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An illustrated key to the species of the genus *Narella* (Cnidaria, Octocorallia, Primnoidae)

Stephen D. Cairns[1], Michelle L. Taylor[2]

1 *Department of Invertebrate Zoology, National Museum of Natural History. Smithsonian Institution, Washington, DC, 20560, USA* **2** *School of Biological Sciences, University of Essex, Wivenhoe Park, Colchester, CO4 3SQ, UK*

Corresponding author: *Stephen D. Cairns* (cairnss@si.edu)

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Abstract

A history of the description of the 50 valid species of *Narella* is given, beginning with the first species described in 1860. To help differentiate the various species, a tabular and a polychotomous key are provided. The species in the keys are arranged using nine characters or character sets that are believed to be of value at the species level. New characters or new significance given to previously described characters used in our keys include: 1) the nature of the dorsolateral edge of the basal scale, being ridged or not, 2) the thickness of the body wall scales, and 3) the arrangement of the coenenchymal scales (imbricate or mosaic), their thickness (thin or massive), and their outer surface ornamentation (ridged or not). All characters used in the keys are illustrated.

Keywords

Alcyonacea, Calcaxonia, dichotomous key, Primnoidae, tabular key

Introduction

The first species of *Narella* was described as *Primnoa regularis* by Duchassaing and Michelotti (1860) collected off Guadeloupe, Lesser Antilles at an unknown depth. This is somewhat remarkable in that 366 m is the shallowest depth from which this species is known, and it was thus collected at a time when deep-water animals were not thought to occur below approximately 200 m. *Primnoa regularis* was made the type (by monotypy) of the newly described genus *Narella* by Gray (1870), calling it that name perhaps because the polyps resembled a series of small noses (Latin *naris* = nostril). The holotype is deposited at the Turin Museum (Volpi and Benvenuti 2003) but because of its poor condition was set aside to be replaced by a neotype (Cairns and Bayer 2004; ICZN 2005).

The next species to be described in the genus, *Stachyodes regularis* Wright & Studer, 1889, from the Kermadec Islands, was unfortunately also called *regularis*, but placed in the newly described genus *Stachyodes* Wright & Studer, 1887 in Studer (1887), a junior synonym of *Narella*. Because Versluys (1906) considered it and *P. regularis* of Duchassaing and Michelotti (1860) to be in the same genus, the Wright & Studer species was thought to be a junior homonym and thus it required a new name, which he gave as *S. studeri* Versluys, 1906. It also became the type species of *Stachyodes*. Yet another genus name that was subsequently synonymized with *Narella* was proposed by Wright and Studer (1889) as *Calypterinus*, the type species being *C. allmani* Wright & Studer, 1889 (Fiji).

In the first of several species to be described based on specimens collected by the US Fish and Wildlife Service vessel *Albatross*, Studer (1894) described *Stachyodes* (= *Narella*) *ambigua* from off the Galapagos Islands.

Next followed Versluys' (1906) beautifully illustrated and finely described revision of the deep-water octocorals of the *Siboga* Expedition from Indonesia, which included the description of seven new species, all of which he also placed in *Stachyodes.* This work set the standard for future morphological descriptions within the genus.

In the next ten years a flurry of new species were described from around the world: four from off Japan (Kinoshita 1907), one from off Sumatra (Kükenthal 1907), one from the Hawaiian Islands (Nutting 1908), three from the North Atlantic (Hickson 1909; Kükenthal 1912, 1915), and one from the southwest Indian Ocean (Thomson 1911). *Narella elegans* Tixier-Durivault & Lafargue, 1968 is believed to be a junior synonym of *N. versluysi* (Hickson, 1909), originally described in Stephens and Hickson (1909). Thomson also described a species from the southwest Indian Ocean, *S. capensis* Thomson, 1917, which was later synonymized with *N. gilchristi* (Thomson, 1911). But most notable from this time period was Kükenthal's (1919) report on the deep-water octocorals of the *Siboga* expedition, in which he re-described all the species of *Narella* (as *Stachyodes*) and provided a morphological key to the 18 valid species. One hundred years later these are still the characters used to discriminate species and form the basis for the keys presented herein.

Aurivillius (1931) described one new species from off Japan, and Deichmann (1936) two new species from the northwest Atlantic Ocean. Finally, the "modern" era of *Narella* taxonomy was introduced by Bayer (1951), who finally synonymized *Stachyodes* and *Calypterinus* with *Narella*, and also described a new species from Indonesia. He later described two new species from off the Hawaiian Islands (Bayer 1995, 1997), one of them, *N. nuttingi* Bayer, 1997, later being synonymized with *N. dichotoma* (Cairns & Bayer, 2007). In collaboration with Cairns, Bayer also revised the *Narella* species from the northwest Atlantic (Cairns and Bayer 2003), describing two new species, and from the Hawaiian Islands (Cairns and Bayer 2007), describing six new species. They subsequently also placed the genus in phylogenetic perspective in a morphology-based cladogram, and listed the 38 known species at that time (Cairns and Bayer 2009). Also in 2007, Cairns and Baco (2007) described five new species from deep seamounts in the Gulf of Alaska.

Cairns described five more new species from the New Zealand region (Cairns 2012) and six from the northern and central Pacific (Cairns 2018), which prompted the need for this synthetic key to the species. Cairns (2018) also made one previously described species of *Narella*, *N. mesolepis* Cairns, 2012, the basis for a new genus, *Pseudonarella*. Taylor and Rogers (2015) placed *Narella* in a phylogenetic perspective using molecular data, and listed the 44 species known at that time, although *S. regularis* should be considered as junior synonym of *N. studeri*, and Cairns (2018) considered *N. irregularis* to be a junior synonym of *N. horrida*. Finally, Taylor and Rogers (2017) described three new species from the southwest Indian Ocean, and listed all species known at that time.

The genus *Narella* represents a highly successful adaptive radiation within the primnoids and more species are expected to be discovered. This is the reason why we here present two keys (a tabular and polychotomous key), the first since Kükenthal's (1919) work, i.e., to facilitate comparison of species for identification purposes, and to examine this genus before new species are described.

Materials and methods

Many of the descriptions and diagnoses are based on original literature, which is duly cited. Descriptive terms used are found in the trilingual glossary of Bayer et al. (1983). Reviewing holotypes involved preparing sclerites for viewing under a light microscope following procedures well-documented elsewhere (Alderslade 1998; Fabricius and Alderslade 2001; Cairns 2016).

Taxonomy

Subclass Octocorallia
Order Alcyonacea
Suborder Calcaxonia
Family Primnoidae Milne Edwards, 1857

Genus *Narella* Gray, 1870

Narella Gray, 1870: 49; Cairns and Bayer 2009: 43.
Stachyodes Wright & Studer in Studer 1887: 49.
Calypterinus Wright & Studer in Studer 1887: 49–50.

Diagnosis. Colonies branched dichotomously (laterally or equal), pinnately, in a lyrate fashion, or unbranched. Polyps arranged in whorls, all polyps facing downward in contracted condition. Each polyp covered with three (rarely four) pairs of abaxial body wall scales (i.e., one pair of basals, one or rarely two pairs of medials, and one pair of buccals) and a variable number of pairs of smaller adaxial scales, nonetheless leaving the adaxial face largely naked. Articular ridge not present on basal scales. Paired infrabasal scales often present. Opercular scales keeled on inner surface. Coenenchymal scales thin and imbricate or thick and mosaic in placement, and sometimes prominently ridged.

Type species. *Primnoa regularis* Duchassaing & Michelotti, 1860, by monotypy.

Discussion. Currently there are 50 valid species in the genus *Narella*, the most speciose in the family Primnoidae (Taylor and Rogers 2015). The species in both keys (tabular (Table 1) and polychotomous, below) are roughly presented in an order that follows the major characters as outlined below, these characters we purport to be valuable in the distinction of species of *Narella*.

***Dorsolateral edge of basal scale ridged or not ridged*:** The dorsolateral edge (the point of inflexion of the scale from the dorsal region to the lateral region) of the basal scale is consistently ridged or not ridged (Fig. 1E) in each species, with the only exception of *N. macrocalyx*, which is inconspicuously ridged, and sometimes (rarely) lacks the ridge. This external ridging may help give strength to basal sclerites. The ridge may be single and extend from the base to the tip of the scale (Fig. 1A, B), or partial, occurring only at the base of the scale (Fig. 1C). Or, there may be multiple short ridges occurring in this region of the scale (Fig. 1D). The ridges may be tall or low. This character is relatively easy to observe, but usually requires the removal of a polyp from a whorl, drying the specimen, and then applying a dye to help see the characteristic ridging structure.

***Number of pairs of body wall scales*:** Most species of *Narella* have three pairs of abaxial body wall scales (basal, medial, and buccal, Fig. 1F), but in three species there is consistently an extra pair of medial scales (Fig. 1G). Also, specimens of some species that have otherwise three pairs of body wall scales will have occasional polyps with four pairs of body wall scales. This is a fairly easily observed character when using a dissecting microscope.

***Worm commensalism*:** The commensal association with a polychaete worm, usually a polynoid (Cairns and Bayer 2008, Cairns 2012, Britayev et al. 2014, Serpetti et al. 2017), is considered to be characteristic of the species, and is easily observed even without a microscope. The facing basal scales of two adjacent polyps are greatly enlarged and modified (reflexed) in order to make an elongate cylindrical tube for the worm (Fig. 1H, I).

***Branching mode*:** The mode of branching, and thus colony shape, is considered to be characteristic of the species. Modes include: unbranched (Fig. 1J), branching from a common basal coenenchyme or bolus (Fig. 1K, L), sparse equal dichotomous branching (Fig. 1M), equal dichotomous branching (Fig. 1N), and lyrate (Fig. 1O), which is often followed by dichotomous branching. Lyrate branching might be considered as a special case of dichotomous branching in which the outer component of each bifurcation maintains a straight line while the inner branches remain roughly parallel to one another.

***Body wall scale thickness*:** In some species the body wall scales are quite thick, or massive (Figs 1P, 2A). This trait is often correlated with having thick coenenchymals as well (see next character). This character is best seen using scanning electron microscopy of individual sclerites.

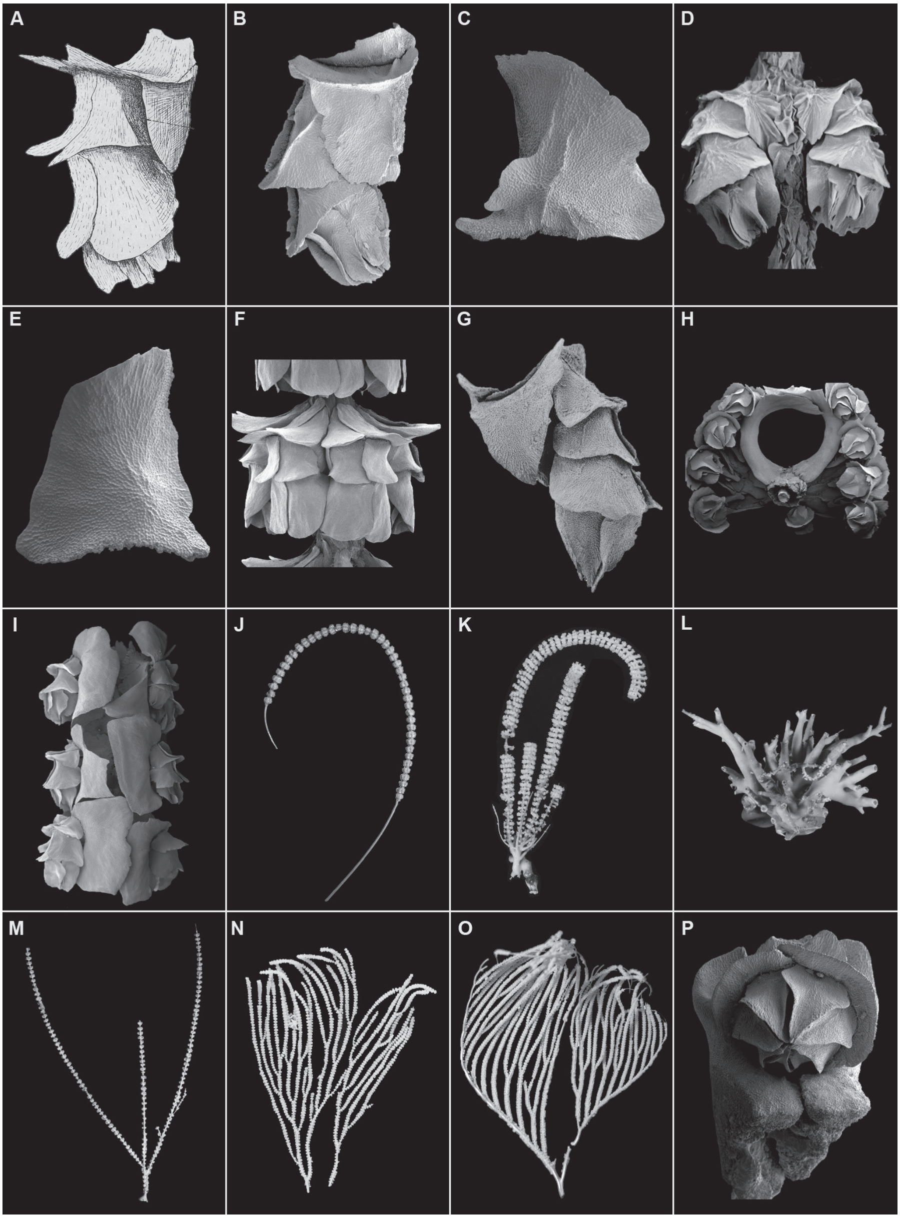

Figure 1. A, B lateral view of a polyp showing dorsolateral ridge for entire height of basal scale (**A** *N. parva* from Versluys (1906) **B** *N. bayeri*) **C** basal scale of *N. hawaiinensis* showing dorsolateral ridge only on lower half of scale **D** whorl of polyps of *N. pauciflora* showing multiple dorsolateral ridges on the basal scales **E** basal scale of *N. vulgaris* showing the lack of a dorsolateral ridge, and a lobate distal edge **F** polyp whorl of *N. bellissima* showing the three pairs of body wall scales **G** polyp of *N. laxa* having four pairs of body wall scales **H** polyp whorl of *N. hypsocalyx* showing highly modified basal scales forming a cross section view of a cylindrical worm tube **I** polyp whorl of *N. vulgaris* showing highly modified basal scales forming a lateral view of a cylindrical worm tube **J** unbranched colony of *N. versluysi* **K, L** branching from a basal bolus of *N. hypsocalyx* **M** sparse, dichotomous branching of *N. macrocalyx* **N** equal, dichotomous branching of *N. vulgaris* **O** lyrate branching of *N. bellissima* **P** massive basal scales of *N. clavata*.

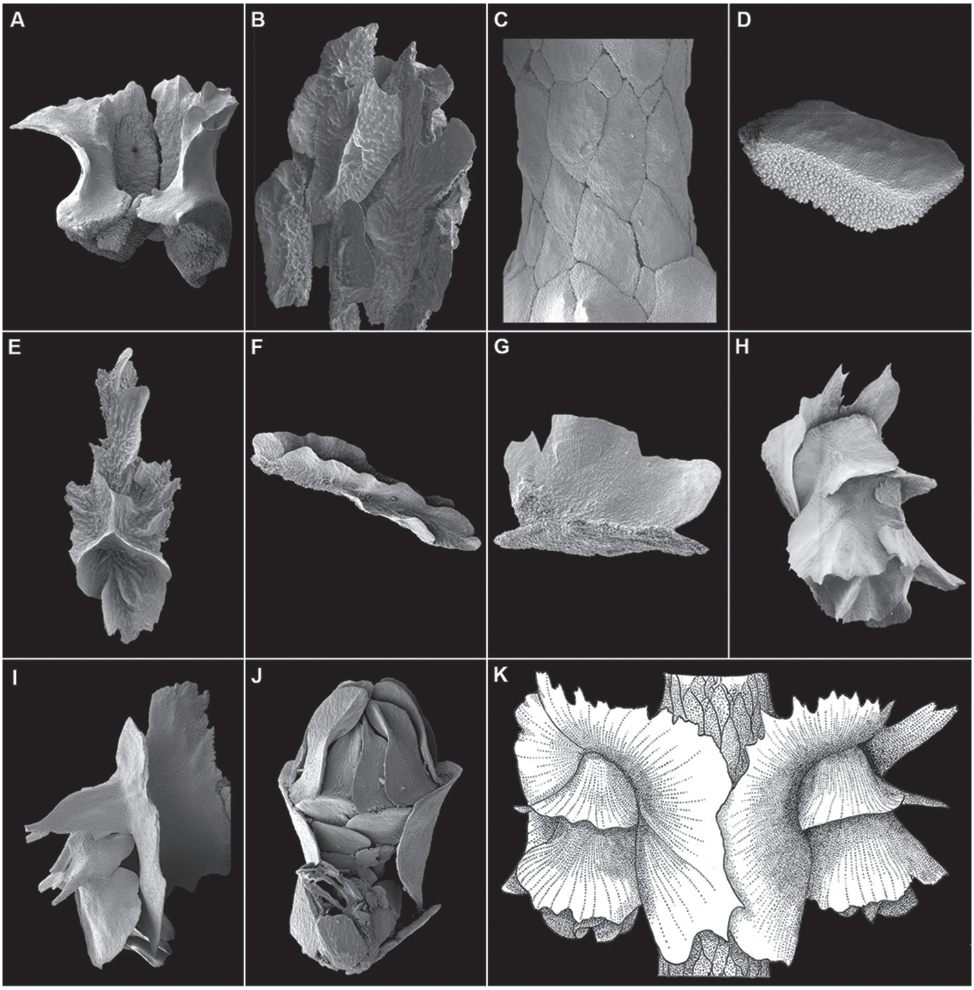

Figure 2. A massive basal scales of *N. clavata* **B** thin, imbricate coenenchymal scales of *N. fordi* **C** thick, mosaic arranged coenenchymal scales of *N. mosaica* **D** individual thick coenenchymal scale of *N. mosaica* with a finely granular outer surface **E** complexly ridged coenenchymal scale of *N. muzikae* **F** single medial coenenchymal ridge of *N. pauciflora* **G** sail scale of *N. spectabilis* **H** serrate distal margin of body wall scales of *N. bowersi* **I** spinose body wall scales of *N. horrida* **J** adaxial body wall scales of *N. dampieri* **K** polyp pair of *N. leilae* showing extensive cowl and serrate distal edges of body wall scales (from Bayer, 1951).

***Coenenchymal scales arrangement and ornamentation*:** The coenenchymal scales of most species are relatively thin, having the same thickness as a body wall scale, and have edges that slightly overlap those of other adjacent coenenchymal scales (Fig. 2B). But some species have quite thick scales (Fig. 2C–D) that are so massive that they cannot overlap adjacent scales and thus produce a mosaic, polygonal, or tessellate pattern, also called "cobblestone" (Williams 1992). The term mosaic is used herein. Coenenchymal scales usually have a finely granular outer surface (Fig. 2D), but many

Table 1. Tabular Key to the species of the genus *Narella*.

Species	Dorsolateral edge of basal scale	Pairs of body wall scales	Polychaete commensalism	Branching mode	Body wall scale thickness	Coenenchymal scales: imbricate, thickness; ridged	Polyps/ whorl; whorl diameter (mm)	Polyp length (mm)	Distal edge of basal scales	Other characters	Geographic and depth range
N. macrocalyx Cairns & Bayer, 2007	Small ridge	3	Present	Sparse,	Thin	Thin, imbricate; rarely ridged	4–6; 7–11	4.5–5.5	Lobate, smooth		Hawaiian Islands, 1206–1807 m
N. gilchristi (Thomson, 1911)	Small ridge	3	Present	lyrate, secondarily dichotomous	Thin	Thick, mosaic; unridged	4–8; 4–9	2—3	Lobate, smooth		Southwest Indian Ocean, 90–1365 m
N. ferula Cairns, 2018	Multi-ridged	3	Absent	Unbranched	Thin	Thin, imbricate; ridged	2–3; 3.6	2.3–2.5	Serrate cowl, spurs	Medial scales also with serrate margin	Palmyra Atoll, 1023 m
N. hawaiinensis Cairns & Bayer, 2007	Inconspicuous basal ridge	3	Absent	Unbranched	Thin	Thin, imbricate; ridged	3–5; 5–6	3.4–4.1	Lobate, smooth		HI, Johnston Atoll, 1492–1944 m
N. muzikae Cairns & Bayer, 2007	Multi-ridged	3	Absent	Common coenosteum (bolus)	Thin	Thin, imbricate; ridged	3–6; 3–4	1.7–2.2	Lobate, serrate	Base strongly calcified	Hawaiian Islands, 326–381 m
N. merga Cairns, 2018	Two ridges basally	3	Absent	Y-shaped	Thin	Thin, imbricate; ridged	3; 4.4	4	Lobate (short cowl)		Wake Island, 2575 m
N. fordi Cairns, 2018	Multi-ridged	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged	3;3.4–3.5	2.1–2.6	Lobate, smooth	Medial scales ridged	Phoenix Islands, 1899 m
N. cristata Cairns & Baco, 2007	Single ridge	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged (sail scales)	2–4; 3.4	2.1–3.0	Lobate, smooth	Medial and buccals ridged; occasionally four pairs of bw scales	Gulf of Alaska seamounts, 3385 m
N. alvinae Cairns & Bayer, 2003	Single ridge	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged	4; 3.8	2.7–3.1	Lobate. smooth	Medial scales elongate	Bermuda, 3419 m
N. bayeri Cairns & Baco, 2007	Single ridge	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged (sail scales)	5–7; 3.5	2.2–3.4	Lobate, smooth	Medial scales ridged	Gulf of Alaska seamounts, 3277–4091 m
N. alaskensis Cairns & Baco, 2007	Low ridge	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged (sail scales)	5–9; 7.5	2.7–3.2	Lobate (narrow), smooth	Medial scales ridged	Gulf of Alaska seamounts, 2377–3075 m
N. arbuscula Cairns & Baco, 2007	Tall, short ridge	3	Absent	Sparse, equal dichotomous	Thin	Thin, imbricate; ridged (sail scales)	6–7; 6.8	3.4–4.7	Lobate, smooth	Whorls crowded	Gulf of Alaska seamounts, 2775–3465 m
N. pauciflora Deichmann, 1936	Multi-ridged	3	Absent	Equal dichotomous	Thin	Thin, imbricate; complex ridging	2–5; 4	2.6–2.8	Lobate, smooth	Adaxial buccals as ridged ascus scales	Northwest Atlantic, 738–1473 m
N. bowersi (Nutting, 1908)	One ridge basally	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	3–4; 4.5	2.5–3.2	Tall, serrate	Buccal scales serrate	Hawaiian islands, 1218–1758 m
N. gaussi (Kükenthal, 1912)	Multi-ridged	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	4–5; 3	2.1–3.0	Lobate (low), smooth	Radial ridges on all body wall scales	Antarctica, 2450 m
N. parva (Versluys, 1906)	Multi-ridged	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	4–6; 2.5–3.2	2.0–2.4	Tall, narrow, smooth	Adaxial buccal scales ridged	Southwest Pacific, 920–2400 m

Species	Dorsolateral edge of basal scale	Pairs of body wall scales	Polychaete commensalism	Branching mode	Body wall scale thickness	Coenenchymal scales: imbricate, thickness; ridged	Polyps/ whorl; whorl diameter (mm)	Polyp length (mm)	Distal edge of basal scales	Other characters	Geographic and depth range
N. regularis (Duchassaing & Michelotti., 1860)	Multi-ridged	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	4–5; 3.2	2.0–2.3	Lobate, smooth	Medial and buccals ridged	Northwest Atlantic, 366 – 792 m
N. valentine Taylor & Rogers, 2017	One tall ridge	3	Absent	Lyrate, secondarily dichotomous	Thin	Thin, imbricate; flat	4–5; 2.4–2.8	1.5–1.8	Tooth-like apex	Medials ridged	Southwest Indian Ocean, 383–444 m
N. virgosa Cairns, 2018	Multi-ridged	3	Absent	Lyrate, secondarily dichotomous and bushy	Thin	Thin, imbricate; ridged (sail scales)	3–4; 3.3–4.2	2.6–2.8	Lobate, smooth	Medials and buccals ridged	Hawaiian Islands and Johnston Atoll; 1901–1985 m
N. bellissima (Kükenthal, 1915)	Low ridge basally	3	Absent	Lyrate, secondarily dichotomous	Thin	Thin, imbricate; ridged (sail scales)	3–8; 3.15	2.0–2.2	Lobate, smooth		Amphi-Atlantic, 161–1968 m
N. ornata Bayer, 1995	Multi-ridged	3	Absent	Unknown	Thin	Thin, imbricate; ridged	3–4; 3.5	3	Serrate distal margin	All scales, including adaxial buccals, radially ridged	Hawaiian Islands, 748–1007 m
N. spectablis Cairns & Bayer, 2003	One tall ridge	4	Absent	Unbranched	Thin	Thin, imbricate; ridged (sail scales)	3; 2.8	3.5	Lobate, smooth (low)	All body wall scales ridged	Bahamas, 1485 m
N. abyssalis Cairns & Baco, 2007	Multi-ridged	4	Absent	Sparse, dichotomous	Thin	Thin, imbricate; ridged (sail scales)	2–4; 2.8	1.9–2.4	Lobate, smooth (low)	All body wall scales ridged	Gulf of Alaska seamounts, 4594 m
N. laxa Deichmann, 1936	Absent	4	Absent	Equal dichotomous	Thin	Thin, imbricate; multiple ridges	3–5; 3.6	3	Lobate, smooth	3 pairs of adaxial buccal scales	Amphi-North Atlantic, 2980–3186 m
N. horrida (Versluys, 1906)	Absent	3	Present	From common bolus	Massive	Thick, mosaic; unridged	5–6; 6–9	2.0–3.4	Spinose (massive)	Medial scales also spinose	Indonesia, 204 m
N. hypsocalyx Cairns, 2012	Absent	3	Present	From common bolus	Thin	Thin, imbricate; unridged	9; 13	2.7	Tall and serrate	Adaxial buccals elongate	New Zealand, 510–1118 m
N. clavata (Versluys, 1906)	Absent	3	Present	Sparse, dichotomous	Massive	Thick, mosaic; unridged	4–14; 7–8	2—3	Tall, narrow, smooth	Adaxial buccals numerous	Indonesia, Philippines, 128–335 m
N. ambigua (Studer, 1894)	Absent	3	Present	Sparse, dichotomous	Thin	Thick, mosaic; unridged	5–7; 6–7	2.5–3.0	Lobate, tall, smooth	3 pairs adaxial buccals	Galapagos, Gulf of Panama, 702– 1463 m
N. aurantiaca Cairns, 2018	Absent	3	Present	Sparse, dichotomous	Thin	Thin, interlocking; ridged	4–6; 6.5–7.0	2.8–3.2	Lobate, smooth		Wake Island, 745 m
N. leilae Bayer, 1951	Absent	3	Present	Sparse, dichotomous	Thin	Thin, imbricate; ridged (sail scales)	4–6; 5.2–5.6	2.0–2.5	Serrate cowl	Edges of buccals undulate	Indonesia, 740 m
N. alata Cairns & Bayer, 2007	Absent	3	Present	Equal dichotomous	Thin	Thin, imbricate; medial scale	4–5; 4–5	2.5–3.1	Lobate, tall (cowl), smooth	Whorls closely spaced	Hawaiian Islands, 477–750 m
N. vermifera Cairns & Bayer, 2007	Absent	3	Present	Equal dichotomous	Thin	Thick, mosaic; very low ridges	3–5; 4	1.8–2.0	Lobate, tall, smooth	Buccals in closed position	Hawaiian Islands, 275–527 m

Species	Dorsolateral edge of basal scale	Pairs of body wall scales	Polychaete commensalism	Branching mode	Body wall scale thickness	Coenenchymal scales: imbricate, thickness; ridged	Polyps/ whorl; whorl diameter (mm)	Polyp length (mm)	Distal edge of basal scales	Other characters	Geographic and depth range
N. allmani (Wright & Studer, 1889)	Absent	3	Present	Equal dichotomous	Thin	Thick, mosaic; unridged	4–7;5	3	Tall, serrate		Fiji, depth unknown
N. obscura (Versluys, 1906)	Absent	3	Present	Equal dichotomous	Thin	Thick, mosaic; unridged	4–6; 6–7	2.7–2.8	Lobate (undulate), smooth (cowl)		Indonesia, 984 m
N. dampieri Cairns, 2012	Absent	3	Present	Equal dichotomous	Thin	Thick, mosaic; unridged	5–8; 7	1.4–1.9	Lobate, tall, narrow	Numerous adaxial buccal scales	Lord Howe Islands, 342 m
N. mosaica Cairns, 2012	Absent	3	Present	Equal dichotomous	Massive	Thick, mosaic; unridged	3–5; 5–6	2.7–3.1	Lobate, slender, smooth		New Zealand, 228–294 m
N. vulgaris Cairns, 2012	Absent	3	Present	Equal dichotomous	Massive	Thick, mosaic; unridged	4–6; 4–5	2.0–2.4	Lobate, smooth	2 pairs adaxial buccals are ridged	New Zealand, 335–1165 m
N. orientalis (Versluys, 1906)	Absent	3	Present	Unknown	Thin	Thin, imbricate; unridged (concave)	6; 5.8	2.2–3.0	Lobate, smooth		Indonesia, 520 m
N. calamus Cairns, 2018	Absent	3	Absent	Unbranched	Thin	Thin, imbricate; ridged (sail sacles)	4; 5	4.5–5.0	Serrate, blunt		Wake Island, 2073 m
N. versluysi (Hickson, 1909)	Absent	3	Absent	Unbranched or very sparsely	Thin	Thin, imbricate; medial ridge	4–7; 5–7	3.2–3.7	Lobate, smooth	Basal scale ridged internally	Amphi-North Atlantic, 550–3100 m
N. speighti Taylor & Rogers, 2017	Absent	3	Absent	Sparse, dichotomous	Thin	Thin, imbricate; unridged	3–4; 2.5–3.6	2.0–2.2	Lobate (slender), smooth		Southwest Indian Ocean, 870 m
N. grandiflora (Kükenthal, 1907)	Absent	3	Absent	Sparse, dichotomous	Thin	Thick, mosaic; unridged	4–5; 4.5	3	Lobate, smooth	Numerous adaxial buccal scales	Indonesia, 805 m
N. studeri (Versluys, 1906)	Absent	3	Absent	Equal dichotomous	Massive	Thick, mosaic; unridged	4–8; 4–5	3.0–3.3	Lobate, smooth	Smooth body wall scales	New Zealand, Indonesia, 732–1392 m
N. biannulata (Kinoshita, 1907)	Absent	3	Absent	Equal dichotomous	Massive	Thick, mosaic; unridged	6–7; 4.8	1.8–2.0	Lobate, smooth	Adaxial buccals absent; medial scales closed	Japan, depth unknown
N. candidae Taylor & Rogers, 2017	Absent	3	Absent	Equal dichotomous	Thin	Thick, mosaic; unridged (smooth)	4–6; 4–5	2.0–2.4	Lobate, smooth		Southwest Indian Ocean, 763 m
N. japonensis (Aurivillius, 1931)	Absent	3	Absent	Equal dichotomous	Thin	Thin, imbricate; unridged	3–6; 3.5–4.0	2—3	Lobate, smooth	Stem stiff	Japan, 732 m
N. gigas Cairns & Bayer, 2007	Absent	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	10–14; 9–12	2.5–3.0	Lobate, tall, narrow, smooth		Hawaiian Islands, 362–399 m
N. dichotoma (Versluys, 1906)	Absent	3	Absent	Equal dichotomous	Thin	Thin, imbricate; low ridges	3–5; 4–5	2.8–3.1	Lobate, smooth		Hawaiian Islands, Malaysia, 204–1448 m
N. megalepis (Kinoshita, 1908)	Absent	3	Absent	Equal dichotomous	Thin	Thin, imbricate; ridged	5–8; 6–7	2.5–3.0	Lobate, smooth	Numerous small adaxial buccal scales	Japan, depth unknown
N. compressa (Kinoshita, 1908)	Absent	3	Absent	Lyrate	Massive	Thick, mosaic; unridged	7–8; 3	2	Lobate, smooth		Japan, Phoenix Islands, 501 m

species have scales that bear a single longitudinal (Fig. 2F) or multiple complexly arranged ridges (Fig. 2E). If these ridges are quite tall they have been termed sail scales (Cairns 2016)(Fig. 2G). Mosaic coenenchymals are not usually ridged (Fig. 2D). This character is best seen using SEM.

***Polyps/whorl*; *whorl diameter*:** Although every specimen and species has a range of polyps/whorl and whorl diameter, sometimes these numbers help to differentiate species. This character is easily determined using a dissecting microscope.

***Polyp length*:** As above, this character has a range for every specimen and species, but can sometimes differentiate among species. The polyp length is essentially the horizontal length of the polyp, which consist of the length of the buccal scale and whatever part of the operculars protrude from the buccal scale. This character is easily determined using a dissecting microscope.

***Shape of the distal edge of basal scales*:** The distal edge of the basal scales are usually slightly lobate and smooth (Fig. 1E), but in some species are serrate (Fig. 2H, K) or even spinose (e.g., *N. horrida*, Fig. 2I). It may extend far beyond its junction with the proximal edge of the medial scales as a cowl (Fig. 2K) or be quite short (Fig. 1D). This character is also easily determined using a dissecting microscope.

***Other characters*:** Other characters that are used to describe and differentiate species but are not consistently addressed in the keys include: shape and number of adaxial body wall scales (Fig. 2J), external ridging of the medial and buccal scales, closure of the body wall rings, aspects of the opercular scales, body wall formula (i.e., ratio of length of basal: medial: buccal scales), and number of polyps per cm.

Geographic and depth range. All ocean basins, 128–4594 m (Cairns 2012).

Polychotomous key to the species of the genus *Narella*

1a	Dorsolateral edge of basal scale bears a longitudinal ridge or ridges (Fig. 1A, D)	**2**
1b	Dorsolateral edge of basal scale unridged (smooth) (Fig. 1F)	**9**
2a	Three pairs of body wall scales per polyp (Fig. 1A, B, F)	**3**
2b	Four pairs of body wall scales per polyp (Fig. 1G)	**18**
3a	Polychaete commensalism present, causing extreme modification of basal scales to form a tube (Fig. 1H, I)	**4**
3b	Polychaete commensalism absent (no tubes)	**5**
4a	Colony branching sparse (Fig. 1M); coenenchymal scales thin and imbricate in arrangement (Fig. 2B); Hawaiian Islands	***N. macrocalyx***
4b	Colony branching lyrate (Fig. 1O); coenenchymal scales thick and mosaic in arrangement (Fig. 2C, D); South West Indian Ocean	***N. gilchristi***
5a	Colonies unbranched (Fig. 1J)	**6**
5b	Branches of colony originate from a common base or from a basal bolus (Fig. 1K, L)	***N. muzikae***
5c	Branching in a Y-shape	***N. merga***

5d	Branching sparse, dichotomous (Fig. 1M)	**7**
5e	Branching equal, dichotomous (Fig. 1N)	**12**
5f	Branching lyrate, sometimes with subsequent dichotomous branching (Fig. 1O)	**16**
5g	Branching pattern unknown; all scales radially ridged	***N. ornata***
6a	Multiple ridges on dorsolateral edge of basal scales (Fig. 1D); polyps less than 2.5 mm in length	***N. ferula***
6b	Single inconspicuous ridge on dorsolateral edge of basal scales (Fig. 1A, B); polyps greater than 3.5 mm in length	***N. hawaiinensis***
7a	Polyps less than 4 mm in length	**8**
7b	Polyps more than 5 mm in length	**10**
8a	Multiple ridges on dorsolateral edge of basal scales	***N. fordi***
8b	Single ridge on dorsolateral edge of basal scales	**9**
9a	Buccal scales ridged (Fig. 1D); medial scales short; Gulf of Alaska	***N. cristata***
9b	Buccal scales unridged; medial scales elongate; Bermuda	***N. alvinae***
10a	Whorl diameter less than 4 mm	***N. bayeri***
10b	Whorl diameter greater than 6 mm	**11**
11a	Polyp length 3.4–4.7 mm	***N. arbuscula***
11b	Polyp length 2.7–3.2 mm	***N. alaskensis***
12a	Extremely few polyps per whorl (occasionally only two)	***N. pauciflora***
12b	More numerous polyps per whorl (up to six)(Fig. 1F)	**13**
13a	Whorl diameter greater than 3.5 mm	**14**
13b	Whorl diameter less than 3.5 mm	**15**
14a	Multiple ridges on dorsolateral edge of basal scales; Antarctica	***N. gaussi***
14b	Single ridge on dorsolateral edge of basal scales; Hawaiian Islands	***N. bowersi***
15a	Medial and buccal scales ridged; northwest Atlantic Ocean	***N. regularis***
15b	Medials and buccals not ridged; Indonesian region	***N. parva***
16a	Coenenchymal scales unridged (granular)(Fig. 2C, D)	***N. valentine***
16b	Coenenchymal scales ridged (Fig. 2E–G)	**17**
17a	Polyps 2.6–2.8 mm in length; South Pacific	***N. virgosa***
17b	Polyps 2.0–2.2 mm in length; Northwest Atlantic	***N. bellissima***
18a	Colony unbranched; single ridge on dorsolateral edge of basal scales	***N. spectabilis***
18b	Colony sparsely dichotomous; multiple ridges on dorsolateral edge of basal scales	***N. abyssalis***
19a	Four pairs of body wall scales per polyp (Fig. 1G)	***N. laxa***
19b	Three pairs of body wall scales per polyp	**20**
20a	Polychaete commensalism present, causing extreme modification of basal scales to form a tube	**21**
20b	Polychaete commensalism absent (no tubes)	**32**
21a	Branches of colony originate from a common base or from a basal bolus (Fig. 1K, L)	**22**
21b	Branching sparse, dichotomous (Fig. 1M)	**23**

21c Branching equal, dichotomous (Fig. 1N) **26**

21d Branching pattern unknown; margin of basolateral scales tall and serrate .... ***N. orientalis***

22a Body wall scales massive (Figs 1P, 2A); coenenchymal scales mosaic in arrangement; margin of basal scale spinose........ ***N. horrida***

22b Body wall scales thin (normal); coenenchymal scales imbricate; margin of basal scale serrate .... ***N. hypsocalyx***

23a Coenenchymal scales thick (mosaic) and unridged (Fig. 2C, D) **24**

23b Coenenchymal scales thin and ridged **25**

24a Body wall scales massive; numerous small adaxial buccal scales; western Pacific (Figs 1P, 2A) .... ***N. clavata***

24b Body wall scales thin; 3 pairs of large adaxial buccals (Fig. 2J); eastern Pacific........ ***N. ambigua***

25a Polyps 2.8–3.2 mm in length; distal margin of basal scales lobate and smooth (Fig. 1C)........ ***N. aurantiacus***

25b Polyps 2.0–2.5 mm in length; distal margin of basal scales a serrate cowl (Fig. 2K)........ ***N. leilae***

26a Coenenchymal scales ridged (Fig. 2E–G)........ **27**

26b Coenenchymal scales not ridged (Fig. 2C, D)........ **29**

27a Coenenchymal scales thin and imbricate in arrangement; polyps 2.5–3.1 mm in length .... ***N. alata***

27b Coenenchymal scales thick (Fig. 2D) and mosaic in arrangement; polyps 1.8–2.0 mm in length........ ***N. vermifera***

28a Whorl diameter more than 6 mm........ **29**

28b Whorl diameter less than 6 mm........ **30**

29a Polyp length 2.7–2.8 mm; few adaxial scales........ ***N. obscura***

29b Polyp length 1.4–1.9 mm; numerous small adaxial scales (Fig. 2J) .... ***N. dampieri***

30a Polyp length 2.7–3.1 mm; adaxial scales not ridged .... ***N. mosaica***

30b Polyp length 2.0–2.4 mm; adaxial scales ridged .... ***N. vulgaris***

31a Colonies unbranched........ **32**

31b Branching sparse, dichotomous........ **33**

31c Branching equal, dichotomous **34**

31d Branching lyrate, sometimes with subsequent dichotomous branching .... ***N. compressa***

32a Polyp length 4.5–5.0 mm; distal margin of basal scales serrate.... ***N. calamus***

32b Polyp length 3.2–3.7 mm; distal margin of basal scales lobate and smooth .... ***N. versluysi***

33a Coenenchymal scales thick and mosaic in arrangement; polyp length approximately 3 mm .... ***N. grandiflora***

33b Coenenchymal scales thin and imbricate in arrangement; polyp length 2.0–2.2 mm........ ***N. speighti***

34a Body wall scales massive (Fig. 1P) **35**

34b Body wall scales thin (normal) **36**

35a Medial scales in open position; polyp length 3.0–3.3 mm............***N. studeri***
35b Medial scales in closed position (fused); polyp length 1.8–2.0 mm ....***N. biannulata***
36a Coenenchymal scales unridged (granular) **37**
36b Coenenchymal scales ridged...**38**
37a Coenenchymal scales thick and mosaic in arrangement; South West Indian Ocean .... ***N. candidae***
37b Coenenchymal scales thin and imbricate in arrangement; Japan..***N. japonensis***
38a Polyps per whorl fewer than 5..***N. dichotoma***
38b Polyps per whorl 5–8 .... ***N. megalepis***
38c Polyps per whorl more than 9 ....***N. gigas***

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RESEARCH ARTICLE

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Three new species of the spider genus *Luzonacera* Li & Li, 2017 from Philippines (Araneae, Psilodercidae)

Wan-Jin Chang[1,2], Fengyuan Li[1], Shuqiang Li[1]

1 *Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China* **2** *University of Chinese Academy of Sciences, Beijing, China*

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

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Abstract

Three new species of *Luzonacera* Li & Li, 2017 are described: *L. francescoballarini* Li & Li, **sp. n.** (♂♀), *L. lattuensis* Li & Li, **sp. n.** (♂♀) and *L. peterjaegeri* Li & Li, **sp. n.** (♂♀). Prior to this study, the genus was known by two species, both from Luzon Island, Philippines. So far, the genus and all five species are endemic to Luzon Island and can be found in dry or humid caves in a dark environment.

Keywords

cave, endemic, Luzon Island, Southeast Asia, tropical

Introduction

The spider family Psilodercidae Machado, 1951 contains eleven genera and 116 species (World Spider Catalog 2018, Li and Quan 2017). All species are restricted to tropical Asia and known from Sri Lanka and India to Philippines (World Spider Catalog 2018). Currently, five species of Psilodercidae belonging to four genera are known to occur in Philippines (World Spider Catalog 2018): *Psiloderces egeria* Simon, 1892 from Luzon, *Althepus noonadanae* Brignoli, 1973 from Mindanao, *Leclercera negros* Deeleman-Reinhold, 1995 from Negros, and *Luzonacera chang* Li & Li, 2017 and *L. duan* Li & Li, 2017 from Luzon.

The recently described genus *Luzonacera* Li & Li, 2017 was known from two species, *L. chang* Li & Li, 2017 and *L. duan* Li & Li, 2017 (World Spider Catalog 2018). While studying new material collected on Luzon Island, we recognized three new species of the genus. The goal of this paper is to provide detailed descriptions of these new species.

Materials and methods

All specimens were collected in Luzon Island and preserved in 95% ethanol solution. All types are deposited in the Institute of Zoology, Chinese Academy of Sciences in Beijing (IZCAS) and Senckenberg Research Institute in Frankfurt (SMF). A Leica M205 C stereomicroscope was used to measure and examine the specimens. Morphological details of the specimens were studied with an Olympus BX41 compound microscope. An Olympus C7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus SZX12 stereomicroscope was used to take photos. The images were generated using Helicon Focus 6.7.1 image stacking software and further revised with Adobe Photoshop. Leg measurements are shown as total length (femur, patella, tibia, metatarsus, and tarsus). Leg segments were measured from their retrolateral side except for *L. peterjaegeri* sp. n. which was measured from the prolateral side. All measurements are given in millimetres (mm). Terminology follows that of Li et al. (2014), Tong and Li (2007) and Deeleman-Reinhold (1995).

The extraction of genomic DNA from legs followed Li and Li (2018). Primer sets for the PCR and cycle sequencing reactions used for cytochrome c oxidase subunit I (COI) in this study are from Folmer et al. (1994). All sequences were analysed using BLAST. The GenBank accession numbers are provided in Table 1. The COI dataset of the three sequences obtained in this study and two sequences from GenBank were aligned using MAFFT version 7 (http://mafft.cbrc.jp/ alignment/server/). MEGA7.0.16 (Kumar et al. 2016) was used for subsequent manual adjustment of the sequences and calculation of pairwise comparisons of uncorrected K2P-distances.

Table 1. The accession numbers for each species in this paper.

Species	Length (bp)	GenBank accession number
Luzonacera francescoballarini sp. n.	651	MK238752
Luzonacera lattuensis sp. n.	651	MK238753
Luzonacera peterjaegeri sp. n.	651	MK238754

Taxonomy

Family Psilodercidae Machado, 1951

Genus *Luzonacera* Li & Li, 2017

Type species. *Luzonacera chang* Li & Li, 2017

Emended diagnosis. *Luzonacera* resembles *Althepus* Thorell, 1898 and *Leclercera* Deeleman-Reinhold, 1995. However, *Luzonacera* can be differentiated by the combination of the following characteristics: 1) absence of a conductor (versus presence of a conductor in both *Althepus* and *Leclercera*); 2) absence of a retrolateral protrusion on the tibia or cymbium of the male palp (versus presence of a retrolateral protrusion on the tibia or cymbium of the male palp in *Althepus* and *Leclercera*); 3) remarkably inflated tibia of the male palp; 4) pyriform bulb with spirally extended embolus; and 5) two pairs of spermathecae, the lateral spermathecae with longer stalks than the medial spermathecae.

Composition. *L. chang* Li & Li, 2017 (the type species), *L. duan* Li & Li, 2017, *L. francescoballarini* sp. n., *L. lattuensis* sp. n. and *L. peterjaegeri* sp. n.

Distribution. Philippines.

Illustrated key to the males of *Luzonacera*

1 Embolus and bulb equal in length; embolus and bulb ratio approximately equal to 1 (Fig. 1i) .... ***L. chang***
– Embolus short (bulb ca. 2 times longer than the embolus); embolus and bulb ratio: 0.40–0.57 (Fig. 1ii–v) **2**
2 Slight constriction of the central part of bulb (Fig. 1iii) .... ***L. francescoballarini* sp. n.**
– Pronounced constriction of the central part of bulb (Fig. 1ii, iv, v) **3**
3 Bulb with smooth surface dorsally (Fig. 1v) .... ***L. peterjaegeri* sp. n.**
– Bulb with a notch (NO) dorsally (Fig. 1ii & iv) **4**
4 The tip of the bulb without protrusion (PT) (Fig. 1ii) .... ***L. duan***
– The tip of the bulb with protrusion (PT) (Fig. 1iv) .... ***L. lattuensis* sp. n.**

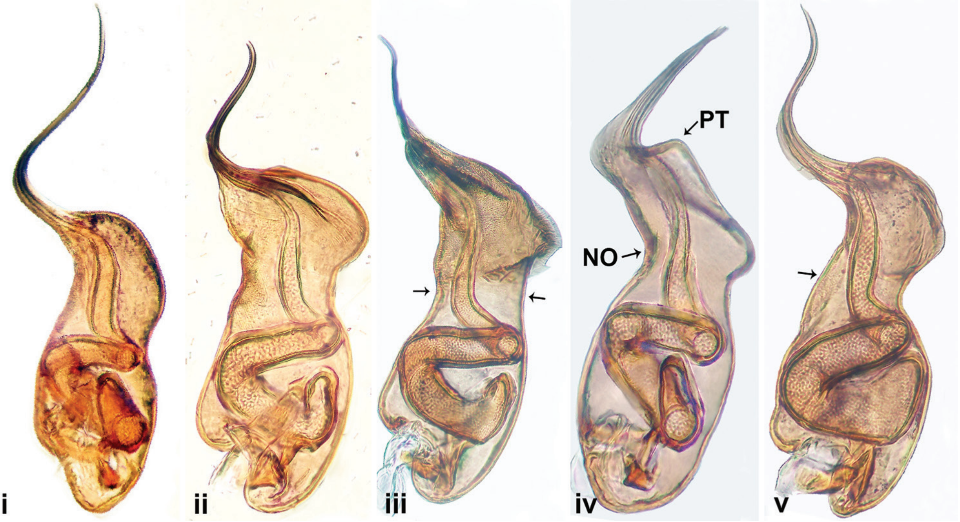

Figure 1. Prolateral view of male palp bulbs of *Luzonacera* species: **i** *L. chang* **ii** *L. duan* **iii** *L. francescoballarini* sp. n. **iv** *L. lattuensis* sp. n. and **v** *L. peterjaegeri* sp. n. Abbreviations: **PT** = protrusion, **NO** = notch.

Illustrated key to the females of *Luzonacera*

1 Two pairs of similar spermathecae (a–d) **2**
– Two pairs of dissimilar spermathecae (medial pair oblique, tube-shaped) (e)... .... ***L. peterjaegeri* sp. n.**

2 Spermathecae without globose distal part (with swollen distal ends) (Fig. 2a) .... ***L. chang***
– Spermathecae with globose distal part (Fig. 2b–d) **3**
3 Two pairs of spermathecae pointed almost the same direction (Fig. 2b, d) .. **4**
– Two pairs of spermathecae pointed opposite directions (Fig. 2c) .... ***L. francescoballarini* sp. n.**
4 Relatively short stalks of medial spermathecae; distal part and stalk ratio approximately 0.5 (Fig. 2d) .... ***L. lattuensis* sp. n.**
– Relatively long stalks of medial spermathecae; distal part and stalk ratio approximately 0.25 (Fig. 2b) .... ***L. duan***

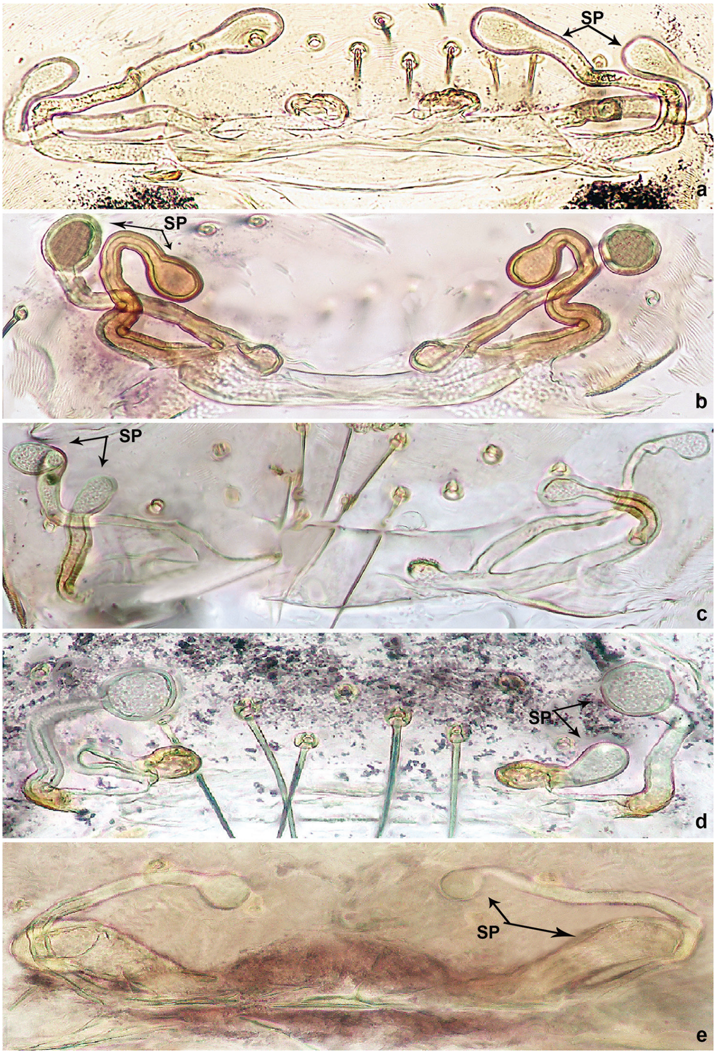

Figure 2. Female internal genitalia of five different species of *Luzonacera*: **a** *L. chang* **b** *L. duan* **c** *L. francescoballarini* sp. n. **d** *L. lattuensis* sp. n. and **e** *L. peterjaegeri* sp. n. Abbreviation: **SP** = spermathecae.

Luzonacera francescoballarini **Li & Li, sp. n.**

http://zoobank.org/EEE59EF0-7FF6-4F7D-BB5E-6FE76729FB76

Figs 3, 4, 9, 10

Types. Holotype: ♂ (IZCAS), Philippines, Luzon Island, Bulacan Province, San Miguel City, near Biak-Na-Bato National Park, Bayukbok Cave, 15°10'5.4"N, 121°5'4.3"E, 125 m, 21.V.2015, F. Ballarin and Y. Li. **Paratypes:** 1♂, 1♀ (IZCAS), same data as holotype.

Etymology. The species is named after Francesco Ballarin, who collected the type series; name in genitive case.

Diagnosis. *Luzonacera francescoballarini* sp. n. resembles *L. lattuensis* sp. n. in having a short embolus, and two pairs of twisted spermathecae globose at distal parts. Males can be distinguished from the latter species by the smooth dorsal surface of the bulb (Figure 3B); females can be distinguished by having longer spermathecae (Figure 4A; versus shorter in *L. lattuensis* sp. n. in Figure 6A).

Description. Male (Holotype). Total length 4.81; carapace 1.60 long, 1.28 wide; abdomen 3.20 long, 0.96 wide. Colour faded. Carapace round, pale yellow, with ovoid brown patch medially and rounded brown patch posterior to ocular area. Fovea shallow. Anterior margin of thoracic region distinctly elevated. Chelicerae light brown with lamina, promargin with a single tooth and retromargin with two small teeth (Figure 7A). Clypeus slanting, light brown. Labium slanting, pale brown. Sternum pale brown with large patch of brown spots medially. Abdomen elongated with complex patterns dorsally and ventrally. Legs light brown; measurements: I 22.44 (6.73, 0.64, 6.41, 3.21, 5.45), II 17.63 (5.13, 0.64, 5.13, 5.45, 1.28), III 12.05 (3.53, 0.32, 3.40, 3.20, 1.60), IV 23.07 (7.05, 0.64, 7.05, 6.41, 1.92). Palp (Figure 3A–E): tibia swollen at the base, length/width = 2.40; cymbium swollen with distal protrusion and numerous long setae; length/width = 2.33; bulb light brown, pyriform; embolus forms a slender spiral extending from tip of bulb.

Female (paratype). Similar to male in coloration and general features but slightly larger (Figure 4D, E). Measurements: total length 3.59; carapace 1.20 long, 1.40 wide; abdomen 2.20 long, 0.80 wide. Leg measurements: I 14.11(4.17, 0.32, 4.17, 4.17, 1.28), II 10.88 (3.50, 0.32, 3.53, 3.21, 0.32), III 9.26 (2.56, 0.50, 2.60, 2.60, 1.00), IV 14.06 (4.49, 0.40, 4.17, 4.00, 1.00). Internal genitalia: two pairs of slender spermathecae with long stalks (ca. 6 times longer than distal globular parts), spermathecae distal parts not wider than basal width of stalks, both pairs equal in width (Figure 4A).

Distribution. Type locality only (Figure 10).

Natural history. Collected in a dark and rather humid cave, close to the ground, along the wall of the cave with huge rocks.

Comments. Based on the 651 bp aligned sequences, the COI uncorrected K2P-distance between *L. francescoballarini* sp. n. and *L. chang* is 13.5%, between *L. francescoballarini* sp. n. and *L. duan* is 15.0%, between *L. francescoballarini* sp. n. and *L. lattuensis* sp. n. is 14.9%, and between *L. francescoballarini* sp. n. and *L. peterjaegeri* sp. n. is 13.9%.

