 16A–D) ..... **4**
- 4 Metatibial spurs white; scutellum slightly truncate apically (Fig 10E); notauli comparatively less impressed (Fig. 10B); T2 comparatively less transverse, its medial length 0.80 × its width at posterior margin (Fig. 10C) [Kenya] ..... ***Philoplitis masneri* Fernandez-Triana & Goulet, 2009**
- Metatibial spurs yellow or yellowish-brown; scutellum longer and not truncate (Figs 2D, 4A, 6D, 13B, 14D, 15B); notauli comparatively deeply impressed (Figs 4A, 6D, 12D, 13B, 14D); T2 comparatively more transverse, its medial length less than 0.50 × its width at posterior margin (Figs 3C, 4B, 6E, 6F, 13D, 15C) ..... **5**
- 5 T2 dark brown, transversely striate medially and longitudinally striate latero-apically (Figs 12F, 13D); T1 length less than 1.80 × its apical width [India, Sri Lanka] ..... ***Philoplitis striatus* Fernandez-Triana & Goulet, 2009**
- T2 yellowish-white or yellowish brown and almost completely smooth (Figs 3C, 4B, 6E, 6F, 15C); T1 length more than 2.00 × its apical width ..... **6**

- 6 Body color mostly reddish-brown (Figs 2, 3); T1 length  $2.20 \times$  its apical width; T2 with medial length more than  $0.40 \times$  its width at apex; palpi usually brown or light brown with apical segments yellowish .....7
- Body color mostly black (Figs 6, 14, 15); T1 length more than  $2.20 \times$  its apical width; T2 with medial length less than  $0.40 \times$  its width at apex; palpi brown.....8
- 7 F2 L/W  $2.30 \times$  and F15 L/W  $2.70 \times$ ; maxillary palps 3–5 yellowish-white; notauli deeply impressed (Fig. 4A); tarsal claw with 2–3 teeth; T1 without shallow longitudinal groove, apically orange-yellow (Fig. 4B); T2 with median zone outlined by shallow and quite divergent grooves (Fig. 4B) [Philippines and southeastern China] .....***Philoplitis coniferens* Nixon, 1965**
- F2 L/W  $3.00 \times$  and F15 L/W  $1.90 \times$ ; maxillary palps 3–5 dark brown (Fig. 3A); notauli faintly impressed (Figs 2D, 3A); tarsal claw with one tooth; T1 with distinct shallow longitudinal groove extending beyond middle of the tergite, apically yellow (Fig. 2F); T2 without median zone outlined by shallow and quite divergent grooves (Fig. 3C) [India].....***Philoplitis adustipalpus* Ahmad, 2005**
- 8 Occiput medially with three pits right above and before occipital carina (Fig. 16 C); mesopleuron impressed medially (Fig. 14C); fore wing infuscated only beneath pterostigma (Figs 14A, 15C); fore wing with length of vein r  $1.00 \times$  length of vein 3RSa, and length of vein 3RSa  $1.10 \times$  length of vein 2M (Figs 14A, 15C); tarsal claw with one tooth; metafemur length  $3.40 \times$  its maximum width; T1 with longitudinal groove extending beyond half of tergite (Fig. 14F); T2 orange-brown (Fig. 15C) [India] ....***Philoplitis trifoveatus* Ranjith & Fernandez-Triana, sp. n.**
- Occiput medially with one pit right above and before occipital carina (Fig 16B); mesopleuron not impressed medially (Fig. 6C); fore wing infuscated throughout beneath pterostigma (Figs 6A, 7B); fore wing with length of vein r  $1.60 \times$  length of vein 3RSa, and length of vein 3RSa  $0.47 \times$  length of vein 2M (Figs 6A, 7B); tarsal claw with two teeth; metafemur length  $3.70 \times$  its maximum width; T1 with longitudinal groove not extending beyond half of tergite (Fig. 6E); T2 yellow (Figs 6E, 6F) [India] .....  
.....***Philoplitis keralensis* Ranjith & Fernandez-Triana, sp. n.**

## Species descriptions and notes

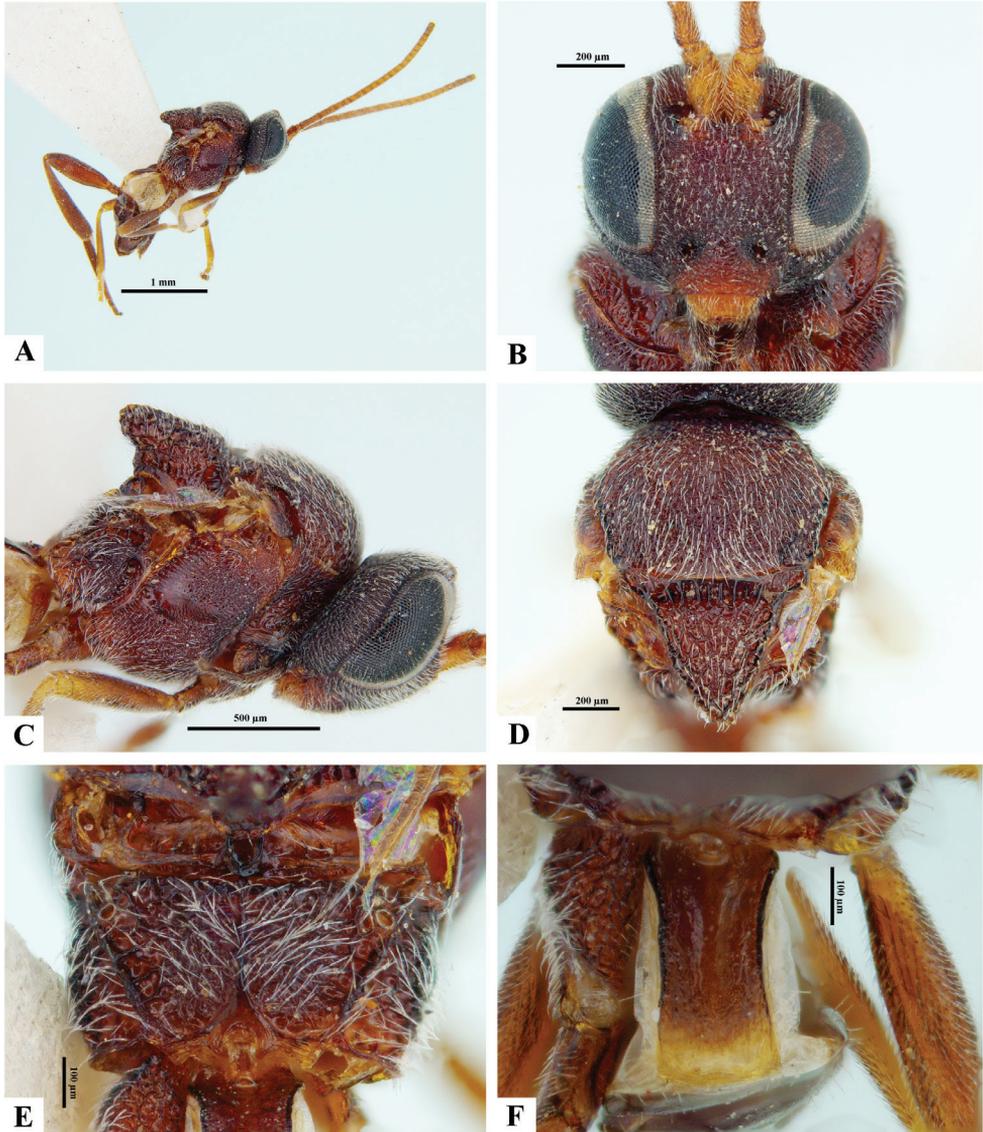
### ***Philoplitis adustipalpus* Ahmad, 2005**

Figs 2–3, 16A

*Philoplitis adustipalpus* Ahmad, 2005: 1736, original description.

