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- Introduction
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- Results
- Discussion
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In Focus

The cover picture shows *Xenapates gaullei* (Konow, 1896).

See paper of **Liston, Goergen & Koch** The immature stages and biology of two *Xenapates* species in West Africa (Hymenoptera, Tenthredinidae)

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Abstract & Indexing Information

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Thysanoptera disjunct distribution between western America and the Mediterranean with a new *Psilothrips* species (Thripidae) from Iran

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http://zoobank.org/96E838D7-137A-4109-A9A1-C2864E39F7A1

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Abstract

The genus *Psilothrips* Hood, 1927 is one of several Thysanoptera taxa with a disjunct distribution between the west coast of North America and the Mediterranean. Despite being considered a member of the *Anaphothrips* genus-group, two species of *Psilothrips* have long pronotal posteroangular setae, thus a revised generic diagnosis is provided. One new species, *P. zygophylli* sp.n. is described from Iran, *P. indicus* Bhatti, 1967 is proposed as a new synonym of *P. bimaculatus* (Priesner, 1932), and a key is provided to the five recognized species.

Key Words

Introduction

More than 100 of the 235 genera of the Thysanoptera sub-family Thripinae each include only a single species (ThripsWiki 2014), usually known from a single locality. In contrast, only three genera each include more than 100 species, *Frankliniella* Karny, 1910, *Scirtothrips* Shull, 1909 and *Thrips* Linnaeus, 1758 and each of these genera is found worldwide, and thus equally uninformative about biogeographic relationships. The genus considered in this paper, *Psilothrips* Hood, 1927, is one of the smaller genera. It is of interest because it shows a remarkable disjunct distribution between Western America and Mediterranean countries. Due to incorrect observations based on poorly prepared slide-mounted specimens, and despite a recent critical study (Bhatti and de Borbon 2008), the available literature for *Psilothrips* is confusing and its relationships are not clearly defined.

The objectives of this paper are to clarify the generic diagnosis, to describe a new species from Iran, and to suggest a new synonymy for a species recorded from India and China.

Material and methods

The specimens of new species described in this paper were collected into 95% ethanol, and subsequently mounted onto slides in Canada balsam using a form of the protocol given in ThripsWiki (2014). The photomicrographs (except Fig. 10) were prepared using a Leica DM2500 microscope using D.I.C. illumination and Automontage imaging software, and line drawings were sketched using a drawing tube attachment to Zeiss Standard 20 microscope. The measurements as well as Fig. 10 were obtained using a Motic BA310

microscope with attached camera. Terminology follows zur Strassen (2003) and Hoddle et al. (2014).

The following collection acronyms are used for the institutions cited in this paper:

ANIC   Australian National Insect Collection, Canberra.
BMNH   Natural History Museum, London.
PPSU   Department of Plant Protection, College of Agriculture, Shiraz University, Shiraz.
SMF   Senckenberg Museum, Frankfurt.

The holotype and a male paratype have been deposited in BMNH. Most other specimens listed in this paper are deposited in PPSU, and a few in the ANIC.

Results

Psilothrips Hood, 1927

*Psilothrips* Hood, 1927: 198. Type species *P. pardalotus* Hood, 1927, by monotypy.

Remarks. Members of this genus can be distinguished from other Thripinae by the lack of a comb of microtrichia on the posterior margin of tergite VIII, and the presence of a particularly long pair of setae arising in a unique position on the antecostal ridges of tergites III–VII (Figs 11, 13). Only one other genus shares these two character states, *Apsilothrips* Bhatti & de Borbon, 2008 from western Argentina (Mendoza and Jujuy). The single species placed in that genus could equally well be interpreted as an unusual species of *Psilothrips*, but is weakly distinguished by the presence of small cilia on the anterior margin of the fore wing and complete absence of sternal discal setae. In contrast, other Thripinae taxa in which the median tergal setae are unusually long have these setae arising just posterior to the antecostal ridge; they also usually have a comb on tergite VIII, and cilia present on the anterior margin of the fore wing. A generic definition of *Psilothrips* was provided by O'Neill (1960), but that failed to mention several important character states, including the number of ocellar setae, the presence

of six prominently pigmented facets ventrally on each compound eye, and the presence of a prominent spinula on both the meso and metafurca. The number of ocellar setae is particularly important because of the failure of earlier workers to note the presence of ocellar setae pair I in front of the first ocellus, including O'Neill's failure to illustrate these setae (see her Fig. 1/6). This led Bhatti (1967) to refer to an "additional" pair of anteocellar setae when describing *P. indicus* as a new species. This pair of setae is often very small, and is difficult to see due to the curvature of the head except when a specimen is very well cleared or the head crushed (Figs 1, 2).

Generic diagnosis. Macropterous Thripinae. Antennae 8-segmented (Fig. 9), segment I with no dorso-apical setae, II with no long setae, sense cones on III–IV forked, III–VI with rows of microtrichia. Head transverse, with 3 pairs of ocellar setae, pair III near anterior margins of triangle (Figs 1, 2); maxillary palps 2-segmented; compound eyes with 6 pigmented facets (Fig. 2). Pronotum transverse (Figs 3, 4, 5, 6), weakly sculptured, discal setae small; with 4 pairs of posteromarginal setae, of which one posteroangular pair sometimes longer than other pairs. Meso- and metafurca with spinula. Mesonotal anterior campaniform sensilla absent, median pair of setae distant from posterior margin. Metanotal sculpture irregularly reticulate, median setae arise medially; no campaniform sensilla (Figs 6, 7, 8). Tarsi 2-segmented. Fore wing costa with setae but no cilia (Fig. 10); first vein with 3 widely spaced setae on distal half; second vein with continuous, widely spaced, row of setae; clavus with 4 veinal setae and one discal seta; posterior fringe straight. Tergites with weak transverse reticulation, posterolaterally these lines bear small microtrichia; II–VIII with setae S1 (median pair) elongate (Figs 11, 12, 13), on III–VII arising on antecostal ridge; V–VII with setae S2 unusually elongate, almost as long as S1; tergites without ctenidia, VIII with no posteromarginal comb; tergite IX with one pair of campaniform sensilla (Fig. 12), without discal microtrichia (except *P. priesneri*), X with no median split (Fig. 12); pleurotergites with or without discal setae; sternites III–VII with 3 pairs of marginal setae (lateral pair on VII sometimes absent), discal setae varying in number from zero to eight. Male with sternal pore plates present or absent.

Key to species of *Psilothrips*

1   Pronotum with 1 pair of posteroangular setae as long as, or longer than, width of antennal segment II (Figs 5, 6); pleurotergal discal setae absent 2
–   Pronotum with no elongate setae, posteroangular setae less than 0.5 times as long as width of antennal segment II (Figs 3, 4); pleurotergal discal setae present or absent 3
2   Metanotum posterior third with concentric sculpture lines (Fig. 6); major setae on pronotum setiform; western USA ... .*pardalotus*
–   Metanotum posterior third with equiangular reticulation (Fig. 8); major setae on pronotum longitudinally grooved; Iran... ....*zygophylli* sp.n.
3   Metanotum posterior third with many complex markings within each reticle (Fig. 7); tergite IX anterior third with prominent transverse band of microtrichia (Fig. 12); western USA ....*priesneri*
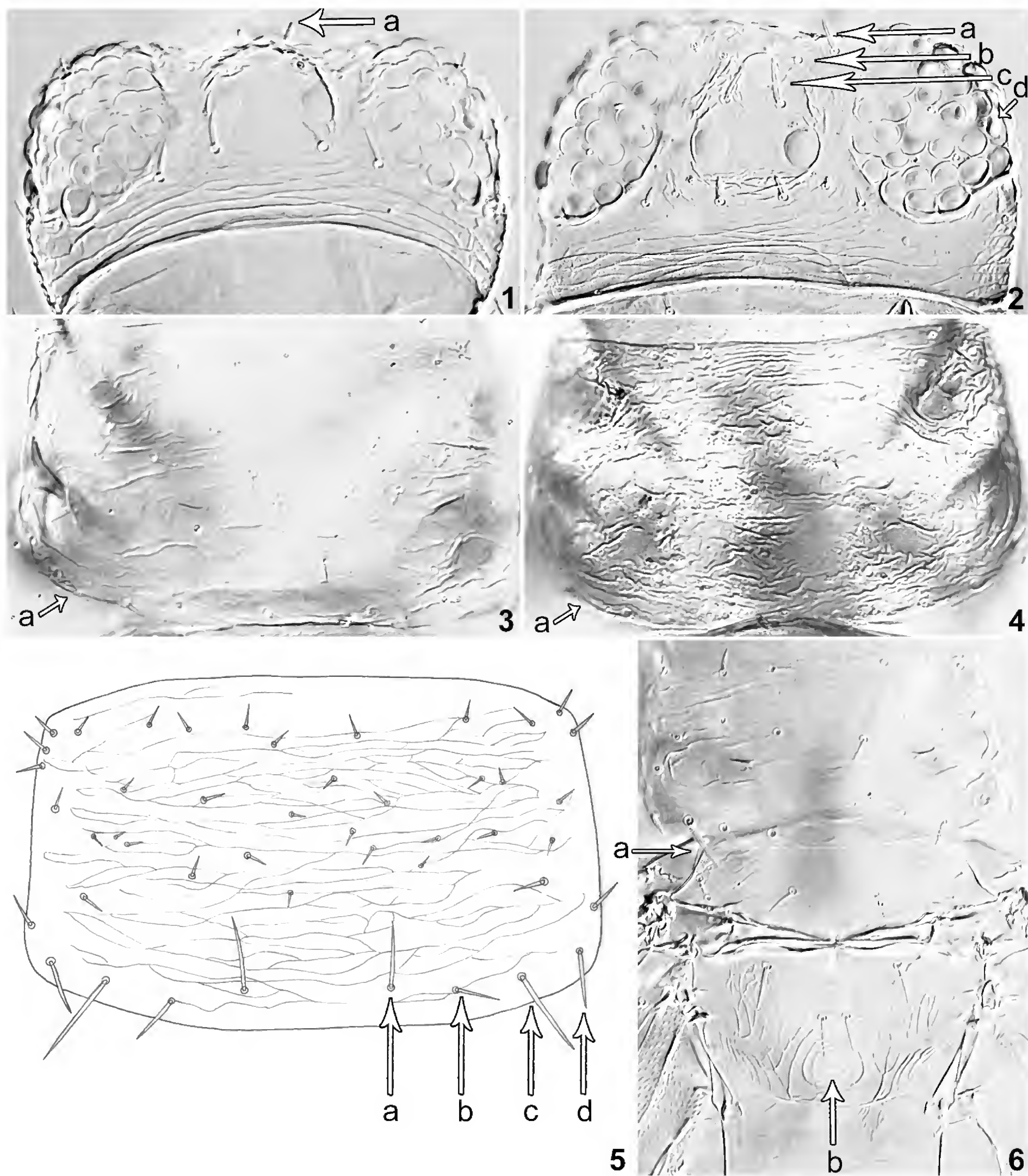
Figures 1–6. *Psilothrips* spp: Head **(1)** *P. pardalotus*; female (a: ocellar setae I) **(2)** *P. zygophylli*; paratype (a, b, c: ocellar setae I-III; d: pigmented facet). Pronotum **(3)** *P. bimaculatus*; female (a: no elongate posteroangular setae) **(4)** *P. priesneri*; female (a: no elongate posteroangular setae) **(5)** *P. zygophylli*; holotype (a: S1, b: S2, c: S3, d: S4). Pro, meso and metanotum **(6)** *P. pardalotus*; female (a: posteroangular setae, b: metanotal sculpture).

– Metanotal reticles with few or no internal markings; tergite IX with no prominent microtrichia 4

4 Head and body uniformly brown (in life with bright red internal pigment); macropterae and micropterae; Canary Islands ....*minutus*

– Head and pronotum yellow with brown areas, tergites II–VII yellow posterolaterally (in life with orange pigment in pterothorax); only macropterae known; Morocco, Egypt, Yemen, Israel, India, China...*bimaculatus*

Psilothrips bimaculatus (Priesner, 1932)

Fig. 3

Thamnothrips bimaculatus Priesner, 1932: 3.
Psilothrips indicus Bhatti, 1967: 12. **Syn.n.**

Remarks. Widespread in southern Mediterranean countries, from Morocco to Israel and Yemen, also in Iran from siris trees (*Albizia* sp., Fabaceae) in Khozestan Province (Alavi and Mohiseni 2002), this species is here interpreted to include records from India and central China. The type specimens of *P. indicus*, three females collected in Delhi on *Ipomoea carnea* (Convolvulaceae), are not available for study but are presumably in the "J.S. Bhatti Private collection" (Bhatti and de Borbon 2008). The proposed new synonymy is based on the original description, together with two females from Ningxia, China, collected from *Lycium halimifolium* (Solanaceae), 20.VII.1980, and identified as *P. indicus* by Han Yun-fa (in BMNH and SMF). These two females have been compared with females from Morocco, Egypt, Israel and Yemen. The colour, as described by Bhatti (1967) is distinctive, with abdominal tergites II–VII sharply paler posterolaterally, and the metanotal equiangular reticulations with few or no internal markings. This species, under the name of *P. indicus*, has been considered a pest on Chinese wolfberry (*Lycium* spp.) in China (Li et al. 2012).

Psilothrips minutus zur Strassen, 1965

Psilothrips minutus zur Strassen, 1965: 27.

Remarks. Known only from the Canary Islands on *Suaeda fruticosa*, this species is unusually dark, and is the only member of the genus for which micropterous individuals are known. None of the available specimens are suitably cleared, but pleurotergal discal setae are not discernable. The tergal antecostal ridge is weaker in this species than among the other members of this genus, and the micropterae have the median tergal setae irregular in size and on some tergites arising posterior to the antecostal ridge.

Psilothrips pardalotus Hood, 1927

Figs 1, 6, 11

Psilothrips pardalotus Hood, 1927: 198.

Remarks. As recognised by O'Neill (1960), the metanotal sculpture of this species is diagnostic (Fig. 6), and the major pronotal posteroangular setae are about 30 μm long. The species is recorded from Arizona, California, Idaho, Nevada, New Mexico, Texas, and Utah, and appears to be associated with *Sarcobatus vermiculatus*. In contrast to *P. priesneri*, the abdominal pleurotergites lack discal setae, and tergite IX lacks discal microtrichia.

Psilothrips priesneri (Moulton, 1926)

Figs 4, 7, 12

Anaphothrips priesneri Moulton, 1926: 123.

Remarks. The metanotal reticulation of this species, with extensive markings inside each reticle as illustrated by O'Neill (1960), is diagnostic for this species (Fig. 7). The pleurotergites bear several discal setae, and tergite IX has a distinctive transverse band of microtrichia (Fig. 12). This species has been recorded in western USA from Arizona, California, and Texas.

Psilothrips zygophylli sp. n.

http://zoobank.org/203380BE-3F22-4BF2-83C0-073E8EFF8D23
Figs 2, 5, 8, 9, 10, 13

Female macroptera. Body yellow to light brown, antennal segments I, III and IV pale, remaining segments shaded; head and pronotum with posterior margins weakly shaded; pterothorax light brown medially, including metascutellum; abdominal tergites I–VIII yellow laterally but with light brown patch medially; fore wings weakly shaded.

With the character states in the generic diagnosis; antennal segments slender (Fig. 9) with reduced microtrichia. Head weakly reticulate in basal third, ocellar setae III on anterior margins of ocellar triangle (Fig. 2).

Pronotum with irregular transverse sculpture lines; 4 pairs of posteromarginal setae, S1 and S3 longer than S2 and S4 (Fig. 5). Metanotum with equiangular reticulation on posterior half, median setae often asymmetric in position (Fig. 8). Fore wing relatively broad; first vein with two setae distally, second vein with about 11 setae (Fig. 10); apex with small sub-apical lobe bearing many long microtrichia ventrally. Abdominal tergites with transverse reticulation medially (Fig. 13), setae S2 slightly shorter than setae S1; tergites IV–VI with striate sculpture laterally bearing a few short microtrichia; sternites III–VII with about eight discal setae.

Measurements (holotype female; measurements in micrometer). Table 1.

Male macroptera. Similar to female but paler. Tergite IX without any processes or stout setae; sternites apparently without pore plates.

Table 1. Measurements of various parts of holotype female and paratype male in micometer.

Feature	Female	Male
Body distended length	1440	800
Head length (width)	124 (212)	82 (140)
Pronotum length (width)	133 (240)	93 (142)
Posteroangular setae	36	24
Fore wing length (median width)	1048 (115)	567 (50)
Tergite II S1 setae	48	-
Ovipositor length	240	-
Antennal segments III–VIII length	46, 43, 40, 56, 18, 21	36, 35, 34, 42, 15, 19
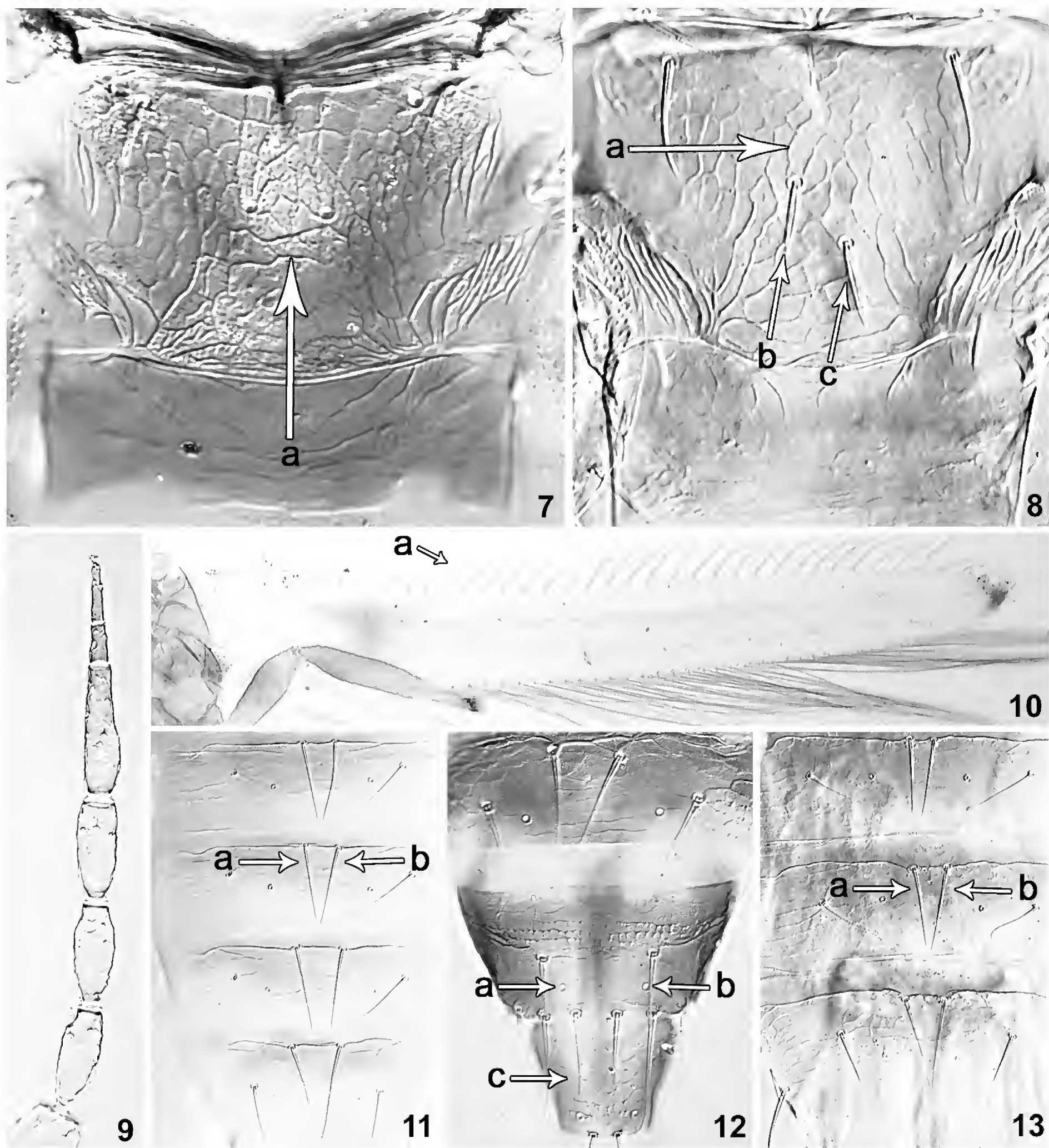
Figures 7–13. Metanotum **(7)** *P. priesneri*; female (a: metanotal sculpture) **(8)** *P. zygophylli*; paratype (a: metanotal sculpture; b, c: median setae). Antenna (segments II–VIII) **(9)** *P. zygophylli*; paratype. Forewing **(10)** *P. zygophylli*; paratype (a: setae). Abdominal tergites **(11)** *P. pardalotus* (V–VIII); female (a, b: median tergal setae) **(12)** *P. priesneri* (VIII–X); female (a, b: campaniform sensilla; c: tergite X without split) **(13)** *P. zygophylli* (VI–VIII); paratype (a, b: median tergal setae).

Measurements (paratype male; measurements in micrometer). Table 1.

Specimens examined (slide-mounted). Holotype female, **IRAN**, **Fars Province**, Sarvestan, 100 km west of Shiraz, from leaves of *Zygophyllum* sp. (Zygophyllaceae), 17.IV.2014 (KM 1151) (in BMNH).

Paratypes: 7 females, taken with the holotype; 17 females, 6 males, 4 larvae, **IRAN**, **Fars Province**, Sarves-

tan, from leaves of *Zygophyllum* sp., 9.V.2014 (KM 1185) (in PPSU), 2 females, 1 male, 1 larva, **IRAN**, **Fars Province**, Sarvestan, from leaves of *Zygophyllum* sp. (in ANIC).

Etymology. This species is named after the genus of plant from which it was collected.

Comments. This new species shares many character states with the North American species *P. pardalotus*.

It differs in the form of the metanotal sculpture, longer major setae on the head and pronotum which are more prominently longitudinally grooved, shorter setae S2 on the abdominal tergites, and more slender antennae.

Discussion

Disjunct distribution in Thysanoptera

This paper considers the interesting zoogeographical distribution of the five species now recognised in the Thripinae genus *Psilothrips*. Two of the species are from the drier areas of western North America, whereas three are from similar low rainfall areas across North Africa and Asia. Among Thysanoptera, a similar distribution pattern is found in the genus *Orothrips* Moulton, 1907 of the family Aeolothripidae, with three species from western North America and one from the Mediterranean region (Marullo and Mound 1993), and at genus level in the family Stenurothripidae that comprises two monobasic genera in western USA and one small genus in the Mediterranean region (Mound 1983, Mound and Marullo 1999). Similarly the genus *Ankothrips* Crawford, 1909 in the family Melanthripidae shows remarkable disjunction, with seven species from western North America, one from Namibia in south-west Africa, and five from the western Palaearctic including one recently described from Iran (Minaei et al. 2012). Regardless of any possible historical component involved in such disjunctions, for *Psilothrips* the distribution is probably related to ecological conditions and the available flora. Available records of plants from which *Psilothrips* adults have been collected include many that are typical of semi-arid areas: *Amaranthus* (Amaranthaceae), *Allenrolfea*, *Atriplex*, *Sarcobatus* and *Suaeda* (Chenopodiaceae), *Calotropis* (Asclepiadaceae), *Lycium* (Solanaceae), and *Nitraria* and *Zygophyllum* (Zygophyllaceae).

Pronotal setal lengths and Thysanoptera systematic relationships

The new species described above emphasizes one of the problems involved in assessing systematic relationships among Thysanoptera. *Psilothrips* is presumed to be a member of the *Anaphothrips* group of genera, in which species do not bear any long setae on the pronotum (Bhatti 1978, Mound and Masumoto 2009). Certainly three of the species are essentially "anaphothripoid", but two have prominent posteroangular setae on the pronotum and, if considered in isolation, might well be considered unrelated. Although setal lengths have traditionally been considered important in assessing relationships among the taxa within several families, there is increasing evidence that reduction in setal length (i.e. loss of long setae) occurred convergently in widely unrelated genera (Mound and Palmer 1981, Pereyra and Mound 2009, Minaei et al. 2012). In contrast, it appears that within *Psilothrips* one

or more reversions from an *Anaphothrips*-like condition to long pronotal posteroangular setae have taken place.

Acknowledgements

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The immature stages and biology of two *Xenapates* species in West Africa (Hymenoptera, Tenthredinidae)

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http://zoobank.org/487EDA35-E3B2-4044-A15C-BE663CE1F173

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Abstract

The immature stages and host plants of *Xenapates* Kirby, 1882 were hitherto unknown. We describe the larvae, prepupae and pupae of *X. braunsi* (Konow, 1896) and *X. gaullei* (Konow, 1896), and record observations on aspects of their biology. The relationship of *Xenapates* to other taxa currently placed in the Allantinae and Blennocampinae of the Tenthredinidae remains unclear. Most larval characters of *Xenapates* resemble those described for West Palaearctic Allantini (Allantinae) and some Blennocampinae, but unique amongst exophytic larvae of Tenthredinoidea is the complete absence of cuticular appendages on the dorsum of the trunk in the two *Xenapates* species studied. The setose outer surface of the abdominal prolegs of *Xenapates*, and the presence of a mesal ridge only on the left mandible, are character states that have not so far been recorded in other genera currently placed in the Allantinae or Blennocampinae. Larval host plants of *X. braunsi* are *Digitaria horizontalis*, *Pennisetum purpureum*, *Setaria barbata* and *Zea mays* (all Poaceae). *X. gaullei* larvae feed on two *Commelina* species (Commelinaceae). Larvae of both species are easy bleeders.

Introduction

Xenapates Kirby, 1882 contains forty-seven described species that are currently considered to be valid (Taeger et al. 2010, Koch 2012a, b) and is thus one of the largest genera of Tenthredinidae in the Afrotropical Region, to which it is confined. It has been placed by most recent specialists in the subfamily Allantinae. Benson (1938) erected the tribe Xenapateini for *Xenapates* and some similar Oriental taxa, based solely on characters of wing venation that have since proved to be of limited value in the taxonomy of Blennocampinae and Allantinae (Koch and Liston 2012). Koch (1996) redefined the Xenapateini using characters of the adult mouthparts. As applies to many Afrotropical sawflies (Koch 2005), nothing was known about the larvae of *Xenapates* or their host plants. Here, we document observations on the immature stages of *X. braunsi* (Konow, 1896) and *X. gaullei* (Konow,

1896). Both species have extensive ranges in western and central parts of the Afrotropical Region, where their adults are the most frequently encountered *Xenapates* and can be locally abundant. *X. braunsi* was placed by Koch (1995) in the *africanus* species group, and *X. gaullei* in the *variator* group.

Material and methods

By chance, *Xenapates braunsi* and *X. gaullei* were found to occur in the vegetation of fallow areas on the campus of the International Institute of Tropical Agriculture (IITA), near Cotonou, Republic of Benin, 6.44°N 2.33°E. All specimens were collected or reared, and field observations made there, by Georg Goergen (hereafter abbreviated to GG), between June 2011 and August 2014. Larvae of *X. gaullei* were first detected
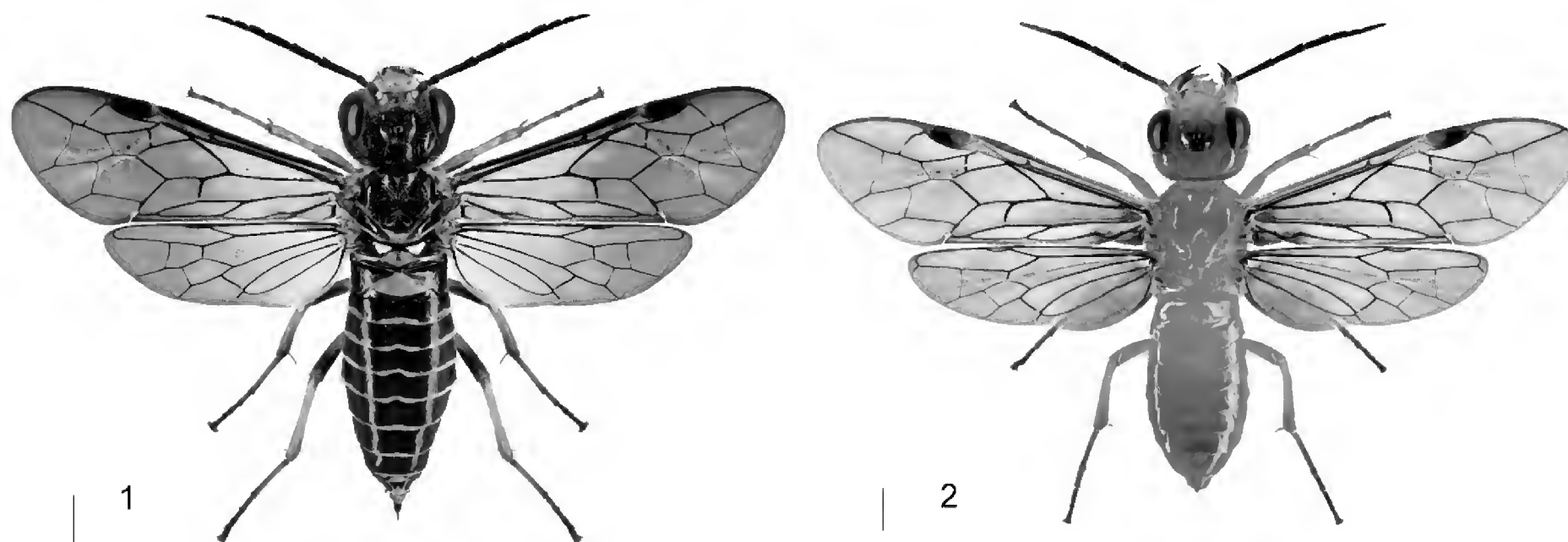
Figures 1–2. *Xenapates* adult females, reared from larvae: **1.** *X. braunsi.* **2.** *X. gaullei.* Scale bars = 1 mm.

by close examination of *Commelina communis* plants, growing near to where adults had been observed courting. Further searching led to the discovery of a few larvae of *X. braunsi*, feeding on adjacent plants of *Setaria barbata*. The first attempts to rear larvae in the laboratory, using rearing cages, ended with the death of all larvae after only a few days. After several failed attempts, larvae of both species were reared (Table 1) to the adult stage on their respective potted host plants by enclosing them under netting supported by wire frames, and placing the pots in the open air at the corner of a building, under an approximately 80 cm wide roof overhang, in a position mostly shaded from direct sunlight. Conditions during rearing were thus close to ambient climatic conditions, i.e. at near to the locally recorded values for mean annual temperature of 27.4°C (mean minima 24.3°C; mean maxima 30.1°C) and mean annual relative humidity of 80.5%. Further, the size of pot used was increased to 35 cm diameter and 10 cm depth in response to complete mortality caused by nematodes, of prepupae reared on hosts planted in smaller pots. The amount of sand in the soil mixture was simultaneously increased, to provide better drainage. Before use, the sand was spread in a thin layer and baked in the sun for several days, to make it more sterile. These modifications led to greatly improved survival during rearing. After the first successful rearing, larval development of each species was studied separately, by introducing adults of both sexes to cages containing potted host plants, in which they laid eggs. *Setaria barbata* was usually offered as a host to *X. braunsi*, but a few larvae collected on *Zea mays* in the field were allowed to complete their development on the same host in captivity. *Commelina communis* was offered to *X. gaullei*. Adults were provided throughout with 50% honey solution. The pupal stage proved particularly challenging to observe, because of its short duration. Some cocoons were extracted from the soil in the rearing pots and an aperture was cut in the wall of each cocoon. They were kept in dark, ventilated containers next to

the rearing pots and checked every week for up to six months (November–April). Determination of the sawfly species by Frank Koch is based on reared adults (Figs 1, 2). AC Tehou and PO Agbani (National Herbarium of Benin, Abomey-Calavi University, Benin) determined the host plants, or confirmed the initial identifications by GG.

Habitus images were taken by GG of living or freshly prepared adults and various immature stages, with a Q Imaging Micropublisher 5.0 RTV digital camera mounted on a Leica Wild M10 binocular microscope. Stacks of photographs were processed using Auto-Montage Pro (version 5.03) software (Syncroscopy) to produce composite images, then enhanced using Adobe Photoshop CS5 software. Specimens of larvae, prepupae and pupae were preserved in ethanol and deposited together with dry mounted adults in the collections of the Biodiversity Centre (IITA, Calavi, Benin) and the Museum für Naturkunde (Berlin, Germany).

Larvae preserved in ethanol were subsequently studied by Andrew Liston. Vouchers are deposited in the Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany).

It was not possible to establish to which instars these belonged. *Xenapates braunsi* material comprised four larvae of probably at least two instars, based on their head capsule widths: 1.2, 1.5–1.7 mm). *X. gaullei* was represented by twelve larvae, probably of at least three instars: head capsule widths 0.5–0.8, 1.2, 1.7, 2.1 mm. Some body parts were photographed with a Leica DFC295 camera through an Olympus SZX12 microscope. Composite images with an extended depth of field were created from stacks of images using the software CombineZ5.3, and finally arranged and partly enhanced with Ulead PhotoImpact X3.

Morphological terminology follows Viitasaari (2002). Setal counts are for the whole of the body part referred to. Note that Lorenz and Kraus (1957) give setal counts only for one half of the body, or for half of a bilaterally symmetrical organ.

Results

Descriptions of larvae

Descriptions are based mainly on the final feeding instars. Examination of larvae by GG, and his photographs of reared larvae at various stages, showed that the mature larvae differ very little in morphology or colouration from earlier instars. However, the colour pattern, particularly the black markings, becomes more strongly developed as the larva matures.

Xenapates Kirby, 1882

Figs 3–12

[based on the larvae of *X. braunsi* and *X. gaullei*]

Description. *Head.* Slightly wider than high (to epistomal suture). Without surface sculpture. Antenna with 5 antennomeres on large subconic antacorium. 4 basal antennomeres ring-like, apical antennomere peg-like. Clypeus with 4 setae. Postclypeus about half as long as preclypeus. Preclypeus with medial, laterally sclerotised (brown), transverse division (ca. medial third unsclerotised). Labrum slightly asymmetric (right lobe larger than left), undivided by longitudinal or transverse depressions, with 6 setae. Stipes and palpifer of maxilla each with a prominent lobe directed towards mandibles. Left mandible (Figs 3, 4) with straight-edged blade on outer (dorsal) surface, ending with a tooth on left side; a long tooth medially, contiguous with a well-developed mesal ridge, its edge produced in two rounded lobes, separated by a wide, rounded emargination (Fig. 3); inner surface with three well-defined teeth. Right mandible (Fig. 5) outer surface similar to left mandible, but straight-edged blade not ending in tooth; medial tooth very broad; inner surface with one wide, asymmetrical tooth closely adjoined by a pair of short, narrow teeth on a shared, rectangular flange; to left of this a straight, unsclerotised edge, about as long as three adjacent teeth together, and much lower than these; no mesal ridge present.
Cuticle of thorax and abdomen. Without dorsal macrostructures such as tubercles, spines, or longer setae, but with reticulate-spiculate surface structure on dorsum reaching to just above spiracles (Fig. 7), sometimes also on subspiracular and surpedal lobes (Fig. 8). To the naked eye, these parts appear "velvety", but at magnifications of 40–90× under a stereo microscope they might almost be described as "scaly". The cuticle thus strongly resembles that of the easy bleeder species *Rhadinoceraea micans* (Klug, 1816) (Blennocampinae) as described by Boevé (2009).
Thorax. Meso- and metathoracic substigmal lobes strongly protruding laterally. Prothorax with more or less strongly developed dorso-lateral lobes. Legs with 5 articles, bearing numerous long setae. Coxa longer than basal width. Trochanter wider than long; about half as long as coxa. Femur apically expanded on inner surface (Fig. 6); femur thus much wider apically than apical width of trochanter, and about twice as wide as base of tibia.
Abdomen. Segments 1–8 with 6 dorsal annulets. Prolegs on segments 2–8 and 10; 1.5–1.7× as long as basal width, with 16–20 setae on outer surface (Fig. 8) and 12–20 on inner surface. Apex of suranal lobe and antero-dorsal surface of subanal lobe with numerous short setae.

Xenapates braunsi (Konow, 1896)

Figs 3–5, 8–9, 11

Description. *Colour* (Fig. 9). Head including posterior vertex yellow, changing to white on genae. A black patch, not more than 4× as long as ocularium, surrounds stemmatum and does not reach an imagined horizontal line extended from dorsal apex of frons. Thoracic legs pale brown, except for black coxal suture. Trunk pale green, appearing dorsally darker because contents of gut show through; subspiracular lobes and anal area including anal prolegs pale orange.
Head (Fig. 11). With a pair of large, pale depressions, one each side of coronal suture dorsal of junction with frontal suture. Setae on vertex and parietals very short (less than third diameter of antennomere 1) and pale. Some setae on genae and mouthparts as long as antenna. Right lobe of labrum about twice as long as visible part of left lobe.
*Trunk.* Prothorax dorsal annulets 1 and 2 laterally fused. Annulet 2 medially divided; lateral lobes very much higher than lateral parts of 1 or 3. Dorsal surface of lobes on annulet 2 with partly pigmented spicules that are more strongly developed than on other parts of thoracic dorsum. Surface of integument of abdomen above spiracles almost smooth, with very minute, unpigmented spicules. Some partly dark spicules on hypopleurite, surpedal and substigmal lobes (Fig. 8).
Length of fully grown larvae: 19–20 mm (n = 16).

Xenapates gaullei (Konow, 1896)

Figs 6–7, 10, 12

Description. *Colour* (Fig. 10). Head yellow, with large medial black fleck on posterior vertex. Fleck about as long as wide and not reaching to vertical furrows or frons. Large black patch, at least 5× as long as ocularium, surrounds stemmatum and extends above level of dorsal apex of frons. Trunk dorsally grey to supraspiracular line, paler below this except for grey ventral edges of subspiracular and surpedal lobes. Coxae basally ringed with black. Anal area including anal prolegs pale orange. Note: dark coxal markings only become conspicuous in last feeding instars.
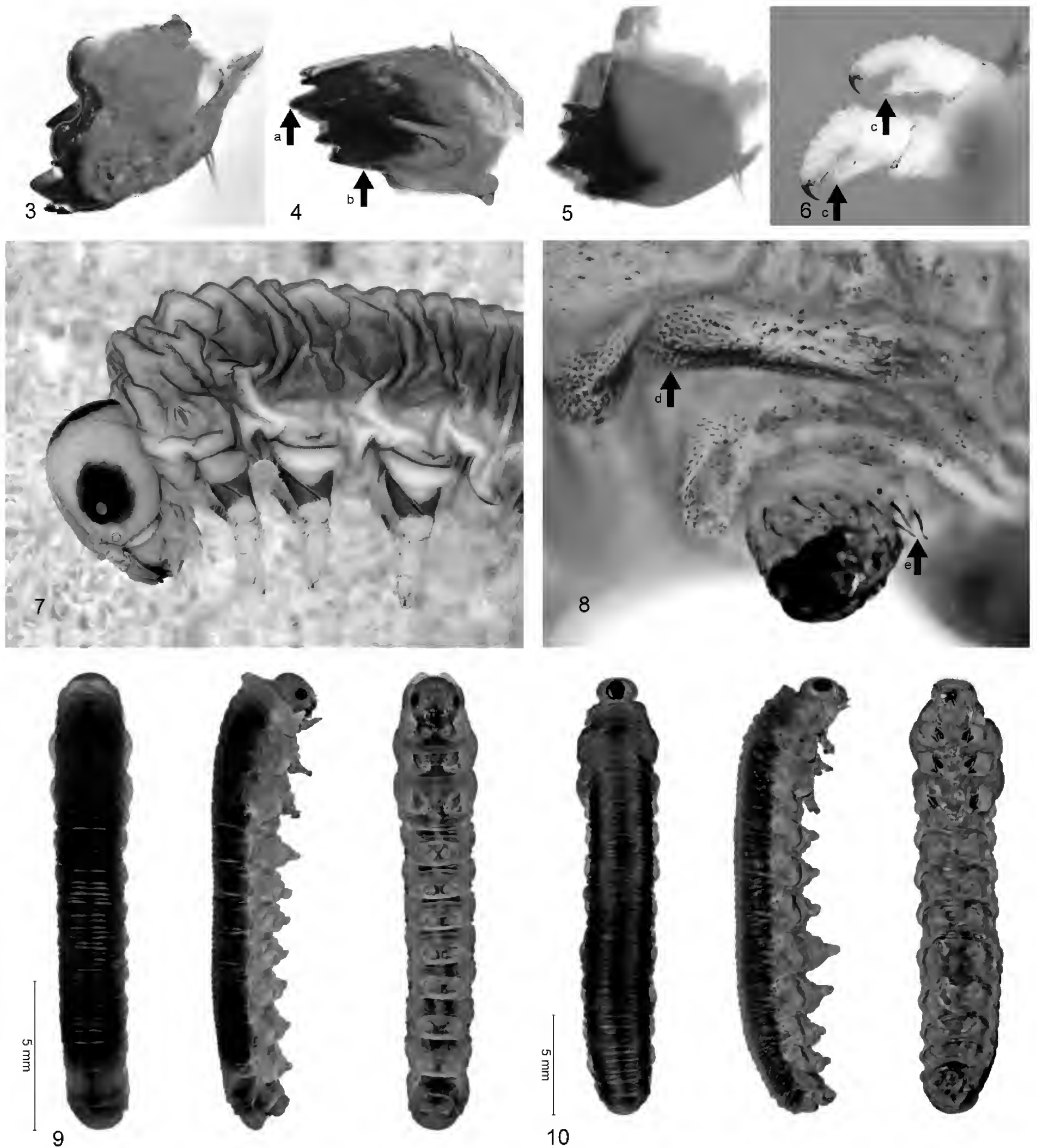
Figures 3–10. *Xenapates* larvae: **3.** *X. braunsi* left mandible, outer face; green line along edge of mesal ridge. **4.** *X. braunsi* left mandible, ventral; (**a**) medial tooth, (**b**) inner face. **5.** *X. braunsi* right mandible, inner face. **6.** *X. gaullei* right pro- and mesothoracic legs; (**c**) expanded apex of femur. **7.** *X. gaullei* thorax, lateral. **8.** *X. braunsi* proleg and ventral part of abdominal segment 8, external surface; (**d**) reticulate-spiculate surface structure on surpedal lobe; (**e**) setae on proleg (some missing). **9.** *X. braunsi* mature larva; dorsal, lateral and ventral (from left). **10.** *X. gaullei* mature larva.