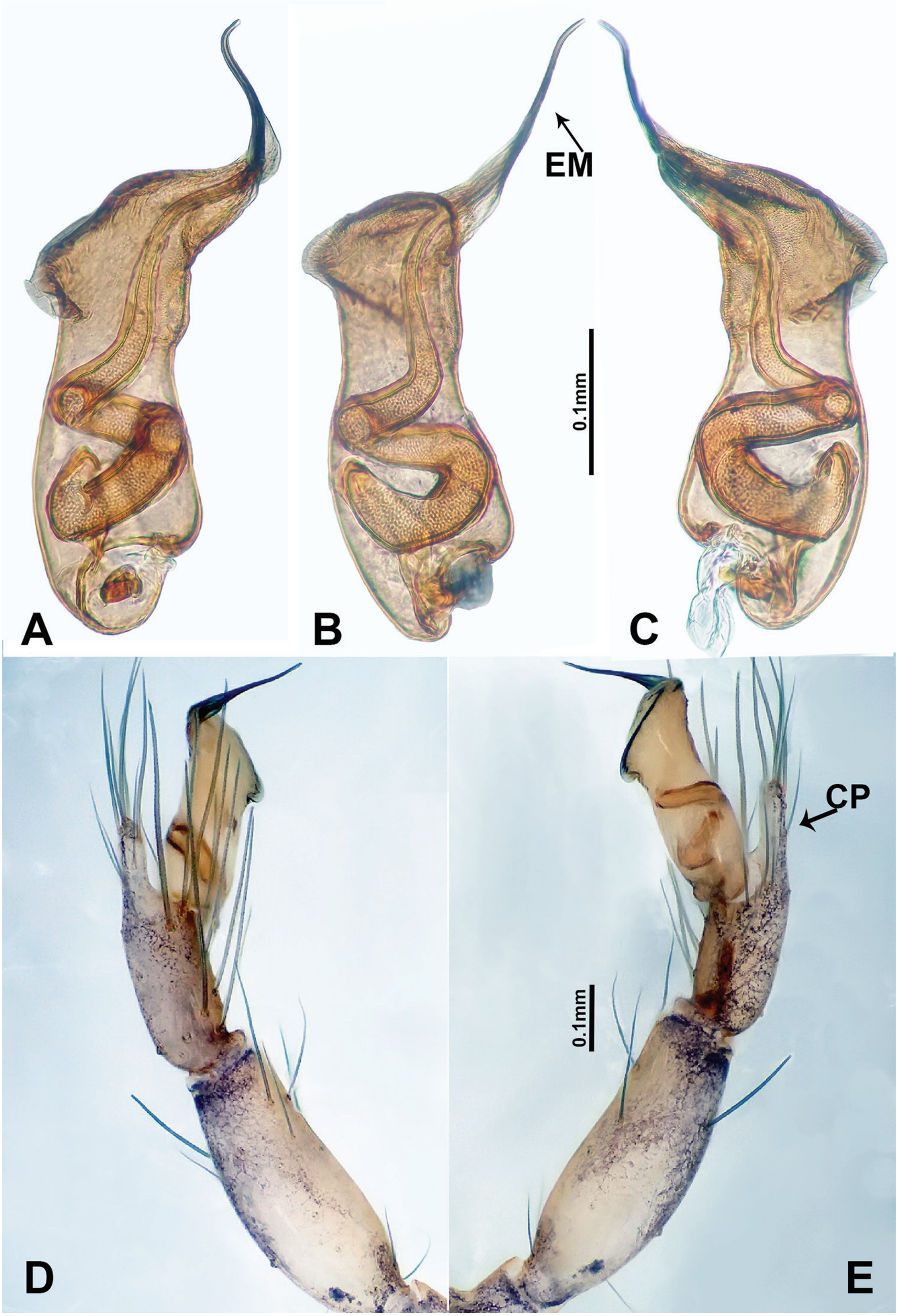

Figure 3. *Luzonacera francescoballarini* sp. n., male holotype **A** palp bulb, retrolateral view **B** palp bulb, ventral view **C** palp bulb, prolateral view **D** palp, prolateral view **E** palp, retrolateral view. Abbreviations: **EM** = embolus; **CP** = cymbial protrusion.

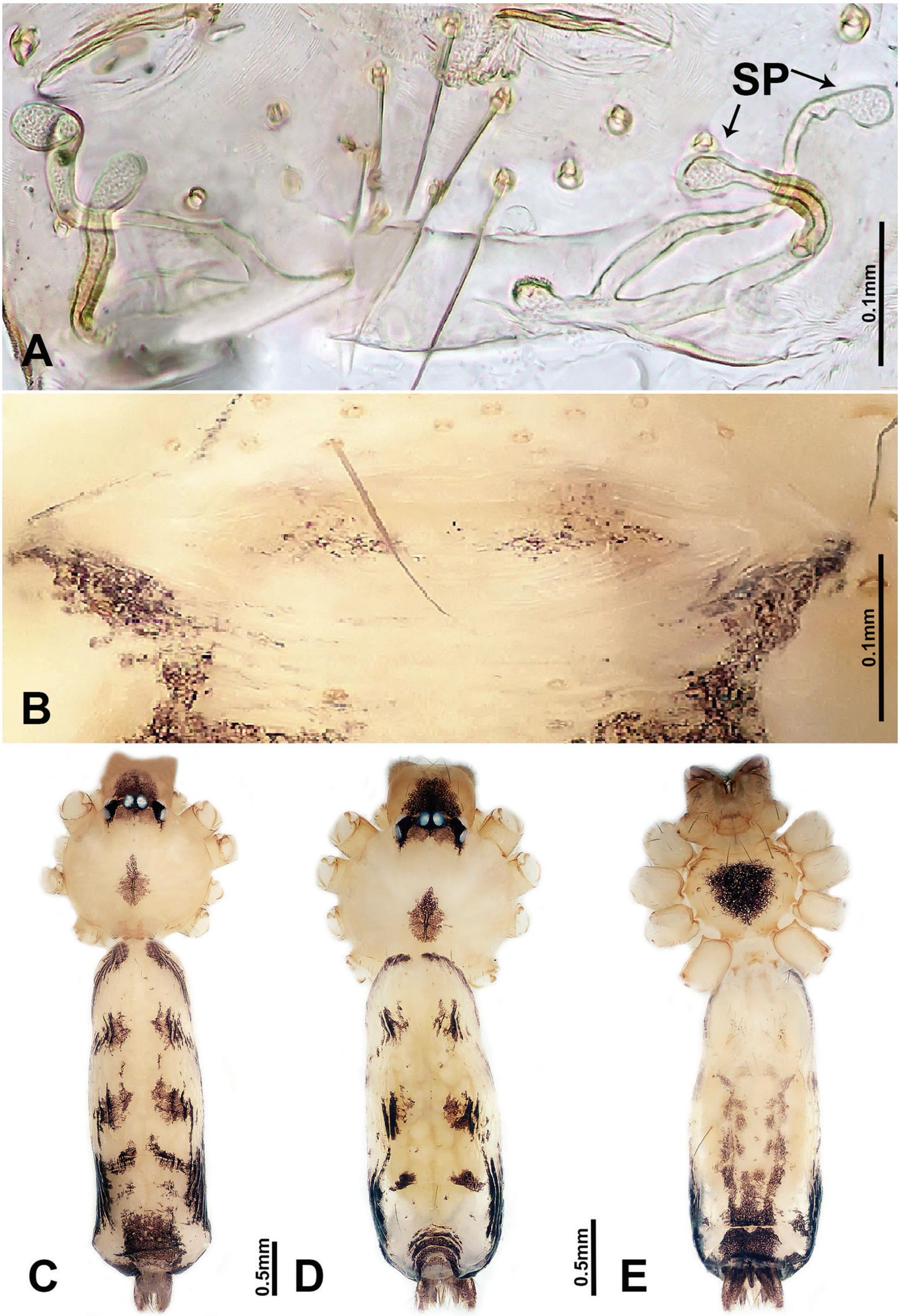

Figure 4. *Luzonacera francescoballarini* sp. n., male holotype and female paratype **A** internal genitalia, dorsal view **B** female epigastric furrow, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: **SP** = spermathecae.

Luzonacera lattuensis Li & Li, sp. n.

http://zoobank.org/0D355C5B-450C-4F82-805E-0062E14381F0
Figs 5, 6, 9, 10

Types. Holotype: ♂ (IZCAS), Philippines, Luzon Island, Cagayon Province, Tuguegarao City, Penablanca Village, Lattu-Lattuc Cave, 17°42'23"N, 121°49'2"E, 111 m, 31.V.2015, F. Ballarin and Y. Li. **Paratypes:** 1♂, 1♀ (IZCAS), same data as holotype.

Etymology. The species name is an adjective referring to the type locality.

Diagnosis. Both sexes of *L. lattuensis* sp. n. and *L. francescoballarini* sp. n. are very similar. Males of *L. lattuensis* sp. n. can be distinguished from *L. francescoballarini* sp. n. by the bulb with a dorsal notch (Figure 5A) and a relatively longer cymbium tip (Figure 5E); females can be distinguished by having shorter spermathecae with more widely spaced bases (Figure 6A; versus longer spermathecae with more narrowly spaced bases in *L. francescoballarini* sp. n. in Figure 7A).

Description. Male (Holotype). Total length 3.85; carapace 1.28 long, 0.96 wide; abdomen 2.56 long, 0.75 wide. Carapace round and brown, with three longitudinal brown bands; the central band is 3 times wider than the lateral bands (Figure 6C). Fovea shallow, brown. Anterior margin of thoracic region distinctly elevated. Chelicerae brown with lamina, promargin with one tooth and retromargin with two small teeth (Figure 9B). Clypeus slanting, brown with two pale rounded areas laterally and two triangular projections basally. Labium slanting, dark brown. Sternum pale brown with three dark brown patches laterally. Abdomen elongated, with complex patterns dorsally and ventrally. Legs brown with white annulations; measurements: I & II missing, III 7.80 (2.24, 0.32, 2.24, 2.00, 1.00), IV missing. Palp (Figure 5A–E): tibia swollen at the base, length/width = 2.50; cymbium with distal protrusion, length/width = 2.0; bulb light brown, pyriform; embolus forms a slender spiral extending subapically from bulb.

Female (paratype). General features and coloration are similar to the male, but the female is slightly larger (Figure 6D, E). Measurements: total length 3.81; carapace 1.25 long, 1.00 wide; abdomen 2.56 long, 1.40 wide. Leg measurements: I 11.05 (3.25, 0.40, 3.20, 3.20, 1.00), II 10.57 (3.20, 0.32, 2.88, 3.21, 0.96), III 6.74 (2.00, 0.32, 1.92, 1.75, 0.75), IV 13.35 (3.75, 0.31, 3.80, 4.49, 1.00). Internal genitalia: two pairs of twisted spermathecae, medial spermathecae with globose distal parts and short stalks, and lateral spermathecae with globose distal parts and long stalks (stalks ca. 3 times longer than distal parts) (Figure 6A).

Distribution. Type locality only (Figure 10).

Natural history. Collected close to the ground along the wall of a dark, rather dry and dusty secondary cave with huge rocks.

Comments. Based on the 651 bp- aligned sequences, the COI uncorrected K2P-distance between *L. lattuensis* sp. n. and *L. chang* is 12.4%, between *L. lattuensis* sp. n. and *L. duan* is 11.5%, and between *L. lattuensis* sp. n. and *L. peterjaegeri* sp. n. is 13.6%.

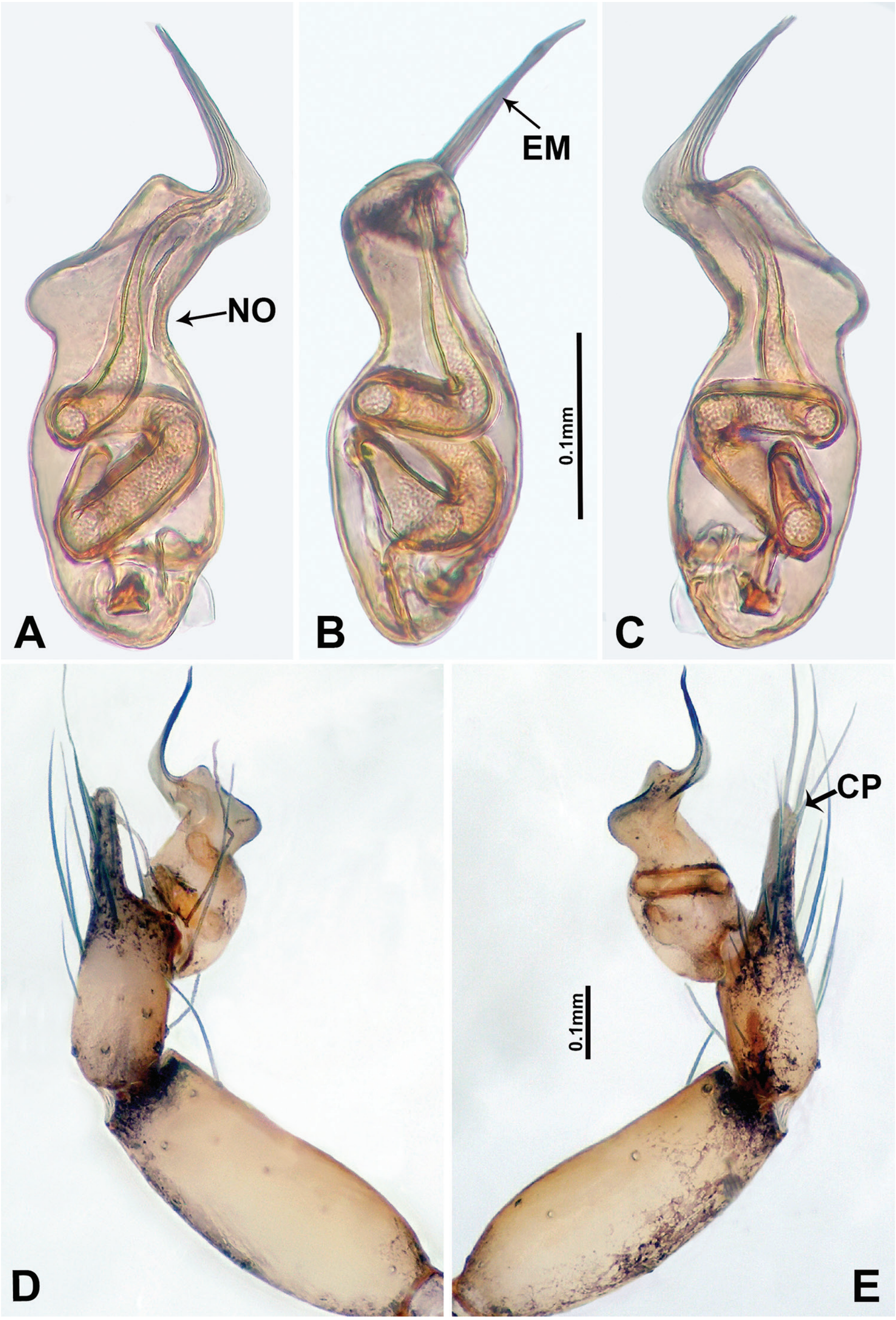

Figure 5. *Luzonacera lattuensis* sp. n., male holotype **A** palp bulb, retrolateral view **B** palp bulb, ventral view **C** palp bulb, prolateral view **D** palp, prolateral view **E** palp, retrolateral view. Abbreviations: **EM** = embolus; **CP** = cymbial protrusion; **NO** = notch.

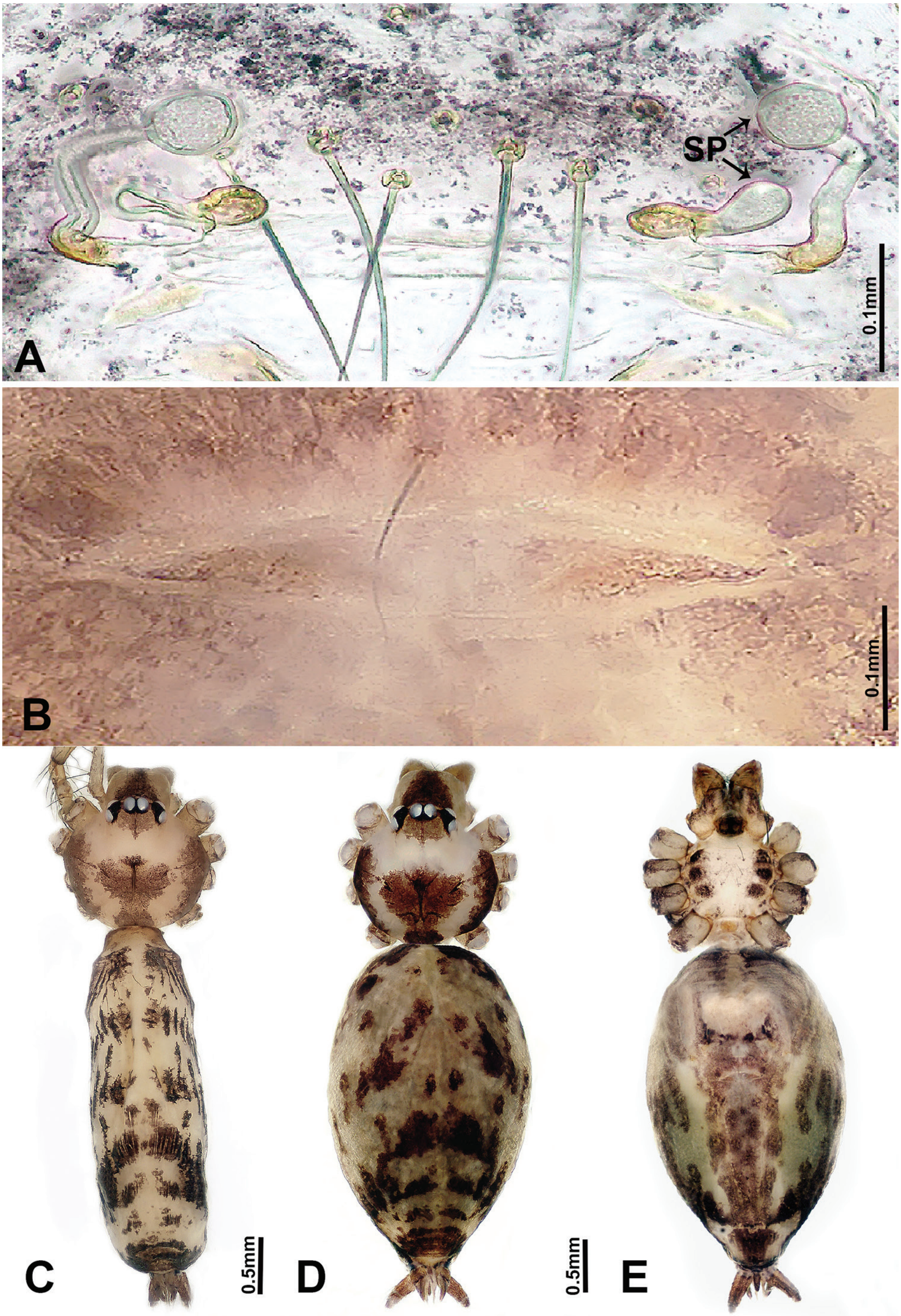

Figure 6. *Luzonacera lattuensis* sp. n., male holotype and female paratype **A** internal genitalia, dorsal view **B** female epigastric furrow, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: **SP** = spermathecae.

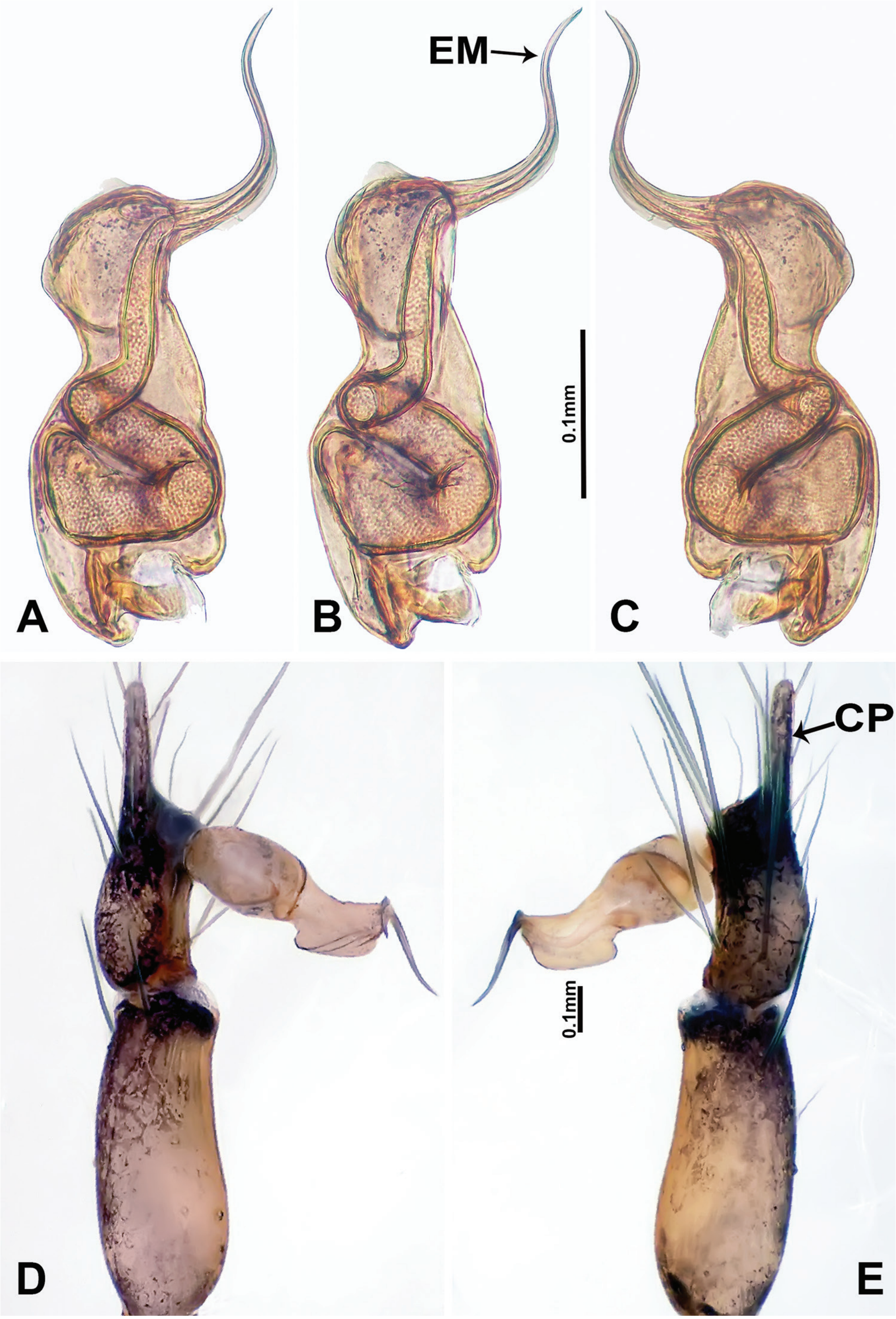

Figure 7. *Luzonacera peterjaegeri* sp. n., male holotype **A** right palp bulb, retrolateral view **B** right palp bulb, ventral view **C** right palp bulb, prolateral view **D** right palp, prolateral view **E** right palp, retrolateral view. Abbreviations: **EM** = embolus; **CP** = cymbial protrusion.

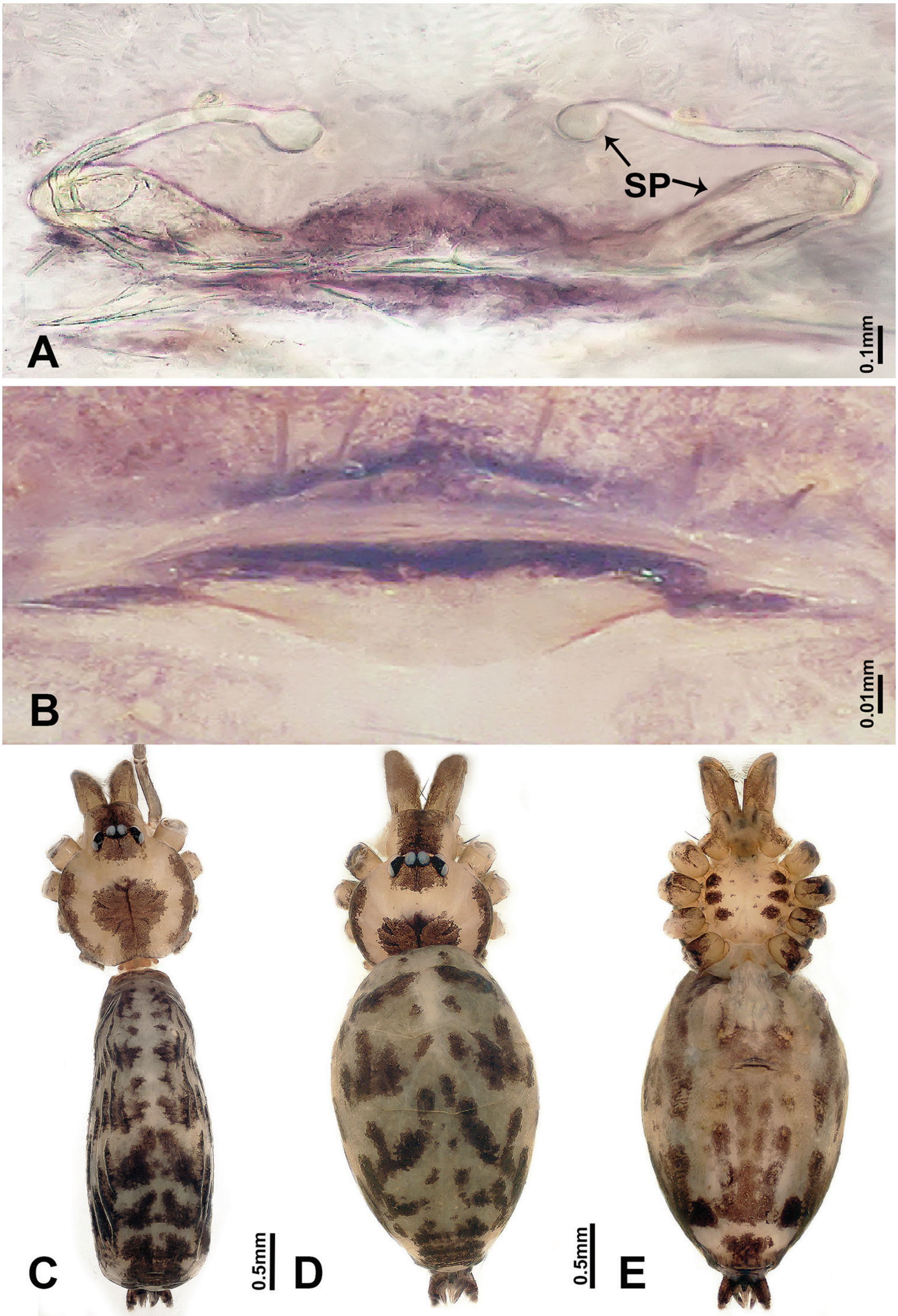

Figure 8. *Luzonacera peterjaegeri* sp. n., male holotype and female paratype **A** internal genitalia, dorsal view **f** female epigastric furrow, ventral view **C** male habitus, dorsal view **D** female habitus, dorsal view **E** female habitus, ventral view. Abbreviation: **SP** = spermathecae.

Luzonacera peterjaegeri **Li & Li, sp. n.**

http://zoobank.org/ B57BC1C9-4645-4662-90C1-CE3FFC211E96
Figs 7–9

Types. Holotype: ♂ (SMF), Philippines, Northern Luzon Island, Teresita State, Cagayan Province, Lower Kimmabalyu Cave, 18°11'35.4"N, 121°52'10.3"E, 22.I.2015, H. Steiner. **Paratypes:** 1♂, 2♀ (SMF), same data as holotype.

Etymology. The species is named after Peter Jäger in honour of his contribution to the study of spiders from Asia; name in genitive case.

Diagnosis. *Luzonacera peterjaegeri* sp. n. can be distinguished from all other known species of the genus by a distinct constriction on the central part of the bulb (Figure 7A); females can be distinguished by two types of spermathecae: one pair of slender spermathecae bearing a globose distal part, and one pair of oblique, tube-shaped spermathecae (Figure 8A; versus both pairs of spermathecae bearing a globose distal part in other species). Moreover, both sexes of *L. peterjaegeri* sp. n. have longer chelicerae (Figure 8; versus shorter chelicerae in other species).

Description. Male (Holotype). Total length 4.00; carapace 1.50 long, 1.40 wide; abdomen 2.50 long, 1.00 wide. Carapace round, pale brown, with three longitudinal brown bands, with the middle band 3 times wider than the lateral bands (Figure 8C). Fovea shallow and brown. Anterior margin of thoracic region distinctly elevated. Chelicerae long, brown with lamina, promargin with one tooth, and retromargin with two small teeth (Figure 9C). Clypeus brown with two pale rounded areas laterally and two relatively longer protrusions basally. Labium brown. Sternum brown with three dark brown patches laterally. Abdomen elongated, with complex patterns

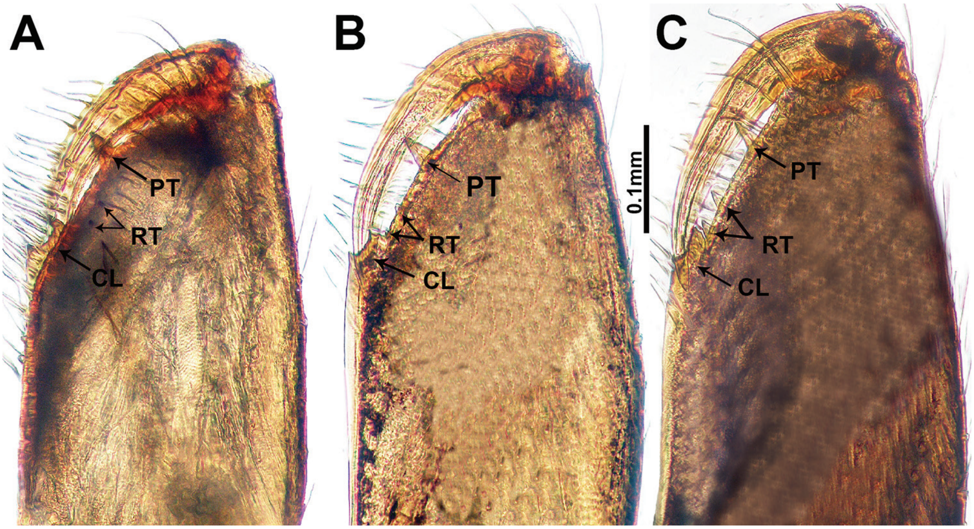

Figure 9. Cheliceral retromargin **A** *L. francescoballarini* sp. n. **B** *L. lattuensis* sp. n. **C** *L. peterjaegeri* sp. n. Abbreviations: **PT** = promargin teeth; **RT** = retromargin teeth; **CL** = cheliceral lamina.

dorsally and ventrally. Leg measurements: all legs missing. Right palp (Figure 7A–E): tibia swollen at the base, length/width = 2.25; cymbium with distal protrusion, length/width = 3.4; bulb light brown, pyriform; embolus forms a slender spiral elongating terminally from bulb.

Female (paratype). General features and coloration are similar to male, but the female is slightly larger (Figure 8D, E). Measurements: total length 4.17; carapace 1.60 long, 1.28 wide; abdomen 2.56 long, 1.5 wide. Legs missing. Internal genitalia: two pairs of spermathecae, one pair of spermathecae globose distally with long stalks (ca. 6 times longer than distal parts), the other pair are oblique, tube-shaped spermathecae (Figure 8A).

Distribution. Type locality only (Figure 10).

Comments. Based on the 651 bp aligned sequences, the COI uncorrected K2P-distance between *L. peterjaegeri* sp. n. and *L. chang* is 15.9%, and between *L. peterjaegeri* sp. n. and *L. duan* is 13.9%.

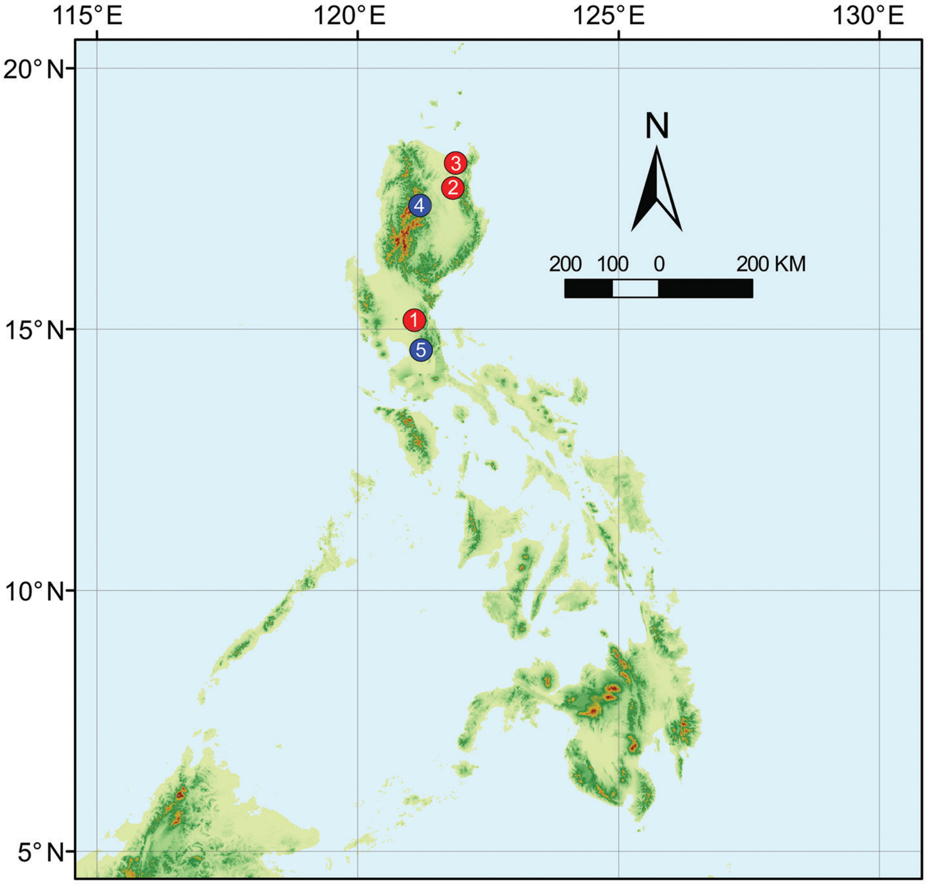

Figure 10. Distribution of five *Luzonacera* in Philippines **1** *Luzonacera francescoballarini* sp. n. **2** *L. lattuensis* sp. n. **3** *L. peterjaegeri* sp. n. **4** *L. duan* **5** *L. chang*.

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RESEARCH ARTICLE

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New discoveries of the family Epicopeiidae from China, with description of a new species (Lepidoptera, Epicopeiidae)

Si-Yao Huang[1], Min Wang[1], Wa Da[2], Xiao-Ling Fan[1]

[1] Department of Entomology, College of Agriculture, South China Agricultural University, Guangzhou 510642, Guangdong, China **[2]** *Tibet Plateau Institute of Biology, Lhasa 850001, Xizang Autonomous Prefecture, China*

Corresponding author: *Xiao-Ling Fan* (fanxiaol66@scau.edu.cn)

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Abstract

Some new discoveries of the family Epicopeiidae Swinhoe, 1892 from China are reported. A new species, *Mimaporia owadai* Huang & Wang, **sp. n.** is described from W. Sichuan. *Burmeia* Minet, 2003 and *Psychostrophia endoi* Inoue, 1992 are reported as new to China, with the female genitalia of the former described for the first time. The females of *Psychostrophia endoi* Inoue, 1992 and *Deuveia banghaasi* Hering, 1932 are reported for the first time. Adults and genitalia of all species aforementioned are illustrated.

Keywords

Geometroidea, Himalaya, Indochina, Oriental swallowtail moth, taxonomy

Introduction

The family Epicopeiidae Swinhoe, 1892 is a small group belonging to Geometroidea hitherto comprised of ten genera and approximately 25 species restricted in the Asian Palaearctic and Oriental regions (Wei and Yen 2017). They are well known as mimics of many other lepidopterous families such as Papilionidae, Riodinidae, Pieridae, Nymphalidae, Zygaenidae, Geometridae, and Erebidae (Wei and Yen 2015). Members of this family usually share the following autapomorphies: head without ocelli, forewing without an areole and in forewing venation vein R_5 usually stalked with vein M_1 (Minet 2003). Nearly all of the species in Epicopeiidae are day-flying creatures, with the exception of *Amana angulifera* Walker, 1855, which is nocturnal and can be attracted to light in the night (Wei and Yen 2015). Early stage is poorly known in this family, but in a few cases that have already been revealed, the larva and pupa are mainly covered by waxy matter on the surface (Janet and Wytsman 1903, Sugi 1972, Nakamura 2006).

In mainland China, this family is poorly studied. Most of the genera included in Epicopeiidae in modern concept were placed and studied in Epipleminae (formerly Epiplemidae, now regarded as a subfamily of Uraniidae) in Chinese literatures, except for the genus *Epicopeia* Westwood, 1844. In Zhu (1981), three genera and three species placed in Epiplemidae and one genus, five species, and two subspecies placed in Epicopeiidae are all belonging to the Epicopeiidae in modern concept. In Zhu et al. (2004), three genera and nine species of Epicopeiidae have been recorded (all in Epiplemidae). In the present study, nine genera and 22 species of Epicopeiidae are recorded in mainland China, and most of them are distributed in rather high altitudes in the mountainous region of western China (Fig. 1). During the research of the lepidopterous collection of South China Agricultural University, we found a male belonging to a previously undescribed species of the genus *Mimaporia* Wei & Yen, 2017, which has already been figured in Wei and Yen (2017). The examination of the genitalia proves it to be a distinct species of this genus and is described herein. Meanwhile, female individuals of three little known species, viz. *Burmeia leesi* Minet, 2003, *Psychostrophia endoi* Inoue, 1992, and *Deuveia banghaasi* (Hering, 1932) are also found in the collection and female genitalia of these three species are illustrated for the first time. Among them, *Burmeia leesi* Minet and *Psychostrophia endoi* Inoue are recorded for the first time in China.

Materials and methods

Specimens examined in this study were all collected in daytime by an insect net, and are deposited in the collection of South China Agricultural University (SCAU), Guangzhou. All adult photos were taken by a Nikon CoolPix S7000 camera, the adults in wild and habitat photos are taken by Sony DSC-TX100 and Sony DSC-RX100 v1.00 cameras. Abdomens were removed and macerated in 10% KOH for examination of male and female genitalia. Photographs of the male genitalia of *Mimaporia owadai* sp. n. were taken under a Zeiss SteReo Discovery V.12 digital microscope, and genitalia photos of other species were all taken under a Keyence VHX-5000 digital microscope. Adult and genitalia photos were all processed by Adobe Photoshop CS5 software. Terminology of adult and genitalia follows Klotz (1970), Kristensen (2003), Minet (2003), and Wei and Yen (2017). New records are indicated by asterisk (*).

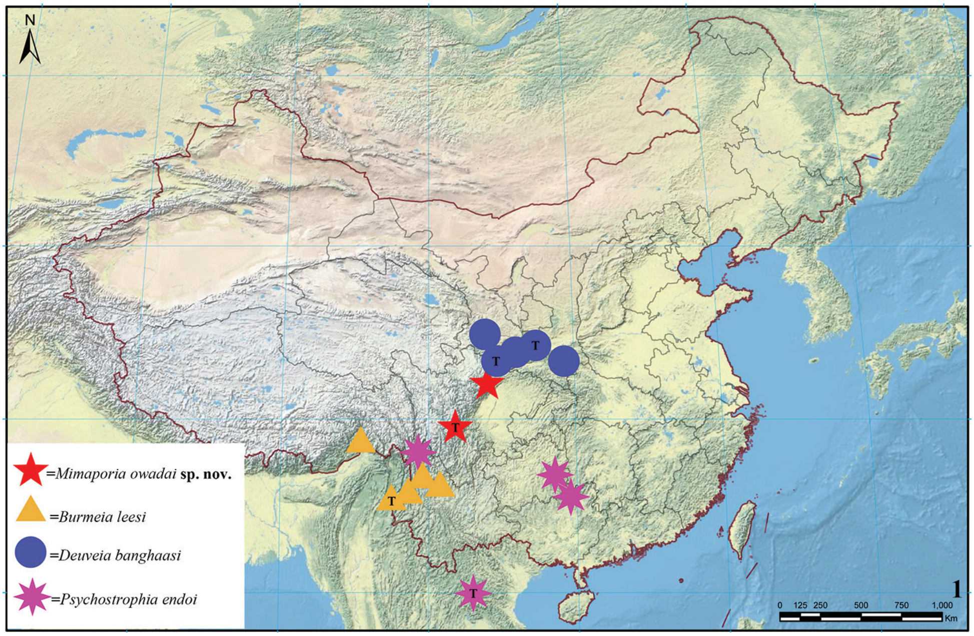


Figure 1. Distribution of part of the Epicopeiidae species in China. The T refers to the type locality of each species. Records of distribution are taken from Zhu et al. (2004), Wei and Yen (2017), Hering (1932), Minet (2003), and results of this work.

Taxonomy

Mimaporia Wei & Yen, 2017

Mimaporia Wei & Yen, 2017: 542, type species: *Mimaporia hmong* Wei & Yen, 2017.

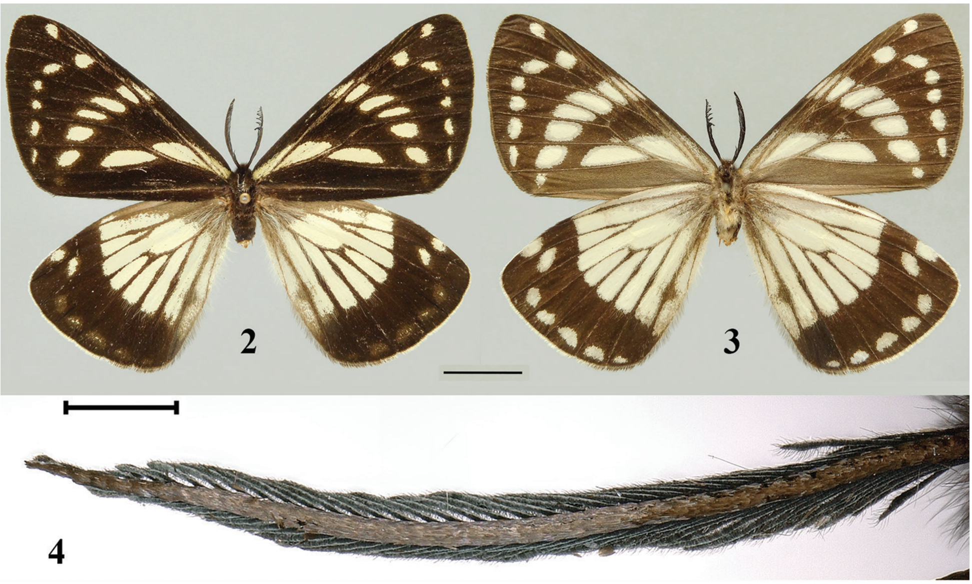
Diagnosis. The genus *Mimaporia* is characterized by the following characters: chaetosemata absent, forewing vein M_2 situated closer to vein M_3 than to the stem of vein R_5 and M_1 and aedeagus with a strongly sclerotized shaft.

Mimaporia owadai Huang & Wang, sp. n.

http://zoobank.org/73A9A812-E80B-4CF8-BC60-770D04D113FE
Figs 2–9

Mimaporia sp.: Wei & Yen, 2017, 544, 547, fig. 11.

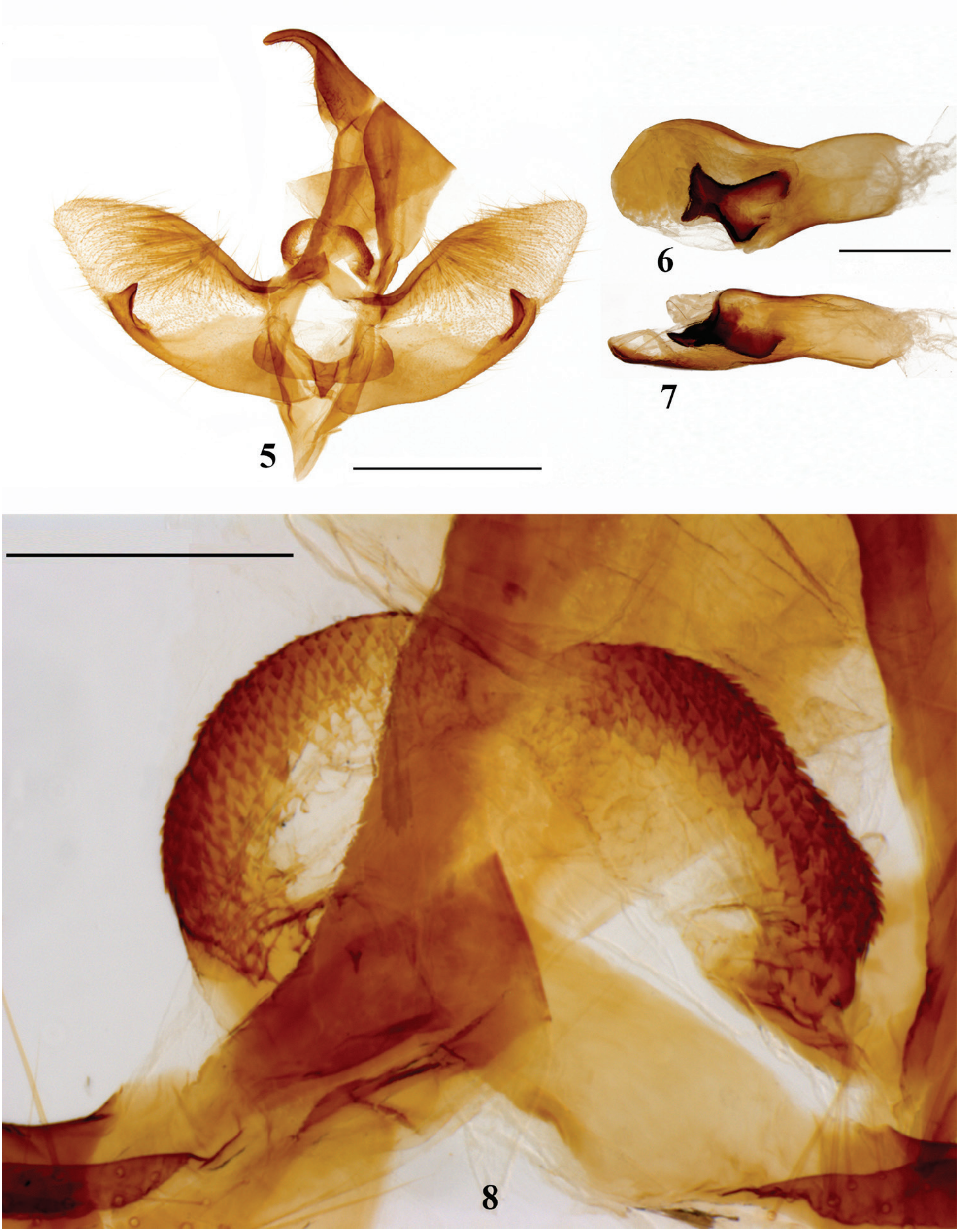
Type material. Holotype: male, altitude 2800 m, 3.VIII.2004, Moxi Town, Luding County, Ganzi Tibetan Autonomous Prefecture, PR China, leg. Min Wang (SCAU).



Figures 2–4. *Mimaporia owadai* sp. n., adult: **2** upperside **3** underside **4** enlarged antenna. Scale bars: 1 cm (**2, 3**); 1 mm (**4**).

Diagnosis. Externally, male of *Mimaporia owadai* sp. n. is similar to that of the type species of the genus, *M. hmong* Wei & Yen, 2017, but it can be immediately distinguished from the latter externally by the bipectinate antenna, more yellowish patterns on upper side of both wings, hindwing upper side with a well-developed grayish basal zone and with submarginal band weakly developed, with only trails in cell M_1 to cell CuA_2. In male genitalia, *Mimaporia owadai* sp. n. can be distinguished easily from *M. hmong* by the tip of the valve obviously narrowing and ending with a sharper apex, praesacculus ending with a single-branched process, juxta with a median triangular process directing ventrally and with the sclerotized shaft in aedeagus narrowing in the middle part. The individual figured in Wei and Yen (2017: 544, fig. 11) is identical with the holotype in external features, which should be regarded as the same species.

Description. Male (Figs 2–4). Length of forewing 35 mm, wingspan 62 mm. Head black; frons wide, covered with long blackish brown hairy scales and white scales; vertex covered with long blackish brown hair; compound eye black and large; antenna black, bipectinate. Thorax black; patagia covered with white scale and long blackish brown hairy scales; tegula covered with long blackish brown hairy scales and brownish scales, and surrounded by short white scales; abdomen covered with black scales and long blackish brown hair dorsally and yellowish white hair ventrally. Forewing upper side ground color black, all patterns creamy white, cilia black. Costa with a slender stripe at base; a triangle cell bar present at the base of discoidal cell; median band consisted of six patches of different sizes and shape extending from costa to cell CuA_1; postmedian band consisted of six dots of different sizes and shape extending from cell R_4 to cell CuA_1 and shifting outwards at cell R_5 and M_1; a single rounded dot present



Figures 5–8. Male genitalia of *Mimaporia owadai* sp. n.: **5** genitalia capsule ventral view **6** aedeagus dorsal view **7** aedeagus lateral view **8** enlarged area of genitalia capsule showing costula. Scale bar: 1 mm.

in cell R_3 at subapical zone. Forewing under side ground color blackish brown, paler at basal area; patterns similar to upper side. Hindwing upper side ground color black, all patterns creamy white, cilia yellowish white from apex to vein CuA_1, and gradually become blackish brown from vein CuA_1 to anal angle. Wing base and about half of the

Figure 9. Habitat of *Mimaporia owadai* sp. n. in Moxi County.

hindwing costa grayish brown; median zone with a single large patch extending from costa to dorsum, and are divided into smaller and slender patches by darkened veins. Two dots present at subapical zone; submarginal band poorly-developed, with only trail of paler patches extending from cell m_1 to cell CuA_2. Hindwing underside ground color similar to forewing underside, submarginal band well-developed and represented by five separated yellowish white patches extending from cell M_1 to CuA_2; other patterns similar to the upper side.

Male genitalia (Figs 5–8). Uncus well developed, bending downwards at distal one third. Tegumen broad. Costula (Fig. 8) presents at the junction of tegumen and vinculum, semi-circular and concaves shallowly at the middle, its surface scobinated by numerous small spines at both side of marginal area of the concave portion. Transtilla broad, slightly sclerotized. Juxta broad, U-shaped, with a triangular process at the middle part. Saccus narrow, triangular. Valva broad, gradually narrowing towards apex and ending with a rounded tip; its inner surface densely setose. Costa strongly sclerotized. Sacculus sclerotized, broad at base and narrowing towards tip. Praesacculus strongly sclerotized, ending with a triangular process directed dorsally. Aedeagus short and stout, narrowing at the middle and expanding near the apex in dorsal view. A strongly pigmented and sclerotized shaft present in the aedeagus, with middle part narrowing.

Female. Unknown.

Distribution. This species is currently known to occur in Luding and Wenchuan counties (Wolong) in western and northwestern Sichuan province at present.

Etymology. The specific name *owadai* is named in honor of Dr. Mamoru Owada (Tsukuba, Japan) who provided us with assistance and some literature.

Remarks. This new species flew like a *Neptis* (Nymphalidae) butterfly in conifer-broadleaf forest (Fig. 9) at the altitude about 2800 m. Actually, the wing maculation of forewing of the genus *Mimaporia* is also similar to certain species in the genus *Neptis*, for example *Neptis alwina* (Bremer & Grey, 1852), *Neptis dejeani* Oberthür, 1894 and *Neptis philyroides* Staudinger, 1887, by upper side sharing similar median and postmedian band and cell bar on forewing as well as postmedian band on hindwing. The distribution area of *Mimaporia owadai* sp. n. is within the distribution area of the former two species, while distribution area of *M. hmong* (northern Vietnam) falls within the distribution area of the last species. So we suspect that the genus *Mimaporia* might probably also a mimicker of the genus *Neptis* Fabricius, 1807 (Nymphalidae).

Burmeia Minet, 2003

Burmeia Minet, 2003: 470, type species: *Burmeia leesi* Minet, 2003.

Diagnosis. The genus *Burmeia* is a monotypic genus characterized by the following characters: antennal flagellum of male without scale, hindwing termen obviously angulate between vein M_2 and vein M_3 and in male genitalia tegumen and vinculum synscleritous. The female genitalia of *Burmeia* are also diagnostic and they differ from the ground plan of that of *Psychostrophia* in following aspects (female genitalia of other species in the genus *Psychostrophia* have been figured by Zhu et al. 2004): antrum membranous, while sclerotized in *Psychostrophia*; ductus bursae sclerotized, while membranous in *Psychostrophia*; corpus bursae nearly the same size of the 8th abdominal segment, while much larger in *Psychostrophia*; corpus bursae with an appendix bursae of similar size, while without an appendix bursae in *Psychostrophia*. Regarding the characters of female genitalia given above, *Burmeia* is definitely a distinct genus from *Psychostrophia*.

Burmeia leesi Minet, 2003

Figs 10–24

Burmeia leesi Minet, 2003: 473, fig. 2, 8, 10, 18–23.
Psychostrophia nymphidiaria: Zhu et al. 2004: 222, fig. 154, pl. VI, fig. 1 [misidentification].

Material examined. 28 males, 1 female, altitude 2700 m, 18–21.VII.2017, 62K, Motuo County, Linzhi Division, Xizang Autonomous Region, leg. Si-yao Huang & Shuqin Ji; 1 male, altitude 2500 m, 15.VII.2018, Yaojiaping, Lushui County, Nujiang Lisu Autonomous Prefecture, Yunnan Province, leg. Si-yao Huang; 1 male, altitude 3000 m, 16.VII.2016, Yulong Naxi Autonomous County, Lijiang City, Yunnan Province, leg. Si-yao Huang.

Figures 10, 11. *Burmeia leesi* adult: **10** male, Xizang **11** female, Xizang. Scale bar: 1 cm.

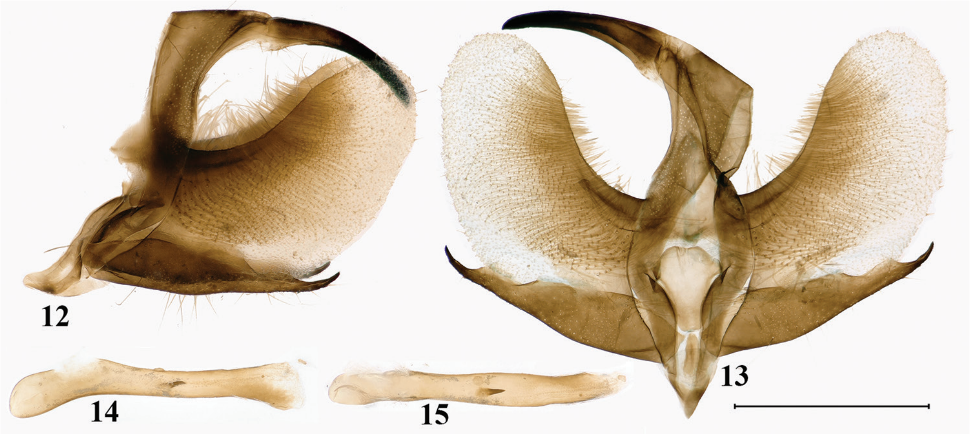
Diagnosis. *Burmeia leesi* Minet is unique among the Epicopeiidae by the morphological characters mentioned above in the generic diagnosis. The female genitalia are recorded here for the first time and the description is given below. The male genitalia (Figs 12–15) have already been described precisely by Minet (2003).

Female genitalia (Figs 16, 17). Papillae anales slightly sclerotized, rectangular in lateral view, with rounded tip. Apophyses posteriores and anteriores slender; the former nearly twice the length of the latter. Antrum membranous and slender. Ostium bursae narrower than antrum. Ductus seminalis short, arising from ductus bursae just below the ostium bursae. Lamella antevaginalis rectangular in lateral view and blunt arrow-shaped in ventral view, strongly sclerotized. Lamella postvaginalis sclerotized and somewhat rectangular in lateral view. Ductus bursae sclerotized, long and broad. Corpus bursae oval, with a strongly sclerotized broad U-shaped signum. Appendix bursae oval and membranous, nearly the same size as corpus bursae.