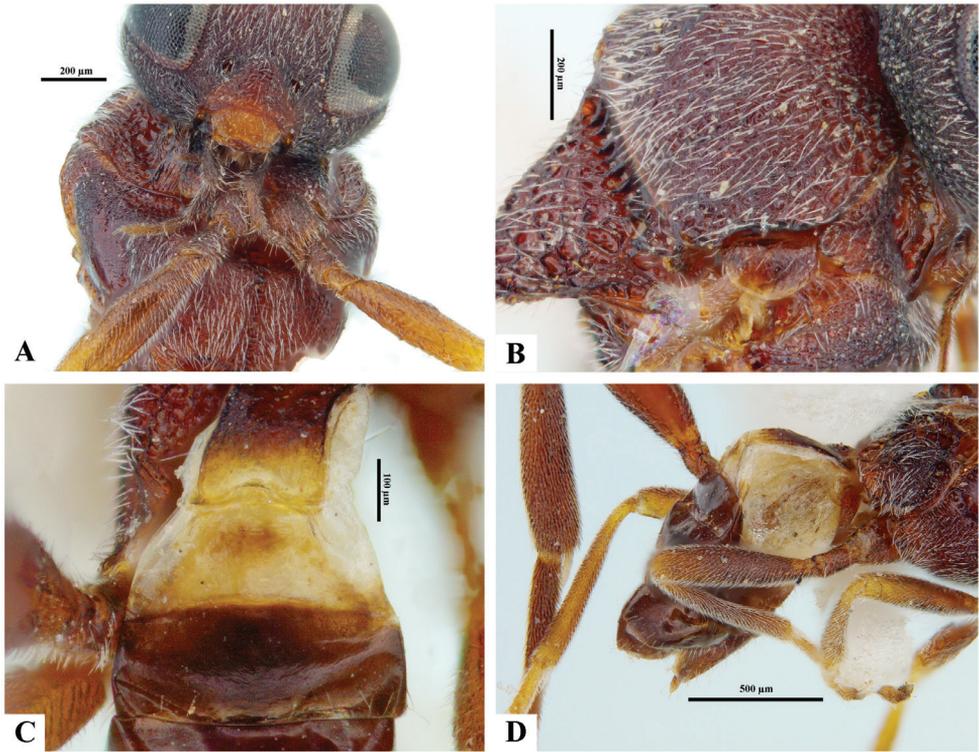
**Material examined. Holotype:** Female, INDIA (ZDAMU). Holotype locality: India, Uttar Pradesh, Etawah, 13.iv.2002, M Shamim leg.

**Diagnosis.** *Philoplitis adustipalpus* is similar to *P. coniferens* Nixon by its body colour, but it can be distinguished by having mesopleuron mostly rugose (punctate in *P. coniferens*), and metatibial spurs whitish yellow (orange-yellow in *P. coniferens*).



**Figure 2.** *Philoplitis adustipalpus*, female holotype **A** habitus, lateral view **B** head, frontal view **C** head and mesosoma, lateral view **D** mesosoma, dorsal view **E** propodeum, dorsal view **F** metasomal tergite I, dorsal view.

**Redescription.** Head distinctly rugose, frons transversely striated. Occipital carina strongly defined and crenulate. Moderately smooth and shiny area centrally between posterior ocelli and occipital carina. Antennae long, L of F2  $3.00 \times$  its W, L of F15  $1.90 \times$  its W. Mesosoma mostly covered with silver setae. Anteromesoscutum coarsely rugose. Notauli faintly impressed with impressed postero-lateral area above tegula. Scutellar disc L/W ratio  $1.20 \times$ , and its length  $0.80 \times$  that of anteromesoscutum. Mes-



**Figure 3.** *Philoplitis adustipalpus*, female holotype **A** head and mesosoma, ventral view **B** mesosoma, oblique view **C** metasomal tergites 2, 3, dorsal view **D** metasoma, lateral view.

opleuron rugose anteriorly, smooth to sparsely punctate medially, rugose posteriorly with a median, smooth area centrally. Metapleuron rugose. Propodeum rugose with complete, medial longitudinal carina, lateral carinae forming crenulations. Tarsal claws with one tooth and with arolium subequal to claw length. Metafemur L  $3.47 \times$  its maximum width. Inner spur of metatibia  $0.39 \times$  L of first metatarsomere. T1 finely striate, slightly emarginate medially with smooth triangular area medio-apically, T1 with shallow, median longitudinal groove extending beyond half of tergite length, T1 L  $2.20 \times$  its W at posterior margin. T2 smooth, medial zone outlined by divergent carinae on either side, T2 medial L  $0.47 \times$  its W at posterior margin. T3+ smooth, sparsely setose.

**Colour.** Head reddish brown, clypeus reddish brown, mandibles brown, palpi brown, antennae yellowish brown, gena laterally black, mesosoma reddish brown with silver pubescence, tegula brown, procoxa and protrochanter brown, profemur brown basal half apically yellow, protibia and protarsomeres yellow, mid leg and hind leg brown, metatibial spurs whitish yellow, metasoma dark brown, T1 black laterally, apically yellow, T2 yellow with light brownish area medially, laterotergites 1 and 2 yellowish white.

**Male.** Unknown.

**Distribution.** India (Uttar Pradesh).

***Philoplitis coniferens* Nixon, 1965**

Fig. 4

*Philoplitis coniferens* Nixon, 1965: 267, original description.

**Notes.** This species was redescribed and diagnosed by Fernandez-Triana and Goulet (2009). Here we report additional specimens (2 females, 4 males) from a different locality in Philippines, Cavite, Maragondon, 14°15.97'N 120°42.71'E, iv-v.2011, Malaise trap, H Ngo leg. (CNC).

***Philoplitis dzangasangha* Fernandez-Triana & Ranjith, sp. n.**

<http://zoobank.org/3EFD60B4-54DC-40B7-9E4D-60E9A4D0DABF>

Fig. 5

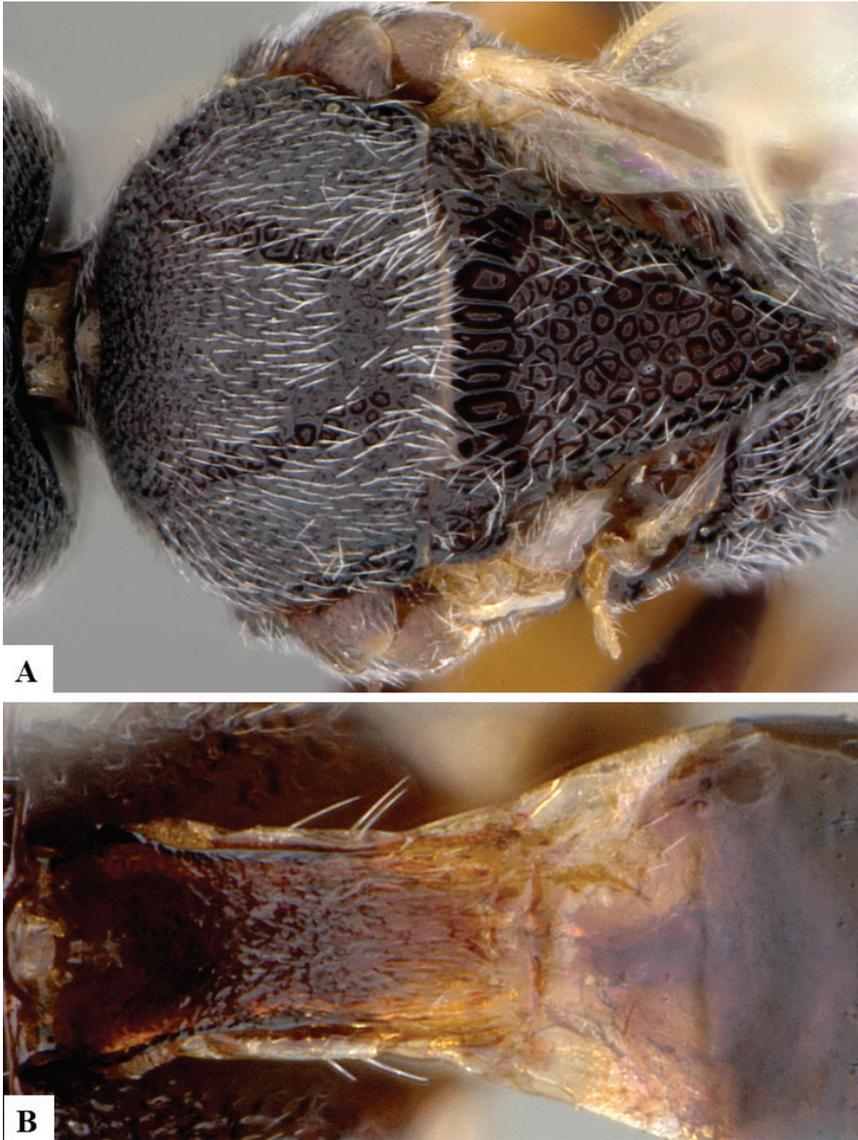
**Holotype.** Male, CENTRAL AFRICAN REPUBLIC (CNC). Holotype locality: Central African Republic, Dzanga-Sangha Reserve, 2°55'N 16°15'E, 320 m, 5-16.vii.1998, Malaise trap, J Carpenter & J Wensel leg.

**Paratypes.** Four males, REPUBLIC OF THE CONGO (CNC), Sangha province, Bomassa, 2.2105 16.1929, 365 m, mixed forest with *Maranthaceae* sp., 30.x.2012, Cysquet, Darlina & Lyenguet leg.