Head (Fig. 12). No depression present on each side of coronal suture dorsal of junction with frontal suture. Setae on vertex and parietals slightly darkened and as long as diameter of antennomere 1. Setae on lower frons and genae longer (as long as antenna) and paler. Right lobe of labrum only slightly larger than left.

Trunk. Prothorax with dorsal annulets clearly separated. Annulet 3 medially divided and lateral lobes slightly higher than lateral parts of 1 and 2. Entire surface of integument on dorsum above spiracles, and partly on subspiracular and surpedal lobes, densely and uniformly spiculate (Fig. 7); each spicule apically darkened.

Length of fully grown larvae: 20–21 mm (n = 7).

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Prepupae and pupae

Figs 13–16

The colour pattern of the larva of *Xenapates gaullei* is largely lost at the moult to the prepupal stage (Fig. 14), whereas the prepupae of *X. braunsi* (Fig. 13) retain, for example, extensive black markings on the head, and the orange anal area. The pale depressions on the faces of larvae of *X. braunsi* (not present in *X. gaullei*) at the base of the coronal suture adjoining the frons are retained in the prepupa (Fig. 13), thus further facilitating their separation. The pupae are at first only weakly pigmented. At this stage they can nevertheless be distinguished by colour: *X. braunsi* (Fig. 15) is predominantly bright green, whereas *X. gaullei* (Fig. 16) has a yellow ground colour with only the abdomen tinged slightly green. As pigmentation develops, the much more extensively dark colour pattern of *X. braunsi* easily distinguishes it from *X. gaullei*.

Host plants

X. braunsi: Poaceae: *Digitaria horizontalis* Willdenow (Jamaican crabgrass), *Pennisetum purpureum* Schumacher (elephant grass), *Setaria barbata* (Lamarck) Kunth (bristly foxtail grass), *Zea mays* Linnaeus (maize).

All four plant species were observed to be hosts under field conditions. Though adults were regularly found on *Z. mays* during the wet seasons, larvae were rarely observed feeding on this species, compared to the other host plants. A few larvae collected in the field on maize were successfully reared to the cocoon stage on potted maize plants.

X. gaullei: Commelinaceae: *Commelina benghalensis* Linnaeus (Bengal dayflower) and *C. communis* Linnaeus (Asiatic dayflower). Both species were found to be hosts under field conditions.

Biology

Adults of *Xenapates braunsi* and *X. gaullei* were frequently observed courting and mating on leaves of *Alternanthera brasiliana* (Linnaeus) Kuntze (Amaranthaceae), which offer a relatively large surface area on which the sawflies can engage with each other. These activities took place particularly during sunny periods following rainfall. Neither oviposition nor occurrence of larvae was observed on *A. brasiliana*. Despite the provision of honey solution, adults never lived longer than three days in captivity. Compared to other sawflies, the incubation period of *X. braunsi* and *X. gaullei* eggs is extremely short (lasting a maximum of five days: see Table 1 and below). Larvae of both species are easy bleeders (Boevé 2009). Rupture of the cuticle and emission of haemolymph was induced even by light contact with a 000 size paint brush. No parasitoids were observed or reared, but attacks on cocoon stages by nematodes were frequent when the soil was too wet.

X. braunsi: Oviposition was not observed during this study, but 3 mm long larvae were detected on young leaves of *Setaria barbata* five days after the introduction of adults to the experimental cages. Larval feeding followed a similar pattern to *X. gaullei*, except that early instars first grazed on the leaf surface without perforating it. Later, the still young larvae moved to the leaf edge and fed on its margin. They were then also observed to feed on older leaves. When mature, larvae stopped feeding and entered the ground, without moulting. The cocoon (Fig. 17), made of sand grains bound together by a secretion, was ellipsoidal with largest dimensions approximately 7 by 11 mm. The external surface of the cocoon was rough, the inner surface smooth. It was not possible to remove the sand grains from the fabric of the cocoon without destroying it. The larva moulted slowly to the prepupal stage, shedding its exuvia caudally. The pupa became fully developed only a few days before emergence of the adult. The intensely green-coloured haemolymph of the cocoon stages of *X. braunsi* was striking, and remained highly visible through the integument of freshly emerged adults (Fig. 1).

X. gaullei: Eggs were found mostly singly on sub-apical leaves, but not on the youngest, apical leaves. Oviposition was into a slit cut in the mesophyll from the upper side of a leaf, at no specific locus: eggs were found close to the leaf edge or at some distance from it, but never in the mid-rib. On average, larvae left their egg cavities (Fig. 18) to feed externally 5 days after oviposition (n = 11). The first moult, however, takes place just before the larva exits the leaf. It seems likely that larvae of the first instar, which must be of very short duration, feed within the leaf. Although such feeding was not observed directly, the cavities surrounding hatched eggs appeared too large to have been caused by mere disruption during oviposition, or eclosion of the larva. Whereas young larvae made feeding holes in the leaf blade, close to where they eclosed (Fig. 18), older instars fed directly on the leaf margin. One to two days before they burrowed into the soil, mature larvae stopped feeding, evacuated their gut and thereby became slightly smaller. Each larva then made a cocoon in the earth, close to the bottom of the plant pot. Cocoons were never recovered from within the root system of the host plant. The cocoon resembled that of *X. braunsi*.

Phenology and voltinism

Although too few adults were reared to allow definite conclusions to be drawn on voltinism, field observations of adults in 2012 through 2014 indicated that *Xenapates braunsi* and *X. gaullei* are multivoltine, with two or three generations per year. Possibly the number of generations depends on prevailing weather conditions. The first generation emerges at the beginning of the main wet season, which lasts from April to late July. In years with early and sustained rainfall such as 2013, a second generation of *X. braunsi* can emerge as early as 11–14 days after the first larvae have burrowed into the ground, i.e. 34–36 days after the egg was laid (Table 1). In *X. gaullei* the equivalent
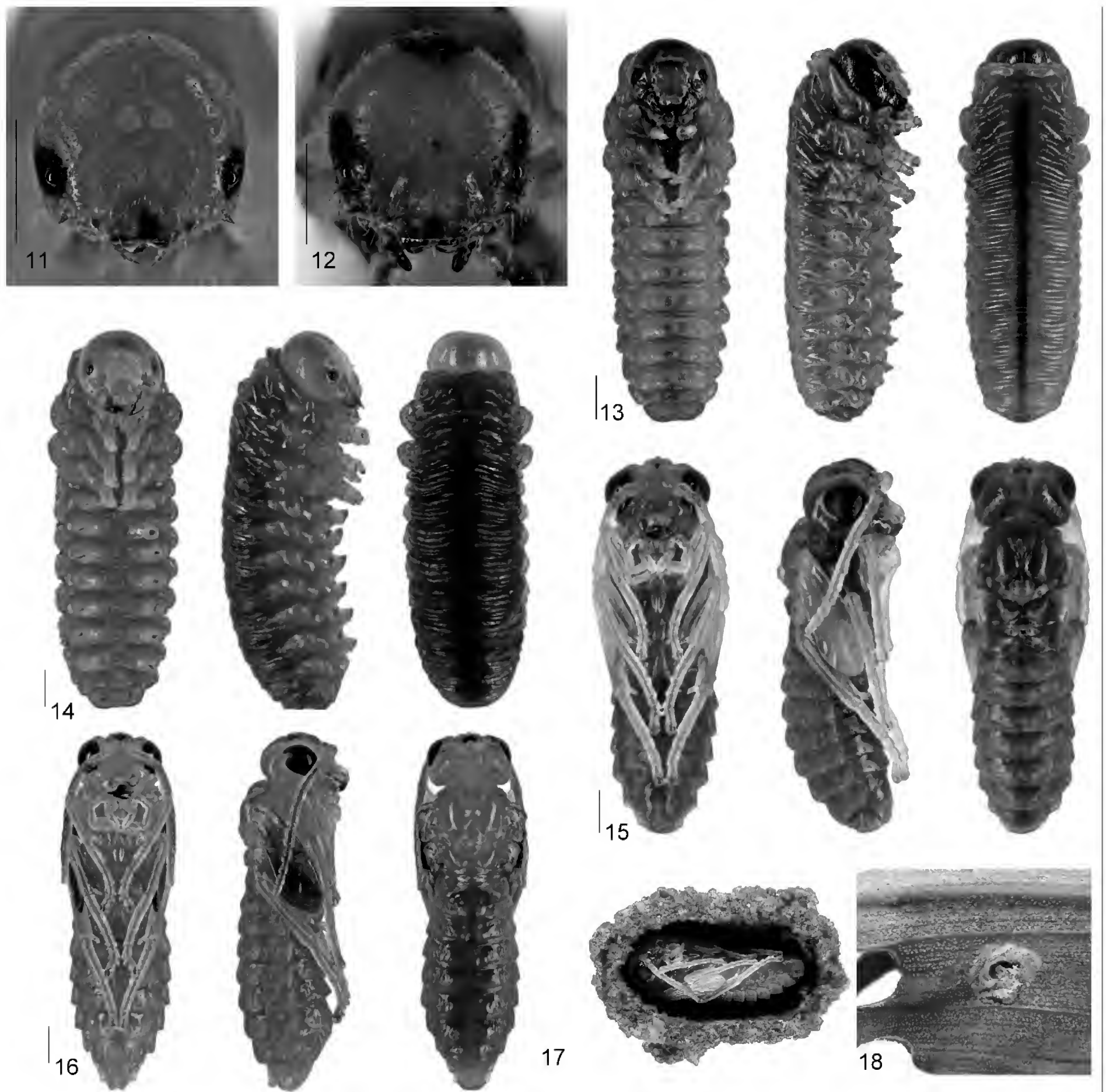
Figures 11–18. *Xenapates* immature stages: Larva; head frontal. **11.** *X. braunsi* **12.** *X. gaullei.* Prepupa; ventral, lateral and dorsal (from left). **13.** *X. braunsi* **14.** *X. gaullei.* Pupa; ventral, lateral and dorsal (from left). **15.** *X. braunsi* **16.** *X. gaullei.* **17.** *X. braunsi*: cocoon containing pupa. **18.** Vacated egg pocket of *X. gaullei*, exuvia of first instar larva visible in perforation, with feeding hole (at left) made by second instar. Scale bars = 1 mm.

Table 1. Ex ova rearing chronologies of *Xenapates braunsi* and *X. gaullei*, using respectively *Setaria barbata* and *Commelina communis* as host plants, between 2012 and 2014. Numerous unsuccessful rearings are not listed.

Year	Introduction of adults to cages	First observation of larvae	Larvae burrowed into soil	Adult emergence
X. braunsi				
2012	26 October	31 October	15–17 November (n=3)	No emergence
2013	18 May	23 May	8–9 June (n=4)	19–22 June (n=3)
2013	03 October	08 October	28–30 October (n=9)	13–14 April 2014 (n=3)
X. gaullei				
2012	4 May	9 May	25–26 May (n=4)	No emergence
2013	6 June	11 June	1–2 July (n=5)	18–20 July (n=2)
2013	27 September	4 October	27–28 October (n=4)	17 April 2014 (n=2)

period spent in the ground was 19 days, and complete development from the egg took 40–42 days (Table 1). However, in years with normal onset of rain (e.g. 2012 and 2014), the immature stages take longer to develop, and adults of the second generation emerge during the short, less intense wet season that starts between late September and early November. Offspring that have developed during the latter period undergo a prolonged diapause and adults emerge in April of the following year, after having spent about 193 days in the soil in *X. braunsi* and 202 days in *X. gaullei* (Table 1). Under field conditions in southern Benin, three generations were less often observed in *X. gaullei* than in *X. braunsi*. Whereas *X. braunsi* appeared to have an approximately 1:1 sex ratio during the short wet season, females of *X. gaullei* seemed far less frequent than males during the same period. During the long wet season, females were apparently equally frequent in both species. Slight protandry was observed to be usual, in both species.

Discussion

Phylogenetic position of *Xenapates*

The phylogenetic position of *Xenapates* within the Tenthredinidae, as in several other lineages traditionally placed in the Allantinae, remains unclear. *Xenapates* larvae differ from previously described exophytic tenthredinid larvae (Lorenz and Kraus 1957), in lacking on the dorsal annulets of the trunk any cuticular appendages such as tubercles or setae. Other sawfly taxa whose larvae have an extremely reduced complement of macroscopic cuticular structures belong notably to the tribes Waldheimini (e.g. *Waldheimia*) and Blennocampini (e.g. *Tomostethus*) of the Blennocampinae (Smith 1969, Smith and Williams 2014). The complete absence of these structures might be an apomorphy of *Xenapates*. However, as long as this character state remains unknown in most other Afrotropical and Oriental genera placed in the Allantinae and Blennocampinae, its taxonomic significance cannot be evaluated. Of the taxa that were included in the Xenapateini by Koch (1996), only the larva of *Takeuchiella pentagona* Malaise, 1935 has been described (Okutani 1959): annulets 2 and 4 of the abdominal segments carry conical tubercles and setae. In some characters, the larvae of *Xenapates* agree with those of Allantini as characterised by Lorenz and Kraus (1957): antenna with 5 members, clypeus with 4 setae, abdominal segments with 6 annulets, and abdominal prolegs on abdominal segments 2–8 and 10. However, the same combination of character states is also found in some Blennocampinae (Smith 1969). Noteworthy is that the lobed stipes and palpifer of the maxilla of *Xenapates* are found together only in the allantine genera *Allantus* and *Taxonus*, and Tenthredininae (Lorenz and Kraus 1957). On the other hand, larvae of the Allantinae and Blennocampinae taxa described by Lorenz and Kraus (1957) and Smith (1969, 1979) are without setae on the external surface of the abdominal prolegs, whereas *Xenapates* has at least 16 setae. According to Lorenz and Kraus (1957), in the Tenthredinidae some Athaliinae, Nematinae, Selandriinae and Tenthredininae share this character. The abdominal prolegs of the larva of *T. pentagona* are setose only on the inner surface (Okutani 1959). The mandibles of *Xenapates* larvae resemble those of Blennocampinae in that only one mandible has a mesal ridge, rather than the Allantinae, in which both mandibles have a mesal ridge (Smith 1969, 1979). However, in all the Blennocampinae studied by Smith (1969), the right mandible has a mesal ridge, whereas in *Xenapates* it is only developed on the left mandible. *Xenapates* also differs from Allantini in its use of monocots as larval hosts. The easy bleeding trait exhibited by *X. braunsi* and *X. gaullei* larvae is shared by a number of species in various lineages of Tenthredinidae: Athaliinae, Selandriinae, Tenthredininae and particularly the Blennocampinae, but is not known in the Allantinae (Boevé 2009; note subsequent alteration to family group taxonomy by Malm and Nyman 2014). Although we called the structure made by the last larval instar of *Xenapates* a cocoon, one could alternatively regard it as a cell formed in the soil, which is held together by a secretion. Smith (1969) notes that Blennocampinae which enter the ground form a cocoon. On the other hand, Smith (1979) states that Allantinae rarely, if ever, spin cocoons and that those which enter the soil form an earthen cell. However, it has seldom been recorded whether or not any secretion was used to hold the walls together, and perhaps in some cases this does occur.

Monocots as host plants of Afrotropical sawflies

The spectrum of host plants utilised by Tenthredinoidea is very large, with larvae of most taxa feeding on angiosperms, but a large minority on gymnosperms, and rather fewer on ferns, horsetails and mosses (Liston 1995, Vikberg and Nuorteva 1997). However, most available data on host plant associations relate to the temperate zones of the Palaearctic and Nearctic. Very little is known about host plant associations of Afrotropical sawflies, and the pattern in this region might therefore ultimately prove to be quite different. All hosts of the two *Xenapates* species in this study are placed in the monocots, within a clade called the commelinids, respectively in the Commelinaceae of the Commelinales (*X. gaullei*) and Poaceae of the Poales (*X. braunsi*) (APG 2009). Worldwide, the number of tenthredinoid lineages so far known to be attached to monocots in general, and grasses (Poales) in particular, is relatively low. The grass-feeders comprise only some tenthredinid species in the Holarctic and partly Oriental genera *Selandria*, *Dolerus* (Selandriinae), *Eutomostethus* (Blennocampinae), *Tenthredo*, *Tenthredopsis* (Tenthredininae) and *Euura* (as *Pachynematus* in Lorenz and Kraus 1957; see Prous et al. 2014 on generic placement) (Nematinae) (Lorenz and Kraus 1957). As far as we are aware, *X. braunsi* is so far the only sawfly whose larvae have been found feeding on *Zea mays*.

Until now, only one record existed of an Afrotropical sawfly species using a member of the Poales as a larval host. Larvae of a *Distega* species (Blennocampinae),

identified as *Distega* aff. *nigeriae* Fors.[ius, 1927], were stated to feed on "Mil" (French for millet; cultivated *Pennisetum* spp.) in Senegal by Risbec (1950). He noted that during his stay in Senegal, feeding damage to crops by this sawfly did not seem very significant. It is difficult, because of the brevity of the published information and lack of voucher material, to assess the accuracy of identification of the sawfly involved in this record. In particular, it is not stated whether adults were reared from the larvae. The drawing of the larva in Risbec (1950) lacks any indication of the presence of cuticular processes on the dorsum, and its very strongly developed prothoracic lobes also closely resemble those of *X. braunsi*, which in this study was found to use *Pennisetum* as a host. Furthermore, Risbec referred only to the presence of setae on the front of the head and on the abdominal prolegs, not mentioning any setae on other parts of the body. This resembles the distribution of setae that we observed in *Xenapates* larvae. The velvety appearance of the cuticle described by Risbec suggests that it, too, was an easy bleeder. On the other hand, his larvae exhibited a conspicuous row of lateral black spots, just above the spiracles, which are not found in *X. braunsi* or *X. gaullei*. We conclude that Risbec's identification of *Pennisetum* as a host of *Distega* requires reinvestigation, because the sawfly larva involved may have been misidentified.

In the Holarctic, some species of Selandriinae and Nematinae whose larvae feed on Poaceae reach levels of abundance sufficient to make them ecologically important in grasslands (for example, the larvae are a major source of nutrition for some bird species: Potts 1986), and occasionally they may damage crops of grass fodder (Mühle and Wetzel 1965), or grain crops (Miller and Pike 2002). It remains to be seen, if grass-feeding sawflies perform similar roles in the Afrotropical Region.

Conclusions

All four of the larval hosts of *X. braunsi* identified in this study are of greater or lesser importance as cereal or fodder crops in Benin and throughout tropical and sub-tropical Africa (Akoegninou et al. 2006). The host plants of *X. gaullei* are also of direct interest to man. Leaves of *Commelina benghalensis* are eaten as a vegetable in Africa and parts of Asia (Grubben and Denton 2004), whereas *C. communis* is better known internationally as a troublesome invasive weed, for example in parts of Europe and North America (Zheng et al. 2006). Both *Xenapates* species could therefore be regarded as potential crop pests. On the other hand, *X. gaullei* might be a candidate for biological control of invasive *Commelina* spp. We therefore recommend that additional studies on the biology of *Xenapates* species be undertaken. Ideally, some attention should also be paid to identifying the still unknown hosts and larvae of other relatively speciose genera of Afrotropical tenthredinids, such as *Distega*.

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Recognition and identification of bumblebee species in the *Bombus lucorum*-complex (Hymenoptera, Apidae) – A review and outlook

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Abstract

The recognition of cryptic species represents one of the major challenges in current taxonomy and affects our understanding of global diversity. In practice, the process from discovery to acceptance in the scientific community can take an extensive length of time. A prime example is the traditionally difficult taxonomy of the cryptic bumblebee species belonging to the *Bombus lucorum*-complex. The status of the three European species in the group – *Bombus lucorum* and the closely related *Bombus cryptarum* and *Bombus magnus* – has recently become widely accepted, primarily due to investigations of nucleotide sequences and marking pheromones. In contrast, doubts prevail concerning the validity of species identification based on morphology. As a consequence, our knowledge of the species is muddled in a mire of unreliable and confusing literature data from a large number of authors over the centuries. To clarify this issue, this paper provides a recapitulation of the historical literature and highlights the milestones in the process of species recognition. Further, the possibility of a morphologically based species identification is discussed in the context of new molecular data. Finally, this review outlines the current challenges and provides directions for future issues.

Introduction

Bumblebees (*Bombus* Latreille, 1802) are considered to be a striking feature of Europe's pollinator fauna (e.g., Corbet et al. 1991, Neumayer and Paulus 1999, Goulson et al. 2007, Goulson 2010). In contrast to most other bee genera, bumblebees are readily recognizable and rarely confused with other bees (Amiet 1996, Gokcezade et al. 2010, Amiet and Krebs 2012). Yet species determination requires expertise, and reliable identification in the field is often impossible. Reasons for this are the relatively monotonous morphology (Michener 2007), enormous variability in coloration and size which is often associated with biogeographical distribution (e.g., Vogt 1909, Vogt 1911, Krüger 1951, Løken 1973, Pekkarinen 1979) and the fact that the same or similar color-patterns are often repeated in various species (Dalla Torre 1880, Reinig 1939, Amiet 1996, Williams 2007 and references therein). One of these groups with very similar morphology consists of the European species of the subgenus *Bombus*

s. str.: *Bombus terrestris* L., 1758, *B. lucorum* L., 1761, *B. cryptarum* Fabricius, 1775, *B. magnus* Vogt, 1911 and *B. sporadicus* Nylander, 1848. Two species of this group, *B. lucorum* and particularly *B. terrestris*, are of great economic interest since the extensive use of bumblebees for commercial greenhouse pollination (Velthuis and van Doorn 2006, Winter et al. 2006). In the past decades, there has been much disagreement on the taxonomy of this group. Especially the status of *B. lucorum* and the closely related *B. cryptarum* and *B. magnus*, forming the so-called *Bombus lucorum*-complex, has been intensively discussed. This can be traced to an exceptionally high degree of synonymisation: Williams (1998) reported far more than 100 infrasubspecific names just for *Bombus lucorum* s.l. In contrast, the species status of the three distinct species in Europe is widely accepted nowadays, primarily based on investigations of nucleotide sequences of the mitochondrial COI gene (Bertsch et al. 2005, Murray et al. 2008, Bertsch 2009, Carolan et al. 2012, Williams et al. 2012) and male labial gland secretions (Bertsch 1997,

Bertsch et al. 2004, Bertsch et al. 2005). Still, serious doubts remain concerning the validity of species identification based on morphology and the reliability of certain distinguishing characters have been challenged (e.g., Williams 2000, Carolan et al. 2012). As a consequence of this doubtful delineation, our current knowledge about the species is muddled in a mire of unreliable literature data from numerous authors over the centuries. Only few studies on the species exist that are backed up by reliable species identification using molecular methods. In addition, information about diagnostic characters in the literature are often confusing or based on insufficient underlying data sources. To rectify the problem, this review provides an overview on species recognition and the differentiation of the *Bombus lucorum*-complex. Further, it provides an urgently required reappraisal to pave the way for future investigations.

Bombus lucorum vs. Bombus magnus

Bombus lucorum and *B. terrestris* were described by Linnaeus in 1761 and 1758, respectively. Their species status has been widely accepted in the last century. Only few authors doubted their status and lumped them together (e.g., Faester and Hammer 1970, Warncke 1981, Warncke 1986). More than a century later, *B. magnus* was described by Vogt (1911) in a single sentence as a 'forma nova *magnus*' without detailed information. It was probably the same species that was described as *Bombus terrestris* var. *flavoscutellaris* by Trautmann and Trautmann (1915). The species description of *B. magnus* was made by Krüger (1951, 1954) with detailed descriptions of all castes and several *races* and *ethna*, which are difficult to comprehend from today's view. Some earlier experts failed to distinguish *B. lucorum* and *B. magnus* (Elfving 1960, Ander 1965), others primarily highlighted the need of further studies (Alford 1975, Delmas 1981). Løken (1973) conducted a grand morphometric analysis and advocated their species status, primarily based on measurements of queens, whereas the distinguishability of workers and males remained uncertain. Her work was confirmed and enhanced by further specific indices by Tkalců (1974). At that time, the first biochemical results in the form of male labial gland marking pheromones emerged (Kullenberg et al. 1970, Bergström et al. 1973, Bergström et al. 1981). For *B. lucorum*, two similar but distinctly different profiles could be identified related to a 'dark' and a 'blonde' form, supporting Løken's (1973) view. However, common to all of the above mentioned literature is the fact that a previously unknown species, *B. cryptarum*, occurs sympatrically with *B. lucorum* and *B. magnus* and probably biased their results due to a species mix in their samples. This is likely the reason why the results from Pekkarinen (1979) are not in line with the others. Even though other authors also overlooked a possible third taxon (Scholl and Obrecht 1983, Pamilo et al. 1984), their results based on enzyme electrophoresis strongly supported the idea that *B. lucorum* is not a single species.

A third species comes into play

Using morphological and morphometric methods, Rasmont (1981a, 1981b) was the first who recognized a putative third species and attributed it to *Bombus lucocryptarum* Ball which was later synonymized with *Bombus cryptarum* Fabricius (Rasmont 1983). Interestingly this taxon was also previously described as *Bombus lucorum* var. *pseudocryptarum* Skorikov from Russia and Poland (Skorikov 1913). Rasmont (1981b) provided a determination table for the queens. Tables for both female castes (Rasmont 1984) and males (Rasmont et al. 1986) followed, even if those for the latter were of limited applicability. His keys were supported by remarkable crossing experiments between the three putative species (De Jonghe 1982, De Jonghe and Rasmont 1983, Rasmont and De Jonghe 1985). His cross breeding of the three putative taxa ultimately failed, even though copulation and egg deposition were observed. Nonetheless, his breeding within the examined taxa succeeded. In contrast, no interspecific mating was observed in the experiments of Bučánková et al. (2011). In short, the results strongly indicate that reproductive isolation is present but, due to the limited sample sizes, this conclusion cannot be entirely reliable. In general, although the conviction that *B. lucorum* consisted of more than one taxon grew, the species were still lumped together by some authors (Warncke 1986, Westrich 1990). Williams (1991, 1998) provisionally synonymized the potential species. The confirmation of a third species with biochemical methods remained open for some time (Obrecht and Scholl 1984, Scholl et al. 1990, Scholl et al. 1992, Pamilo et al. 1997), probably due to the similar enzyme genetic profiles of *B. cryptarum* and *B. magnus*. However, it is likely that the samples of *B. cryptarum* and *B. magnus* used for analyses were mixed, a point that Bertsch et al. (2004) presupposed for Pamilo et al. (1997). With recurring theme, the morphometric attempts of Baker (1996) were of restricted value, since *B. cryptarum* was not considered as a separate species and the same applies for Macdonald (1999). He advocated *B. lucorum* and *B. magnus* as good species based on the coloration of the pile (extended yellow collar of queens of *B. magnus*; for a review of morphological traits see below) and observations concerning their ecology. In retrospect, it seems highly likely that at least some of the examined specimens from his study were in fact *B. cryptarum*, since this species occurs most frequently in the mainland of northern Scotland (Macdonald, personal communication). This may explain why Williams (2000) could not find a clear gap in collar extension between *B. lucorum* and *B. magnus*: *B. cryptarum* queens have on average a collar extension between the latter two species (Carolan et al. 2012) which may have critically biased the measurements.

The first sufficient biochemical evidence for all three species was conducted by Bertsch (1997) and Bertsch et al. (2004) by the identification of three distinct male labial gland secretion profiles: the profiles of *B. cryptarum* and

B. magnus are similar and share ethyl dodecanoate as the main component. Yet they clearly differ in minor components such as alcohols (Bertsch et al. 2004, Bertsch et al. 2005). Recently the great stability of the labial gland secretion composition of *B. cryptarum* over great geographical ranges was shown, a fact that supports their value for species recognition (Bertsch and Schweer 2012).

Nucleotide sequence data improved our understanding

The debate gained new life with the application of phylogenetic analyses using nucleotide sequences of the mitochondrial cytochrome oxidase I gene (COI). With this method, the composition of three distinct molecular operational taxonomic units (MOTUs) in the European *B. lucorum*-complex was convincingly confirmed multiple times (Bertsch et al. 2005, Murray et al. 2008, Bertsch 2009, Carolan et al. 2012). In contrast, the taxonomic state of knowledge remains incomplete in the global context and additional cryptic taxa of the subgenus *Bombus* s. str. occur in the Far East (Williams et al. 2012). Several Asiatic taxa are most closely related to *B. cryptarum* based on COI (Bertsch et al. 2010) and the difficulty of defining the respective taxonomic units is an ongoing process (Bertsch et al. 2014). Admittedly, although COI barcoding and its applicability for species recognition has been criticized (e.g., Will and Rubinoff 2004, DeSalle et al. 2005, Meyer and Paulay 2005, for a review see Taylor and Harris 2012), the results for the European *B. lucorum*-complex seem convincing. The interspecific genetic divergences of the species are considerably larger than the intraspecific divergences and these patterns are stable over wide geographic ranges of Europe. In measureable terms, the genetic divergences between the species, based on the Kimura 2-parameter model of DNA sequence evolution (Kimura 1980), from Carolan et al. (2012) ranged from 0.033 to 0.044, whereas intraspecific distance was from 0.002 to 0.004. In the analysis by Murray et al. (2008), which was based on Tamura-Nei (Tamura and Nei 1993), the distances are slightly smaller. The interspecific distance ranges from 0.023–0.036 and intraspecific from 0.001-0.004. Based on their divergences and missing intermediates, Murray et al. (2008) concluded that their results "provide strong support for the existence of *B. cryptarum, B. lucorum, B. magnus* and *B. terrestris* as species that are discrete genotypic clusters" with respect to the Genotypic Cluster Concept of species (Mallet 1995).

Additionally, the COI sequences are suitable for inexpensive and fast analyses by restriction fragment length polymorphisms (RFLP), if only the species identity and not the individual sequence is of interest. Therefore Murray et al. (2008) provided a protocol which was successfully applied by Waters et al. (2011). An enhanced version was published recently (Vesterlund et al. 2014). This more time consuming approach works well with smaller COI fragments and hence is better suited for degraded DNA. However, it should be mentioned that none of the RFLPs protocols worked with the so-called *Folmer re-gion* PCR primers (derived from the primers presented in Folmer et al. (1994)), which are widely used for DNA 'barcode' collections such as BOLD (Ratnasingham and Hebert 2007).

In conclusion, both the labial gland secretion profiles and the results from the analyses of the nucleotide sequences reveal sufficient support for three distinct species in the European *B. lucorum*-complex. Additional support comes from the morphological implications, the phenological data presented in Bertsch et al. (2004) and the cross-breeding experiments. To further enhance our knowledge in this respect, an investigation of nuclear genes of the three species is urgently needed and will be a key issue in understanding the closer phylogenetic relationships in the species complex. In the best case, data from nuclear genes may help clarify the status of the described subspecies of *B. cryptarum* (cf. Rasmont 1984).

Can the species be distinguished by morphology?

While the biochemical and genetic methods for determination are widely accepted today, the published information on the morphological distinguishability of the species is confusing. Fortunately molecular and biochemical methods used nowadays allow for the verification or invalidation of potential discriminatory morphological traits. Currently, the key in Rasmont (1984) is the most important reference for the determination of females since most other keys (e.g., Mauss 1994, Amiet 1996, Bertsch et al. 2004, Dorow 2004) share crucial traits with that of Rasmont or are based on it. In general, the characters of coloration have been examined much more intensively. It should be mentioned that in using Rasmont (1984), the entirety of characters are only recognizable in queens. In this respect, the occurrence of the first collar is particularly important, since this may be the only character that is accessible in the field (Rasmont 1984, Bertsch 1997, Bertsch et al. 2004).

Identification of queens

Three distinct forms of the first collar have been suggested to identify queens from the *B. lucorum*-complex. The first describes the lateral border of the yellow collar, which has been mentioned as a characteristic trait many times (e.g., Skorikov 1913, Ball 1914, Trautmann and Trautmann 1915, Alford 1975, Rasmont 1981b, Rasmont 1984, Amiet 1996, Bertsch 1997, Bertsch et al. 2004). If the border extends down onto the episternum, it is associated with *B. magnus* (Fig. 5) and *B. cryptarum* (Fig. 3). For *B. magnus*, the collar was reported to extend far below the tegulae and become very broad below them. In contrast, a higher lateral border that is almost exclusively restricted to the pronatal lobes points to *B. lucorum* (Figs 1–2). In the literature, this trait is often vaguely described as "below tegula" or not, which is not entirely correct,
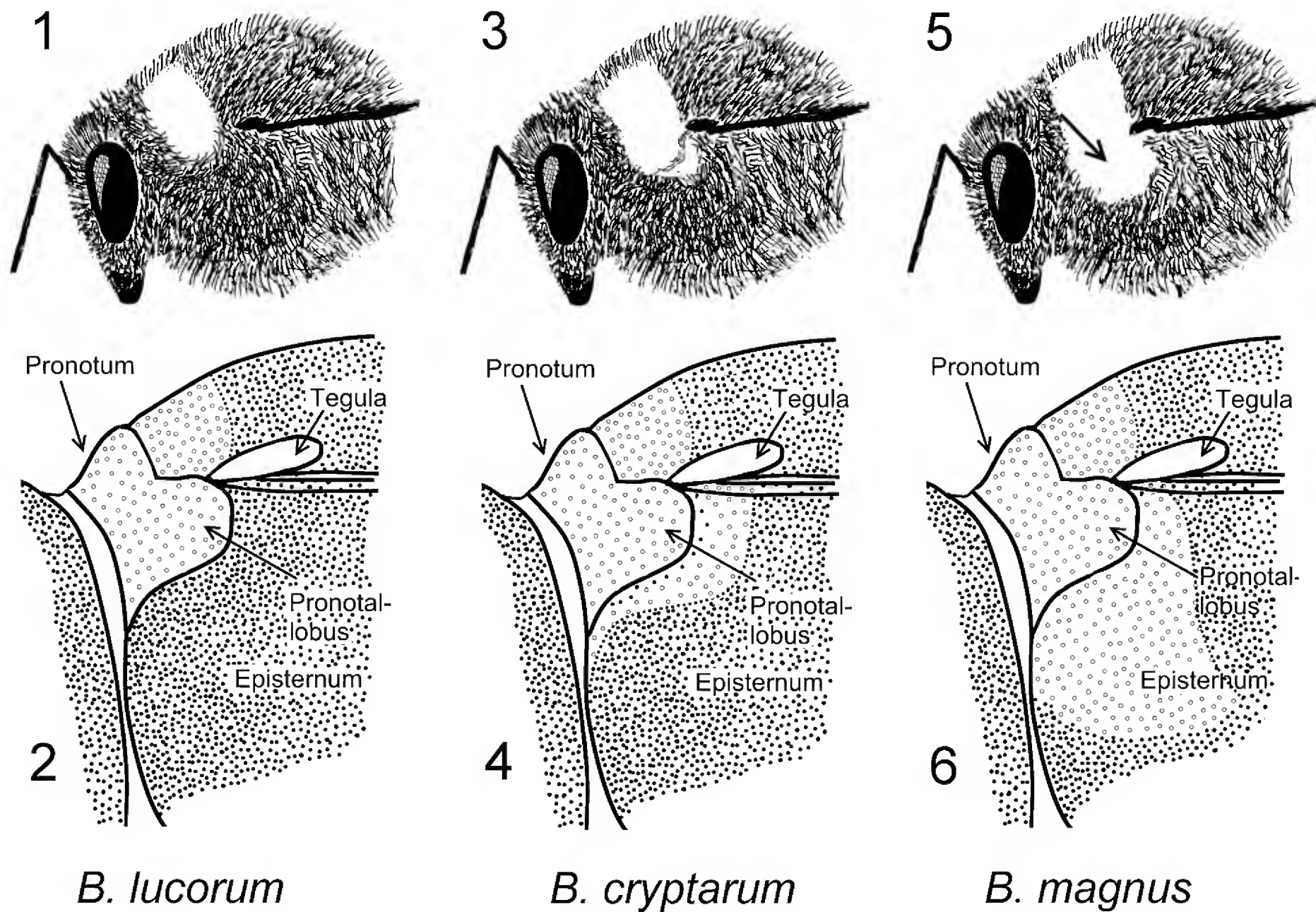
Figures 1–6. Shape of first collar as described in the literature. Head and parts of the mesosoma of the respective species are shown in a lateral view. **1–2.** *B. lucorum*; **3–4.** *B. cryptarum*; **5–6.** *B. magnus*. The drawings were provided by Johann Neumayer and are based on Bertsch et al. (2004).

since the border of the episternum is slightly below the tegula. The second trait is a so-called "S" or "5" shape that can be found within the collar. The pile along the border of the pronatal lobes and the episternum may be black and forms the "S" shape (Figs 3–4). It is associated with *B. cryptarum*.

Another hint comes from a strong melanization of the collar which has been reported for *B. cryptarum*. However, this trait is regionally restricted (Bertsch et al. 2004, Bertsch et al. 2005) and on rare occasions may occur in the other species, too (Carolan et al. 2012).

Bertsch (2009) was able to assign all but three investigated queen specimens to the correct species with the above mentioned characters, according to the biochemical evidence (n = 28). In contrast, using a larger sample from the British Isles and Denmark (n = 67), Carolan et al. (2012) showed that especially the collar-characters are not reliable for species diagnosis since they show overlap (see Fig. 4: doi: 10.1371/journal.pone.0029251. g004). However, not every voucher of this figure is convincing: A close look at specimen "h" from their study, identified by morphology as "*lucorum*", reveals an obvious collar extension far below the tegula and onto the episternum. Since there is no "S"-shape, the specimen should therefore be associated with *B. magnus*, which is actually the case according to the DNA barcode. More-

over, specimen "c", which was identified as "*magnus*" based on morphology, reveals a faint black "S"-shape, exactly as described in Bertsch et al. (2004). It remains unclear why this voucher was assigned to *B. magnus* and not *B. cryptarum*. Thirdly, specimen "f" is not a typical *B. magnus*-morphotype since it does not show a clear broad collar below the tegula. Against this background, their conclusion that "each species can be morphologically identified as belonging to all 3 taxa" cannot be upheld. The study gave sufficient evidence that the extension of the anterior band of *B. cryptarum* queens can vary and that it critically resembles the traits of the other species. Yet it does not show that queens of *B. lucorum* and *B. magnus* resemble each other.