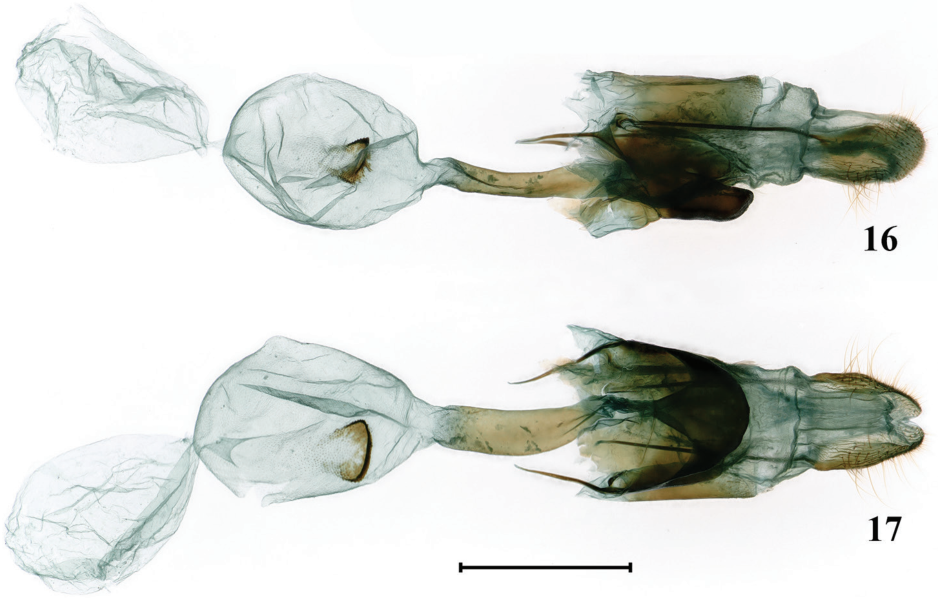
Remarks. The female genitalia are illustrated here for the first time. This little known species has not been recorded elsewhere after Minet described it in 2003 from northeastern Myanmar.

Biology. The flying period of this species in China is from early July to late July. Adults are usually found flying slowly above bushes and trees at edge of evergreen broad-leaved forest (Fig. 18) or conifer-broadleaf forest (Fig. 19) in altitude ranging from 2500 m to 3000 m along river or stream. They can fly in both cloudy days and sunny days. Males can be found sucking nutrients on human feces, damp ground, and wet stone (Figs 20–22). In 62K, Motuo County, this species was occasionally attracted to light trap in night (Fig. 23). Sometimes males can gather on damp ground (Fig. 24). In Yaojiaping, Western Yunnan, this species was found flying together with *Psychostrophia nymphidiaria* (Oberthür, 1893).

Distribution. China* (Yunnan, Xizang), Myanmar (Htawgaw)



Figures 12–15. Male genitalia of *Burmeia leesi*: **12** genitalia capsule lateral view **13** genitalia capsule ventral view **14** aedeagus lateral view **15** aedeagus dorsal view. Scale bar: 1 mm.



Figures 16, 17. Female genitalia of *Burmeia leesi*: **16** lateral view **17** ventral view. Scale bar: 1 mm.

Figures 18, 19. Habitats of *Burmeia leesi*: **18** Yaojiaping, Lushui County **19** 62K, Motuo County.

Figures 20–24. *Burmeia* living adult: **20** sucking on human feces **21** sucking on damp ground **22** sucking on wet stone **23** attracted to light trap **24** gathering and sucking on damp ground. Photographs taken in 62K, Motuo County.

Psychostrophia Butler, 1877

Psychostrophia Butler, 1877: 401, type species: *Psychostrophia melanargia* Butler, 1877.

Diagnosis. The genus *Psychostrophia* is characterized by the following characters: hindwing with cilia mostly black, except the part between vein M_1 and M_3 white; uncus long, thin and tubular for most of its length; aedeagus with a bunch of slender cornuti and coecum well developed and long.

Psychostrophia endoi Inoue, 1992

Figs 25–29

Psychostrophia endoi Inoue, 1992: 149, figs 1, 2.

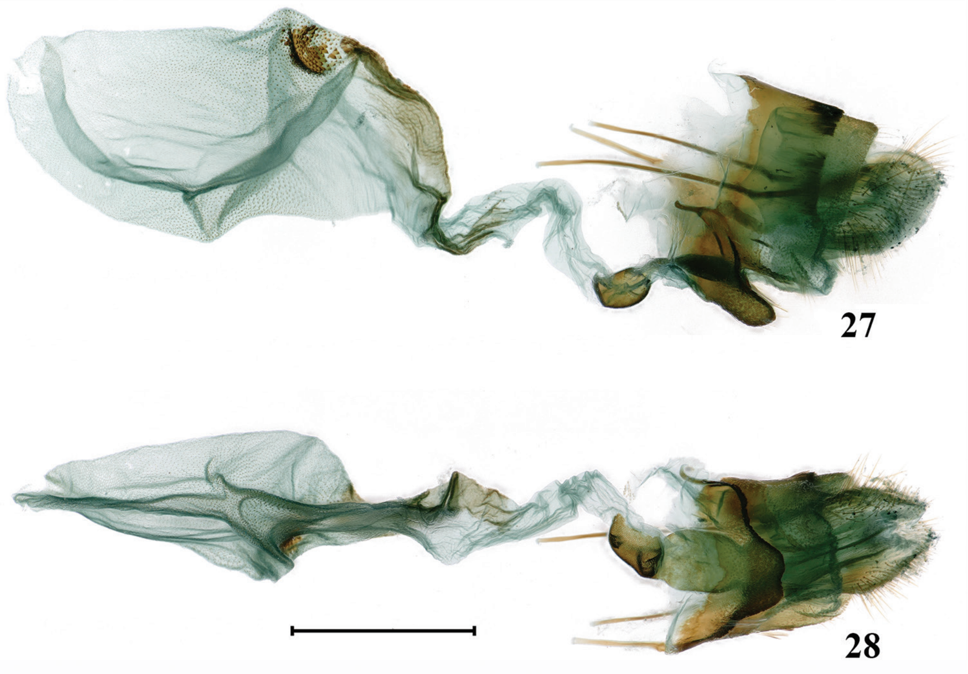
Material examined. 1 female, 30.VII.2003, Jiuwanshan Natural Reserve, Rongshui Miao Autonomous County, Liuzhou, Guangxi Zhuang Autonomous Region, leg. Min Wang; 1 female, 9.VI.2014, Deqin County, Diqing Tibetan Autonomous Prefecture, Yunnan Province, leg. Jia-qi Wang.

Diagnosis. *Psychostrophia endoi* is closely related to *P. picaria* Leech, 1897 from central and western China in external features, but it can be distinguished from it by the following combination of characters: on forewing upper side the postmedian band forming two obviously connected teeth in cell M_3 and CuA_1, pointing to termen in both sexes; the submarginal spots absent in male and the submarginal band below the subapical spot weak and represented by separated minute white dots in female; on hindwing upper side the postmedian band is obsolete and represented by white dots in male and the postmedian band ill-developed and represents by separated white dots in female; in male the genitalia valva more protruding at apex; in female genitalia the lamella antevaginalis is trapezoid in ventral view.

Description. Length of forewing 21–22 mm, female differs from male in larger size and having submarginal series on both wings better developed. Head black; antenna filiform, black; forewing ground color black, cilia black from apex to vein R_5, white from R_5 to median portion of cell M_1 and becoming black again from median portion of cell M_1 to tornus; postmedian band white, extending from middle of the cell M_1 to dorsum, with its inner edge wavy and outer edge forming two prominent connected tooth in cell M_3 and CuA_1; subapical spot white and well-developed, oval shape; submarginal band consisted of four or five separated white dots situated from cell M_1 to cell CuA_2; hindwing ground color black, cilia black from apex to vein M_1, white from M_1 to median portion of cell M_2 and becoming black again from median portion of cell M_2 to tornus; median band white and broad, becoming wider towards costa; postmedian fascia consisted of separated white dots of different size running from apex to tornus.

Female genitalia (Figs 27, 28). Papillae anales slightly sclerotized, elliptical in lateral view, with tip rounded. Apophyses posteriores and anteriores slender; and the lat-

Figures 25, 26. *Psychostrophia endoi* female, adult: **25** Yunnan **26** Guangxi. Scale bar: 1 cm.



Figures 27, 28. Female genitalia of *Psychostrophia endoi*: **26** lateral view **27** ventral view. Scale bar: 1 mm.

ter are slightly shorter than the former. Antrum well-developed and forming a strongly sclerotized chamber. Ostium bursae nearly the same width as antrum. Lamella antevaginalis strongly sclerotized, rectangular in lateral view and trapezoid in ventral view, with edge shallowly concave in the middle. Lamella postvaginalis slightly sclerotized and poorly developed, horn-shaped in lateral view. Ductus bursae membranous, long and curved medially, its anterior part near the corpus bursae slightly sclerotized and pigmented. Corpus bursae membranous, large and oval shape, scobinated with numer-

Figure 29. *Psychostrophia endoi* living male adult, Leishan County, Guizhou Province. Photograph by Gui-qiang Huang.

Figure 30. Habitat of *Psychostrophia endoi* in Leishan County, Guizhou Province. Photograph by Gui-qiang Huang.

ous small spines; its dorsal ridge near ductus bursae sclerotized and pigmented; next to the sclerotized ridge a sclerotized signum presents, consisting of larger spines.

Remarks. The female of *P. endoi* (Figs 25, 26) is recorded here for the first time. This little known species has not been recorded elsewhere after Inoue described it in 1992 from northern Laos. The differences in the sizes of the submarginal series between females and males (Inoue 1992: fig. 1), due to sexual difference, is rather common.

Biology. The flying period of this species is from early June to late July. The male (Fig. 29) of this species could be found sucking nutrient on wet ground on road of farmlands near evergreen broad-leaved forest (Fig. 30).

Distribution. China*(Yunnan, Guizhou, Guangxi), Laos (Sam Neua).

***Deuveia* Minet, 2003**

Deuveia Minet, 2003: 467, type species: *Amana banghaasi* Hering, 1932.

Diagnosis. The genus *Deuveia* is characterized by the following characters: forewing with three thick yellow stripes, juxta bilobate and spoon-like in each lobe and aedeagus with junction piece ventrally.

***Deuveia banghaasi* (Hering, 1932)**

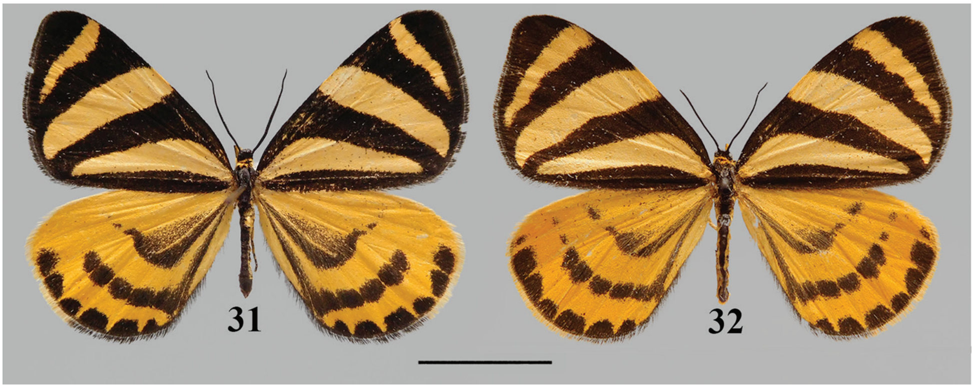
Figs 31–36

Amana banghaasi Hering, 1932: 28.
Deuveia banghaasi (Hering): Minet 2003: 467, figs 1, 7, 9, 12–17.

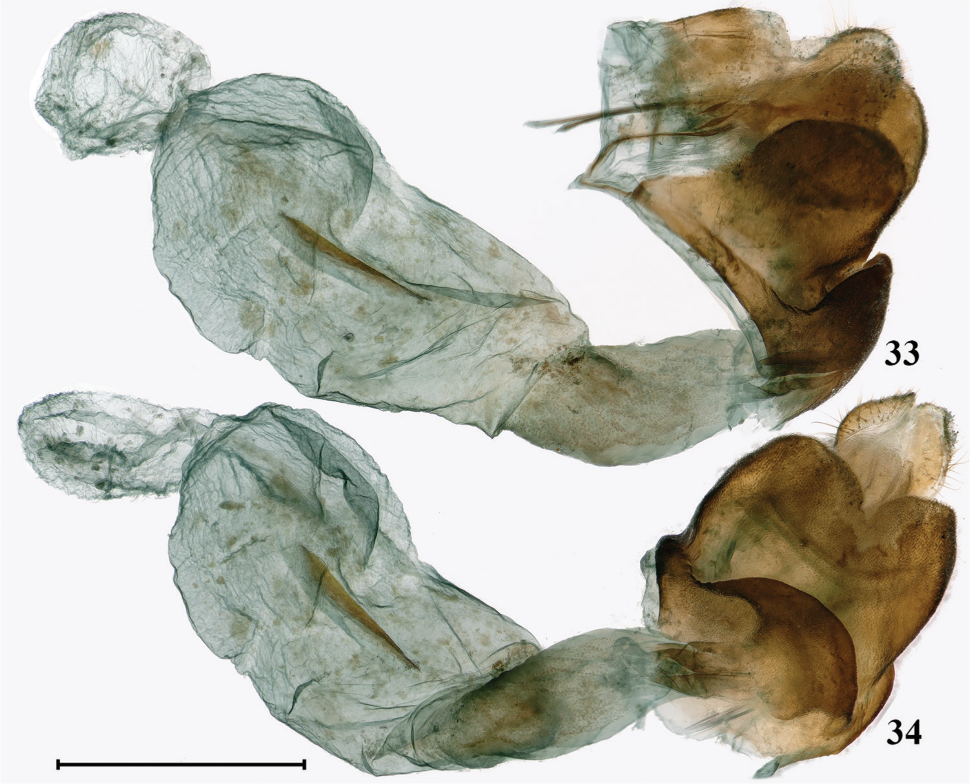
Material examined. 1 female, altitude 1500–1800 m, 5.VI.2018, Yueheping, Ningshan County, Ankang City, Shaanxi Province, leg. Li-ping Zhou; 1 male, 1400–1600 m, 6.VI.2018, Liuba County, Hanzhong City, Shaanxi Province, leg. Li-ping Zhou; 1 male, altitude 2700 m, 17.VI.2016, Li County, Aba Tibetan and Qiang Autonomous Prefecture, Sichuan Province, leg. Hao Huang; 5 males, 22–24.VI.2017, altitude 2600 m, Pingwu County, Mianyang City, Sichuan Province, leg. Shu-qin Ji; 3 males, altitude 2600 m, 21.VII.2015, Lazikou, Diebu County, Gannan Tibetan Autonomous Prefecture, Gansu Province, leg. Si-yao Huang.

Diagnosis. *Deuveia banghaasi* is unique among epicopeiid moths for forewing having three broad yellow stripes and hindwing with yellowish ground color and unmistakable black patterns. The female (Fig. 32) is recorded for the first time and a description is given below, the male (Fig. 31) has already been described precisely by Minet (2003).

Description. Female. Length of forewing 19 mm, female differs from male in having forewing termen more rounded, postmedian band on forewing upper side broader and longer, and hindwing discoidal cell with less black scale. Forewing ground color black, cilia blackish brown; upper side with three yellowish broad stripes, the basal one extending from



Figures 31, 32. *Deuveia banghaasi* adult: **31** male, Shaanxi **32** female, Shaanxi. Scale bar: 1 cm.



Figures 33, 34. Female genitalia of *Deuveia banghaasi*: **33** lateral view **34** ventral view. Scale bar: 1 mm.

Figures 35, 36. Habitats of *Deuveia banghaasi*: **35** Yueheping, Ningshan County, photograph by Di Lu **36** Lazikou, Diebu County.

wing base across the base of discoidal cell and ending at tornus; the median one extending from middle of the costa and ending at tornus; the postmedian one extending from costa near apex and ending at vein CuA_1. Hindwing ground color orange yellow, cilia yellow from apex to vein CuA_1, and black from vein CuA_1 to dorsum, patterns blackish. Median band extending from vein $Sc+R_1$ to distal end of discoidal cell, ending in a long stripe connected to wing base; postmedian band consisted of separated square spots extending from vein $Sc+R_1$ to dorsum, and ending in a long stripe connected to wing base. Marginal band consisted of separated rounded spots extending from apex to tornus.

Female genitalia (Figs 33, 34). Papillae anales small, slightly sclerotized, rounded in lateral view. Apophyses posteriores moderately long, Apophyses anteriores short and broad, triangular in lateral view. Antrum broad, sclerotized. Ostium bursae narrower than antrum. Lamella antevaginalis strongly sclerotized, triangular in lateral view and broad shield-like in ventral view. Lamella postvaginalis strongly sclerotized, rounded in lateral view and rectangular in ventral view, its edge deeply concave in the middle and forming a V-shaped gap. Ductus bursae slightly sclerotized, short and stout. Corpus bursae membranous, large and oval in lateral view, with a sclerotized blade-like signum in the middle. Appendix bursae presents, globular in lateral view.

Biology. This species is usually found at edge of evergreen broad-leaved forest (Fig. 35) and conifer-broadleaf forest (Fig. 36) in altitude ranging from 1500 m to 3000 m. The flying period is from early June to late July. Adults usually come out around middle of the day when sunshine is abundant and flying slowly.

Distribution. China (Sichuan, Gansu, Shaanxi).

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Taxonomic study of the genus *Aoyuanus* Ding & Chen, with descriptions of two new species (Hemiptera, Fulgoromorpha, Delphacidae)

Zheng-Xiang Zhou[1,2], Lin Yang[1], Xiang-Sheng Chen[1,3,4]

1 *Institute of Entomology, Guizhou University, Guiyang, Guizhou, 550025, China* **2** *College of Agriculture, Anshun University, Anshun, 561000, China* **3** *Guizhou Key Laboratory for Plant Pest Management of Mountainous Region, Guizhou University, Guiyang, Guizhou, 550025, China* **4** *Special Key Laboratory for Development and Utilization of Insect Resources of Guizhou, Guizhou University, Guiyang, Guizhou, 550025, China*

Corresponding author: *Xiang-Sheng Chen* (chenxs3218@163.com)

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Abstract

The delphacid planthoppers genus *Aoyuanus* Ding & Chen, 2001 is reviewed. Two new species, *A. spathulus* **sp. n.** and *A. varius* **sp. n.**, are described and illustrated from China to give the genus three species in total, and the generic characteristics are redefined. A short description and illustrations are also given for *A. furcatus*. A key to all known species of *Aoyuanus* based on male genitalia is provided.

Keywords

Delphacid, Fulgoroidea, new taxa, planthopper, taxonomy

Introduction

The planthopper tribe Delphacini Leach, 1815 (Hemiptera: Fulgoromorpha: Delphacidae: Delphacinae) occurs in all ecoregions (excluding Antarctica). It is the largest clade of Delphacidae, including approximately 1639 species in 322 genera (Bourgoin 2018), and the group promises to continue to grow as new diversity is discovered (Yang 1989; Bartlett and Kunz 2015; Ren et al. 2015; Campodonico 2017; Remes Lenicov and Brentassi 2017).

The planthopper genus *Aoyuanus* was established by Ding and Chen (2001) for a single species *Aoyuanus furcatus* Ding & Chen, 2001 from China (Chen et al. 2001). In this paper, two new species are described and illustrated from Yunnan Province, China, which were collected from weeds along a roadside. A key is given to separate all species.

Materials and methods

Morphological terminology follows Ding (2006). Measurements of body length equal the distance between the apex of vertex and tip of tegmen. All measurements are in millimeters (mm). Dry specimens were used for the description and illustration. Color illustrations for adult habitus were obtained by KEYENCE VHX-1000. External morphology was observed under a stereoscopic microscope (Leica Mz 12.5) and characters were measured with an ocular micrometer. The genital segments of the examined specimens were macerated in 10% KOH and drawn from preparations in glycerin jelly using Olympus CX41 and Leica MZ 12.5 stereomicroscopes. Illustrations were scanned with Canon CanoScan LiDE 220 and imported into Adobe Photoshop 6.0 for labeling and plate composition.

The type specimens of the new species are deposited in the Institute of Entomology, Guizhou University, Guiyang, Guizhou Province, China (**GUGC**).

Taxonomy

Aoyuanus Ding & Chen, 2001

Aoyuanus Ding & Chen, 2001: 328; Ding, 2006: 358.

Type species. *Aoyuanus furcatus* Ding & Chen, 2001, by original designation.

Diagnosis. Small sized. Frons with median carina forked at base (Figs 5, 24, 44). Pygofer asymmetrical in posterior view (Figs 12, 31, 51). Aedeagus forked at base (Figs 15, 16, 34, 35, 54, 55). Parameres simple, asymmetrical (Figs 17, 18, 36–38, 56–59).

Description. *Coloration.* General color yellow to black (Figs 1, 2, 20, 21, 40, 41). Head with vertex, frons, face and antennae yellow to dark brown (Figs 4–6, 23–25, 43–45). Postclypeus paler than frontoclypeus (Figs 5, 24, 44). Pronotum and mesonotum yellow to yellowish brown (Figs 4, 23, 43). Forewings hyaline, with dark marking at apex (Figs 4, 23, 43). Legs yellow to yellowish brown (Figs 1, 2, 21, 22, 40, 41). Abdomen black, with yellow marking at lateral margins (Figs 1, 2, 21, 22, 40, 41).

Structure. Head including eyes narrower than pronotum (Figs 4, 23, 43). Vertex subquadrate, apically arched or truncate, keeled carinae project or not, narrower at apex than at base, submedian carinae not uniting at apex (Figs 4, 23, 43). Frons with median carina forked between eyes, longer at middle line than wide at widest part, widest at top of ocelli, lateral carinae distinctly narrowed dorsally between eyes (Figs 4, 5, 23, 24, 43, 44). Antennae cylindrical, with basal segment shorter than second, reaching postclypeus suture (Figs 5, 24, 44). Pronotum with lateral carinae almost attaining hind margin (Figs 4, 23, 43). Posttibial spur with approximately 12–20 teeth.

Male genitalia. Pygofer in profile distinctly wider ventrally than dorsally, asymmetrical in caudal view. Medioventral process at ventral margin of pygofer opening (Figs 10–12, 29–31, 49–51). Diaphragm broad, with dorsal margin incised, V-shaped (Figs 12, 31, 51). Aedeagus forked at base (Figs 15, 16, 34, 35, 54, 55). Parameres simple, asymmetrical (Figs 17, 18, 36–38, 56–59). Suspensorium present, Y-shaped, relative length between anal segment and aedeagus (Figs 19, 39, 60). Anal segment with a pair of processes or none (Figs 13, 14, 32, 33, 52, 53).

Distribution. Oriental region (China).

Remarks. This genus is extremely similar to *Indozuriel* Fennah, 1973 in appearance and is similar to *Javesella* Fennah, 1963 in shaped of aedeagus, but can be easily distinguished from the latter by the pygofer asymmetrical in caudal view (pygofer symmetrical in caudal view in *Indozuriel* and *Javesella*); parameres asymmetrical (parameres symmetrical in *Indozuriel* and *Javesella*).

Key to species of genus *Aoyuanus* (males)

1 Pygofer with three medioventral processes (Fig. 12); anal segment without process (Figs 13, 14) .... ***A. furcatus***

– Pygofer with a medioventral process (Figs 31, 51); anal segment with a pair of processes (Figs 32, 33, 52, 53) **2**

2 Medioventral process not forked at apex (Fig. 31); anal segment with processes symmetrical, broad at apex (Figs 32, 33) ....***A. spathulus* sp. n.**

– Medioventral process forked at apex (Fig. 51); anal segment with two asymmetrical processes, pointed at apex (Figs 52, 53) ....***A. varius* sp. n.**

Aoyuanus furcatus Ding & Chen, 2001

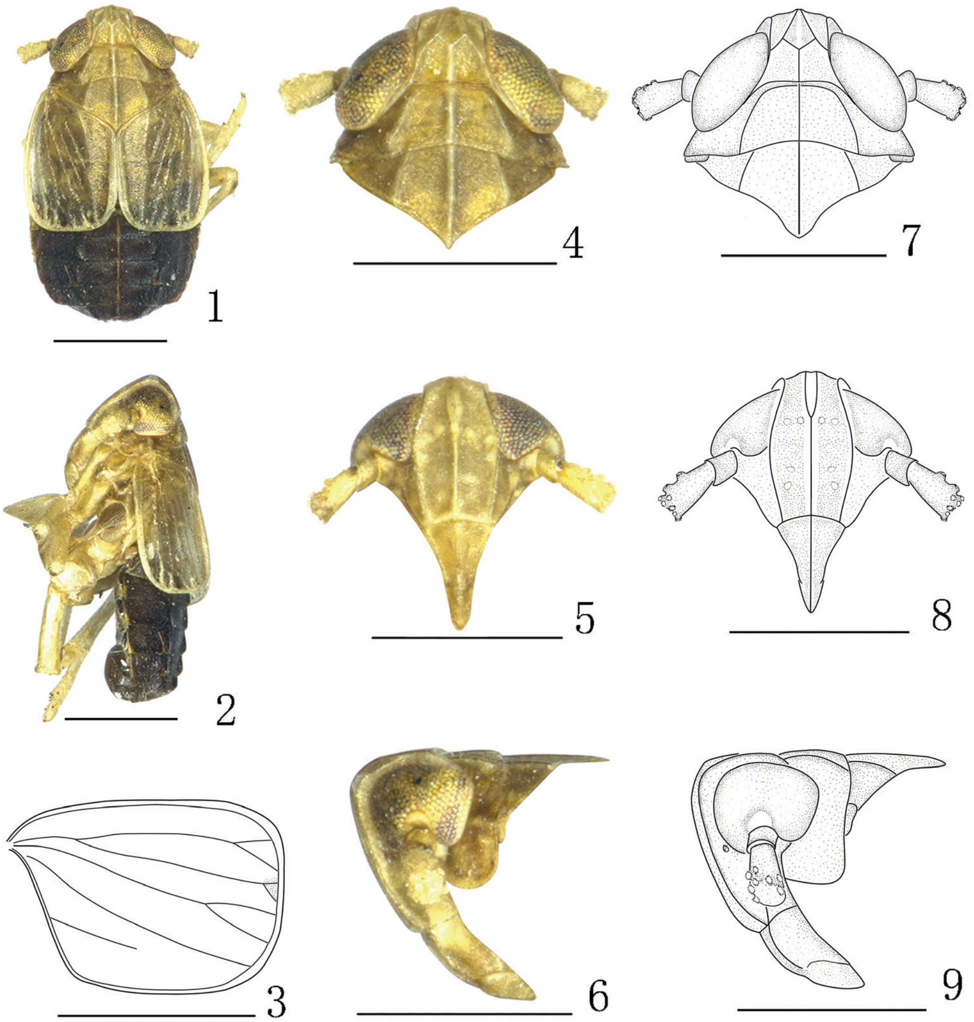
Figs 1–19

Aoyuanus furcatus Ding & Chen, 2001: 328–329, figs 33–40; Ding, 2006: 358–360, fig. 189.

Material examined. 15 ♂♂, China: Hubei, Yingshan County, Dabieshan, 2 Jul 2014, Z-X Zhou. 6 ♂♂, Hunan, Wugang County, Yunshan, 18 Aug 1999, X-S Chen.

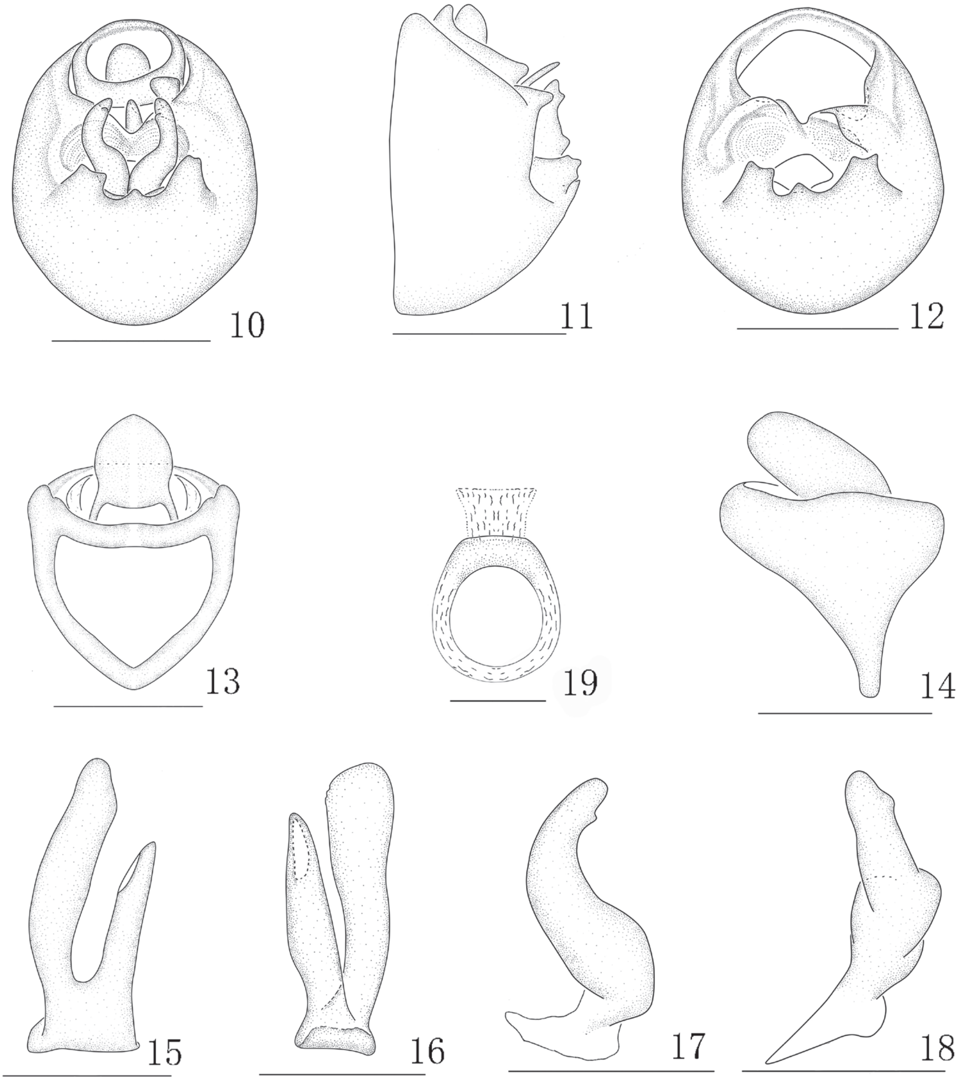
Short redescription. Pygofer and parameres asymmetrical. Suspensorium ring-shaped, membranous.

Distribution. Hubei, Guizhou, Hunan, Zhejiang.



Figures 1–9. *Aoyuanus furcatus* Ding & Chen, 2001, male. **1–2** male habitus (dorsal and lateral views) **3** forewing **4, 7** head and thorax, dorsal view **5, 8** front **6, 9** head and thorax, lateral view. Scale bars: 0.5 mm.

Remarks. Based on the illustrations (Figs 1–19) and description by Ding and Chen (2001), this species can be distinguished from other species of the genus by the following characters: pygofer with three medioventral processes; anal segment without process, suspensorium ring-shaped. This species is also similar to *Indozuriel rostri* Ding & Zhou, 1973 in appearance, but can be easily distinguished from the latter by the parameres without curved apically (parameres with curved apically in *I. rostri*). This species is also similar to *Javesella salina* (Haupt, 1924) in the shaped of aedeagus, but can be easily distinguished from the latter by the pygofer having a medioventral processes (pygofer without medioventral process in *J. salina*).

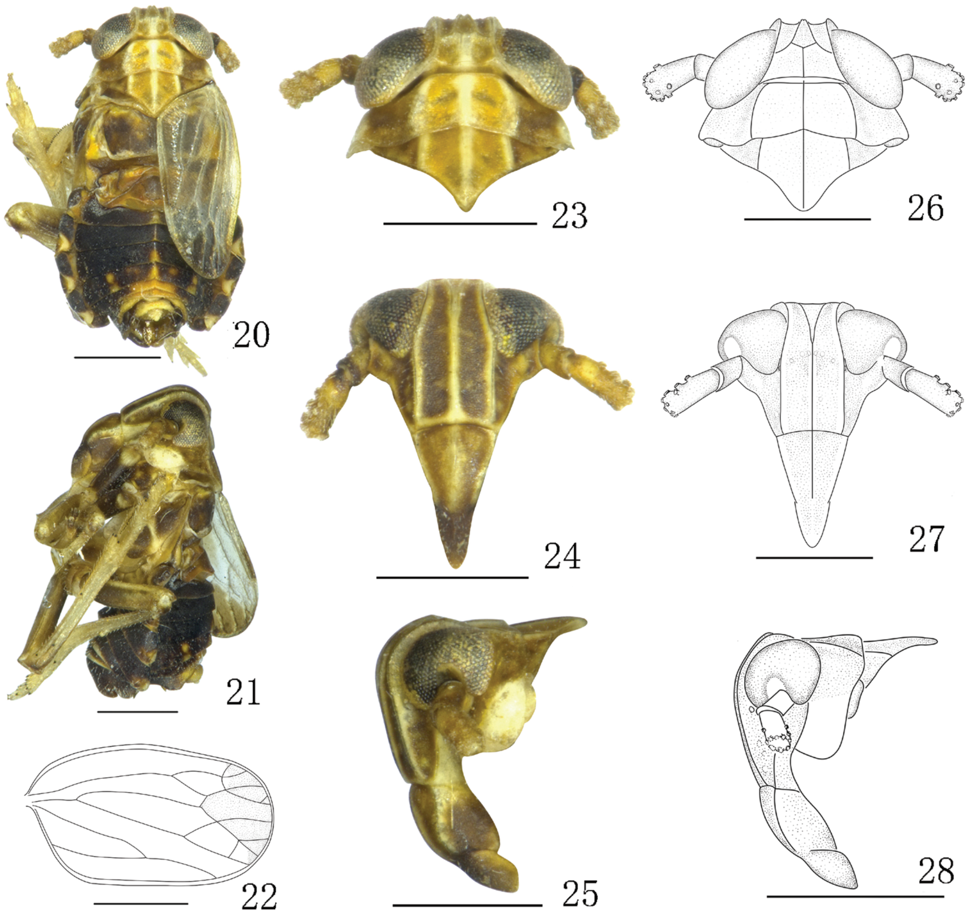


Figures 10–19. *Aoyuanus furcatus* Ding & Chen, 2001, male. **10** genitalia, caudal view **11** genitalia, lateral view **12** diaphragm, caudal view **13** anal segment, caudal view **14** anal segment, left view **15** aedeagus, left view **16** aedeagus, ventral view **17** left paramere, caudal view **18** left paramere, left lateral view **19** suspensorium. Scale bars: 0.2 mm (**10–14**); 0.1 mm (**15–19**).

Aoyuanus spathulus sp. n.

http://zoobank.org/0B63176F-93FB-454A-8F80-0E271F0148B4
Figs 20–39

Type material. Holotype: ♂, **China**: Yunnan, Simao County, Caiyanghe (22°56'N, 101°20'E), 23 Aug 2014, Z-X Zhou. Paratypes: 2♂♂, same data as holotype.



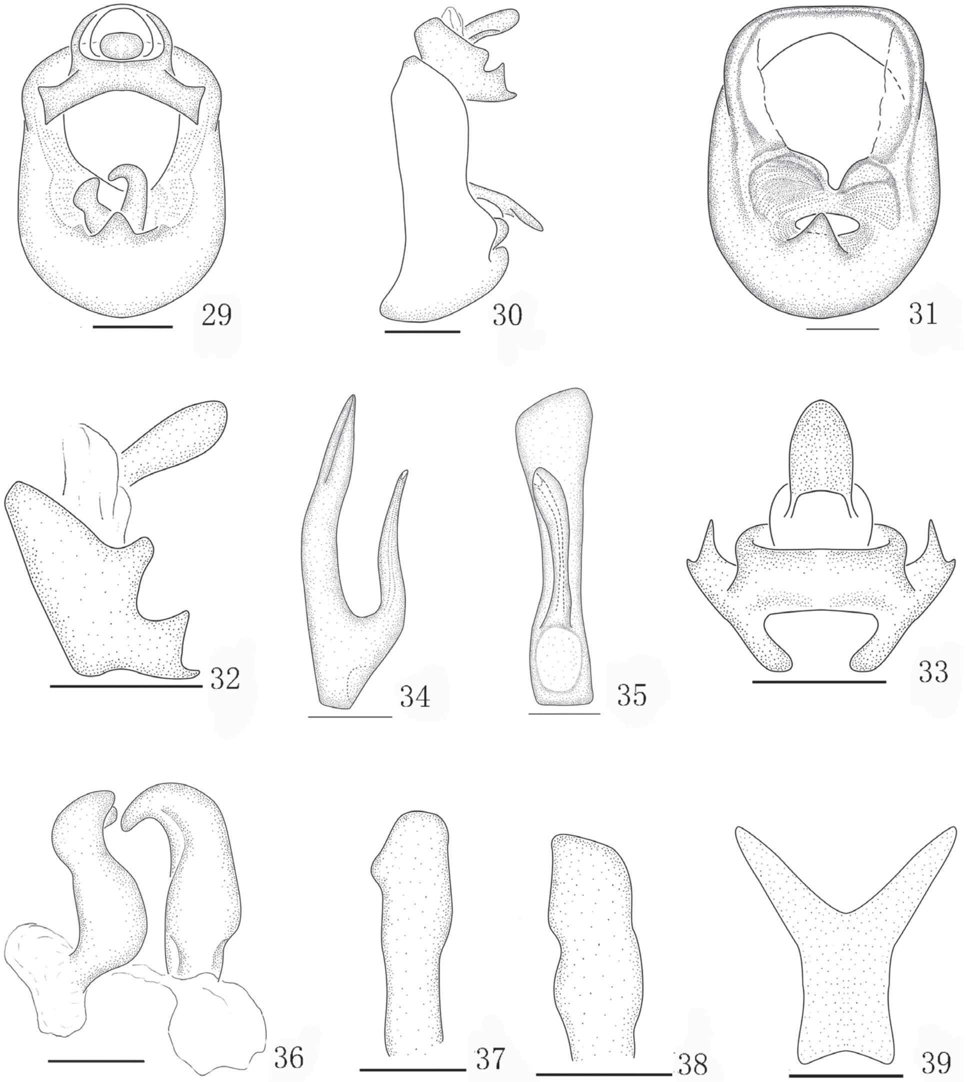
Figures 20–28. *Aoyuanus spathulus* sp. n., male. **20–21** male habitus (dorsal and lateral views) **22** forewing **23, 26** head and thorax, dorsal view **24, 27** front **25, 28** head and thorax, lateral view. Scale bars: 0.5 mm.

Type locality. China: Yunnan, Simao County, Caiyanghe (22°56'N, 101°20'E), 1368 m.

Measurements (n = 3). Body length (from apex of vertex to apex of forewing): male 1.90–2.00 mm; forewing length: male 0.80–0.87 mm.

Diagnosis. Forewings with brown marking at apex (Figs 20, 21). Aedeagus forked at approximately basal one-third, with dorsal one broad, flat and rounded at apex (Figs 34, 35). Anal segment with two processes at laterocaudal margins, broad and large, broadened at apex (Figs 32, 33).

Description. *Coloration.* General color yellowish white to dark brown (Figs 20, 21, 23–25). Head yellowish white to yellowish brown (Figs 23–25). Vertex yellowish white (Fig. 23). Frons black-brown, except middle carina and lateral margins yellow (Fig. 24). Clypeus yellowish brown (Fig. 24). Rostrum yellowish brown, with



Figures 29–39. *Aoyuanus spathulus* sp. n., male. **29** genitalia, caudal view **30** genitalia, lateral view **31** diaphragm, caudal view **32** anal segment, left view **33** anal segment, caudal view **34** aedeagus, left view **35** aedeagus, ventral view **36** parameres, caudal view **37** left paramere, left lateral view **38** right paramere, right lateral view **39** suspensorium. Scale bars: 0.2 mm (**29–33**); 0.1 mm (**34–39**).

apex brown. Genae yellowish brown (Figs 24, 25). Eyes generally yellowish brown (Figs 20, 21, 23–25); ocellus yellow (Fig. 25). Antennae with first segment yellowish brown and black at apex and with second segment yellow (Fig. 24). Pronotum and mesonotum yellow, except carinae yellowish white (Fig. 23). Forewings with brown marking at apex (Figs 20, 21). Legs yellowish white to yellowish brown, tibiae yellow and yellowish brown basally, tarsomeres yellow (Figs 20, 21). Abdomen black, except lateral margins and middorsum with pale markings and segments 7–9 pale dorsally (Figs 20, 21).

Structure. Head and thorax. Head including eyes narrower than pronotum, ratio 0.98:1 (Figs 23, 26). Vertex with lateral carinae slightly concave, shorter submedially than wide at base, ratio 0.76:1, narrower at apex than at base, ratio 0.90:1 (Figs 23, 26). Frons longer in middle line than wide at widest part, ratio 1.77:1 (Figs 24, 27). Postclypeus wider at base than frons at apex, slightly longer than wide at base (Figs 24, 27). Antennae with basal segment as long as wide, shorter than second, ratio 0.45:1 (Figs 24, 27). Pronotum longer than vertex, ratio 1.06:1 (Figs 23, 26). Mesonotum shorter than pronotum and vertex combined, ratio 0.81:1 (Figs 23, 26). Posttibial spur with 16–20 distinct teeth along hind margin. Brachypterous forewings distinctly not reaching apex of abdomen, longer than widest part, ratio 1.76:1, widest at middle (Fig. 22).

Male genitalia. Pygofer with a medioventral process (Figs 29–31). Aedeagus forked in approximately basal one-third and dorsal one broad and flat, rounded at apex (Figs 34, 35). Parameres small, with apical half-turned mesad (Figs 36–38). Suspensorium Y-shaped, with arms as long as stem (Fig. 39). Anal segment with two processes at laterocaudal margins, large, broadened at apex (Figs 32, 33).

Reported hosts. None.

Distribution. China (Yunnan).

Etymology. The specific name is derived from the Latin word *spathulus* (narrow and flattened), referring to the male anal segment with two spatulate processes.

Remarks. The new species is similar to *Aoyuanus furcatus* Ding & Chen, 2001 in the shape of the aedeagus, but can be easily distinguished from the latter by the male anal segment with processes (without processes in *A. furcatus*); and the pygofer with a medioventral process (with three processes in *A. furcatus*). This new species is also extremely similar to *Aoyuanus varius* sp. n. in the shape of aedeagus, but can be easily distinguished from the latter by the anal segment with lateroapical angles symmetrical (anal segment with lateroapical angles asymmetrical in *A. varius* sp. n.); pygofer with one medioventral process not forked at apex (pygofer with medioventral process forked at apex in *A. varius* sp. n.); suspensorium Y-shaped, with arms as long as stem (suspensorium with stem longer than arms in *A. varius* sp. n.).

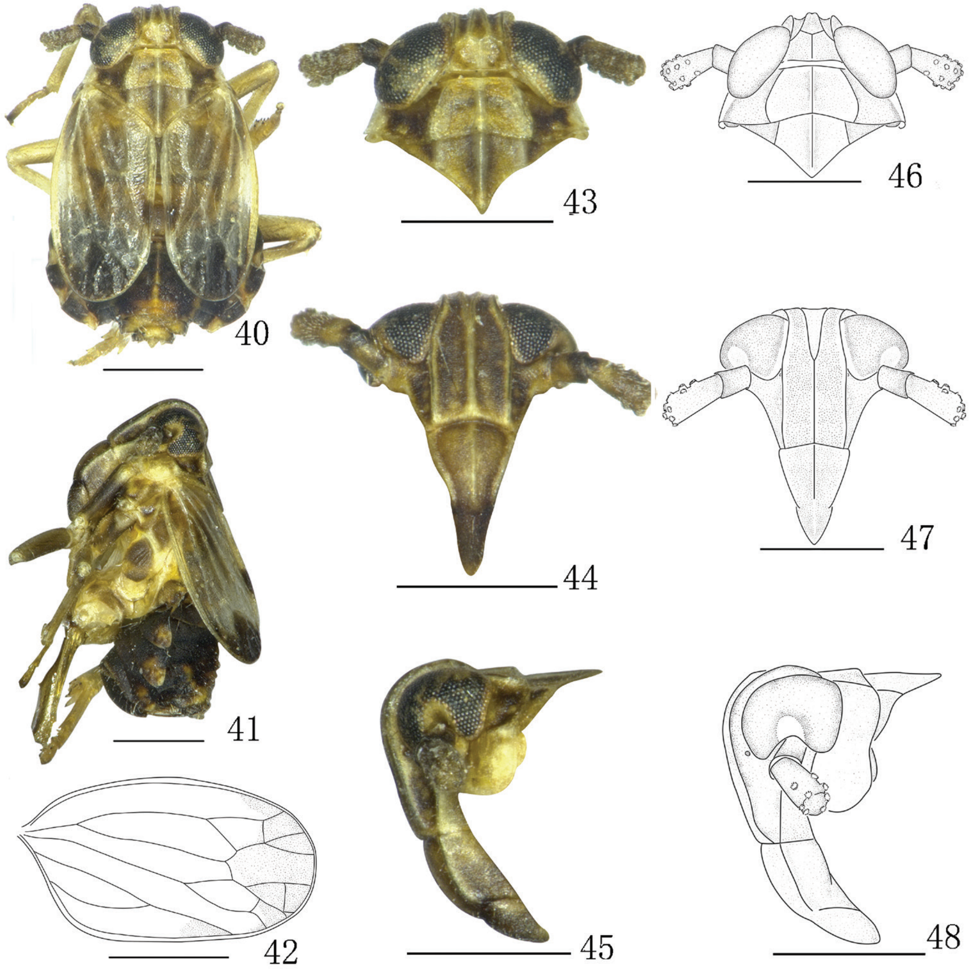
***Aoyuanus varius* sp. n.**

http://zoobank.org/ECED68F4-41EC-40C4-8BED-E6766E23F4D2
Figs 40–60

Type material. Holotype: ♂, **China**: Yunnan, Dali County, Xiaguan (25°58'N, 100°22'E), 4 Aug 2006, Q-Z Song. Paratype: 1♂, same data as holotype.

Type locality. China: Yunnan, Dali County, Xiaguan (25°58'N, 100°22'E), 1988 m.

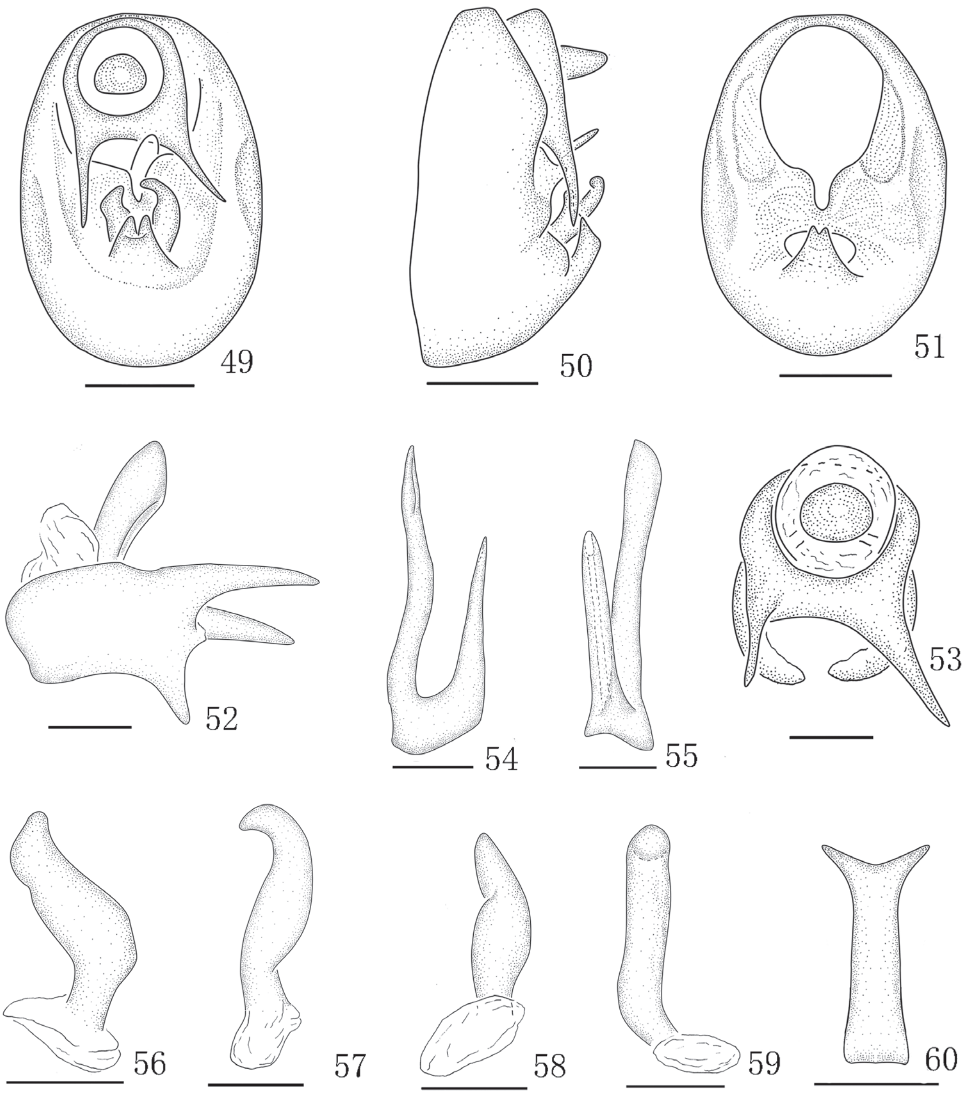
Measurements (n = 2). Body length (from apex of vertex to apex of forewing): male 2.00–2.02 mm; forewing length: male 1.07–1.10 mm.



Figures 40–48. *Aoyuanus varius* sp. n., male. **40–41** male habitus (dorsal and lateral views) **42** forewing **43, 46** head and thorax, dorsal view **44, 47** front **45, 48** head and thorax, lateral view. Scale bars: 0.5 mm.

Diagnosis. Forewings pale yellow with dark black marking at apex (Figs 40, 41). Aedeagus forked at basal quarter, dorsal one broadened at apex in ventral view, longer than ventral one (Figs 54, 55). Anal segment with two processes at laterocaudal margins, processes asymmetrical (Figs 52, 53).

Description. *Coloration.* General color yellow to black (Figs 40, 41, 43–45). Head yellow to yellowish brown (Figs 40, 41, 43–45). Vertex yellowish brown (Figs 40, 43). Frons black brown, except middle carina and lateral margins yellowish brown (Fig. 44). Clypeus yellowish brown to dark brown (Fig. 44). Rostrum yellowish brown, with apex brown. Genae yellowish brown (Figs 44, 45). Eyes usually yellowish brown (Figs 40, 41, 43–45); ocellus black (Fig. 45). Antennae with basal segment yellowish brown and black at apex and with second segment yellowish brown (Figs 40, 41,



Figures 49–60. *Aoyuanus varius* sp. n., male. **49** genitalia, caudal view **50** genitalia, lateral view **51** diaphragm, caudal view **52** anal segment, left view **53** anal segment, caudal view **54** aedeagus, left view **55** Aedeagus, ventral view **56** left paramere, caudal view **57** right paramere, caudal view **58** Left paramere, left lateral view **59** right paramere, right lateral view **60** suspensorium. Scale bars: 0.2 mm (**49–53**); 0.1 mm (**54–60**).

43–45). Pronotum and mesonotum yellowish brown (Figs 40, 43). Forewings pale yellow with dark black marking at apex and midline dorsal margin (Figs 40, 41). Legs yellow to yellowish brown, tibiae yellow and yellowish brown basally, tarsomeres yellow (Figs 40, 41). Abdomen black, except lateral margins and dorsal apex with some small yellow markings (Figs 40, 41).

Structure. Head and thorax. Head including eyes narrower than pronotum, ratio 0.92:1 (Figs 43, 46). Vertex with longer than wide at base, ratio 1.18:1, narrower at apex than at base, ratio 0.81:1 (Figs 43, 46). Frons longer in middle line than wide at widest part, ratio 1.76:1 (Figs 44, 47). Postclypeus wider at base than frons at apex, slightly longer than wide at base (Figs 44, 47). Antennae with basal segment longer than wide, ratio 1.4:1, shorter than second, ratio 0.58:1 (Figs 44, 47). Pronotum shorter than vertex, ratio 0.87:1 (Figs 43, 46). Mesonotum shorter than pronotum and vertex combined, ratio 0.54:1 (Figs 43, 46). Posttibial spur with 18 distinct teeth along hind margin. Brachypterous forewings distinctly not reaching apex of abdomen, longer than widest part, ratio 1.73:1, widest at middle (Figs 40, 41).

Male genitalia. Pygofer with one medioventral process, which forked at apex (Figs 49–51). Aedeagus forked at basal quarter, dorsal one longer and broader at apex than ventral one in ventral view (Figs 54, 55). Parameres small, with apical half-turned mesad (Figs 56–59). Suspensorium Y-shaped, stem longer than arms, ratio 2.5:1 (Fig. 60). Anal segment with two processes at laterocaudal margins, processes asymmetrical (Figs 52, 53).

Reported hosts. None.

Distribution. China (Yunnan).

Etymology. The specific name is from the Latin word *varius* (meaning different, changeable), which alludes to the anal segment with two processes, which are asymmetrical.

Remarks. This new species is extremely similar to *Aoyuanus spathulus* sp. n., but can be distinguished from them by the anal segment with lateroapical angles asymmetrical (anal segment with lateroapical angles symmetrical in *A. spathulus* sp. n.).

Discussion

The genus *Aoyuanus* was erected by Chen and Ding (2001) and placed in the tribe Delphacini because of its spinal formula of the hind leg 5–7–4, large, thin and flattened tibial spur, bearing a row of fine and black-tipped teeth on the posterior margin, a developed diaphragm, and the presence of a suspensorium (Yang 1989; Ding 2006). It can be distinguished from other genera of the tribe Delphacini by the pygofer and parameres that are asymmetrical in caudal view. In this study, although the suspensorium of the two new species are Y-shaped, we place them in *Aoyuanus* because of their small size; the head which includes eyes narrower than pronotum; the pygofer and parameres that are asymmetrical in caudal view; and the aedeagus forked at its basal third, with the dorsal branch flattened and ventral branch tubular. We extend the definition of the genus to include a head with the anterior margin arched or transverse, the keeled carinae may or may not project; pygofer and parameres asymmetrical in caudal view; suspensorium ring and membranous or Y-shaped.

Emeljanov (1993) established the subtribe Numatina within Delphacini, based on the region between the anal segment and phallus having a suspensorium. According to the criteria of Emeljanov (1993), *A. furcatus* Ding & Chen, 2001 belongs to the subtribe Numatina but the two new species, *A. spathulus* sp. n. and *A. varius* sp. n., do not. Nevertheless, the monophyly of the subtribe classification was not directly tested. Hence, Urban et al. (2010) considered doubtful the subtribe classification and divided Delphacini into three major clades. Recently, Huang et al. (2017) supported the general concept of subtribe Numatina and supported the division of this tribe into three clades, but they are composed differently from those of Urban et al. (2010). According to Huang et al. (2017), *A. furcatus* belongs to the subtribe Numatina, but two new species are not clearly placed. Therefore, in this paper, we provisionally place the two new species in the genus *Aoyuanus*, but more taxon samples and molecular data are still required to confirm the relationships within Delphacini in the future.

Acknowledgments

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RESEARCH ARTICLE

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Ceratophysella species from mushrooms in China (Collembola, Hypogastruridae)

Wanda Maria Weiner[1], Zhijing Xie[2,3], Yu Li[4], Xin Sun[2,4,5]

1 *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland* **2** *Key laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China* **3** *University of Chinese Academy of Sciences, Beijing 100049, China* **4** *Engineering Research Center of Chinese Ministry of Education for Edible and Medicinal Fungi, Jilin Agricultural University, Changchun 130118, China* **5** *J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, 37073 Göttingen, Germany*

Corresponding author: *Xin Sun* (sunxin@iga.ac.cn)

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Abstract

Four species of the genus *Ceratophysella* living on mushrooms are reported from China, including a new species, *Ceratophysella skarzynskii* Weiner & Sun, **sp. n.**, which is described from alpine mushrooms. The new species belongs to the *Ceratophysella* group of species with a dorsal chaetotaxy of type B and differs from the other species in a combination of characters. *Ceratophysella skarzynskii* **sp. n.** is distinguished by its small body size (maximum length 1.09 mm), number of peg-like s-chaetae (30–32) in the ventral sensory file, the trilobed apical vesicle of antennal segment IV, five modified chaetae on dens, and serrated dorsal chaetae. A key to the Chinese species of the genus has been provided.