**Non type material examined.** One female, same locality and collecting date than paratypes.

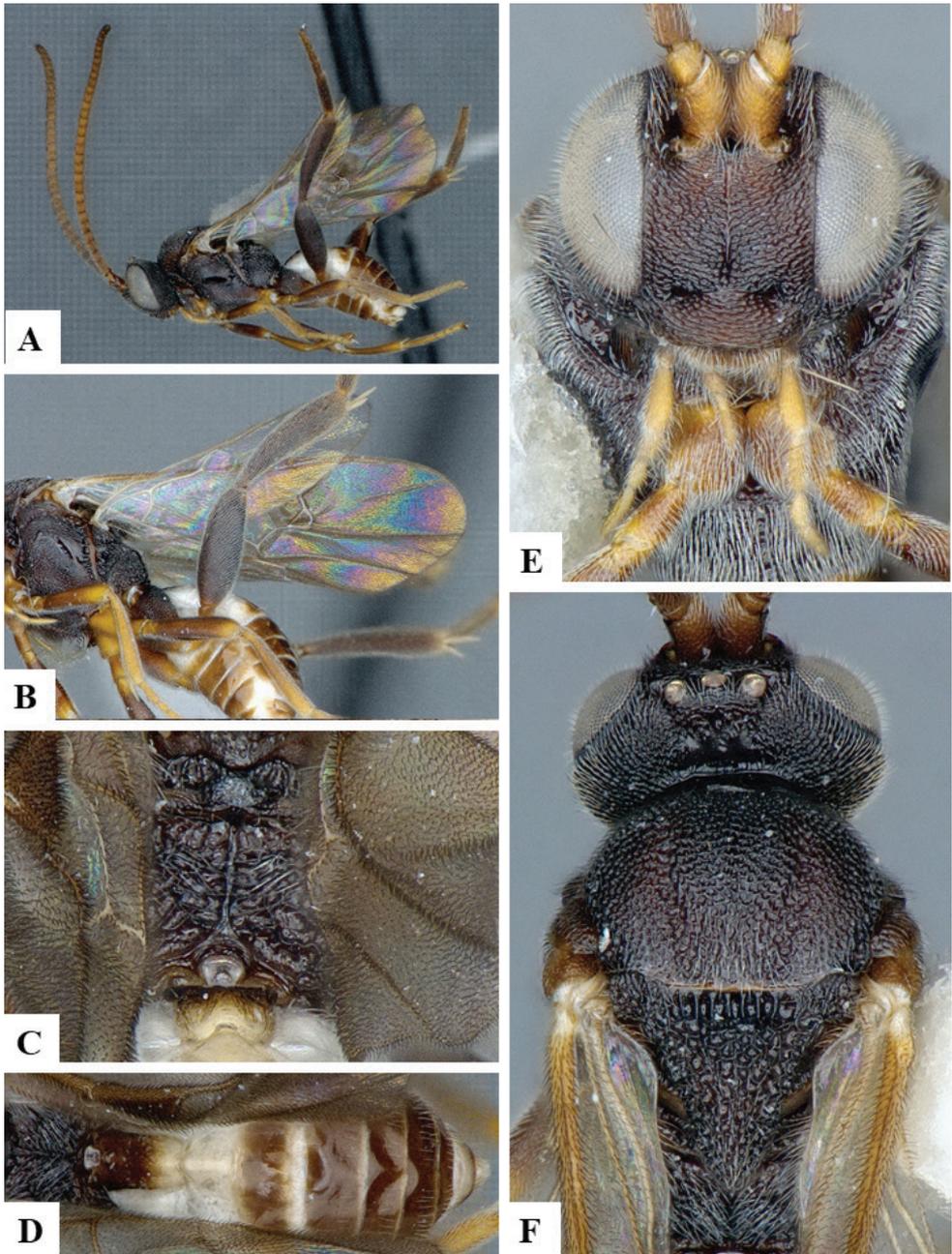
**Diagnosis.** *Philoplitis dzangasangha* sp. n. differs from all other species by its generally lighter coloration with palpi, pro- and mesocoxae yellow, and flagellomeres light brown.

**Description.** Head distinctly rugose. Frons transversely striate, with a median, longitudinal carina. Occipital carina strongly defined and crenulate. Smooth and shiny area centrally between posterior ocelli and occipital carina. Antennae longer than body length, L of F2 2.50 × its W, L of F15 3.00 × its W. Mesosoma mostly covered with silver setae. Anteromesoscutum coarsely rugose. Notauli deeply impressed, and with impressed postero-lateral area above tegula. Scutellar disc coarsely rugose, more or less straight in lateral view. Scutellar disc L/W ratio 1.20 ×, and its L 0.80 × that of anteromesoscutum. Mesopleuron mostly rugose or striate, but with median, smooth area centrally. Meta-pleuron rugose. Propodeum rugose with complete mid longitudinal carina. Fore wing ratios, r/3RSa: 2.00 ×; r/r-m: 2.80 ×; r/2RS: 1.00 ×; 3RSa/2M: 1.10 ×; 2RS/2M: 0.90 ×; r-m/2M: 0.60 ×; r/(r-2M): 0.51 ×; height of second sub marginal cell/(r-2M): 0.33 ×. Tarsal claws with one tooth and with arolium longer than claw length. Metafemur L 3.20 × its maximum width, inner spur of metatibia 0.54 × L of first metatarsomere. T1 mostly sculptured on posterior 0.7 (anterior 0.3 mostly smooth), T1 with shallow, median longitudinal groove extending half of tergite length, T1 L 3.00 × its width at posterior margin. T2 smooth, subtriangular, poorly defined by divergent grooves (grooves only distinct on anterior half of T2 length), T2 medial L 0.50 × its W at posterior margin (but that value is approximate as W at posterior margin is not clearly defined by the grooves). T3+ smooth.



**Figure 4.** *Philopltis coniferens*, female **A** mesosoma, dorsal view **B** metasomal tergites 1–3, dorsal view.

**Colour.** Head and mesosoma dark brown to black; scape and pedicel yellow; flagellomeres light brown; palpi yellow; pro- and mesocoxae yellow; pro- and mesofemorae and protibia yellow, mesotibia partially brown and partially yellow; hind legs mostly dark brown (except for trochanter and trochantellus yellow); metatibial spurs light yellow; most wing veins light yellow to transparent, except for pterostigma surrounding veins (r, 2RS, 3RSa, r-m, 2M, R1) which are brown; area beneath pterostigma very light brown, slightly darker than rest of wing and forming a cloud that extends to vein



**Figure 5.** *Philoplitis dzangasangha*, male holotype **A** habitus, lateral view **B** wings and part of meso- and metasomae, lateral view **C** propodeum (partially), dorsal view **D** metasoma, dorsal view **E** head, frontal view **F** head and mesosoma, dorsal view.

2M; metasoma dorsally mostly brown, except for posterior 0.2 of T1 and entire T2 which are yellow-white; laterotergites 1–3 yellowish white, rest mostly brown.

**Female.** Unknown, but see Notes below.

**Distribution.** Central Africa Republic, Dzanga Sangha Reserve.

**Etymology.** Named after the type locality, part of the important Dzanga Sangha Protected Area Complex, as recognition of the value that complex has to protect the biodiversity of central Africa.

**Notes.** Among the specimens we studied there was a female collected on the same place and date than the paratypes; however, some morphological characters are different. With so few specimens available it is not possible at the time to conclude if the female belongs to the same species or a different one. For the time being we prefer to keep within the species, although we did not include it as a paratype.