Aside from this confusing information, the work of Carolan et al. (2012) strongly indicated that the collar characters are not completely reliable and should not be exclusively taken into account for species identification. In addition, the key of Rasmont (1984) uses several characters aside from the coloration of the pile, such as the form of the labrum, punctuations of several structures and the shape of the hindleg metatarsus. However, the reliability of these characters has not been examined against independently verified specimens and through broad geographic sampling. Thus the identification of queens of the *B. lucorum*-complex cannot be made by morphological

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8

9

B. lucorum   B. cryptarum   B. magnus
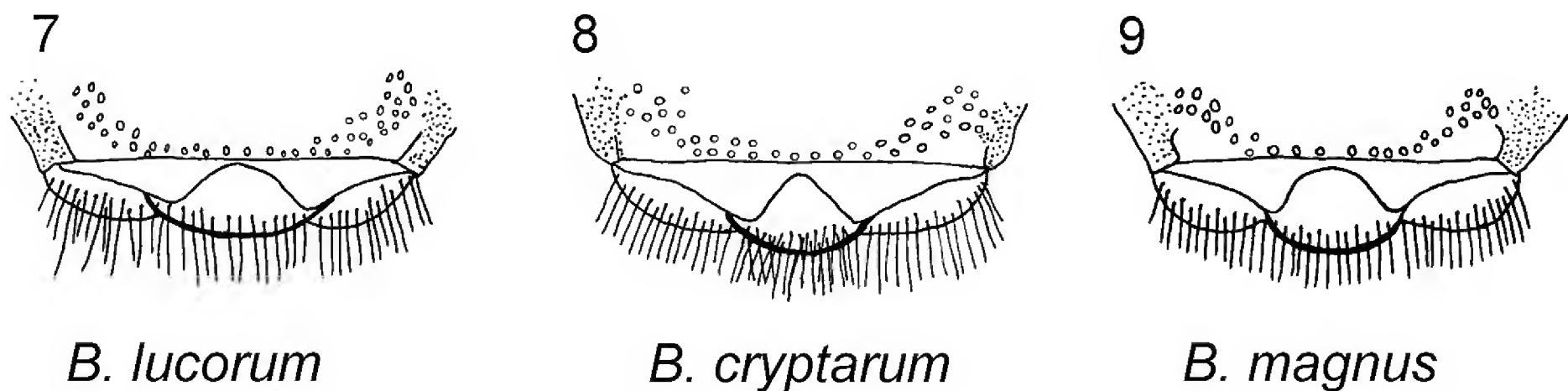
Figures 7–9. Labrum characters in frontal view. **7.** *B. lucorum*; **8.** *B. cryptarum* **9.** *B. magnus*. The drawings were provided by Johann Neumayer and are based on Rasmont (1984).

traits with complete certainty, even if most specimens are probably easily determined as described previously (Bertsch 1997, Bertsch et al. 2004, Bertsch et al. 2005).

Identification of workers

The current state of knowledge concerning the identification of workers is worse than that for queens. Rasmont (1984) postulated that the coloration of workers corresponds approximately to the coloration of queens, implying a potential distinguishability in the shape and extension of the first collar. Unfortunately, the "S"-shape of *B. cryptarum* workers can be inconspicuous or absent (P. Rasmont, personal communication). Indications for the recognition of *B. magnus* can arise if yellow hair is mixed in the black pile of the first tergum (Rasmont 1984). Recently, the distinguishability of the anterior yellow band was examined quantitatively with Scottish (Waters et al. 2011) and Austrian specimens (Bardakji 2013) and was verified with RFLPs and DNA barcodes, respectively. Both studies revealed an uncertain connection of the traits to the species. In Scotland, where all three species occur sympatrically, Waters et al. (2011) was unable to properly distinguish *B. cryptarum* from the other two species. Still there was significant difference in collar extension between *B. lucorum* and *B. magnus*. It seems that the collar extension of the Scottish *B. cryptarum* is moderately variable and therefore constrains the possibility to recognize the other two species. Unfortunately, data on the pile coloration of the first tergum were not recorded, therefore the accuracy of this potential character remains uncertain.

In a study with Austrian specimens (Bardakji 2013), the sample consisted of *B. lucorum* and *B. cryptarum* individuals only. Regarding the extension of the collar, Bardakji (2013) was able to identify a great part (85.5%, 47 of n = 55) of the workers correctly. There were considerably more identification errors in *B. cryptarum*, supporting the view that the extension of the collar of workers of *B. cryptarum* is more variable, in contrast to the others species. Aside from coloration, Rasmont (1984) described two groups of morphological characters that are accessible in queens and workers. **(I)** The first distinguishes characters of the labrum, e. g., the form of the basal area, especially if it is "U"-shaped (*B. lucorum* and *B. magnus*, Figs 7 and 9, respectively) or "V"-shaped (*B.*

cryptarum, Fig. 8). Further, the form of the lamella and punctuation are additional characters of potential value. **(II)** The second group describes the punctuations of the second tergum. Based on this, it was possible only to distinguish *B. lucorum* but not *B. cryptarum* or *B. magnus*. In contrast, Bardakji (2013) tested the reliability of the tergum-trait to differentiate between *B. lucorum* and *B. cryptarum*. It failed in roughly 1 of 5 cases. This is in line with the view of Dorow (2004), who challenged this character by describing greater variation of the second tergum than previously described (Rasmont 1984). In any case, as mentioned above, *B. magnus* was not present in the sample used by Bardakji (2013) and therefore no general statements can be made. Still, it is strongly advised to test these traits on a larger scale with all three species. To avoid misunderstandings it is important to separately name the essential structures. The lamella is the structure directly below the basal area of the labrum and is neither "U" nor "V"-shaped. These shapes refer instead to the basal elevation of the labrum (Figs 7–9).

In summary, the possibility to identify workers of all three species based on morphology has not been verified. Nonetheless, the characters of the labrum and the second tergum are particularly promising. Further morphological comparative examinations, which are supported by DNA barcoding, are necessary to verify these potential identifying characters and to uncover new traits. In the field, the extension of the first collar may be an indicator but is definitely not reliable, especially if all three species co-occur. Additionally, the reliability of the yellowish coloration of the first tergum for workers of *B. magnus* is worthy of further investigation.

Identification of males

Identification of the males is probably the most difficult case. Authors of recently published studies agreed that they are indistinguishable by morphology (Murray et al. 2008, Bertsch 2009, Waters et al. 2011). All three taxa are very similar and show extensive and overlapping variation in color and male genitalia (Rasmont et al. 1986). Therefore, keys based on coloration of the pile of the "face" (e.g., Amiet 1996, Dorow 2004, Gokcezade et al. 2010) are of restricted value, even if they may work for certain geographic regions. In the wider European context, these

keys will fail to properly distinguish all male specimens of the complex. Aggravating this situation is the fact that the males of *B. terrestris* may also be confused with males of the *B. lucorum*-complex, in particular with specimens of *B. cryptarum* that have a dark facial pile. Although, *B. cryptarum* males often show the "S"-shape, it is geographically restricted and especially *B. cryptarum* and *B. magnus* can be more or less identical in morphology (P. Rasmont, personal communication). Aside from coloration, Rasmont et al. (1986) described several potential morphological characters to identify males at the species level. In this respect, the authors highlighted the punctuation of the second tergum as a distinguishing character for *B. lucorum* against *B. cryptarum* and *B. magnus*. Additional characters concern the diameter of the ocelli and the shape of the eighth tergum. The reliability of these traits in the wider European context remains uncertain. As long as no new insights in the distinguishability of the males are gained, completely reliable identification can only be achieved by biochemical or genetic approaches.

Current challenges

Difficulty in species recognition constrains our current knowledge

The long and difficult process of the recognition and acceptance of the species of the *B. lucorum*-complex has caused a number of critical problems concerning our current knowledge of the ecology and distribution of these species. First, the lack of applicable characters that are useful and easy for identification makes it difficult to obtain reliable data from the literature. The great majority of previous studies on these species are based on morphological identification and hence should be viewed cautiously. Additionally, the possibilities of achieving faunistic data by interested amateurs and citizen scientists are very restricted and can barely contribute to scientifically founded statements in this concern. Second, the late redescription of *B. cryptarum* by Rasmont (1981a) implies that practically all data published before the redescription are unreliable since it was not possible to distinguish the species based on the debatable morphological traits. An example from Austria illustrates this point. All reported findings of *B. magnus* from Austria known to the author either before or shortly after the redescription, including the records of Schedl (1982) and Mathis (1982), findings from W. F. Reinig in Aistleitner (2000) and Ressl (1995), and the findings from B. Tkalců in Neumayer and Kofler (2005), were recently reexamined and found to belong to *B. cryptarum* based on morphology (J. Neumayer, personal communication). This demonstrates the importance of verifying older records from the literature and reveals that the unconditional use of references published before that date could lead to confusion, such as the citation of the textbook of Alford (1975) in Murray et al. (2008) or Waters et al. (2011). Third, the predicament is addition-

ally aggravated by the treatment of *B. cryptarum* by authors. Several experts declined to immediately accept *B. cryptarum* as a valid taxon and pooled the available data. In a strict sense, the identification method of every contribution should be reexamined, and the information in several reference textbooks or compilations (e.g., Prŷs-Jones and Corbet 1987, Westrich 1990) unfortunately cannot be regarded as totally reliable. In light of these problems, the number of dependable studies is much reduced. Reliable ecological and distributional data is primarily available in recent studies based on biochemical identification methods. Further, the excellent publications of Pierre Rasmont (Rasmont 1981a, Rasmont 1983, Rasmont 1984, Rasmont et al. 1986, Banaszak and Rasmont 1995) deserve our continued attention regarding the bumblebees of the *B. lucorum*-complex.

Current issues concerning the distribution and ecology

Bertsch et al. (2004) carefully outlined the distribution of the species. Additional data comes from the recent COI-based studies (Murray et al. 2008, Anagnostopoulos 2009, Bertsch 2009, Waters et al. 2011, Carolan et al. 2012, Vesterlund et al. 2014) and from the distribution maps on bumblebees in the Atlas Hymenoptera project (Rasmont and Pauly 2010, Rasmont and Iserbyt 2010–2013). In these works the distribution, especially of *B. cryptarum* and *B. magnus*, appears fragmentary. The isolated finding of *B. cryptarum* in the Balkans (Anagnostopoulos 2009), the lack of doubtless identified *B. magnus* from the Iberian Peninsula south of the Pyrenees and the old records from Eastern Europe reveals the need of further sampling in these regions. Specimens from the Iberian Peninsula are of particular importance since there are indications that queens of *B. lucorum* exhibit a collar coloration similar to *B. magnus* queens in central Spain (Bertsch 2009). Against the background of the false records from the Austrian Alps, the presence of *B. magnus* in the Western Alps and along the southern slopes of the Alps must be verified as well. Species identification accomplished using COI barcodes should contribute to clarify our patchy knowledge on the distribution of the genetic haplotypes and might help outline postglacial recolonization events.

Further investigations are also necessary to understand the factors that drive the species abundances on regional and European scales, since species composition can vary greatly at the regional level (Murray et al. 2008, Waters et al. 2011). One factor that has been claimed to influence the species composition is altitude. For example, Murray et al. (2008) revealed a changing species composition along a relatively low altitudinal gradient, and Neumayer and Paulus (1999) regarded *B. cryptarum* to be a high mountain species. Further, Scholl and Obrecht (1983) concluded that one *B. lucorum* s.l. taxon occurs at higher relative frequency in the Alps. In contrast, the fact that all species can be found to live sympatrically in various lowland habitats in greater parts of Europe means that altitude cannot be the determining factor for a species' distribu-

tion. However, the association of *B. cryptarum* with the high altitudes of the Alps and the observation of Pamilo et al. (1997) that *B. cryptarum*/*B. magnus* becomes predominant in northernmost Finland justify further investigation into the ecological factors that change with increasing altitude and latitude. Additional research is still pending concerning habitat use and nesting biology. Waters et al. (2011) made significant inroads to understand habitat usage but the study was restricted to relatively few habitats in northwestern Scotland. Regarding continental Europe, most recent studies specify the habitat types of the collection areas, but comparative studies concerning the used habitat or nesting sites over a sufficient geographic area are not available. Especially the exact habitat use of *B. magnus* appears unclear. The occurrence of this species seems to be very patchy but regionally common (Bertsch et al. 2004). Further, it is frequently associated with heathlands (Banaszak and Rasmont 1994, Waters et al. 2011) and visits species of Ericaceae (Rasmont 1984, Bertsch et al. 2004). Yet, the species is neither restricted to heathland nor does it rely on Ericaceae. Of particular note is that the species seems to occur in habitats with a very low diversity of flowering plant species, such as mass-flowering Ericaceae in heathlands or *Melampyrum pratense* in commercial forests (personal observation). Comparative studies are also necessary to improve our knowledge of the species bionomies, e.g., by examining exact nesting sites, and might confirm the phenological differences suggested by Bertsch et al. (2004).

The importance of regionally stable characters

Traditionally, a significant part of the faunistic data of bumblebees in Europe is contributed by dedicated amateurs from the public rather than institutional scientists. At present, the restrictive possibility of identifying specimens by morphology has prevented reports of species of the *Bombus lucorum*-complex by citizen science. However, observations described in the literature suggest that species of the complex exhibit certain characters in certain regions such as the characteristic melanized collar, probably restricted to queens of *B. cryptarum* in northern Germany (Bertsch et al. 2005), or the "pinkish-buff" on the metasoma of fresh *B. magnus* queens that was reported from Northern Scotland (Macdonald 1999). It should be worthwhile to consider the reliability and stability of such characters to allow the public to make use of them for morphologically based identifications in particular regions. In this respect, particularly promising is the coloration of clypeal hairs in males. Admittedly males show extensive color variation in facial hair (Rasmont et al. 1986, Table 2), yet there are indications that regionally stable characters exist. The keys of Amiet (1996), Dorow (2004) and Gokcezade et al. (2010) share the same color-based system to distinguish males of all species from Switzerland, Hessia (Germany) and Austria, respectively. An examination of the reliability of these traits in the mentioned regions is of particular value, since the rele-

vant characters are accessible in the field and hence might serve as a window to achieve distributional data without the need for molecular or biochemical analyses.

Future tasks

1. Investigations of nuclear genes of the species from the *Bombus lucorum*-complex will contribute to underpin the species' status and help to estimate more accurate phylogenies.
2. New genetic sequence data, especially from the Mediterranean peninsulas, will enhance the current knowledge about the genetic diversity within the complex and might help to evaluate potential postglacial recolonization events.
3. The reported distinguishing morphological characters must be tested for all castes of all species in a wider European context against a biochemical control and on a sufficiently large scale. Further, it would be of particular importance to discover new distinguishing characters.
4. Investigations to determine regionally stable morphological or coloration characters might facilitate the acquisition of new distributional and ecological data by citizen scientists.
5. The reexamination of museum specimens, at best, backed up with a sequencing of COI fragments, can allow the correct assignment of historic records and will help to highlight incorrect species identifications.
6. Additional acquisition of good ecological and distributional data from accurately identified specimens will increase our knowledge about the species' ecology. Among others, future studies should focus on altitudinal differences, nesting sites and habitat use of the species.

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PENSOFT.

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Internal ornamentation of the first proctodeal segment of the digestive tube of Syntermitinae (Isoptera, Termitidae)

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Abstract

The ornaments inside the first proctodeal segment of the digestive tube in thirty-three species of the termite subfamily Syntermitinae are described and illustrated, encompassing all genera of the subfamily. The occurrence, type and pattern of the ornamentation reveal a wide morphological diversity. A first proposal for classification and nomenclature of these structures and coverage patterns is included, as well as a discussion of possible functions.

Key Words

Introduction

The termite gut is specialized for the digestion of lignocellulosic resources. Unlike other insects, the hindgut is compartmentalized, and five segments can be recognized: ileum, or first proctodeal segment (P1); enteric valve, or second proctodeal segment (P2); paunch, or third proctodeal segment (P3); colon, or fourth proctodeal segment (P4); and rectum, or fifth proctodeal segment (P5) (Noirot 1995). During the evolution of termites, many groups evolved more anatomically and physiologically complex adaptations that allowed them to diversify their diet. For example, members of the subfamily Cubitermitinae, a well-characterized soil-feeder group, have a specialized diverticulum connected to the P3, and a complex physiology that regulates the pH and the oxygen supply in the gut compartments (Brune 2014). The digestive process, mediated by symbionts, occurs mainly in the P3, but the entire gut is important for digestion.

The gut characters are important for termite taxonomy. One of the first comprehensive studies employing gut anatomy was that of Sands (1972), who reorganized a complex of soldierless termite species and described 16 new genera, based mainly on these characters; additionally, Sands revamped the entire classification of Termitidae. Although Sands never employed the P1 ornaments, his work is a good example of how the morphology of the gut can be taxonomically informative for Isoptera. Although the internal ornaments have been widely used in termite systematics, the major focus has been on P2, and published information about other segments is sparse.

Kovoor (1969) contributed the first comparative study of the anatomy of the digestive tube of termites, including species of Syntermitinae (at that time considered as part of Nasutitermitinae). She described the gut of *Cornitermes cumulans*, *Labiotermes pelliceus*, *Procornitermes triacifer*, *Rhynchotermes nasutissimus*, *Syntermes dirus* and an unspecified species of "*Armitermes*" (probably *Silvestritermes euamignathus*), emphasizing important morphological differences between the "mandibulate nasutes" and "true nasutes", which today are assigned to the Syntermitinae and Nasutitermitinae, respectively. Kovoor (1969) mentioned the existence of ornamentation inside the (P1) in Syntermitinae, describing and

illustrating this ornamentation for *Syntermes dirus* (only by a small indication, without details) and describing a slightly different arrangement of spines for other species of the *Syntermes*-group. However, she did not discuss the possible significance of the differences or make a detailed microscopic examination of the ornamentation.

The papers of Noirot (1995, 2001) systematized the knowledge of termite gut anatomy, establishing a nomenclature and comparing a wide range of species from all families and subfamilies of Isoptera, and also the wood roach *Cryptocercus*, the sister-group of termites (Krishna et al. 2013). Noirot (1995) described the first proctodeal segment in lower termites. In these groups the P1 is very short and has six internal cushions, with tri-radial symmetry and ornamented with small spines, similar to *Cryptocercus*. Noirot (2001) indicated that the ornamentation, although reduced, persists in the subfamily Macrotermitinae, but for the other groups of Termitidae it is not clear if there is a pattern.

Except for the study of Kovoor (1969), the P1 internal ornaments are neglected in termite literature, particularly for species of Termitidae. Even in the most comprehensive termite treatises that include information about the gut anatomy (Grassé 1982; Krishna et al. 2013; Noirot 1995, 2001), the existence of these ornaments is only mentioned, and there is no specific description, categorization or hypothesis respecting their function. As mentioned above, Noirot (1995, 2001) described a generalized pattern for the families of lower termites, but except for few notes about Macrotermitinae, almost nothing is mentioned for Termitidae, which comprise two-thirds of Isoptera species. Besides, Termitidae have a much larger food repertoire compared with the lower termites, that feed strictly wood (Brune 2014).

Herein we describe and compare the internal ornamentation of the first proctodeal segment for a comprehensive set of Syntermitinae species, and propose, for the first time, a comparative nomenclature for these structures and coverage patterns. There is wide variation within the subfamily, and insights about the taxonomic value, classification by feeding habits, and function in termite digestion are discussed.

Materials and methods

The specimens studied are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. We dissected individuals of 36 species of Syntermitinae, covering all genera (Table 1). These represented nearly one-third of the 101 described taxa of Syntermitinae, and were chosen by a previous examination of all subfamily species to include the most representative.

The arrangement of the ornamentation is represented by schematic drawings. Since in the Syntermitinae the P1 is inflated and globose, it is impossible to photograph or illustrate the complete coverage exactly as it exists *in situ* and on the actual scale. The plan of the dissections is explained in Fig. 1.

Table 1. Genera and species studied.

Genera (total number of described species)	Studied species
Acangaobitermes (1)	*A. krishnai*
Armitermes (3)	*A. armiger*
	A. bidentatus
	A. spininotus
Cahuallitermes (2)	*C. intermedius*
Cornitermes (14)	*C. acignathus*
	C. cumulans
	C. bolivianus
	C. silvestrii
Curvitermes (2)	*C. odontognathus*
Cyrilliotermes (4)	*C. angulariceps*
Embiratermes (14)	*E. brevinasus*
	E. festivellus
	E. heterotypus
	E. ignotus
	E. robustus
	E. silvestrii
Ibitermes (3)	*I. curupira*
	I. tellustris
Labiotermes (10)	*L. emersoni*
	L. labralis
	L. leptothrix
	L. orthocephalus
Macuxitermes (1)	*M. triceratops*
Mapinguaritermes (2)	*M. peruanus*
Noirotitermes (1)	*N. noiroti*
Paracurvitermes (1)	*P. manni*
Procornitermes (5)	*P. araujoi*
	P. lespesii
	P. triacifer
Rhynchotermes (7)	*R. nasutissimus*
	R. perarmatus
Silvestritermes (7)	*S. euamignathus*
Syntermes (23)	*S. molestus*
	S. spinosus
Uncitermes (1)	*U. teevani*

The structures were removed, mounted in glycerin, and photographed under an optical microscope (Zeiss Microscope Axionskop 2 coupled to a computer). The terminology adopted for the digestive tube follows Noirot (2001).

Results

The analysis of the P1 ornamentation revealed a wide diversity of structures and patterns (Figs 2–25). The structures can be categorized by form and relative arrangement, and the ornamentation by the types of spines and their abundance. As a specific nomenclature for these structures does not exist, we propose some terms that are discussed below.

Categories of structures

Aciculiform spines are slender and straight. They vary in size from relatively large (around 20 μm; for example, Figs 5b, 10b, 18c, 22b, 22c) to relatively small (around 5
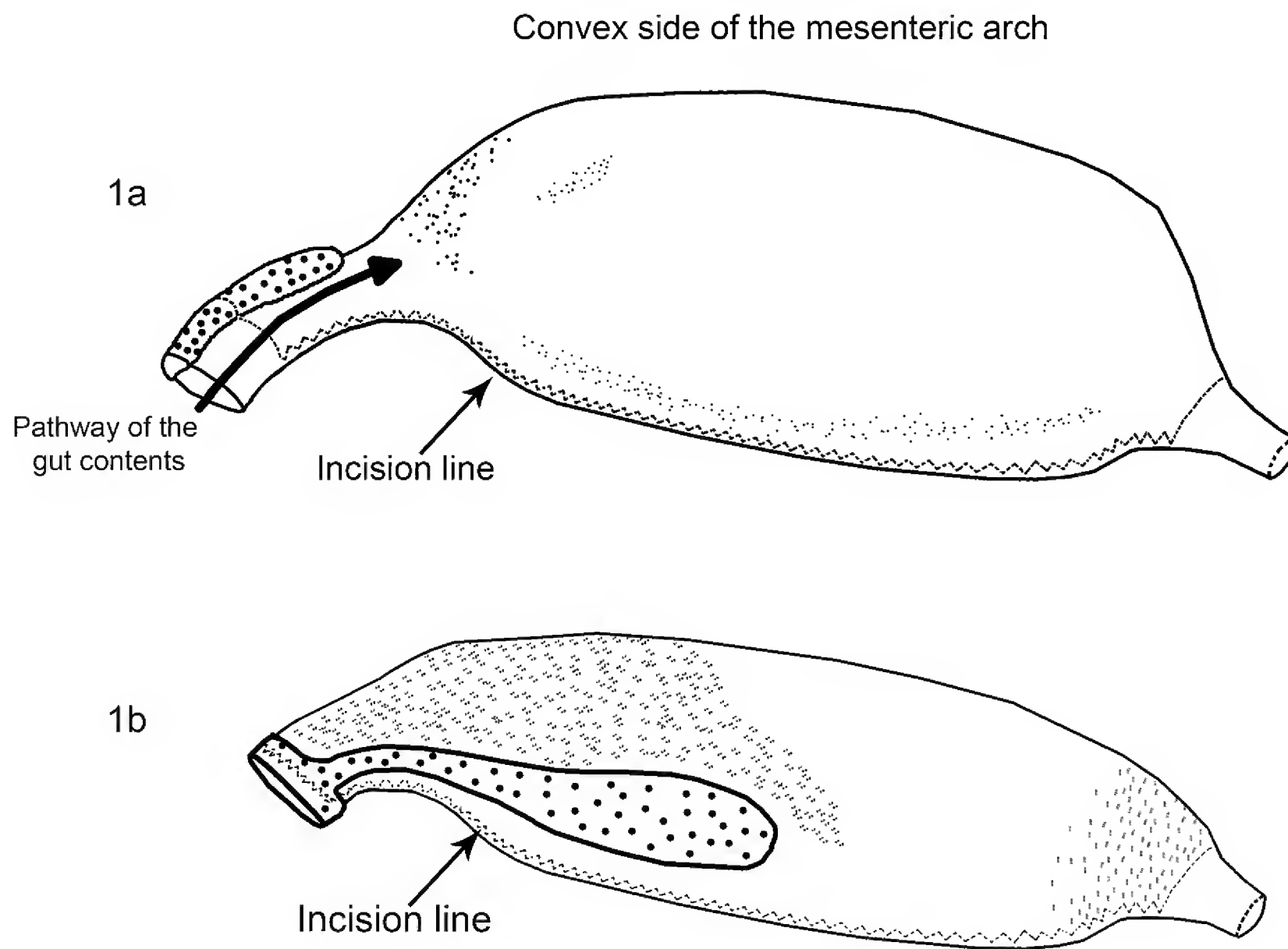
Figure 1. First proctodeal segment (P1), diagrammatic illustrations showing the line of incision most often used in this study. **(a)** *Silvestritermes euamignathus*, mesenteric tongue and ornamentation situated on convex side of mesenteric arch; **(b)** *Rhynchotermes nasutissimus*, ornamentation situated on convex side of mesenteric arch and mesenteric tongue twisted.
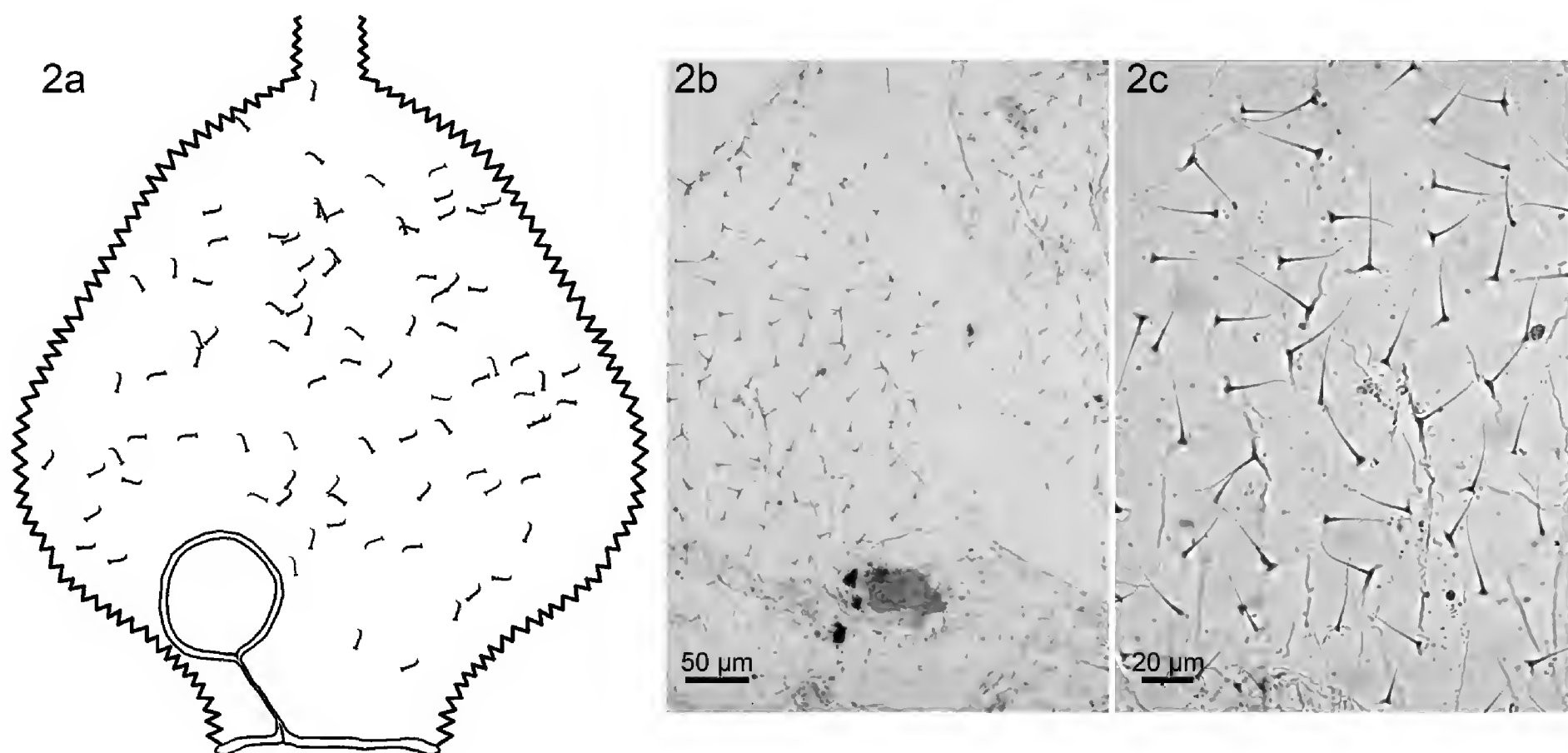

Figure 2. *Armitermes spininotus*. **(a)** Schematic drawing of P1 showing arrangement of ornamentation. **(b, c)** Photomicrographs: **(b)** General view; **(c)** Detail of ornamentation of thin setae.

μm, Figs 6b, 6c), and in some species these spines have a sclerotized base (Figs 3b, 21b, 23d, 23e, 24c). Two variations of the aciculiform type are the trifurcated spines (Fig. 8b) and thin setae (Fig. 2c).

Robust spines are relatively short (around 10 μm), with a simple conical shape. They are sparsely distributed (Figs 16b, 25b).
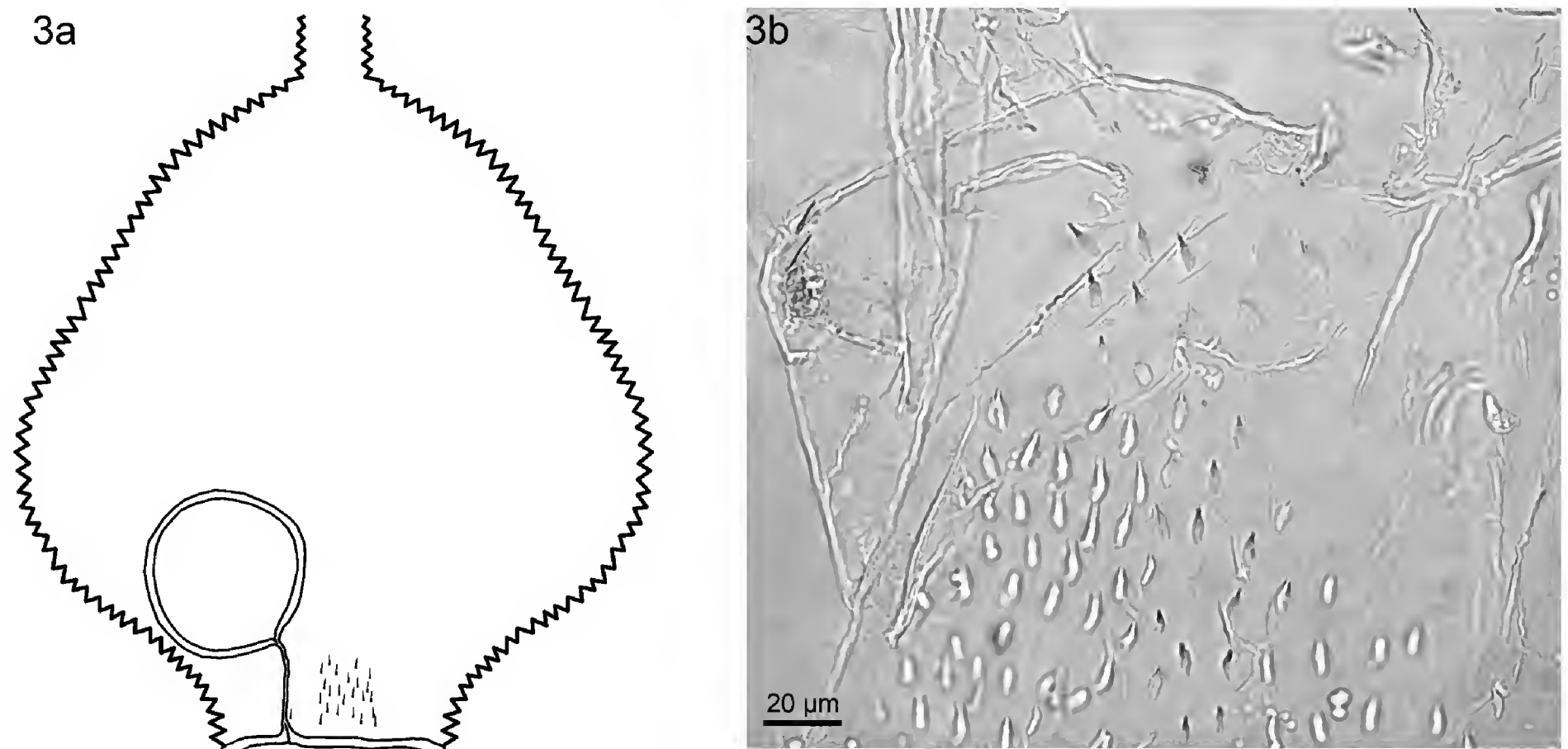
Figure 3. *Cornitermes bolivianus.* **(a)** Schematic drawing of P1 showing arrangement of spines; **(b)** Photomicrograph showing detail of spines with sclerotized bases.
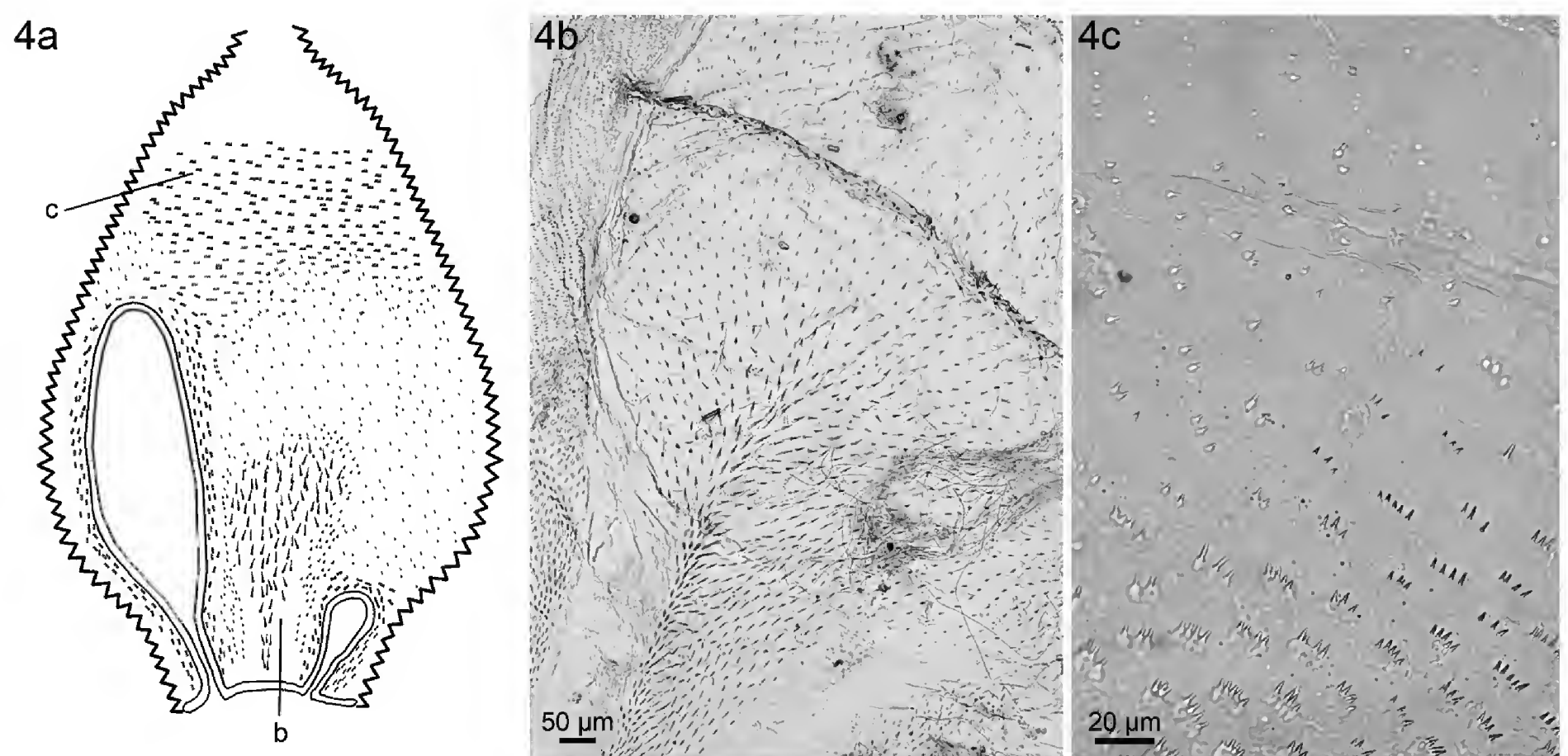

Figure 4. *Cornitermes cumulans.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Aciculiform spines, situated between the mesenteric tongues; **(c)** Detail of short spines in rows, present around the mesenteric tongues and next to P2.

Stout spines are similar to robust spines, but larger and sometimes slightly curved; they may be arranged longitudinally (Figs 11c, 16c) or regularly alternating (Fig. 12d).

The central ridges, present in some species of *Labiotermes* (Figs 13c, 14c, 15c), are single structures, composed of spines with their bases fused, arranged in a helical pattern. These ridges are probably homologous to the longitudinal arrangement of stout spines in *Ibitermes curupira* and *Mapinguaritermes* (Figs 11c, 16c), since their placements are equivalent inside P1.

Small spines in rows (Figs 4c, 21c, 23c, 23f) are tiny and have a typical transverse arrangement in units of 2–6 spines.

Patterns of ornamentation

The coverage and abundance of spines can be categorized in four types of patterns.