Keywords

Ceratophysella skarzynskii sp. n., key, new species, taxonomy

Introduction

The genus *Ceratophysella* Börner, 1932 is distributed worldwide, having more than 130 species (Bellinger et al. 1996–2018). The main diagnostic characters for the genus are the pigmented body, 8 + 8 ocelli, body chaetae mostly differentiated into micro- and macrochaetae, an eversible integumental sac usually present between antennal segments III and IV, the ventral side of antennal segment IV with a sensory file often well-developed of short, erect, curved, and flattened at tips s-chaetae, unguiculus with broad basal lamella, furca well developed, mucro usually boat-like with a spoon-like apex and distinct lamella, and anal spines usually long and curved.

Until now, fourteen species of the genus *Ceratophysella* have been reported from China (Zhao 1992, Shen 1993, Liu et al. 1998, Zhao et al. 1997, Jia et al. 2010). As a common group of Collembola living on mushrooms, species have often caused significant economic damage in China (Wei 2002; Zhu 2012). Within a large collection of the mushroom Collembola in China, three known species, *C. communis* (Folsom, 1898), *C. denticulata* (Bagnall, 1941), *C. liguladorsi* (Lee, 1974), and the new species described here, *C. skarzynskii* sp. n., are reported in the present paper.

Materials and methods

Specimens were collected by hand using a brush and stored in ethanol; they were then cleared in lactic acid and KOH, and mounted in Marc André II medium. Drawings and measurements were made using a phase contrast microscope LEICA DM2500 equipped with a camera lucida.

Mushroom species were determined by the third author, Yu Li.

Abbreviations used in the descriptions:

Abd.	abdominal segments,
Ant.	antennal segments,
av	apical vesicle
AIIIO	sensory organ of Ant. III,
l.p.	lateral processus on labial palp,
ms	s-microsetae (ms) (microsensillum),
or	subapical organite
PAO	postantennal organ,
S	sensillum,
s-chaetae	sensorial chaetae on Th. and Abd.
Th.	thoracic segments,
VT	ventral tube,
IGA-CAS	Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences;
ISEA-PAS	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.

Terminology for the descriptions follows that given in Fjellberg (1984, 1999), Babenko et al. (1994), and Thibaud et al. (2004).

Taxonomy

Ceratophysella skarzynskii Weiner & Sun, sp. n.

http://zoobank.org/BA3F1CD5-D62C-4AFA-8450-26FB928994CA
Figs 1–3, Table 1

Type material. *Holotype*: preadult male, China: Jilin: Changbai Mountains, alt. 2000 m, on *Russula* sp., leg. Xin Sun, 29 July 2015. ***Paratypes*:** 10 females and one juvenile, the same data as holotype. Type material: the holotype and 8 paratypes are housed in IGA-CAS, China, two paratypes in ISEA-PAS, Poland.

Diagnosis. Dorsal chaetotaxy of type B with serrated chaetae. Maximal length 1.09 mm. Antennal segment IV with bi- or trilobed apical vesicle and ventral sensory file with 30–32 peg-like s-chaetae. Dens with seven chaetae, five of them modified.

Description. Body length 0.9–1.09 mm (holotype: 1.07 mm). Body colour violet or blue in alive specimens, grey or grey-black in alcohol, ventrally pale. Granulation rather coarse, 10–14 granules between chaetae p_1 on Abd. V (Yosii's parameter).

Antennae. Ant. IV with bilobed or trilobed apical vesicle (av), subapical organite (or), dorso-lateral microsensillum (ms), seven cylindrical, subequal sensilla (dorsal S0, S1–4, dorsolateral S7–8), ca. 30 small, peg-like sensilla and one subcylindrical sensillum in ventral sensory file (sensory rasp) (Fig. 2A, B). Ant. III-organ with two long (external) and two short (internal) curved sensilla (Fig. 2A). Microsensillum on ant. III present. Eversible sac between Ant. III–IV present (Fig. 2B). Ant. I with seven chaetae, Ant. II with 13 chaetae.

Head. Ocelli 8 + 8. Postantennal organ 1.5 times as large as single ocellus with four lobes of which the anterior pair is larger than the posterior pair (Fig. 2C). Accessory boss present (Fig. 2C).

Labrum with 5, 5, 4 chaetae, four prelabrals present. Head of maxilla of the *C. armata*type. Maxillary outer lobe with two sublobal hairs. Labium of the *C. armata* type, with five papillae (A–E) and six proximal chaetae. Guard chaetae a_1, $b_{1–2}$, d_2, e_2 and lateral processus (l.p.) as accessory papillae with short terminal sensillum. Guards $b_{3–4}$, $d_{3–4}$, and $e_{1–6}$ with long sensilla. Dorsal guards $b_{3–4}$, $d_{3–4}$, and e_3 distally expanded and flattened.

Chaetotaxy. Differentiation of dorsal chaetae into micro-/meso- and macrochaetae quite distinct (Figs 1A, 1B, 2D, 3C). Arrangement of chaetae on head typical for the genus, spine-like chaetae absent. Cephalic chaetae $d_{2, 4}$, v_2, $p_{3,4}$, $g_{1, 5}$, l_{01}, l_{11} as macrochaetae. Dorsal chaetotaxy of B type (sensu Gisin 1947, Bourgeois and Cassagnau 1972, and Babenko et al. 1994) (Fig. 1B). Chaetae of medium length, pointed and serrated. Th. I with macrochaetae p_4, without p_2. Th. II–III with macrochaetae p_2 (shifted forward), $p_{5, 6}$, m_5, chaetae m_4 and m_5 (Th. II with $m_{4,}$and microsensillum ms), chaetae p_4 m_6 as sensorial chaetae s, chaetae a_2 as long as a_3. Abd. I–III with macrochaetae $p_{2,6}$, sensorial chaetae s = p_5. Abd. IV with macrochaetae $p_{1, 3, 6}$, s-chaetae as p_4. Abd. V with macrochaetae $p_{1, 5}$, 4 + 4 a-chaetae inside two macrochaetae p5 ($a_{2, 2,}$ absent, chaeta a_5

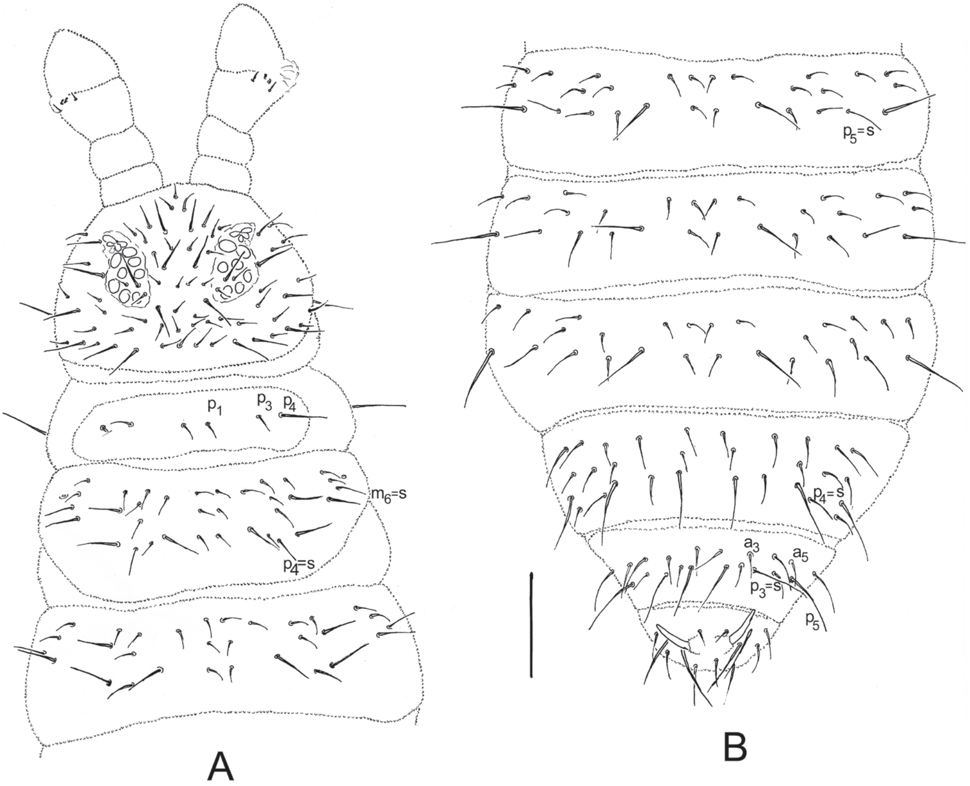

Figure 1. *Ceratophysella skarzynskii* sp. n. **A** Chaetotaxy of head and Th. I–III **B** Chaetotaxy of Abd. I–VI. Scale bars: 0.1 mm.

straight above p_5) (Figs 1B, 3C). Body s-chaetae relatively long, but shorter than macrochaetae, only on Abd. V as long as macrochaetae $p_{1,5}$ (Figs 1A, B, 3C).

Tibiotarsi I, II, III with 19, 19, 18 chaetae respectively, including one acuminate tenent hair A_1 each, femora with 13, 13, 12 chaetae, trochanters with 7, 7, 7 chaetae, coxae with 3, 7, 8 chaetae, subcoxae II with 0, 3, 3 chaetae, subcoxaeI with 1, 2, 3 chaetae. Claws with inner tooth and two pairs of lateral teeth. Empodial appendage with broad basal lamella and apical filament reaching slightly below inner tooth (ratio empodial filament: inner edge of claw = 0.47) (Fig. 3A). Ventral tube with 4 + 4 chaetae.

Retinaculum with 4 + 4 teeth. Furca well developed. Ratio dens + mucro: inner edge of claw III = 2.11: 1, ratio dens: mucro = 1.79: 1. Cuticular skeleton of furca well visible. Dens with uniform granulation and seven dorsal chaetae of which five are modified, two strongly thickened and three moderately so; basal macrochaeta longer than others chaetae, shorter than dens (3/5 of its length). Mucro boat-like with clear outer lamella (Fig. 3B, D).

Anal spines as long as inner edge of claw III slightly curved, situated on basal papillae, colourless (Figs 1B, 3C).

Table 1. Morphological characters for *C. skarzynski* sp. nov. and similar species: *C. denisana* Yosii, 1954 (Yosii 1956), *C. empodialis* Babenko, 1994, *C. longispina* (Tullberg, 1876) and *C. scotica* (Carpenter & Evans, 1899) after authors and Babenko et al. (1994).

Species/characters	*C. denisana*	*C. skarzynskii*	*C. empodialis*	*C. longispina*	*C. scotica*
Maximal body size (mm)	1.20	1.09	1.80	2.00	2.00
Yosii' parameter	14–16 (20)	10–14	8–13	12–16	13–15
Ant.IV: apical vesicle	trilobed	trilobed	simple/slightly bilobed	simple/slightly bilobed	simple
Ant.IV: number of peg-like chaetae in ventral file	>50	30–32	20	max. 15	15–20
Maxillar palp: number of sublobal hairs	2	2	2	2	1
Dorsal chaetae	smooth	serrated	rather smooth	serrated	rather smooth
Th.II–III: length of chaetae s = p_4/p_3	$p_4>p_3$	$p_4>p_3$	$p_4>p_3$	$p_4\approx p_3$	$p_4\approx p_3$
Abd. V: chaetae s = p_3/p_1	$p_3\approx p_1$	$p_3\approx p_1$	$p_3<p_1$	$p_3\approx p_1$	$p_3<p_1$
Tibiotarsial tenent hair	?	pointed	pointed	?	pointed
Empodial appendage : inner edge of claw	±½	±½	±1¼	±½	±1
Empodial basal lamella : inner edge of claw	1/4	1/5	1/5	?	1/5
Lateral teeth of claw	basal 3 pairs	2 pairs	2 pairs	2 pairs	2 pairs
Chaetae on dens: total number/numer of modified chaetae	7/5	7/5	7/2	7(8)/2	7/2

Etymology. The species is cordially dedicated to our colleague and friend Dr Dariusz Skarżyński, a prominent Polish specialist in Hypogastruridae, Collembola.

Remarks. The new species belongs to the *armata*-group of species, group B (Abd. tergum IV with p_1 as macrochaeta) and subgroup B2 (Abd. tergum IV without chaeta p_3) (Bourgeois and Cassagnau 1972). Among the species which could belong to this subgroup,*C. skarzynskii* is most similar to four species: *C. denisana* (Yosii, 1956), *C. empodialis* Babenko, 1994 (in Babenko et al. 1994), *C. longispina* (Tullberg, 1876), and *C. scotica* (Carpenter & Evans, 1899), due to the absence of transformed into spines, spine-like chaetae or spine-like integumentary protuberance on the head or Abd. V. They differ in the shape of the apical vesicle, the number of modified chaetae on the dens, the number of peg-like chaetae in the ventral sensory file on Ant. IV, length of empodial appendage,in the type of dorsal chaetae (serrated or smooth), and in the number of sublobal hairs on maxillary palp (one or two). A comparison of these species is presented in Table 1.

Ceratophysella communis (Folsom, 1898)

Acorutes communis Folsom, 1898: 52.
Syn: *Hypogastrura yuasai* Yosii, 1954: Yosii 1960.

Studied material. China: Henan: Zhengzhou, on *Pleurotus ostreatus*, 7 specimens on slides and 20 in alcohol, leg. Xin Sun, 05 Dec 2014; China: Henan: Zhumadian, on

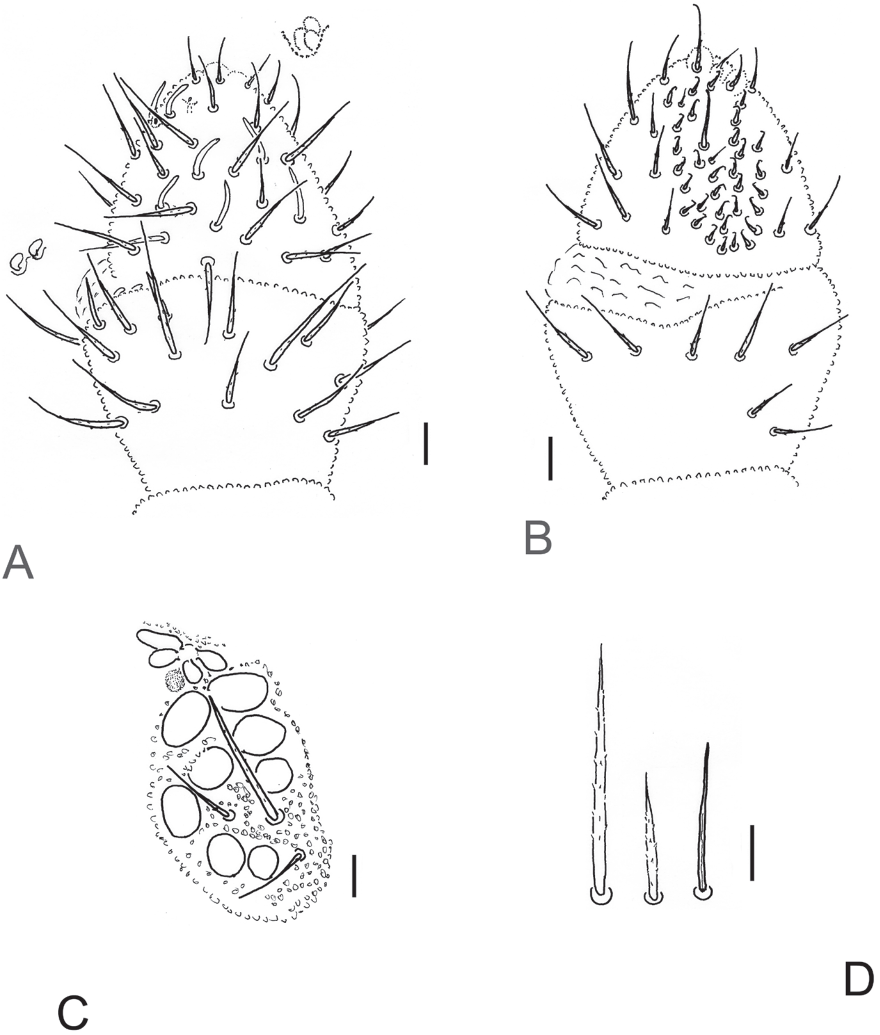

Figure 2. *Ceratophysella skarzynskii* sp. n. **A** ant. III and IV dorsal **B** ant. III and IV dorsal **C** PAO and eyes **D** macro-, microchaetae and s-chaeta. Scale bars: 0.01 mm.

Pleurotus ostreatus, 9 specimens on slides and 50 in alcohol, leg. ZhijingXie, 10 Nov 2017; China: Zhejiang: Pinghu, on *Pleurotus ostreatus*, 13 specimens on slides and 100 in alcohol, leg. Xin Sun, 07 Dec 2014; China: Sichuan: Qingchuan, on *Morchella esculenta*, 4 specimens on slides and 30 in alcohol, leg. Zhijing Xie, 19 Mar 2017.

Ceratophysella denticulata (Bagnall, 1941)

Achorutes denticulatus Bagnall, 1941: 218.
Syn: *Achorutes armata* var. nov. *cuspidate* Axelson, 1905: Thibaud et al. 2004.

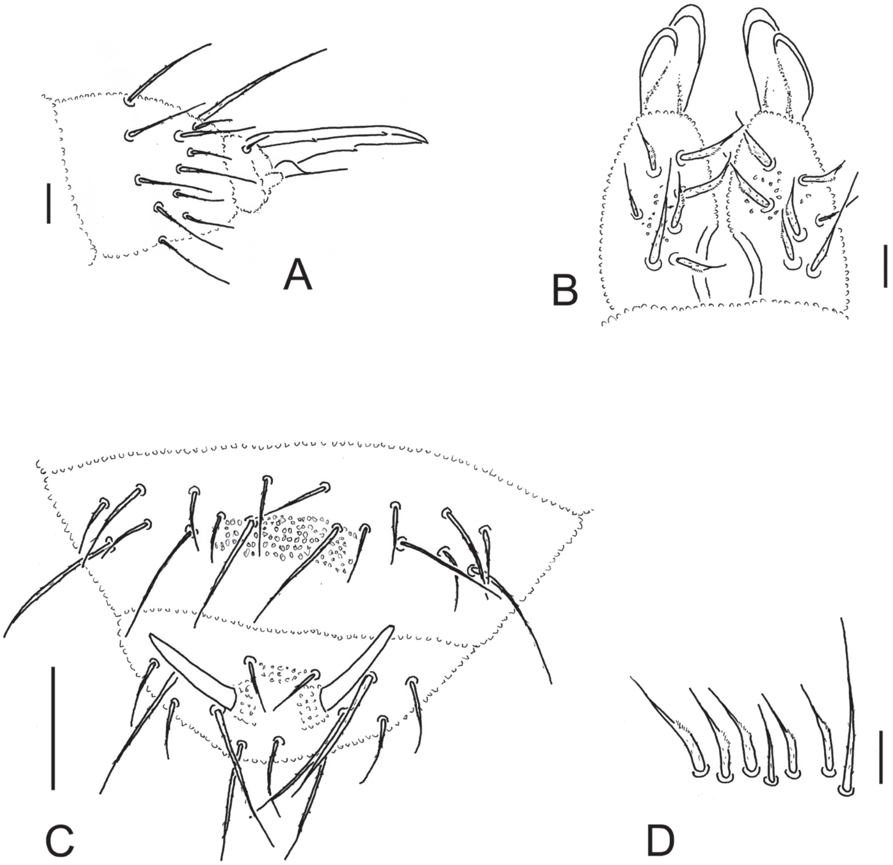

Figure 3. *Ceratophysella skarzynskii* sp. n. **A** tibiotarsus and claw III **B** dens and mucro **C** abd. V and VI **D** set of dens chaetae. Scale bars: 0.01 mm.

Achorutes distinguendus Bagnall, 1941: Thibaud et al. 2004.
Hypogastrura (*Ceratophysella*) *exilis* Yosii, 1956: Yosii 1965.
Hypogastrura (*Ceratophysella*) *afghanistanensis* Stach, 1963: Thibaud et al. 2004.

Studied material. China: Tibet: Lasa, on *Ganoderma* sp., 9 specimens on slides, leg. Weiping Xiong, 27 Mar 2015.

Ceratophysella liguladorsi (Lee, 1974)

Hypogastrura liguladorsi Lee, 1974: 95.

Studied material. China: Zhejiang: Wuyi, on *Lentinus* sp., 11 specimens on slides and 80 in alcohol, leg. Xin Sun, 09 Dec 2014.

Key to the Chinese species of *Ceratophysella*

In 2007 Wu and Yin proposed a key to the six species of the genus *Ceratophysella* known from China. Jia et al. (2010) proposed a list of 14 Chinese species of *Ceratophysella*. The present key includes 15 species. Some of the species are not sufficiently described, but the available characters given in the descriptions are sufficient to include them in the key. The characters for *C. adexilis* have been verified on type material, and for *C. communis* on fresh material from the type locality (Tokyo).

1 Abd. IV with p1 chaeta shorter than p2 chaeta (A-type) **2**
– Abd. IV with p1 chaeta longer than p2 chaeta (B-type).................... **9**
2 Dens with 6 chaetae.................... **3**
– Dens with 7chaetae.................... **5**
3 Unguiculus as long as 1/2–1 of internal edge of claw **4**
– Unguiculus very short, as long as 1/3, claw without teeth.... ***C. zhangi* (Zhao, 1998)**[*]
4 Labial palp with 4 papillae (papilla C absent), macrochaetae rather short, Th. II with p4 = s longer thanmacrochaeta p5.................... ***C. succinea* (Gisin, 1949)**
– Labial palp with 5 papillae (papillae A–E present), macrochaetae long, Th. II with p4 =shorter than macrochaeta p5......... ***C. taiguensis* Jia, Skarżyński & Li, 2010**
5 Body chaetae smooth **6**
– Body chaetae serrated.................... **8**
6 Dens with thickened chaetae.................... **7**
– Dens without thickened chaetae .... ***C. yinae* (Yue & Fu, 2000)**
7 Four internal chaetae on dens thickened, Ant. IV with 8 dorsal sensilla .... ***C. baichengensis* Wu & Yin, 2007**
– Two internal chaetae on dens thickened, Ant. IV with 7 dorsal sensilla.................... ***C. adexilis* Stach, 1964**
8 Abd. V tergum with chaeta a2' present, Ant. IV with simple apical vesicle, Abd. IV tergum with p5=s equal to ½ macrochaetae......... ***C. denticulata* (Bagnall, 1941)**
– Abd. V tergum without chaeta a2, Ant. IV with bi- or trilobed apical vesicle, Abd IV with chaeta p5=s equal to ¾ macrochaetae...... ***C. communis* (Folsom, 1898)**
9 Abd. V tergum with cuticular projection or medial spines.................... **10**
– Abd. V tergum without such projection or spines **11**
10 Abd. V tergum with medial cuticular projection, dens with 7 normal chaetae, ventral sensory file (sensory rasp) with ca. 40 peg-like sensilla .... ***C. liguladorsi* (Lee, 1974)**
– Abd. V tergum with chaetae p1 modified in spines, dens with 7 chaetae among which two modified, central sensory file (sensory rasp) with ca. 25–35 peg-like sensilla .... ***C. duplicispinosa* (Yosii, 1954)**
11 Head with chaetae d5 and sd5 modified into spines.................... **12**
– Head without chaetae modified into spines.................... **13**

---

[*] following the description in Tamura and Zhao 2008

12 Length of unguiculus as 1/3 of inner edge of claw, tibiotarsi with A1 (tenent hair) short (= ½ of inner edge of claw) .... ***C. xiaoi*** **(Tamura, 1998)** (in: Tamura and Zhao 1998)

– Length of unguiculus as 1/2 of inner edge of claw, tibiotarsi with A1 (tenent hair) long (= length of inner edge of claw) ....***C. anshanensis*** **(Wu & Xie, 2007)**

13 Head without a pair of cornea-like convexity **14**

– Head with a pair of cornea-like convexity ....***C. sinensis*** **Stach, 1964**

14 Dens with thickened chaetae, tibiotarsi with prolonged chaeta A1 as pointed tenent hair, claws with one internal tooth and two pairs of lateral teeth .... ***C. skarzynskii*** **sp. n.**

– Dens without thickened chaetae, tibiotarsi without prolonged chaeta A1, claws without internal and lateral teeth .... ***C. flectochaeta*** **Lin & Xia, 1983**

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RESEARCH ARTICLE

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Keys to world Charipinae (Hymenoptera, Cynipoidea, Figitidae)

Mar Ferrer-Suay[1], Jesús Selfa[1], Juli Pujade-Villar[2]

1 *Universitat de València, Facultat de Ciències Biològiques, Departament de Zoologia, Campus de Burjassot-Paterna, Dr. Moliner 50, 46100 Burjassot (València), Spain* **2** *Universitat de Barcelona, Facultat de Biologia, Departament de Biologia Animal. Avda, Diagonal 645, 08028-Barcelona, Spain*

Corresponding author: *M. Ferrer-Suay* (mar.ferrer.suay@gmail.com)

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Abstract

Eight genera of Charipinae are defined, keyed out, and illustrated. Keys for all charipine species within each valid genus, including *Alloxysta*, *Apocharips*, *Dilyta*, *Phaenoglyphis*, and *Thoreauana*, are presented, except for *Dilapothor*, *Lobopterocharips*, and *Lytoxysta*, which are monotypic. Figures are provided to show the diagnostic morphological features as used in the keys.

Keywords

Alloxysta, *Apocharips*, Charipinae, *Dilapothor*, *Dilyta*, key, *Lobopterocharips*, *Lytoxysta*, *Phaenoglyphis*, *Thoreauana*

Introduction

Hymenopteran parasitoids are one of the most important groups of insects in pest control. However, their use in controlling pests is usually difficult because they are impossible to identify at species level; therefore, their employment in pest control is limited. For this reason, the focus of our study is the basic taxonomy of the many hymenopteran groups that are still unknown. This has been our main aim over the last few years.

The Figitidae (Hymenoptera, Cynipoidea) are biologically characterised as parasitoids of the larvae of other insects, principally Diptera and Cyclorrapha (Ronquist 1999), except for the subfamily Charipinae, which is parasitoids of Hemiptera. The members of this subfamily are hyperparasitoids of aphids via Aphidiinae (Hymenoptera, Ichneumonoidea, Braconidae) and Aphelininae (Hymenoptera, Chalcidoidea, Aphelinidae), as well as hyperparasitoids of psyllids via Encyrtidae (Hymenoptera, Chalcidoidea) (Fergusson 1986; Menke and Evenhuis 1991).

Eight genera of Charipinae are recognised in the following regions: *Alloxysta* (Cosmopolitan; Förster 1869), *Apocharips* (Palaearctic and Neotropical; Fergusson 1986), *Dilapothor* (Australia; Paretas-Martínez and Pujade-Villar 2006), *Dilyta* (cosmopolitan, except South America and Australia; Förster 1869), *Lobopterocharips* (Nepal; Paretas-Martínez and Pujade-Villar 2007), *Lytoxysta* (North America; Kieffer 1909), *Phaenoglyphis* (cosmopolitan; Förster 1869), and *Thoreauana* (Australia; Girault 1930). The morphological features of the charipine specimens are dramatically reduced, mainly because they are very small (0.8–2.0 mm), and they generally have shiny, smooth bodies. The combination of these features with the large number of described species over the past 150 years has been the reason for the chaotic taxonomy of the Charipinae. This makes the identification of individual species very difficult.

Nowadays, thanks to many studies carried out the correct state of each species has been rectified, and many new species have been described. The taxonomy of the subfamily Charipinae is now organised and clear, due to studies published over the last nine years (e.g. Ferrer-Suay et al. 2013d, e, f, g, h; 2014a, b, 2015; 2018). Additionally, a website has been developed to collect accurate, up-to-date information on the Charipinae (http://www.charipinaedatabase.com)

Following these studies, and taking into account the importance of the Charipinae in ecology, we have prepared clear and easily followed keys for each of the genera of Charipinae. Figures show the diagnostic characters, as used in the keys. These keys will be helpful for those looking to identify charipine species. The analysis of the morphological features of each species has been crucial to elaborate on these keys.

Material and methods

Specimens were studied using a stereomicroscope (NIKON SMZ-1) and an environmental scanning electron microscope (FEI Quanta 200 ESEM) at the scientific technical services of the University of Barcelona. The field-emission gun environmental scanning electron microscope was used for high-resolution imaging without the need to gold-coat the specimens.

Type materials of each species of Charipinae have been reviewed, as have many additional specimens from all over the world and deposited in the following institutions:

CNCI	(Canadian National Collection of Insects, Ottawa, Canada; G. Gibson)
USNM	(National Museum of Natural History (Smithsonian Institution), Washington, DC, USA; M. Buffington)
BMNH	(Natural History Museum, London, England; D. Notton)
MZLU	(Biologiska Museet, Lund, Sweden; R. Danielsson)
ZSM	(Zoologische Staatssammlung Museum, Munich, Germany; S. Schmidt)

Morphological terms used follow Paretas-Martínez et al. (2007). Measurements and abbreviations include F1–F12, first and subsequent flagellomeres. The width of the forewing radial cell is measured from the margin of the wing to the beginning of the Rs vein. The transfacial line is measured as the distance between the inner margins of compound eyes, measured across the face through the antennal sockets divided by the height of the eye. The malar space is measured by the distance from the lower part of the gena from the mouthparts to the ventral margin of the compound eye, divided by the height of the eye. Females and males of the species have the same characters except where indicated.

Results

Below are explained the morphological features important for species or genera identification in charipines, according to Ferrer-Suay et al. (2012).

Body surface (Fig. 1)

Generic characters. With very fine reticulate sculpture in antennae, head and mesosoma (*Lytoxysta*, Fig. 1[3]) / smooth all other genera (Fig. 1[1, 2]) (except some *Phaenoglyphis* species, which have some very fine imbricate sculpture in scutum).

Head (Fig. 2)

Specific characters. Radial carinae on face (only for *Apocharips* species, Fig. 2[2]) / smooth (rest of the genera) (Fig. 2[1]).

Antenna (Fig. 3)

Generic characters. Number of flagellomeres in female and male: 9–10 (*Thoreauana*, Fig. 3[8]) / 10–11 (*Dilapothor*, Fig. 3[10]) / 11–11 (*Lytoxysta*, Fig. 3[6]) / 11–12 (all other). Shape of last two flagellomeres: wider than the rest and broadly jointed (*Apocharips*, *Dilapothor*, *Dilyta*, *Thoreauana*, Fig. 3[6–10]) / as wide as the previous with constriction between them (*Alloxysta*, *Lobopterocharips*, *Lytoxysta*, *Phaenoglyphis*, Fig. 3[1–6]). Pedicel: cup-shaped (*Lobopterocharips*, Fig. 3[5]) / cylindrical (all others).

Specific characters. Proportions (length and width) of pedicel, F1, F2, F3 and F4. Number of flagellomeres forming of club (in some species some flagellomeres are wider resembling a club). Number of flagellomeres with rhinaria. Males: F1, F2, F3 modified or not (curved, excavated, humped) (Fig. 3[2, 4]).

Pronotum (Fig. 4)

Specific characters. Lateral carinae: absent (Fig. 4[3]) / present (short (Fig. 4[2]) or long (Fig. 4[1]), reaching mesoscutum or not).

Mesopleuron (Fig. 1)

Generic characters. Mesopleural triangle absent (*Lytoxysta*, Fig. 1[3]) / present (all others). Mesopleural sulcus present (*Phaenoglyphis*, Fig. 1[2]) / absent (all others).

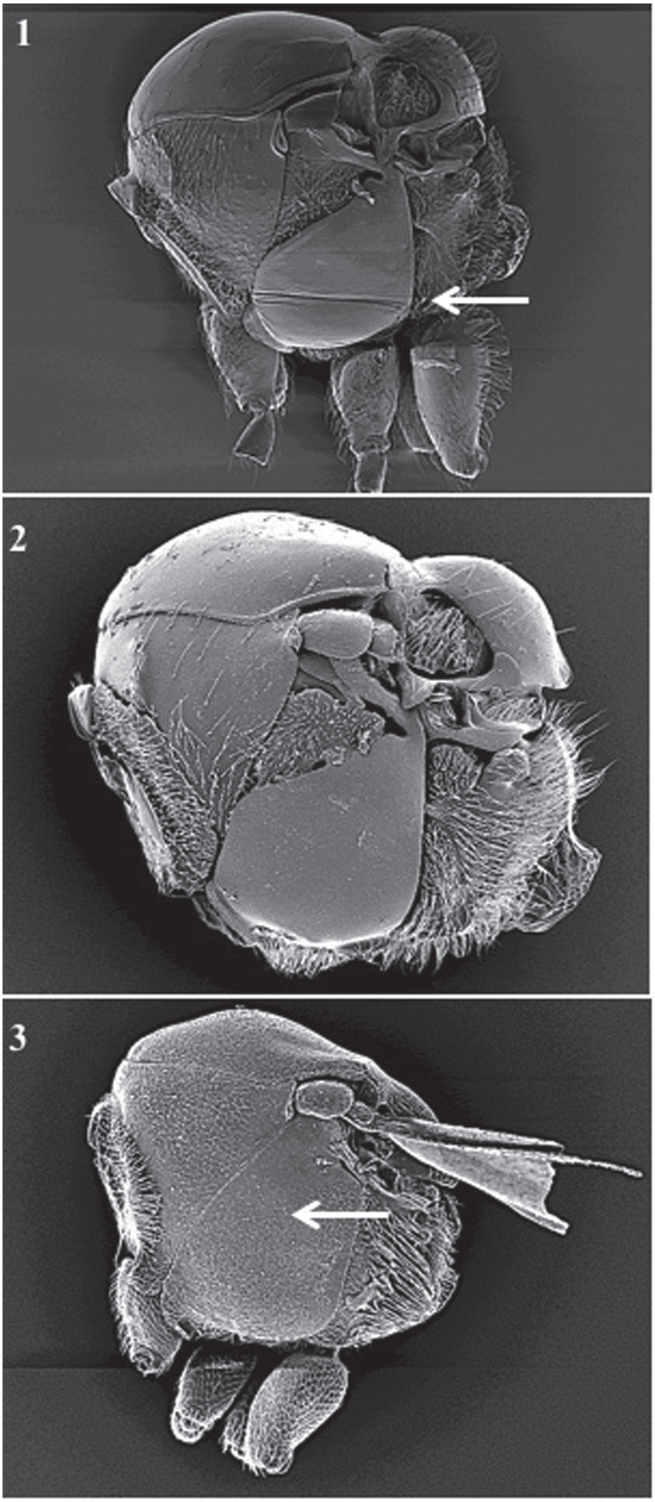

Figure 1. Body surface. *Phaenoglyphis* sp. (**1**); *Alloxysta* sp. (**2**); *Lytoxysta* sp. (**3**).

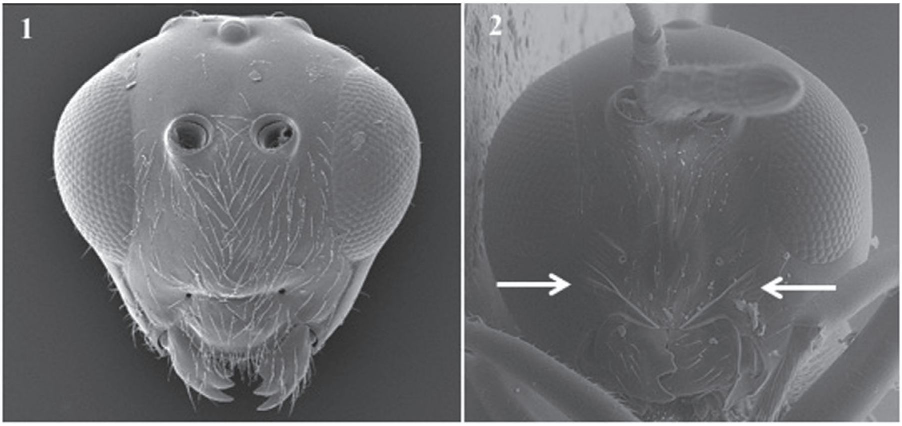

Figure 2. Head. *Phaenoglyphis americana* (**1**); *Apocharips hansoni* (**2**).

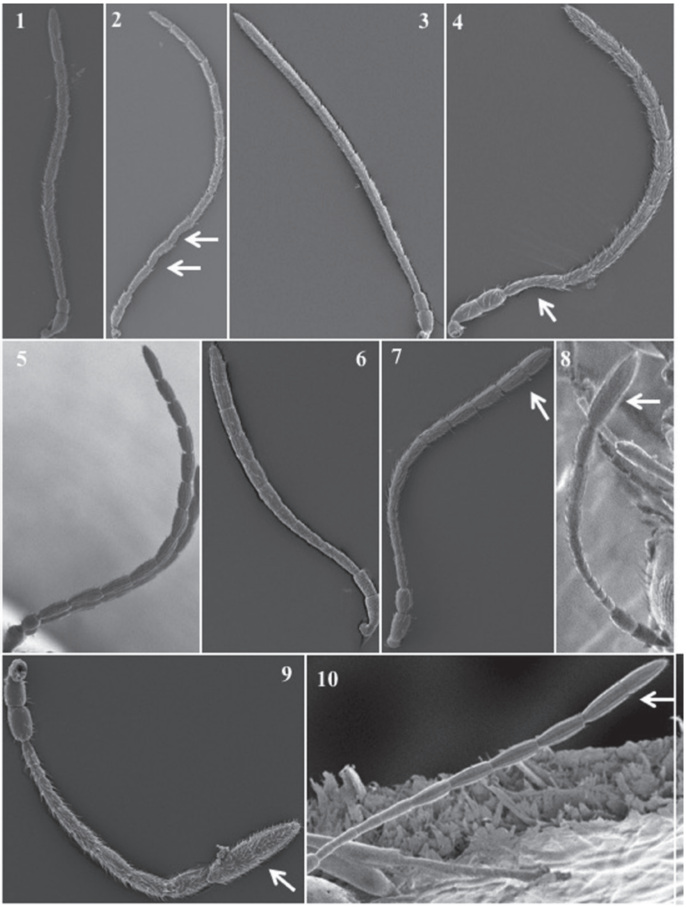

Figure 3. Antenna. *Alloxysta victrix*, female (**1**); *Alloxysta victrix*, male (**2**); *Phaenoglyphis americana*, female (**3**); *Phaenoglyphis americana*, male (**4**); *Lobopterocharips arreplegata*, male (**5**); *Lytoxysta brevipalpis*, female (**6**); *Apocharips trapezoidea*, female (**7**); *Thoreauana mascagnini*, female (**8**); *Dilyta subclavata*, female (**9**); *Dilapothor carverae*, female (**10**).

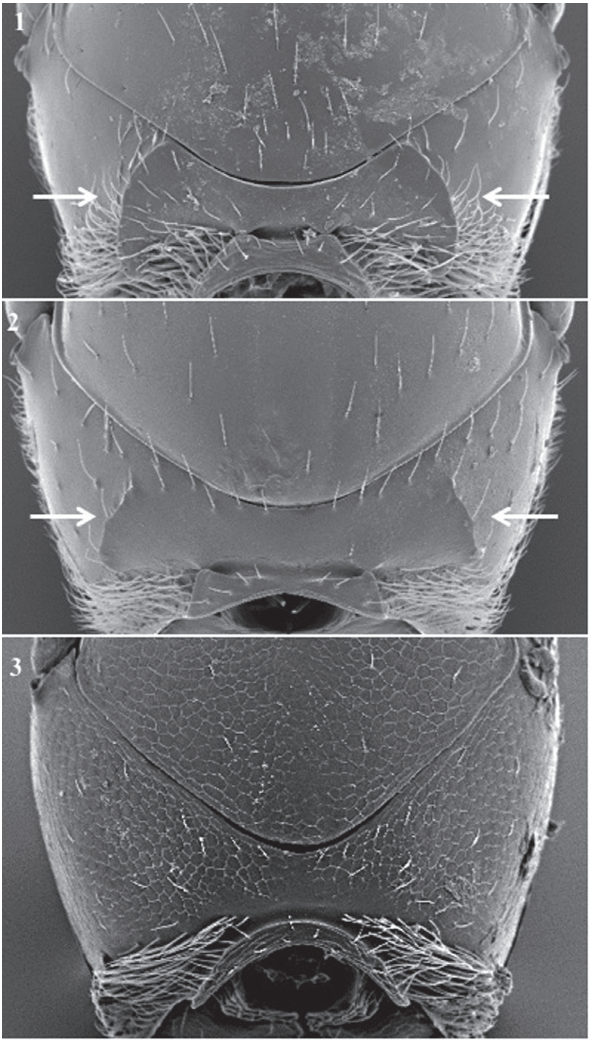

Figure 4. Pronotum. *Dilyta subclavata* (**1**); *Alloxysta xanthopsis* (**2**); *Lytoxysta brevipalpis* (**3**).

Mesoscutum (Fig. 5)

Generic characters. Notauli present (only in †*Protocharips* and some *Phaenoglyphis*, Fig. 5[1,2]) / absent (all others).

Specific characters. Notauli present (Fig. 5[1, 2]) or absent (Fig. 5[4]) (only for *Phaenoglyphis* species). Presence or absence of very fine imbricate sculpture in basal areas of scutum (for *Phaenoglyphis* species, Fig. 5[3]).

Scutellum (Figs 6, 7)

Generic characters. Scutellar foveae present (only in some *Phaenoglyphis*, Fig. 6) / absent (all other). Posterodorsal extensions of axillar strip present (*Alloxysta*,

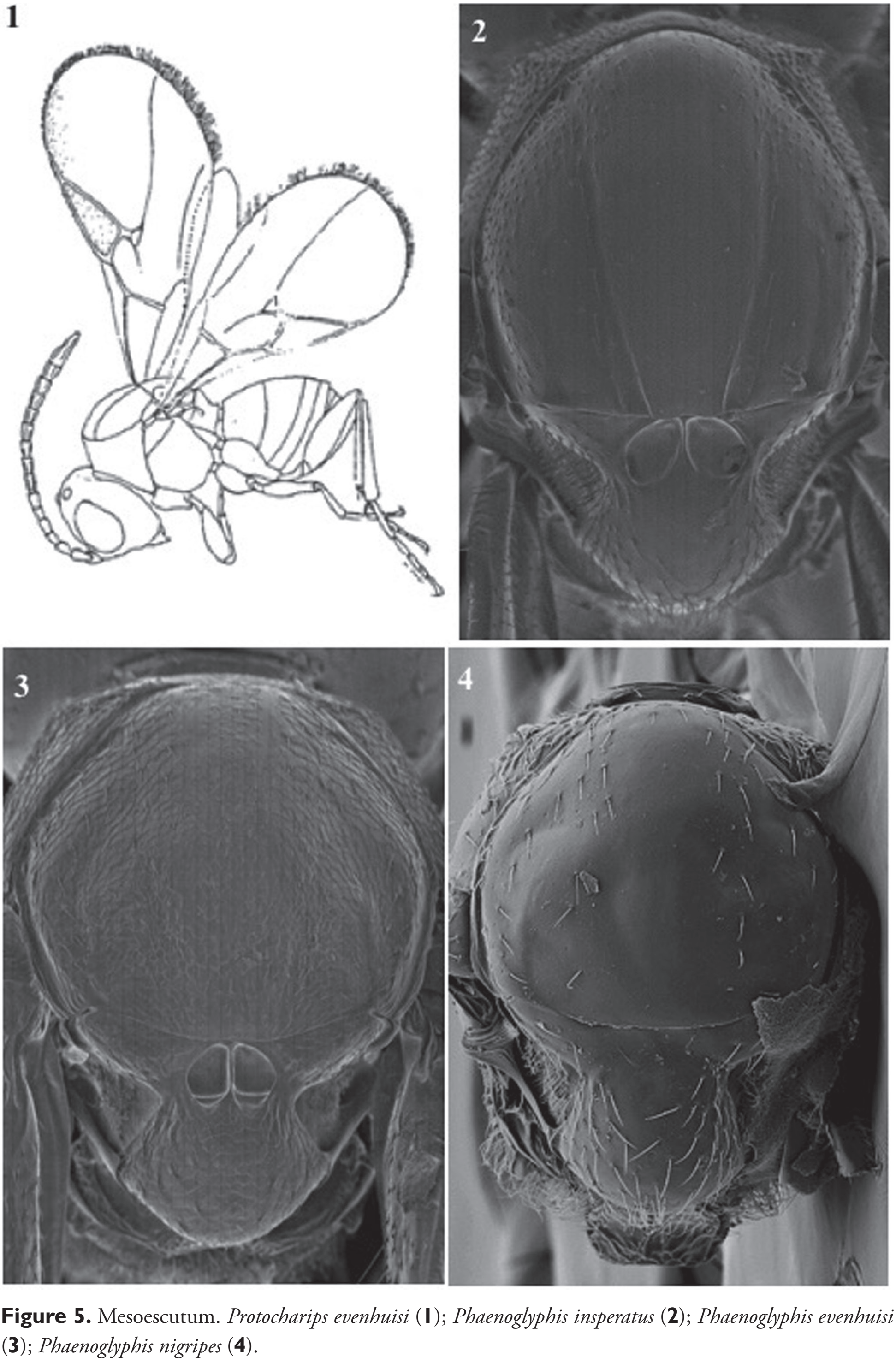

Figure 5. Mesoescutum. *Protocharips evenhuisi* (**1**); *Phaenoglyphis insperatus* (**2**); *Phaenoglyphis evenhuisi* (**3**); *Phaenoglyphis nigripes* (**4**).

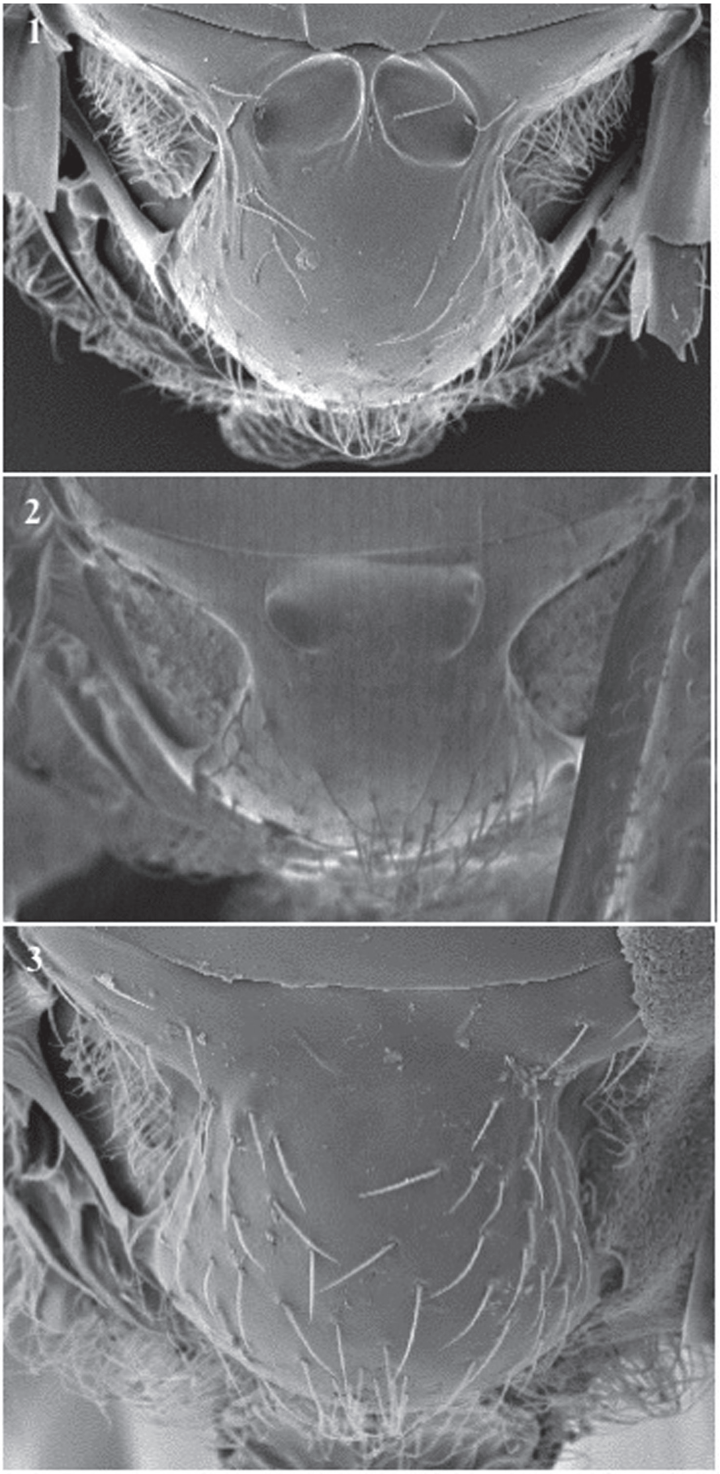

Figure 6. Scutellum. *Phaenoglyphis americana* (**1**); *Phaenoglyphis villosa* (**2**); *Phaenoglyphis laevis* (**3**).

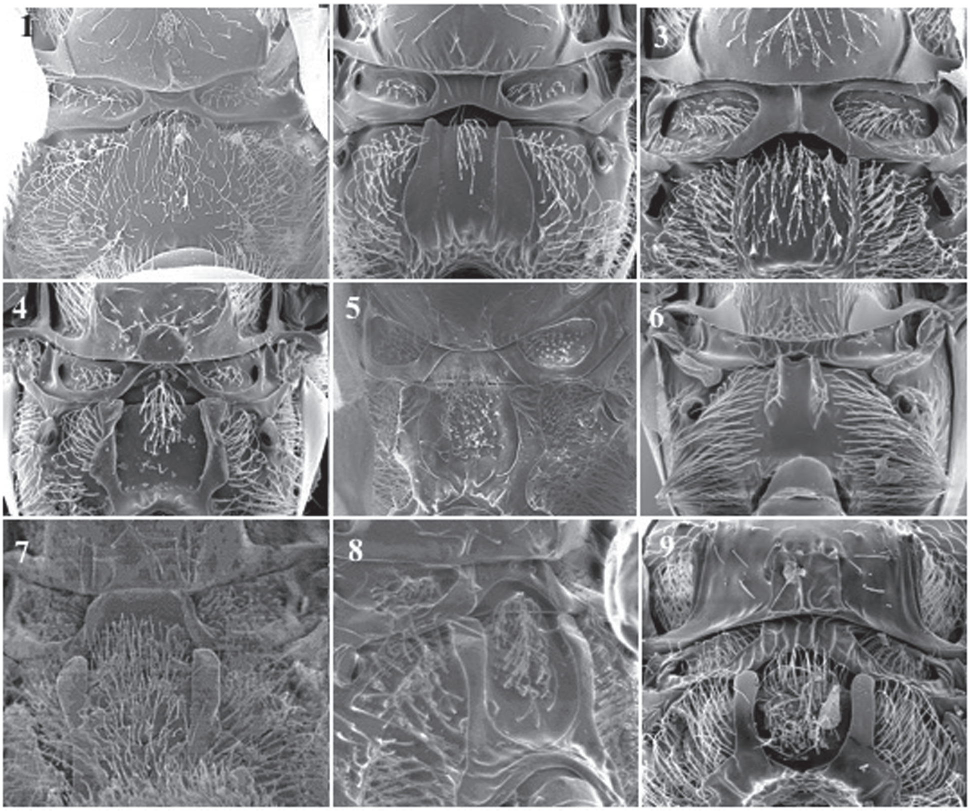

Figure 7. Scutellum and Propodeum. *Alloxysta fuscicornis* (**1**); *Alloxysta xanthopsis* (**2**); *Phaenoglyphis americana* (**3**); *Dilyta subclavata* (**4**); *Dilyta australafricana* (**5**); *Lytoxysta brevipalpis* (**6**); *Dilapothor carverae* (**7**); *Thoreauana mascagnini* (**8**); *Apocharips trapezoidea* (**9**).

Lobopterocharips, *Lytoxysta*, *Phaenoglyphis*, Fig. 10[1]) / absent (*Apocharips*, *Dilapothor*, *Dilyta*, *Thoreauana*, Fig. 10[2]). Carinae on scutellum apex: absent (*Phaenoglyphis*, *Lobopterocharips* and some *Alloxysta*, Newc) / longitudinal carinae at centre (some *Alloxysta*, Fig. 7[1]) / irregular carinae (*Lytoxysta*, Fig. 7[6]) / M-shaped carina at centre (*Apocharips*, Fig. 7[9]) / ∩-shaped carina or two long symmetrical carinae (*Dilyta*, Fig. 7[4, 5]) / two short symmetrical carinae (*Thoreauana*, Fig. 7[8]) / three small carinae at each side (*Dilapothor*, Fig. 7[7]).

Specific characters. Scutellar foveae absent (Fig. 6[3]) or present (fused, Fig. 6[2]; or unfused, Fig. 6[1, 2]) (for *Phaenoglyphis*). Carinae on scutellum apex: absent (Fig. 7[3]) or present (a single carina, Fig. 7[1], to several longitudinal carinae, Fig. 7[2]) (for *Alloxysta* species); two long symmetrical carinae (African *Dilyta*, Fig. 7[5]) or ∩-shaped carina (non-African *Dilyta*, Fig. 7[4]).

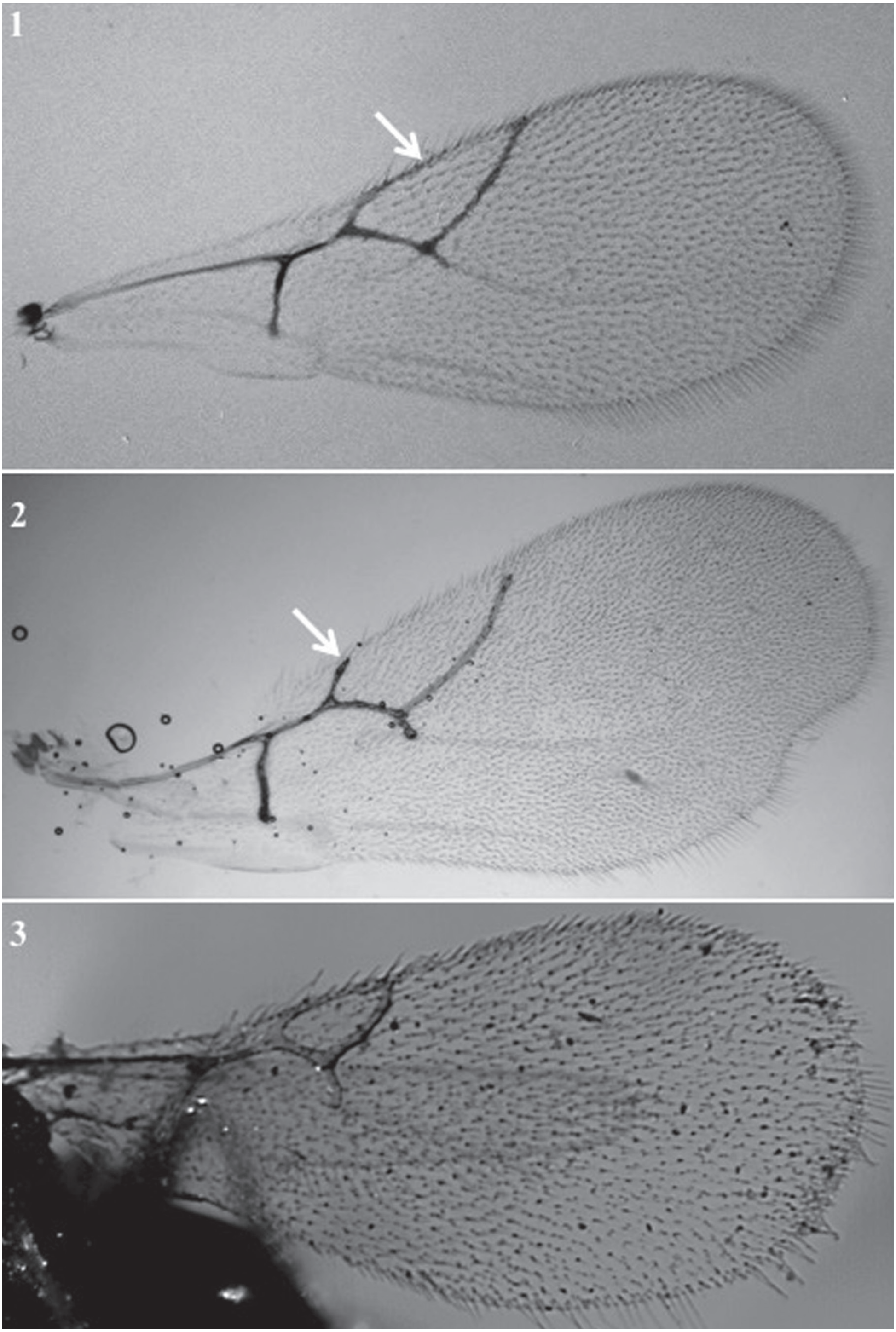

Figure 8. Forewing. *Phaenoglyphis villosa* (**1**); *Lobopterocharips arreplegata* (**2**); *Alloxysta ruficollis* (**3**).