***Philoplitis keralensis* Ranjith & Fernandez-Triana, sp. n.**

<http://zoobank.org/E075CF20-808E-4E98-AAB0-FB7AA5AADAFFD>

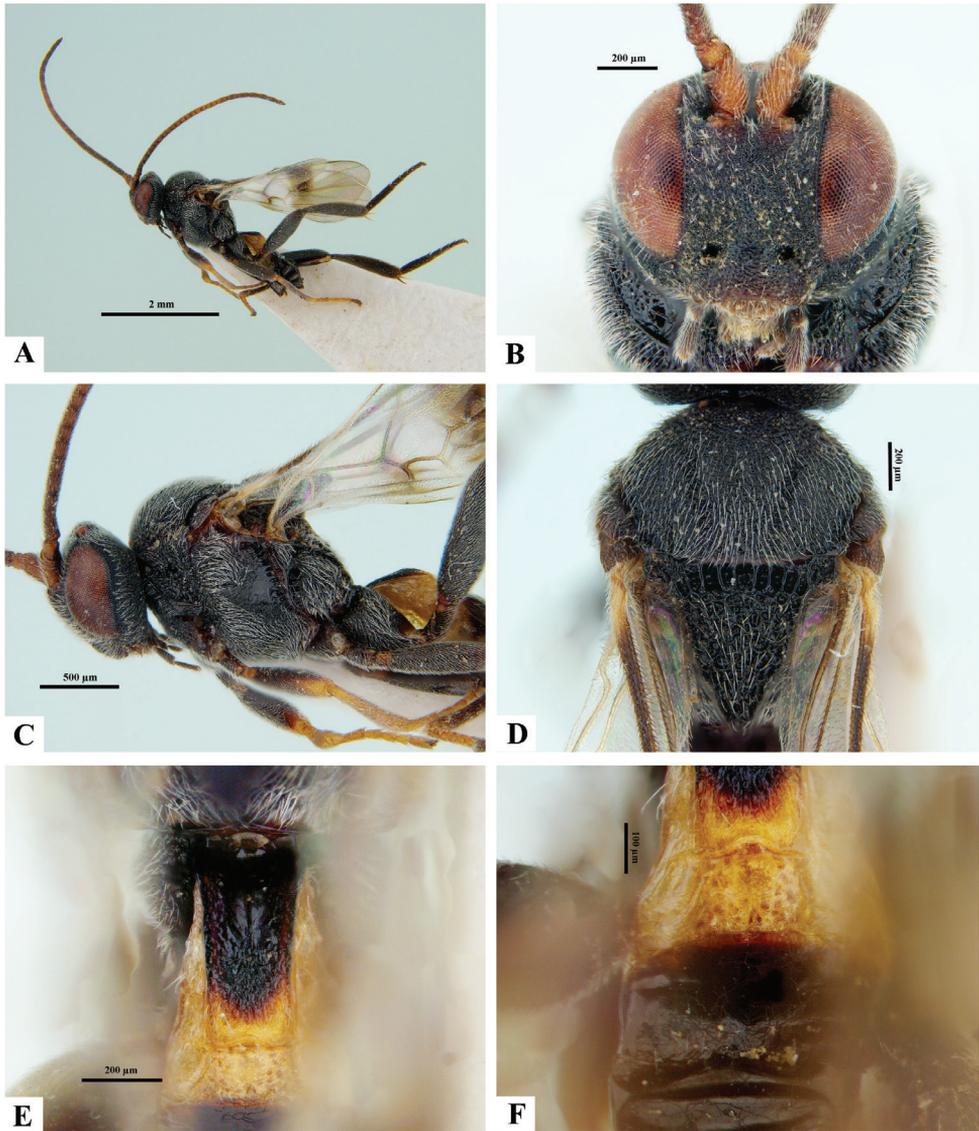
Figs 6–8, 16B

**Holotype.** Female, INDIA (DZUC). Holotype locality: Kerala, Kozhikode, Janakikadu, 31.v.2013, T Veena leg.

**Paratype.** One male, same data than holotype, except 21.v.2013, AP Ranjith leg.

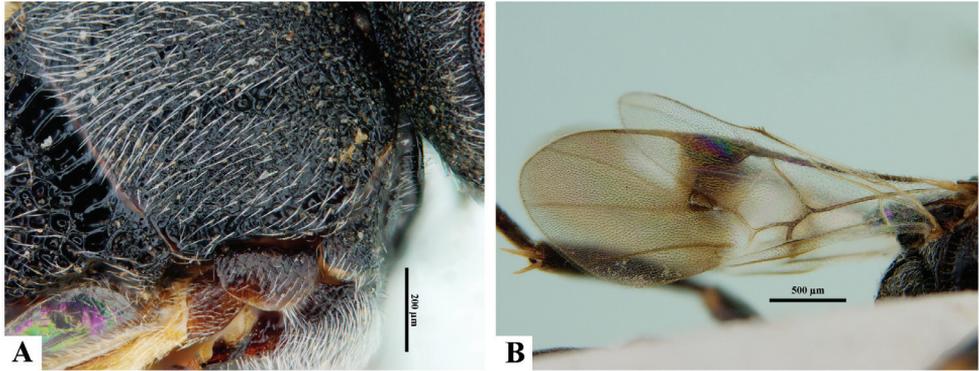
**Diagnosis.** *Philoplitis keralensis* sp. n. is similar to *P. trifoveatus* sp. n., but it can be distinguished from the latter by having different ratios of fore wing veins 2RS/2M 1.13 × (1.30 × in *P. trifoveatus* sp. n.), eyes dark brown (eyes dark yellow in *P. trifoveatus* sp. n.), and fore wing with a small, brownish patch beneath vein 1-CU1 (without small brownish patch beneath 1-CU1 in *P. trifoveatus* sp. n.).

**Description.** Head distinctly rugoso-punctate. Frons transversely striate. Occipital carina strongly defined and crenulated. Area centrally between posterior ocelli and occipital carina mostly coarsely sculptured, with only small, shiny spot right above the occipital carina. Antennae longer than body length, L of F2 3.09 × its W, L of F15 1.94 × its W. Mesosoma mostly covered with silver setae. Anteromesoscutum rugose near notauli, punctate laterally. Notauli impressed, and with impressed surface postero-laterally above the tegula. Scutellar disc coarsely rugose, apex pointing downward in lateral view. Scutellar disc L/W ratio 1.27 ×, and its L 0.90 × that of anteromesoscutum. Mesopleuron mostly rugoso-punctate, but with medial smooth area centrally. Metapleuron rugose. Propodeum rugose, with complete medial longitudinal carina. Fore wing ratios: r/3RSa: 1.60 ×; r/r-m: 2.11 ×; r/2RS: 0.66 ×; 3RSa/2M: 0.47 ×; 2RS/2M: 1.13 ×; r-m/2M: 0.35 ×; r/(r-2M): 0.46 ×; height of second submarginal cell/(r-2M): 0.37 ×. Tarsal claws with two teeth and with arolium subequal to claw length. Metafemur L 3.72 × its maximum width, inner spur of metatibia 0.52 × L of first metatarsomere. T1 rugose, smooth apically, T1 with shallow, median longitudinal groove extending half of tergite length, T1 L 2.42 × its W at posterior margin. T2 smooth, broad, with middle zone outlined by shallow convergent grooves that form a transversely striated triangle, with carinae markedly divergent, smooth, T2 medial L 0.36 × its W at posterior margin. T3+ smooth.

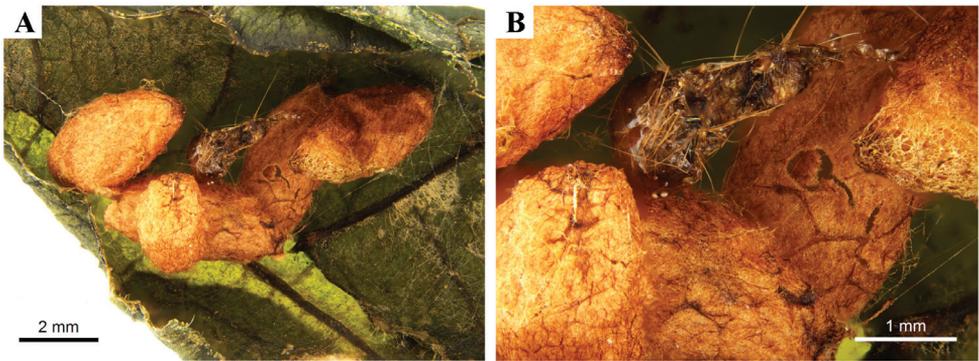


**Figure 6.** *Philoplitis keralensis*, female holotype **A** habitus, lateral view **B** head, frontal view **C** head and mesosoma, lateral view **D** mesosoma, dorsal view **E** metasomal tergite I, dorsal view **F** metasomal tergites 2 and 3, dorsal view.

**Colour.** Head and mesosoma black, scape and pedicel reddish brown, flagellomeres brown, ocelli brown, profemur mostly brown, yellow basally and apically, protibiae and protarsomeres dark brown, mesofemur and metatibia black, mesotarsomeres yellowish brown, hind leg dark brown, metatibial spurs yellowish brown, wing veins and pterostigma brown, except for junction of veins 2CU1, m-cu and 3CU1 which is white, fore wing vein 1SR-M white, with a brownish cloud beneath pterostigma that extends to the posterior margin of the wing, small brownish patch beneath 1-CU1,



**Figure 7.** *Philoplitis keralensis*, female holotype **A** mesoscutum (in part), oblique view **B** wings.



**Figure 8.** *Philoplitis keralensis*, cocoon mass.

fore wing faintly infuscated apically. T1 apically and T2 entirely yellow. Laterotergites 1–3 yellowish-white.