Proximal aciculiform pattern: composed by aciculiform spines, restricted to the proximal region (Figs 5a, 6a, 9a, 10a, 17a, 18a, 20a, 22c), and usually with three groups of small spines in the distal portion (Figs 6c, 9c,
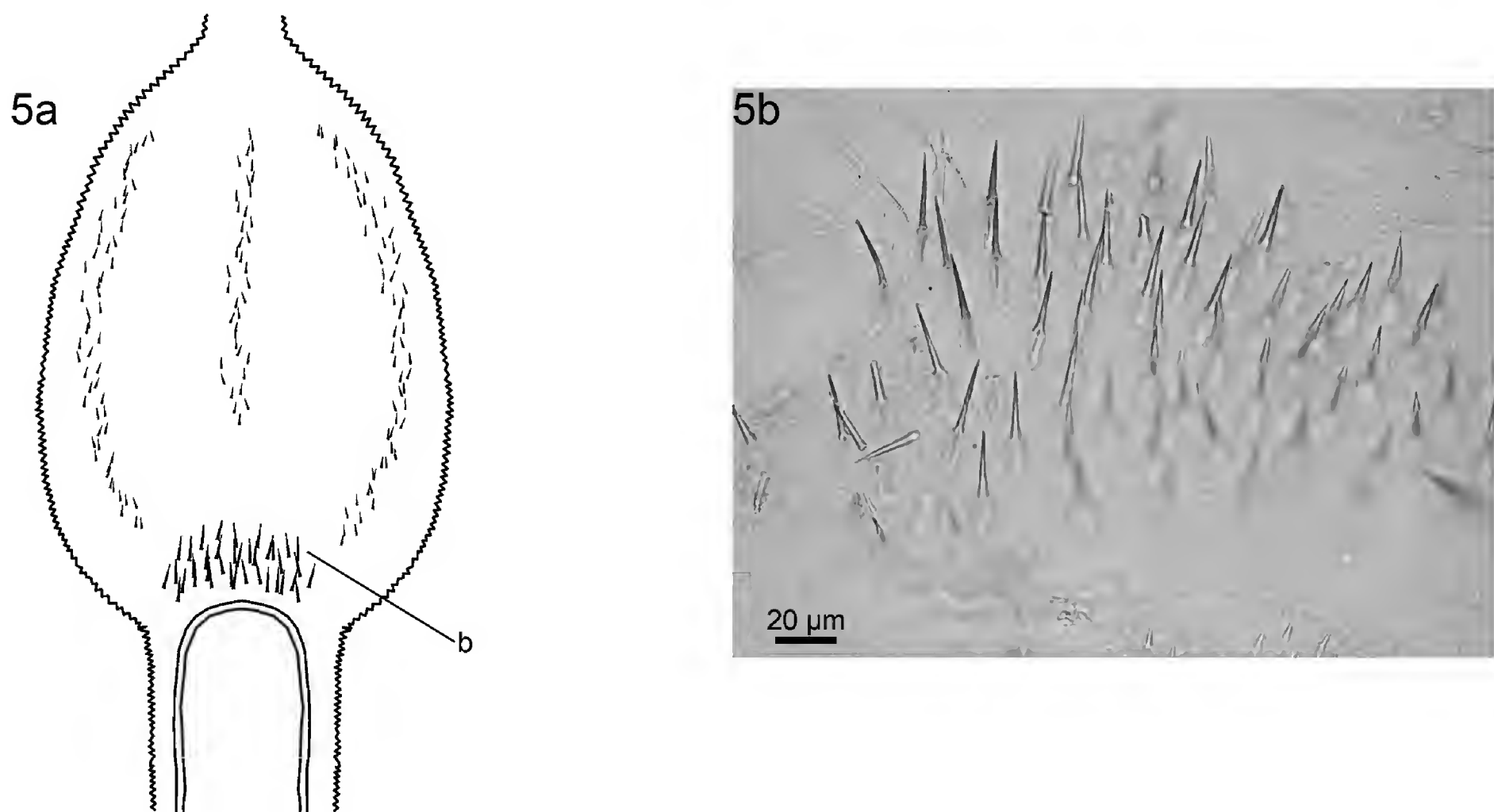
Figure 5. *Curvitermes odontognathus.* (a) Schematic drawing of P1 showing arrangement of spines; (b) Photomicrograph of set of aciculiform spines, positioned just after the mesenteric tongue.
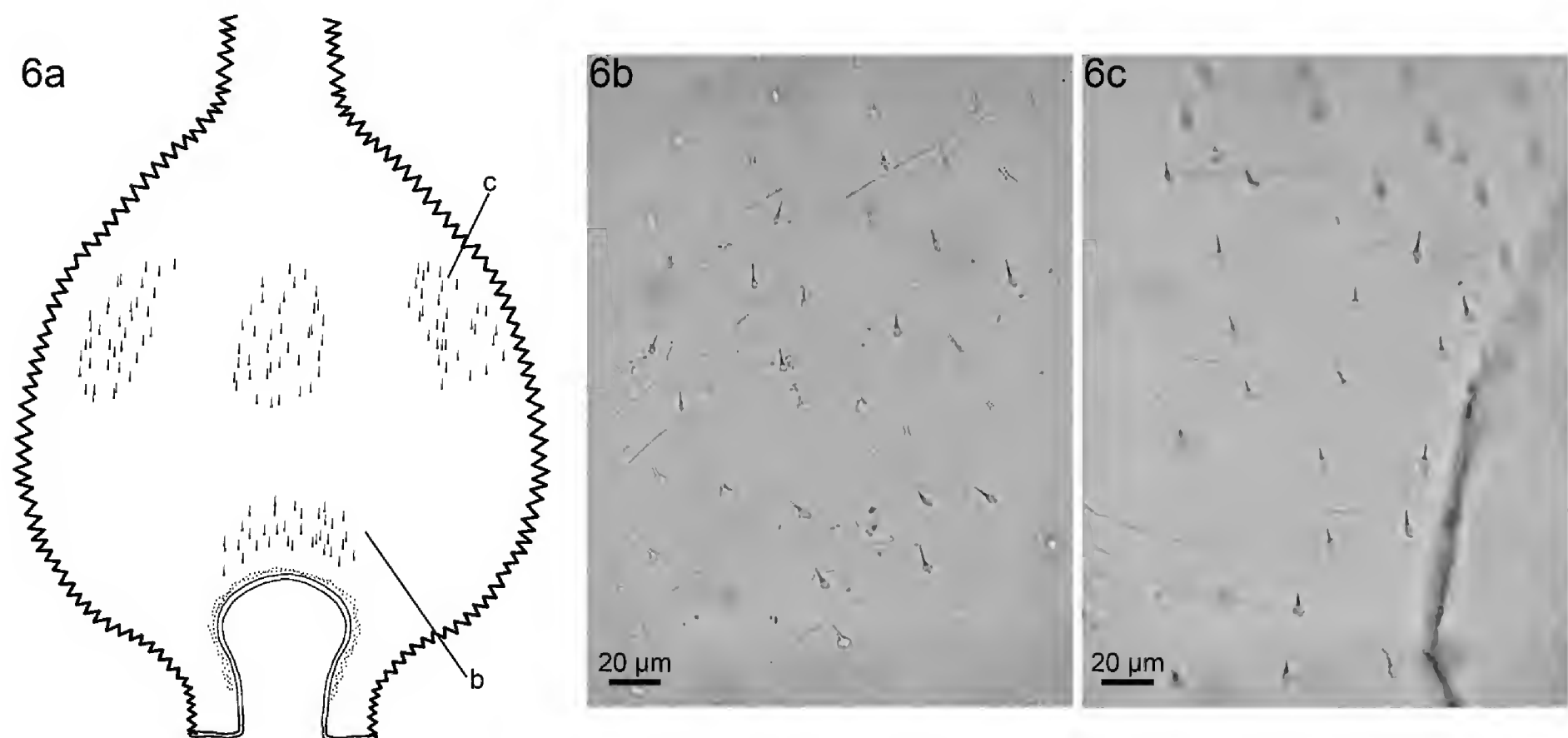

Figure 6. *Cyrilliotermes angulariceps.* (a) Schematic drawing of P1 showing arrangement of spines. (b, c) Photomicrographs: (b) Reduced spines located in proximal region. (c) Spines in distal region.

18b, 20b), the following species can be included in this category:

Acangaobitermes krishnai: Identical to *N. noiroti* (see ahead).

Curvitermes odontognathus (Fig. 5): A group of aciculiform spines is located just after the mesenteric tongue (Fig. 5b), at the distal region three long branches of small spines are present.

Cyrilliotermes angulariceps (Fig. 6): The coverage is composed only by small aciculiform spines, one group located just after the mesenteric tongue (Fig. 6b), and three ovate areas are present at the distal region (Fig. 6c).

Embiratermes brevinasus: identical to *E. ignotus* (see ahead).

Embiratermes festivellus (Fig. 10): A triangular area of aciculiform spines is located just after the mesenteric
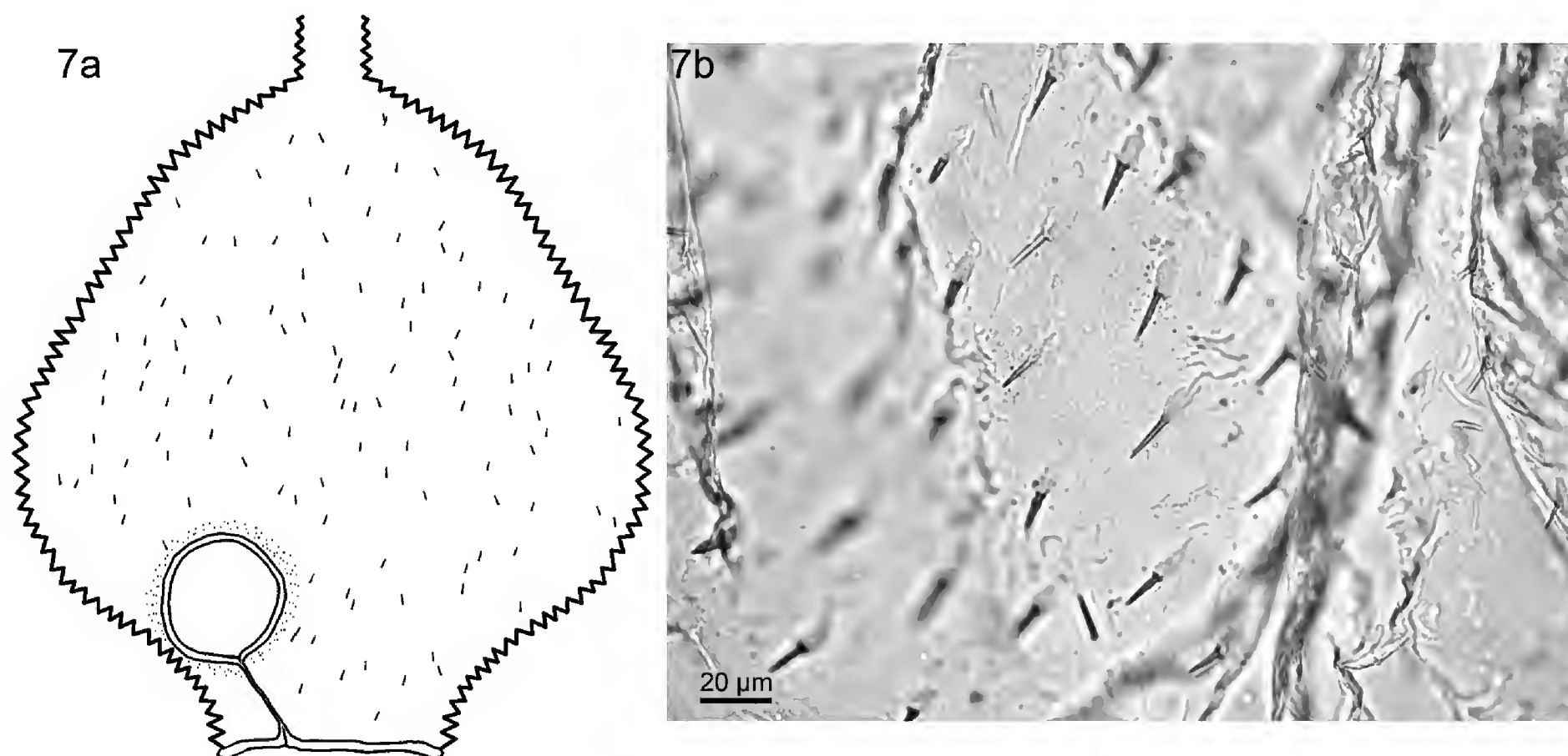
Figure 7. *Embiratermes heterotypus.* **(a)** Schematic drawing of P1 showing arrangement of spines; **(b)** Photomicrograph showing detail of aciculiform spines.
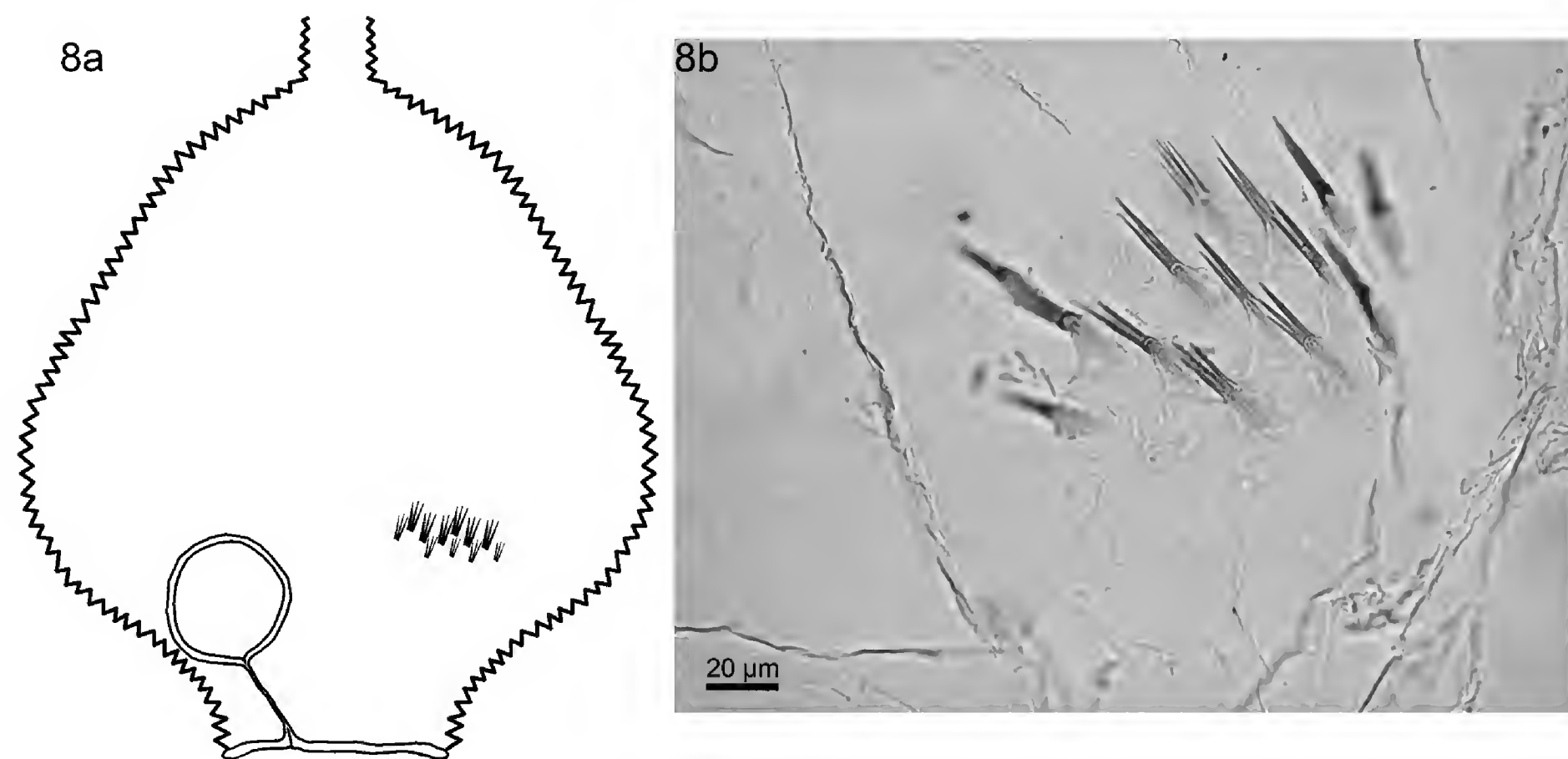

Figure 8. *Embiratermes ignotus.* **(a)** Schematic drawing of P1 showing arrangement of spines; **(b)** Photomicrograph showing detail of trifurcated spines.

tongue (Fig. 10b), and three oval areas, covered with small aciculiform spines, present at the distal region.

Embiratermes ignotus (Fig. 8): The only ornament is a single transversal row of trifurcate spines, placed laterally to the mesenteric tongue (Fig. 8b).

Embiratermes silvestrii (Fig. 9): An oval area of aciculiform spines is located laterally to the mesenteric tongue (Fig. 9b), and three branches of small spines, one long and two shorts, are present at the distal region (Fig. 9c).

Ibitermes tellustris: very similar to *E. silvestrii* (see above).

Macuxitermes triceratops: (Fig. 17): An elongated area of aciculiform spines is placed close and laterally to the mesenteric tongue (Fig. 17c), the distal portion is broadly covered by sparse small spines (Fig. 17b).

Noirotitermes noiroti (Fig. 18): A group of aciculiform spines is located laterally to the mesenteric tongue (Fig. 18c), and at the distal region three long branches of small spines are present (Fig. 18b).

Paracurvitermes manni (Fig. 20): A transversal row of aciculiform spines, placed laterally to the mesenteric tongue is located laterally to the mesenteric tongue
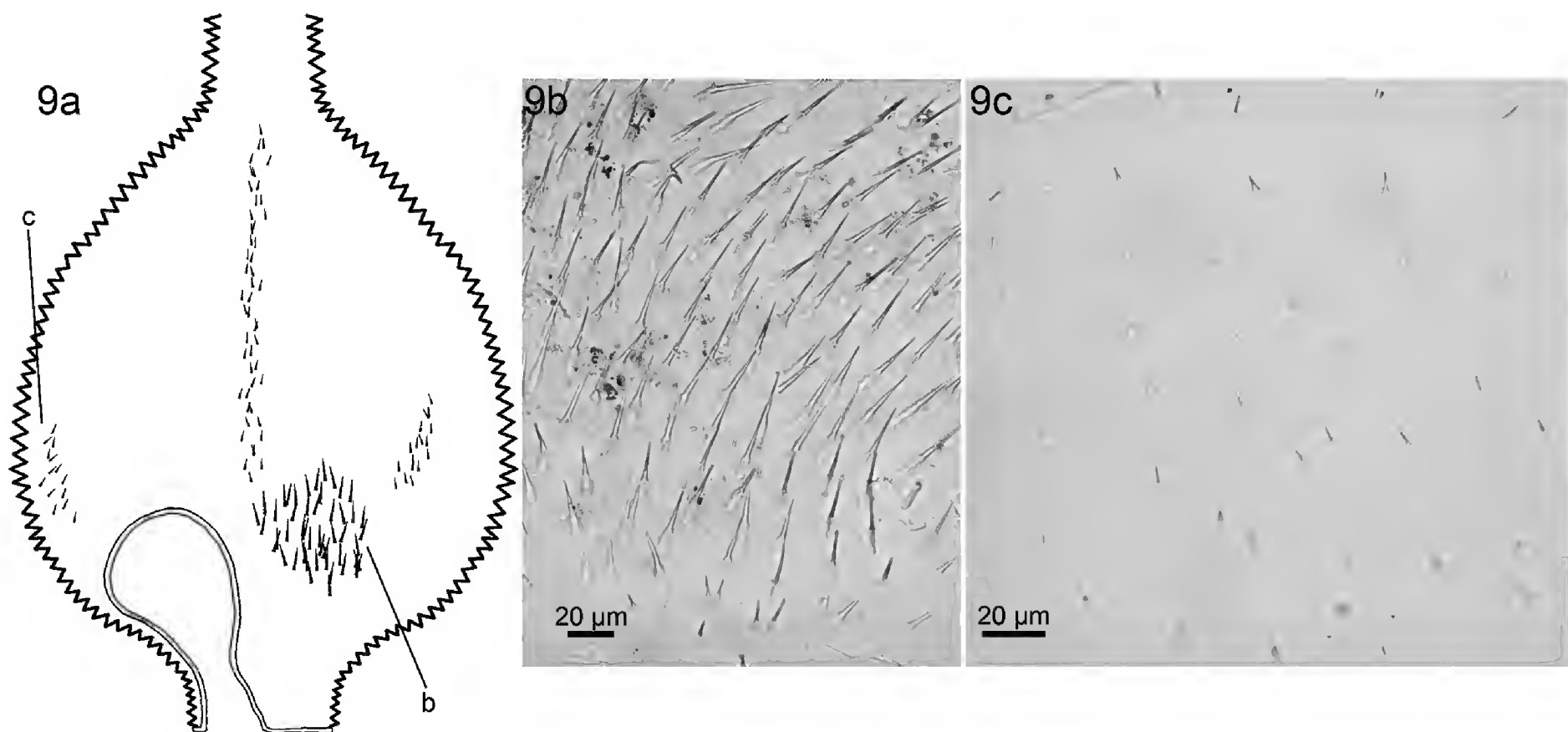
Figure 9. *Embiratermes silvestrii.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Set of aciculiform spines in detail; **(c)** Spines of the distal branches in detail.
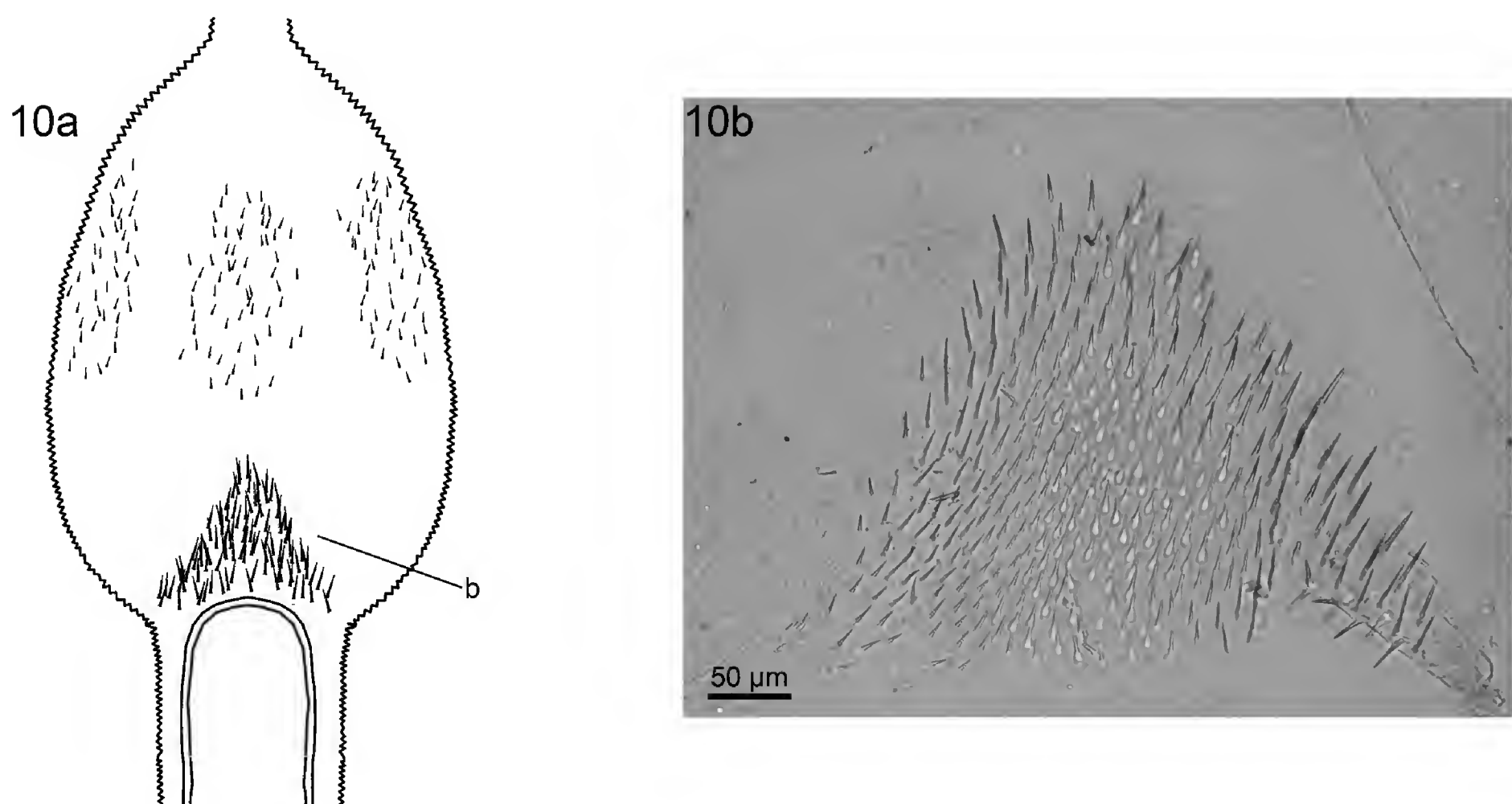

Figure 10. *Embiratermes festivellus.* **(a)** Schematic drawing of P1 showing arrangement of spines; **(b)** Photomicrograph showing detail of aciculiform spines.

(Fig. 20c), and three branches of small spines, one long and two shorts, are present at the distal region (Fig. 20b).

Silvestritermes euamignathus (Fig. 22): A triangular area of aciculiform spines is located just after the mesenteric tongue (Fig. 22c), the aciculiform spines form a singular palisade around the mesenteric tongue (Fig. 22b). Three branches of small spines, one long and two very short, are present at the distal region.

Central ridge pattern: characterized by the presence of a longitudinal row of stout spines (Figs 11a, 16a) or the central ridge (Figs 12a, 13a, 14a, 15a), commonly surrounded by robust spines, the following species can be included in this category:

Embiratermes robustus: very similar to *M. peruanus* (see ahead).

Ibitermes curupira (Fig. 11): The ornaments are concentrated laterally to the mesenteric tongue, a longitudinal
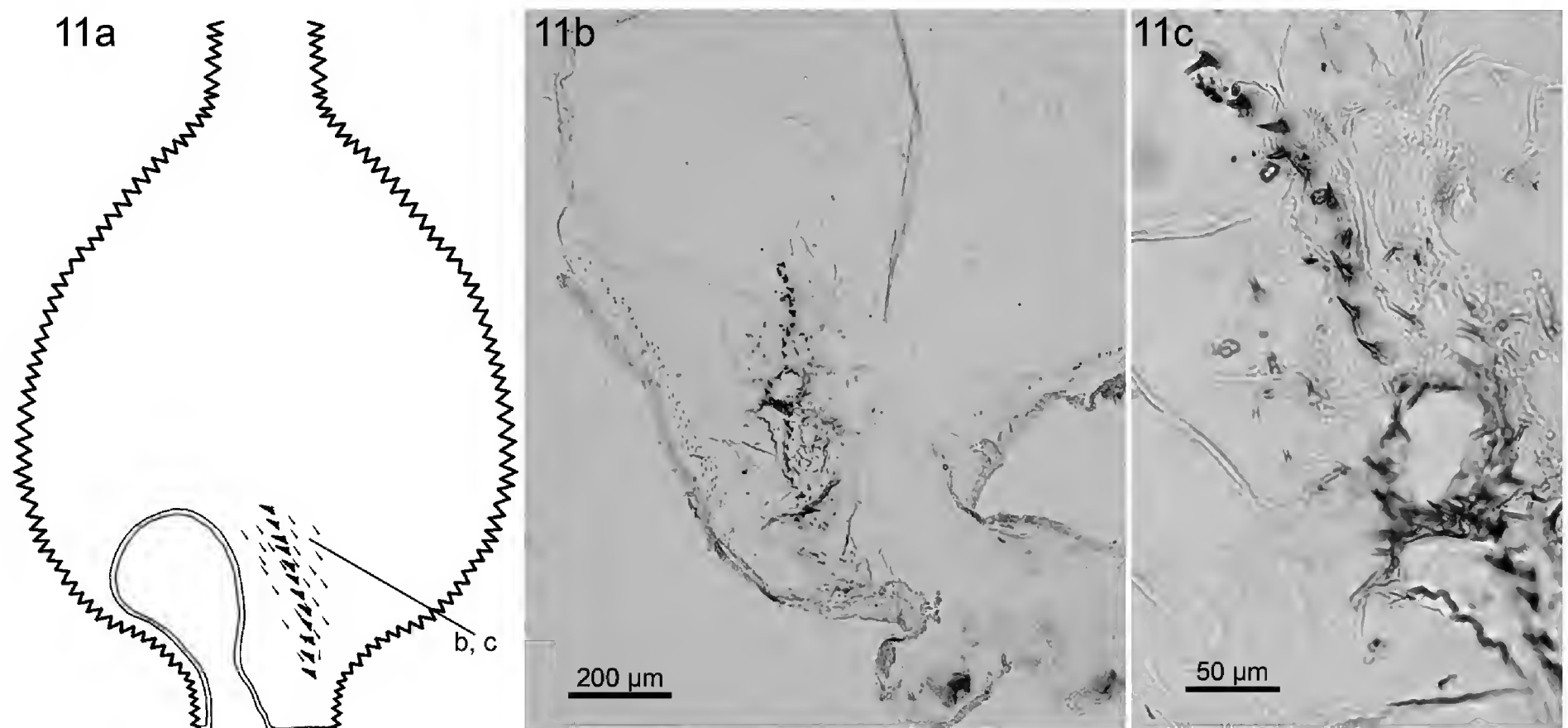
Figure 11. *Ibitermes curupira.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view of longitudinal row of stout spines, with some robust spines nearby (middle of P1 wall slightly damaged); **(c)** Detail of stout spines.
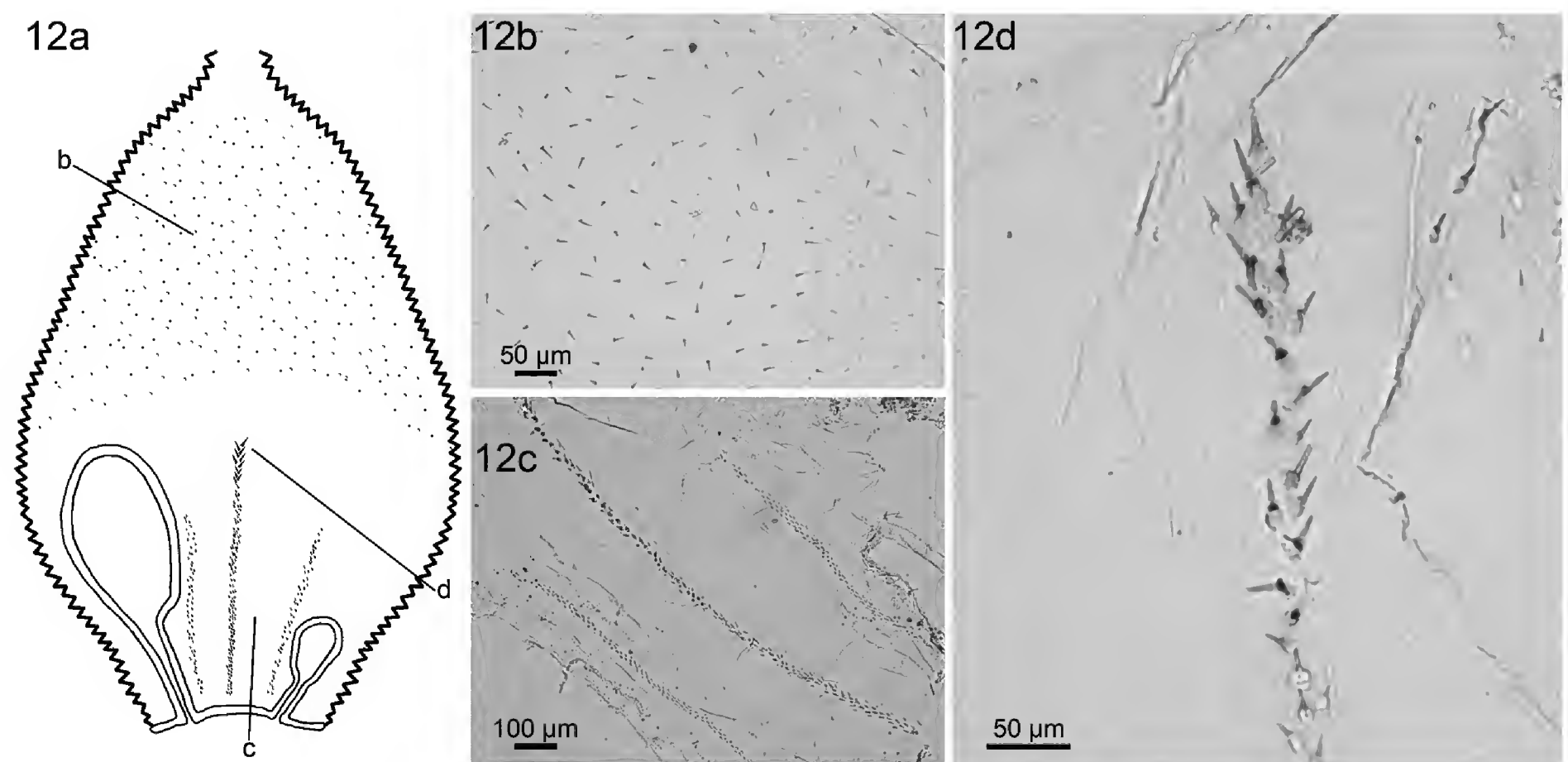

Figure 12. *Labiotermes emersoni.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b–d)** Photomicrographs: **(b)** Detail of spines in the distal region; **(c)** General view of the three branches of spines between the mesenteric tongues; **(d)** Detail of middle branch of spines.

row of 20–25 stout spines (Fig. 11c), and few robust spines spaced distributed around the stout spines.

Labiotermes emersoni (Fig. 12): At the proximal region, between the mesenteric tongues, three longitudinal rows of robust spines (Fig. 12c) with the central ridge at the apex of the middle row (Fig. 12d), distal region covered with spaced small bristles (Fig. 12b).

Labiotermes labralis (Fig. 13): The internal surface is all covered with spaced robust spines (Fig. 13b), with a small central ridge (Fig. 13a).

Labiotermes leptothrix (Fig. 14): The central ridge is "S" shaped, well sclerotized with the fused spines (Fig. 14a), distal region covered with spaced robust spines.

Labiotermes orthocephalus (Fig. 15): The central ridge is composed by 10–15 slightly fused spines (Fig. 15c); distal region is covered with spaced robust spines (Fig. 15b).

Mapinguaritermes peruanus (Fig. 16): The ornaments are concentrated laterally to the mesenteric tongue, a longitudinal row of 15–20 stout spines (Fig. 16c), and robust spines spaced distributed around.
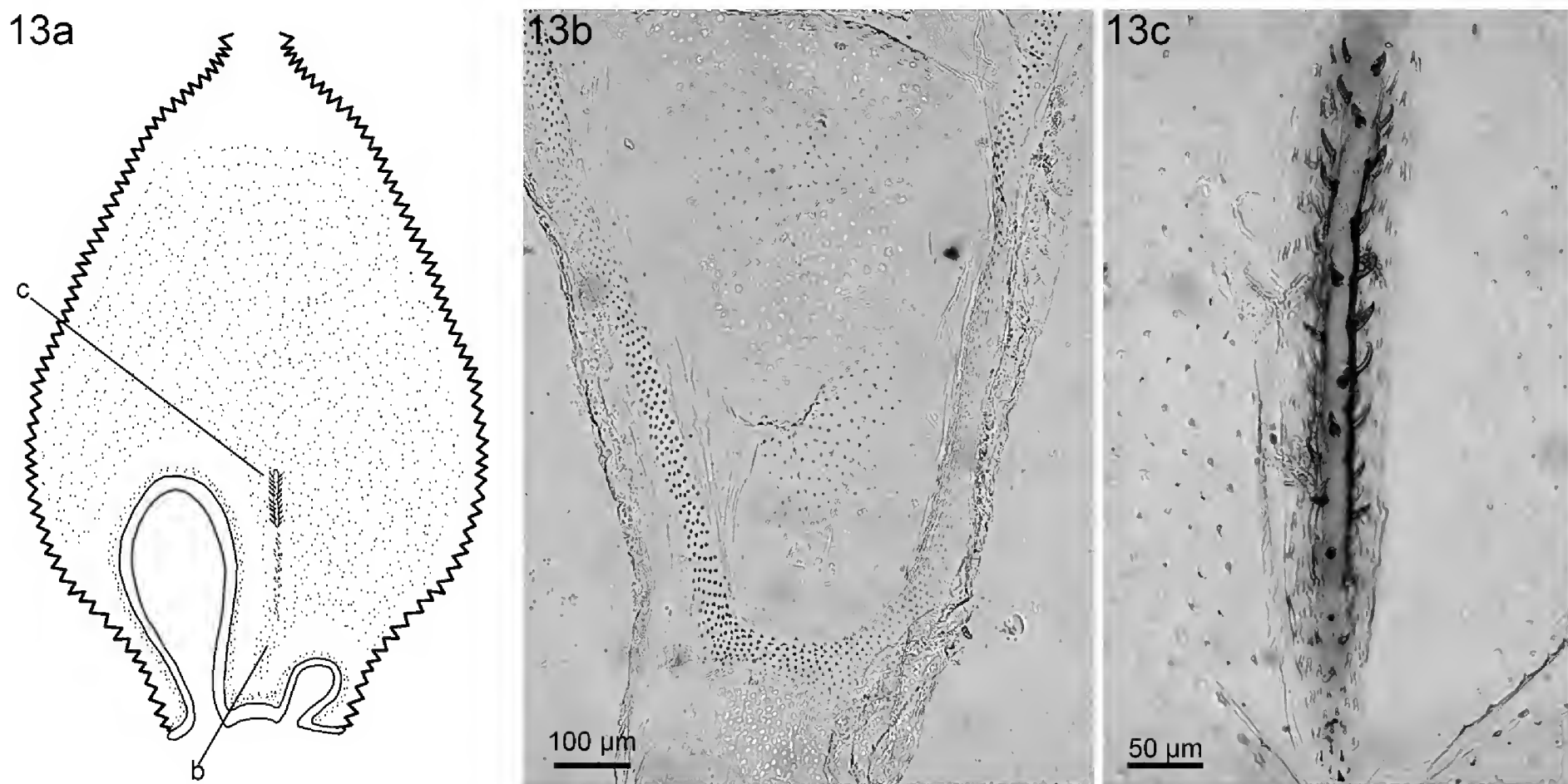
Figure 13. *Labiotermes labralis.* (a) Schematic drawing of P1 showing arrangement of spines. (b, c) Photomicrographs: (b) Detail of the coverage of small robust spines between the mesenteric tongues; (c) Detail of central ridge structure.
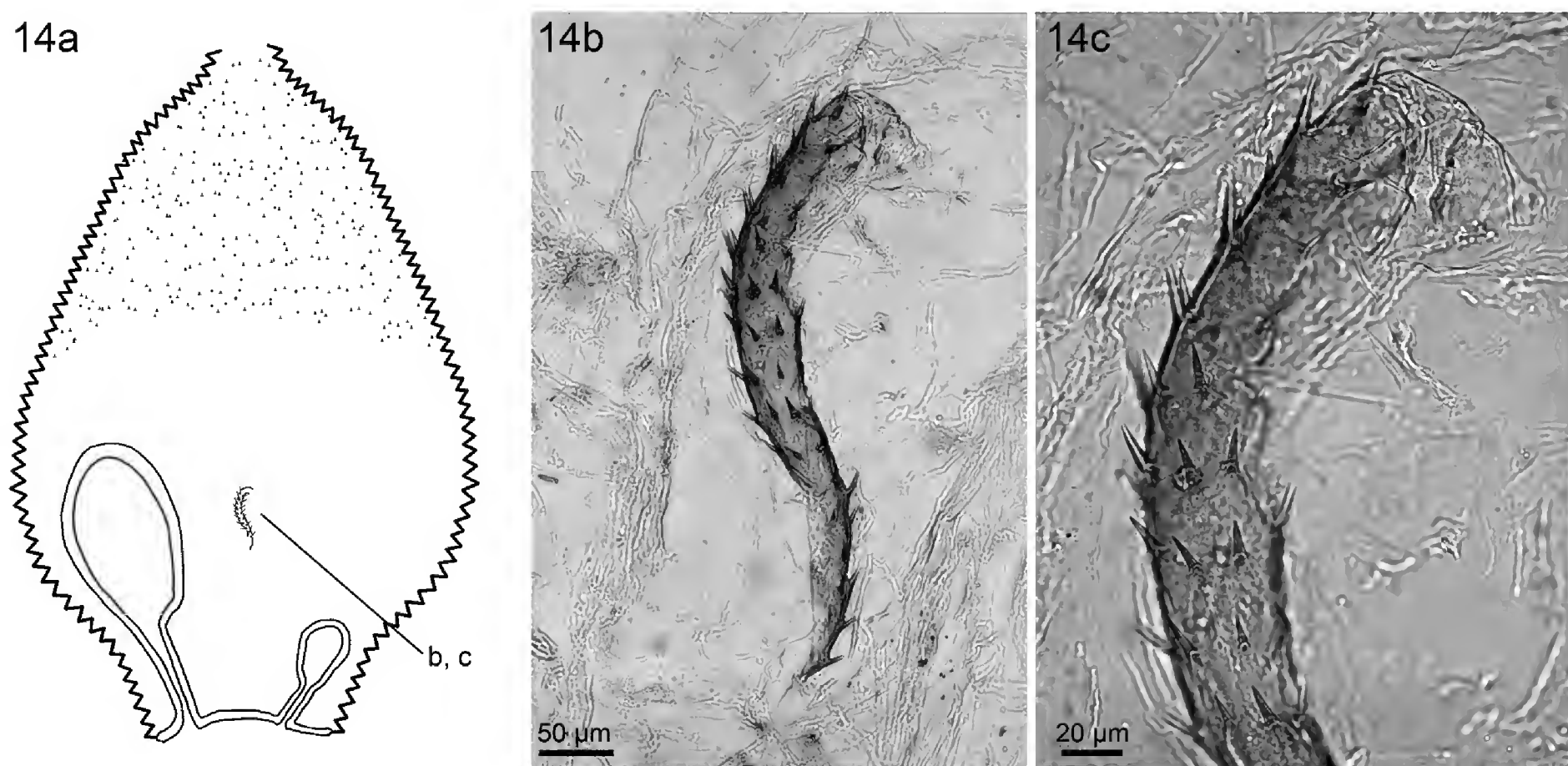

Figure 14. *Labiotermes leptothrix.* (a) Schematic drawing of P1 showing arrangement of spines. (b, c) Photomicrographs: (b) Detail of central ridge structure; (c) Detail of spines on central ridge.