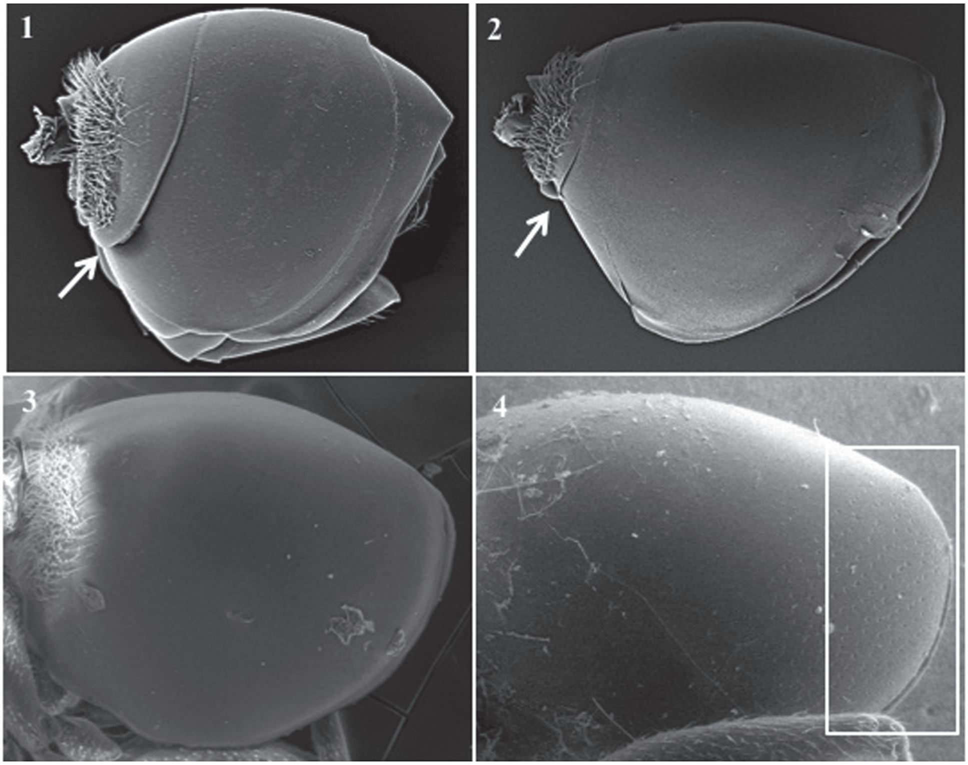

Figure 9. Metasoma. *Alloxysta* (**1**); *Apocharips* (**2**); *Dilyta*, without puntuation on distal area (**3**); *Dilyta*, with puntuation on distal area (**4**).

Propodeum (Fig. 7)

Specific characters. Presence or absence of longitudinal carinae; if present, shape of carinae (short, long, thin, broad, forming a plate). Pubescence.

Forewing (Fig. 8)

Generic characters. Undulation in posteroapical margin of wing present (*Lobopterocharips*, Fig. 8[2]) / absent (all others, Fig. 8[1, 3]). Areola present (only in †*Protocharips*, Fig. 5[1]) / absent (all others).

Specific characters. Shape, size, and length of radial cell (Fig. 8).

Metasoma (Fig. 9)

Generic characters. Metasoma with two visible large terga with subequal dorsomedial lengths (*Alloxysta*, *Lobopterocharips*, *Lytoxysta*, *Phaenoglyphis*, Fig. 9[1]; also in †*Protocharips*, Fig. 5[1]) / with a small basal tergum, terminating just posterior to ring of setae (*Apocharips*, Fig. 9[2]) / not segmented, only one tergite visible (*Dilapothor*, *Dilyta*, *Thoreauana*, Fig. 9[3, 4]).

Specific characters. Punctuation on distal area absent (Fig. 9[3]) or present (Fig. 9[4]) (*Dilyta* species).

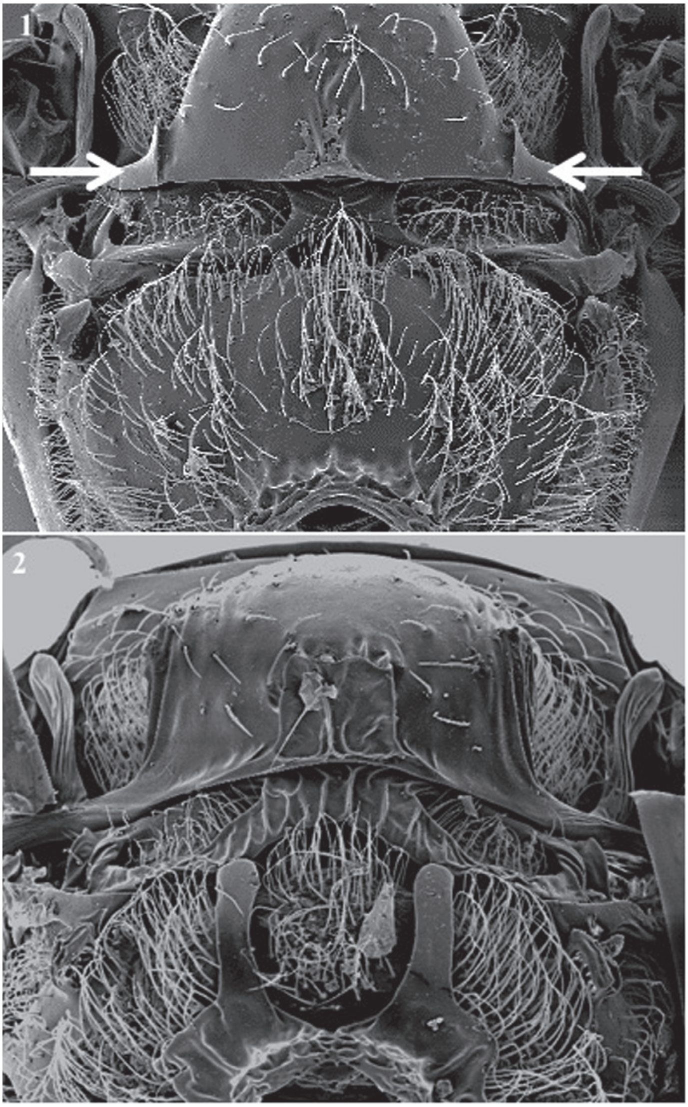

Figure 10. Mesosoma, posterior view. *Alloxysta victrix*, with axillar strip (indicated with arrows) (**1**); *Apocharips trapezoidea*, without axillar strip (**2**).

Key to genera

1 Metasoma with two large terga visible, subequal in length along middorsal line, but basal tergite 1/4–1/3 smaller than second terga in lateral view (Fig. 11[1]). Antenna with all flagellomeres separated by constrictions (Fig. 11[8]).

Posterodorsal extensions of axillar strip present (Fig. 11[11]). Hyperparasitoids of Aphididae (for those genera where it is known) **2**

– Metasoma with a single tergal plate, or if two, then basal tergite much shorter than second along middorsal line (Fig. 11[2, 3]). Antenna with last two flagellomeres broadly jointed or fused (Fig. 11[7]). Posterodorsal extension of axillar strip absent (Fig. 11[12]). Hyperparasitoids of Psyllidae (for those genera where it is known) **5**

2 Mesopleuron with horizontal sulcus in lower part (Fig. 11[4]) .... ***Phaenoglyphis* Förster, 1869**

– Mesopleuron without horizontal sulcus (Fig. 11[5]) **3**

3 Forewing with an undulation in the apical part of the posterior margin (Fig. 11[17]). Antenna with a cup-shaped pedicel (Fig. 11[10]). Known only from Nepal............. ***Lobopterocharips* Paretas-Martínez & Pujade-Villar, 2007**

– Margin of the forewing continuous (Fig. 11[16]). Antenna with a cylindrical pedicel (Fig. 11[9]) **4**

4 Mesopleuron without mesopleural triangle (Fig. 11[6]). Head and mesosoma with fine reticulate sculpture. Nearctic.................... ***Lytoxysta* Kieffer, 1909**

– Mesopleuron with mesopleural triangle (Fig. 11[4, 5]). Head and mesosoma smooth, unsculptured. Cosmopolitan .... ***Alloxysta* Förster, 1869**

5 Metasoma with a small basal tergum, terminating just posterior to ring of setae (Fig. 11[2]). R1 long, reaching wing margin. Palaearctic and Neotropical .... ***Apocharips* Fergusson, 1986**

– Metasoma appearing unsegmented, only one tergite visible (Fig. 11[3]). R1 short, not reaching wing margin **6**

6 Apex of scutellum with a ∩-shaped projected plate (Fig. 11[12]) or with one carina on each side, both symmetrical and parallel higher than axillar strip; distance between them equal to distance between propodeal carinae (Fig. 11[13]). Female antenna with 11 flagellomeres. Cosmopolitan except Neotropics and Australia .... ***Dilyta* Förster, 1869**

– Apex of scutellum without projected plate, with symmetrical carinae longer than axillar strip (Fig. 11[13–15]). Female antenna with less than 11 flagellomeres **7**

7 Head higher than broad in anterior view. Female antenna with 10 flagellomeres, apical club two-segmented. Three carinae at each side of the scutellum apex (Fig. 11[14]). Radial cell large, 2r as long as Sc+R1; Rs long and curved and giving an elongated aspect to the radial cell. Australia .... ***Dilapothor* Paretas-Martínez & Pujade-Villar, 2006**

– Head rounded in anterior view. Female antenna with 9 flagellomeres, apical club not segmented (Fig. 11[7]). One small carina presents at each side of the scutellum apex. (Fig. 11[15]). Radial cell small, 2r shorter than Sc+R1; Rs short and almost straight. Australia .... ***Thoreauana* Girault, 1930**

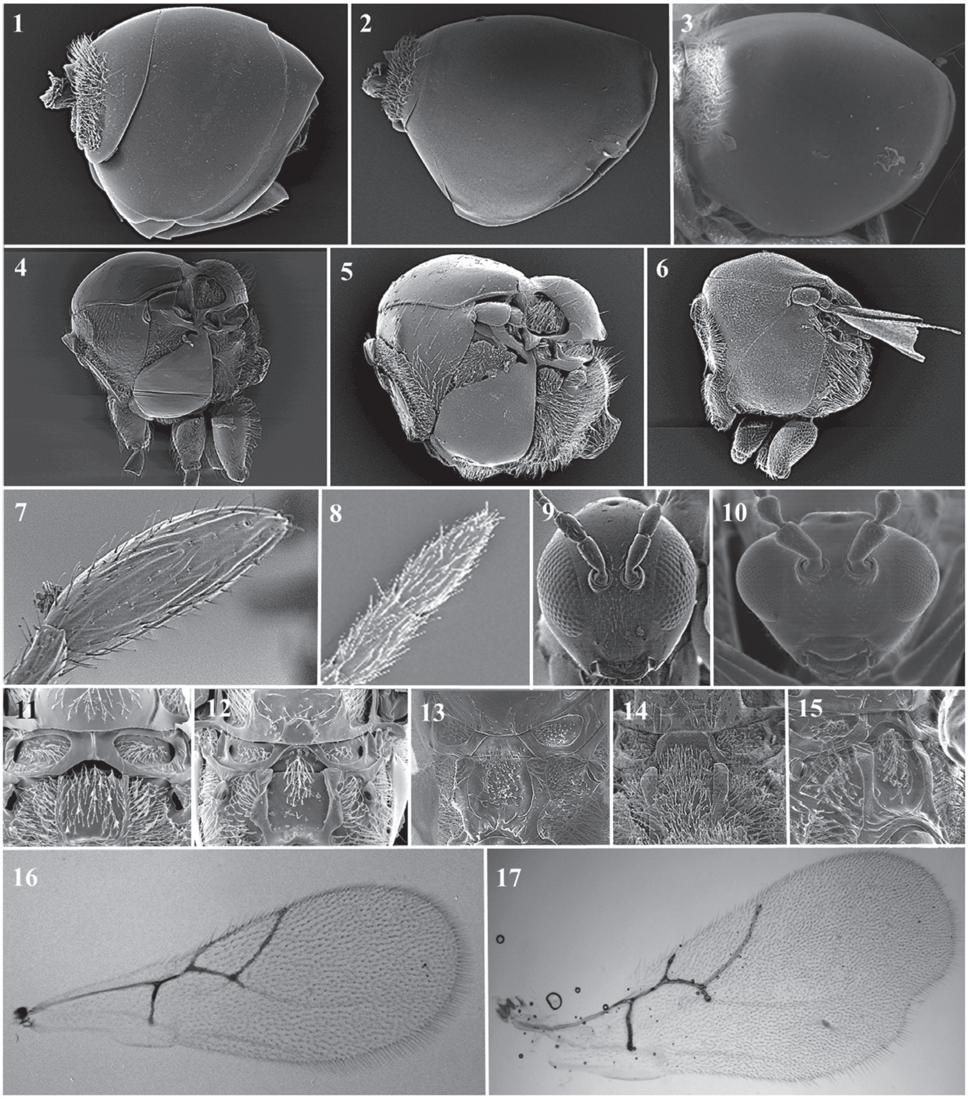

Figure 11. Charipinae general features. metasoma *Alloxysta* sp. (**1**); metasoma *Apocharips* sp. (**2**); metasoma *Dilyta* sp. (**3**); mesosoma *Phaenoglyphis* sp. (**4**); mesosoma *Alloxysta* sp. (**5**); mesosoma *Lytoxysta* sp. (**6**); two last flagellomeres *Thoreauana* sp. (**7**); two last flagellomeres *Phaenoglyphis* sp. (**8**); head *Thoreauana* sp. (**9**) ; head *Lobopterocharips* sp. (**10**); propodeum *Phaenoglyphis* sp. (**11**); propodeum holarctic *Dilyta* sp. (**12**); propodeum african *Dilyta* sp. (**13**); propodeum *Dilapothor* sp. (**14**); propodeum *Thoreauana* sp. (**15**); fore wing *Phaenoglyphis* sp. (**16**); fore wing *Lobopterocharips* sp. (**17**).

Alloxysta Förster, 1869

Allotria Westwood, 1833: 494. Type: *Allotria victrix* Westwood, 1833. Homonym of *Allotria* Hübner, 1823: 280. Synonymized by Hellén (1963: 8).

Xystus Hartig, 1840: 199. Type: *Xystus erythrocephalus* Hartig, 1840. Homonym of *Xystus* Schoenherr, 1826: 310. Synonymized by Hellén (1963: 8).

Alloxysta Förster, 1869: 338. Type: *Xystus macrophadnus* Hartig, 1841.

Pezophycta Förster, 1869: 338. Type: *Xystus brachypterus* Hartig, 1840. Synonymized by Hellén (1963: 8).

Nephycta Förster, 1869: 338. Type: *Nephycta discreta* Förster, 1869. Synonymized by Hellén (1963: 8).

Adelixysta Kierych, 1988: 351. Type: *Adelixysta sawoniewiczi* Kierych, 1988. Synonymized by Menke and Evenhuis (1991: 150).

Carvercharips Kovalev, 1994: 413, 414. Type: *Alloxysta carinata* Carver, 1992. Synonymized by Paretas-Martínez et al. (2007a: 161).

General features. *Head.* Transversally ovate, smooth and shiny, slightly wider than high in anterior view.

Setae found below, between and above toruli, on vertex and multiple setae on the face. Transfacial distance is 0.9–1.3× the height of the compound eye. Malar space is 0.3–0.6× the height of the compound eye (Fig. 12[1]).

Antenna. Female: 13-segmented, filiform. All antennomers covered with sparse setae (Fig. 12[5]). Male: 14-segmented, filiform. All antennomers covered with sparse setae (Fig. 12[6]).

Mesosoma. Pronotum with scattered setae that are differently distributed, depending on the species, with or without carinae (Fig. 12[3]). Mesoscutum is smooth and shiny, round in the dorsal view, with sparse setae. Scutellum is smooth and shiny with scattered setae that are usually more abundant on the apex (Fig. 12[8]). Propodeum with multiple setae, with or without carinae; carinae are separated or fused, forming a variably shaped plate (Fig. 12[7]).

Forewing. Longer than the body, 1.4–1.8× as long as the mesosoma and metasoma together, with dense pubescence; marginal setae present (Fig. 12[2]).

Metasoma. Anterior region has an incomplete ring of setae, is glabrous at centre and is wider laterally. Metasoma is smooth and shiny, with T3 and T4 clearly separated (Fig. 12[4]).

Distribution. Cosmopolitan (Ferrer-Suay et al. 2012)

Hosts. Endoparasitoids of Aphidiinae (Hymenoptera, Braconidae) and Aphelininae (Hymenoptera, Braconidae) that are endoparasitoids of aphids (Hemiptera, Aphididae) (Fergusson 1986; Menke and Evenhuis 1991). Found in a variety of hosts (Ferrer-Suay et al. 2012).

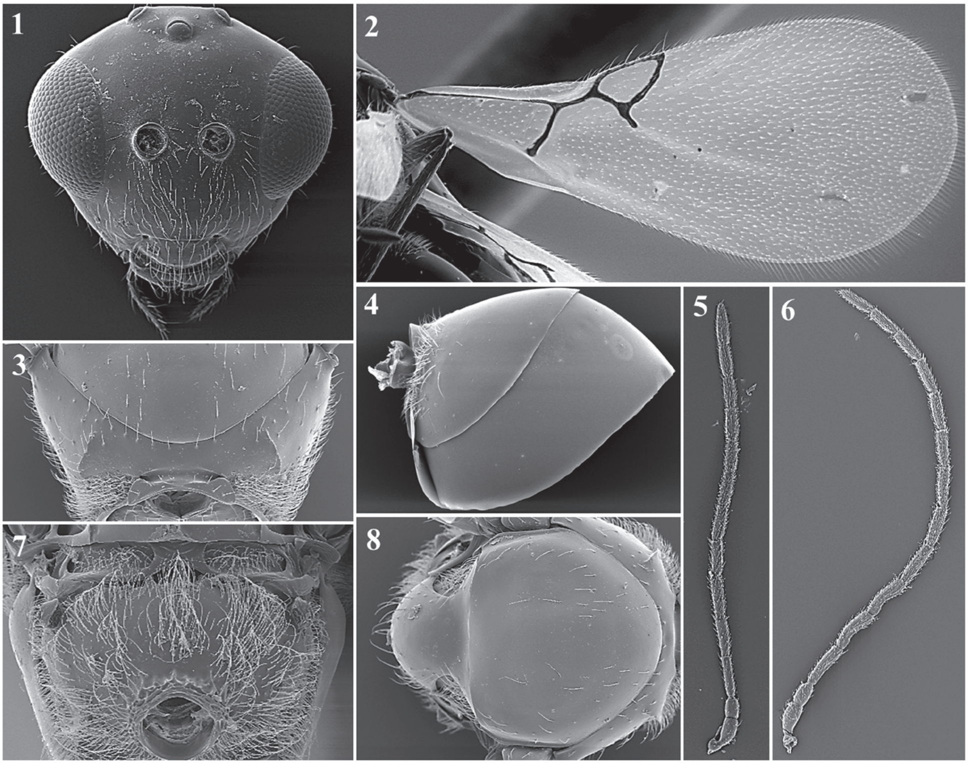

Figure 12. *Alloxysta* general features. Head (**1**); fore wing (**2**); pronotum (**3**); metasoma (**4**); female antennae (**5**); male antennae (**6**); propodeum (**7**); mesoscutum (**8**).

Key to species

1 Brachypterous species **2**
– Fully winged species, usually longer than mesosoma+metasoma **9**
2 Forewing reaching the end of metasoma; visible radial cell **3**
– Forewing reaching the beginning of the metasoma or shorter; without radial cell visible **6**
3 Radial cell completely open (Fig. 18[8]) ....***A. marshalliana* (Kieffer, 1900)**
– Radial cell closed **4**
4 Pronotal carinae absent .... ***A. glebaria* (Hellén, 1963)**
– Pronotal carinae present **5**
5 Propodeal carinae absent ....***A. pseudofuscicornis* (Ferrer-Suay, 2017)**
– Propodeal carinae present .... ***A. curta* (Ferrer-Suay, 2017)**
6 Pronotal carinae present; propodeal carinae absent. Females sometimes brachypterous. Fully winged female has a closed radial cell, 2.4× as long as wide .... ***A. halterata* (Thomson, 1862)**
– Pronotal carinae absent; propodeal carinae absent or present. When present, female always brachypterous 7

7 Propodeal carinae present; F1 shorter than pedicel (Fig. 13[13]).. ***A. brachyptera* (Hartig, 1840)**

– Propodeal carinae absent. F1 shorter or longer than pedicel........................**8**

8 Forewing reaches the beginning of the metasoma. Female: F1 longer than pedicel (Fig. 15[6]). Male: F1 subequal or slightly longer than pedicel, F1–F4 subequal in length.. ***A. pedestris* (Curtis, 1838)**

– Forewing short, practically absent. Female: F1 shorter than pedicel (Fig. 13[6]). Male: unknown................................ ***A. apteroidea* (Hellén, 1963)**

9 Radial cell completely or partially open...**10**

– Radial cell closed..**69**

10 Radial cell completely open **11**

– Radial cell partially open...**41**

11 Propodeal carinae absent...**12**

– Propodeal carinae present **24**

12 Pronotal carinae absent **13**

– Pronotal carinae present...**14**

13 F2 longer than F1 and F3 (Fig. 15[12]); radial cell 2.3× as long as wide (Fig. 18[28]) .... ***A. proxima* (Belizin, 1962)**

– F2 shorter than F1 and subequal to F3 (Fig. 16[5]); radial cell 2.7× as long as wide (Fig. 19[23])............. ***A. huberi* (Ferrer-Suay & Pujade-Villar, 2014)**

14 F2 longer than F1 and F3 (Fig. 16[1]); radial cell 3.8× as long as wide (Fig. 19[19]) .... ***A. alpina* (Ferrer-Suay & Pujade-Villar, 2014)**

– F2 shorter than or subequal to F1 and F3; radial cell shorter **15**

15 Female: unknown. Male: rhinaria and club shape begin at F1; F1 and F2 curved, F1 longer than pedicel and F2, F2–F4 nearly equal in length (Fig. 15[34]); radial cell 4.1× as long as wide (Fig. 19[18]) .... ***A. centroamericana* (Ferrer-Suay & Pujade-Villar, 2013)**

– Female and/or male: rhinaria and club shape begin in different flagellomeres; flagellomere differently proportioned; radial cell shorter **16**

16 Female: unknown. Male: rhinaria and club shape begin at F2; F2 and F3 are curved; F1 shorter than or subequal to F2, F2 subequal to F3, F3 longer than F4 (Fig. 15[29]); radial cell 2.8× as long as wide (Fig. 19[13]) .... ***A. vandenboschi* (Andrews, 1978)**

– Female and/or male: rhinaria and club shape begin at F3 or F4; flagellomere differently proportioned; radial cell not equal to 2.8× as long as wide **17**

17 Female: F1–F4 subequal in length (Fig. 14[16]). Male: F1 with a lateral hump; radial cell 2.7× as long as wide (Fig. 18[7]) .... ***A. mara* (Paretas-Martínez & Pujade-Villar, 2005)**

– Female: F1–F4 subequal in length. Male: F1 without a lateral hump; radial cell longer or shorter, not equal to 2.7× as long as wide...........................**18**

18 Female: F2 subequal to F1, F2 longer than F3 (Fig. 13[11]); radial cell 3.0× as long as wide (Fig. 17[10]). Male: unknown.... ***A. basimacula* (Cameron, 1886)**

– Female: F2 shorter than F1, F2 can be longer, shorter than or subequal to F3; radial cell longer or shorter, not equal to 3.0× as long as wide...................**19**

19 Body is covered in abundant pubescence; radial cell 4.9× as long as wide in females (Fig. 18[25]) and 3.2× as long as wide in males .... ***A. pilosa*** **(Ferrer-Suay & Pujade-Villar, 2013)**

– Body is covered in scattered setae; radial cell < 4.9× as long as wide in females and < 3.2× as long in males **20**

20 F2 longer than F3 (Fig. 13[12]); radial cell 2.7× as long as wide (Fig. 17[11])... .... ***A. brachycera*** **(Hellén, 1963)**

– F2 shorter than or subequal to F3; radial cell shorter or longer than, not equal to 2.7× as long as wide **21**

21 F2–F4 subequal in length (Fig. 13[23]); radial cell 2.8× as long as wide (Fig. 17[21]) .... ***A. crassa*** **(Cameron, 1889)**

– F2–F4 unequal in length; radial cell < 2.8× as long as wide **22**

22 F2 subequal to F3 (Fig. 14[26]); radial cell 2.3× as long as wide (Fig. 18[17]) .... ***A. nipona*** **(Ferrer-Suay & Pujade-Villar, 2013)**

– F2 shorter than F3; radial cell more than 2.3× as long as wide **23**

23 F1 4.4× as long as wide, F3 longer than F4 (Fig. 14[25]); radial cell 2.9× as long as wide, Rs and R1 reach the costal margin (Fig. 17[16]) .... ***A. nigrita*** **(Thomson, 1862)**

– F1 1.4× as long as wide, F3 subequal to F4 (Fig. 15[7]); radial cell 2.8× as long as wide, Rs and R1 do not reach the costal margin (Fig. 18[23]).......... .... ***A. piceomaculata*** **(Cameron, 1883)**

24 Two propodeal carinae well defined, independently reaching the base....... **25**

– Propodeum with two carinae, which form a plate **27**

25 Female: rhinaria and club shape begin at F3; F1 longer than pedicel and F2, F2 shorter than F3, F3 subequal to F4 (Fig. 15[4]); few carinae on apex of scutellum; radial cell 2.4× as long as wide (Fig. 18[21]). Male: unknown...... .... ***A. paretasmartinezi*** **(Ferrer-Suay & Pujade-Villar, 2013)**

– Rhinaria and club shape begin in other flagellomeres; thick, parallel carinae on the apex of scutellum; radial cell shorter or longer than, not equal to 2.4× as long as wide **26**

26 Female: rhinaria and club shape begin at F5; F2 subequal to F3 (Fig. 13[16]); radial cell 2.2× as long as wide (Fig. 17[14]) ......***A. carinata*** **(Carver, 1992)**

– emale: rhinaria and club shape begin at F4; F2 shorter than F3 (Fig. 15[20]); radial cell 2.8× as long as wide (Fig. 19[4]) .... ***A. samurai*** **(Ferrer-Suay & Paretas-Martínez, 2013)**

27 Rhinaria and club shape begin at F2 .... **28**

– Rhinaria and club shape begin in other flagellomere **29**

28 Female: F2–F4 subequal in length (Fig. 15[3]). Male: F2 slightly curved and longer than F3; propodeum with two well defined carinae and separated in the first half with setae present, joining to form a plate in the last half; radial cell 2.6× as long as wide (Fig. 18[20]) .... ***A. pallidicornis*** **(Curtis, 1838)**

– Female: F2 longer than F3, F3 longer than F4 (Fig. 13[1]). Male: F2 shorter than F3; propodeum with two carinae joining to form a thick plate; setae on top and curved sides; radial cell 2.2× as long as wide (Fig. 17[1]) .... ***A. abdera* (Fergusson, 1986)**

29 Female: unknown. Male: rhinaria and club shape begin at F1; F1 curved; F1–F4 subequal in length (Fig. 16[10]); radial cell 3.3× as long as wide (Fig. 19[28]) .... ***A. vicenti* (Ferrer-Suay, 2014)**

– Rhinaria and club shape begin in other flagellomeres; different flagellomere proportions; various sizes of radial cells **30**

30 Rhinaria and club shape begin at F3 .... **31**

– Rhinaria and club shape begin at F4 .... **33**

31 F1 subequal to pedicel, F2 subequal to F3, F3 shorter than F4 (Fig. 16[15]); radial cell 2.4× as long as wide (Fig. 19[33]). Male: unknown...................... .... ***A. nottoni* (Ferrer-Suay & Pujade-Villar, 2015)**

– F1 longer than pedicel **32**

32 Female: F1 2.9× as long as wide, F2 shorter than F3, F3 subequal to F4 (Fig. 15[32]); radial cell 2.4× as long as wide (Fig. 19[16]). Male: unknown......... .... ***A. xanthopa* (Thomson, 1862)**

– A different combination of features.. **33**

33 Pronotal carinae absent **34**

– Pronotal carinae present... **35**

34 Rhinaria and club shape being at F3 (Fig. 14[18]). Male: F1 is 3.9× as long as wide; F2 subequal to F3, F3 shorter than F4; radial cell 2.5× as long as wide in females and 2.3× as long in males (Fig. 18[9]) .... ***A. medinae* (Ferrer-Suay & Pujade-Villar, 2012)**

– Rhinaria and club shape being at F4; radial cell 2.4× as long as wide (Fig. 19[22]) .... ***A. franca* (Ferrer-Suay & Pujade-Villar, 2014)**

35 F1 shorter than or subequal to pedicel **36**

– F1 longer than pedicel **39**

36 F1 shorter than pedicel **37**

– F1 subequal to pedicel **38**

37 F2 slightly longer than F1 and F3 (Fig. 16[9]); radial cell 2.5× as long as wide (Fig. 19[27]) .... ***A. texanae* (Ferrer-Suay & Pujade-Villar, 2014)**

– F2 shorter than F1 and subequal to F3 (Fig. 16[14]); radial cell 2.0× as long as wide (Fig. 19[32]) .... ***A. pascuali* (Ferrer-Suay, 2018)**

38 F2 shorter than F1 and F3 (Fig. 16[2]); radial cell 3.8× as long as wide (Fig. 19[20]); irregular, rounded carina on apex of scutellum .... ***A. areeluckator* (Ferrer-Suay & Pujade-Villar, 2014)**

– F2 subequal to F1 and longer than F3 (Fig. 16[13]); radial cell 2.3× as long as wide (Fig. 19[31]); no carina on apex of scutellum .... ***A. palearctica* (Ferrer-Suay & Pujade-Villar, 2018)**

39 Pronotal carinae thick, long and clearly visible; propodeum with two carinae joining to form a width plate; radial cell 2.2× as long as wide (Fig. 19[25]).... .... ***A. pili* (Ferrer-Suay, 2014)**

– Pronotal and propodeal carinae different; radial cell > 2.2× as long as wide... .... **40**

40 Pronotum with two thick and short carinae covered by few setae; propodeum with two straight and parallel carinae joining at the base and covered by abundant pubescence; radial cell 3.2× as long as wide (Fig. 17[19]) .... ***A. costaricensis* (Ferrer-Suay & Pujade-Villar, 2011)**

– Pronotum with two thick and long carinae, rounded, curving and clearly visible; propodeum with two straight carinae that are well defined on top, forming a plate in the last half, with strongly curved sides; radial cell 2.3× as long as wide (Fig. 19[10]) . ***A. thorpei* (Ferrer-Suay & Pujade-Villar, 2012)**

41 Propodeal carinae absent or only slightly defined on top **42**

– Propodeal carinae present **54**

42 Pronotal carinae absent **43**

– Pronotal carinae present **46**

43 F1 longer than pedicel **44**

– F1 subequal to pedicel **45**

44 Setae absent where the carinae are usually present; F1 5.0× as long as wide (Fig. 16[3]); radial cell 2.8× as long as wide (Fig. 19[21]) .... ***A. buffingtoni* (Ferrer-Suay & Pujade-Villar, 2014)**

– Propodeum completely covered by setae; F1 is 3.0× as long as wide (Fig. 15[25]); radial cell 2.3× as long as wide (Fig. 19[9]) .... ***A. soluta* (Hellén, 1963)**

45 F1 longer than F2, F2 subequal to F3 (Fig. 15[5]); radial cell 2.8× as long as wide; Rs vein does not reach the costal margin (Fig. 18[22]) .... ***A. patens* (Hellén, 1963)**

– F1–F3 subequal in length (Fig. 14[13]); radial cell 2.3× as long as wide; Rs vein reaches the costal margin (Fig. 18[4]) ..... ***A. longiventris* (Baker, 1896)**

46 Thick carinae on apex of scutellum; F1 longer than pedicel and F2, F2–F4 subequal (Fig. 15[16]) ..... ***A. rubidus* (Ferrer-Suay & Pujade-Villar, 2012)**

– Carinae absent on apex of scutellum; different flagellomere proportions **47**

47 F1 subequal to pedicel (Fig. 14[21]). Male: F2 and F3 curved. Radial cell 2.5× as long as wide (Fig. 18[12]) .... ***A. minuscula* (Andrews, 1978)**

– F1 longer than pedicel; various sizes of radial cells **48**

48 F2–F4 subequal in length **49**

– F2–F4 unequal in length **52**

49 Rhinaria and club shape begin at F4; F1 longer or slightly shorter than F2 (Fig. 14[2]) .... ***A. fuscipes* (Thomson, 1862)**

– Rhinaria and club shape begin in other flagellomere **50**

50 Rhinaria and club shape begin at F1 (Fig. 15[23]); radial cell 2.9× as long as wide (Fig. 19[7]). Male: unknown .... ***A. sharkeyi* (Ferrer-Suay & Pujade-Villar, 2013)**

– Rhinaria and club shape begin at F3; radial cell longer or shorter, not equal to 2.9× as long as wide **51**

51 Female: F1 is 6.3× as long as wide, F2 4.6× as long as wide (Fig. 15[18]); radial cell 2.6× as long as wide (Fig. 19[2]). Male: unknown.......................... ....***A. salicicola*** **(Belizin, 1973)**

– Female: F1 is 3.5× as long as wide, F2 is 2.1× as long as wide (Fig. 15[22]); radial cell 2.7× as long as wide (Fig. 19[6]). Male: rhinaria and club shape begin at F4; F1 longer than F2, F2 longer than F3, F3 shorter than F4 ....***A. semiaperta*** **(Fergusson, 1986)**

52 Female: rhinaria and club shape begin at F4 (Fig. 13[20]). Male: rhinaria and club shape begin at F2; none of the flagellomere are curved; F1 longer than pedicel, F1–F3 subequal, F3 shorter than or subequal to F4; radial cell 2.2× as long as wide (Fig. 17[18]) ....***A. commensuratus*** **(Andrews, 1978)**

– Female and/or male: rhinaria and club shape begin at F3; flagellomere differently proportioned; size of radial cells diverse...**53**

53 Female: F1 subequal to F2, F2 longer than F3, F3 subequal to F4 (Fig. 14[15]). Male: F2 and F3 curved; F1 subequal to F2, F2 longer than F3, F3 longer than F4; large radial cell 3.0× as long as wide in both males and females (Fig. 18[6])..................................***A. macrophadna*** **(Hartig, 1841)**

– Female: F1 longer than F2, F2 shorter than or subequal to F3, F3 shorter than F4 (Fig. 15[2]). Male: flagellomeres not curved; F1 longer than F2, F2 longer than F3, F3 shorter than F4; radial cell < 3.0× as long as wide in both sexes (Fig. 18[19])..**54**

54 Radial cell 2.5× as long as wide; Rs-2 strongly curved and radial cell wide open ....***A. simplex*** **(Watanabe, 1950)**

– Radial cell 2.7× as long as wide; Rs-2 not strongly curved and radial cell not wide open ....***A. obscurata*** **(Hartig, 1840)**

55 Propodeal carinae do not protrude; F1 subequal to pedicel in both sexes; rhinaria and club shape begin at F4 (Fig. 13[19]); radial cell 2.1× as long as wide (Fig. 17[17])..***A. citripes*** **(Thomson, 1862)**

– Propodeal carinae well defined and protruding; without the combination of characters as above **56**

56 Propodeum with two well-defined carinae, which independently reach the base; carinae thick with curved sides; rhinaria and club shape begin at F3 in female (Fig. 15[10]); F1–F3 slightly curved in male; radial cell is small with a straight Rs vein (Fig. 18[26]) ....***A. pleuralis*** **(Cameron, 1879)**

– Propodeum with two carinae, which form a plate or join together only at the base; without the combination of characters as above...............................**57**

57 Propodeal carinae thick, well defined, with curved sides joined at the base. Female: F1 subequal to pedicel, F1 longer than F2, F2 shorter than F3, F3 shorter than F4 (Fig. 13[8]). Male: F1 shorter than pedicel, F2–F4 subequal . ...***A. asiatica*** **(Ferrer-Suay & Pujade-Villar, 2013)**

– Propodeal carinae joined at the base, forming a complete plate; male and female flagellomeres not proportioned as above **58**

58 Rhinaria begin at F3 and club shape begins at F2; F3 subequal to pedicel and shorter than F4 (Fig. 14[14]); apex of scutellum has thick carinae .... ***A. luismii*** **(Ferrer-Suay, 2011)**

– Rhinaria and club shape begin in the same flagellomere; F3 unequal to pedicel; no apex of scutellum without carinae...................................... **59**

59 Female: unknown. Male: rhinaria and club shape begin at F2; F1 longer than F2, F2–F4 subequal; F2 slightly curved (Fig. 16[11]); radial cell 2.8× as long as wide (Fig. 19[29]).......... ***A. viellae*** **(Ferrer-Suay & Pujade-Villar, 2013)**

– Rhinaria and club shape begin in other flagellomeres; variety of combinations of the features explained above...................................... **60**

60 Rhinaria and club shape begin at F4...................................... **61**

– Rhinaria and club shape begin at F3...................................... **67**

61 Pronotal carinae absent...................................... **62**

– Pronotal carinae present...................................... **64**

62 Female: F3 subequal to pedicel (Fig. 15[17]); propodeum with two carinae that form a plate with straight sides .... ***A. rufiventris*** **(Hartig, 1840)**

– Female: F3 unequal to pedicel; propodeum with two carinae that form a plate with curved sides **63**

63 Female: F1 longer than pedicel (Fig. 13[4]); propodeum with two carinae that form a plate with curved sides; radial cell 2.1× as long as wide (Fig. 17[4]).... .... ***A. antsirananae*** **(Ferrer-Suay & Pujade-Villar, 2012)**

– Female: F1 shorter than pedicel (Fig. 15[24]); propodeum with two carinae that form a plate with only slightly-curved sides; radial cell 2.2× as long as wide (Fig. 19[8])........... ***A. slovenica*** **(Ferrer-Suay & Pujade-Villar, 2013)**

64 F1 subequal to pedicel...................................... **65**

– F1 longer than pedicel...................................... **66**

65 Body brown; pronotum with scattered setae; found in *Aphis* sp.................... .... ***A. postica*** **(Hartig, 1841)**

– Body bicolored; pronotum with abundant setae; found in *Neuquenaphis* sp... .... ***A. nothofagi*** **(Andrews, 1976)**

66 Female: F2 subequal to F3 (Fig. 13[17]); radial cell 2.3× as long as wide (sometimes the club shape begins at F3) (Fig. 17[15])....***A. castanea*** **(Hartig, 1841)**

– Female: F2 shorter than F3 (Fig. 13[9]); radial cell 3.0× as long as wide (Fig. 17[8]). Male: unknown...................................... ***A. aurata*** **(Belizin, 1968)**

67 Female: F3 subequal to pedicel (Fig. 14[20]). Male: F1 longer than pedicel and F2, F2 subequal to F3; radial cell 2.0× as long as wide (Fig. 18[11]) .... ***A. melanogaster*** **(Hartig, 1840)**

– F1 longer than pedicel and F2; without combination of characters as above....**68**

68 Apex of scutellum without carina present; plate propodeum with straight sides...................................... ***A. longipennis*** **(Hartig, 1841)**

– Apex of scutellum with a thick carina present; plate propodeum with curved sides and few setae on top .... ***A. andrewsi*** **(Ferrer-Suay & Pujade-Villar, 2011)**

69 Propodeal carinae present **70**

– Propodeal carinae absent.. **91**

70 Propodeal carinae independent, slightly fused at bottom............................ .... ***A. barbotini*** **(Ferrer-Suay & Pujade-Villar, 2016)**

– Propodeal carinae fused, forming a plate.. **71**

71 Pronotal carinae present... **72**

– Pronotal carinae absent **98**

72 Female: unknown. Male: radial cell 1.8× as long as wide; club shape begins at F2 and rhinaria at F3; F1 longer than pedicel and F2, F2 longer than F3 (Fig. 13[15]); all flagellomeres straight; propodeal carinae with curved sides .... ***A. brevitarsis*** **(Thomson, 1862)**

– Radial cell > 1.8× as long as wide; without combination of characters as above **73**

73 Rhinaria and club shape begin at different flagellomeres **74**

– Rhinaria and club shape begin at the same flagellomeres........................... **75**

74 Female: club shape begins at F2 and rhinaria at F1, F2 subequal to F3 (Fig. 15[31]); apex of scutellum without carinae; propodeal carinae form a wide plate with curved sides; radial cell 2.6× as long as wide (Fig. 19[15]). Male: unknown .... ***A. xanthocera*** **(Thomson, 1862)**

– Female: club shape begins at F3 and rhinaria at F4, F2 shorter than F3. Male: rhinaria and club shape begin at F2, F2 subequal to F3 (Fig. 14[5]); apex of scutellum has a thick carina; propodeal carinae separated on top, forming a plate on the bottom with curved sides...... ***A. hansoni*** **(Pujade-Villar, 2011)**

75 F1 longer than pedicel **76**

– F1 shorter than or subequal to pedicel **85**

76 Propodeal carinae independent **77**

– Propodeal carinae form a plate... **79**

77 Female: rhinaria and club shape begin at F4 (Fig. 13[10]). Male: unknown.. .... ***A. australiae*** **(Ashmead, 1900)**

– Female: unknown. Male: rhinaria and club shape begin at F1 .... **78**

78 Male: rhinaria and club shape begin in the last three-quarters of F1 (Fig. 15[33]) .... ***A. xanthopsis*** **(Ashmead, 1896)**

– Male: rhinaria and club shape both begin at F1 (Fig. 14[8]) .... ***A. japonicus*** **(Ashmead, 1904)**

79 Rhinaria and club shape begin at F2 in both sexes; F1–F4 subequal in length (Fig. 13[27]); radial cell 2.3× as long as wide in females (Fig. 17[25]), 2.6× as long in males ....***A. evenhuisi*** **(Ferrer-Suay & Pujade-Villar, 2012)**

– Rhinaria and club shape begin at F3 or F4 in females, F1 or F2 in males; F1–F4 unequal in length; variety of radial cell sizes.................................. **80**

80 Rhinaria and club shape begin at F4 in females and at F1 in males (when known) **81**

– Rhinaria and club shape begin at F3 in females, F1 or F2 in males **82**

81 Female: radial cell 2.4× as long as wide (Fig. 13[3]). Male: club shape begins at F1 and rhinaria at F3; F1 longer than F2, F2 subequal to F3, F3 shorter than F4; radial cell 2.7× as long as wide (Fig. 17[3]); propodeal carinae well defined, separated by setae on the first half and forming a plate on the last half, straight sides . ***A. antananarivoi* (Ferrer-Suay & Pujade-Villar, 2012)**

– Female: radial cell 2.7× as long as wide (Fig. 14[24]). Male: unknown. Propodeal carinae forming a complete plate with few setae on top and divergent peaks on base .... ***A. nigricans* (Hellén, 1963)**

82 F1 longer than F2, F2 subequal to F3, F3 shorter than F4 (Fig. 14[23]). Male: F1–F4 subequal; radial cell 2.9× as long as wide in females (Fig. 18[14]) and 2.7× as long as wide in males .... ***A. nepalica* (Ferrer-Suay & Pujade-Villar, 2013)**

– With a different combination of characters **83**

83 Propodeal carinae independent, thin on top and bottom, with curved sides; F1–F3 subequal (Fig. 16[6]); radial cell 2.5× as long as wide (Fig. 19[24]) ... . ***A. neartica* (Ferrer-Suay & Pujade-Villar, 2014)**

– Propodeal carinae form a plate; F1–F3 unequal; radial cell less than 2.5× as long as wide **84**

84 Female: F2 shorter than F3 (Fig. 15[13]). Male: rhinaria begins at F1; F3 subequal to pedicel, which is slightly curved; propodeal plate with slightly curved sides; radial cell 2.7× as long as wide in females (Fig. 18[29]) and 2.4× as long as wide in males .... ***A. pusilla* (Kieffer, 1902)**

– Female: F2 subequal to F3 (Fig. 15[8]). Male: rhinaria begins at F2; F3 unequal to pedicel and no curved flagellomere; propodeal plate with curved sides; radial cell 2.4× as long as wide (Fig. 18[24]) .... ***A. pilipennis* (Hartig, 1840)**

85 Rhinaria and club shape begin at F5 in females and F4 in males. Female: F1 subequal to pedicel and longer than F2, F2 shorter than F3, F3 shorter than F4. Male: F1 shorter than pedicel. Two propodeal carinae, narrow, well defined at upper half, wide and forming a plate on the lower half, with sharp edges.. ***A. sawoniewiczi* (Kierych, 1988)**

– Female: rhinaria and club shape begin at different flagellomeres; without combination of characters as above **86**

86 F1 shorter than pedicel **87**

– F1 subequal to pedicel **88**

87 Rhinaria and club shape begin at F5; F1–F3 subequal in length, F3 shorter than F4 (Fig. 14[7]); radial cell 1.9× as long as wide (Fig. 17[30]) .... ***A. heptatoma* (Hellén, 1963)**

– Rhinaria and club shape begin at F1; F1 slightly shorter than F2, F2–F4 subequal in length (Fig. 16[8]); radial cell 2.8× as long as wide (Fig. 19[26]) .... ***A. petchabunensis* (Ferrer-Suay & Pujade-Villar, 2014)**

88 Rhinaria and club shape begin at F4; F1 longer than F2, F2 subequal to F3 (Fig. 15[15]); pronotum with two small carinae (sometimes difficult to see),

separated by setae in the first third, forming a plate in the last two-thirds; radial cell 2.0× as long as wide (Fig. 18[31]) ....***A. ramulifera* (Thomson, 1862)**

– Rhinaria and club shape begin at F3; without combination of characters as above **89**

89 Antennae shorter than body length; flagellomeres short and round; radial cell 2.0× as long as wide, short and round (Fig. 15[21]) .... ***A. sarae* (Ferrer-Suay, 2012)**

– Antennae longer than body length; flagellomeres elongated; radial cell more than 2.0× as long as wide **90**

90 Female: F1 longer than F2, F2 subequal to F3, F3 shorter than F4 (Fig. 13[7]). Male: F1 longer than pedicel and subequal to F2, F2 slightly curved and shorter than F3; propodeum with curved sides; radial cell 2.3× as long as wide (Fig. 17[6]) .... ***A. arcuata* (Kieffer, 1902)**

– F1 longer than F2, F2–F4 subequal in length (Fig. 13[24]); propodeal plate with slightly curved sides; radial cell 2.6× as long as wide (Fig. 17[22]). Male: unknown .... ***A. crassicornis* (Thomson, 1862)**

91 Head yellow; F1 longer than F2, F2–F4 subequal (Fig. 15[30]); radial cell 3.0× as long as wide (Fig. 19[14]); propodeum without setae where usually present in other species .... ***A. victrix* (Westwood, 1833)**

– Head brown; without combination of characters as above......................... **92**

92 Pronotal carinae absent **93**

– Pronotal carinae present... **95**

93 F1–F3 unequal in length.. ***A. kovilovica* (Ferrer-Suay & Pujade-Villar, 2013)**

– F1–F3 subequal in length **94**

94 Female: rhinaria and club shape begin at F4; F1 longer than pedicel (Fig. 13[5]); radial cell 2.4× as long as wide (Fig. 17[5]). Male: with antennae unknown .... ***A. aperta* (Hartig, 1841)**

– Female: unknown. Male: rhinaria and club shape begin at F3; F1 subequal to pedicel (Fig. 15[14]); radial cell 2.5× as long as wide (Fig. 17[30]) .... ***A. quedenfeldti* (Kieffer, 1909)**

95 Female: rhinaria and club shape begin at F3; F1 longer than pedicel, F1 subequal to F2, F2 shorter than or subequal to F3 (Fig. 13[18]). Male: F1–F3 not curved .... ***A. circumscripta* (Hartig, 1841)**

– Rhinaria and club shape begin in other flagellomere; without combination of characters as above **96**

96 Female: rhinaria and club shape begin at F2; F2 shorter than F3 (Fig. 14[11]). Male: F1 curved; radial cell 2.0× as long as wide (Fig. 18[2]) .... ***A. leunisii* (Hartig, 1841)**

– Female: rhinaria and club shape begin at F3 or F4; F2 subequal to F3 (Fig. 13[22]). Male: F1–F3 curved; radial cell 2.7× as long as wide (Fig. 17[20])... .... **97**

97 Often found attacking *Brevicoryne brassicae* (L., 1758) through *Diaeretiella rapae* (M'Intosh, 1855) .... ***A. consobrina* (Zetterstedt, 1838)**

– Often found attacking *Cryptomizus* sp. through *Aphidius ribis* (Haliday, 1834) .... ***A. tscheki* (Giraud, 1860)**

98 F1 longer than pedicel **99**

– F1 shorter than or subequal to pedicel **103**

99 Propodeal carinae straight and independent, widening at the base. Female: rhinaria and club shape begin at F2; F1 longer than pedicel and F2, F2–F4 subequal in length (Fig. 14[10]). Male: rhinaria and club shape begin at F1; F1 longer than pedicel and F2, F2–F4 subequal in length; radial cell 2.5× as long as wide (Fig. 18[1]) .... ***A. lachni* (Ashmead, 1885)**

– Propodeal carinae with different morphology; rhinaria and club shape begin at different flagellomeres; various flagellomere proportions; radial cell < 2.5× as long as wide **100**

100 Female: rhinaria and club shape begin at F3; F1–F3 subequal in length, F3 shorter than F4 (Fig. 14[1]). Male: rhinaria and club shape begin at F3; F1–F3 subequal in length, F3 shorter than F4; F3 curved; propodeal carinae separated and well-defined; radial cell 2.2× as long as wide (Fig. 17[26]) .... ***A. fracticornis* (Thomson, 1862)**

– Flagellomere proportions differ in males and females; propodeal carinae form a plate; radial cell shorter or longer than, not equal to 2.2× as long as wide... .... **101**

101 Female: unknown. Male: rhinaria and club shape begin at F1; F2 longer than F3, F3 subequal to F4 (Fig. 14[19]); propodeal carinae form a plate with slightly-curved sides and few setae on top; radial cell 2.1× as long as wide (Fig. 18[10]) .... ***A. mexicana* (Ferrer-Suay & Pujade-Villar, 2012)**

– Male: unknown. Female: rhinaria and club shape begin at F3; F2 subequal to F3, F3 shorter than F4; propodeal carinae form a plate with sides that are slightly curved or have two peaks; radial cell shorter or longer than, not equal to 2.1× as long as wide **102**

102 Propodeal carinae form a plate; radial cell 1.8× as long as wide (Fig. 15[27]). Male: unknown .... ***A. torresi* (Ferrer-Suay & Pujade-Villar, 2012)**

– Propodeal carinae thin and straight on top, forming a plate on bottom, with peaks on the sides; radial cell 2.2× as long as wide (Fig. 16[29]). Male: unknown .... ***A. hendrickxi* (Benoit, 1956)**

103 F1 subequal to pedicel; F1 longer than F2, F2 subequal to F3 (Fig. 1[22]) ... . ***A. mullensis* (Cameron, 1883)**

– F1 shorter than pedicel, F1–F3 subequal in length, F1 sometimes slightly longer **104**

104 Antennae shorter than body length; forewing with normal marginal setae (the lenght that usually have all other species) .... ***A. brevis* (Thomson, 1862)**

– Antennae subequal or longer than body length; forewing with long marginal setae (longer than the lenght that usually have all other species) .... ***A. darci* (Girault, 1933)**

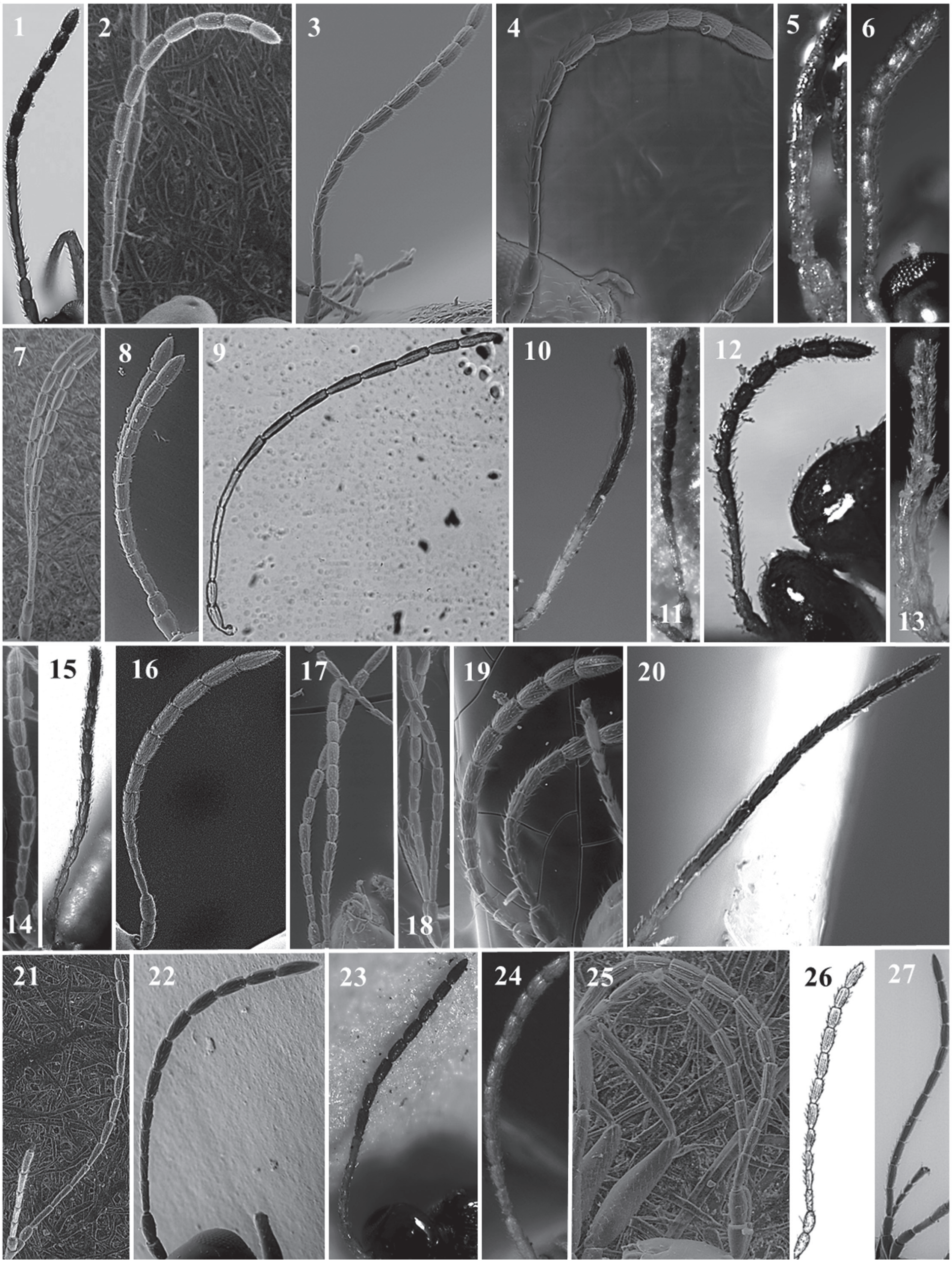

Figure 13. *Alloxysta* antennae. *A. abdera* (**1**); *A. andrewsi* (**2**); *A. antananarivoi* (**3**); *A. antsirananae* (**4**); *A. aperta* (**5**); *A. apteroidea* (**6**); *A. arcuata* (**7**); *A. asiatica* (**8**); *A. aurata* (**9**); *A. australiae* (**10**); *A. basimacula* (**11**); *A. brachycera* (**12**); *A. brachyptera* (**13**); *A. brevis* (**14**); *A. brevitarsis* (**15**); *A. carinata* (**16**); *A. castanea* (**17**); *A. circumscripta* (**18**); *A. citripes* (**19**); *A. commensuratus* (**20**); *A. costaricensis* (**21**); *A. consobrina* (**22**); *A. crassa* (**23**); *A. crassicornis* (**24**); *A. darci* (**25**); *A. desantisi* (**26**); *A. evenhuisi* (**27**).