**Male.** Same as female.

**Host.** Gregarious parasitoid of an unidentified lepidopteran larva (Fig. 8).

**Distribution.** India (Kerala).

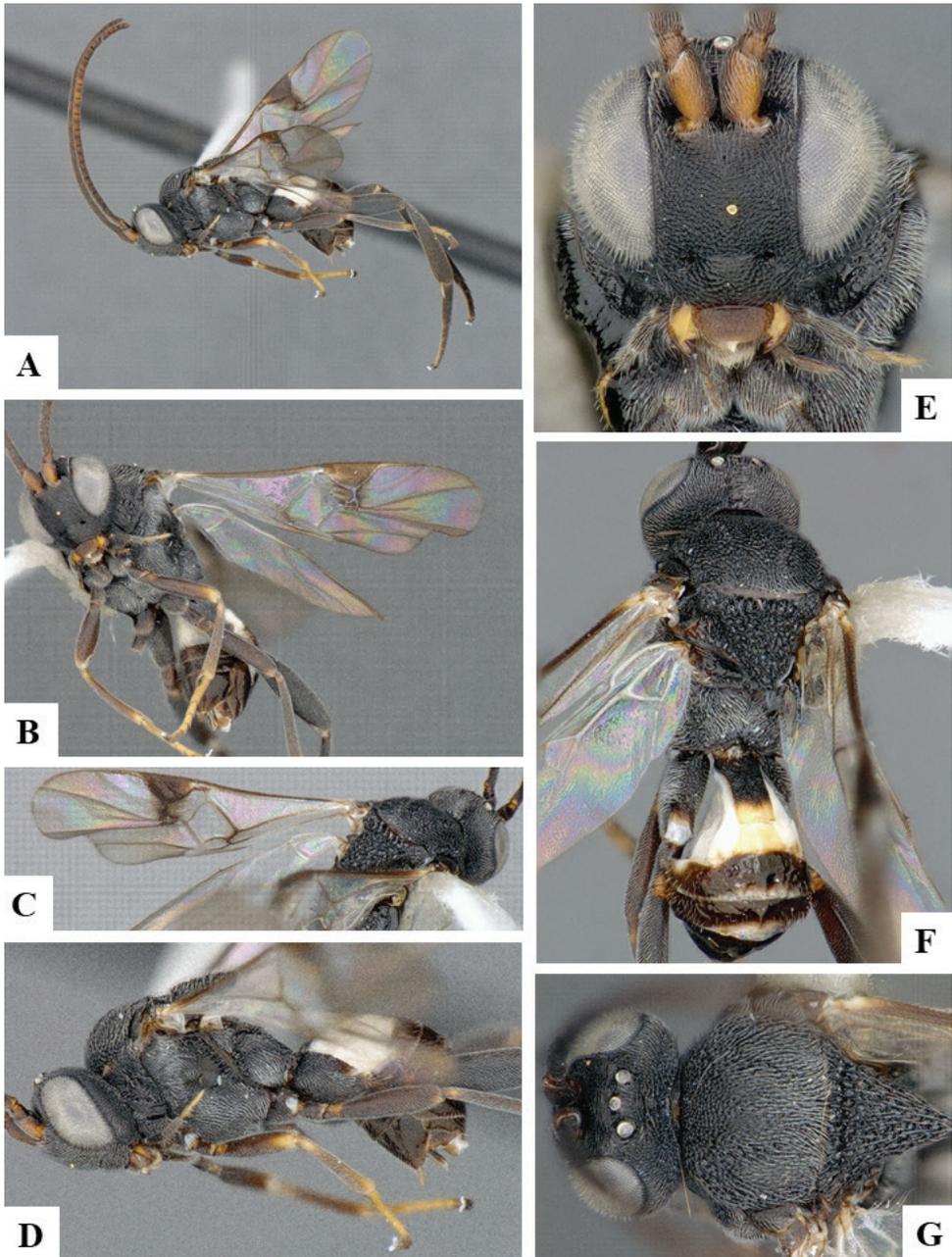
**Etymology.** This new species is named after the Indian state where type locality is found.

***Philoplitis margalla* Fernandez-Triana & Ranjith, sp. n.**

<http://zoobank.org/C04D0DC1-E8C7-45A6-BD51-CA4CF0C4F44D>

Fig. 9

**Holotype.** Female, PAKISTAN (CNC). Holotype locality: Islamabad, Pakistan Museum of Natural History, Shakar Parian, 33°41'9.0"N 73°4'33.60"E, 18.iv.2012, Malaise trap, M Rafique leg. Voucher code: BIOUG02373-G10. Secondary voucher code: CNC469935.



**Figure 9.** *Philoplitis margalla*, female holotype **A** habitus, lateral view **B** body and wings (partially), ventro-lateral view **C** wings **D** body, lateral view **E** head, frontal view **F** body, dorsal view **G** head and mesosoma, dorsal view.

**Paratypes.** One female and one male (BIOUG, CNC). Same locality than holotype but collecting dates 5.xi.2012 and 29.xi.2012 and M Rafique & Q Abbas leg. Voucher codes: BIOUG15337-B11, BIOUG15345-A08.

**Diagnosis.** *Philoplitis margalla* sp. n. is the only known species of *Philoplitis* with sexual dimorphism in the color of the metatibial spurs, which is light yellow in females, dark brown in males.

**Description.** Head distinctly rugose. Frons transversely striate, without median, longitudinal carina. Occipital carina strongly defined and crenulate. Area centrally between posterior ocelli and occipital carina mostly transversally striate, with only very small, shiny spot right above the occipital carina. Antennae longer about same length as body length, L of F2  $2.80 \times$  its W, L of F15  $2.40 \times$  its W. Mesosoma mostly covered by silver setae. Anteromesoscutum coarsely rugose. Notauli deeply impressed, and with impressed postero-lateral area above tegula. Scutellar disc coarsely rugose, slightly downward apically, in lateral view. Scutellar disc L/W ratio  $1.2 \times$ , and its L  $0.86 \times$  that of mesoscutum. Mesopleuron mostly rugose or striate, but with median, smooth area centrally. Metapleuron rugose. Propodeum rugose with complete medial longitudinal carina. Fore wing ratios, r/3RSa:  $1.11 \times$ ; r/r-m:  $3.33 \times$ ; r/2RS:  $0.83 \times$ ; 3RSa/2M:  $0.90 \times$ ; 2RS/2M:  $1.20 \times$ ; r-m/2M:  $0.33 \times$ ; r/(r-2M):  $0.44 \times$ ; height of second submarginal cell/(r-2M):  $0.44 \times$ . Tarsal claws simple and with arolium longer than claw length. Metafemur L  $3.50 \times$  its maximum W, inner spur of metatibia  $0.50 \times$  L of first metatarsomere. T1 fully sculptured, T1 with excavation on anterior 0.2–0.3, then a median longitudinal groove extending to half of tergite length, T1 L  $2.50 \times$  its W at posterior margin. T2 smooth, trapezoidal, relatively well defined by divergent grooves (but grooves only clearly distinct on anterior half of T2), T2 median L  $0.50 \times$  its W at posterior margin. T3+ smooth.

**Colour.** Head and mesosoma black; scape and pedicel orange-yellow; flagellomeres brown to light brown; palpi mostly dark brown to black (only two apical maxillary palpi yellow); all coxae, metafemur, metatibia and metatarsus black; pro- and mesofemorae and pro- and metatibiae mostly dark brown (at most with small yellow spot apically); pro- and mesotarsi yellow; metatibial spurs light yellow; most wing veins and pterostigma brown to light yellow; area beneath stigma light brown, clearly darker than rest of wing which is hyaline; metasoma dorsally mostly dark brown, except for T1 black on anterior 0.8, and for posterior 0.2 of T1 and entire T2 yellow-white; laterotergites 1–3 white, rest dark brown.

**Male.** As female, but with darker body color: palpi, scape, pedicel, most of legs (including metatibial spurs) dark brown to black; metasoma dorsally and laterally darker.

**Distribution.** Pakistan, Islamabad, Margalla Hills National Park.

**Etymology.** The name, to be treated as a name in apposition, refers to the Margalla Hills National Park, a 12,600+ ha protected area in Islamabad Capital Territory, and where the type locality (Shakarparian Park) is located. Despite its small size, the fauna and flora of the Margalla Hills are quite diverse and mostly tropical and constitute a transitional zone between the high mountains to the north and plain areas to the south, providing a corridor for many Himalayan species to disperse south.

***Philoplitis masneri* Fernandez-Triana & Goulet, 2009**

Fig. 10

*Philoplitis masneri* Fernandez-Triana & Goulet, 2009: 292, figs 1, 4, 7, 10, 14 (original description).

**Notes.** This species was described and diagnosed by Fernandez-Triana and Goulet (2009). Here we only provide new images of the species.

***Philoplitis punctatus* Fernandez-Triana & Goulet, 2009**

Fig. 11

*Philoplitis punctatus* Fernandez-Triana & Goulet, 2009: 293, figs 5, 8, 11, 15 (original description).

**Notes.** This species was described and diagnosed by Fernandez-Triana and Goulet (2009). Here we only provide new images of the species, including the first illustrations of a female specimen.

***Philoplitis striatus* Fernandez-Triana & Goulet, 2009**

Figs 12–13, 16D

*Philoplitis striatus* Fernandez-Triana & Goulet, 2009: 294, figs 2, 6, 9, 12, 16 (original description).

**Notes.** This species was described and diagnosed by Fernandez-Triana and Goulet (2009). Here we only provide new images of the species.