Diffuse coverage: composed of a uniform but sparse coverage of spines (Figs 2a, 7a), the following species can be included in this category:

Armitermes spininotus (Fig. 2): All surfaces are covered with spaced thin setae (Figs 2b, 2c).

Embiratermes heterotypus (Fig. 7): All surfaces are covered with a layer of aciculiform spines (Fig. 7b).

Broad coverage: characterized by a dense coverage of spines (Figs 4a, 21a, 23a, 24a), mainly aciculiform, and small spines in rows, with recurrent sclerotized spines, the following species can be included in this category:

Cahuallitermes intermedius: very similar to *C. cumulans* (see ahead).

Cornitermes cumulans (Fig. 4): The surface is covered by different types of spines, laterally to the large mesenteric tongue an elongated area of aciculiform spines (Fig. 4b), the distal region and the edge of the mesenteric tongues are covered with small spines in rows (Fig. 4c), the remain surfaces are covered with spaced robust spines.

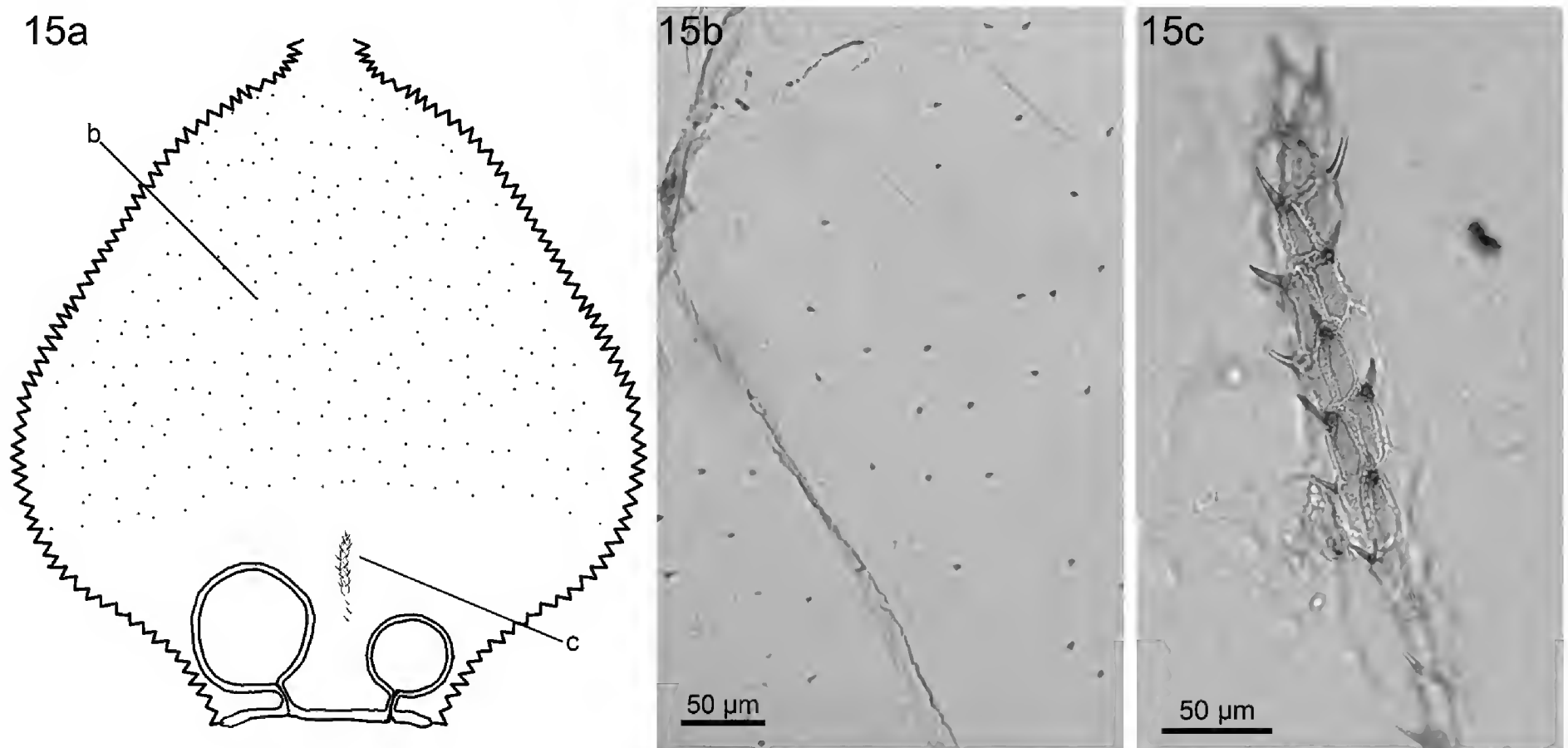*Cornitermes silvestrii, Procornitermes araujoi, Procornitermes triacifer*: very similar to *C. cumulans* (see above).

Figure 15. *Labiotermes orthocephalus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Detail of the sparse short spines in the distal portion; **(c)** Detail of central ridge structure.
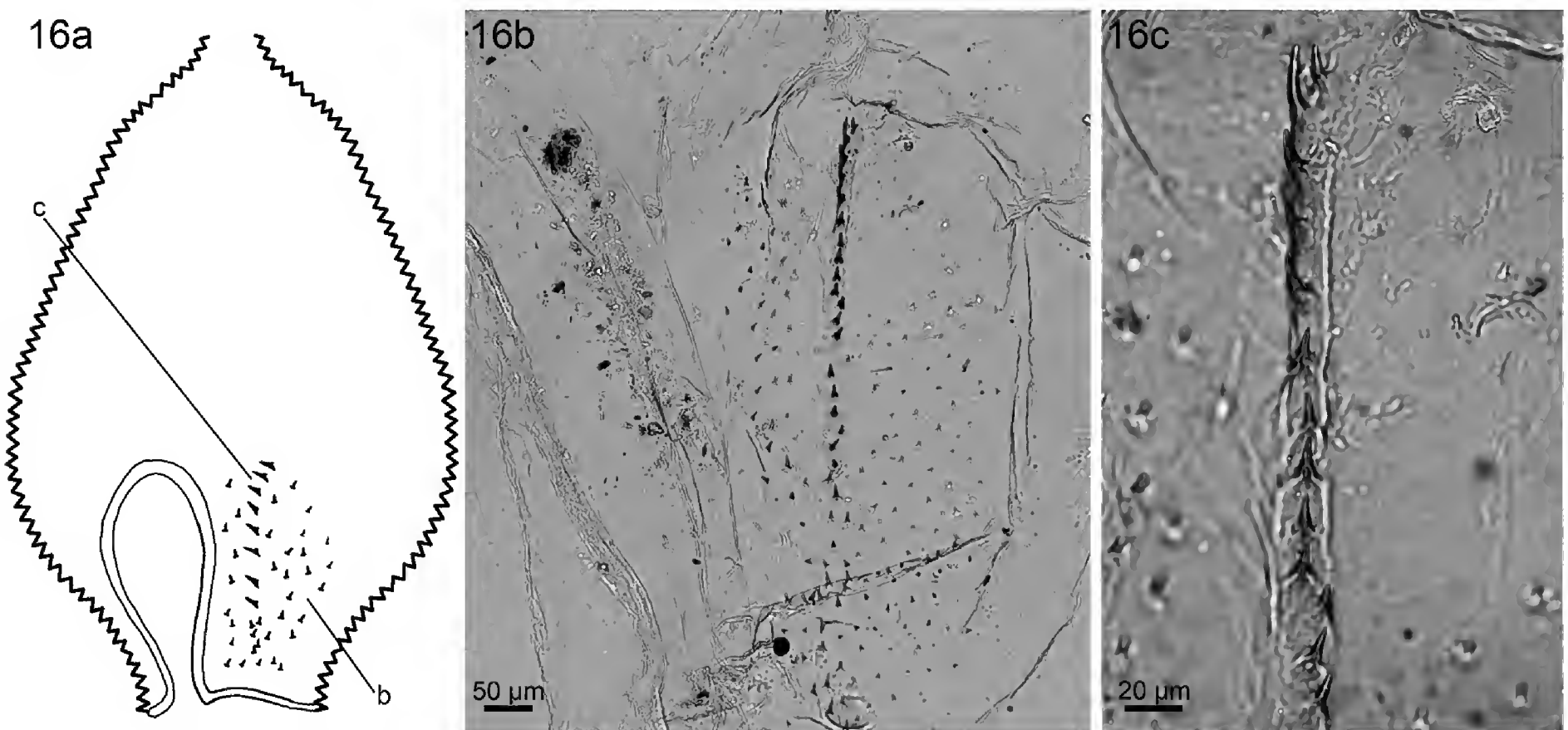

Figure 16. *Mapinguaritermes peruanus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view of the longitudinal row of stout spines, surround by robust spines; **(c)** Detail of stout spines.

Rhynchotermes nasutissimus: very similar to *R. perarmatus* (see ahead).

Rhynchotermes perarmatus (Fig. 21): laterally to the mesenteric tongue there is an elongated area covered with strongly sclerotized aciculiform spines (Fig. 21b), the distal region is covered with small spines in rows (Fig. 21c).

Syntermes molestus (Fig. 23): similar to *C. cumulans*, the surface is covered by different types of spines, laterally to the large mesenteric tongue is an elongated area of strongly sclerotized aciculiform spines (Figs 23b, 23d, 23e), the distal region and the edge of the mes-

enteric tongues are covered with small spines in rows (Figs 23c, 23f) and the remain surfaces are covered with spaced robust spines.

Syntermes spinosus (Fig. 24): laterally to the mesenteric tongue, an elongated area covered with robust spines (Fig. 24b), with a small area with strongly sclerotized aciculiform spines at the middle (Fig. 24c), the edges of the mesenteric tongues are covered with small spines in rows.

The species *A. armiger*, *A. bidentatus* and *U. teevani* (Fig. 25) does not fit clearly in the previous proposed
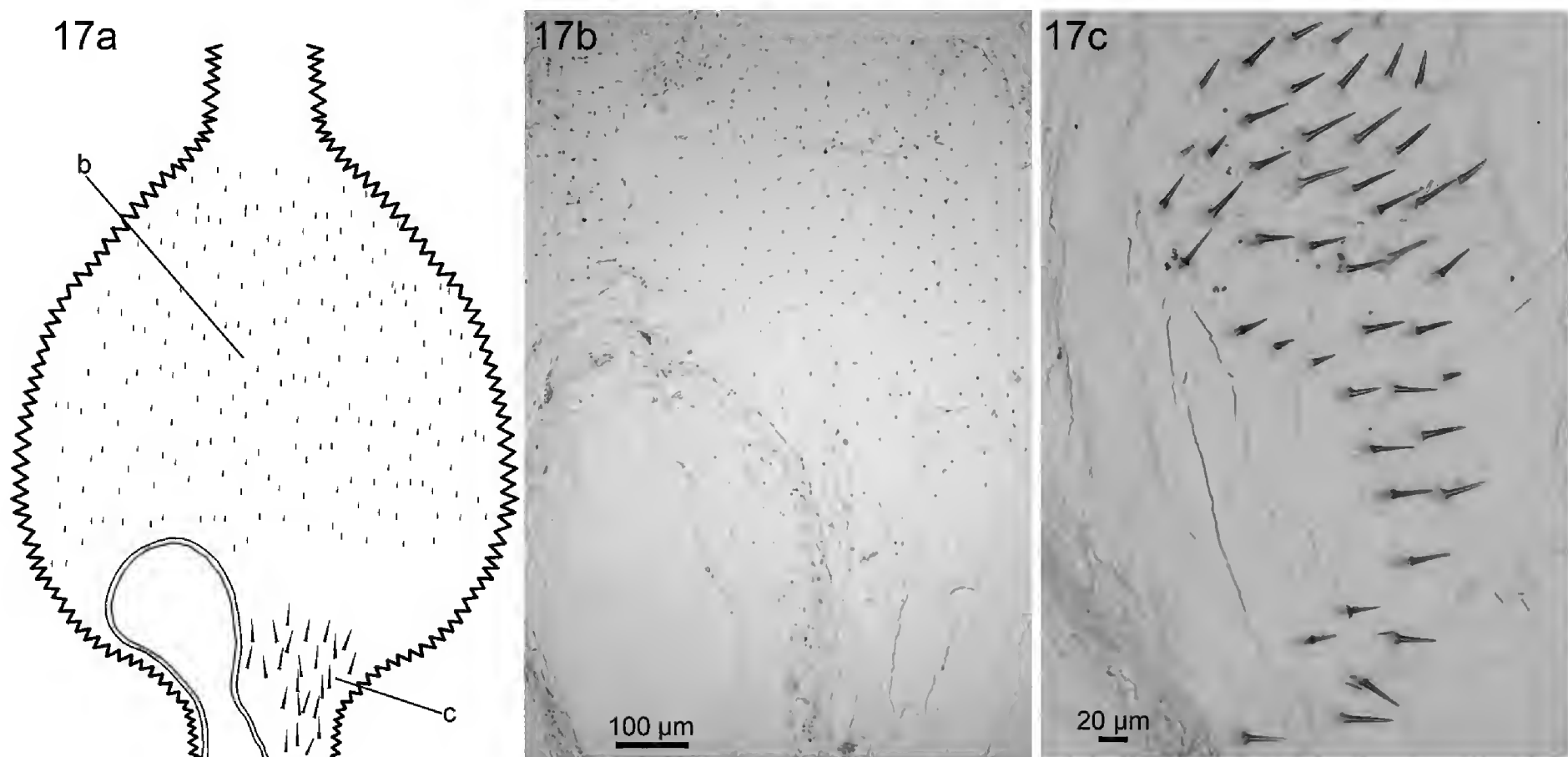
Figure 17. *Macuxitermes triceratops.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view of the short spines in the distal region; **(c)** Set of aciculiform spines in detail.
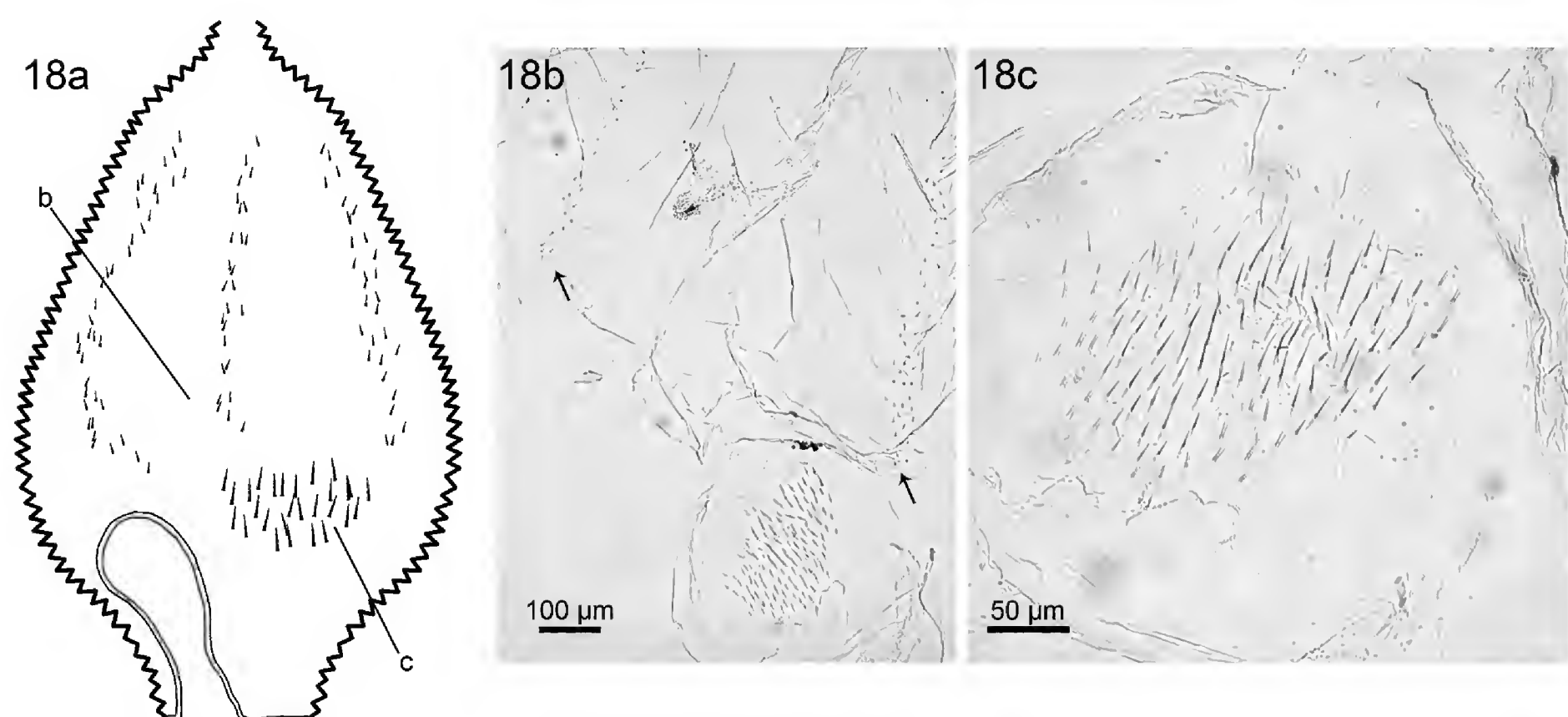
Figure 18. *Noirotitermes noiroti.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view, arrows indicate the distal branches of spines; **(c)** Set of aciculiform spines in detail.

patterns, at the proximal region there is a irregular area covered with robust spines (Figs 25b, 25c), but without the longitudinal row of stout spines or the central ridge, and the distal region is covered with a single longitudinal and large row of spaced small spines, that can not be clearly recognize as equivalent to the broad coverage or the three branches of the proximal aciculiform pattern.

In a few of the species studied, the ornament coverage is reduced to short areas with small, sclerotized, aciculiform spines, i.e. in *C. acignathus, C. bolivianus* (Fig. 3) and *P. lespesii* (Fig. 19).

Discussion

Taxonomic inferences

Considering the four patterns of ornamentation, the Syntermitinae can be generally classified in four distinct groups: proximal aciculiform pattern (*Acangaobitermes, Curvitermes, Cyrilliotermes,* some *Embiratermes* species, *Ibitermes tellustris, Noirotitermes, Silvestritermes*); central ridge pattern (*Embiratermes robustus, Ibitermes curupira, Mapinguaritermes* and *Labiotermes*); diffuse coverage (*Armitermes* and *Embiratermes heterotypus*)
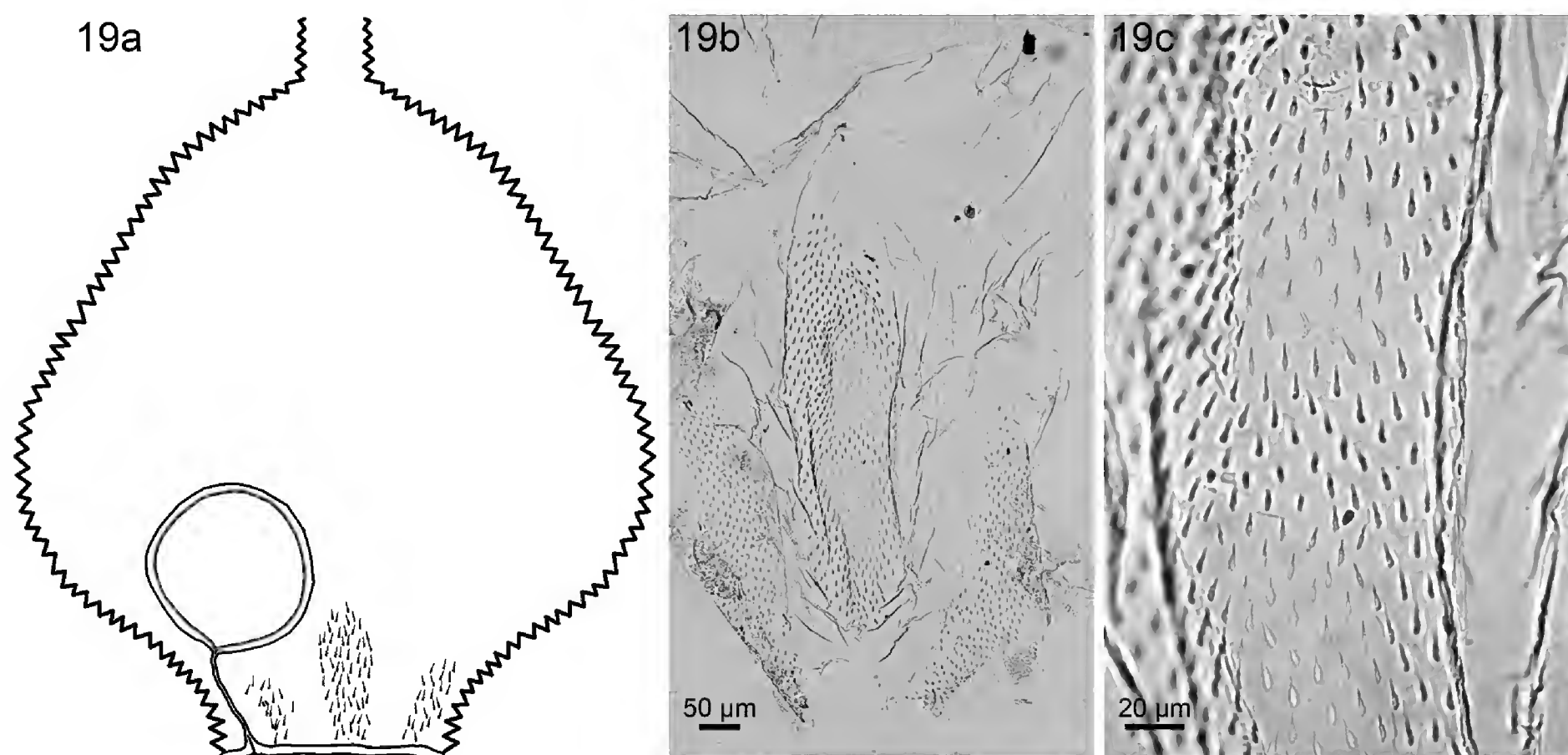
Figure 19. *Procornitermes lespesii*. **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view showing three proximal sets of small spines; **(c)** Small spines with sclerotized base in detail.
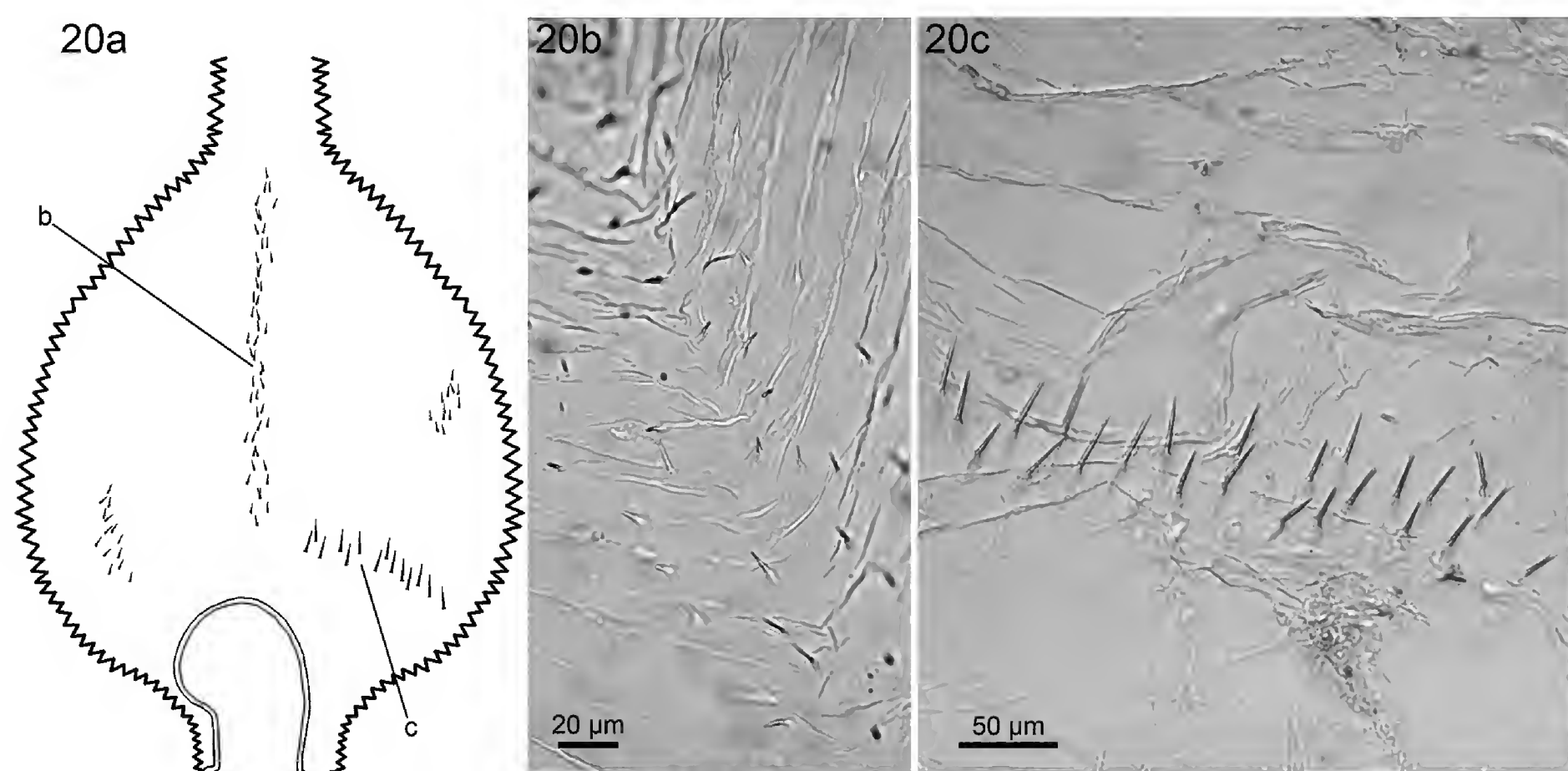
Figure 20. *Paracurvitermes manni*. **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Detail of the middle distal row of spines; **(c)** Transverse row of aciculiform spines in detail.

and broad coverage (*Syntermes, Cornitermes, Rhynchotermes, Procornitermes araujoi* and *Procornitermes triacifer*) (Table 2).

The ornamentation pattern in Syntermitinae is bilaterally symmetrical or asymmetrical (in a few species). The majority of genera of Syntermitinae have a consistent pattern of ornamentation among their species; the exceptions are *Ibitermes, Embiratermes* and *Procornitermes*, particularly *Embiratermes*. This indicates that these genera are not monophyletic, in agreement with observations of other gut anatomical characters (Cancello and Rocha 2013,

for *Procornitermes*; personal observation for *Embiratermes* and *Ibitermes*, manuscript in preparation).

Although these structures may have potential phylogenetic information, their relevance as characters and the congruence with the gut anatomy need to be checked in most comprehensive studies. A preliminary phylogeny of Syntermitinae was proposed in Rocha et al. 2012, but the main objective in the study is just formulate a working hypothesis to test the monophyly of *Armitermes*, a more specific study is necessary to make phylogenetic inferences about the evolution of the ornaments.
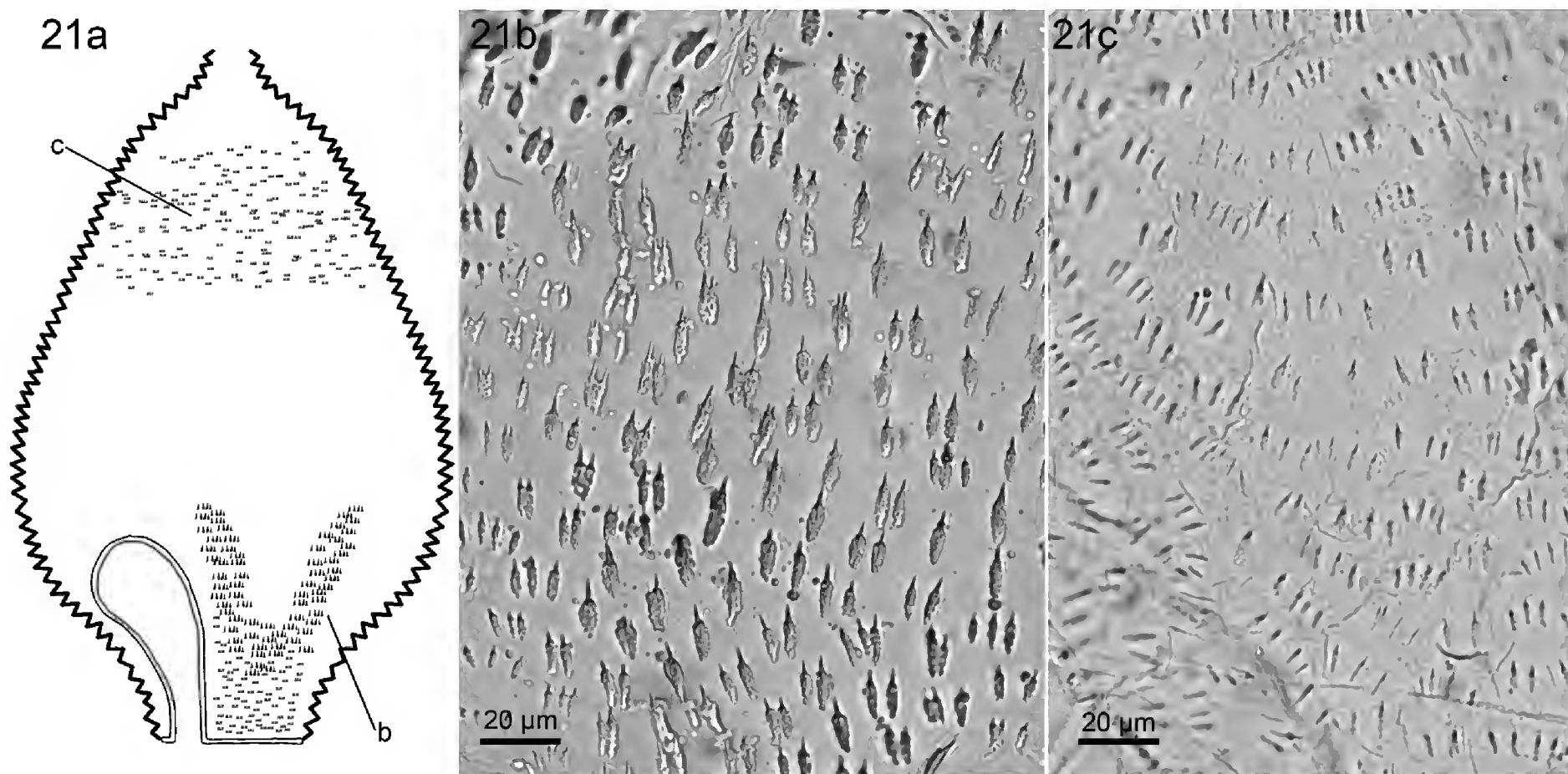
Figure 21. *Rhynchotermes perarmatus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Detail of spines with strongly sclerotized base next to mesenteric tongue; **(c)** Detail of rows of small spines in the distal region.
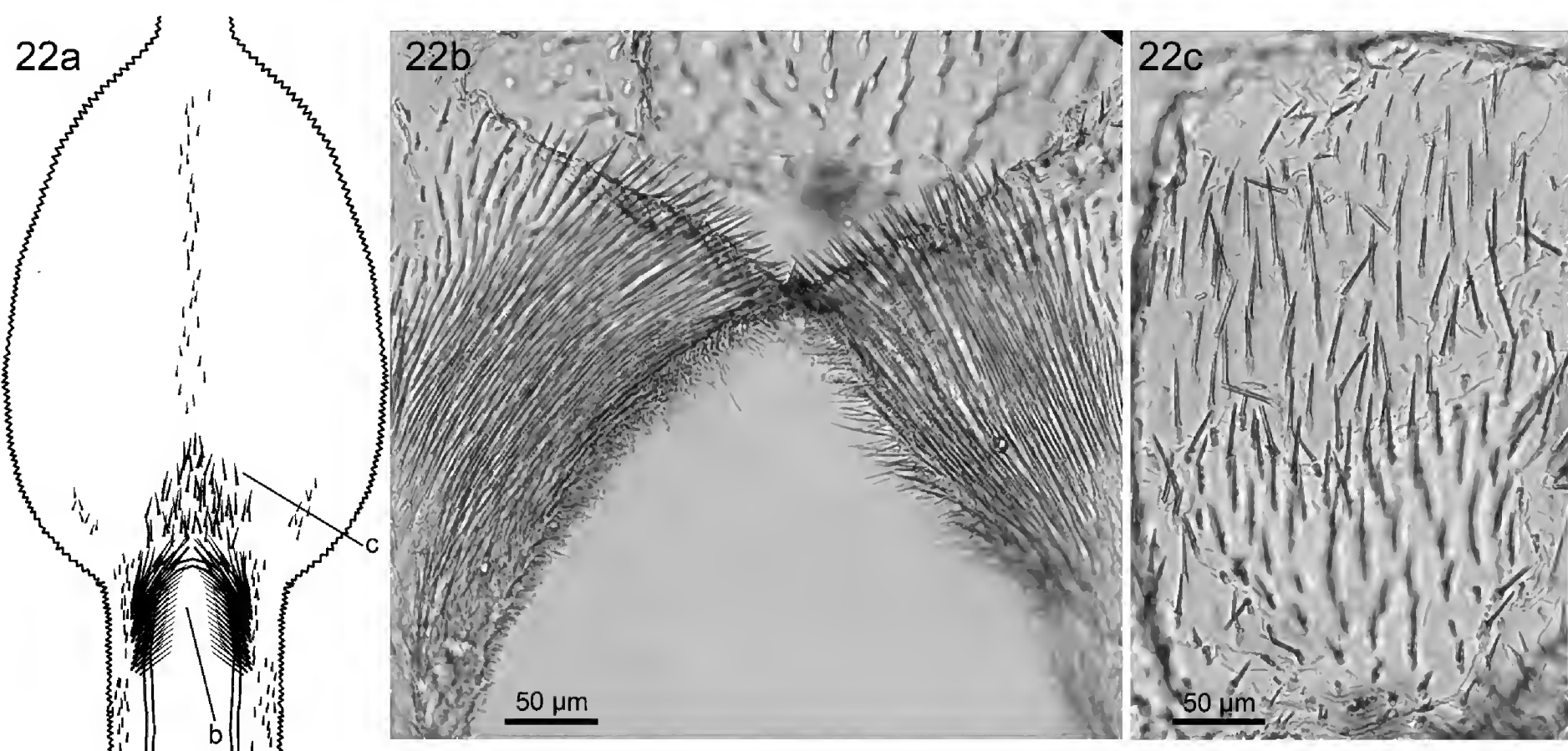
Figure 22. *Silvestritermes euamignathus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** Palisade of thin aciculiform spines around the mesenteric tongue; **(c)** Detail of aciculiform spines just after the mesenteric tongue.

Feeding habit inferences

In studies of termite faunas, the species are commonly classified by diet. The categories are defined by a humification gradient, which ranges from whole plant matter (such as wood and dead leaves) to decomposed cellulosic compounds dispersed in the soil (see Donovan et al. 2001 for a more detailed description). Although the classification by feeding groups is widely used, more recent studies have indicated that there is a continuum among termite feeding preferences (Bourguignon et al. 2010).

No specific proposal has been made for a classification of the feeding habits of all Syntermitinae species. Based on field notes accompanying specimens deposited in the MZUSP, and inferences from worker mandibles and gut morphology, we made a compilation and a classification for their diet, and compared feeding habits and P1 patterns of ornamentation among the species examined (Table 2).