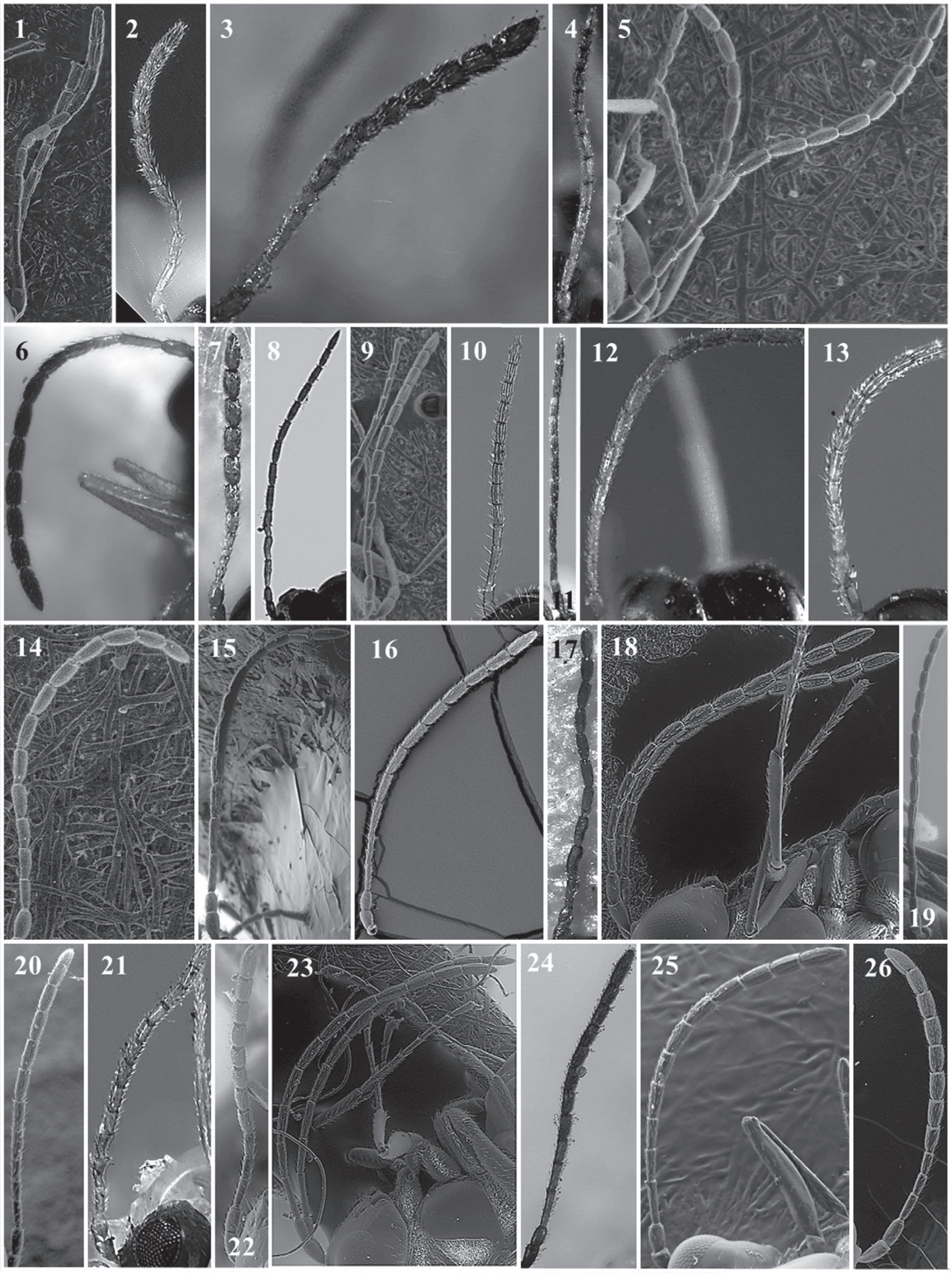

Figure 14. *Alloxysta* antennae. *A. fracticornis* (**1**); *A. fuscipes* (**2**); *A. glebaria* (**3**); *A. halterata* (**4**); *A. hansoni* (**5**); *A. hendrickxi* (**6**); *A. heptatoma* (**7**); *A. japonicus* (**8**); *A. kovilovica* (**9**); *A. lachni* (**10**); *A. leunisii* (**11**); *A. longipennis* (**12**); *A. longiventris* (**13**); *A. luismii* (**14**); *A. macrophadnus* (**15**); *A. mara* (**16**); *A. marshalliana* (**17**); *A. medinae* (**18**); *A. mexicana* (**19**); *A. melanogaster* (**20**); *A. minuscula* (**21**); *A. mullensis* (**22**); *A. nepalica* (**23**); *A. nigricans* (**24**); *A. nigrita* (**25**); *A. nipona* (**26**).

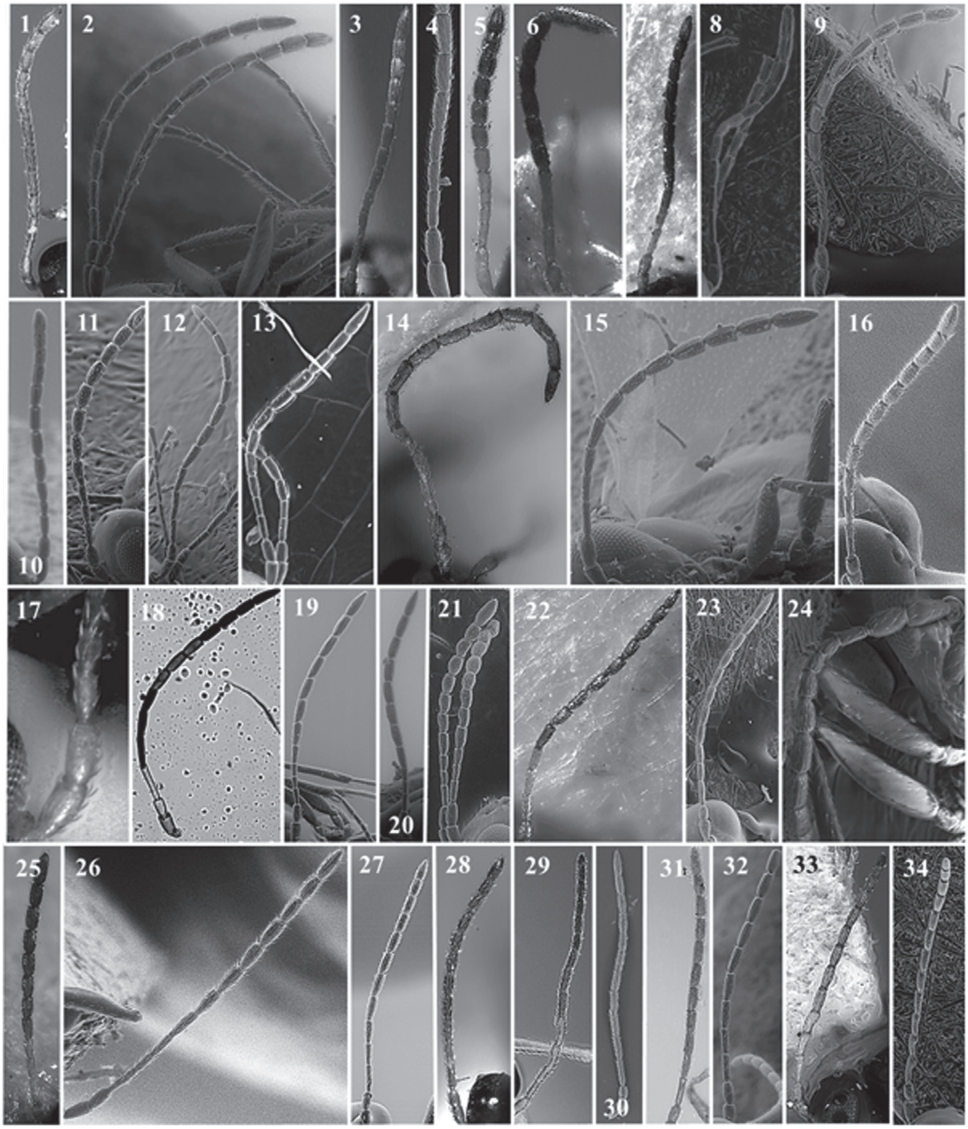

Figure 15. *Alloxysta* antennae. *A. nothofagi* (**1**); *A. obscurata* (**2**); *A. pallidicornis* (**3**); *A. paretasmartinezi* (**4**); *A. patens* (**5**); *A. pedestris* (**6**); *A. piceomaculata* (**7**); *A. pilipennis* (**8**); *A. pilosa* (**9**); *A. pleuralis* (**10**); *A. postica* (**11**); *A. proxima* (**12**); *A. pusilla* (**13**); *A. quedenfeldti* (**14**); *A. ramulifera* (**15**); *A. rubidus* (**16**); *A. rufiventris* (**17**); *A. salicicola* (**18**); *A. sawoniewiczi* (**19**); *A. samurai* (**20**); *A. sarae* (**21**); *A. semiaperta* (**22**); *A. sharkey* (**23**); *A. slovenica* (**24**); *A. soluta* (**25**); *A. thorpei* (**26**); *A. torresi* (**27**); *A. tscheki* (**28**); *A. vandenboschi* (**29**); *A. victrix* (**30**); *A. xanthocera* (**31**); *A. xanthopa* (**32**); *A. xanthopsis* (**33**); *A. centroamericana* (**34**).

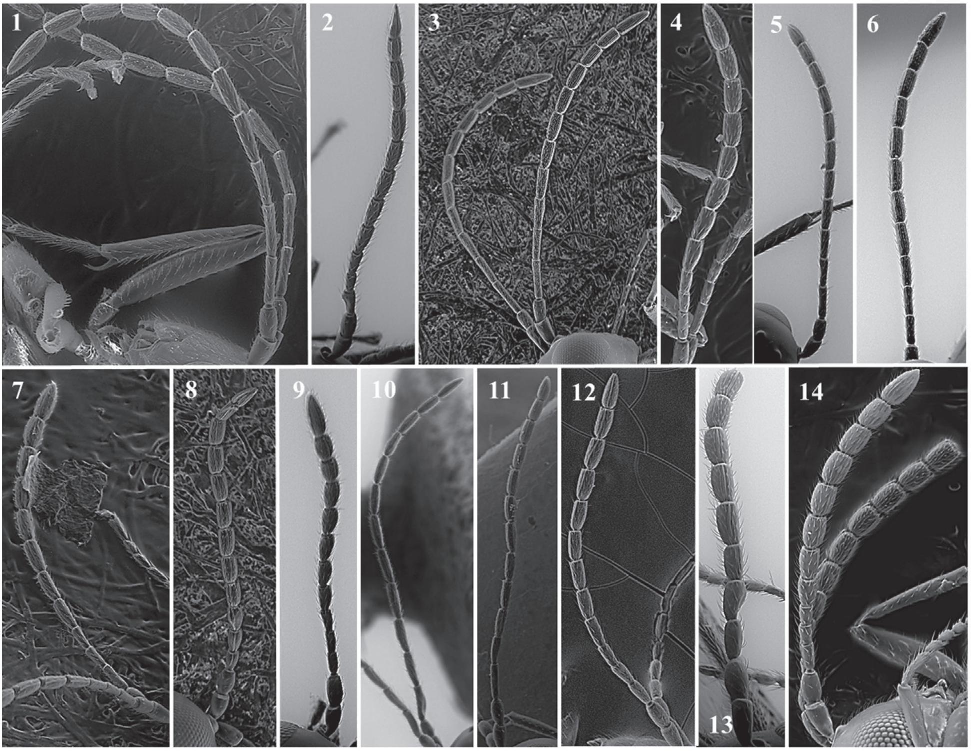

Figure 16. *Alloxysta* antennae. *A. alpina* (**1**); *A. areeluckator* (**2**); *A. buffingtoni* (**3**); *A. franca* (**4**); *A. huberi* (**5**); *A. neartica* (**6**); *A. pili* (**7**); *A. petchabunensis* (**8**); *A. texanae* (**9**); *A. vicenti* (**10**) ; *A. viellae* (**11**); *A. corta* (**12)**; *A. palearctica* (**13**); *A. pascuali* (**14**); *A. nottoni* (**15**).

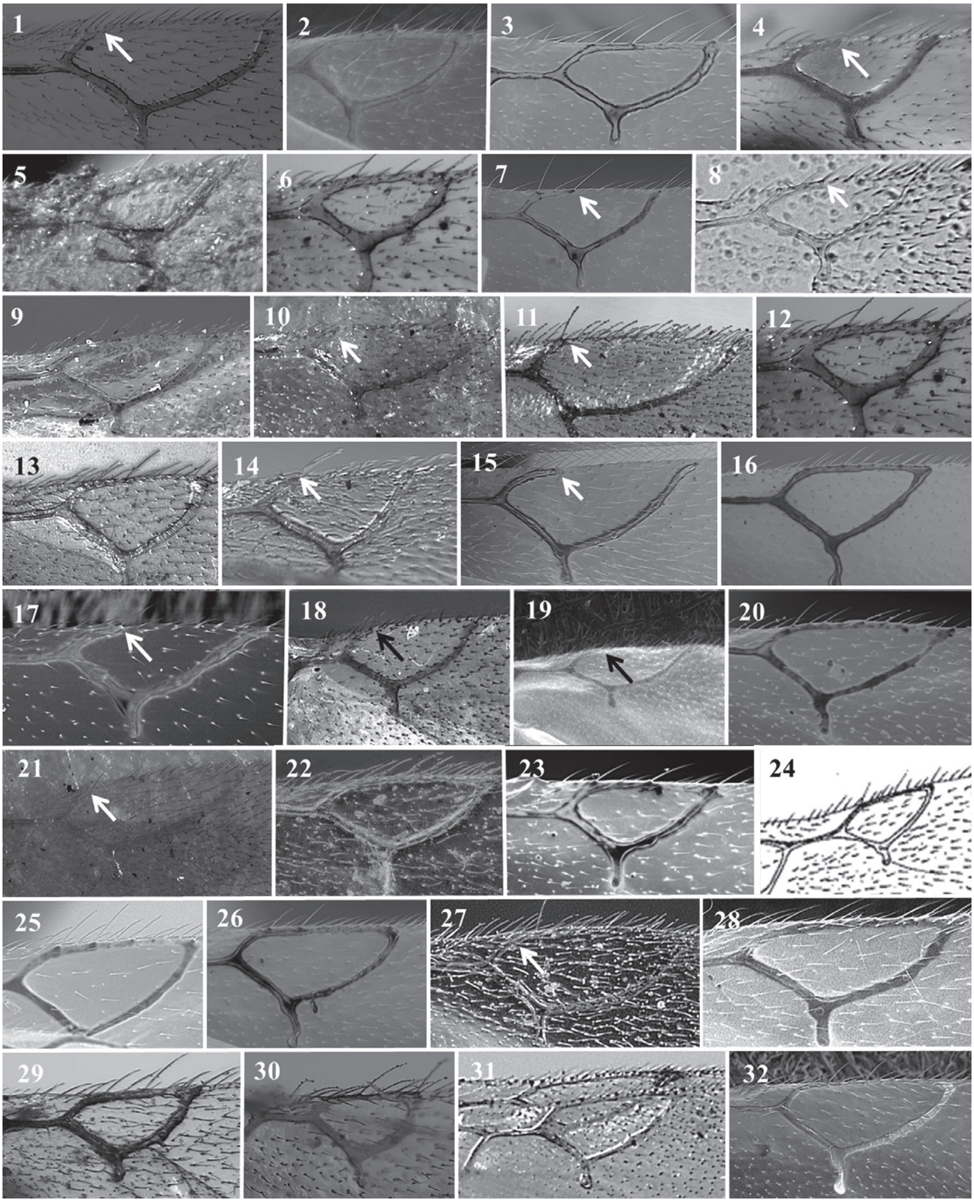

Figure 17. *Alloxysta* radial cell. *A. abdera* (**1**); *A. andrewsi* (**2**); *A. antananarivoi* (**3**); *A. antsirananae* (**4**); *A. aperta* (**5**); *A. arcuata* (**6**); *A. asiatica* (**7**); *A. aurata* (**8**); *A. australiae* (**9**); *A. basimacula* (**10**); *A. brachycera* (**11**); *A. brevis* (**12**); *A. brevitarsis* (**13**); *A. carinata* (**14**); *A. castanea* (**15**); *A. circumscripta* (**16**); *A. citripes* (**17**); *A. commensuratus* (**18**); *A. costaricensis* (**19**); *A. consobrina* (**20**); *A. crassa* (**21**); *A. crassicornis* (**22**); *A. darci* (**23**); *A. desantisi* (**24**); *A. evenhuisi* (**25**); *A. fracticornis* (**26**); *A. fuscipes* (**27**); *A. hansoni* (**28**); *A. hendrickxi* (**29**); *A. heptatoma* (**30**); *A. japonicus* (**31**); *A. kovilovica* (**32**).

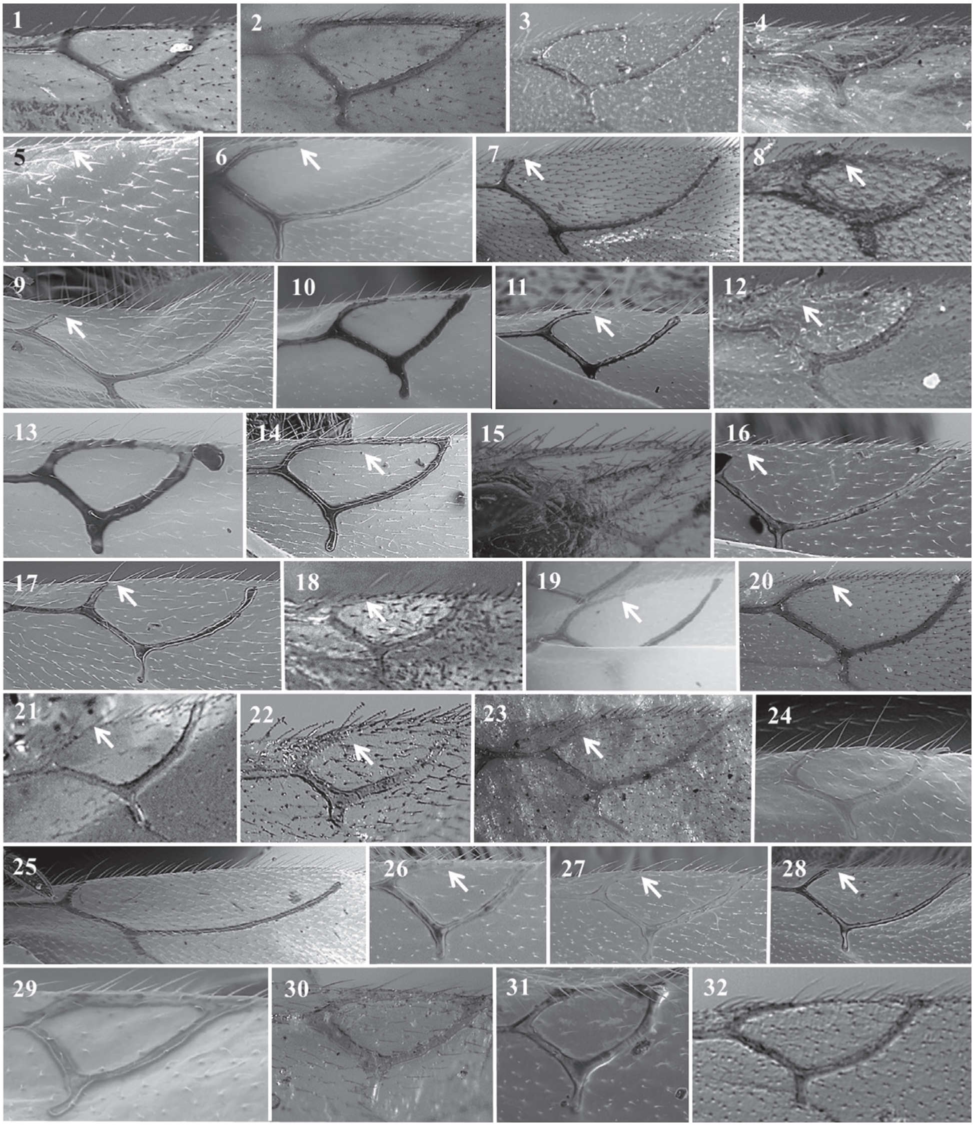

Figure 18. *Alloxysta* radial cell. *A. lachni* (**1**); *A. leunisii* (**2**); *A. longipennis* (**3**); *A. longiventris* (**4**); *A. luismii* (**5**); *A. macrophadna* (**6**); *A. mara* (**7**); *A. marshalliana* (**8**); *A. medinae* (**9**); *A. mexicana* (**10**); *A. melanogaster* (**11**); *A. minuscula* (**12**); *A. mullensis* (**13**); *A. nepalica* (**14**); *A. nigricans* (**15**); *A. nigrita* (**16**); *A. nipona* (**17**); *A. nothofagi* (**18**); *A. obscurata* (**19**); *A. pallidicornis* (**20**); *A. paretasmartinezi* (**21**); *A. patens* (**22**); *A. piceomaculata* (**23**); *A. pilipennis* (**24**); *A. pilosa* (**25**); *A. pleuralis* (**26**); *A. postica* (**27**); *A. proxima* (**28**); *A. pusilla* (**29**); *A. quedenfeldti* (**30**); *A. ramulifera* (**31**); *A. rubidus* (**32**).

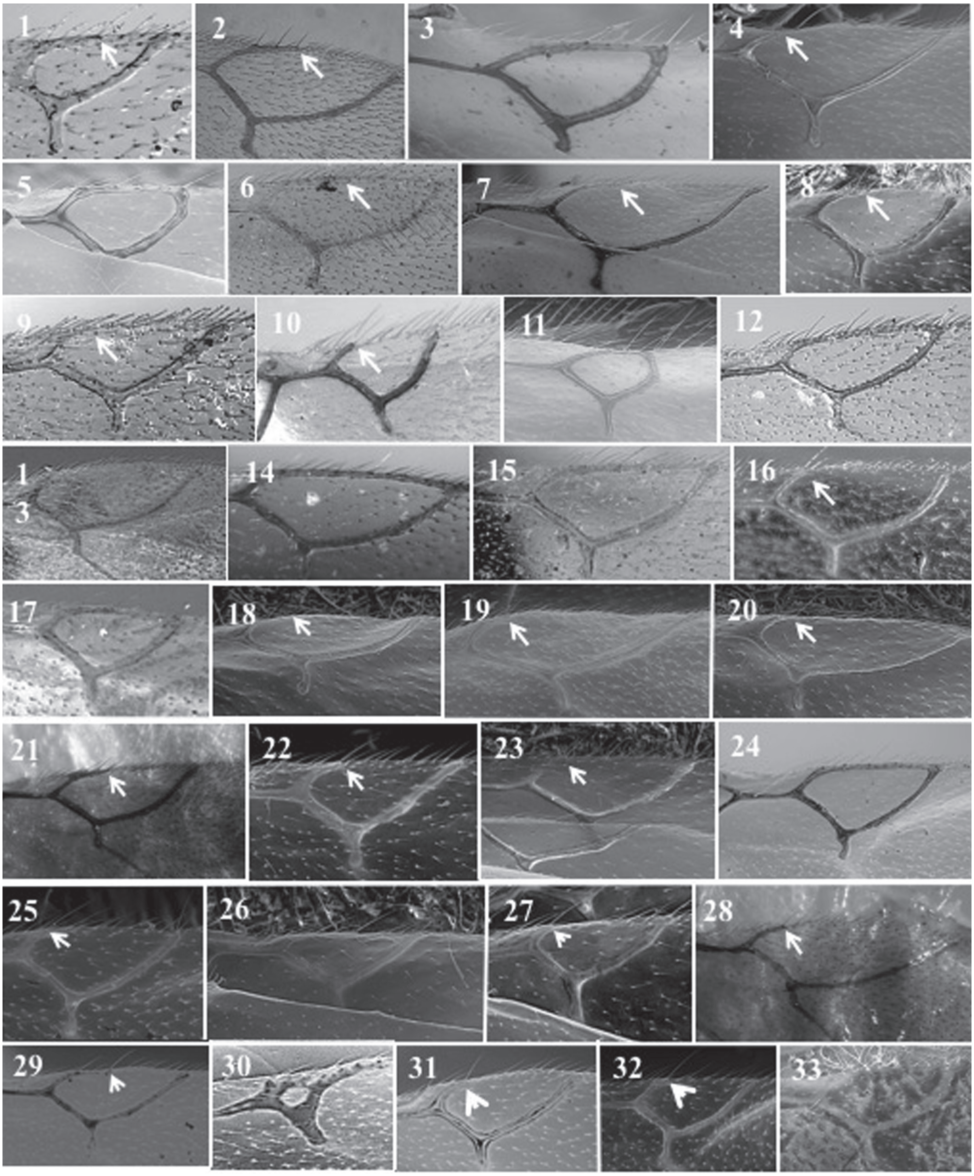

Figure 19. *Alloxysta* radial cell. *A. rufiventris* (**1**); *A. salicicola* (**2**); *A. sawoniewiczi* (**3**); *A. samurai* (**4**); *A. sarae* (**5**); *A. semiaperta* (**6**); *A. sharkey* (**7**); *A. slovenica* (**8**); *A. soluta* (**9**); *A. thorpei* (**10**); *A. torresi* (**11**); *A. tscheki* (**12**); *A. vandenboschi* (**13**); *A. victrix* (**14**); *A. xanthocera* (**15**); *A. xanthopa* (**16**); *A. xanthopsis* (**17**); *A. centroamericana* (**18**); *A. alpina* (**19**); *A. areeluckator* (**20**); *A. buffingtoni* (**21**); *A. franca* (**22**); *A. huberi* (**23**); *A. neartica* (**24**); *A. pili* (**25**); *A. petchabunensis* (**26**); *A. texanae* (**27**); *A. vicenti* (**28**); *A. viellae* (**29**); *A. curta* (**30**); *A. palearctica* (**31**); *A. pascuali* (**32**); *A. nottoni* (**33**).

Apocharips Fergusson, 1986

Apocharips Fergusson, 1986: 16. Type: *Allotria xanthocephala* Thomson, 1862.

General features. *Head*. Triangular, higher than it is wide, smooth and shiny. Setae present below and between toruli with few setae above toruli. Scattered setae on vertex, many setae on frons. Transfacial line 0.9–0.8× the height of the compound eye. Malar space 0.3–0.4 × the height of the compound eye (Fig. 20[1]).

Antenna. Female: 13-segmented, filiform. All antennomers covered with sparse setae (Fig. 20[2]). Male: 14-segmented, filiform. All antennomers covered with sparse setae.

Mesosoma. Pronotum with setae; two thick, curved, long carinae (Fig. 20[4]). Mesoscutum smooth and shiny, round in dorsal view with sparse setae. Scutellum smooth and shiny with scattered setae, an M-shaped carina on the apex of scutellum. Propodeum with abundant setae; two propodeal carinae separated by setae in first third, forming a plate in last two-thirds, with strongly-curved sides (Fig. 20[5]).

Forewing. Longer than the body, 1.1–1.5× as long as the mesosoma and metasoma combined, with dense pubescence and marginal setae. Open radial cell in variable sizes. Shape of R1 and Rs veins vary.

Metasoma. Has a small basal metasomal tergum, terminating just posterior to the ring of setae at the base of the metasoma (Fig. 20[6]).

Distribution. Holarctic, Neotropical and African regions (Ferrer-Suay et al. 2013).

Biology. Endoparasitoids of Encyrtidae (Hymenoptera: Chalcidoidea) that are endoparasitoids of psyllids (Hemiptera: Psyllidae) (Fergusson 1986; Menke and Evenhuis 1991). Until now it has been cited in: *Euphyllura olivine* and *Euphyllura aethiopica* by Silvestri (1915: 274).

Key to species

1 Radial cell is short, 1.2× as long as wide, with parallel R1 and Rs (Fig. 22[5])... .... ***A. trapezoidea* (Hartig, 1841)**

– Radial cell is longer, 2.0–2.8× as long as wide; R1 and Rs non-parallel **2**

2 Lower face with small radial carinae around clypeus.................................... .... ***A. hansoni* Menke, 1993**

– Face smooth, without carinae.. **3**

3 Last two flagellomeres well-differentiated, not broadly joined **4**

– Last two flagellomeres broadly joined... **5**

4 Many long setae under toruli. Female: rhinaria and club shape (antenna widening) begin at F5; F1 longer than F2 which is subequal to F3 (Fig. 21[1]); propodeal carinae are thick and separated; apex of scutellum has carinae (Fig. 22[1]). Male: unknown......***A. angelicae* (Pujade-Villar & Evenhuis, 2002)**

– Short, scattered setae under toruli. Female: rhinaria and club shape begin at F2; F1 = F2 < F3 (Fig. 21[2]); propodeal carinae form a plate with strongly curved margins; apex of scutellum does not have carinae (Fig. 22[2]). Male: unknown ....***A. colombiana* (Ferrer-Suay & Pujade-Villar, 2013)**

5 Male: rhinaria and club shape begin at F4; F1 = F2 < F3 (Fig. 21[6]); Rs is curved, reaching wing margin (Fig. 22[6]). Female: unknown ....***A. tropicale* (Ferrer-Suay & Paretas-Martínez, 2013)**

– Male: rhinaria and club shape begin at F5; F1 > F2 = F3 (Fig. 21[4]); Rs is straight and does not reach wing margin (Fig. 22[4]). Female: unknown ....***A. tamanii* (Paretas-Martínez & Pujade-Villar, 2013)**

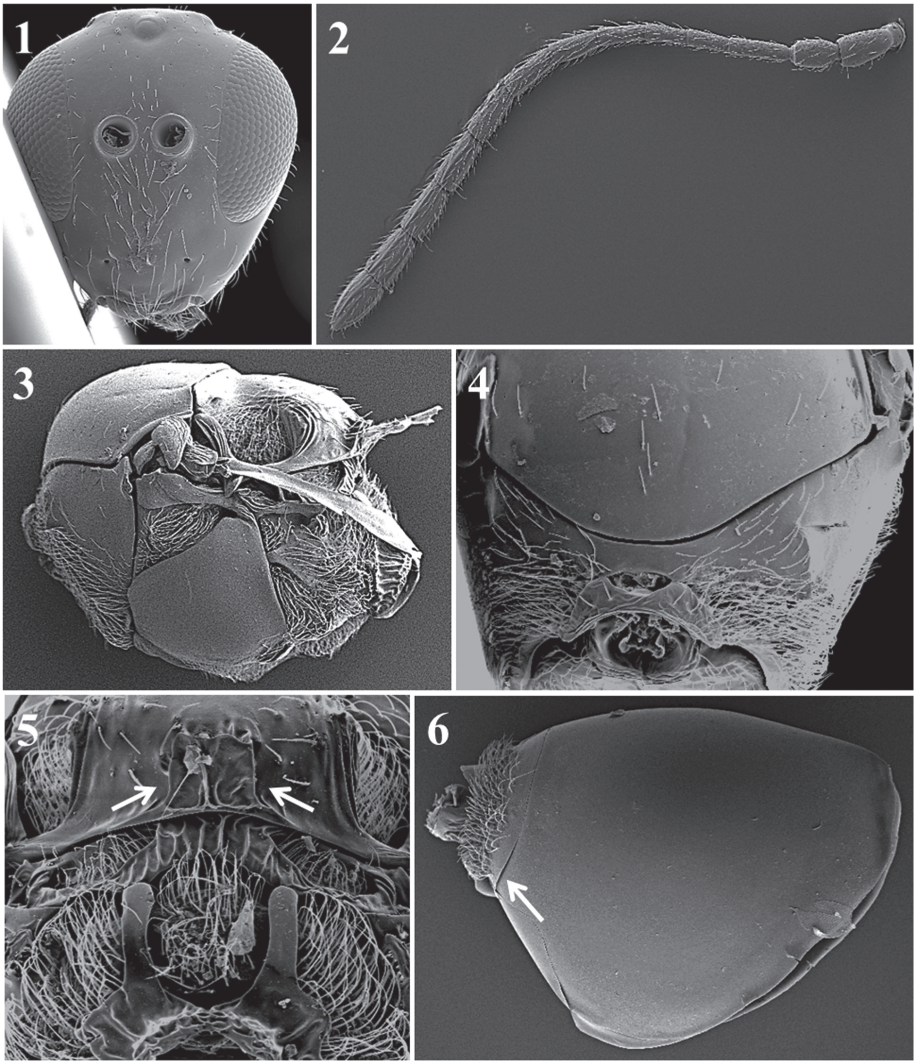

Figure 20. *Apocharips* general features. Head (**1**); antenna (**2**); mesosoma (**3**); pronotum (**4**); propodeum (**5**); metasoma (**6**).

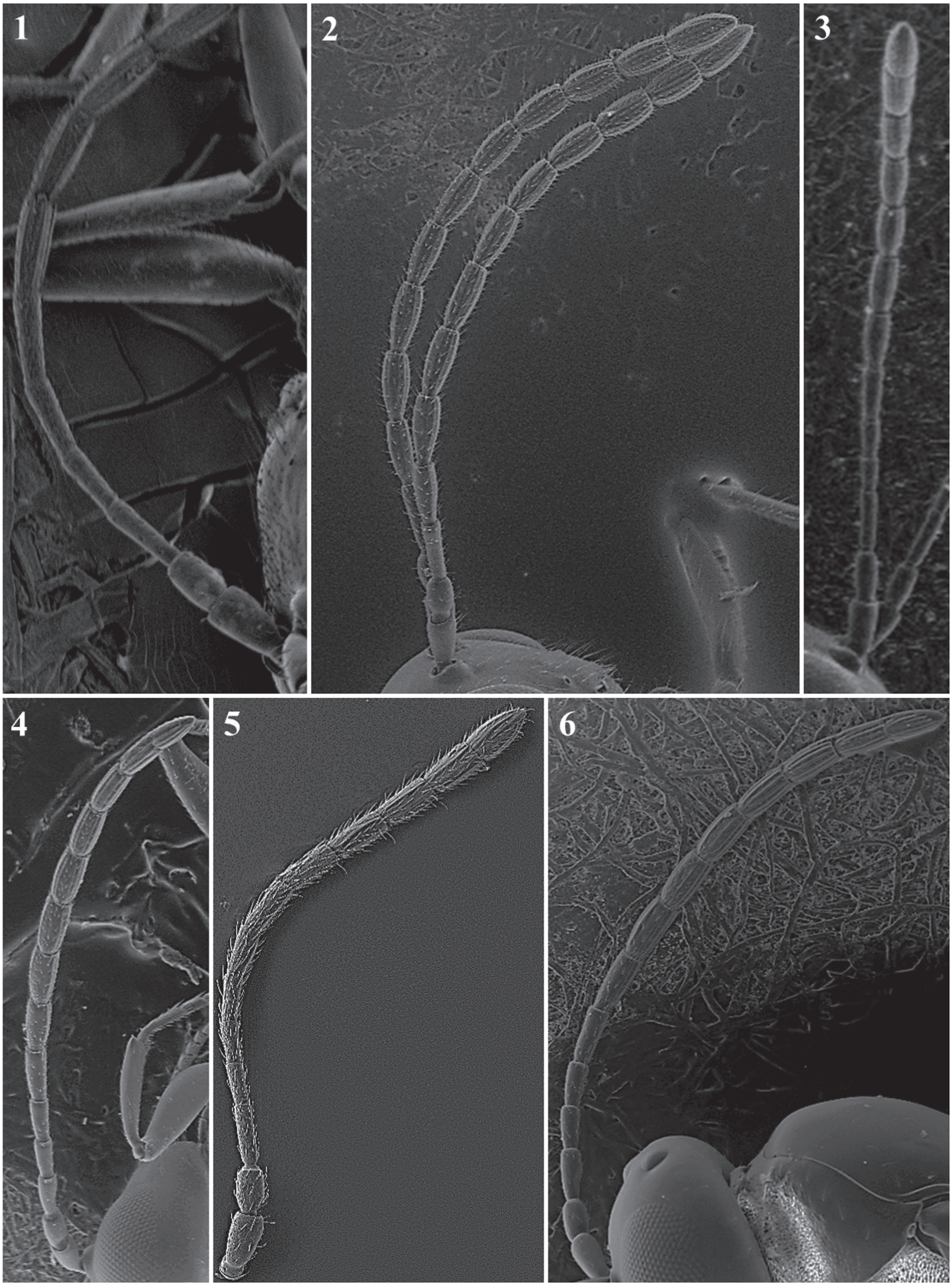

Figure 21. *Apocharips* antennae. *A. angelicae* (**1**); *A. colombiana* (**2**); *A. hansoni* (**3**); *A. tamani* (**4**); *A. trapezoidea* (**5**); *A. tropicale* (**6**).

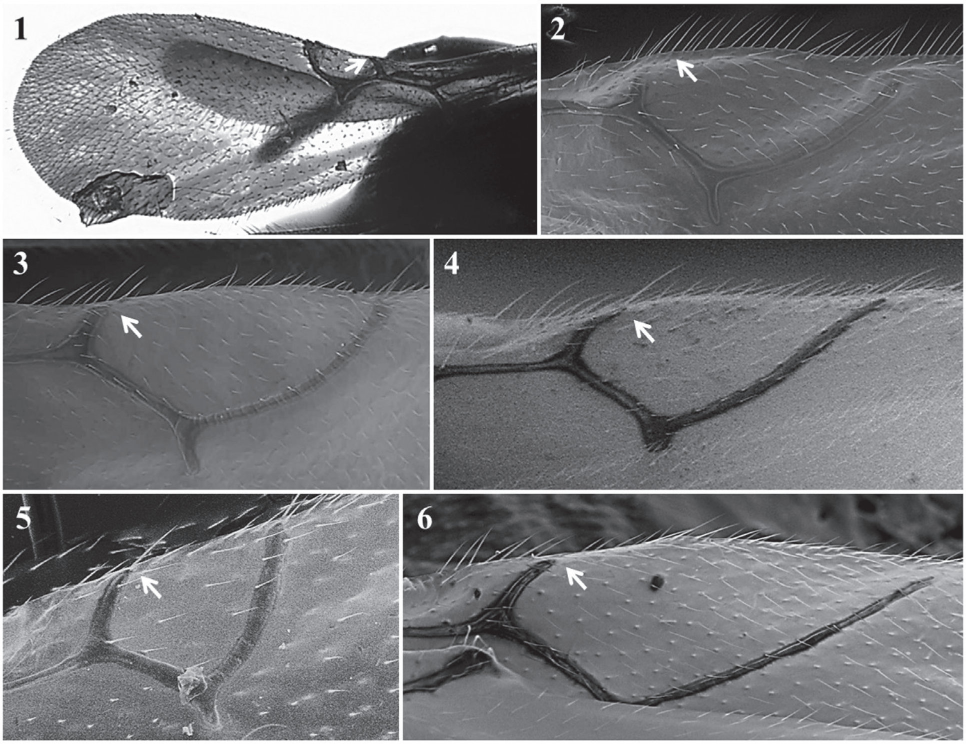

Figure 22. *Apocharips* radial cell. *A. angelicae* (**1**); *A. colombiana* (**2**); *A. hansoni* (**3**); *A. tamanii* (**4**); *A. trapezoidea* (**5**); *A. tropicale* (**6**).

Dilapothor Paretas-Martínez & Pujade-Villar, 2006

Dilapothor Paretas-Martinez & Pujade-Villar, 2006: 224. Type: *Dilapothor carverae* Paretas-Martínez & Pujade-Villar, 2006.

General features. *Head*. Elongated in anterior view, eyes located at the higher part of the head, malar space is more than double the distance from the external margin of the lateral ocellus to the dorsal margin of the compound eye, measured in the anterior view of the head. With some setae below the toruli; sparse setae on frons (Fig. 23[5]).

Antenna. Female: 12-segmented, clavate. Flagellomeres separate except the last two, which are broadly joined, all antennomers are covered with sparse setae. Each flagellomere expands towards its distal end (Fig. 23[2]).

Mesosoma. Pronotal carinae small, only slightly indicated. Mesoscutum is smooth, shiny, and is almost completely without setae (Fig. 23[6]). No sutures on the mesopleuron. Scutellum has three carinae on each side of the scutellar apex that are symmetrical, with a distance between them equivalent to the distance between the propodeal carinae. Propodeum has two strong, broad carinae (Fig. 23[3]).

Forewing. Large, longer than body and covered with dense pubescence; marginal setae are present, but not very long. Large radial cell is completely open; 2r as long as Sc + R1; Rs are long and curved, giving an elongated, large appearance to radial cell; R1 is very short and does not reach the costal margin; 2rm is very short, almost absent; Cu1a, M + Cu1a, Rs + M and M veins absent (Fig. 23[1]).

Metasoma. Proximal part of metasoma has a complete ring of setae. Metasoma not segmented, only one big tergite visible (Fig. 23[4]).

Comments. Until now there is only one species known of this genus, *Dilapothor carverae* Paretas-Martínez & Pujade-Villar, 2006.

Distribution. Only known from Australia (Paretas-Martínez and Pujade-Villar 2006).

Hosts. Unknown (Paretas-Martínez and Pujade-Villar 2006).

Dilyta Förster, 1869

Dilyta Förster, 1869: 340. Type: *Dilyta subclavata* Förster, 1869: 340.

Dylita Förster, 1869: 338. An incorrect original spelling (rejected by Menke and Evenhuis 1991:152, first revisers), unavailable.

Charips Haliday in Marshall, 1870: 181. Type: *Charips microcera* Haliday in Marsall, 1870. Synonymized by Hellén (1963: 4).

Allotria (*Glyptoxysta* Thomson, 1877: 881).

Glyptoxysta Thomson, 1877 in Ashmead (1903: 142). Type: *Glyptoxysta heterocera* Thomson, 1877. Synonymized by Hellén (1963: 4).

General features. *Head*. Rounded in anterior view, eyes located at middle line of head, malar space subequal to the distance from external margin of the lateral ocellus to the dorsal margin of the compound eye, measured in anterior view of the head. Surface completely smooth, without any strigose, malar impression, epistomal sulcus or clypeo-pleurostomal lines. Clypeus almost straight, slightly projecting over mandibles, without marginal inflection. Setae sparse, concentrated principally below the toruli (Fig. 24[3]).

Antennae. Size of pedicel and flagellomeres vary among species. Female: 13-segmented, slightly clavate; two last segments (F10–F11) broadly jointed. Male: 14-segmented, slightly clavate or filiform; two last segments (F11–F12) broadly jointed.

Mesosoma. Pronotum have setae only in the anterior part; pronotal carinae is long, clearly indicated, and extends from scutum to the anterior part of pronotum (Fig. 24[4]). Mesoscutum smooth, shiny, and almost without setae. Mesopleuron smooth, without any longitudinal ridge in lower part (Fig. 24[2]). Scutellum smooth, with scarce setae at posterior and lateral parts. Propodeum with two strong, broad carinae. Apex of scutellum: *Holarctic* spp. ∩-shaped carina (Fig. 24[5]). *Afrotropical* spp. with one carina on each side, both symmetrical and parallel, with a distance between them equivalent to the distance between the propodeal carinae (Fig. 24[6]).

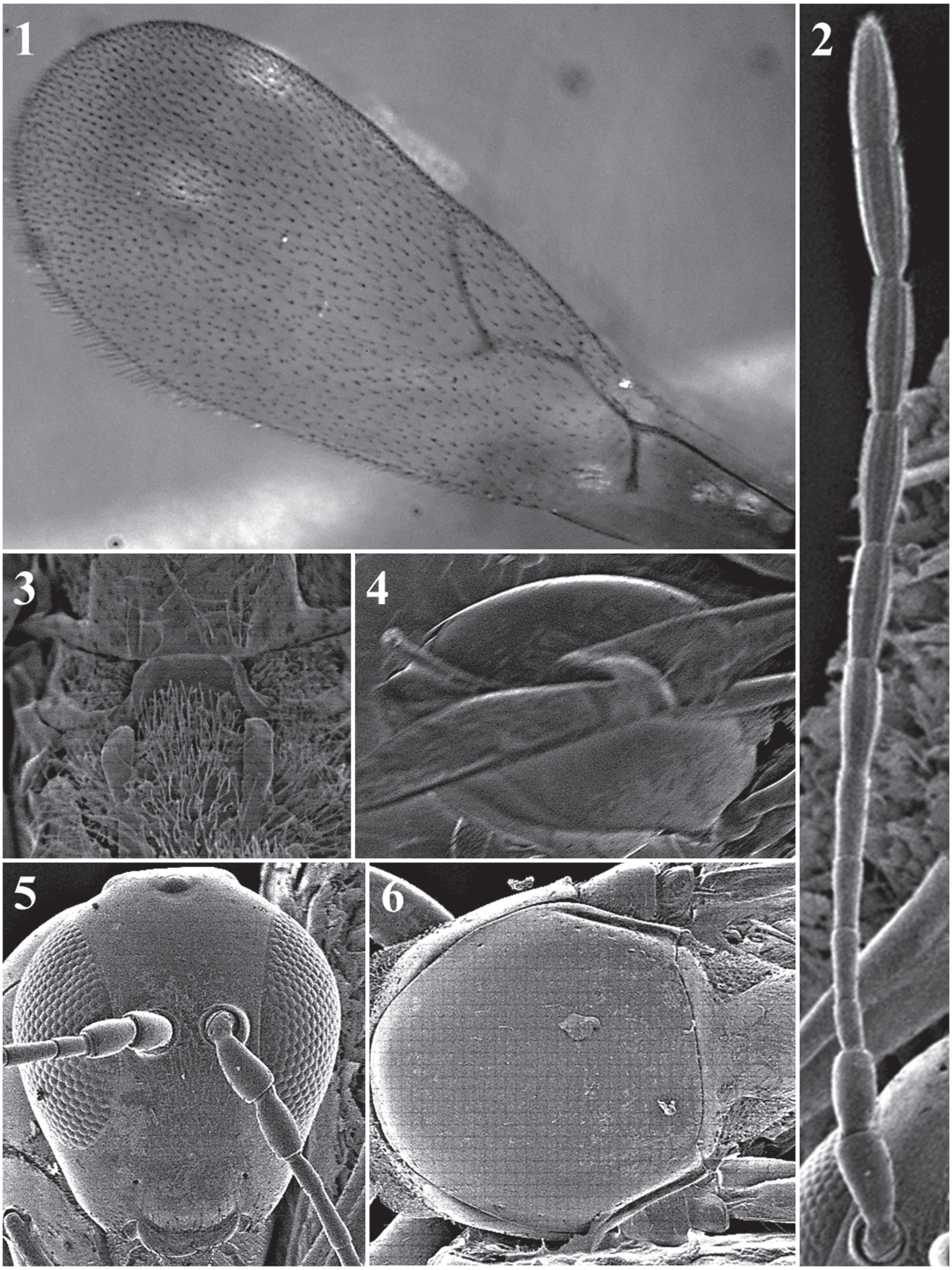

Figure 23. *Dilapothor carverae* Paretas-Martínez and Pujade-Villar, 2006. Fore wing (**1**); antenna (**2**); propodeum (**3**); metasoma (**4**); head (**5**); mesoscutum (**6**).

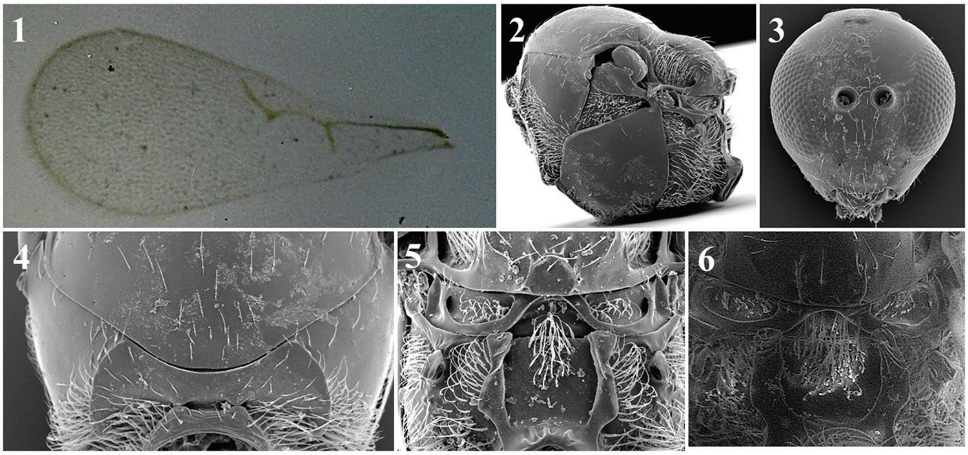

Figure 24. *Dilyta* general features. Forewing (**1**); mesosoma (**2**); head (**3**); pronotum (**4**); propodeum holarctic species (**5**); propodeum african species (**6**).

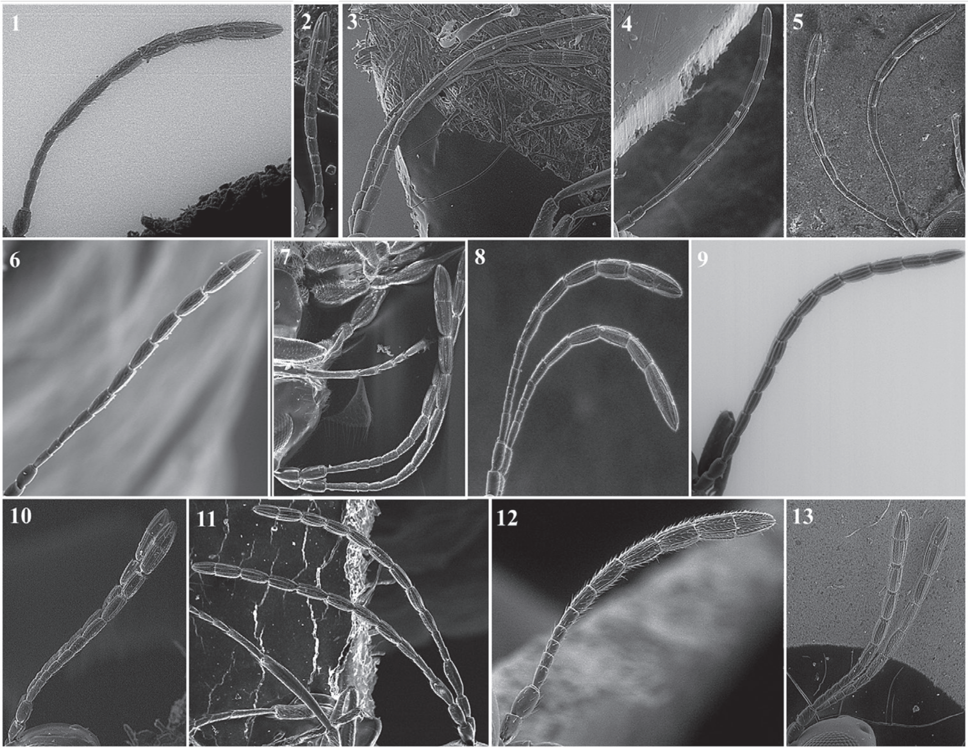

Figure 25. *Dilyta* antennae. *D. africana* (**1**); *D. alevae* (**2**); *D. australafricana* (**3**); *D. ghanana* (**4**); *D. japonica* (**5**); *D. kenyana* (**6**); *D. longinqua* (**7**); *D. orientalis* (**8**); *D. paretasmartinezi* (**9**); *D. rathmanae* (**10**); *D. sinica* (**11**); *D. somaliana* (**12**); *D. subclavata* (**13**).

Forewing. Large, longer than body, covered with dense pubescence; marginal, long setae present; brown veins; radial cell small and completely open along anterior margin; R1 very short and barely reaches costal margin (Fig. 24[1]).

Distribution. Holarctic, Afrotropical and Oriental regions (Paretas-Martínez et al. 2011).

Hosts. Endoparasitoids of Encyrtidae (Hymenoptera: Chalcidoidea) that are endoparasitoids of psyllids (Hemiptera: Psyllidae) (Fergusson 1986; Menke and Evenhuis 1991). Until now it has been cited in: *Cacopsylla alba*, *Cacopsylla pyricola*, *Psylla pyri*, *Psyllopsis fraxini* by Menke and Evenhuis (1991: 152); *Trioza erytreae* by Paretas-Martínez et al. (2009: 211) and Psyllidae on *Firmiana simplex* by Paretas-Martínez et al. (2011: 34).

Key to species

1 Apex of scutellum has one carina on each side, both symmetrical, parallel and higher than axillar strip, distance between them equivalent to distance between the propodeal carinae (Fig. 24[6]) **2**

– Apex of scutellum a ∩-shaped, projected plate (Fig. 24[5]) **6**

2 Metasoma with a punctuated area on distal part **3**

– Metasoma does not have punctures **4**

3 Female: F1 subequal or slightly longer than pedicel, F2 and F3 much shorter than F1, F4 longer than F3 but shorter than F1; F5–F11 wider than previous segments, antenna slightly clavate from F5; sensilla beginning at F4–F5 (Fig. 25[1]). Male: F1 slightly longer than pedicel, F2 much shorter than F1, F3 shorter than F1 but longer than F2, F4 longer than F3 but shorter than F1, F5 wider than and as long as F1; overall, antenna slightly wider from F5 to F12 ...... ***D. africana* (Benoit, 1956)**

– Female: F1 subequal to pedicel, F2 much shorter than F1, F3 wider than and subequal in length to F1; F3–F11 wider than previous segments; antenna slightly clavate from F3; sensilla beginning on F3 (Fig. 25[4]). Male: unknown ...... ***D. ghanana* (Paretas-Martínez, Pujade-Villar & Melika, 2009)**

4 Female: F1 subequal to pedicel; F2 to F4 each shorter than F1; F5 subequal to F1 in length but wider; F5–F11 wider than previous segments, antenna slightly clavate from F5; sensilla beginning on F5–F6 (Fig. 25[3]). Male: unknown ...... ***D. australafricana* (Paretas-Martínez & Pujade-Villar, 2009)**

– F1 shorter than pedicel; different combination of flagellomeres **5**

5 Female: F1 shorter than pedicel, F2 and F3 shorter than F1 but not subquadrate, longer than they are wide, F4 longer than F1; F4–F11 wider than previous segments, antenna slightly clavate from F4; sensilla beginning on F4–F5 (Fig. 25[6]). Male: F1 subequal to pedicel; F2 shorter than F1, F3 shorter than F1 but slightly longer than F2, F4 wider than and as long as F1; antenna

slightly wider from F4 to F12 ....*D. kenyana* **(Paretas-Martínez & Pujade-Villar, 2009)**

– Female: F1–F5 very short, each shorter than pedicel; F1 and F5 subequal in length, F2–F4 subquadrate, as wide as they are long, and shorter than F1; F1–F6 wider than previous segments, antenna slightly clavate from F6; sensilla begin at F6 (Fig. 25[12]). Male: F1 straight; F1–F3 each similar to pedicel, subquadrate, and < 1.5 as long as wide; sensilla abundant on F1...... .... ***D. somaliana*** **(Paretas-Martínez, Pujade-Villar & Evenhuis, 2009)**

6 Metasoma with distinct, visible punctuation on distal half.........................**7**

– Metasoma does not have punctures, or at most has very few, scattered punctures on distal half that are not clearly visible **11**

7 Female: unknown. Male: F1 very long, wide and arched, F1 much longer than pedicel (almost double), F1 longer than F2 and F3 combined, F2 slightly shorter than or subequal to F3, F4 longer than F2 and F3, F4–F12 wider than previous segments; antenna slightly clavate from F4, sensilla begin at F4 (Fig. 25[11]) .... ***D. sinica*** **(Ferrer-Suay & Paretas-Martínez, 2011)**

– Male, when known, has different features than given above **8**

8 Female: F1 very long, thin, almost twice as long as pedicel; F1 longer than F2–F5, F1 nearly as long as F2, F3 and F4 combined (Fig. 25[5]). Male: unknown .... ***D. japonica*** **(Paretas-Martínez & Ferrer-Suay, 2011)**

– F1 similar in length to pedicel, F1 shorter than or subequal to F2 and F3 combined...**9**

9 Female: unknown. Male: rhinaria and club shape begin at F1; F1 slightly curved; F1–F3 subequal (Fig. 25[9])... .... ***D. paretasmartinezi*** **(Pujade-Villar & Ferrer-Suay, 2012)**

– Rhinaria and club shape begin in different flagellomeres; F1–F3 unequal . 10

10 Female: F1 slightly shorter than or subequal than pedicel, F2 subequal to F3, F4 slightly shorter than F1 but longer than F2 and F3, F1 subequal to F5, F6 longer than F5 (Fig. 25[13]). Male: F1 slightly longer than pedicel; F2 and F3 each shorter than F1; F1 subequal to F4; F4–F12 wider than previous flagellomeres, antenna slightly clavate from F4; sensilla begin at F4 .... ***D. subclavata*** **(Förster, 1869)**

– Female: F1 subequal to pedicel or slightly longer, F2 shorter than F3, F3 shorter than F4, F4 shorter than F5, F1 subequal to F5 (Fig. 25[7]). Male: F1 subequal to pedicel, F2 shorter than F1 or F3, F3 subequal to F1; F3–F12 wider than previous flagellomeres; antenna slightly clavate from F3; sensilla begin at F3..........***D. longinqua*** **(Paretas-Martínez & Pujade-Villar, 2011)**

11 Female: F1 narrow, slightly longer or subequal to pedicel; F1 longer than F2, F3 and F4; F2 slightly shorter than or subequal to F3; F4 longer than F2 and F3 (Fig. 15[8]). Male: unknown ....***D. orientalis*** **(Ferrer-Suay & Paretas-Martínez, 2011)**

– F1 markedly or only slightly shorter than pedicel; flagellomere differently proportioned than as above..**12**

12 Female: F1 almost double the length of F2, F3 and F4; F2 and F3 subequal to F4 but sometimes F2 seems slightly shorter than F3 or F4; F5 longer than F4; F5 longer than F4 but shorter than F1; F7–F11 wider than previous flagellomeres; antenna slightly clavate from F6 (Fig. 25[10]). Male: F1 as long as pedicel; F2 slightly shorter than F3; F4 as long as F1 but thinner; sensilla begin at F4................................***D. rathmanae* (Menke & Evenhuis, 1991)**

– Female: F1 longer than F2, F2 slightly longer than F3 and F4, F3 subequal to F4, F5 longer than F4 but as long as F1; F6–F10 wider than previous flagellomeres; antenna slightly clavate from F5 (female antenna has only 10 flagellomeres) (Fig. 25[2]). Male: F1 longer than pedicel, F2 subequal to F3, F4 wider and as long as F1; sensilla begin at F6 .... ***D. aleevae* (Pujade-Villar & Paretas-Martínez, 2011)**

***Lobopterocharips* Paretas-Martínez & Pujade-Villar, 2007**

Lobopterocharips Paretas-Martínez et al., 2007: 475. Type: *Lobopterocharips arreplegata* Paretas-Martínez & Pujade-Villar, 2007.