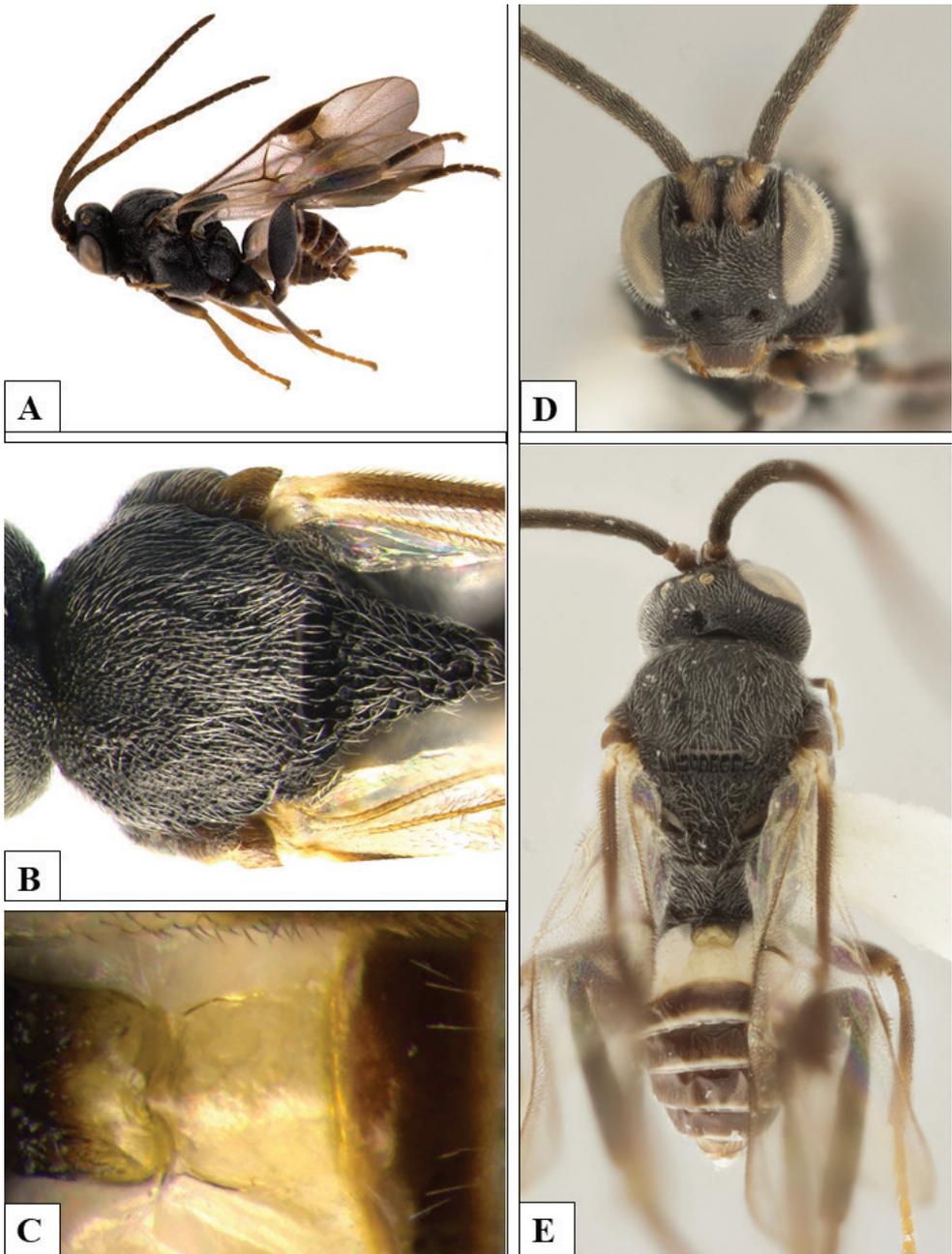
***Philoplitis trifoveatus* Ranjith & Fernandez-Triana, sp. n.**