The pattern of ornamentation in Syntermitinae appears to be generally related to the feeding habit, and reflects the humification gradient. Species that feed lower
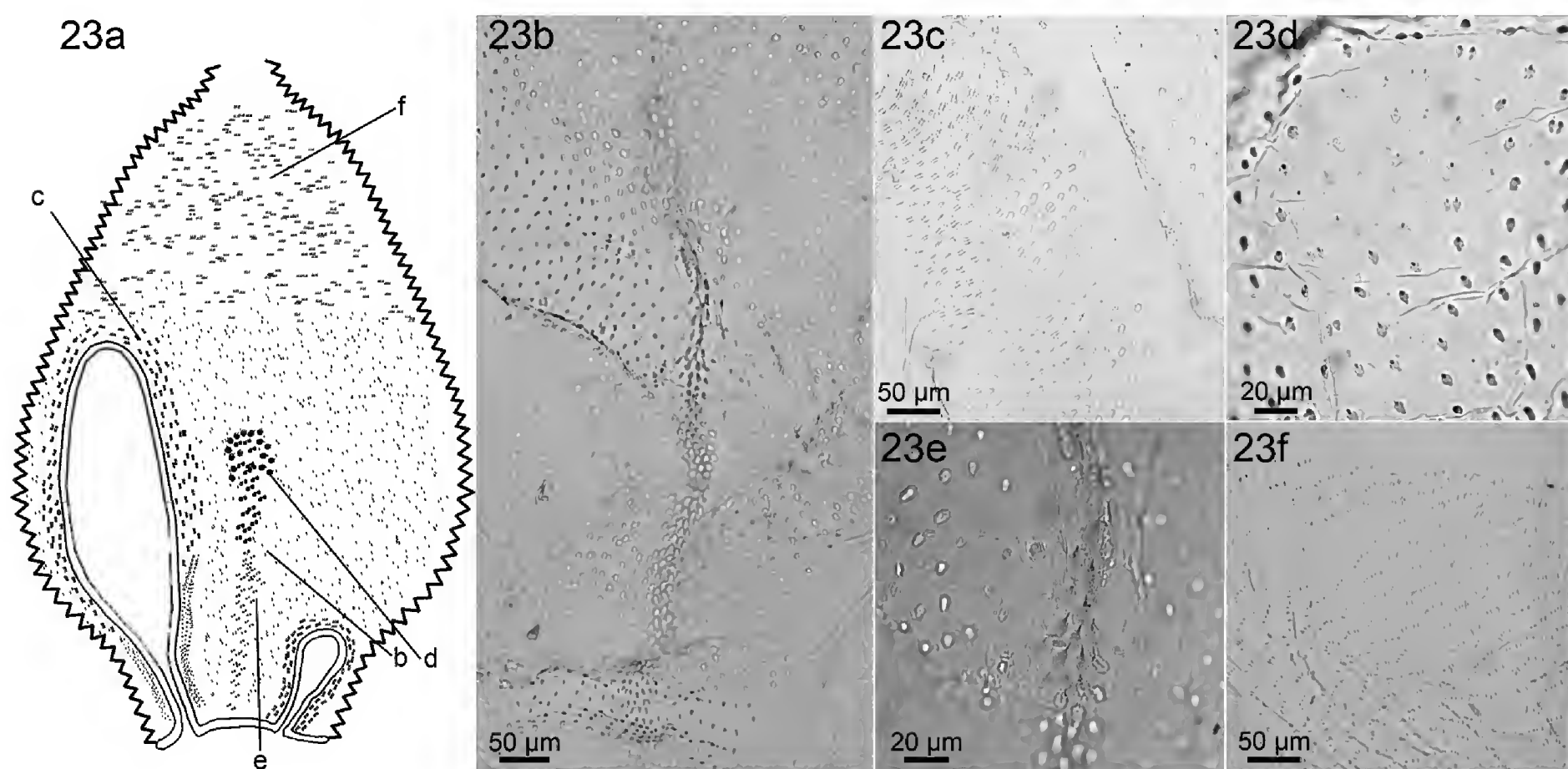
Figure 23. *Syntermes molestus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b–f)** Photomicrographs: **(b)** General view of the region between the mesenteric tongues; **(c)** Detail of small spines in rows adjacent to the mesenteric tongue; **(d)** Detail of spines with strongly sclerotized base between the mesenteric tongues; **(e)** Detail of strongly sclerotized spines in the middle of the region between the mesenteric tongues; **(f)** Detail of the small spines in rows in the distal region.
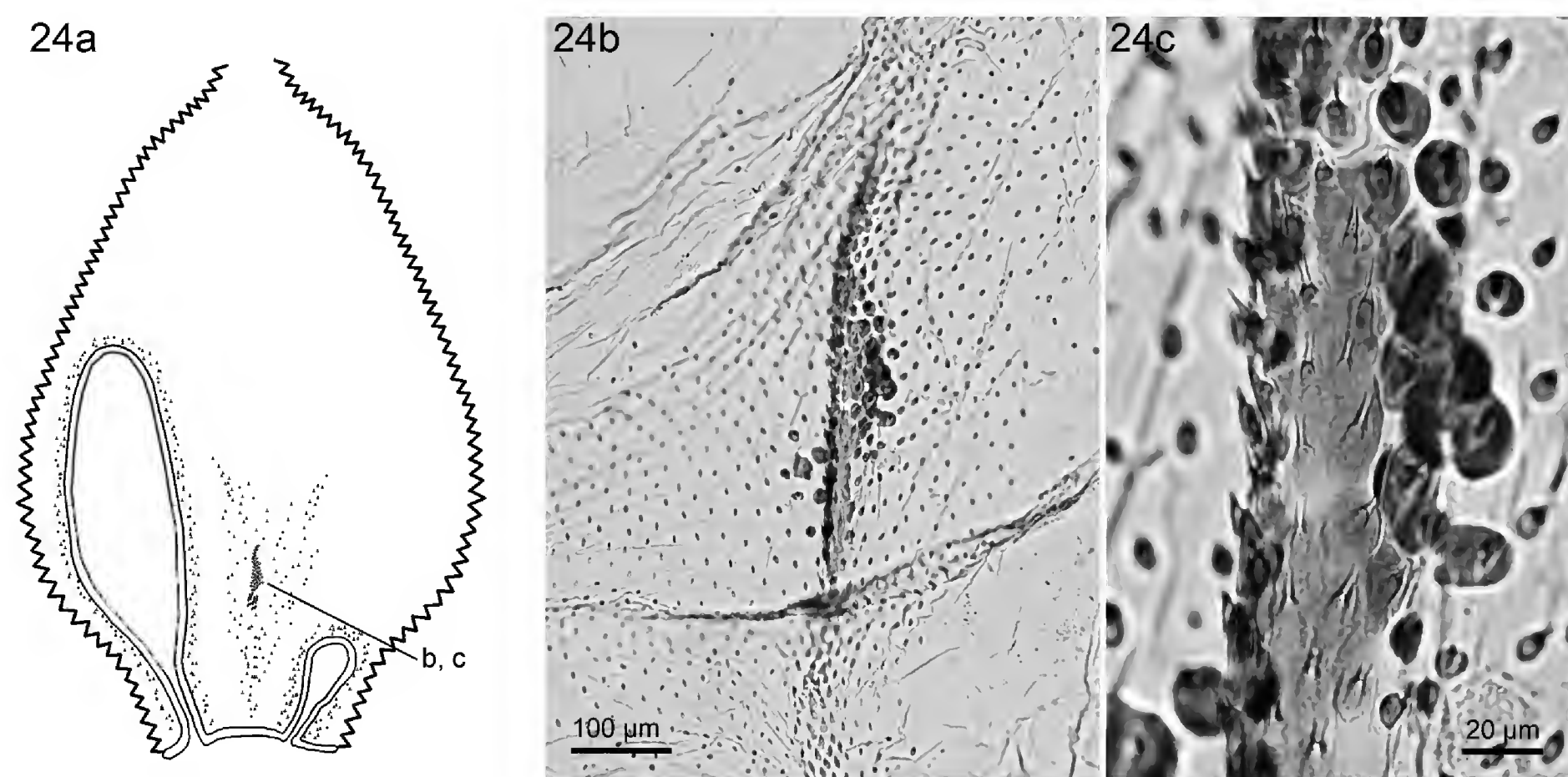
Figure 24. *Syntermes spinosus.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view of sclerotized spines between the mesenteric tongues; **(c)** Detail of the strongly sclerotized spines with their bases merged.

in the humification gradient (litter-feeders, grass-feeders and wood-feeders) mainly display a mosaic pattern, with a wide and heterogeneous coverage of small spines (for example *Syntermes*, *Cornitermes*, *Rhynchotermes*). Species that feed on humidified resources (intermediate- and soil-feeders) have a more centralized pattern, with structures concentrated only in the proximal region of P1 (for example *Silvestritermes*, *Curvitermes*, *Mapin-*

guaritermes, *Labiotermes*) (see Table 2). This inference may be useful as an additional character to determine the species' diet, combined with other characteristics of the gut. However, some of the species examined in this study are exceptions; for instance, *P. lespesii* and *C. bolivianus* are known as, respectively, wood-feeder and litter-feeder species, although their P1 ornamentation is much reduced.

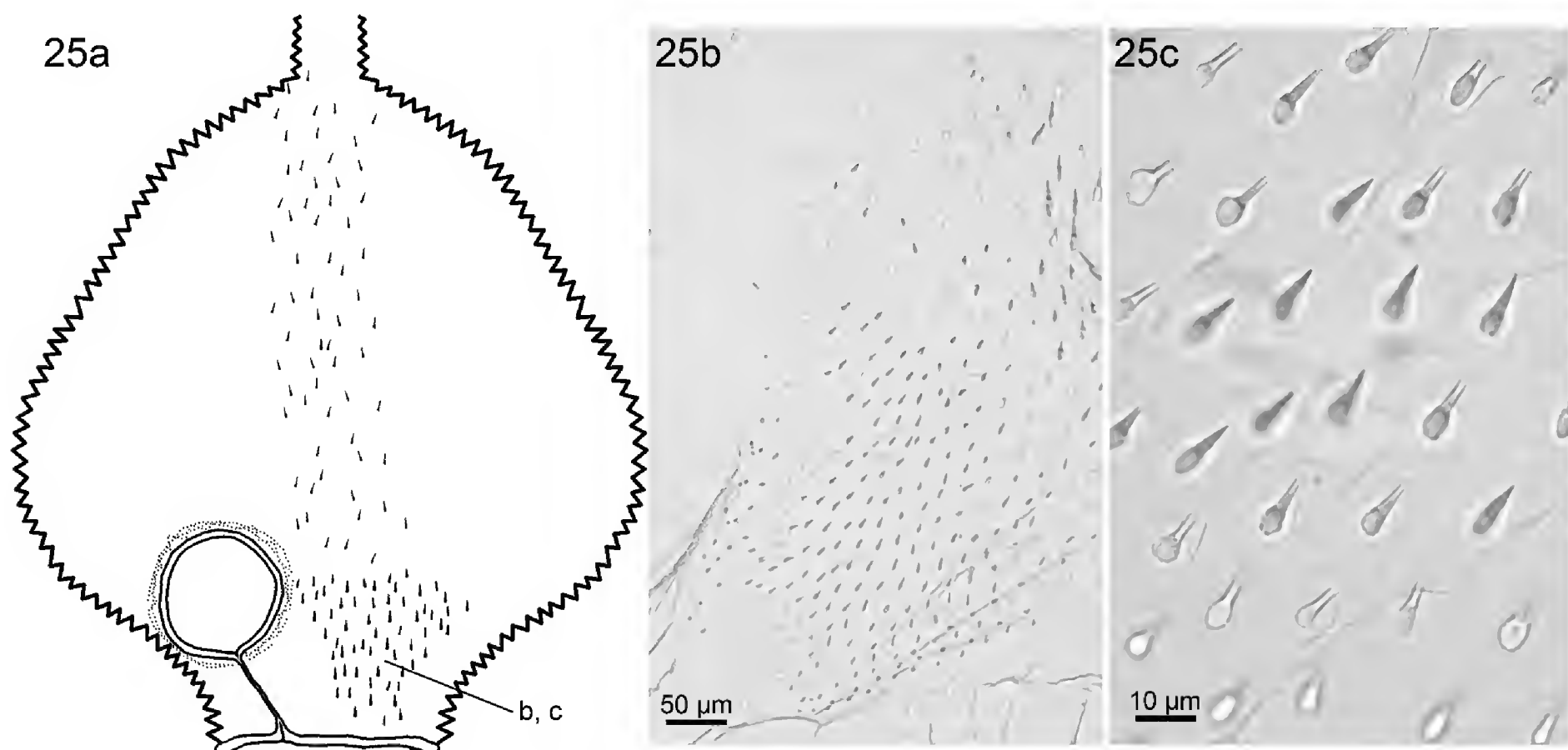**Figure 25.** *Uncitermes teevani.* **(a)** Schematic drawing of P1 showing arrangement of spines. **(b, c)** Photomicrographs: **(b)** General view of the robust spines covering the proximal portion; **(c)** Detail of robust spines.

Table 2. Association between patterns of ornaments for the species studied, and their feeding habits.

Species	Pattern of ornaments	Feeding habit
Acangaobitermes krishnai	Proximal aciculiform	Soil-feeder
Curvitermes odontognathus	Proximal aciculiform	Soil-feeder
Cyrilliotermes angulariceps	Proximal aciculiform	Soil-feeder
Embiratermes brevinasus	Proximal aciculiform	Intermediate
Embiratermes festivellus	Proximal aciculiform	Intermediate
Embiratermes ignotus	Proximal aciculiform	Intermediate
Embiratermes silvestrii	Proximal aciculiform	Intermediate
Ibitermes tellustris	Proximal aciculiform	Intermediate
Noirotitermes noiroti	Proximal aciculiform	Intermediate
Macuxitermes triceratops	Proximal aciculiform	Intermediate
Paracurvitermes manni	Proximal aciculiform	Soil-feeder
Silvestritermes euamignathus	Proximal aciculiform	Intermediate
Armitermes armiger	Unclear	Intermediate
Armitermes bidentatus	Unclear	Intermediate
Armitermes spininotus	Diffuse coverage	Intermediate
Uncitermes teevani	Unclear	Intermediate
Embiratermes heterotypus	Diffuse coverage	Intermediate
Embiratermes robustus	Central ridge	Intermediate
Ibitermes curupira	Central ridge	Intermediate
Labiotermes emersoni	Central ridge	Intermediate
Labiotermes labralis	Central ridge	Intermediate
Labiotermes leptothrix	Central ridge	Intermediate
Labiotermes orthocephalus	Central ridge	Intermediate
Mapinguaritermes peruanus	Central ridge	Intermediate
Cahuallitermes intermedius	Broad coverage	Litter-feeder
Cornitermes acignathus	Reduced coverage	Litter-feeder
Cornitermes cumulans	Broad coverage	Litter-feeder/ Grass-feeder
Cornitermes bolivianus	Reduced coverage	Litter-feeder
Cornitermes silvestrii	Broad coverage	Litter-feeder
Procornitermes araujoi	Broad coverage	Wood-feeder/ Litter-feeder
Procornitermes lespesii	Reduced coverage	Wood-feeder

Species	Pattern of ornaments	Feeding habit
Procornitermes triacifer	Broad coverage	Wood-feeder/ Litter-feeder
Rhynchotermes nasutissimus	Broad coverage	Litter-feeder/ Grass-feeder
Rhynchotermes perarmatus	Broad coverage	Litter-feeder/ Grass-feeder
Syntermes molestus	Broad coverage	Grass-feeder
Syntermes spinosus	Broad coverage	Grass-feeder

Function in termite digestion

As the P1 ornaments have never been described in detail for Termitidae species, we can only speculate as to their function. Investigating their specific function is outside the scope of this paper, but we can make some suggestions based on morphological inference and analogies with the functions of P2 suggested by Donovan et al. (2000).

These structures may function as an abrasive surface for the food mass that enters from the midgut. This hypothesis is supported by the location of the ornaments, only in the proximal part of the convex side of the mesenteric arch (see Fig. 1). However, in some cases the ridges may be irrelevant for this function, for example the isolated central ridges in *Labiotermes* (Figs 12–15) measure around 50–100 μm and the P1 diameter varies between 1–2 mm, and it is difficult to explain how a single structure of this size can act on the food mass.

Another possible explanation is microbial inoculation. This hypothesis is supported by the usual presence of what appears to be a bacterial film covering the spines, and some points regarding this possibility need to be considered. The pH and oxygenation conditions inside the first proctodeal segment may be very differ-

ent from the third proctodeal segment, which implies that the bacterial flora will also necessarily be different. Bignell and Eggleton (1995) studied the pH conditions inside each segment of the digestive tract in various termite species, and found that P1 may be more alkaline than P3. Schmitt-Wagner et al. (2003) demonstrated for two *Cubitermes* species (African soil-feeder termites) that inside each hindgut compartment (P1–P5) the symbiont assemblage is composed of distinct types and proportions of microbial groups; this reinforces a microbial-inoculation hypothesis. The mean size of the ornamentation is approximately 20 µm, suggesting an association of the bacteria of the micro-oxic region, the peripheral region of the lumen, of approximately 100 µm, with oxygen availability (Brune and Friedrich 2000). To confirm this, more-detailed studies are needed to bolster this hypothesis.

In other groups of Termitidae, with the same range of feeding habits, ornamentation appears to be absent. For example, in Nasutitermitinae the species have a variety of feeding habits that cover the entire humification gradient, but we never find ornaments in their first proctodeal segment (personal observation). This suggests that in the course of termite evolution, many different strategies have emerged in response to the problems of digesting similar types of food.

Conclusion

Additional information is needed in order to determine the functions and importance of these structures in termite digestion, although the variability among the species clearly shows the taxonomic value of the structure. This character may have taxonomic value in other termite groups, especially for Termitinae and Apicotermitinae, although further studies are needed to confirm this possibility.

Acknowledgments

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PENSOFT.

New species and new combinations of Asian *Batrisodes* Reitter (Coleoptera, Staphylinidae, Pselaphinae), and synonymy of *Batrisodellus* Jeannel with *Batrisodes*

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http://zoobank.org/EA8D190E-0E7C-4E04-9E96-65EC0E75D6D1

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Abstract

Continuing surveys on the pselaphine fauna in China have revealed four undescribed species of the genus *Batrisodes*: *Batrisodes angustelytratus* **sp. n.** (with *Pachycondyla* ant) and *B. longwangshanus* **sp. n.** from Zhejiang, *B. bamian* **sp. n.** (with *Pseudolasius* ant) from Hunan, and *B. songxiaobini* **sp. n.** (with *Formica* ant) from Yunnan. The genus *Batrisodellus* is placed as a junior synonym of *Batrisodes*, **syn. n.**; this taxonomic act results in eight **new combinations**: *Batrisodes cerberus*, *B. coprea*, *B. cristatus*, *B. fengtingae*, *B. laticollis*, *B. longulus*, *B. palpalis*, and *B. punctipennis*. The Russian Far East species *Basitrodes cornutus* is transferred to *Batrisodes*, **comb. n.**

Key Words

Introduction

The fauna of the largely Holarctic genus *Batrisodes* Reitter in China is poorly explored. Currently only four species of this genus have been known: two from the mainland and two from Taiwan. Three of them, *B. masatakai* Nomura, *B. babaianus* Nomura, and *B. simplex* Yin & Li, are placed in the subgenus *Excavodes* Park (Nomura 2007, Yin and Li 2013), and one, *B. pruinosus* (Reitter), in the nominotypical subgenus (Besuchet 1981). Recent surveys on the pselaphine beetles in eastern, central, and southwestern China in 2013 and 2014 have revealed four undescribed *Batrisodes* species that are described herein. Of them, three were collected from colonies of the ant genera *Pachycondyla* Smith, *Pseudolasius* Emery, and *Formica* Linnaeus. Due to the weak concept of subgenera applied for the eastern Asian *Batrisodes*, the subgeneric system is not used in this paper.

After an examination of the newly collected material, as well as types, photos, and the original descriptions of the described species, we found that all characters used to define *Batrisodellus* Jeannel to be weak. Since *Batrisodellus* cannot be clearly separated from *Batrisodes*, it is placed in synonymy with the latter. In addition, *Basitrodes cornutus* Kurbatov is transferred to *Batrisodes* based on the characters extracted from its original description and figures, and a photo of an identified male.

Material and methods

The type material of the new species is housed in the Insect Collection of Shanghai Normal University, Shanghai, China (**SNUC**).

The collecting data of the material are quoted verbatim. A slash is used to separate different labels. Authors'

supplementary notes are included in square brackets. Each type specimen bears the following label: 'HOLO-TYPE [red] (or PARATYPE [yellow]), ♂ (or ♀), *Batrisodes* + specific name sp. n., det. Yin & Shen, 2015, SNUC'. Morphological terminology follows Chandler (2001), except our use of 'ventrite' instead of 'sternite' when describing meso- and metathoracic structures.

The following abbreviations are applied: AL—length of the abdomen along the midline; AW—maximum width of the abdomen; EL—length of the elytra along the sutural line; EW—maximum width of the elytra; HL—length of the head from the anterior clypeal margin to the occipital constriction; HW—width of the head across eyes; PL—length of the pronotum along the midline; PW—maximum width of the pronotum. Length of the body is a combination of HL + PL + EL + AL.

Taxonomy

Description of new species

Batrisodes angustelytratus Yin, Shen & Li, sp. n.

http://zoobank.org/93776461-DB0B-42F9-B90E-A3C3827E0D2A
Figs 1A, 2

Type material (3 ♂♂). **Holotype: China:** ♂, labeled 'China: S. Zhejiang, Longquan [龙泉], Fengyang Shan [凤阳山], creek valley nr. hotel, 27°54'42"N, 119°11'52"E, ant nest under rock, 1175 m, 28.iv.2014, X.-B. Song' (SNUC). **Paratypes: China:** 2 ♂♂, same label data as holotype (SNUC).

Description. Male (Fig. 1A). Body reddish brown, BL 2.12–2.18 mm. Head about as long as wide, HL 0.48–0.49 mm, HW 0.47–0.49 mm; with large vertexal foveae; frons flat, lacking modification, concave between moderately raised antennal tubercles; clypeus coarsely punctate, with round anterior margin; lateral vertexal carinae faintly present from frons to anterior margins of vertexal foveae, median vertexal carina distinct, extending from level of posterior margins of vertexal foveae to base; each eye composed of about 45 facets, lacking ocular canthi; postgenal area with many long erect setae visible in dorsal view. Antennal club (Fig. 2A) formed by apical three antennomeres, IX and X strongly transverse, unmodified, XI large, with distinct, apically-truncate basal denticle. Pronotum about as long as wide, PL 0.48–0.47 mm, PW 0.47–0.46 mm; disc slightly convex; median and lateral longitudinal sulci distinct; lacking median antebasal fovea; with small antebasal tubercles. Elytra much wider than long, EL 0.60–0.63 mm, EW 0.74–0.76 mm; base distinctly constricted; each elytron with three large nude basal foveae; lacking discal striae; marginal striae complete. Mesofemora (Fig. 2B) with thin but distinct ventral spine near middle, mesotibiae (Fig. 2C) with triangular preapical spur; metatibiae (Fig. 2D) with long apical tuft of setae. AL 0.56–0.59 mm, AW 0.79–0.81 mm; abdominal tergite IV (first visible tergite) with strongly oblique

marginal carinae; discal carinae short. Length of aedeagus (Fig. 2E–G) 0.44 mm, median lobe broadened in dorso-ventral view, split at apex.

Female. Unknown.

Differential diagnosis. The new species is most similar to *Batrisodes fengtingae* (Yin & Nomura) [previously placed in *Batrisodellus*, transferred to *Batrisodes* due to the synonymy of these two genera, see below] by sharing similar modification on antennomeres XI and spines on the legs, and an asymmetric aedeagus. *Batrisodes angustelytratus* can be readily separated from *B. fengtingae* and all other congeners by the strongly constricted elytral base, as well as the unique form of aedeagus.

Biology. Adults were collected from a colony of a *Pachycondyla* ant nesting under a rock.

Distribution. Eastern China: Zhejiang.

Etymology. The species epithet refers to the strongly constricted base of the elytra.

Batrisodes bamian Yin, Shen & Li, sp. n.

http://zoobank.org/6900B5E9-19A3-4467-9C0D-957A56275962
Figs 1B, 3

Type material (5 ♂♂, 1 ♀). **Holotype: China:** ♂, labeled 'China: Hunan, Guidong Co. [桂东县], Bamian Shan [八面山], 25°59'46"N, 113°41'59"E, 1825 m, colony of *Pseudolasius* sp. nesting under moss on rock, 04.vi.2014, Peng & Shen' (SNUC). **Paratypes: China:** 4 ♂♂, 1 ♀, same label data as holotype (SNUC).

Description. Male (Fig. 1B). Body reddish brown, BL 2.92–2.93 mm. Head about as long as wide, HL 0.55–0.57 mm, HW 0.54–0.55 mm; with small vertexal foveae; frons lacking modification, slightly concave between moderately raised antennal tubercles; clypeus medially impunctate, with round anterior margin; lateral vertexal carinae present from level of midpoints of eyes to posterolateral margins of head, median vertexal carina short; each eye composed of about 60 facets, lacking ocular canthi; postgenal area with numerous long erect setae visible in dorsal view. Antennae lacking distinct club (Fig. 3A–B), IX strongly protruding at lateral margins, X unmodified, XI large, with distinct basal denticle. Pronotum slightly longer than wide, PL 0.63–0.66 mm, PW 0.55–0.57 mm; disc slightly convex; median longitudinal sulcus thin and shallow, lateral sulci more distinct; lacking median antebasal fovea; with indistinct antebasal tubercles. Elytra wider than long, EL 0.88–0.91 mm, EW 1.02–1.03 mm; each elytron with three nude basal foveae; with short discal striae; marginal striae present in posterior half of flank. Mesofemora (Fig. 3C) with small, blunt ventral spine near middle, mesotibiae (Fig. 3D) with small ventral denticle and apical spur; metatibiae lacking long apical tuft of setae. AL 0.79–0.86 mm, AW 0.93–0.95 mm; abdominal tergite IV (first visible tergite) with oblique marginal carinae; discal carinae as short, triangular ridges. Length of aedeagus (Fig. 3E–G) 0.79 mm, median lobe symmetric, endophallus comprising two sclerites.
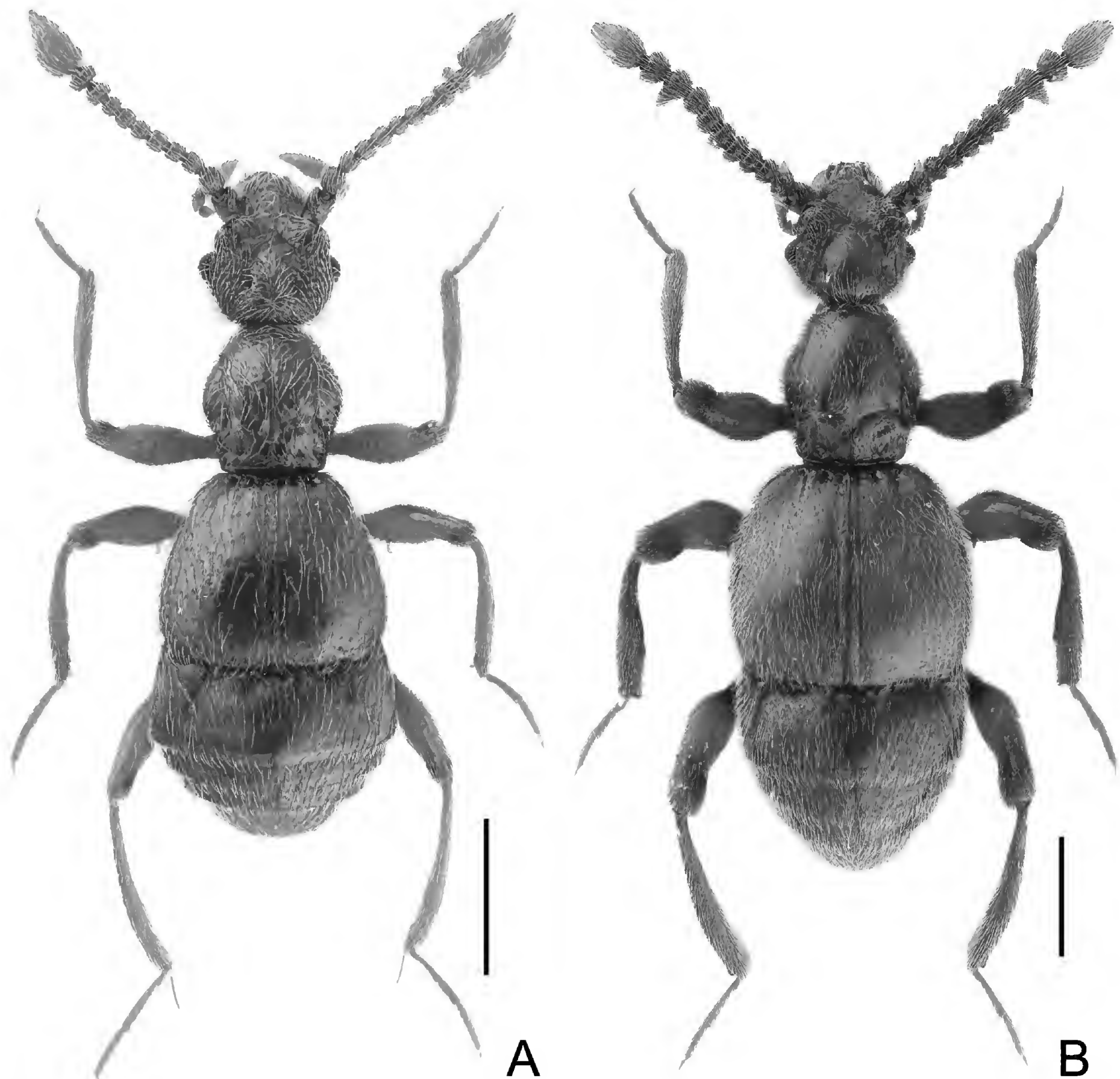
Figure 1. Male habitus of *Batrisodes* species. **A.** *B. angustelytratus*; **B.** *B. bamian*. Scales: 0.5 mm.

Female. Much smaller than male, antennae and legs lacking modification and spine; each eye composed of about 40 facets. Tergite VIII (Fig. 3H) and sternite VIII (Fig. 3I) transverse. Genital complex (Fig. 3J) well-sclerotized, width 0.37 mm. BL 2.67 mm, HL 0.52 mm, HW 0.53 mm, PL 0.59 mm, PW 0.53 mm, EL 0.78 mm, EW 0.93 mm, AL 0.78 mm, AW 0.86 mm.

Differential diagnosis. The stout habitus and modified antennomere IX, combined with the unique form of the aedeagus readily separates the new species from all other congeners.

Biology. The adults were collected from colonies of a *Pseudolasius* ant nesting under moss on rocks.

Distribution. Central China: Hunan.

Etymology. The specific epithet refers to the type locality of the new species, Bamian Mountain.

Batrisodes longwangshanus Yin, Shen & Li, sp. n.

http://zoobank.org/ADCBAF9B-F5F1-43FE-B192-9D5B8F7B3F92
Figs 4A, 5

Type material (6 ♂♂, 3 ♀♀). **Holotype: China:** ♂, labeled 'China, Zhejiang, Anji County [安吉县], Longwang Shan N. R. [龙王山], Qianmutian–Qianmu Peak [千亩田－千亩峰], 30°23'47"N, 119°26'17"E, 1250–1450 m, mixed leaf litter, sifted, 14.v.2013, Chen & Pan' (SNUC). **Paratypes: China:** 5 ♂♂, 3 ♀♀, same label data as holotype (SNUC).

Description. Male (Fig. 4A). Body reddish brown, BL 2.23–2.24 mm. Head slightly wider than long, HL 0.46–0.48 mm, HW 0.50–0.51 mm; with big vertexal foveae; frons lacking modification, slightly concave between moderately raised antennal tubercles; clypeus granulate along
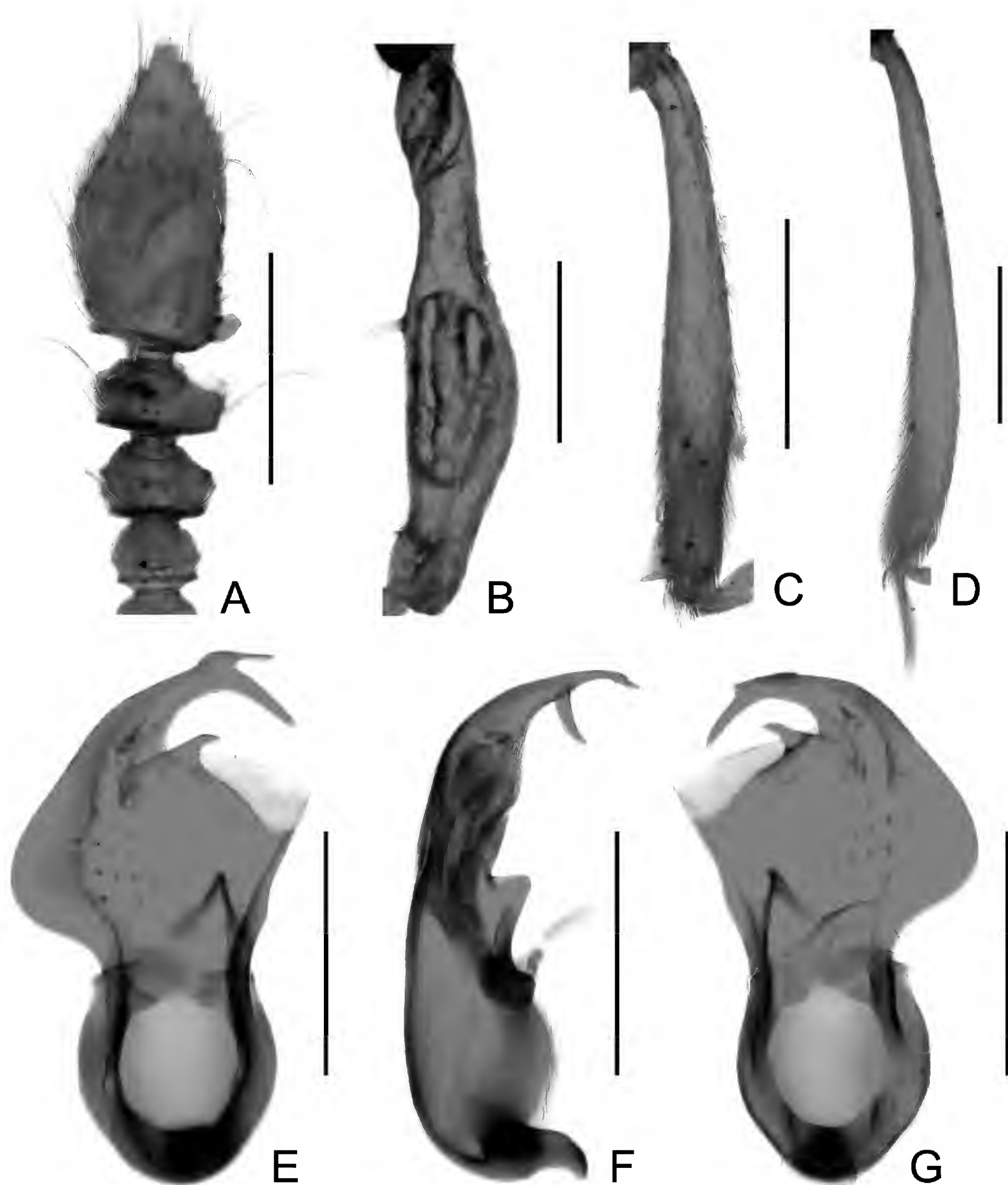
Figure 2. Diagnostic features of *Batrisodes angustelytratus*, male. **A.** antennal club; **B.** mesotrochanter and mesofemur; **C.** mesotibia; **D.** metatibia; **E.** aedeagus, in dorsal view; **F.** same, in lateral view; **G.** same, in ventral view. Scales: 0.2 mm.

round anterior margin; lateral vertexal carinae present from level of midpoints of eyes to posterolateral margins of head, lacking median vertexal carina; each eye composed of about 15 facets, with ocular canthi; postgenal area with numerous long erect setae visible in dorsal view. Antennal clubs (Fig. 5A) loosely formed by apical three antennomeres, lacking modification. Pronotum slightly longer than wide, PL 0.47–0.50 mm, PW 0.46–0.47 mm; disc slightly convex; median and lateral longitudinal sulci distinct; lacking median antebasal fovea; with discal and antebasal tubercles along discal ridges, with distinct basolateral tubercles. Elytra wider than long, EL 0.61–0.62 mm, EW 0.73–0.74 mm; each elytron with three large nude basal foveae; with shallow discal striae; marginal striae com-

Dtsch. Entomol. Z. 62 (1) 2015, 45–54

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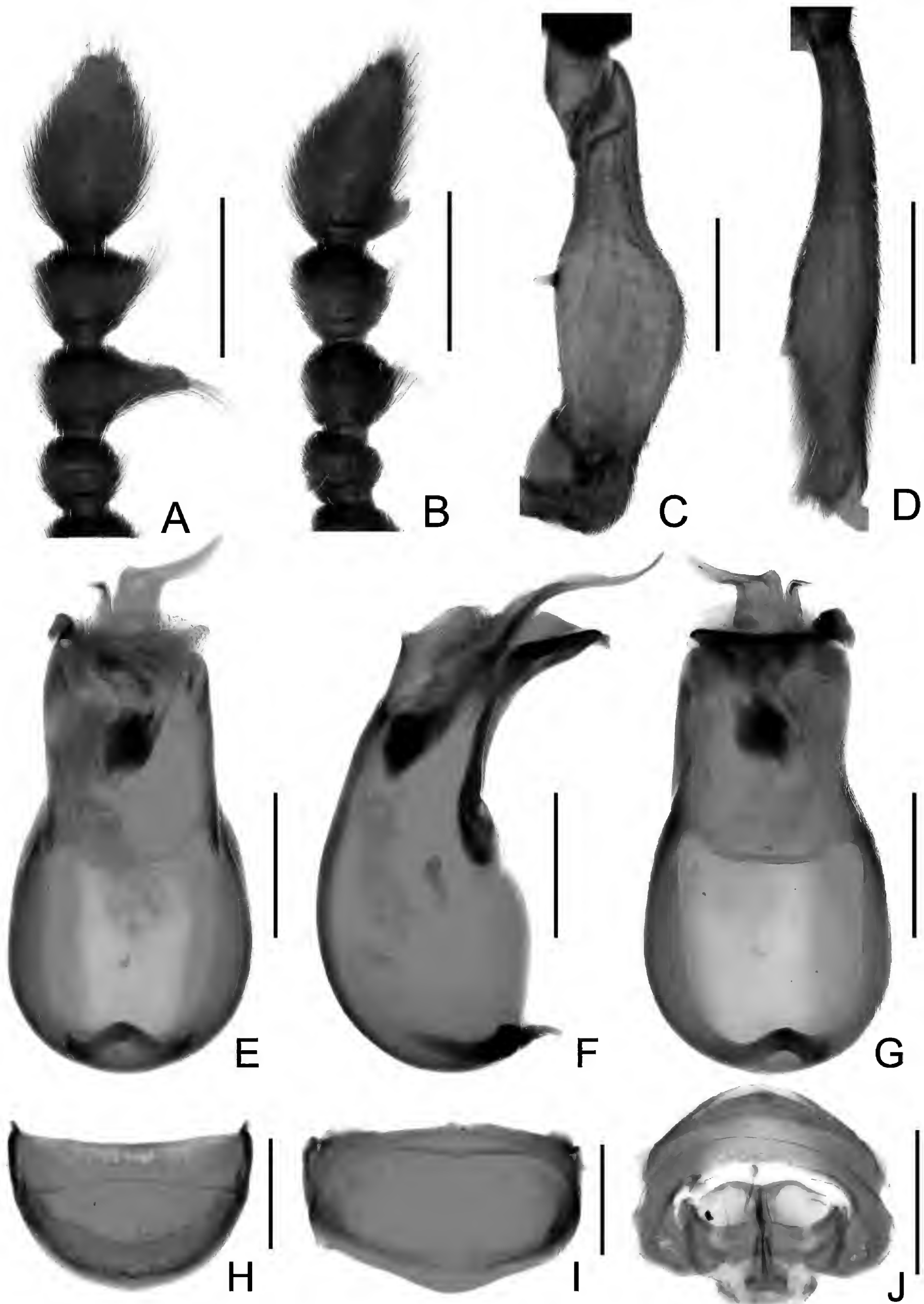
Figure 3. Diagnostic features of *Batrisodes bamian* (**A–G.** male; **H–J.** female). **A–B.** antennal club; **C.** mesotrochanter and mesofemur; **D.** mesotibia; **E.** aedeagus, in dorsal view; **F.** same, in lateral view; **G.** same, in ventral view; **H.** tergite VIII; **I.** sternite VIII; **J.** genital complex. Scales: 0.2 mm.
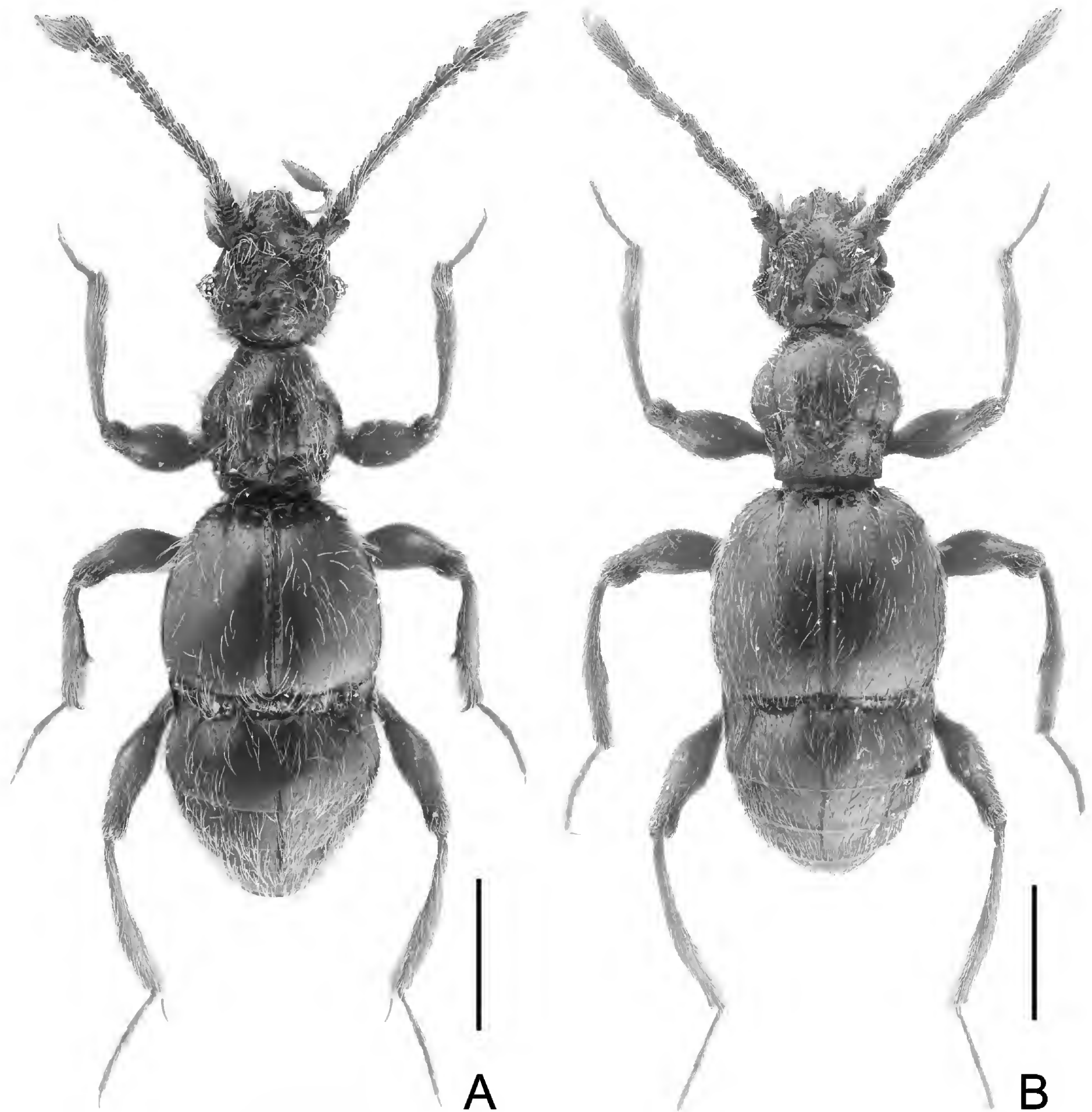
Figure 4. Male habitus of *Batrisodes* species. **A.** *B. longwangshanus*; **B.** *B. songxiaobini.* Scales: 0.5 mm.

plete. Protibiae (Fig. 5B) constricted at apical third; mesotrochanters (Fig. 5C) with big ventral spine, mesofemora (Fig. 5C) with small, blunt ventral spine, mesotibiae (Fig. 5D) with sharp ventral denticle and acute apical spur; metatibiae (Fig. 5E) with long apical tuft of setae. AL 0.64–0.69 mm, AW 0.70–0.72 mm; abdominal tergite IV (first visible tergite) with oblique marginal carinae; discal carinae short. Length of aedeagus (Fig. 5F–H) 0.37 mm, median lobe nearly symmetric, with one thin, short and another large, curved styli at right side of apicolateral margin.