General features. *Head.* Transversely ovate, slightly wider than high in anterior view. Smooth surface, without sculpturing or ridges. Clypeus broadly projected over mandibles, marginal inflection well defined. Epistomal sulcus and clypeo-pleurostomal lines well defined. Toruli wrinkled in inferior area. Malar impression absent (Fig. 26[4]).

Antennae. Male: 14-segmented, filiform. Antennomers completely separate, covered with sparse setae. Abundant rhinaria in all flagellomers (Fig. 26[5]).

Mesosoma. Pronotal carinae very small, only slightly indicated. Mesopleuron smooth, without wrinkles or furrows (Fig. 26[2]). Mesoscutum smooth, shiny, without notauli or other impressions, and almost with no setae. Parascutal sulcus ending anteriorly next to tegula. Scutellum evenly rounded without distinct sculpture, smooth, no foveae or sculpture on apex. Posterodorsal extensions of axillar strips present. Metascutellum not constricted, with one longitudinal medial carina. Propodeum with two narrow longitudinal carinae (Fig. 26[3]).

Forewing. With dense pubescence; marginal setae present. Radial cell completely open, large; 2r as long as Sc+R1; Rs long, curved, ending just before wing margin; R1 reaching wing margin; 2rm well defined; Cu1a, M+Cu1a, Rs+M, M veins present, slightly visible; Rs+M vein pointing to middle part of basal vein. Undulation present in apical part of posterior margin (Fig. 26[1]).

Metasoma. Proximal area with incomplete ring of setae, not present in dorsal area. T2-T3 with subequal dorsomedial lengths, covering most of metasoma.

Comments. Until now there is only one species known of this genus, *Lobopterocharips arreplegata* Paretas-Martinez et al. 2007b.

Distribution. Only known from Nepal (Paretas-Martínez et al. 2007: 475).

Hosts. Unknown (Paretas-Martínez et al. 2007: 475).

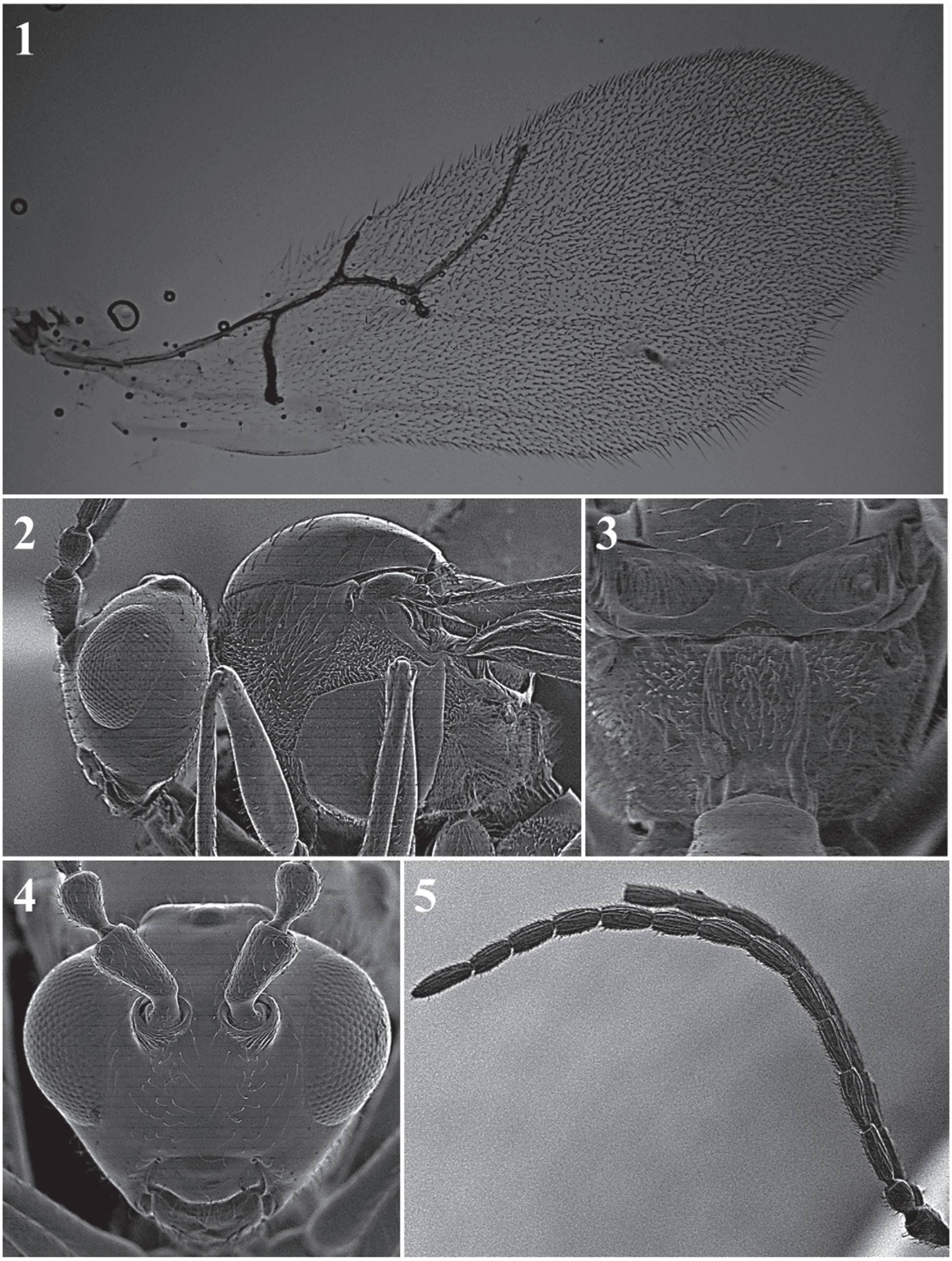

Figure 26. *Lobopterocharips arreplegata* Paretas-Martinez and Pujade-Villar, 2007. Fore wing (**1**); mesosoma, lateral view (**2**); propodeum (**3**); head, anterior view (**4**); antenna (**5**).

Lytoxysta Kieffer, 1909

Lytoxysta Kieffer, 1909: 479. Type: *Lytoxysta brevipalpis* Kieffer, 1909.

General features. *Head*. Triangular, higher than it is wide, covered by fine reticulated sculpture. Covered by very few scattered setae (Fig. 27[9]).

Antenna. Female: 13-segmented, filiform (Fig. 27[2]). Male: 13-segmented, filiform (Fig. 27[3]).

Mesosoma. Entirely covered by fine reticulated sculpture (Fig. 27[7]). Pronotum has no carinae present (Fig. 27[8]). Apex of scutellum has irregular carinae (Fig. 27[5]). Propodeum covered by abundant long setae; two thin and short propodeal carinae on top (Fig. 27[4]).

Forewing. Longer than body with dense pubescence and marginal setae. Radial cell is open. R1 and Rs are short and do not reach the costal margin (Fig. 27[1]).

Metasoma. Anterior part with an incomplete ring of setae, glabrous at centre and wider laterally. Metasoma smooth and shiny, T3 and T4 clearly distinguished.

Comments. Until now there is only one species known of this genus, *Lytoxysta brevipalpis* Kieffer, 1909.

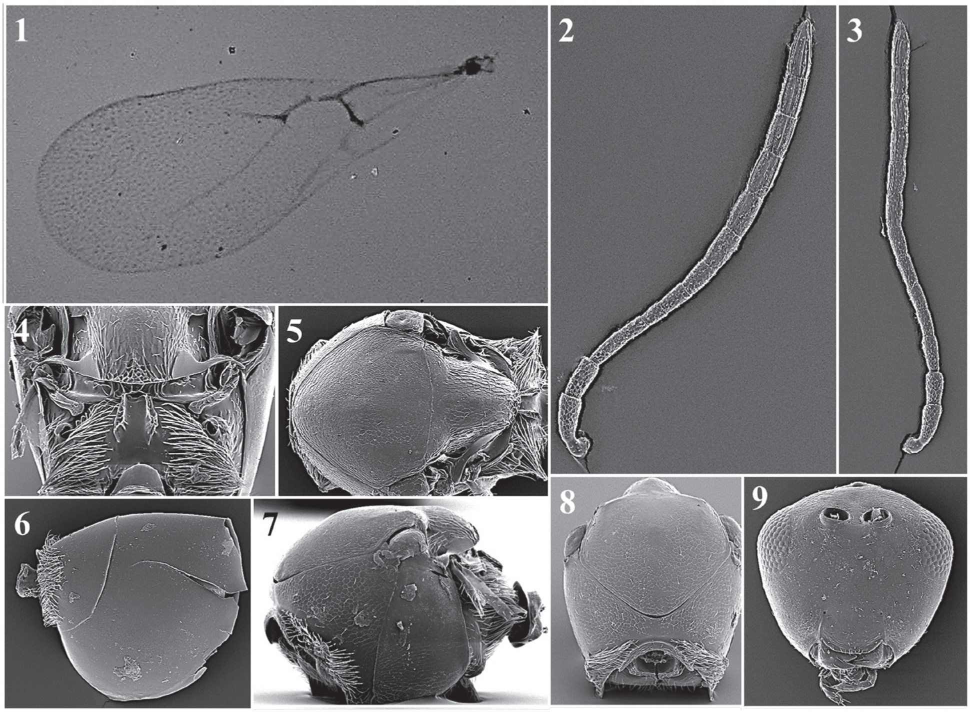

Figure 27. *Lytoxysta brevipalpis* Kieffer, 1909. Fore wing (**1**); antenna female (**2**); antenna male (**3**); propodeum (**4**); mesoscutum (**5**); metasoma (**6**); mesosoa, lateral view (**7**); pronotum (**8**); head, anterior view (**9**).

Distribution. Canada (British Columbia and Manitoba) and USA (California) (Andrews 1978: 24); USA (Massachusetts) (Kieffer 1909: 480).

Hosts. Cited in *Chaitophorus salicicorticis*, *Aphis* sp. and *Dactynotus* sp. throughout *Aphidius* sp. and *Lysiphlebus* sp. (Andrews 1978: 24).

Phaenoglyphis Förster, 1896

Phaenoglyphis Förster, 1869: 338. Type: *Phaenoglyphis xanthochroa* Förster, 1869.

Hemicrisis Förster, 1869: 338. Type: *Hemicrisis ruficornis* Förster, 1869. Synonymized by Evenhuis (1973: 218). See the history of placement in Pujade-Villar and Paretas-Martínez (2006).

Glyptoxysta Thomson, 1877: 812. Type: *Auloxysta nigripes* Thomson, 1877, by subsequent designation (Ashmead 1903: 142) (vide Rohwer and Fagan 1919: 237). Synonymized by Hellén (1963: 5).

Bothrioxysta Kieffer, 1902: 11. Type: *Auloxysta nigripes* Thomson, 1877, by subsequent designation (Rohwer and Fagan 1917: 362). Synonymized by Hellén (1963: 5).

Charipsella Brèthes, 1913: 159. Type: *Charipsella laevigata* Bréthes, 1913. Synonymized by Quinlan and Evenhuis (1980: 428).

General features. *Head*. Transversally ovate, smooth and shiny, slightly wider than it is high from the anterior view. Setae below and between toruli, without setae above toruli. Setae few and scattered on vertex, many setae on face. Transfacial line 1.1–1.2× height of compound eye. Malar space 0.3–0.4× height of compound eye (Fig. 28[1]).

Antenna. Female: 13-segmented, filiform. All antennomers have sparse setae (Fig. 28[7]). Male: 14-segmented, filiform. All antennomers have sparse setae (Fig. 28[3]).

Mesosoma. Pronotum entirely covered by long setae; two thick and long carinae are clearly visible (Fig. 28[6]). Mesoscutum smooth, shiny and round in dorsal view with scattered setae (Fig. 27[2, 5]). Scutellum smooth and shiny with scattered setae that are more abundant on apex. Propodeum covered with setae; two thin carinae are well-separated (Fig. 28[9]).

Forewing. Longer than body, 1.3–1.6× as long as mesosoma and metasoma combined. Covered with dense pubescence; marginal setae present. Radial cell usually closed, very few species with partially or completely open radial cell.

Metasoma. Anterior part has an incomplete ring of setae, is glabrous at centre and wider laterally. Metasoma smooth and shiny, T3 and T4 clearly distinguished (Fig. 28[9]).

Distribution. Cosmopolitan (Ferrer-Suay et al. 2012).

Hosts. Endoparasitoids of Aphidiinae (Hymenoptera: Braconidae) and Aphelininae (Hymenoptera: Braconidae) that are endoparasitoids of aphids (Hemiptera: Aphididae) (Fergusson 1986; Menke and Evenhuis 1991).

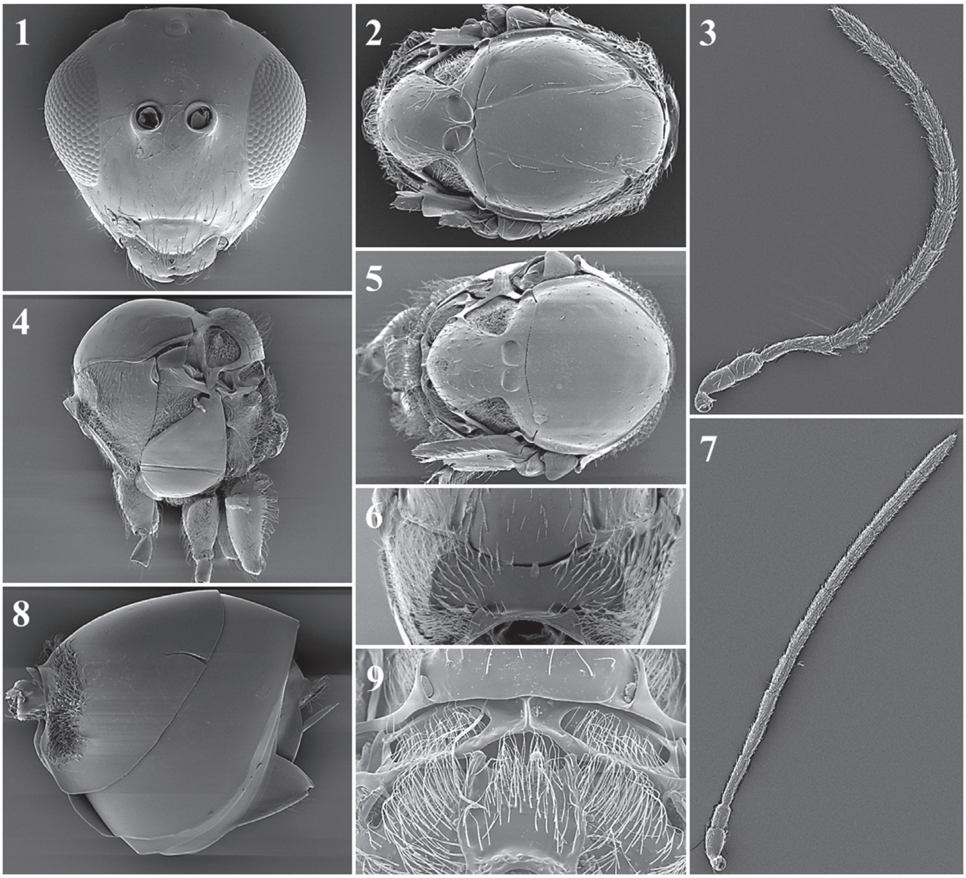

Figure 28. *Phaenoglyphis* general features. Head (**1**); mesoscutum with notauli (**2**); male antenna (**3**); mesosoma (**4**); mesoscutum without notauli (**5**); pronotum (**6**); female antenna (**7**); metasoma (**8**); propodeum (**9**).

Key to species

1 Notauli present, at least on the posterior half of mesoscutum and/or scutum sculpture (Fig. 28[2]) **2**
– Notauli completely absent and scutum smooth and shining (Fig. 28[5]) **23**
2 Mesoscutum covered by imbricated sculpture (except mesopleura) **3**
– Mesoscutum smooth, without imbricated sculpture.................................**6**
3 Mesoscutum mostly smooth, with a few wrinkles on the distal side of the notauli **4**
– With distinctive imbricate sculpturing on all surfaces **5**
4 Notaulus very faint; radial cell 2.4× as long as wide.......... .... ***P. izhizawai* (Watanabe, 1950)**
– Distinct notaulus; radial cell 2.7× as long as wide .... ***P. ruficornis* (Förster, 1869)**

5 Rhinaria and club shape begin at F1 (Fig. 29[23]); thick pronotal carinae do not reach mesoscutum; mesoscutum entirely covered by many setae; notauli present, only insinuated on the anterior part and well-marked on the back; scutellar foveae open on the bottom (Fig. 31[23]); central part of metascutellum smooth, with only a central carina. Male: unknown ... ***P. pubicollis* (Thomson, 1877)**

– Rhinaria and club shape begin at F4 (Fig. 29[7]); long pronotal carinae reach the mesoscutum; mesoscutum with few, scattered setae; notauli only insinuated; scutellar foveae completely defined with a transverse posterior carina inside (Fig. 31[7]); central part of metascutellum with imbricated sculpture. Male: unknown ... ***P. evenhuisi* (Pujade-Villar & Paretas-Martínez, 2006)**

6 Head, mesosoma and metasoma are yellowish brown ... **7**

– Head, mesosoma and metasoma are dark brown ... **8**

7 Pedicel 1.5× as long as wide; F2 shorter than F3, F3–F10 subequal in length, width and shape (Fig. 29[29]); notauli deeply excavated; median mesoscutal impression not evident; rounded scutellar foveae but with a straight interior side; mesoscutum and scutellum have few scattered setae (Fig. 31[29]); mesoscutum and scutellum covered by scattered setae; propodeal carinae are independent and slightly curved in the last third; closed radial cell with all veins of the same thickness. Male: unknown ... ***P. xanthochroa* (Förster, 1869)**

– F2–F10 subequal in length, width and shape (Fig. 29[21]); notauli deeply excavated with the median mesoscutal impression evident on the first two-thirds; large and oval scutellar foveae (Fig. 31[21]); mesoscutum and scutellum completely covered in long setae; central part of propodeum has few setae; propodeal carinae well-defined, straight and parallel; closed radial cell with the first half of R1 thinner than the second half only in females. Male: rhinaria and club shape begin at F2; F1 curved and longer than pedicel and F2, F2–F12 subequal; notauli is finer than in the females; veins of radial cell normal ... ***P. pilosus* (Andrews, 1978)**

8 Completely open radial cell; scutellar foveae absent ... ***P. indica* (Ferrer-Suay & Pujade-Villar, 2013)**

– Closed radial cell; scutellar foveae present ... **9**

9 Antennae longer than body ... **10**

– Antennae subequal or shorter than body ... **16**

10 Rhinaria and club shape begin at F1 ... **11**

– Rhinaria and club shape begin in other flagellomeres ... **13**

11 Rhinaria and club shape begin in all parts of F1; F2 subequal to F3, F3 shorter than F4 (Fig. 29[17]); mesoscutum smooth and with few scattered setae that are only present on the anterior and lateral margins and few or none at the central part; scutellar foveae with a straight top and sides, open at the bottom (Fig. 31[17]); apex of scutellum with few setae; radial cell 2.7× as long as wide; Rs is slightly curved. Male: unknown ... ***P. longicornis* (Hartig, 1840)**

– Rhinaria and club shape begin in last three-quarters of F1; different flagellomere proportions; mesoscutum has many scattered setae; different scutellar foveae; apex of scutellum has abundant setae; various radial cell sizes; Rs is straight **12**

12 Last flagellomere 2.5× as long as wide (Fig. 29[27]); scutellar foveae has straight sides and open at top and bottom (Fig. 31[27]); propodeal carinae independent; radial cell 2.4× as long as wide. Male: unknown .... ***P. stricta* (Thomson, 1877)**

– Last flagellomere 4.3× as long as wide (Fig. 29[13]); rounded scutellar foveae, slightly open at bottom (Fig. 31[13]); propodeal carinae joined at base; radial cell 2.9× as long as wide. Male: unknown .... ***P. insperatus* (Belizin, 1973)**

13 Rhinaria and club shape begin in same flagellomere **14**

– Rhinaria and club shape begin in different flagellomeres **15**

14 Rhinaria and club shape begin at F2; pedicel shorter than F1, F1–F3 unequal in length (Fig. 29[26]); scutellar foveae slightly fused (Fig. 31[26]); propodeal carinae slightly curved; radial cell 2.9× as long as wide. Male: unknown .... ***P. stenos* (Andrews, 1978)**

– Rhinaria and club shape begin at F3; pedicel longer than F1, F1–F3 subequal in length, (Fig. 29[11]); scutellar foveae not fused and open at top and bottom (Fig. 31[11]); propodeal carinae well-defined and straight; radial cell 2.7× as long as wide. Male: rhinaria and club shape begin at F3; F1 slightly curved and longer than pedicel and F2, F2 shorter than F3, F3 subequal to F4 .... ***P. heterocera* (Hartig, 1841)**

15 Rhinaria begin at F1 and club shape begins at F2; F1 is 2.1× as long as pedicel (Fig. 29[2]); notauli clearly visible with two extensions at the base of mesoscutum just above foveae (Fig. 31[2]); longitudinal carinae present in metascutellum do not branch at base. Male: rhinaria and club shape begin at F2; F1 very curved and longer than pedicel and F2, F2 shorter than F3, F3 subequal to F4 .... ***P. americana* (Baker, 1896)**

– Rhinaria begin at F1 and club shape begins at F3; F1 is 1.3× as long as pedicel (Fig. 29[9]); notauli deeply excavated on the aterior part and weakly on the back, straight mesoscutum base (Fig. 31[9]); longitudinal carinae present in metascutellum branch at base. Male: rhinaria begins at F5 and club shape at F3; F2 subequal to F3, F3 shorter than F4........... ***P. fuscicornis* (Thomson, 1877)**

16 F1 longer than pedicel **17**

– F1 subequal or shorter than pedicel **19**

17 Female: unknown. Male: rhinaria and club shape begin at F1; F2 thick and curved; F1 longer than pedicel and F2, F2–F4 subequal in length; scutellar foveae incomplete at top and bottom .... ***P. jeffersoni* (Ferrer-Suay & Pujade-Villar, 2014)**

– Female: rhinaria and club shape begin at F3; different relations between flagellomeres; scutellar foveae completely defined or only slightly open on bottom. Male: unknown **18**

18 F1 is 1.1× as long as pedicel, F1 longer than F2, F2 shorter than F3, F3–F4 subequal in length (Fig. 29[25]); mesoscutum with a line of setae next to each notaulus, notauli weakly present (Fig. 31[25]); scutellar foveae completely

defined with two lines at top; propodeum has two short, straight carinae independently reach base. Male: unknown......... ***P. salicis* (Cameron, 1883)**

– F1 is 1.3× as long as pedicel, F1 longer than F2, F2–F4 subequal in length (Fig. 29[10]); mesoscutum without setae in central part; notauli more marked on back than in front; scutellar foveae slightly open on bottom (Fig. 31[10]; propodeum with two well-defined carinae, slightly curved in last half. Male: unknown .... ***P. gutierrezi* (Andrews, 1978)**

19 Rhinaria begins at F2; F1 longer than F2, F2–F4 subequal in length; radial cell 2.7× as long as wide.................................... ***P. proximus* (Belizin, 1966)**

– Rhinaria begins at F3; different flagellomere proportions; various radial cell sizes **20**

20 Female: F1–F4 subequal in length (Fig. 29[18]); scutellar foveae rounded and separated by a thin carina (Fig. 31[18]); abundant setae on apex of scutellum; propodeum with narrow carinae (sometimes difficult to see). Male: rhinaria and club shape begin at F3; F1 not curved; F1 longer than pedicel and F2, F2 shorter than F3, F3–F4 subequal .... ***P. moldavica* (Ionescu, 1969)**

– F1 longer than F2; without combination of characters as above................ **21**

21 F2 shorter than F3, F3 subequal to F4 (Fig. 29[1]); scutellar foveae completely defined (Fig. 31[1]). Male: unknown .... ***P. abbreviata* (Thomson, 1877)**

– F2 subequal to F3, F3 subequal or shorter than F4; scutellar foveae incomplete.. **22**

22 F3 subequal to F4 (Fig. 29[15]); notauli clearly visible; scutellar foveae has superior and inferior margins that are not clearly delimited (Fig. 31[15]) .... ***P. japonica* (Ferrer-Suay & Pujade-Villar, 2013)**

– F3 shorter than F4; notauli present but slightly insinuated; scutellar foveae not delimited on bottom.. .... ***P. montoliui* (Ferrer-Suay & Pujade-Villar, 2013)**

23 Scutellar foveae not present... **24**

– Scutellar foveae present, sometimes superficially **29**

24 Open radial cell; body entirely covered by setae **25**

– Closed radial cell; body covered by scattered setae.................................... **27**

25 Completely open radial cell that is 3.1× as long as wide .... ***P. chiangmaiensis* (Ferrer-Suay & Pujade-Villar, 2014)**

– Partially open radial cell that can be different sizes **26**

26 Rhinaria and club shape begin at F3 (Fig. 19[6]); radial cell 3.8× as long as wide (Fig. 31[6])................... ***P. china* (Ferrer-Suay & Pujade-Villar, 2013)**

– Rhinaria and club shape begin at F2 (Fig. 19[3]); radial cell 2.6× as long as wide (Fig. 31[3])............... ***P. asiatica* (Ferrer-Suay & Pujade-Villar, 2013)**

27 Female: unknown. Male: rhinaria and club shape begin at F3; F1 long and curved; F2 slightly longer than F3, F3 subequal to F4; radial cell 3.1× as long as wide................................. ***P. kenai* (Ferrer-Suay & Pujade-Villar, 2014)**

– Female: rhinaria and club shape begin at F3 or F5; different sizes and ratios between flagellomeres; radial cell 2.5–2.6× as long as wide........................ **28**

28 Rhinaria and club shape begin at F5; F2 long and only slightly shorter than F1 (Fig. 29[16]); mesoscutum with abundant setae only in first half (Fig. 31[16]); mesopleural triangle open on anterior margin .... ***P. laevis* (Andrews, 1978)**

– Rhinaria and club shape begin at F3 (sometimes difficult to see); F2 shorter than F1 (Fig. 29[19]); mesoscutum has setae present on anterior and lateral margins (Fig. 31[19]); complete mesopleural triangle .... ***P. nigripes* (Thomson, 1877)**

29 Radial cell partially open along anterior margin; F1 and F2 subequal; F1 curved in males (Fig. 29[28]) .... ***P. villosa* (Hartig, 1841)**

– Radial cell closed; F1 and F2 subequal or F1 longer than F2..................... **30**

30 Propodeal carinae form a plate .... ***P. wongchaiensis* (Ferrer-Suay & Pujade-Villar, 2014)**

– Propodeal carinae are independent.. **31**

31 Rhinaria and club shape begin at F2 .... **32**

– Rhinaria and club shape begin at F3 .... **33**

32 Rounded scutellar foveae are separated by a carina and open at the bottom (Fig. 29[8]); scutellum has abundant setae; straight propodeal carinae are well-defined and join at the base; Rs slightly curved. Male: rhinaria and club shape begin at F2; F1 curved and longer than pedicel and F2, F2–F4 subequal .... ***P. falcata* (Andrews, 1978)**

– Scutellar foveae practically absent (Fig. 29[20]); scutellum has few setae; propodeal carinae are slightly curved in the last third, clearly defined and reach the base independently. Male: unknown .... ***P. palmirae* (Pujade-Villar & Melika, 2018)**

33 Pedicel longer than F1, F1 longer than F2 (Fig. 30[1]); scutellar foveae almost completed (Fig. 32[1]); two propodeal carinae are well-defined at the top and undefined at the bottom; radial cell 2.7× as long as wide. Male: unknown.... .... ***P. belizini* (Pujade-Villar, 2018)**

– Pedicel shorter than F1; different flagellomere proportions; mesoscutum has few scattered setae; incomplete scutellar foveae; two propodeal carinae that are well-defined; radial cell 2.7–2.8× as long as wide................................ **34**

34 F2 shorter than F3 (Fig. 29[5]); mesoscutum not gibbous; scutellum has few setae that are not abundant on the apex (Fig. 31[5]); propodeal carinae are slightly curved, well-defined at top and form a plate on bottom; radial cell 2.7× as long as wide. Male: F1 curved and longer than pedicel and F2, F2 subequal to F3 .... ***P. calverti* (Andrews, 1978)**

– F2 longer than F3 (Fig. 29[14]); mesoscutum characterised as very gibbous (Fig. 31[14]); scutellum with many setae, abundant on apex; propodeal carinae straight, well-defined and independently reaching base; radial cell 2.8× as long as wide. Male: unknown .... ***P. insularis* (Belizin, 1973)**

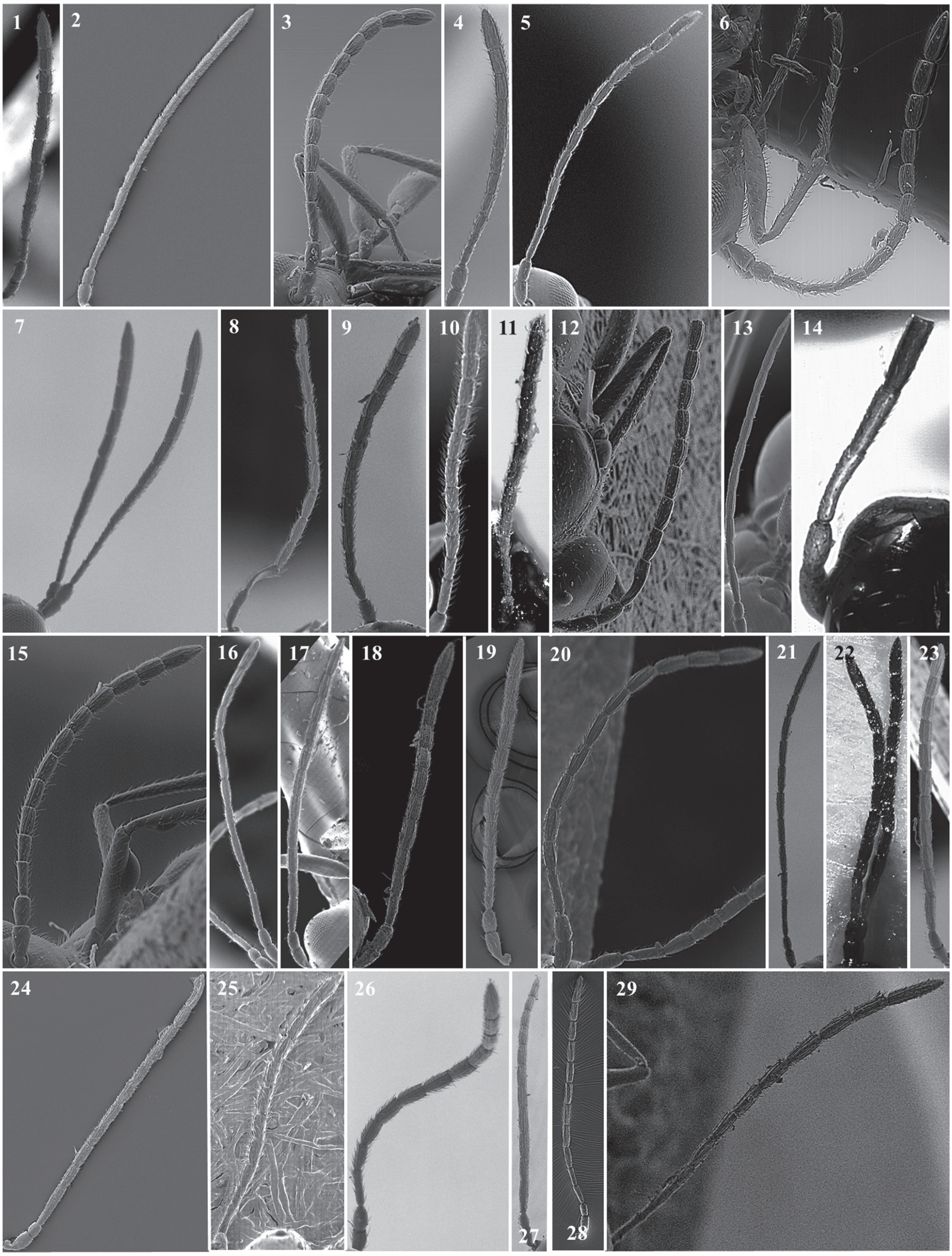

Figure 29. *Phaenoglyphis* antennae. *P. abbreviata* (**1**); *P. americana* (**2**); *P. asiatica* (**3**); *P. belizini* (**4**); *P. calverti* (**5**); *P. china* (**6**); *P. evenhuisi* (**7**); *P. falcata* (**8**); *P. fuscicornis* (**9**); *P. gutierrezi* (**10**); *P. heterocera* (**11**); *P. indica* (**12**); *P. insperatus* (**13**); *P. insularis* (**14**); *P. japonica* (**15**); *P. laevis* (**16**); *P. longicornis* (**17**); *P. moldavica* (**18**); *P. nigripes* (**19**); *P. palmirae* (**20**); *P. pilosus* (**21**); *P. proximus* (**22**); *P. pubicollis* (**23**); *P. ruficornis* (**24**); *P. salicis* (**25**); *P. stenos* (**26**); *P. stricta* (**27**); *P. villosa* (**28**); *P. xanthochroa* (**29**).

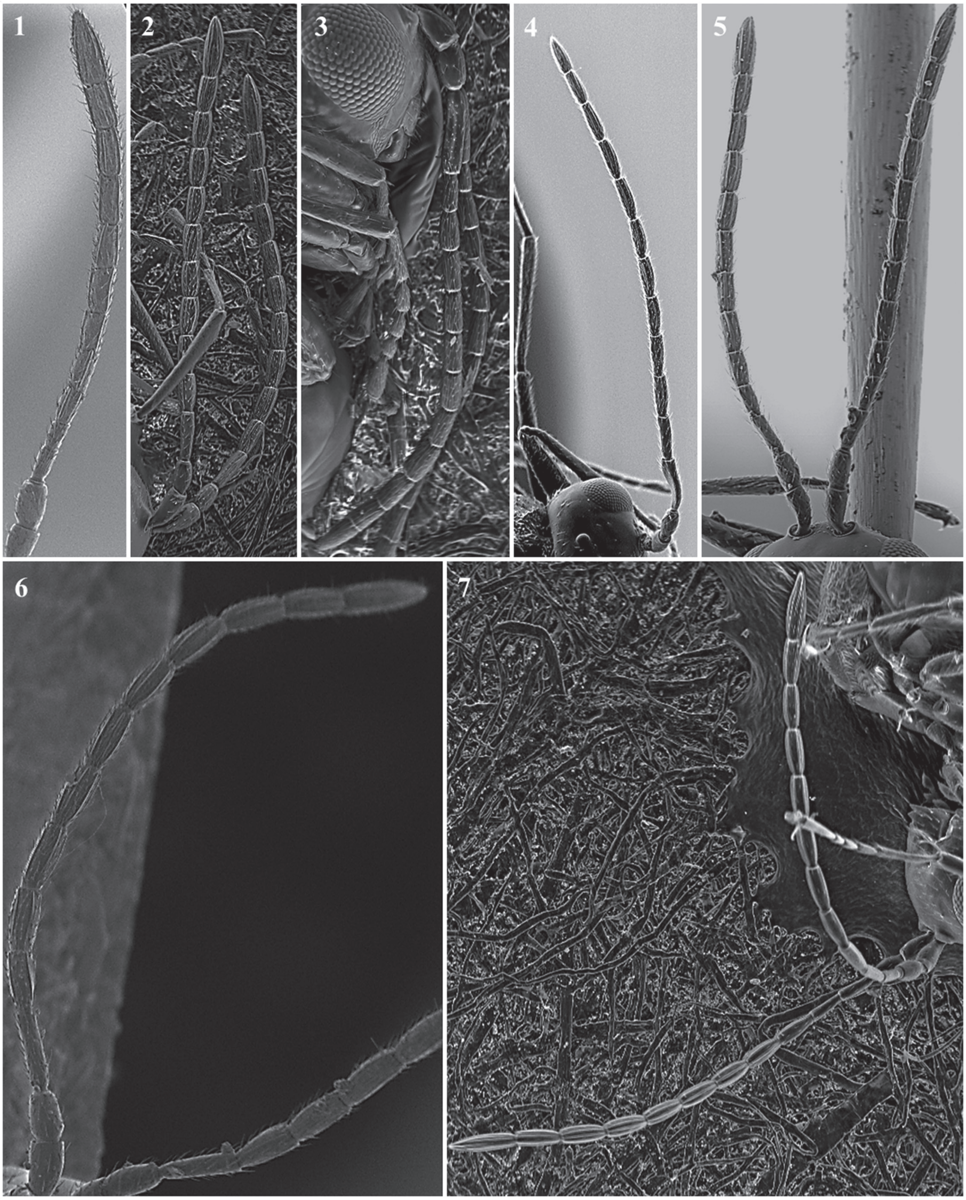

Figure 30. *Phaenoglyphis* antennae. *P. belizini* (**1**); *P. chiangmaii* (**2**); *P. jeffersonii* (**3**); *P. kenai* (**4**); *P. montoliu* (**5**); *P. palmirae* (**6**); *P. wongchaii* (**7**).

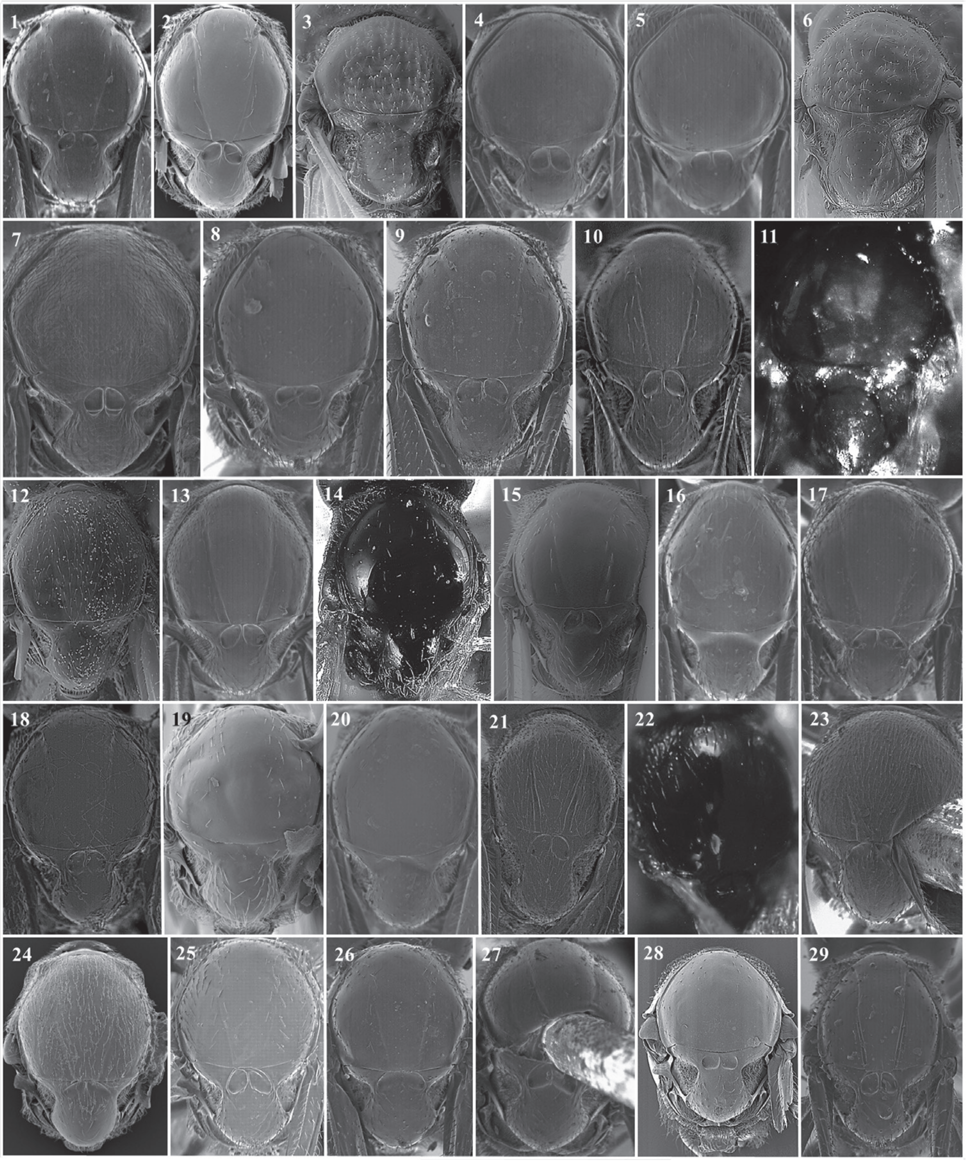

Figure 31. *Phaenoglyphis* mesoscutum. *P. abbreviata* (**1**); *P. americana* (**2**); *P. asiatica* (**3**); *P. belizini* (**4**); *P. calverti* (**5**); *P. china* (**6**); *P. evenhuisi* (**7**); *P. falcata* (**8**); *P. fuscicornis* (**9**); *P. gutierrezi* (**10**); *P. heterocera* (**11**); *P. indica* (**12**); *P. insperatus* (**13**); *P. insularis* (**14**); *P. japonica* (**15**); *P. laevis* (**16**); *P. longicornis* (**17**); *P. moldavica* (**18**); *P. nigripes* (**19**); *P. palmirae* (**20**); *P. pilosus* (**21**); *P. proximus* (**22**); *P. pubicollis* (**23**); *P. ruficornis* (**24**); *P. salicis* (**25**); *P. stenos* (**26**); *P. stricta* (**27**); *P. villosa* (**28**); *P. xanthochroa* (**29**).

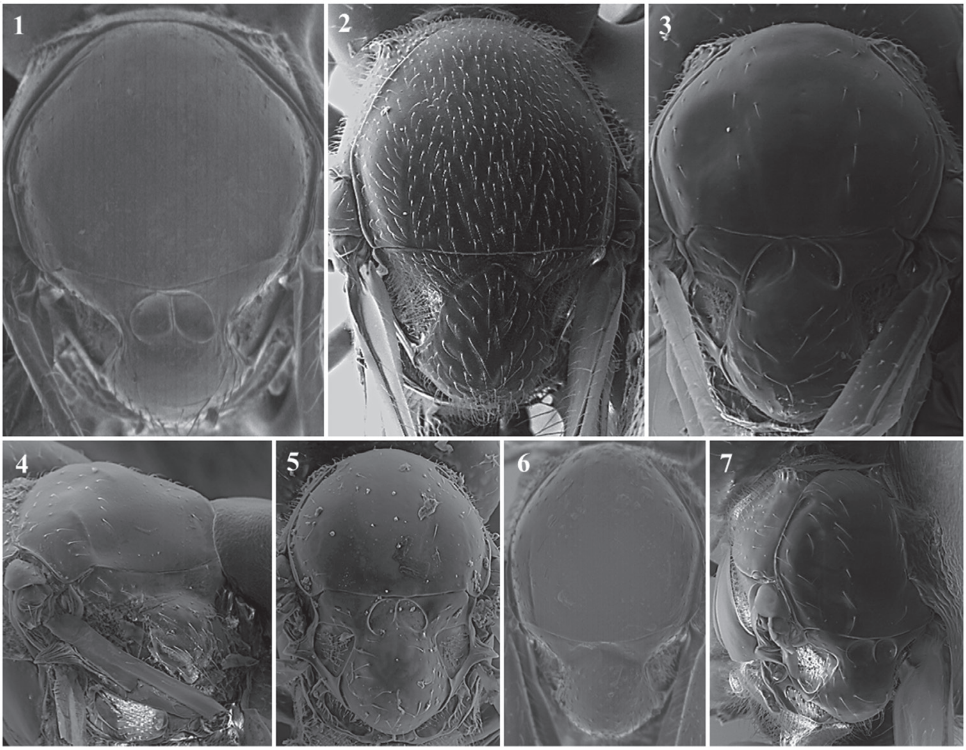

Figure 32. *Phaenoglyphis* mesoscutum. *P. belizini* (**1**); *P. chiangmaii* (**2**); *P. jeffersonii* (**3**); *P. kenai* (**4**); *P. montoliu* (**5**); *P. palmirae* (**6**); *P. wongchaii* (**7**).

Thoreauana Girault, 1930

Thoreauana Girault, 1930: 2. Type: *Thoreauana nativa* Girault.

General features. *Head*. Rounded in anterior view, eyes at the midline of the head, malar space subequal to the distance from the external margin of the lateral ocellus to the dorsal margin of the compound eye, measured in the anterior view; abundant setae below the toruli; sparse setae on frons (Fig. 33[1]).

Antenna. Female: 11-segmented, clavate. Male: 12-segmented, clavate (Fig. 33[3]).

Mesosoma. Pronotum with setae only on its anterior part; pronotal carinae are small and only slightly indicated (Fig. 33[5]). Mesoscutum is smooth, shiny and almost without setae. No sutures on the mesopleuron (Fig. 33[4]). Scutellum smooth with sparse setae on its posterior and lateral parts; one small carina on each side of scutellum apex that are symmetrical, with a distance between them equivalent to the distance between the propodeal carinae. Propodeum with two strong and broad carinae (Fig. 33[5]).

Forewing. Large, longer than body, covered in dense pubescence; marginal setae present and long; veins yellow to light brown; radial cell small and completely open;

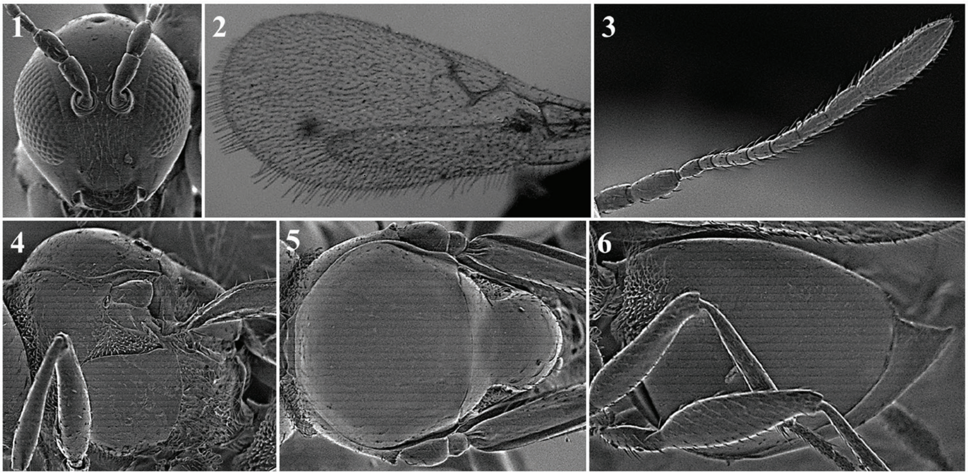

Figure 33. *Thoreauana* general features. Head (**1**); forewing (**2**); antenna (**3**); mesosoma (**4**); mesoscutum (**5**); metasoma (**6**).

R1 is very short, incomplete and does not reaching the costal margin; 2r is shorter than Sc + R1; Rs is short and nearly straight, reaching the wing margin; Cu1a, M + Cu1a, R s + M and M veins absent (Fig. 33[2]).

Metasoma. Proximal part has a complete ring of setae; metasoma non-segmented, only one tergite visible (Fig. 33[6]).

Distribution. Australia (Girault 1930: 274, 1935: 2; Paretas-Martínez and Pujade-Villar 2006: 224).

Hosts. Unknown.

Key to species

1 Female: unknown. Male: club shape begins at F3; F1 and F2 small and combined, shorter than pedicel and F3, F10 twice as long as other flagellomeres, but not wider, forming a slender club (Fig. 34[1]) .... ***T. giraulti* (Paretas-Martínez & Pujade-Villar, 2006)**

– Club shape begins beyond F3; various size and combination of flagellomeres **2**

2 Head with abundant, long setae on face (Fig. 34[4]); F1 shorter than pedicel but F1+ F2 longer than pedicel; F1–F3 long and subequal. Club shape begins at F4; F9 (F10 in males) forms a small club at the apex of the antenna; in females club dilated, in males club slender ..... ***T. thoreauini* (Girault, 1935)**

– Head with scattered setae on face. F1 shorter than pedicel and F1+F2 shorter than pedicel. F1–F3 very short and sometimes subequal. Club shape begin beyond F4 .... **3**

3 Female: F2 shorter than F1 and F3; club shape begins at F6. Male: F1–F3 subequal; club shape begins at F4 (Fig. 34[2]) .... ***T. mascagnini* (Girault, 1935)**

– Female: F1–F3 subequal; club shape begins at F8 (Fig. 34[3]). Male: unknown .... ***T. nativa* (Girault, 1930)**

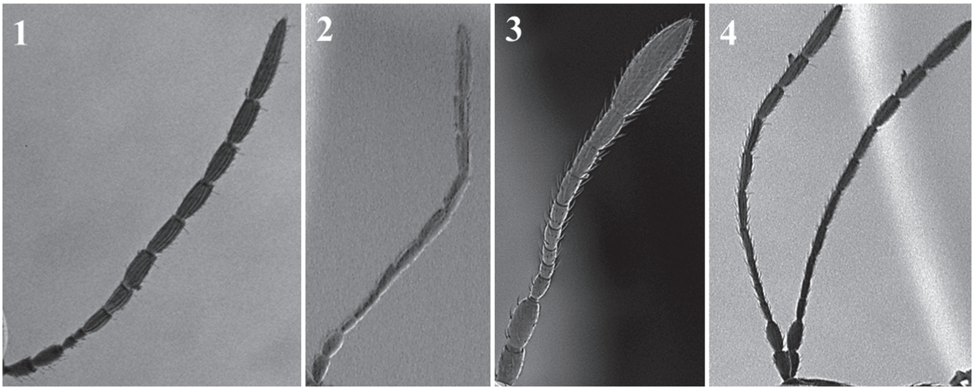

Figure 34. *Thoreauana* antennae. *T. giraulti* (**1**); *T. mascagnini* (**2**); *T. nativa* (**3**); *T. thoreauini* (**4**).

Acknowledgements

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RESEARCH ARTICLE

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Revision of the ant-eating spider genus *Mallinus* Simon, 1893 (Araneae, Zodariidae)

Charles R. Haddad[1], Arnaud Henrard[2,3], Rudy Jocqué[2]

1 *Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa* **2** *Department of Zoology, Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium* **3** *Earth and life Institute, Biodiversity Research Center, Université catholique de Louvain, B-1348, Louvain-la-Neuve, Belgium*

Corresponding author: *Charles R. Haddad* (haddadcr@ufs.ac.za)

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Abstract

The zodariine spider genus *Mallinus* Simon, 1893 is redescribed and diagnosed. The type species, *M. nitidiventris* Simon, 1893 from South Africa, was originally described from subadult specimens. Adults of both sexes of *M. nitidiventris* are described for the first time, based on recently collected material, and the genus is rediagnosed, redescribed, and its relationships discussed. A single aberrant male specimen from Namibia is here described as a morphospecies, as it is presumed to only be superficially related. A second species, *M. defectus* Strand, 1906 from Tunisia, is considered a '*species inquirenda*', as the type specimens could not be traced, but this species is in any case unlikely to be congeneric. The genus is one of 10 cases of a monotypic genus in the Zodariidae. Notes are provided on the biology of *M. nitidiventris*.

Keywords

Arid, endemic, myrmecophagous, Nama Karoo, South Africa, Zodariinae

Introduction

The Zodariidae is a medium-sized family of spiders, with 1140 species in 85 genera globally (World Spider Catalog 2018). The subfamily Zodariinae is of particular interest from a biological perspective, as most of the species are exclusively myrmecophagous (Cushing 2012, Pekár et al. 2012, Pekár and Toft 2015, Komatsu 2016), which reflects its derived phylogenetic position in the family (Jocqué 1991).

The genus *Mallinus* Simon, 1893 remains one of the most poorly understood genera of Zodariinae. Initially described from a single South African locality, the type species (*M. nitidiventris* Simon, 1893) has never been properly redescribed, as the type series consists of a subadult male and subadult female (Jocqué 1991), not adult specimens as indicated by Simon (1893). A second species, *M. defectus* Strand, 1906, was described from Tunisia (Strand 1906) in the Palaearctic Region, but it was doubtfully placed in *Mallinus* originally, and as explained in the discussion it is unlikely to belong to this genus. Simon (1893) placed *Mallinus* in his "Zodarieae" together with *Zodarion* Walckenaer, 1826 and *Diores* Simon, 1893, although the concept of this subfamily has expanded significantly since then through a series of revisions led by the third author (Jocqué 1991; World Spider Catalog 2018).

The recent collection of adult specimens in South Africa fitting Jocqué's (1991) illustrations of *M. nitidiventris* served as the impetus to redescribe the type species and assess whether other congeneric species may occur in Africa. Examination of museum collections yielded several additional records of *M. nitidiventris*, indicating a surprisingly broad distribution of the species in the arid Nama Karoo Biome of South Africa, but also extending into the Succulent Karoo and the arid parts of the Savanna Biome. A revised diagnosis and description, aided by scanning electron micrographs, are provided to recognize *Mallinus* from other Zodariinae spiders.

A single male from northern Namibia is here described as "*Mallinus*" sp. Although the shape and the texture of the cephalothorax and the abdomen are similar to that of *M. nitidiventris,* we suppose that it belongs to a different genus, mainly due to the absence of a conductor on the male palp and the extremely unusual eye pattern: the AME are much larger than the remainder and the ALE are very wide apart, situated in the far lateral corners of the clypeus. However, we have refrained from describing a new genus on the base of a single male, and await further material to place it.

Materials and methods

The specimens examined in the current study were preserved in 70% ethanol and examined using a Nikon SMZ800 stereomicroscope for measurements and descriptions. The female genitalia and male palps were drawn with a WILD M10 stereomicroscope (Leica). The female genitalia were then dissected and digested using half a tablet of Total Care Enzima product (protein removal system originally for cleaning contact lenses and containing subtilisin A-0.4 mg per tablet; Abbott Medical Optics, Santa Ana, CA) in a few millilitres of distilled water overnight, and then immersed in 75% ethanol. These female genitalia and male palps were photographed with a Leica MZ16 using the Leica Application Suite (LAS) automontage software (ver. 3.8; Leica, https://leicacamera.com).