<http://zoobank.org/3B38C228-5D59-426E-AAF8-AD47C3DE7BB0>

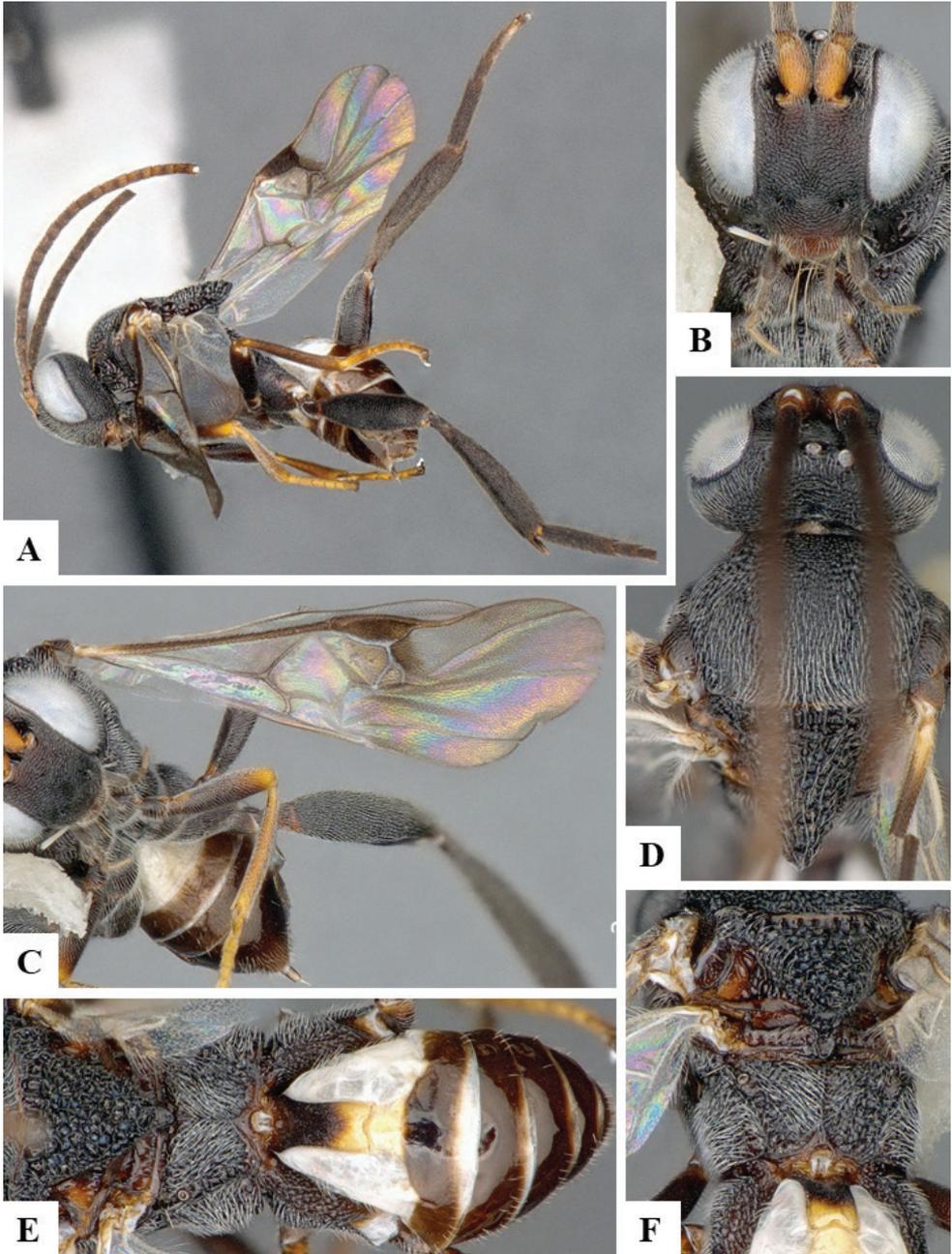
Figs 14, 15, 16C

**Holotype.** Female, INDIA (DZUC). Holotype locality: Karnataka, MSS SRF, Malaise trap, 1-19.ii.2007.

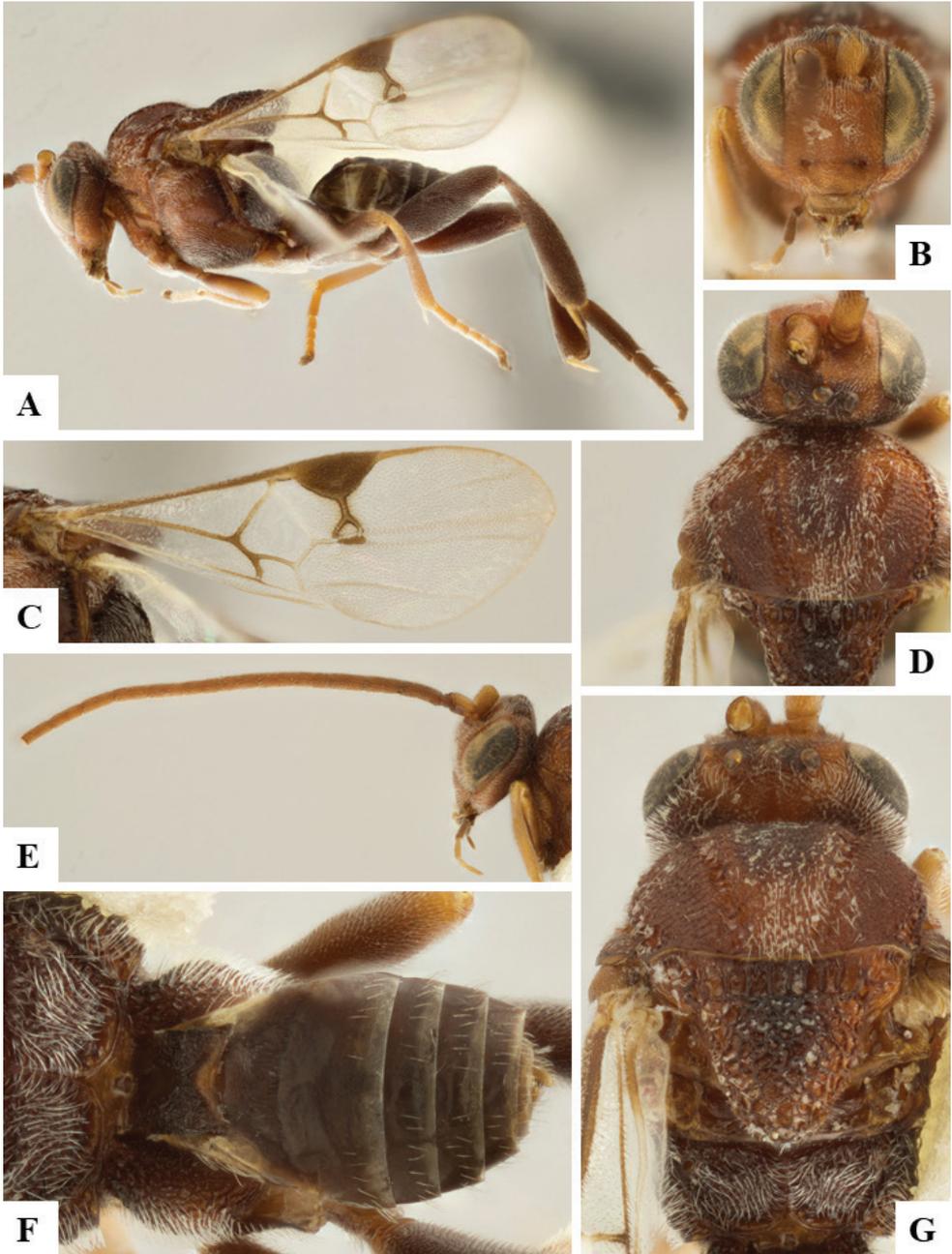
**Diagnosis.** *Philoplitis trifoveatus* sp. n. differs from all other species by having the occiput medially with three pits. This new species can be separated from *P. keralensis* sp. n. by having scutellar disc L/W ratio 1.10 ×, and its L 0.90 × that of anteromesoscutum (scutellar disc L/W ratio 1.27 ×, its length 1.10 × that of anteromesoscutum in



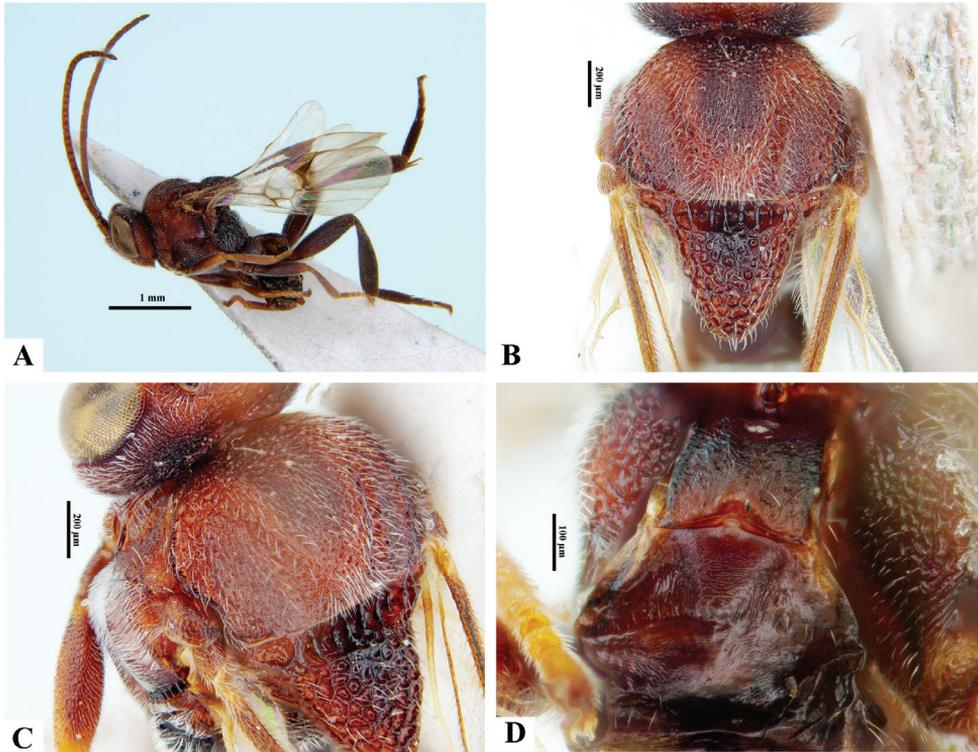
**Figure 10.** *Philoplitis masneri*, male holotype **A** habitus, lateral view **B** mesosoma, dorsal view **C** metasomal tergites 1-3 (partially), dorsal view **D** head, frontal view **E** body, dorsal view.



**Figure 11.** *Philoplitis punctatus*, female **A** habitus, lateral view **B** head, frontal view **C** wings and body (partially) ventral view **D** head and mesosoma, dorsal view **E** metasoma, dorsal view **F** Scutellum and propodeum, dorsal view.



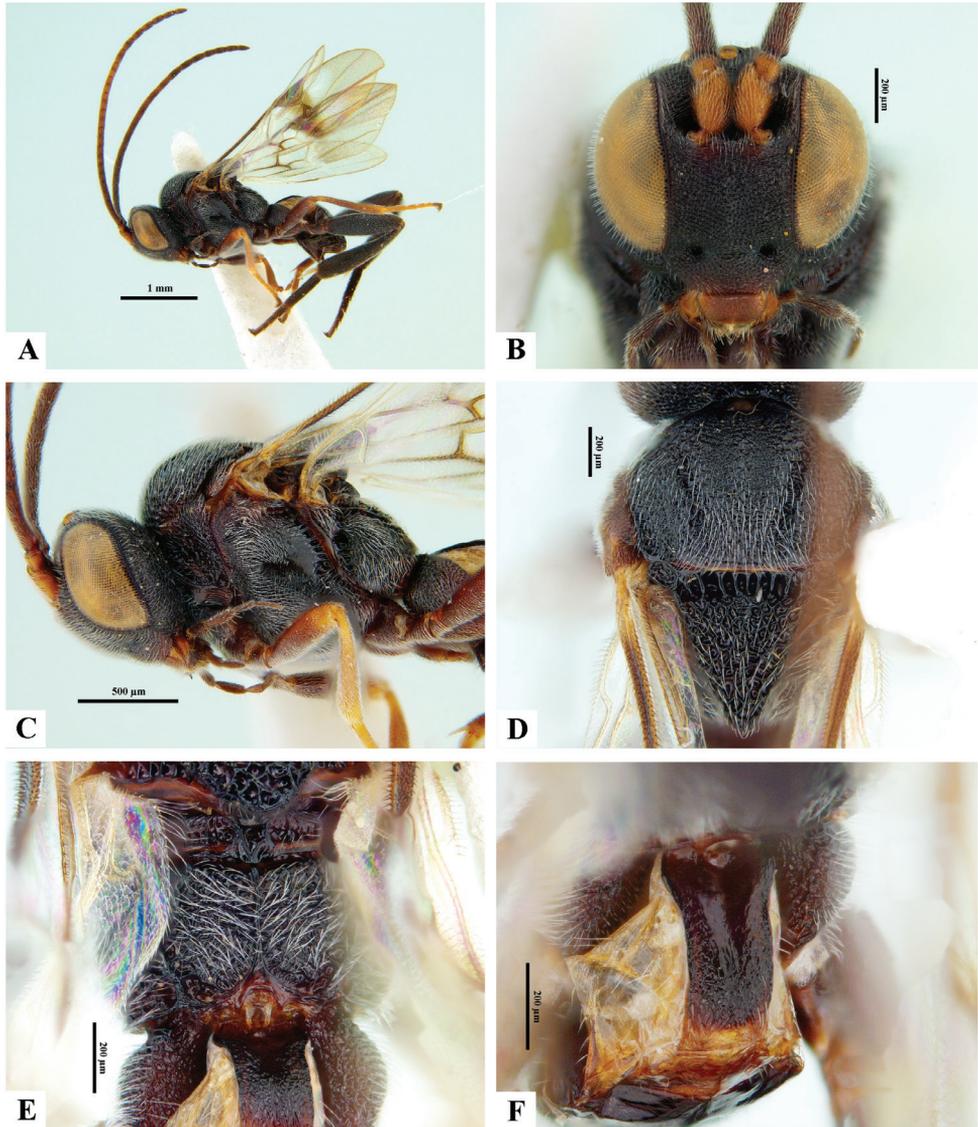
**Figure 12.** *Philopltis striatus*, male holotype **A** habitus, lateral view **B** mesosoma, dorsal view **C** wings **D** head and mesosoma, dorsal view **E** head and antenna, lateral view **F** metasoma, dorsal view **G** head and mesosoma, dorsal view.