Female. Slightly smaller than male, legs lacking modification and spine; each eye composed of about 8 facets. Tergite VIII (Fig. 5I) and sternite VIII (Fig. 5J) transverse. Genital complex (Fig. 5K) weakly sclerotized,

width 0.23 mm. BL 2.05–2.14 mm, HL 0.42–0.46 mm, HW 0.48–0.52 mm, PL 0.45–0.46 mm, PW 0.43–0.45 mm, EL 0.57–0.60 mm, EW 0.70–0.72 mm, AL 0.61–0.62 mm, AW 0.65–0.67 mm.

Differential diagnosis. *Batrisodes longwangshanus* can be separated from all other congeners by a combination of the simple antennal club, the presence of the ocular canthi, the dentate mesotrochanter, mesofemora, and mesotibiae, and the unique form of the aedeagus.

Biology. All adults were collected from leaf litter samples in a mixed forest.

Distribution. Eastern China: Zhejiang.

Etymology. The specific epithet refers to the type locality of the new species, Longwang Mountain.
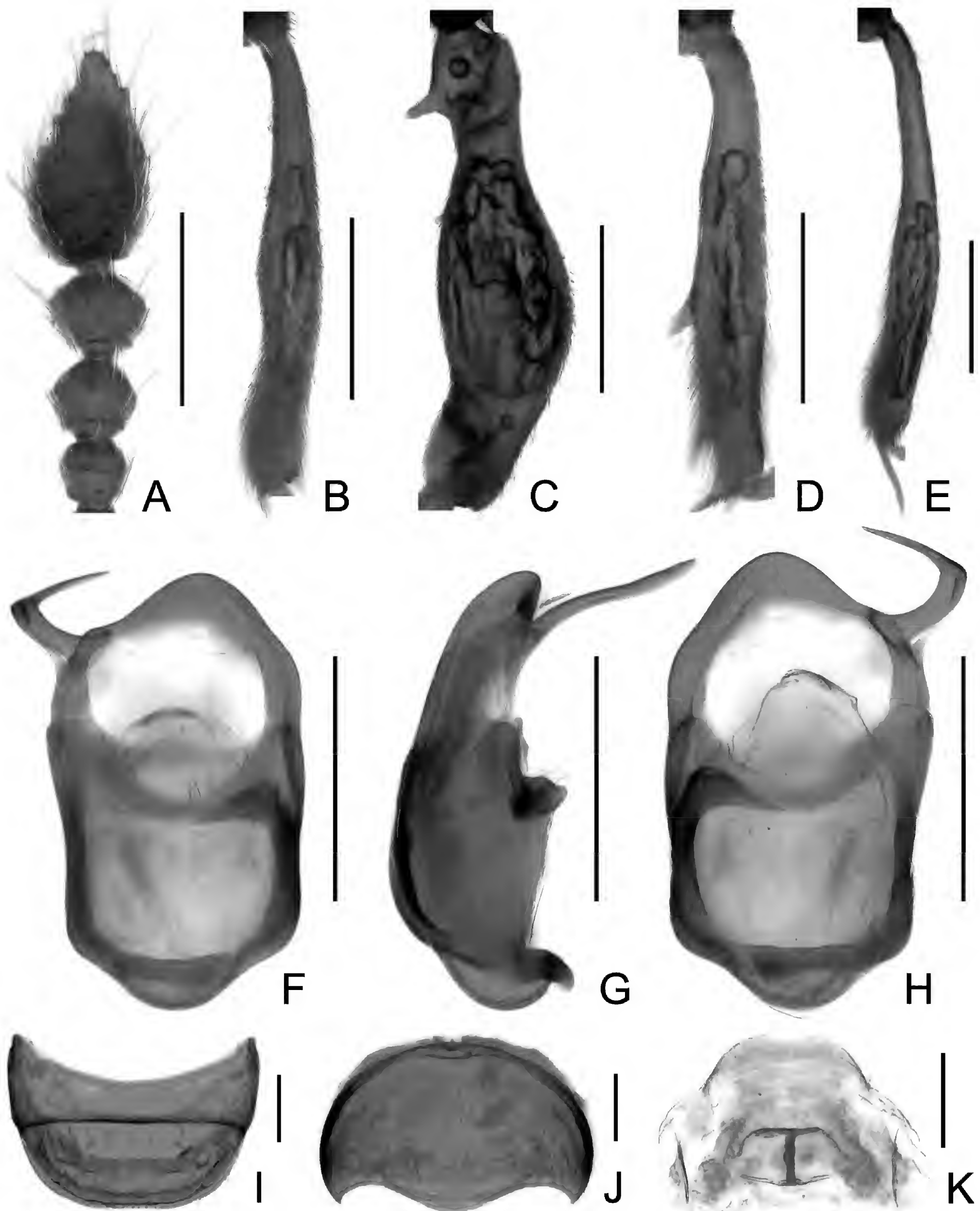
Figure 5. Diagnostic features of *Batrisodes longwangshanus* (**A–H.** male; **I–K.** female). **A.** antennal club; **B.** protibia; **C.** mesotro-chanter and mesofemur; **D.** mesotibia; **E.** metatibia; **F.** aedeagus, in dorsal view; **G.** same, in lateral view; **H.** same, in ventral view; **I.** tergite VIII; **J.** sternite VIII; **K.** genital complex. Scales: A–H = 0.2 mm; I–K = 0.1 mm.
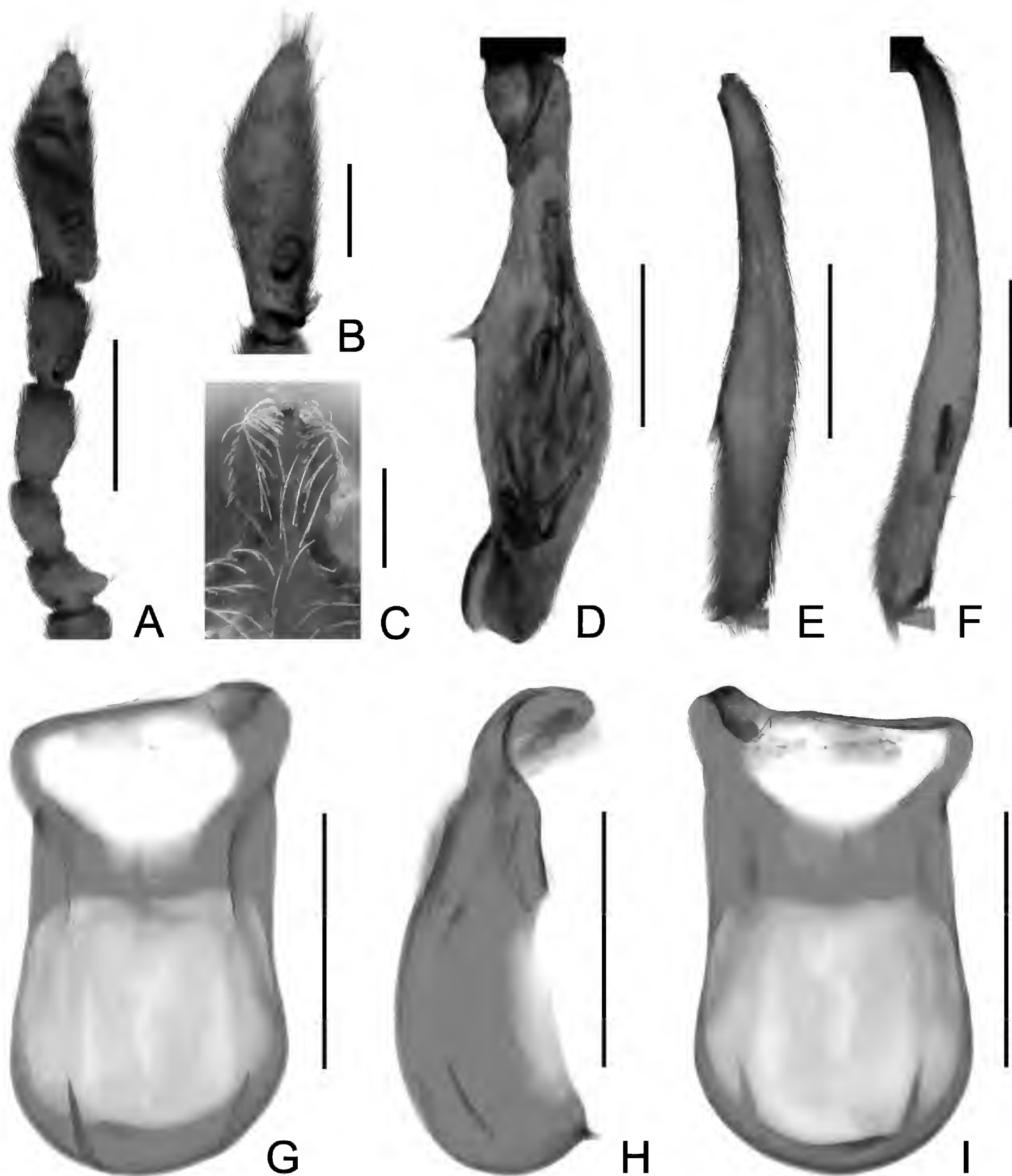
Figure 6. Diagnostic features of *Batrisodes songxiaobini*, male. **A.** antennomeres VII–XI; **B.** antennomere XI, enlarged; **C.** median projection of frons; **D.** mesotrochanter and mesofemur; **E.** mesotibia; **F.** metatibia; **G.** aedeagus, in dorsal view; **H.** same, in lateral view; **I.** same, in ventral view. Scales: A, D–I = 0.2 mm; B, C = 0.1 mm.

Batrisodes songxiaobini Yin, Shen & Li, sp. n.

http://zoobank.org/832A74D6-8C31-4BC7-A927-AF864F5ACFAF
Figs 4B, 6

Type material (6 ♂♂). **Holotype: China:** ♂, labeled 'China: Yunnan, Tengchong Co. [腾冲县], Mingguang Town [明光乡], Zizhi Vill. [自治村], Donghe [东河],

25°42'55''N, 98°34'52''E, 2100 m, 01.v.2014, X.-B. Song, [from a nest of *Formica* sp.]' (SNUC). **Paratypes: China:** 5 ♂♂, same label data as holotype (SNUC).

Description. Male (Fig. 4B). Body reddish brown, BL 2.54–2.60 mm. Head slightly longer than wide, HL 0.52–0.55 mm, HW 0.53–0.54 mm; with small vertexal foveae; frons strongly protruding anteriorly at middle (Fig. 6C);

clypeus lacking punctation, with round anterior margin; lateral vertexal carinae present from level of anterior margins of eyes to posterolateral margins of head, with short median vertexal carina; each eye composed of about 55 facets, lacking ocular canthi; postgenal area with many long erect setae visible in dorsal view. Antennal clubs (Fig. 6A) formed by apical three antennomeres; antennomeres VII expanded at base, with one long, thick seta at apex of expansion, antennomeres VIII–XI each elongate, XI (Fig. 6B) with small denticle at base. Pronotum slightly longer than wide, PL 0.57–0.59 mm, PW 0.51–0.57 mm; disc slightly convex; with distinct median and lateral longitudinal sulci; lacking median antebasal fovea; with small basolateral tubercles. Elytra wider than long, EL 0.75–0.77 mm, EW 0.88–0.90 mm; each elytron with three large nude basal foveae; with shallow discal striae; marginal striae complete. Mesofemora (Fig. 6D) with small, sharp ventral spine, mesotibiae (Fig. 6E) with small ventral denticle and small, acute apical spur; metatibiae (Fig. 6F) with short apical tuft of setae. AL 0.68–0.71 mm, AW 0.77–0.78 mm; abdominal tergite IV (first visible tergite) with oblique marginal carinae; discal carinae short. Length of aedeagus (Fig. 6G–I) 0.40 mm, median lobe nearly symmetric, with one spine-like sclerite at middle of anterior margin of foramen.

Female. Unknown.

Differential diagnosis. The protruding anterior margin of the frons is shared in a number of Asian species, e.g. *Batrisodes cornutus* (Kurbatov) (transferred from the genus *Basitrodes*, see below), and *Batrisodes acutifrons* Jeannel. But the characteristic forms of the antennomeres VII–XI and protruding frons in the male, as well as the aedeagal structure readily separate this new species from all other congeners.

Biology. Adults were collected from a colony of a *Formica* ant nesting under a rock.

Distribution. Southwestern China: Yunnan.

Etymology. The species epithet recognizes the collecting efforts of Xiao-Bin Song, who collected the type series and many other interesting pselaphines.

New synonymy and new combinations

René Jeannel (Jeannel 1958) in his treatment of Japanese Pselaphinae created a number of new genera placed near *Batrisodes*, e.g. *Basitrodes* Jeannel, *Petaloscapus* Jeannel, *Batrisodellus*, *Kigatrodes* Jeannel, and *Speobatrisodes* Jeannel. All of these taxa were defined based on weak characters which are either variable in a genus, or merely male sexual features, e.g. the form of the aedeagus, and the modification of male antennomeres. In our opinion their diagnoses and relationships to *Batrisodes* must be revised in the future.

The genus *Batrisodellus* (type species: *Batrisodes nipponensis* Raffray), comprising nine species from Japan and one species from China (Shibata et al. 2013; Yin, Nomura and Zhao 2011), was originally characterized by the presence of a basal denticle on male antennomeres XI, the dentate male mesofemora and mesotibiae, and the

symmetric, scaphoid aedeagus (Jeannel 1958). In fact, the aedeagus in the Chinese species presents an asymmetric form, while the other characters frequently occur in many *Batrisodes* species. Since none of these characters can be used to effectively separate *Batrisodellus* from *Batrisodes*, the two genera are synonymized here, with *Batrisodellus* being the junior synonym of *Batrisodes*, **syn. n.** As a consequence, all ten species currently placed in *Batrisodellus* are transferred to *Batrisodes*: *Batrisodes acuminatus* (Sharp) **comb. rev.**, *Batrisodes cerberus* (Tanabe & Nakane) **comb. n.**, *Batrisodes coprea* (Tanabe & Nakane) **comb. n.**, *Batrisodes cristatus* (Jeannel) **comb. n.**, *Batrisodes fengtingae* (Yin & Nomura) **comb. n.**, *Batrisodes laticollis* (Jeannel) **comb. n.**, *Batrisodes longulus* (Jeannel) **comb. n.**, *Batrisodes nipponensis* Raffray **comb. rev.**, *Batrisodes palpalis* (Sharp) **comb. n.**, and *Batrisodes punctipennis* (Sharp) **comb. n.**

According to the original description (Kurbatov 1984), the Russian Far East species *Basitrodes cornutus* Kurbatov lacks the unique aedeagal form of *Basitrodes*, but shares many characters typical of *Batrisodes*. After an examination of a high-resolution photo of an identified male [collecting data: Kunashir Is., cordon Alekhinskij, rotten *Abies*, 31.VII.2011, Kurbatov leg.], this species is here moved to *Batrisodes* **comb. n.**

Nomenclatural change

The name *Batrisodes* (*Excavodes*) *simplex* Yin & Li, 2013 is a primary junior homonym of *Batrisodes simplex* (LeConte, 1878), the latter is a junior synonym of *Batrisodes* (*Pubimodes*) *striatus striatus* (LeConte, 1849) (Chandler 1997). Hence we propose a **new replacement name**: *Batrisodes* (*Excavodes*) *pengzhongi*.

Etymology. The new name is dedicated to Zhong Peng, who collected most specimens of the type series of this species.

Acknowledgements

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Taxonomic notes of the Neotropical alderfly genus *Ilyobius* Enderlein, 1910 (Megaloptera, Sialidae), with description of a new species

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http://zoobank.org/0F16CC5E-DF15-4D6D-862C-CB83B0FC4B6C

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Abstract

The alderfly genus *Ilyobius* Enderlein, 1910 is one of the rare groups of Sialidae and mainly distributed in the Neotropical region. Here we describe a new species, *I. curvata* sp. n., from Panama and Colombia. Furthermore, we provide re-description on two described species of *Ilyobius*, i.e., *I. flavicollis* (Enderlein, 1910) and *I. nubila* (Navás, 1933). A key to the species of *Ilyobius* is given. The geographical distribution pattern of extant *Ilyobius* species is also summarized.

Key Words

Introduction

The alderfly genus *Ilyobius* Enderlein, 1910 is one of the distinct but rare groups of Sialidae. This genus was previously treated to be a junior synonym of *Protosialis* van der Weele, 1909 (Penny 1981), but was recently recovered to be valid based on a comprehensive phylogenetic study on the world Sialidae (Liu et al. 2015). The adults of *Ilyobius* are characterized by the distinct coloration (generally orange, sometimes with dark markings) of head and pronotum, the wing venation (Rs with two simple branches, MP with one simple anterior and one bifurcate posterior branch), the presence of male endophallus with blackish thorny setae, the female sternite 7 being distinctly prominent at the posterior middle, and the female gonocoxites plus gonapophyses 8 together presenting as a sclerotized complex. Currently, *Ilyobius* comprises all extant Neotropical alderflies except *Protosialis bifasciata*

(Hagen, 1861), which is still placed in *Protosialis* (Liu et al. 2015). Moreover, because of the similar wing venations, three fossil species are also placed in *Ilyobius*, i.e., †*Ilyobius casca* (Engel & Grimaldi, 2007) from the Miocene Dominican amber, †*Ilyobius baltica* (Wichard, 1997) from the Eocene Baltic amber, and †*Ilyobius herrlingi* (Wichard, 2002) also from the Eocene Baltic amber, the latter two of which have tentative generic placement (Liu et al. 2015).

Compared with the other alderfly genera, the genus *Ilyobius* is still poorly known due to its rareness (Contreras-Ramos 2008). Among the eight described species of *Ilyobius*, five of them, i.e., *I. chilensis* (McLachlan, 1871), *I. flammata* (Penny, 1981), *I. hauseri* (Contreras-Ramos, Fiorentin & Urakami, 2005), *I. mexicana* (Banks, 1901), and *I. ranchograndis* (Contreras-Ramos, 2006), have modern descriptions or re-descriptions (Contreras-Ramos 2006, 2008; Contreras-Ramos et al. 2005), but the

remaining three, i.e., *I. bimaculata* (Banks, 1920), *I. flavicollis* (Enderlein, 1910), and *I. nubila* (Navás, 1933), are known only from their original descriptions, which are generally inadequate.

In this paper, based on our examination of some *Ilyobius* specimens from several historical collections, we provide some new information on this rare alderfly genus, including the re-descriptions of *I. flavicollis* and *I. nubila*, and the description of a new species from Panama and Colombia. The first key to the extant species of *Ilyobius* is also given.

Methods

Specimens for the present study are deposited in the Museum für Naturkunde (MFN), Berlin, Germany; the Warsaw Museum of the Institute of Zoology (MZPW), Polish Academy of Sciences, Warsaw, Poland; the Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany; and the National Museum of Natural History (USNM), Smithsonian Institutions, Washington, D.C., U.S.A. Genitalic preparations were made by clearing the apex of the abdomen in a cold, saturated KOH solution for 8–10 h. After rinsing the KOH with acetic acid and water, the apex of the abdomen was transferred to glycerin for further dissection and examination. After examination it was moved to fresh glycerin and stored in a microvial pinned below the specimen. The terminology of the genitalia follows that of Aspöck and Aspöck (2008).

Taxonomy

Genus *Ilyobius* Enderlein

Ilyobius Enderlein, 1910: 381. Type species: *Sialis flavicollis* Enderlein, 1910: 380, original designation.

Diagnosis. Forewing length ~7.0–17.0 mm in males; ~9.0–19.5 mm in females. Body generally blackish brown, but usually with pale head and prothorax. Head generally orange to reddish brown, sometimes with dark markings on frons and vertex. Antennae pilose, more than half the length of the forewing. Compound eyes strongly prominent. Labrum ~4.0–5.0 times wider than long, lateral margins rounded, front margin slightly emarginated. Prothorax >2.0 times wider than long, pronotum uniformly orange to reddish brown, or blackish brown with pale markings. Forewing ~2.5–3.5 times longer than wide, minutely hirsute, margins pilose; costal area feebly or distinctly dilated proximally, with 5–10 distinct costal crossveins; sc-r present; Rs 2-branched; MA 2-branched; MP 2-branched, anterior branch simple, posterior branch bifurcated; CuA 2-branched, CuP simple; 1A simple, 2A 2-branched, 3A simple; 3 r-rs present. Hindwing ~2.5–3.0 times as long as wide; 2–5 distinct costal crossveins present proximally; sc-r absent; Rs 2-branched; MA

2-branched; MP 2-branched; CuA 2-branched, CuP simple; 1A simple, 2A 2-branched, 3A simple; 3 r-rs present. Male tergite 9 transversely arched; sternite 9 broadly lingulate, posteriorly sometimes with elongate median projection; gonocoxites 9 widely separated from each other, generally short and ovoid, but complicatedly shaped in some species; ectoproct paired, or largely paired but medially connected by feebly sclerotized, narrow region; gonocoxites 11 transversely arched, posteriorly with a pair of median processes (= gonostyli 11), which are variously shaped among species; endophallus internally with blackish thorny setae. Female sternite 7 broad, usually with a tubercular median projection near posterior margin; fused gonocoxites 8 and gonapophyses 8 forming a strongly sclerotized complex; tergite 9 strongly broadened ventrally, separating an independent dorsal region, which is much narrower and extending ventrad; gonocoxites 9 valvate, ovoid, posteriorly bearing rather small gonostyli 9.

Distribution. The extant described species are recorded from Argentina, Bolivia, Brazil, Chile, Colombia, Mexico, Panama, Peru, and Venezuela. In addition, an undetermined species was recorded in Ecuador (Contreras-Ramos 2008). Considering fossils, *Ilyobius* might have been distributed in Eurasia based on the two species described from the Eocene Baltic ambers (Wichard 1997, 2002) although their generic placements need further clarification (Liu et al. 2015). Another species from the Miocene Dominican amber (Engel and Grimaldi 2007) indicates the past occurrence of *Ilyobius* in Dominica.

Ilyobius curvata sp. n.

http://zoobank.org/CB200390-6333-4696-B8EB-47BDBB51535F
Figs 1–2, 5–11, 15

Description. Male. Forewing length 7.0–8.6 mm, hindwing length 5.6–7.8 mm.

Head (Figs 1, 5) smoothly orange, slightly brown on clypeus, with dense short yellowish pilosity; a pair of blackish brown markings present and expanded from entire inner margins of compound eyes, with bifurcate extension medially and trifurcate extension posteriorly; raised scars indistinct. Compound eyes brown. Antennae brown. Mouthparts blackish brown.

Prothorax (Figs 1, 5) brown throughout, pronotum with anterior margin reddish brown; meso- and meta thorax blackish brown. Legs pale brown, bearing dense brownish setae; tarsal claws reddish brown. Wings smoky brown, slightly darker on costal areas and proximal portions; veins pale brown. Forewing about 2.4 times as long as wide; costal area with 13 crossveins (eight proximal ones distinct); sc-r present; Rs with two simple branches; MA with two simple branches; MP proximally fused with CuA, having simple anterior branch and bifurcate posterior branch; CuA bifurcated, CuP simple; 1A simple, 2A with two simple branches, 3A simple; three r-rs present. Hindwing slightly narrower than forewing, about
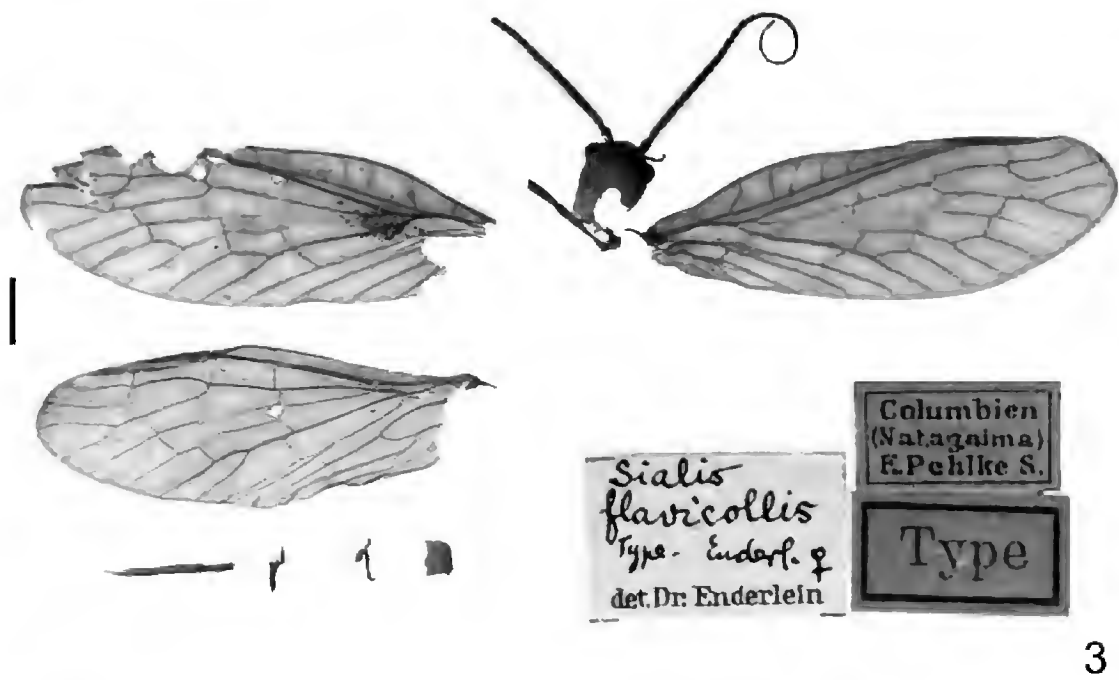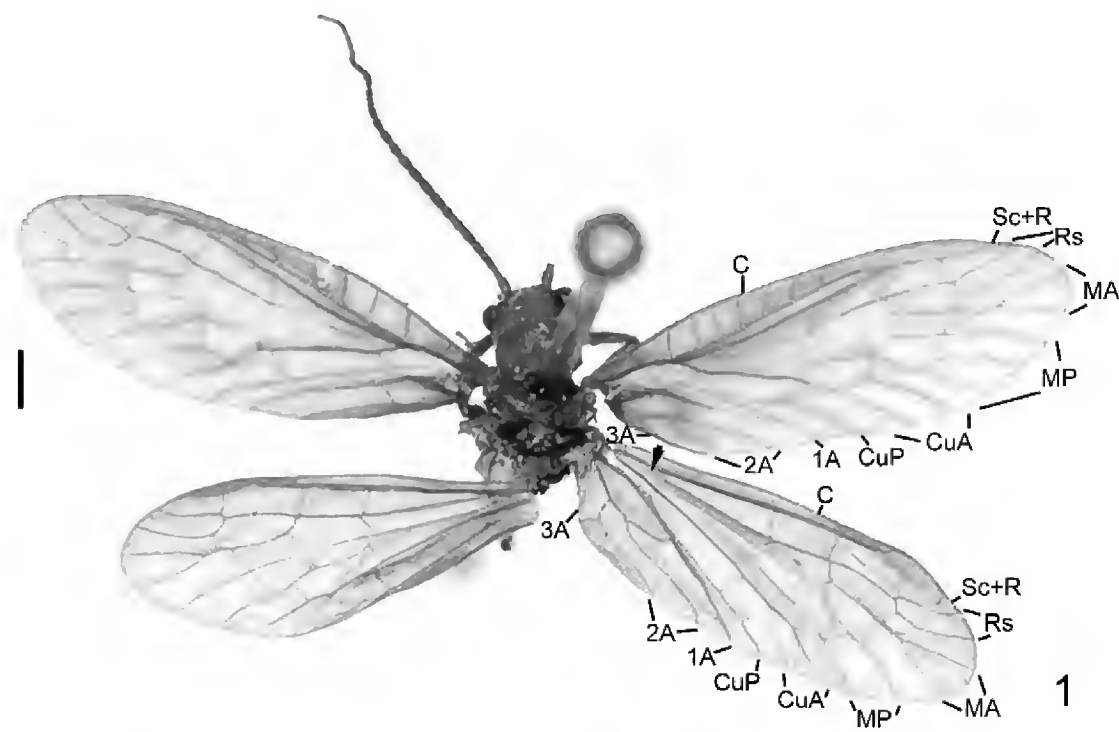
Figures 1–4. Habitus images of *Ilyobius* spp. **1.** *I. curvata* sp. n., male holotype; **2.** *I. curvata* sp. n., female paratype; **3.** *I. flavicollis* (Enderlein), female holotype and its labels; **4.** *I. nubila* (Navás), female holotype and its labels. Arrow indicates the base of hindwing MA. Scale bars: 1.0 mm.
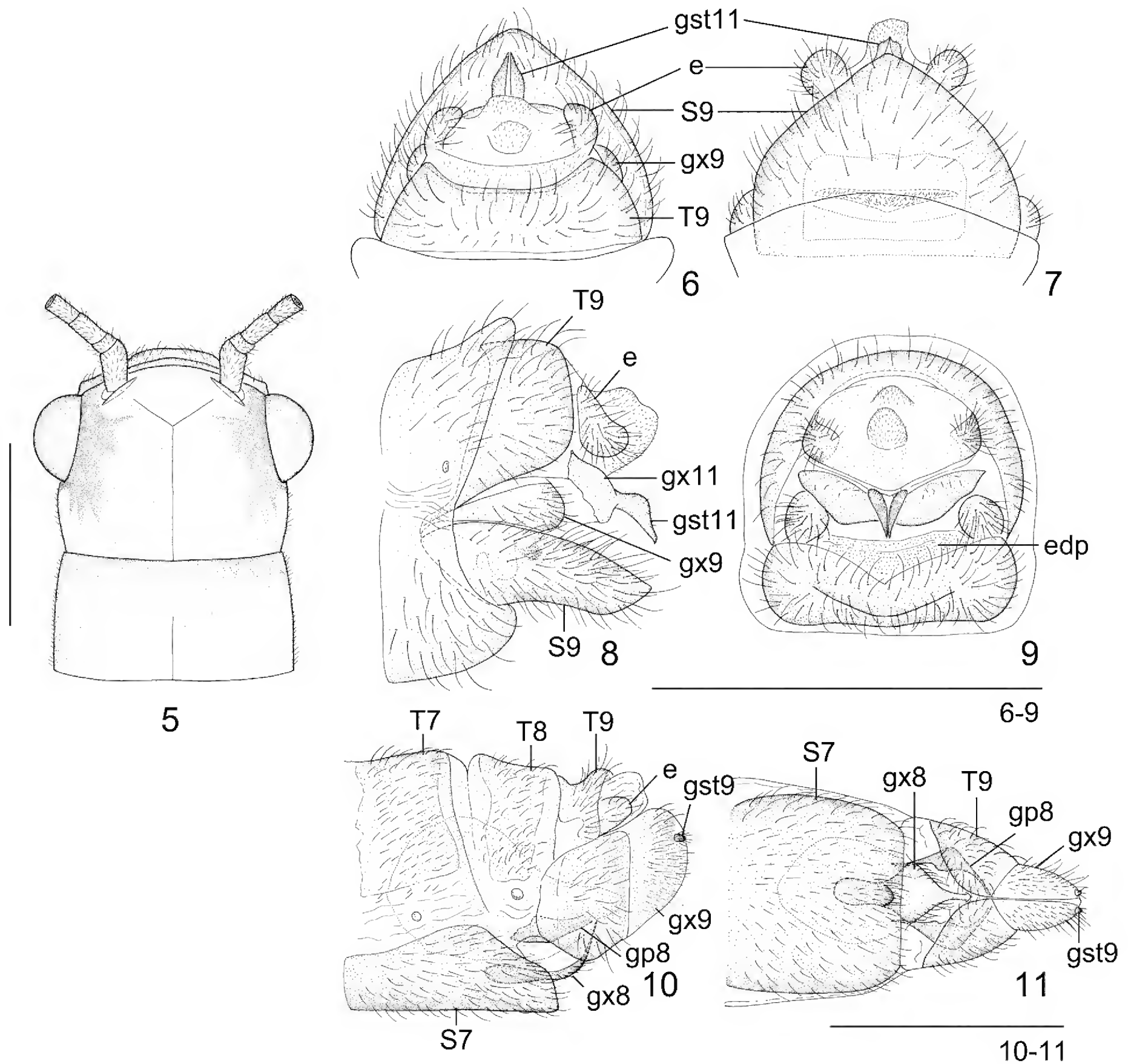
Figures 5–11. *Ilyobius curvata* sp. n. **5.** Male head and pronotum, dorsal view; **6.** Male genitalia, dorsal view; **7.** Male genitalia, ventral view; **8.** Male genitalia, lateral view; **9.** Male genitalia, caudal view; **10.** Female genitalia, lateral view; **11.** Female genitalia, ventral view. e: ectoproct; edp: endophallus; gp8: gonapophyses 8; gst9 and 11: gonostylus 9 and 11; gx8, 9, and 11: gonocoxite 8, 9 and 11; S7 and 9: sternite 7 and 9; T7–9: tergite 7–9. Scale bars: 1.0 mm.

2.9 times as long as wide; costal area with seven costal crossveins (two proximal ones distinct); branching condition of longitudinal veins mostly same as that of forewing, except for MP having two simple branches; MA proximally leaving a short oblique veinlet fused with MP; M separated from R.

Abdomen blackish brown. Tergite 9 (Fig. 6) in dorsal view nearly 3.0 times as wide as long, anterior margin truncate, posterior margin slightly concaved. Sternite 9 (Fig. 7) lingulate, about twice as long as tergite 9, posteromedially slightly pointed. Gonocoxite 9 (Fig. 8) ovoid, slightly shorter than tergite 9, gradually widened posteriad, with rounded apex. Ectoprocts (Fig. 6) largely paired, ovoid, medially connected by a feebly sclerotized transverse zone. A short ovoid lobe present beneath anus

(Fig. 9). Gonocoxites 11 (Figs 8–9) transversely arched proximally, median processes (= gonostyli 11) close to each other and strongly curved ventrad, with unguiform tips. Endophallus (Figs 7–8) present between tergite and sternite 9, internally with a narrow, transversely bandlike, and densely scabrous membrane.

Female. Body length 9.0 mm; forewing length 9.0–9.5 mm, hindwing length 8.4–8.7 mm.

Sternite 7 (Figs 10–11) broad, subtrapezoidal in lateral view and subquadrate in ventral view, with truncate posterior margin and a small tubercular projection subdistad. Fused gonocoxites 8 (Figs 10–11) narrowly elongated, and posteriorly curved dorsad in lateral view; in ventral view nearly rhombic, longitudinally depressed as a canal from a rather narrowed posterior portion to a roundly in-

flated anterior portion, which is inserted beneath sternite 7; gonapophyses 8 (Figs 10–11) distinctly sclerotized, strongly convex posteriad, and widened laterally. Tergite 9 laterally separating into short, narrow dorsal region and broad, subtrapezoidal ventral region. Gonocoxite 9 (Fig. 10) broadly valvate, arcuately margined ventrad, posteriorly with a small gonostylus 9 at tip. Ectoprocts (Fig. 10) short, ovoid.

Type materials. Holotype ♂, "Columbien [= Colombia], Moritz/*ruficeps* Mor[itz]. i.det. [= identified] Columb[ia]. Mor[itz]." (MFN). Paratypes 1♀, "Columbien [= Colombia], Moritz" (MFN). 1♀, "Tabernilla [ca. 9°08'N; 79°48'W], Canal Zone, Panama/May 4–07/Collected by August Busck/*Protosialis mexicana* (Bks. [= Banks]) ♀, det. A. Contreras[-Ramos], [20]05" (NMNH); 2♂, Pacora [ca. 9°04'N; 79°17'W], Panama, II-19-[19]45, H.H. Stage/Plot F Sheet, 24 hrs [= hours], 45–4519/*Protosialis mexicana* (Bks. [= Banks]) ♂, A. Contreras-R[amos]., det. 2005" (NMNH).

Distribution. Colombia; Panama (Panama Province).

Etymology. The specific epithet "*curvata*" refers to the strongly ventrally curved median processes (gonostyli) of the male gonocoxites 11 in the new species.

Remarks. The new species is closely related to *Ilyobius mexicana* (Banks, 1901) by having similar cephalic marking patterns and general genitalic characteristics. The three paratypes of the new species from Panama were even identified to be *I. mexicana* by Contreras-Ramos (2008). However, *I. curvata* differs from *I. mexicana* by the male gonocoxites 11 with median processes close to each other and strongly curved ventrad and by the female fused gonocoxites 8 strongly narrowed posteriad. In *I. mexicana* the median processes of male gonocoxites 11 are straightly directed and the female fused gonocoxites 8 is bluntly prominent posteriorly. These genitalic differences are stable based on our examination of several specimens of both species. Moreover, concerning the body-size, *I. curvata* is smaller than *I. mexicana*, with the forewing length less than 9.0 mm in males and 10.0 mm in females, while the forewing length of *I. mexicana* is more than 11.0 mm in males and 12.0 mm in females.

Ilyobius flavicollis (Enderlein)

Figs 3, 15

Sialis flavicollis Enderlein, 1910: 380. Type locality: Colombia (Natagaima).

Re-description. Female. Body length 12.0 mm; forewing length 14.5 mm, hindwing length 13.0 mm.

Head (Fig. 3) blackish brown, but dark orange on median portion of vertex, with dense brownish pilosity; vertex with few raised scars. Compound eyes blackish brown. Antennae blackish brown. Mouthparts brown.

Pronotum (Fig. 3) uniformly orange, other parts of thorax damaged. Only one foreleg preserved, blackish brown, bearing dense brownish setae. Wings smoky

brown, with brownish veins. Forewing about 2.5 times as long as wide, with several transparent patches on proximal costal cells; costal area proximally distinctly dilated, with 10 distinct crossveins; sc-r present; Rs with two simple branches; MA with two simple branches; MP proximally fused with CuA, having simple anterior branch and bifurcate posterior branch; CuA bifurcated, CuP simple; 1A simple, 2A with two simple branches, 3A simple; three r-rs present. Hindwing about 2.5 times as long as wide; costal area proximally with four distinct crossveins; branching condition of longitudinal veins mostly same as that of forewing, except for MP having two simple branches; MA proximally leaving a short oblique veinlet fused with MP; M separated from R.

Abdomen damaged.

Type material. Holotype ♀, "Columbien [= Colombia] (Natagaima [a town of Tolima Department, ca. 3°35'N; 75°05'W]), E[rnst]. Pehlke S./Type/*Sialis flavicollis* Enderl[ein]. ♀, Type, det. Dr. Enderlein" (MZPW).

Distribution. Colombia (Tolima).

Remarks. *Ilyobius flavicollis* is the type species of the genus *Ilyobius*. Unfortunately, the primary type of *I. flavicollis* is largely damaged with the abdomen lost. Nevertheless, *I. flavicollis* is highly possible to be the same genus with the other Neotropical alderflies based on the alternately black-orange body coloration and the wing venations with two simple Rs branches and a bifurcated posterior branch of MP. The cephalic color pattern of *I. flavicollis* is different from all the other *Ilyobius* species, suggesting that this species should be valid.

Ilyobius nubila (Navás)

Figs 4, 12–15

Protosialis nubila Navás, 1933: 36. Type locality: Brazil (São Paulo).
Protosialis brasiliensis Navás, 1936: 725. Type locality: Brazil (São Paulo: Ipiranga).