All measurements are given in millimetres (mm). Measurements of somatic morphological structures were taken from one specimen of each sex, as indicated, while total length measurements were taken for all available specimens to determine size variation. Leg lengths are presented as the sequence from femur to tarsus, and total. Digital photographs of the dorsal and lateral habitus of both sexes of *M. nitidiventris* were taken with a Nikon D5-L3 camera system attached to a Nikon SMZ800 stereomicroscope. To increase depth of field, a series of images was taken and stacked using the CombineZM imaging software (http://www.hadleyweb.pwp.blueyonder.co.uk).

Material for scanning electron microscopy (SEM) was freshly collected from the farm Bankfontein in the western Free State, South Africa (see Material examined) and immediately preserved in 100% ethanol (see below). Prior to SEM, material was transferred to fresh 100% ethanol overnight, critical point dried in an argon chamber, glued to aluminium stubs using double-sided tape, and sputter coated with gold. Somatic and genitalic structures were examined in a JEOL JSM-7800F FE-SEM at 3 kV and digital photographs were taken.

The following abbreviations are used in the descriptions: **AER** – anterior eye row; **AH** – abdomen height; **AL** – abdomen length; **ALE** – anterior lateral eye; **ALS** – anterior lateral spinneret; **AME** – anterior median eye; **AW** – abdomen width; **CL** – carapace length; **CW** – carapace width; **F** – femur; **FL** – fovea length; **imm.** – immature; **MA** – median apophysis; **MOQ** – median ocular quadrangle; **MOQAW** – median ocular quadrangle anterior width; **MOQL** – median ocular quadrangle length; **MOQPW** – median ocular quadrangle posterior width; **PER** – posterior eye row; **PERW** – posterior eye row width; **PLE** – posterior lateral eye; **PLS** – posterior lateral spinneret; **PME** – posterior median eye; **PMS** – posterior median spinneret; **RTA** – retrolateral tibial apophysis; **SL** – sternum length; **ST** – spermatheca; **SW** – sternum width; **T** – tibia; **TL** – total length; **v** – ventral.

The examined material was obtained from the Muséum National d'Histoire Naturelle, Paris, France (**MNHN**, Christine Rollard), Royal Museum for Central Africa, Tervuren, Belgium (**MRAC**, Rudy Jocqué), State Museum of Namibia, Windhoek (**SMN**, Eryn Griffin) and the National Collection of Arachnida, ARC – Plant Protection Research, Pretoria, South Africa (**NCA**, Petro Marais).

Taxonomy

Family Zodariidae

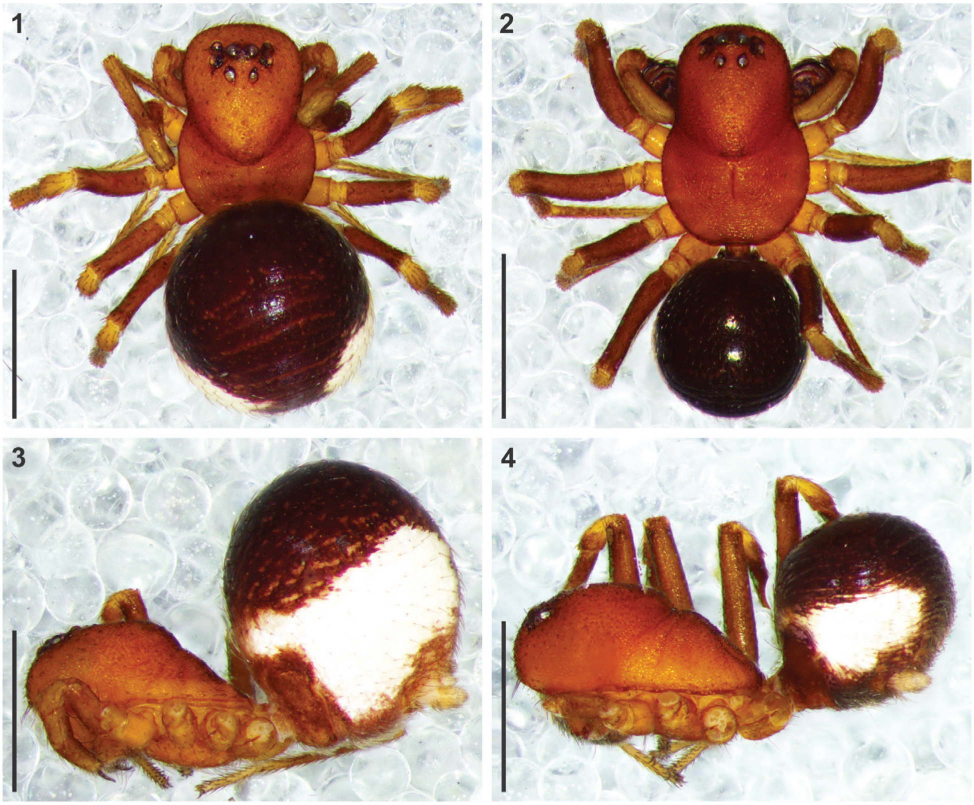
Genus *Mallinus* Simon, 1893

Mallinus Simon, 1893: 436; Jocqué 1991: 136.

Type species. *Mallinus nitidiventris* Simon, 1893, by monotypy.

Diagnosis. *Mallinus* can be distinguished from other zodariine spiders by the relatively smaller size of the anterior median eyes, which are only slightly larger than the lateral and posterior eyes, while generally much larger than the other eyes in other zodariines. *Mallinus* shares with *Palfuria* Simon, 1910 the scale-like extensions on the endites and the considerably raised cephalic region, but lacks the carapace modifications at the posterior end of the cephalic region typical for most *Palfuria* (Szüts and Jocqué 2001); rather, the carapace slopes steeply at the posterior end of the cephalic region, with only a shallow transverse depression. *Mallinus* also have a very globose abdomen, which is usually higher than long in both sexes, a rare condition amongst other zodariines.

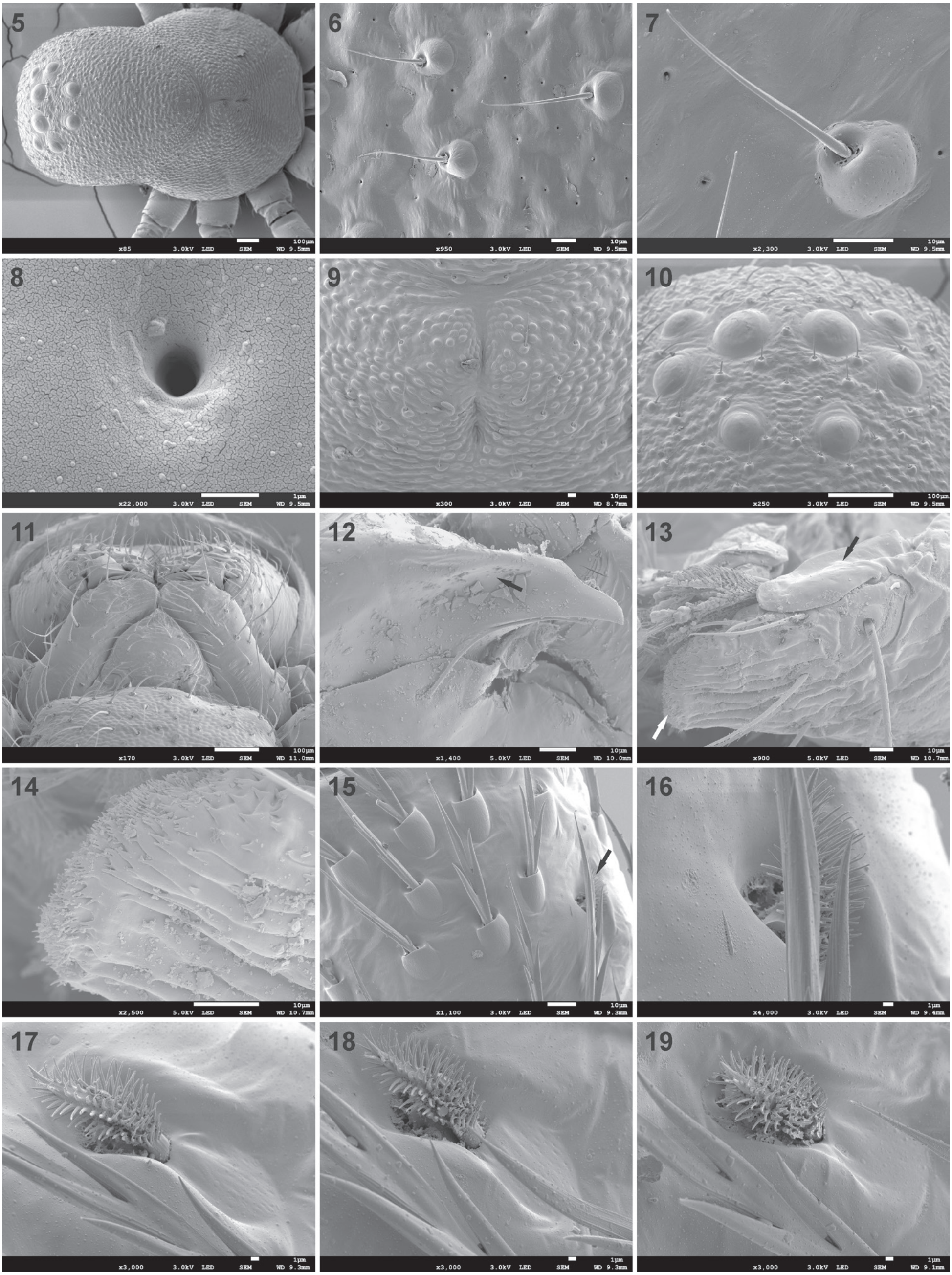
Description. Small spiders, 2.13–2.72 mm in length. Carapace longer than wide, with cephalic region similar in length to thoracic region; cephalic region rounded anteriorly, parallel-sided laterally, thoracic region almost circular, broadest at middle of coxa II (Figs 1, 2, 5); cephalic width about 0.77 times thoracic width in males and 0.88 times maximum width in females (cephalic width measured on posterior tangent of PME); carapace in lateral view with strongly convex clypeus, raised behind PER, highest at coxa I, with steep slope in posterior half (Figs 3, 4); surface deeply granulate, sparsely covered in short straight setae with swollen bases, with scattered small pores (Figs 6–10); fovea slit-like, on posterior slope, at two-thirds carapace length (Figs 2, 5, 9). Eye region reasonably broad, AER procurved, PER strongly procurved (Figs 5, 10), with anterior margin of PME behind posterior margin of PLE; all eyes surrounded by black rings; MOQ width equal anteriorly and posteriorly, slightly longer than wide (Fig. 10). Chilum absent. Chelicerae small, narrowed distally, directed posteroventrally; fangs very short and thick (Fig. 11), with posterior groove that anterior margin of endites fits into (Fig. 12); cheliceral promargin with anteromesal cusp provided with one small tooth; setae scarce, each plastron with two long setae; endites almost parallel-sided, rounded distally, converging at midline in front of labium, apically with scale-like extension (Fig. 13), prolateral edge with field of flattened denticles (Fig. 14); labium subtriangular, broader than long (Fig. 11); sternum shield-shaped, as long as broad (Figs 55, 57), surface deeply granulate, covered in scattered erect setae; pleural bars isolated; precoxal triangles small, distinct; intercoxal sclerites absent between coxae I & II, present between coxae II & III and III & IV. Leg formula 4321 (*contra* 4123 in Jocqué 1991), leg IV clearly longer than others; legs covered in mix of short straight, finely barbed setae and incised setae (Fig. 15); femoral organ present on all legs, with single brush-like, densely barbed seta, lying in faint groove riddled with small pits, similar in structure on all four femora (Figs 16–19); patellae without distinct indentation, with lyriform organ retrolaterally at half their length (Figs 20, 21); metatarsi with dense field of short chemosensory setae dorsally (Figs 22, 23), single distal trichobothrium (Figs 24, 25), scattered longer chemosensory setae and barbed setae; metatarsus stopper present, weakly elevated dorsally (Fig. 25); metatarsi without distinct preening comb, metatarsi II–IV with four longer thicker incised setae distally (Figs 26, 27); tarsi ventrally with paired rows of short needle-like setae; tarsal claws paired, with large teeth on margin facing opposing claw (Figs 28, 29), several trichobothria (Fig. 30), chemosensory setae (Fig. 31), subdistal suture (Fig. 29) and weakly elevated oval tarsal organ (Fig. 32); female palpal tarsus conical, with single large claw with three large teeth, turned inward more than 45° (Fig. 33), palpal patella with lyriform organ retrolaterally (Fig. 34). Abdomen globose, higher than long in females, similar in males, with circumferential folds laterally (Fig. 35) and shiny scutum covering dorsum in both sexes (Figs 1–4); petiole short (Fig. 36); abdominal dorsum with sparse covering of short straight setae with fine brachiae, denser ventrally (Fig. 37); epigastric



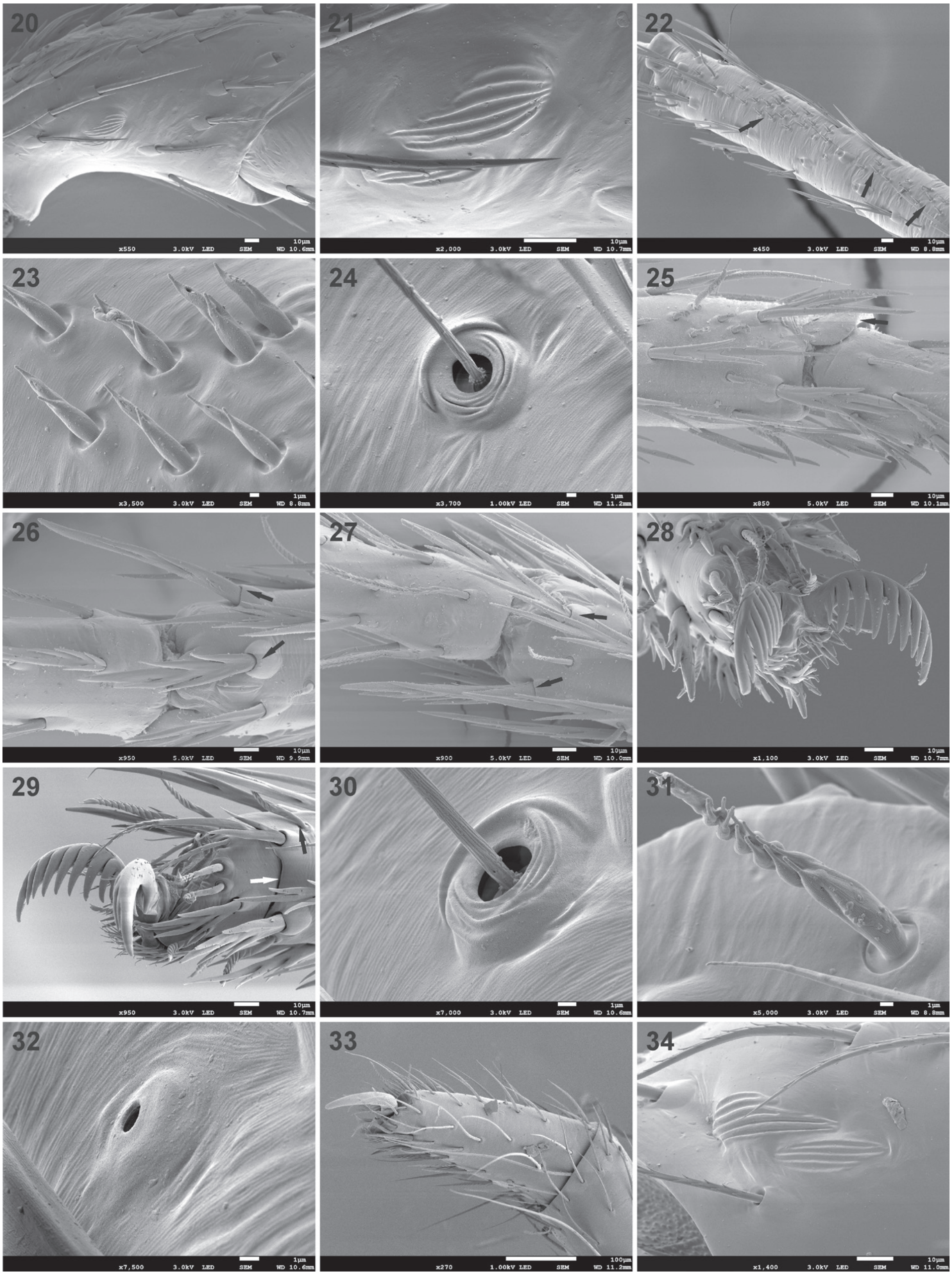
Figures 1–4. Somatic morphology of *Mallinus nitidiventris* female (**1, 3**) and male (**2, 4**) from Bankfontein, Free State (NCA 2015/1818) **1, 2** habitus, dorsal view **3, 4** same, lateral view. Scale bars: 1.0 mm.

region weakly sclerotised; venter only with inframamillary sclerite present, transversely broad, with row of flattened setae (Figs 38, 39). Spinnerets: ALS of females (Figs 38, 40) and males (Figs 41, 42) long, conical, with central major ampullate gland spigot surrounded by several piriform gland spigots; PMS and PLS of females not studied by SEM, absent in males. Epigyne simple, with median lobe and two adjacent lateral lobes posteriorly incorporating copulatory openings (Figs 43, 47, 50); entrance ducts short, directed slightly laterally, entering lateral spermathecae with three spirals (Fig. 51). Male palp with unmodified femur and patella; tibia with single sharp triangular RTA, curved distally, extending approximately one-quarter the cymbium length (Figs 44, 48, 49, 52, 53); tarsus with triangular cymbium (Fig. 44), with baso-retrolateral process, with broad distal claw and single modified toothed seta prolaterally (Figs 45, 46); embolus long, whip-like, originating retrolaterally, curving around proximal and prolateral margins of tegulum, fine at distal end, tip associated with narrow membranous conductor; MA originating medially on tegulum, C-shaped, with swollen base but sharp end (Figs 48, 52).

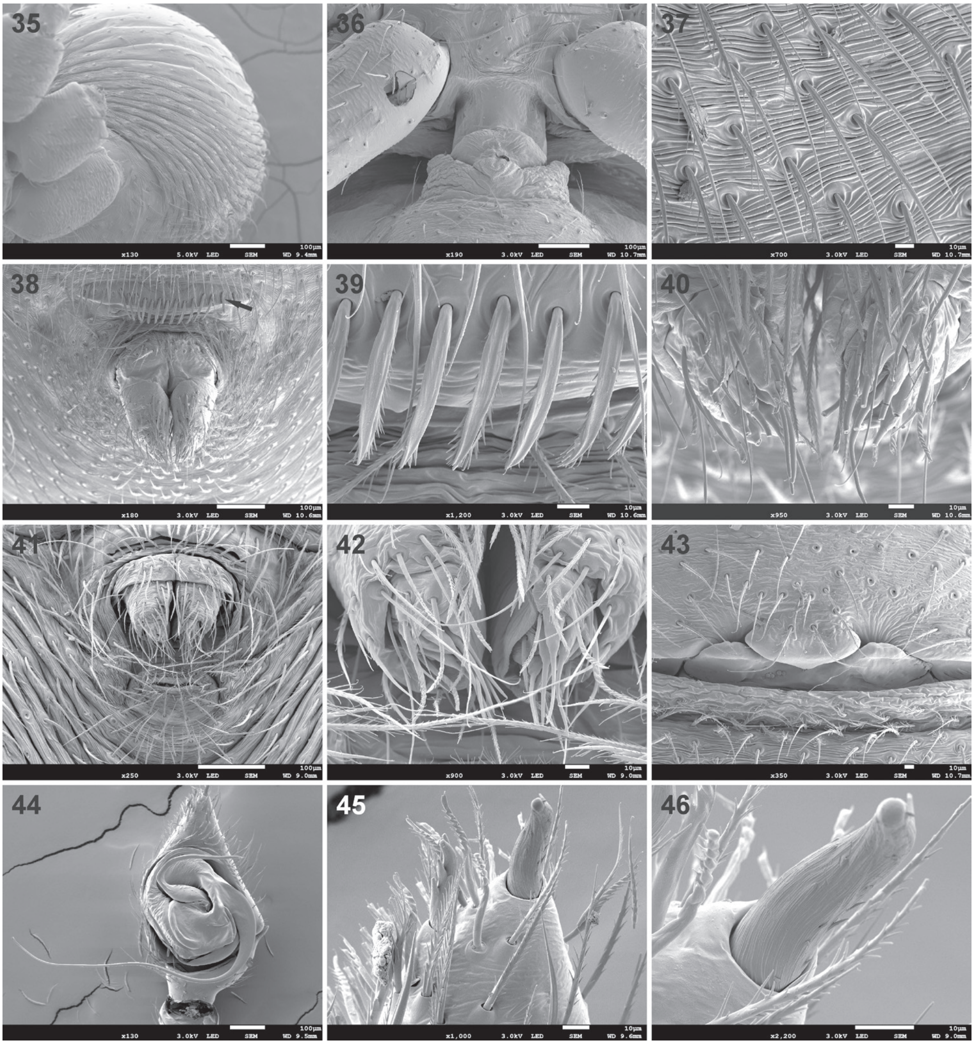
Relationships. In a morphological phylogeny of Zodariidae, Jocqué (1991) placed *Mallinus* in the Zodariinae, as sister group to *Ranops* Jocqué, 1991 + *Zodarion*. However,



Figures 5–19. Scanning electron microscope photographs of *Mallinus nitidiventris* male (**5–10, 12–19**) and female (**11**) **5** carapace, dorsal view **6** detail of carapace integument **7** same, detail of carapace setae **8** same, detail of carapace pore **9** fovea **10** eye region, dorsal view **11** endites, labium and anterior end of sternum **12** distal end of chelicera, arrow indicating posterior groove of fang **13** distal end of endite, black arrow indicating distal endite scale, white arrow indicating prolateral field of flattened denticles **14** prolateral margin of endite, showing detail of flattened denticles **15** femur I, dorsal view, incised setae and femoral organ (black arrow) **16–19** femoral organ on legs I–IV, respectively.



Figures 20–34. Scanning electron microscope photographs of *Mallinus nitidiventris* female (**20, 21, 28, 29, 33, 34**) and male (**22–27, 30–32**) **20** patella IV, retrolateral view **21** same, detail of lyriform organ **22** metatarsus I, incised setae and dorsal fields of short chemosensory setae (black arrows) **23** same, detail of short chemosensory setae **24** metatarsus I, trichobothrium **25** metatarsus III, arrow indicating metatarsal stopper **26** metatarsus III, arrows indicating thickened ventral terminal setae **27** same, metatarsus IV **28** tarsus I, paired claws in distal view **29** same, prolateral distal view, black arrow indicating chemosensory seta, white arrow indicating subdistal suture of tarsus **30** same, trichobothrium **31** same, chemosensory seta **32** same, tarsal organ **33** palpal tarsus and claw **34** palpal patella, lyriform organ.



Figures 35–46. Scanning electron microscope photographs of *Mallinus nitidiventris* male (**35, 41, 42, 44–46**) and female (**36–40, 43**) **35** abdomen, ventrolateral view **36** petiole, ventral view **37** ventral abdominal setae **38, 41** spinnerets, ventral view, arrow in **38** indicating sclerite in front of tracheal spiracle **39** detail of setae on sclerite in front of tracheal spiracle **40, 42** detail of anterior lateral spinnerets **43** epigyne, ventral view **44** palp, ventral view **45** detail of palpal claw and thickened distal prolateral seta **46** detail of palpal claw.

its position would have been clearer had adult specimens been available for study. This lack resulted in a considerable number of missing entries in the character matrix relating to genitalic morphology. Henrard and Jocqué (unpubl.) include a single male *M. nitidiventris* (from Tswalu Kalahari Reserve, MRAC 216253) in their molecular phylogeny of Zodariidae. Their results suggest that *Mallinus* is most closely related to *Palfuria*.

This sister group relationship is also well supported by morphological characters. *Mallinus* shares with *Palfuria* the deeply granulate tegument of the carapace, the strongly raised cephalic region with a steep slope in the posterior half, the scale-like extensions on the endites, the circumferential folds of the abdomen (this character is conspicuous in males and females when the abdomen is not distended), and the subdistal suture on the tarsi. The subdistal suture was also observed in *Akyttara* Jocqué, 1987 and *Heradida* Simon, 1893, to which they are also closely related. In the phylogeny of Henrard and Jocqué (unpubl.), *Ranops* appears to be placed as the sister group of a clade containing *Akyttara*, *Heradida*, *Mallinus* and *Palfuria*, forming a strongly supported monophyletic group. Those zodariines belong to a monophyletic clade characterized by the presence of a unique femoral organ on the legs (Henrard and Jocqué 2017).

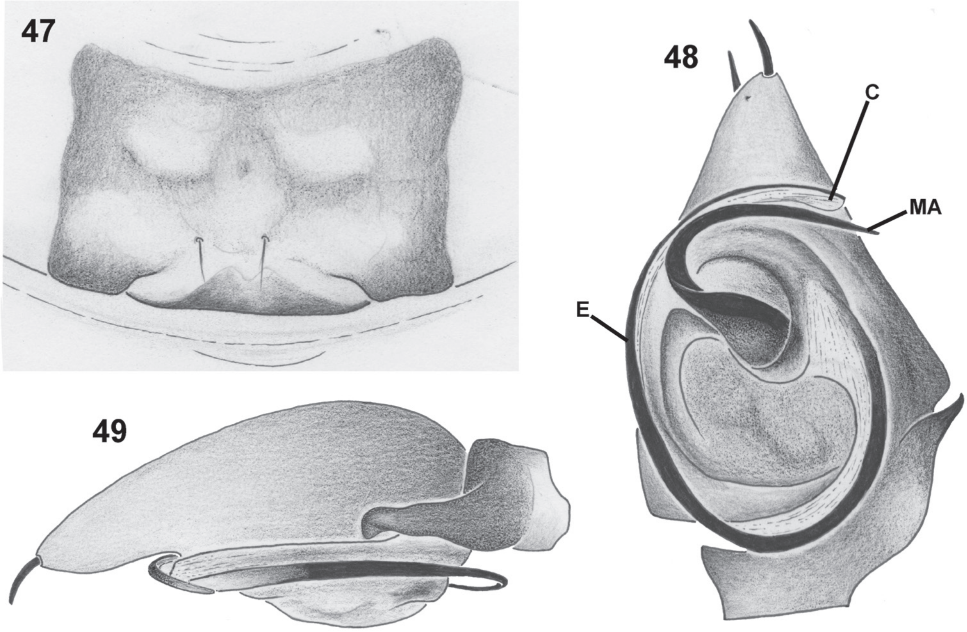
Mallinus nitidiventris Simon, 1893

Figs 1–57

Mallinus nitidiventris Simon, 1893: 436, figs 409–410 (juv.); Jocqué 1991: 136, figs 334–335 (juv.).

Type material. Subadult ♂ lectotype and subadult ♀ paralectotype: SOUTH AFRICA: Western Cape: Matjiesfontein, 33°15'S, 20°40'E, MNHN AR 3280 – examined by Jocqué (1991).

Other material examined. SOUTH AFRICA: *Eastern Cape*: Aberdeen district, Farm Bokvlei, 32°25.8'S, 23°21.0'E, 14.XII.2007, leg. D.H. Jacobs (pitfall traps, karoo), 2♂ (NCA 2008/4662); Aberdeen district, Farm De Pannen, 32°41.4'S, 23°25.8'E, 14.XII.2007, leg. D.H. Jacobs (pitfall traps), 1 imm. 4♂ (NCA 2011/604); Aberdeen district, Farm Juriesfontein, 32°31.8'S, 23°25.8'E, 11.XII.2007, leg. D.H. Jacobs (pitfall traps), 1♂ (NCA 2008/4665); Aberdeen district, Farm Nuwejaarsfontein, 32°57.0'S, 24°23.4'E, 14.XII.2007, leg. D.H. Jacobs (pitfall traps, karoo), 2 imm. 7♂ 1♀ (NCA 2008/2612). *Free State*: Luckhoff district, Farm Bankfontein, 30°04.980'S, 24°54.170'E, 22.I.2015, leg. C. Haddad (base of grass tussocks, wetland margin), 1♂ (NCA 2015/1655); Same locality, 30°04.421'S, 24°53.017'E, 6–8.IV.2015, leg. C. Haddad (hand collecting, Nama Karoo veld), 1♂ 1♀ (NCA 2015/1818), 2♂ 1♀ (S.E.M. preparations); Same locality, 30°04.421'S, 24°53.038'E, 26.III.2017, leg. C. Haddad & R. Booysen (hand collecting, Nama Karoo veld), 3 imm. 5♂ (NCA 2017/1447); Same locality, 30°04.974'S, 24°54.297'E, 2–6.IV.2015, leg. University of the Free State students (pitfall traps, Nama Karoo veld), 1♂ (NCA 2015/2398); Same locality, Research camp, 30°04.421'S, 24°53.013'E, 1185 m a.s.l., 24–26.XI.2015, leg. C. Haddad & R. Booysen (night collecting), 1♂ (NCA 2015/2231). *Northern Cape*: Pofadder, 29°22'S, 19°07'E, 15.X.2006, leg. L. Spangenberg (pitfall traps), 1♀ (MRAC 222264); Tswalu Game Reserve, man-made dam, 27°15'S, 22°27'E, 1176 m a.s.l., 6.II.2005, leg. R. Jocqué (savanna shrubland, by hand), 1♂ (MRAC 216253).



Figures 47–49. *Mallinus nitidiventris*, female (**47**) and male (**48, 49**) genitalic morphology (NCA 2008/2612) **47** epigyne, ventral view **48** palp, retrolateral view **49** same, ventral view. Abbreviations: C–conductor; E–embolus; MA–median apophysis. Scale bars: 0.1 mm.

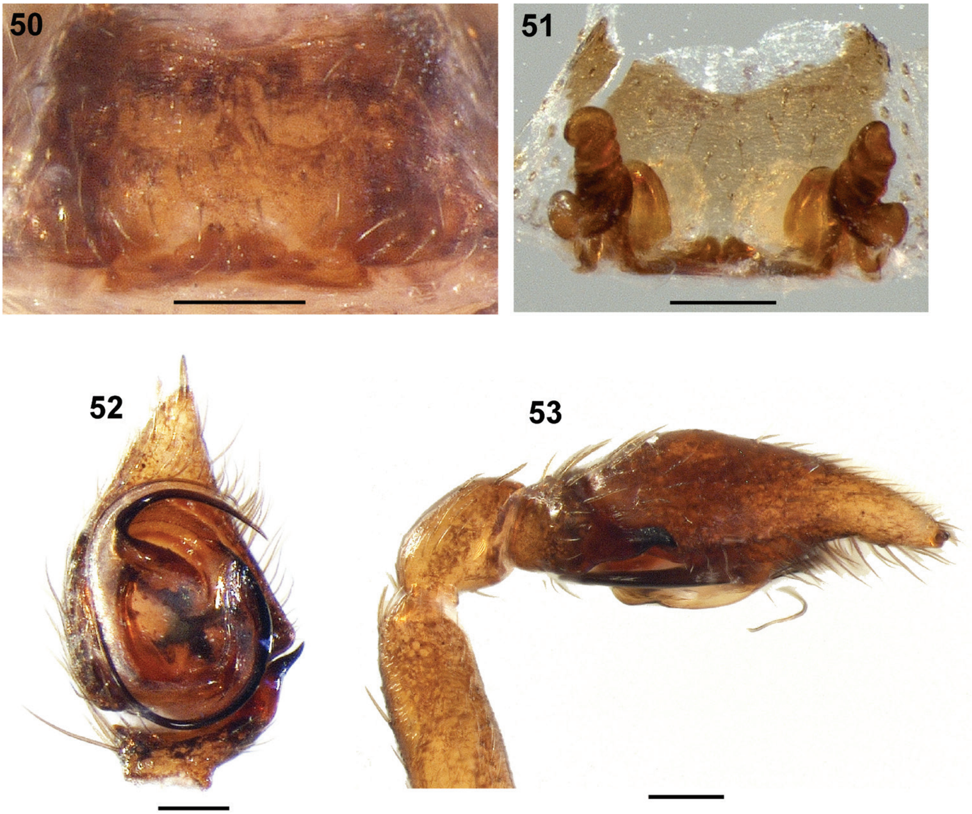
Western Cape: Beaufort West district, Farm Eerste Water, 32°41.4'S, 22°57.6'E, 6.XII.2007, leg. D.H. Jacobs (pitfall traps, karoo), 1 imm. (NCA 2008/2610); Prince Albert, Tierberg, 33°13'S, 22°02'E, 23.IX.1989, leg. R. Dean (old lands), 1♂ (NCA 91/1299), 1♀ (NCA 91/1300).

Unconfirmed record. SOUTH AFRICA: *Northern Cape*: Goepag Nature Reserve, 29°39.906'S, 17°59.838'E, 14–16.VII.2017, leg. R. Booysen, Z. Mbo & R. Christiaan (pitfall traps, Nama Karoo veld), 1 imm. (NCA 2017/1189).

Female (Bankfontein, NCA 2015/1818). Measurements: CL 1.32, CW 0.89, AL 1.39, AW 1.36, AH 1.65, TL 2.60 (2.13–2.70), SL 0.62, SW 0.63, AME–AME 0.06, AME–ALE 0.03, ALE–ALE 0.25, PME–PME 0.09, PME–PLE 0.09, PLE–PLE 0.31, MOQAW 0.21, MOQPW 0.22, MOQL 0.25.

Length of leg segments: I 0.70 + 0.29 + 0.54 + 0.67 + 0.41 = 2.61; II 0.71 + 0.30 + 0.53 + 0.73 + 0.45 = 2.72; III 0.71 + 0.32 + 0.53 + 0.78 + 0.45 = 2.79; IV 0.92 + 0.32 + 0.68 + 1.00 + 0.48 = 3.40.

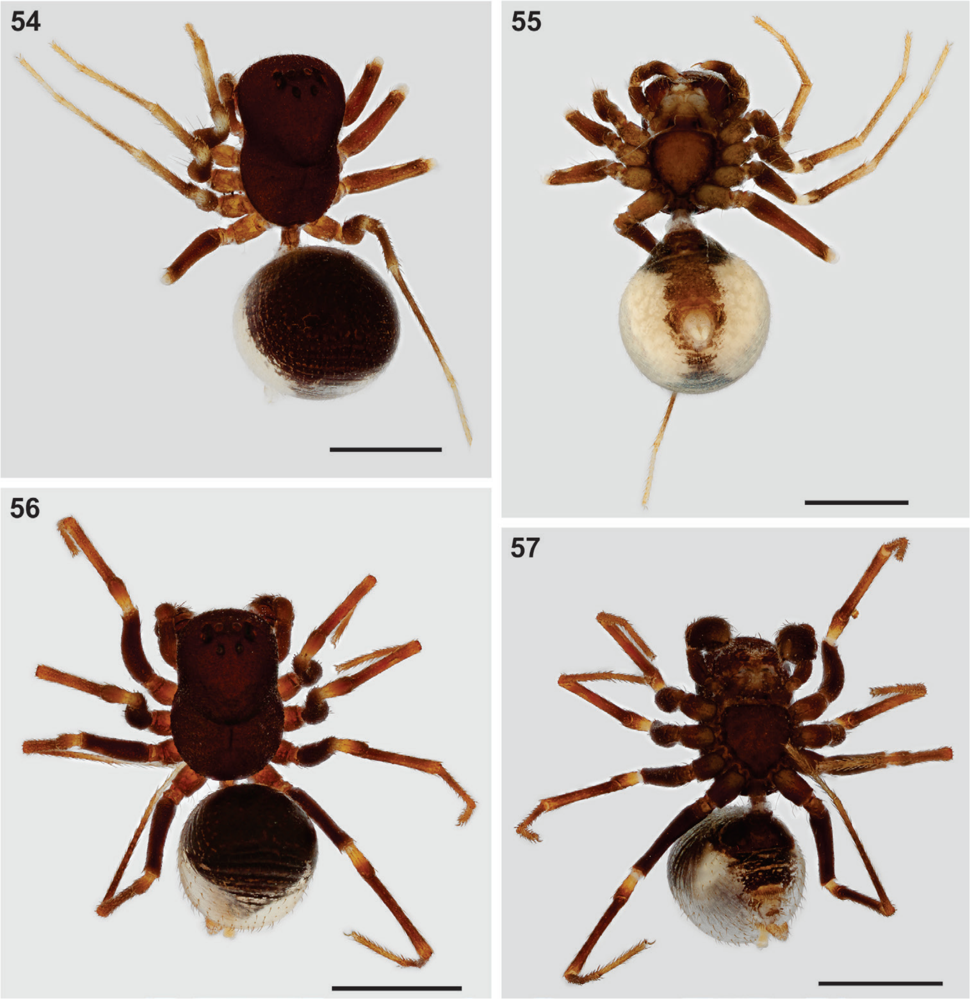
Colour: carapace orange-brown, with faint black mottling and striae (Figs 1, 2); chelicerae orange; endites yellow, slightly darker retrolaterally at midpoint; labium orange, cream distally; sternum orange, cream along anterior margin; leg femora orange-brown; patellae yellow proximally, orange brown distally; tibiae and metatarsi light brown proximally, yellow-brown distally; tarsi yellow; palps yellow-brown; abdomen black dorsally, grey ventrally along midline, with large white patches laterally, fused



Figures 50–53. *Mallinus nitidiventris*, female (**50, 51**) and male (**52, 53**) genitalic morphology (NCA 2008/2612) **50** epigyne, ventral view **51** same, digested, dorsal view **52** palp, ventral view **53** same, retrolateral view. Scale bars: 0.1 mm.

narrowly in ring around anterior of abdomen; spinnerets creamy-yellow. Eyes: AME diameter 1.1 times ALE diameter; AME separated by distance equal to 0.76 times their diameter; AME separated from ALE by 0.4 times AME diameter; clypeus height 4.2 times AME diameter at AME, 4.16 times ALE diameter at ALE; PME and PLE equal in diameter; PME separated by distance equal to 1.15 times their diameter; PME separated from PLE by distance slightly less than 1.21 times PME diameter; CW:PERW = 2.06:1. Legs spineless, covered in short erect setae and incised setae. Abdomen slightly longer than carapace, higher than long or broad, with shiny scutum covering most of dorsum (Figs 1, 2); dorsum sparsely covered in short straight setae, denser on posterior slope and venter. Epigyne as in genus description (Figs 43, 47, 50, 51). Other characters as in genus description.

Male (Bankfontein, NCA 2015/1818). Measurements: CL 1.33, CW 0.88, AL 0.98, AW 0.94, AH 0.98, TL 2.34 (2.23–2.72), SL 0.60, SW 0.59, AME–AME 0.06, AME–ALE 0.03, ALE–ALE 0.25, PME–PME 0.08, PME–PLE 0.08, PLE–PLE 0.29, MOQAW 0.21, MOQPW 0.19, MOQL 0.22.



Figures 54–57. Somatic morphology of *Mallinus nitidiventris* female (**54, 55**) and male (**56, 57**) from Beaufort West, Western Cape (NCA 91/1300 and NCA 2008/2612, respectively) **54, 56** habitus, dorsal view **55, 57** same, ventral view. Scale bars: 1.0 mm.

Length of leg segments: I 0.79 + 0.29 + 0.65 + 0.81 + 0.46 = 3.00; II 0.83 + 0.30 + 0.63 + 0.84 + 0.46 = 3.06; III 0.81 + 0.33 + 0.57 + 0.90 + 0.47 = 3.08; IV 1.03 + 0.33 + 0.75 + 1.15 + 0.53 = 3.79.

Morphology and colouration similar to female (Figs 3, 4), except for the following: AME diameter equals 1.16 times ALE diameter; AME separated by distance 0.67 times their diameter; AME separated from ALE by distance 0.38 times AME diameter; clypeus height 3.85 times AME diameter at AME, 4.0 times ALE diameter at ALE; PME diameter equals 0.89 times PLE diameter; PME separated by distance 1.25 times their diameter; PME separated from PLE by distance 1.25 times PME diameter;

CW:PERW = 2.17:1. Abdomen relatively smaller than female (Figs 3, 4), shorter than carapace, as high as long, slightly longer than broad, with conspicuous circumferential folds. Palp as in genus description (Figs 44, 48, 49, 52, 53).

Variation. Populations from the south-western parts of the species' range (including the type locality) have a clearly darker carapace and legs, which are wine-red in colour (Figs 54–57). It is plausible that populations in this part of its range may associate with a darker species of model ant, affecting their colouration.

Distribution. Widespread in the western half of South Africa, known from the Eastern Cape, Western Cape, Northern Cape and Free State Provinces (Fig. 67).

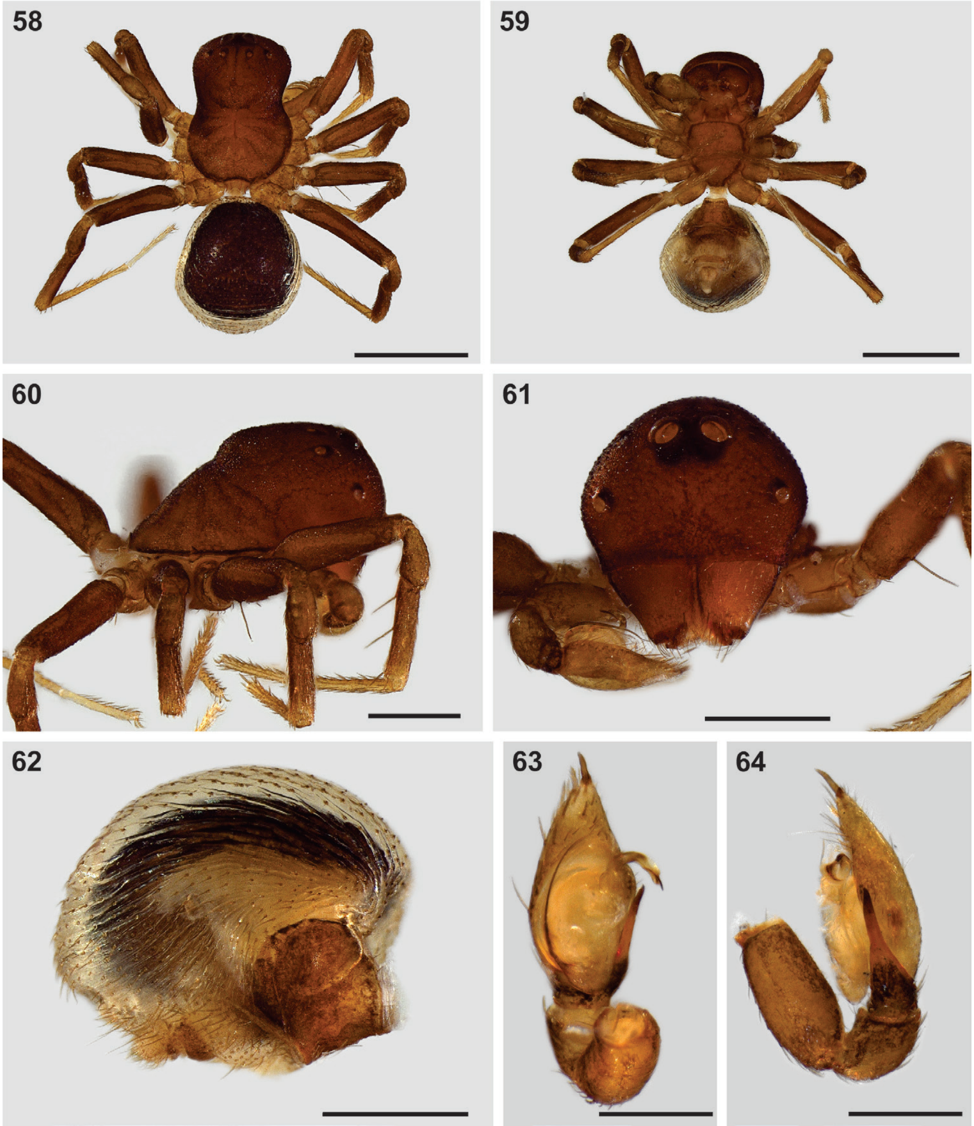
Habitat and biology. *Mallinus nitidiventris* is widespread in the semi-arid and arid western half of South Africa, with records in the Nama Karoo and Succulent Karoo biomes, extending into the arid savannas of the southern Kalahari Desert. Specimens collected at Bankfontein in the western Free State Province were all found in Nama Karoo scrubland, either along a hillside or open plains. The substrate at both sites comprised fine Ecca Shale alluvium, siltstone and sandstone gravels that form part of the Ecca Group of the Karoo Supergroup (A. Odendaal and J. Fourie, pers. comm.). Some of the Bankfontein specimens (NCA 2015/1818) were collected during mid-morning (10:00–12:00) foraging in open ground in the vicinity of various ants, including *Anoplolepis custodiens* F. Smith, 1858, *Camponotus* spp., *Messor* sp. and *Monomorium* sp. Of these, *Mallinus nitidiventris* most closely resembled *Messor* sp. in terms of colouration, although workers of this ant were almost double the body length of the spiders. Only one of these five spiders sampled at this specific site was feeding, a female consuming a *Monomorium* worker ant that measured approximately 2 mm in length, suggesting that this species is myrmecophagous, as are most Zodariinae.

"*Mallinus*" sp.
Figs 58–64

Material examined. NAMIBIA: remote place in north-west Namibia about 50 km from coast, 17°37'S, 12°12'E, 13–16.X.1988, leg. E. Griffin (pitfall traps), 1♂ (SMN 40843).

Remarks. We have included the description of a second species in this paper based on a single poorly preserved male from Namibia without formally naming it, as it shows several clear differences to *M. nitidiventris* that make its generic placement dubious: 1) the lack of a palpal conductor on the palp, and 2) the AME that are much larger than the others, and the ALE that are very wide apart and situated in the far lateral corners of the clypeus. This species most likely represents a new genus, and we hope that its description and illustration here will encourage researchers to find fresh material of both sexes and describe and diagnose this taxon thoroughly.

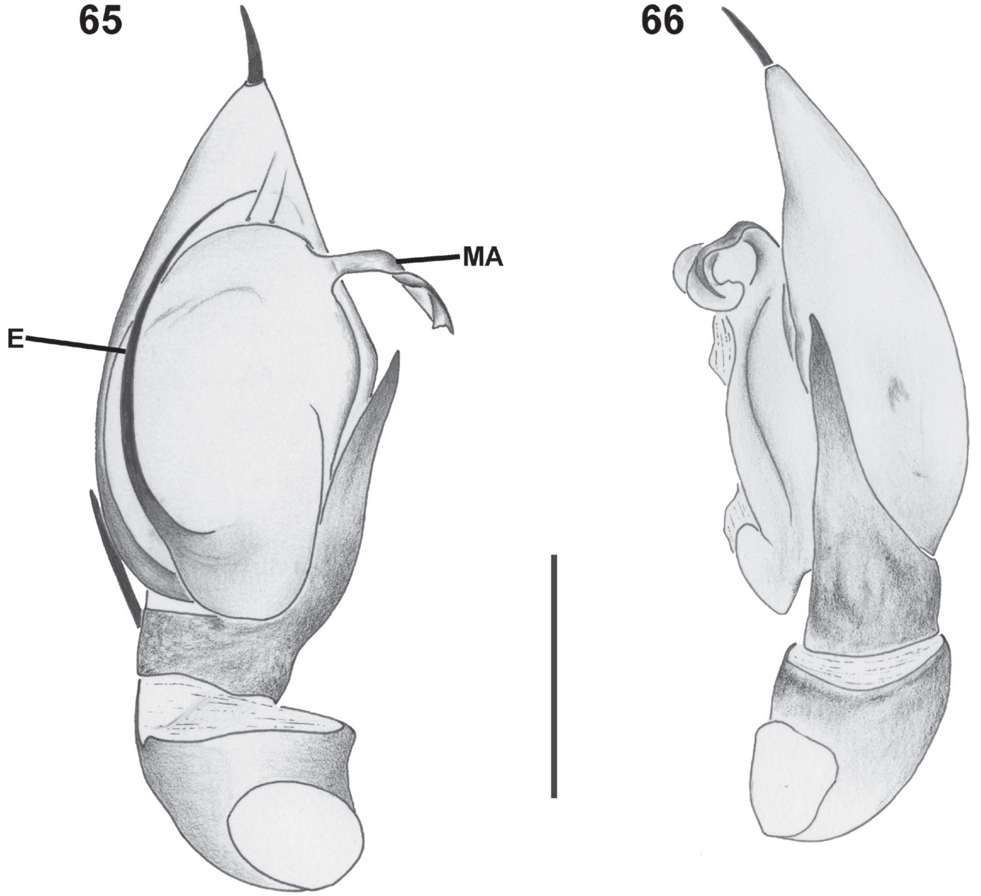
Male (Namibia, SMN 40843). Measurements: CL 1.35, CW 0.92, AL 1.25, AW 1.18, AH 1.12, TL 2.70, SL 0.71, SW 0.64, AME–AME 0.05, AME–ALE 0.25, ALE–ALE 0.69, PME–PME 0.18, PME–PLE 0.13, PLE–PLE 0.53, MOQAW 0.33, MOQPW 0.30, MOQL 0.28.



Figures 58–64. Somatic morphology of "*Mallinus*" sp. male from north-western Namibia (SMN 40843) **58** habitus, dorsal view **59** same, ventral view **60** carapace, lateral view **61** same, anterior view **62** abdomen, lateral view **63** palp, ventral view **64** same, retrolateral view. Scale bars: 1.0 mm (**58, 59**); 0.5 mm (**60–62**); 0.25 mm (**63, 64**).

Length of leg segments: I 0.82 + 0.33 + 0.51 + 0.66 + 0.44 = 2.76; II 0.77 + 0.34 + 0.56 + 0.77 + 0.49 = 2.93; III 0.79 + 0.33 + 0.51 + 0.80 + 0.48 = 2.91; IV 1.00 + 0.36 + 0.74 + 1.15 + 0.54 = 3.79.

Colour: carapace medium brown (Figs 58, 60), with dark area around AME, darker stripe between PME (Fig. 61) and dark radiating striae; chelicerae medium



Figures 65–66. "*Mallinus*" sp., male genitalic morphology (SMN 40843) **65** palp, retrolateral view **66** same, ventral view. Abbreviations: E–embolus; MA–median apophysis. Scale bars: 0.25 mm.

brown; endites and labium pale brown; sternum pale brown, with thin darker margin (Fig. 59); leg femora, patellae and tibiae uniform pale brown; metatarsi and tarsi yellow; abdomen dark sepia dorsally (Fig. 58), pale grey laterally and ventrally, area in front of epigastric furrow yellow; spinnerets creamy-yellow. Carapace: cephalic region very broad, almost as broad as thoracic region (Fig. 58); texture finely granulate, without setae. Eyes: AME largest, diameter 1.9 times ALE diameter; AME separated by distance equal to 0.3 times their diameter; AME separated from ALE by 1.6 times AME diameter; clypeus height 1.9 times AME diameter at AME, 2.9 times ALE diameter at ALE; ALE very far apart, situated in far lateral corners of clypeus (Fig. 61); PME and PLE subequal in diameter; PME separated by distance equal to 3.0 times their diameter; PME separated from PLE by distance slightly less than 2.2 times PME diameter; CW:PERW = 2.06:1. Sternum shield-shaped (Fig. 59), shallowly rebordered along lateral margins, with few scattered short setae. Legs with few spines (spination of

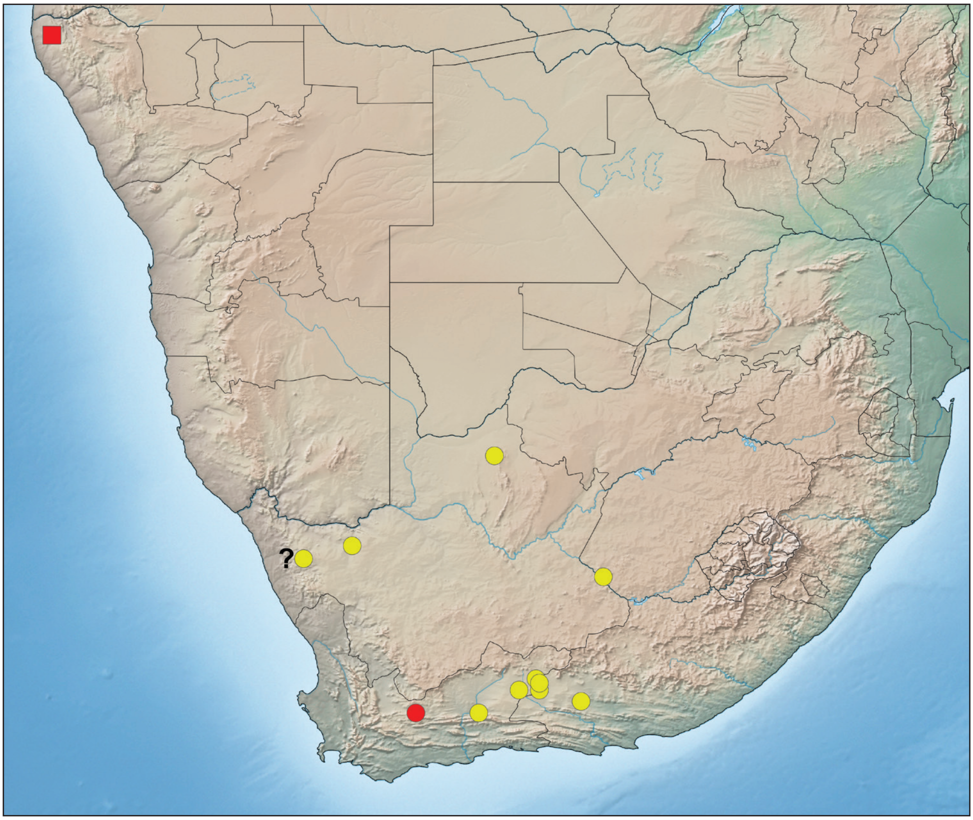


Figure 67. Distribution of *Mallinus nitidiventris* (type locality, red circle; other localities, yellow circles) and "*Mallinus*" sp. (red square) in southern Africa. ? indicates immature specimen requiring confirmation.

specimen probably incomplete: FII v1 III v1; TI v1-1 II v1), with some dispersed short erect setae and incised setae. Abdomen slightly shorter than carapace, almost as high as long or broad, with shiny scutum covering most of dorsum and clear circumferential folds (Fig. 62); dorsum sparsely covered in short straight setae, denser on posterior slope and venter; venter sclerotized in front of epigastric fold, with wide, transverse inframamillary sclerite. Palp with long, straight, strongly tapered, sharp RTA; embolus simple, slightly curved; MA membranous, looping; conductor absent (Figs 63, 64). Other characters as in genus description of *Mallinus*.

Female unknown.

Distribution. Only known from a single locality in north-western Namibia (Fig. 67).

Discussion

Most of the 85 genera in the Zodariidae are known from more than one species or are speciose (e.g. *Mallinella* Strand, 1916 with > 200 species), although 10 genera can be considered monotypic following this revision (World Spider Catalog 2018). *Mallinus*, which is now well defined, appears to be one of the uncommon cases of monotypy. *Mallinus nitidiventris* appears to have a large distribution (Fig. 67), which is also a rare phenomenon in the subfamily Zodariinae. Although it is presently known only from the more arid western half of South Africa, it may possibly also occur in nearby southern Botswana and Namibia. At least for the latter, we could not confirm its occurrence in the country, as the collection of the State Museum in Windhoek, Namibia has no invertebrate curator to currently process specimen loans.

The second species, *Mallinus defectus* Strand, 1906 from Tunisia, was only tentatively attributed to the genus, as Strand (1906) put a question mark behind the genus name: *Mallinus* (?) *defectus*. Considering the predominant distribution patterns of the genera in the Zodariidae, it is most unlikely that the genus occurs both in South and North Africa. It would be the only example of such a distribution. The description of the species by Strand (1906) does not provide a single clue as to the real identity of the genus to which the species belongs. Unfortunately, the type specimens could not be traced, and the species should therefore be considered a '*species inquirenda*'.

The distribution of this monotypic genus thus remains exceptionally large, and it is not clear why it has remained like this.

Acknowledgments

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Supplementary material 1

Table S1. Specimen data of *Mallinus nitidiventris* examined in this study

Authors: Charles R. Haddad, Arnaud Henrard, Rudy Jocqué

Data type: species data

Explanation note: This spreadsheet contains all of the available locality and collecting data of *Mallinus nitidiventris* records included in this study.

Link: https://doi.org/10.3897/zookeys.822.29835.suppl1