**Figure 13.** *Philoplitis striatus*, female **A** habitus, lateral view **B** mesosoma, dorsal view **C** head and mesosoma oblique view **D** metasomal tergites 1-3 (partially), dorsal view.

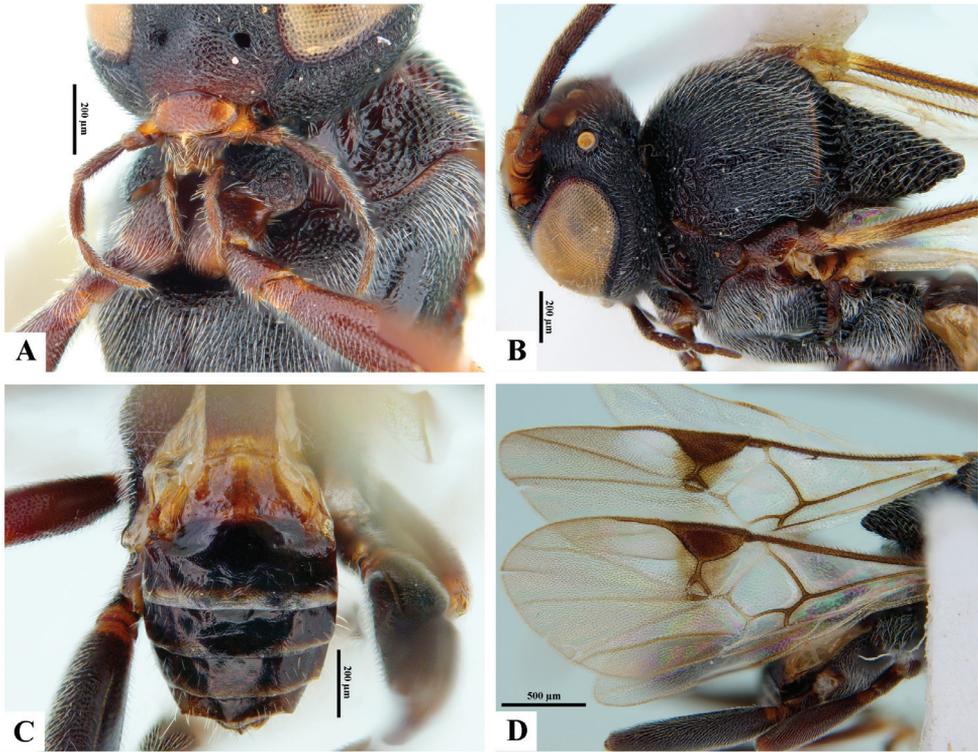
*P. keralensis* sp. n.), and by the ratio of fore wing veins  $r/r-m$  ( $2.50 \times$  in *trifoveatus* sp. n.,  $2.11 \times$  in *keralensis* sp. n.).

**Description.** Head distinctly rugose. Frons transversely striate. Occipital carina strongly defined and crenulate. Area centrally between posterior ocelli and occipital carina mostly transversally striate, with only small, shiny spot right above the occipital carina. Antennae longer than body length, L of F2  $2.90 \times$  its W, L of F15  $2.04 \times$  its W. Mesosoma mostly covered with silver setae. Anteromesoscutum coarsely rugose. Notauli deeply impressed, and with impressed postero-lateral area above tegula. Scutellar disc coarsely rugose, apically downward in lateral view. Scutellar disc L/W ratio  $1.10 \times$ , and its L  $1.10 \times$  that of anteromesoscutum. Mesopleuron sparsely rugose, but with median, smooth area centrally. Metapleuron rugose. Propodeum rugose with complete median, longitudinal carina. Fore wing ratios,  $r/3RSa$ :  $1.00 \times$ ;  $r/r-m$ :  $2.50 \times$ ;  $r/2RS$ :  $0.80 \times$ ;  $3RSa/2M$ :  $1.10 \times$ ;  $2RS/2M$ :  $1.30 \times$ ;  $r-m/2M$ :  $0.44 \times$ ;  $r/(r-2M)$ :  $0.47 \times$ ; height of second sub marginal cell/( $r-2M$ ):  $0.50 \times$ . Tarsal claws with one tooth and with



**Figure 14.** *Philoplitis trifoveatus*, female holotype **A** habitus, lateral view **B** head, frontal view **C** head and mesosoma, lateral view **D** mesosoma, dorsal view **E** propodeum, dorsal view **F** metasomal tergite I, dorsal view.

arolium subequal to claw length. Metafemur L  $3.40 \times$  its maximum width, inner spur of metatibia  $0.49 \times$  L of first metatarsomere. T1 faintly rugose laterally and apically, T1 with shallow median longitudinal groove extending beyond half of its length, T1 L  $2.35 \times$  its W at posterior margin. T2 smooth, broad, with medial zone outlined by



**Figure 15.** *Philoplitis trifoveatus*, female holotype **A** head and mesosoma, ventral view **B** head and mesosoma, oblique view **C** metasoma, dorsal view **D** wings.

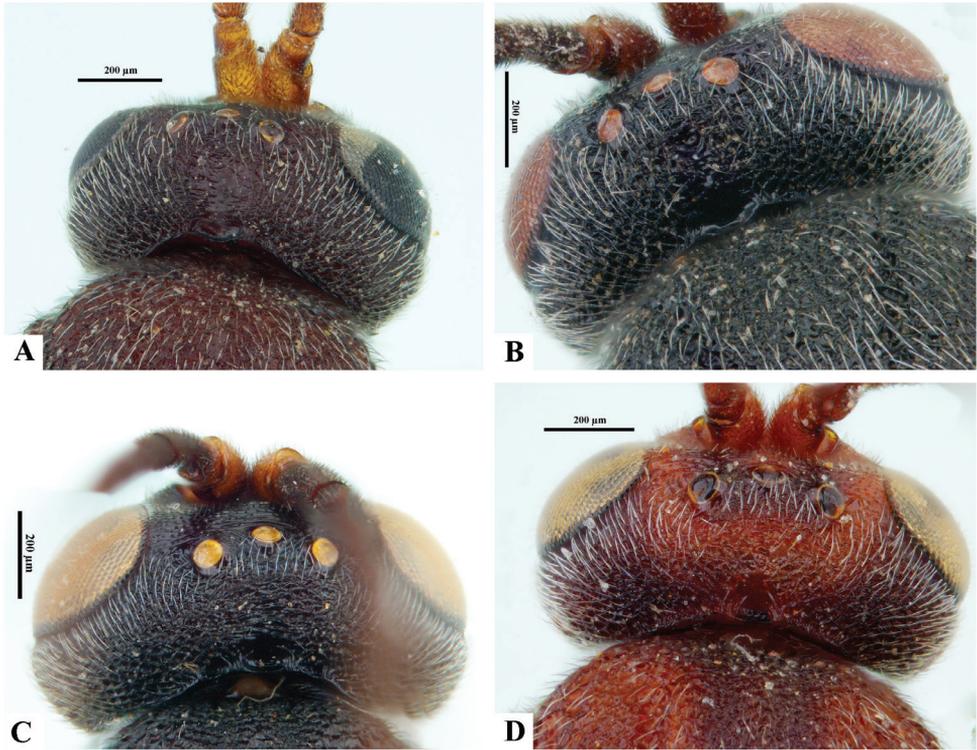
convergent grooves that form a transversely striated triangle, with indistinct carinae markedly divergent, T2 striated medially but without longitudinal striations, T2 medial L  $0.37 \times$  its W at posterior margin. T3+ smooth.

**Colour.** Head reddish brown, scape, pedicel and ocelli dark yellow, flagellomeres brown, palpi brown, mesosoma reddish brown, anteromesoscutum dark yellow at posterior margin, profemur mostly brown, yellow apically, protibia and protarsomeres yellow, mesofemur and mesotibia brown, mesotarsomeres brown, metafemur and metatibia black, metatarsomeres brown, metatibial spurs yellow, wing veins and pterostigma light brown with a brownish cloud beneath that extends to vein 2M, metasoma reddish brown except for T1 apically and T2 entirely brownish-yellow, laterotergite 1-3 yellowish-white.

**Male.** Unknown.

**Distribution.** India (Karnataka).

**Etymology.** This species name alludes to the distinctive three pits present in the occiput.



**Figure 16.** *Philoplitis* spp. from India, dorsal views of heads **A** *P. adustipalpus* **B** *P. keralensis* **C** *P. trifoveatus* **D** *P. striatus*.

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## Supplementary material I

### Neighbour Joining Tree (K2P) of available *Philoplitis* sequences (COI) in the Barcode of Life Data System

Authors: A.P. Ranjith, J. Fernandez-Triana, T. Veena, D.R. Priyadarsanan, M. Nasser  
Data type: molecular data

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