Re-description. Female. Body length 8.0 mm; forewing length 10.0 mm, hindwing length 8.3 mm.

Head (Figs 4, 12) black, slightly paler around epicranial suture, with dense yellowish pilosity; a pair of dark orange areas posteriorly expanded from entire inner margins of compound eyes; vertex with raised scars. Compound eyes blackish brown. Antennae with scape and pedicel blackish brown, flagellum lost. Mouthparts black.

Thorax (Figs 4, 12) black throughout. Legs yellowish brown, bearing dense brownish setae; tarsal claws reddish brown. Wings smoky brown, with brownish veins. Forewing about 3.5 times as long as wide; costal area proximally distinctly dilated, with five distinct crossveins; sc-r present; Rs with two simple branches; MA with two simple branches; MP proximally fused with CuA, having simple anterior branch and bifurcate posterior branch; CuA bifurcated, CuP simple; 1A simple, 2A with two simple branches, 3A simple; three r-rs present. Hindwing
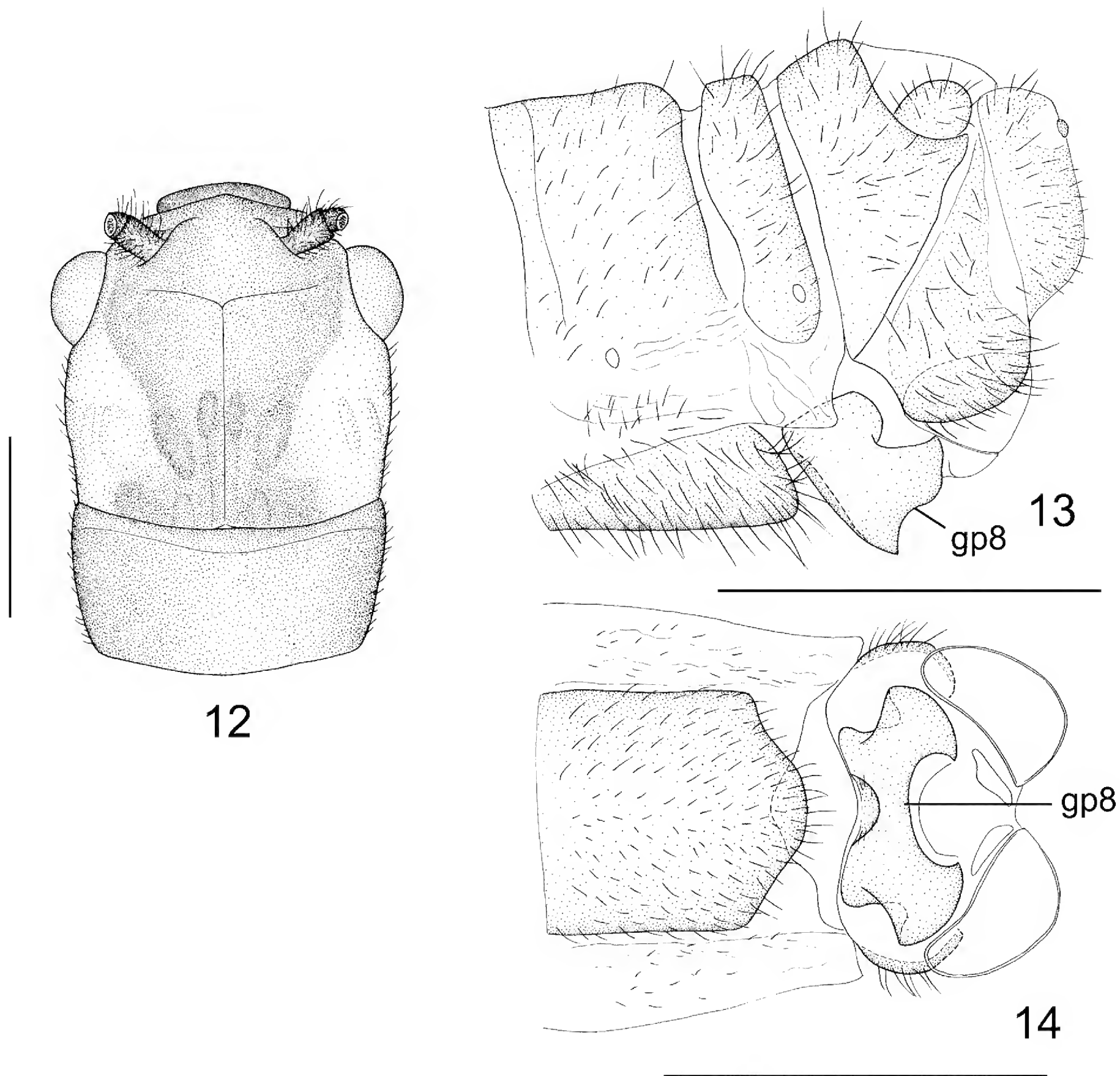
Figures 12–14. *Ilyobius nubila* (Navás). **12.** Female head and pronotum, dorsal view; **13.** Female genitalia, lateral view; **14.** Female genitalia, ventral view. gp8: gonapophyses 8. Scale bars: 1.0 mm.

slightly broader than forewing, about 3.0 times as long as wide; costal area with two distinct crossveins, branching condition of longitudinal veins mostly same as that of forewing, except for MP having two simple branches; MA proximally leaving a short oblique veinlet fused with MP; M separated from R.

Abdomen black. Sternite 7 (Figs 13–14) broad, with posterior margin roundly prominent medially. Fused gonocoxites 8 (Figs 13–14) rather small, sparsely setose, fused at anterior margin of gonapophyses 8; gonapophyses 8 (Fig. 14) composed of a strongly sclerotized plate, which is ventrally depressed and strongly widened on posterior half, with a broadly arched posterior incision, and a pair of broadly semicircular and a pair of tiny, transparent, membranous plates. Tergite 9 laterally separating into narrowly subtrapezoidal dorsal region and narrowly subtriangular ventral region. Gonocoxite 9 (Fig.

13) broadly valvate, arcuately margined ventrad, posteriorly with a small gonostylus 9 at tip. Ectoprocts (Fig. 13) short, ovoid.

Male. Unknown.

Type material. Holotype ♀, "Malto Go-vuros? [unrecognizable handwritten words], Melzer/Brasil - S[ão]. Paulo, Est[at]. S[ão]. Paulo, 20.XI.1927 [collecting data on opposite side of the label]/*Protosialis nubila* Nav[ás]., P. Navás S.J. det./Holotypus" (SDEI).

Distribution. Brazil (São Paulo).

Remarks. *Protosialis brasiliensis* Navás, 1936 was treated to be a junior synonym of *I. nubila* by Liu et al. (2015), but a re-description and a detailed comparison of these two species was not provided in that paper. The evidence for synonymizing these two species is: 1) the same cephalic color patterns with broad black area approaching the compound eyes, 2) the same black pronotum, 3) the
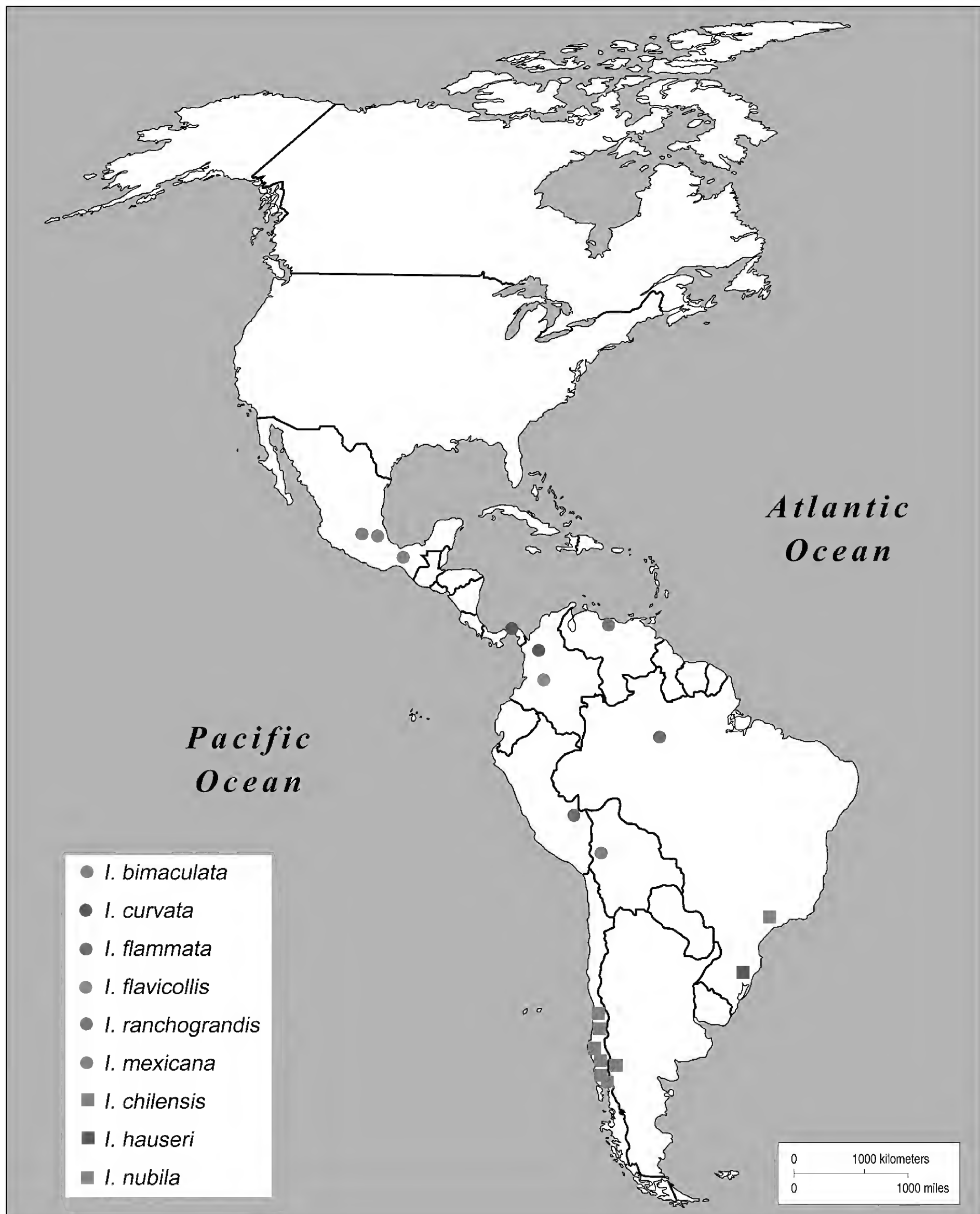
Figure 15. Distribution map of extant species of *Ilyobius*. Besides the present record, other geographical distribution records were obtained from Flint (1973), Penny (1981), Contreras-Ramos (2006, 2008), and Contreras-Ramos et al. (2005).

same wing shape, which is narrowed with distinctly dilated costal area; 4) the same distribution area. The type locality of *I. nubila* was cited to be in the Mato Grosso State of Brazil (Oswald 2014). This record is actually from a very unclear and unrecognizable handwritten la-

bel of the holotype of *I. nubila*. However, the opposite side of this collecting label includes some printed words "Brasil - S. Paulo, Est. S. Paulo" and a possible collecting date "20.XI.1927", which have never been mentioned in the original description (Navás 1933). Therefore, we can-

not exclude the possibility that the holotype of *I. nubila* was collected from São Paulo, where this species occurs, based on the distribution record of *P. brasiliensis* (the junior synonym of *I. nubila*).

This species appears to be closely related to another Brazilian species, *Ilyobius hauseri* (Contreras-Ramos, Fiorentin & Urakami, 2005), by having similar cephalic color patterns with a longitudinal median black stripe,

the black pronotum, and the narrow forewings with distinctly dilated costal area. However, *I. nubila* can be distinguished from *I. hauseri* by the broader cephalic black stripe and the posteriorly broadened female gonapophyses 8 with a broad arcuate posterior notch. In *I. hauseri*, the cephalic black stripe is relatively narrow and not approaching the compound eyes, and the female gonapophysis 8 is convex posteriad without any posterior notch.

Key to species of *Ilyobius*

1 Pronotum pale, uniformly orange to reddish brown (Fig. 1); female fused gonocoxites 8 well developed, gonapophysis 8 with a narrow, arcuate, posteriorly convex sclerite (Fig. 11) 2

– Pronotum dark, usually black, sometimes with pale markings (Fig. 3); female fused gonocoxites 8 reduced, gonapophysis 8 with a broad, plate-like sclerite (Fig. 14) 7

2 Head without posteriorly trifurcate dark marking around compound eyes (Fig. 3).. 3

– Head with posteriorly trifurcate dark markings around compound eyes (Fig. 5).. 4

3 Head blackish brown, but dark orange on median portion of vertex (Fig. 3); **Colombia** ....*I. flavicollis* (Enderlein)

– Head uniformly orange brown (Contreras-Ramos 2006: fig. 1); **Venezuela**................*I. ranchograndis* (Contreras-Ramos)

4 Frons with a pair of ovoid black spots between antennal fossae; **Bolivia** ....*I. bimaculata* (Banks)

– Frons without any dark marking 5

5 Male gonocoxite 9 elongate and strongly directed posterodorsad (Contreras-Ramos 2008: fig. 10); male gonocoxites 11 with median processes directed ventrad (Contreras-Ramos 2008: fig. 10); **Brazil** and **Peru**..............*I. flammata* (Penny)

– Male gonocoxite 9 short, ovoid, not directed posterodorsad (Fig. 8); male gonocoxites 11 with median processes directed posteriad (Fig. 8); **Central America** and **northernmost of South America** 6

6 Forewing length more than 11.0 mm in males and 12.0 mm in females; male gonocoxites 11 with median processes straightly directed posteriad (Liu et al. 2015: fig. 14g); female fused gonocoxites 8 bluntly prominent posteriad (Liu et al. 2015: fig. 15d); **Mexico** .... *I. mexicana* (Banks)

– Forewing length less than 9.0 mm in males and 10.0 mm in females; male gonocoxites 11 with median processes distinctly curved posteroventrad on distal half (Fig. 8); female fused gonocoxites 8 strongly narrowed posteriad (Fig. 11); **Panama** and **Colombia**...*I. curvata* sp. n.

7 Head orange with three broad black markings on frons and lateral portions of vertex, but middle of vertex without dark marking (Contreras-Ramos 2008: fig. 3); male sternite 9 posteriorly with a long, digitiform, median projection, but without any posterolateral projection (Liu et al. 2015: fig. 14b); **Argentina** and **Chile** .... *I. chilensis* (McLachlan)

– Head orange with a median black stripe extending from middle of vertex to frons; male sternite 9 posteriorly with a long, digitiform, median projection and a pair of short lateral projections (Contreras-Ramos et al. 2005: fig. 3); **Brazil**....... 8

8 Head with median black stripe anteriorly not approaching compound eyes (Contreras-Ramos et al. 2005: fig. 1); female gonapophysis 8 posteriorly convex (Contreras-Ramos et al. 2005: fig. 6); **Brazil** . *I. hauseri* (Contreras-Ramos, Fiorentin & Urakami)

– Head with median black stripe anteriorly expanded and approaching compound eyes (Fig. 12); female gonapophysis 8 posteriorly broadly concaved (Fig. 14); **Brazil**.. *I. nubila* (Navás)

Discussion

Liu et al. (2015) separated *Ilyobius* into two species-groups, i.e., the *I. chilensis* group and the *I. mexicana* group, according to a morphology-based phylogenetic analysis of the world's alderfly species. The *I. chilensis* group is composed of *I. chilensis*, *I. hauseri*, and *I. nubila*, and its monophyly is supported by the male sternite 9 with an elongate median projection, the hook-like male ectoprocts, the transversely band-like male gonocoxite 11 with short median processes, and the female fused gonocoxites 8 reduced and fused with gonapophyses 8 (Liu et al. 2015). Four species, *I. flammata*, *I. flavicollis*, *I. mexicana*, and *I. ranchograndis*, were placed in the *I. mexicana* group, whose synapomorphies are the male ectoprocts largely paired but me-

dially connected by a very thin and feebly sclerotized region, the male anus ventrally with a setose lobe, and the female sternite 7 with a tubercular process near posterior margin (Liu et al. 2015). *Iylobius bimaculata* and *I. curvata* are herein considered to be members of the *I. mexicana* group based on the similar cephalic marking patterns and genitalia.

The biogeography of Neotropical Megaloptera is poorly known. Some Neotropical genera of Corydalidae were considered to be diverged due to the splitting of Gondwana during Mesozoic (Penny 1993; Contreras-Ramos 1998; Liu et al. 2012). However, the divergence time of *Ilyobius* with its related genera is still unclear, but was estimated to be very early before the splitting of Pangaea in the Mesozoic (Liu et al. 2015). The only published work on speciation and their bio-

geographical correlation of Neotropical Megaloptera refers to Contreras-Ramos (1998), in which however the biogeographical discussion on the dobsonfly genus *Corydalus* is very general. The uplifting of the Andes, the formation of the Amazonian inland sea, and the northward movement of the Paraná biogeographic province were considered to be the major events for the speciation of *Corydalus* (Contreras-Ramos 1998). Considering *Ilyobius*, the Andes might also have been a significant vicariance for some speciation within this genus. For example, *I. chilensis* is restricted to a narrow area eastern to the Southern Andes, while its congeners, i.e. *I. hauseri* and *I. nubila*, are apparently from the western area to the Southern Andes. Moreover, according to the present distribution pattern of *Ilyobius* (Fig. 15), the two species-groups show more or less disjunctive distributions to each other. The *I. chilensis* group is distributed in southern part of South America, while the *I. mexicana* group ranges from central-eastern South America to Central America. The separation between these two species-groups seems to be correlated with the formation of the Brazilian Plateau where *Ilyobius* has not been collected, probably because this genus prefers the tropical or subtropical lowland forests but not the highland habitats. Nevertheless, due to the incomplete knowledge of the distribution of *Ilyobius* and its phylogeny, any biogeographical consideration on this genus is still premature. The faunal exploration and re-description of the species yet poorly known in *Ilyobius* are still important and will be the basis for further phylogenetic and biogeographic studies, which will be helpful to understand the evolutionary history of this interesting group.

Acknowledgements

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The Sawflies of Crete (Hymenoptera, Symphyta)

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Abstract

Forty-two sawfly species are now known from Crete, including twelve species here recorded for the first time, and excluding earlier published records of *Allantus didymus* (Klug, 1818) based on misidentifications. *Allantus nigrolinearis* (Zirngiebl, 1937) is treated as a distinct species within the *laticinctus-didymus* group. *Aneugmenus oertzeni* (Konow, 1887) is allied to the Sardo-Corsican *A. bibolinii* Zombori, 1979 and belongs to *Aneugmenus* Hartig, 1837 s. str., not *Atoposelandria* Enslin, 1913. *Pristiphora nievesi* Haris, 2002 is a new synonym of *P. tetrica* (Zaddach, 1883). Of the newly recorded species, *Chevinia mediterranea* Lacourt, 2003, *Dolerus puncticollis* Thomson, 1871 and *Empria archangelskii* Dovnar-Zapolskij, 1929 are simultaneously new for the country of Greece. Four species (*Allantus nigrolinearis*, *Aneugmenus oertzeni*, *Periclista cretica* (Schedl, 1981) and *Pristiphora* sp. [*subbifida* group]) have not been recorded outside Crete, and may be endemic. It is not clear whether the morphologically and genetically distinctive Cretan specimens of *Strongylogaster multifasciata* (Geoffroy, 1785) should be regarded as a Cretan endemic species, for which the name *S. cretensis* Konow, 1887 is available, or as an isolated population of *S. multifasciata*. This requires further study, as also the taxonomic status of *Heterarthrus imbrosensis* Schedl, 1981 (only known from Crete) and *H. wuestneii* (Konow, 1905) (widespread in the West Palaearctic). The sympatric occurrence of three related *Pristiphora* species on *Acer sempervirens*, two of which differ in their choice of host individuals that are at different stages of vegetative development, is remarkable. A checklist of the Symphyta of Crete is presented.

Introduction

The Greek island of Crete, in the southern Aegean Sea, is well known for its richness in endemic plant and animal species (Legakis and Kypriotakis 1994). Although the Cretan flora has been studied very intensively, much less is known about many invertebrate groups. The sawfly fauna has been treated by Schedl (1981, 1985, 1993, 2011), who based his studies mainly on material which he collected during six visits to the island, together with specimens made available by other entomologists or housed in public collections. His first paper on this topic (Schedl 1981) also collated the fragmented earlier literature containing records of Cretan sawflies. Schedl (1993) remarked on the general scarcity of Symphyta in Crete,

and stated that only a total of about 150 specimens had been available to him for study. It seemed from his data, that little collecting had been done in the earlier part of spring (March and April). We accordingly chose these months for two visits to Crete in 2013. Many of the species which we encountered, represented by a total of over 600 specimens, were previously recorded in Crete only from very few individuals. For this reason we list all the material that was recently obtained.

Material and methods

A visit to Crete by Liston alone at the end of March was followed by a visit by all three authors at the end of April.

The first visit was centered on Iraklion, with day trips mainly into central Crete. Excursions during the second visit, based at Daratsos near Chania, were mainly in western Crete and focussed on localities in and around the Lefka Ori (White Mountains). Here we paid particular attention to endemic plant species such as *Zelkova abelicea*: a Tertiary relict, endemic Cretan member of the Ulmaceae (Kozlowski, 2013). The two excursions allowed us to do field work at a wide range of localities spread throughout most of the island except for the most easterly part. We collected using aerial nets with extendable handles, mainly by sweeping. Most material, including vouchers of all species, is deposited in the collection of the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI). Additional specimens are in the private collection of H.-J. Jacobs, and some duplicates in the US National Museum, Washington DC. Results of DNA barcoding (sequencing of part of the COI mitochondrial gene) conducted as part of the Barcode of Life Project (BOLD) (Ratnasingham and Hebert 2007) are included for some taxa whose taxonomic status is discussed. The specimen codes used in BOLD are given. Numbers preceded by DEIGISHym refer to specimens deposited in the SDEI; the prefix BC ZSM HYM denotes specimens held by the Zoologische Staatssammlung, Munich, Germany. Tissue for sequencing was obtained by detaching the right-hand mid leg, or part thereof, of pinned, dried specimens. Taxonomy and nomenclature follows Taeger et al. (2010) with modifications by Liston and Prous (2014), Malm and Nyman (2015) and Prous et al. (2014).

The approximate coordinates and altitudes of the collection localities, listed alphabetically under their prefecture (from West to East), are:

Chania. Agia, 35.477°N, 23.930°E, 30 m. Agia Irini, 35.328°N, 23.837°E, 580 m. Askifou, 35.288°N, 24.191°E, 690 m. Daratsos, 35.506°N, 23.974°E, 30 m. Drakona, 35.406°N, 24.020°E, 510 m. Drakona 2, 35.416°N, 24.032°E, 320 m. Fournes, 35.418°N, 23.940°E, 200 m. Fournes-Meskla, 35.417°N, 23.950°E, 320 m. Kakopetros, 35.417°N, 23.750°E, 470 m. Kandanos, 35.333°N, 23.733°E, 420 m. Komitades, 35.208°N, 24.173°E, 170 m. Kournas and Georgiopolis, 35.347°N, 24.273°E, 25 m. Lakki, 35.371°N, 23.896°E, 900 m. Lousakies, 35.458°N, 23.629°E, 260 m. Meskla, 35.401°N, 23.955°E, 210 m. Moni, 35.285°N, 23.822°E, 110 m. Nea Roumata, 35.383°N, 23.850°E, 410 m. Omalos, 35.322°N, 23.913°E, 1100 m. Omalos 2, 35.325°N, 23.891°E, 1060 m. Platanias, 35.500°N, 23.900°E, 20 m. Samonas, 35.407°N, 24.108°E, 310 m. Sempronas, 35.376°N, 23.824°E, 660 m. Strovles, 35.369°N, 23.670°E, 430 m. Theriso-Drakona, 35.400°N, 23.983°E, 600 m. Topolia, 35.424°N, 23.687°E, 270 m.

Rethimnon. Anogeia, 35.289°N, 24.882°E, 750 m. Armeni, 35.295°N, 24.453°E, 400 m. Livadia, 35.303°N, 24.808°E, 395 m. Moni Kato Preveli, 35.171°N, 24.466°E, 170 m.

Iraklion. Krasi, 35.234°N, 25.467°E, 600 m. Marathos, 35.347°N, 24.972°E, 400 m. Mesa Potami, 35.213°N, 25.521°E, 720 m. Potamies, 35.256°N, 25.387°E, 170 m.

Lasithi. Katharo Plateau, Kopraki, 35.147°N, 25.565°E, 1150 m. Mesa Lasithi, 35.181°N, 25.512°E, 820 m. Pinakiano, 35.197°N, 25.464°E, 820 m.

Results

Names of species not previously recorded in Crete are preceded by an asterisk (*) and those for which sequences of COI barcode region of Cretan specimens are available, are indicated by a dagger (†). Unless otherwise stated, specimens were collected by the authors.

We found no evidence that any sawfly species uses *Zelkova abelicea* as a host. However, we only encountered trees and bushes of this species during two visits to Omalos, and further fieldwork at this and other sites should be undertaken.

Argidae

Arge scita (Mocsáry, 1880)

Material. Crete; 1♂, Drakona 2, 22.iv.2013. 1♀, Moni, 28.iv.2013. 2♂♂, Agia Irini, 28.iv.2013.

Cimbicidae

Corynis krueperi (J. Stein, 1876)

Material. Crete; 1♂, Potamies, 27.iii.2013, swept from inflorescences of *Papaver rhoeas*: a known host (Greathead 1978).

The name *C. krueperi* is used instead of *C. similis* (Mocsáry, 1880) for this taxon, as also in Liston and Jacobs (2012), in accordance with a revision of *Corynis* (Jacobs et al., in preparation).

Tenthredinidae
Allantinae

†*Allantus nigrolinearis* (Zirngiebl, 1937), new status

= *Emphytus balteatus* var. *nigrolinearis* Zirngiebl, 1937: 646; ♀, holotype [not examined]. Type locality: Kristallenia (Kreta) [= Panagia Kristalenia, Lasithi Plateau, East Crete]. Blank 1996; synonym of *Allantus balteatus* (Klug, 1818). Lacourt 1999; synonym of *Emphytus laticinctus* (Serville, 1823).
= *Allantus didymus* var. *nigrolinearis* (Zirngiebl, 1937); Schedl 1981; misidentification.

Material. Crete; 2♀♀, 1♂, Agia Irini, 26.iv.2013. 1♀, 1♂, Agia Irini, 28.iv.2013.

Barcode data. The barcodes of two sequenced *A. nigrolinearis* specimens (DEIGISHym20641, 20642) are identical and amongst 34 sequenced specimens of *A. didymus* and *A. laticinctus* sensu lato, are most similar to those of *A. ariadne* Liston and Jacobs, 2012 from Cyprus (DEIGISHym11089, 11093), with divergence of about 3.9%. Minimal divergence
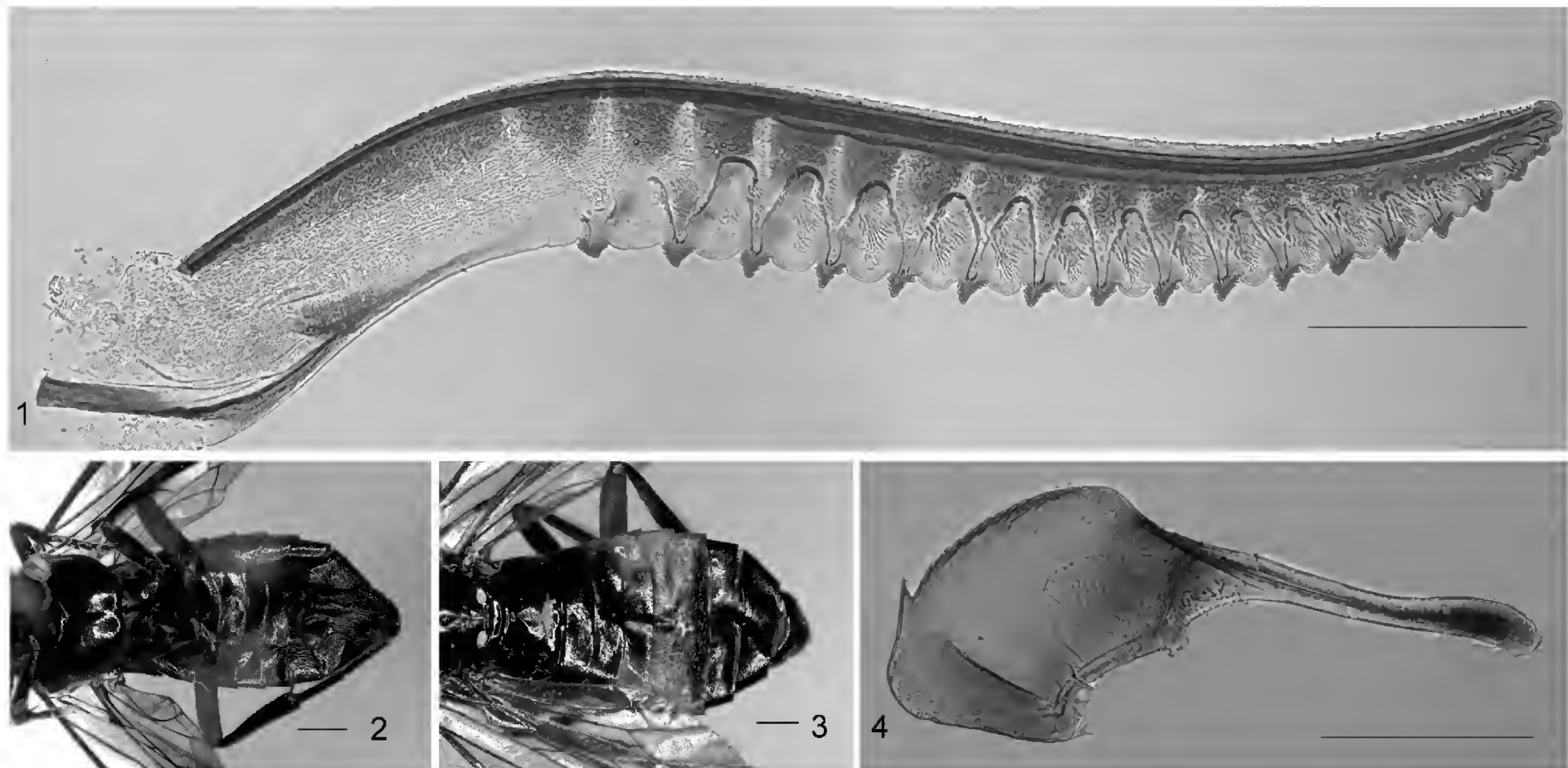
Figures 1–4. *Allantus nigrolinearis*, Crete. **1,** lancet, ♀, scale = 0.2 mm. **2,** underside of abdomen, ♀, scale = 1 mm. **3,** upperside of abdomen, ♀, scale = 1 mm. **4,** penis valve, ♂, scale = 0.2 mm.

of *A. nigrolinearis* from *A. laticinctus* (France BC ZSM 01149 and Italy, Sicily DEIGISHym11042) is 6.4%. Noteworthy is that divergence of 5.3% between *A. nigrolinearis* and *A. didymus* (Klug, 1818) (Italy DEIGISHym18775, and Germany; 10 specimens) is somewhat less than from *A. laticinctus*. Several other segregates cluster around the four named taxa in the barcode similarity tree, indicating that the species group requires revision and may contain more taxa than previously thought.

As noted by Blank (1996), Zirngiebl apparently had no clear concept of species, subspecies and varieties. His var. *nigrolinearis* was described within a paragraph discussing colour variability of a reared series of female *Emphytus balteatus* from Germany. However, his wording does not make it clear what relationship he considered his new variety to have to the other specimens. In the absence of any clear indication that Zirngiebl considered *nigrolinearis* to be of infrasubspecific rank, the name is available (ICZN 1999, Article 45.6.4.).

Female *A. nigrolinearis* differ from those of *A. laticinctus* and *A. ariadne* in having an uninterrupted, broad, median, black vitta through the otherwise red sterna of the abdomen (Fig. 2). In the other species a number of sterna are entirely red. The metatibia of *A. nigrolinearis* females is also darker: apical half, and base narrowly, fuscous. In the other species the metatibia is entirely red except for apex. In two *A. nigrolinearis* the otherwise red abdominal terga 3–6 have a median black stripe (Fig. 3). In the third female, this stripe is interrupted on tergum 5 and the metatibia is somewhat paler than in the other specimens. The four basal serrulae of the lancet of *A. nigrolinearis* (Fig. 1) are subtriangular and similar to the other serrulae, whereas the four basal serrulae of *A. laticinctus* and *A. ariadne* are more rounded than the others (Liston and Jacobs 2012, Figs 4, 6). The males of *A. nigrolinearis* and

A. ariadne are indistinguishable, apparently including their penis valves (*A. nigrolinearis*: Fig. 4. *A. ariadne*: Liston and Jacobs 2012, Fig. 7), but differ in leg colour from *A. laticinctus*. In *A. nigrolinearis* and *A. ariadne* the mid femur is almost entirely black except for the apex, but in *A. laticinctus* approximately the apical half of the mid femur is pale. The holotype of var. *nigrolinearis* was mistakenly considered by Schedl (1981, 1993) to belong to *Allantus didymus* (Klug, 1818) (Schedl 2011). Schedl (2011) added a record from Crete of a male specimen which he determined as *A. didymus*. However, confusion of *A. didymus* with *A. laticinctus* (sensu lato) has been widespread, particularly of the males (Koch 1988). Until more convincing evidence for the occurrence of *A. didymus* in Crete is presented, the name should be removed from the faunal list of the island.

A. laticinctus has only definitely been reared from *Rosa*, in central and western Europe (Taeger et al. 1998, Knight 2006). The host(s) of *A. nigrolinearis* are likely to be Rosaceae (because the known hosts of other species in this complex are Rosaceae), but as for *Empria archangelskii* (see below), several host species seem possible.

**†Allantus viennensis* (Schrank, 1781)

Material. Crete; 1♀, 6♂♂, Daratsos, on roses (garden cultivar) in hotel garden, 21–25.iv.2013. 1♂, Meskla, 22.iv.2013, near roses (garden cultivar). *Rosa* spp. are the known hosts: Taeger et al. 1998.

The garden habitat and association of the Cretan specimens with horticultural varieties of rose, suggest that *A. viennensis* may have been introduced to the island. *A. viennensis*, probably native to southern and central Europe, is also an introduced and established species in the eastern USA (Smith 2003).

*†*Ametastegia glabrata* (Fallén, 1808)

Material. Crete; 1♀, Strovles, 24.iv.2013.

One of the most cosmopolitan of sawflies, introduced to North America, South America and Australia from its (presumed) native range in the Palaearctic (Liston and Zerafa 2012).

Empria archangelskii Dovnar-Zapolskij, 1929

Material. Crete; 1♀ "Ajos Joánnis Ep. Ajos Wássilis" 21.iii.1925 , leg. A. Schulz, Museum für Naturkunde, Berlin. 1♀, Agios Nicolaos, Almyros (Lasithi), 11.iv.1976, leg. Matti Viitasaari, Viitasaari Collection, Helsinki. 1♀, Mesa Potami, 28.iii.2013, swept from *Crataegus monogyna*. 1♀, Anogeia, 29.iii.2013, swept from flowering *Acer sempervirens*. 1♀, 1♂, Katharo Plateau, Kopraki, 30.iii.2013, swept from low vegetation on riverbank. 1♀, Agia Irini, 26.iv.2013, swept from low vegetation on a dry slope.

Based on the serrulae of the lancet, Prous (2012) treated the Cretan specimens preliminarily as a different species (sp4) from *E. archangelskii*. Serrulae in Cretan specimens are narrower and more protruding (Fig. 5) than in mainland specimens (Fig. 6). Although the three studied lancets of Cretan females are very similar to each other and slightly different from the two specimens studied from the mainland (one from Crimea, and the syntype of *E. archangelskii* from Tuapse, Krasnodar Krai, Russia), the penis valves of males appear to be indistinguishable (Figs 9–10). Because no consistent external differences were detected between the specimens from Crete and elsewhere, and a normal variability of lancets cannot be excluded, we consider them conspecific. *Selandria labialis* Brullé, 1832, currently treated as a synonym of *E. immersa* (Klug, 1818) (Taeger et al. 2010), was described from Methoni [Plaine de Modon], Messenia, Peloponnese, an area with habitats probably similar to those in Crete. The description of *S. labialis* can be interpreted as referring to *E. immersa* or *E. archangelskii*, although "Chaperon très-peu échancré" [clypeus very slightly emarginate] fits better with the former. Neither of these species has otherwise been recorded from mainland Greece. The Cretan *E. archangelskii* are the first recorded from Greece and are the most westerly records of the species, which is otherwise known from the North coast of the Black Sea (Russia, Ukraine), Cyprus, Israel, Lebanon and Syria (Prous 2012).

The closest species to *E. archangelskii* is *E. excisa* (Thomson, 1871). *E. archangelskii* can be easily distinguished by the red-yellow pale colour of its legs, with femora mainly pale (black and whitish in *E. excisa*, with femora mainly black). There appear also to be slight differences between lancets and penis valves: serrulae are more protruding in *E. archangelskii* (Figs 5–6) than in *E. excisa* (Figs 7–8) and valviceps of penis valves might be slightly narrower and differently shaped in *E. archangelskii* (Figs 9–10) than in *E. excisa* (Figs 11–12).

The hostplant(s) of *E. archangelskii* are unknown. However, the larvae of *Empria* species which are morphologically and genetically closest to *E. archangelskii* all feed on non-woody Rosaceae. The plants from which the specimens were collected and were growing near the collecting sites did not offer clues as to the identity of a possible host. The only Rosaceae obviously present at all Cretan collecting sites was *Crataegus monogyna*, but presumably the widespread *Sanguisorba minor*, *Sarcopoterium spinosum* and *Rubus sanctus* were also present somewhere not too distant.

Athaliinae

Athalia circularis (Klug, 1815)

Material. Crete; 1♂, Agia, 29.iv.2013, netted from *Veronica* sp. growing in wet bed of a stream. *Veronica* spp. are known hosts (Taeger et al. 1998).

†*Athalia cordata* Serville, 1823

Material. Crete; 1♂, Potamies, 27.iii.2013. 4♀♀, Mesa Potami, 28.iii.2013. 1♀, Krasi, 28.iii.2013. 1♂, Daratsos, pool at hotel, 21.iv.2013. 1♀, 6♂♂, Omalos, 21.iv.2013. 1♀, Sempronas, 21.iv.2013. 1♂, Drakona, 22.iv.2013. 1♀, 8♂♂, Thériso-Drakona, 22.iv.2013. 1♂, Askifou, 23.iv.2013. 3♂♂, Kakopetros, 24.iv.2013. 1♀, 1♂ Strovles, 24.iv.2013. 3♀♀, 14♂♂, Omalos 2, 25.iv.2013. 14♀♀, 25♂♂, Agia Irini, 26.iv.2013. 1♂, Samonas, 27.iv.2013. 7♂♂, Moni, 28.iv.2013. 2♀♀, 3♂♂, Agia Irini, 28.iv.2013. 4♂♂, Agia, 29.iv.2013.

We did not collect all male specimens that were seen. During both visits to Agia Irini, males were very abundant in the uppermost part of the gorge.

†*Athalia rosae* (Linnaeus, 1758)

Material. Crete; 1♂, Strovles, 24.iv.2013.

Blennocampinae

*†*Chevinia mediterranea* Lacourt, 2003

Material. Crete; 1♀, Drakona, 22.iv.2013, swept from *Quercus* sp. (either *Q. ilex* or *Q. coccifera*).

C. mediterranea was described from localities on the Mediterranean coast of mainland France and Corsica (Lacourt 2003). Specimens recorded as ? *Chevinia* sp. from Thessaly, mainland Greece, by Standfuss et al. (2010) also belong to this species (comparison with paratypes of *C. mediterranea* by A. Mol, S. Blank and A. Liston, 2013). The mainland specimens were also collected from *Quercus* spp. (K. Standfuss, personal communication), so perhaps the larval host is one or more oak species.

Halidamia affinis (Fallén, 1807)

Material. Crete; 1♀, Daratsos, pool at hotel, 22.iv.2013. 1♀, Meskla, 22.iv.2013. 2♀♀, Fournes-Meskla, 22.iv.2013.
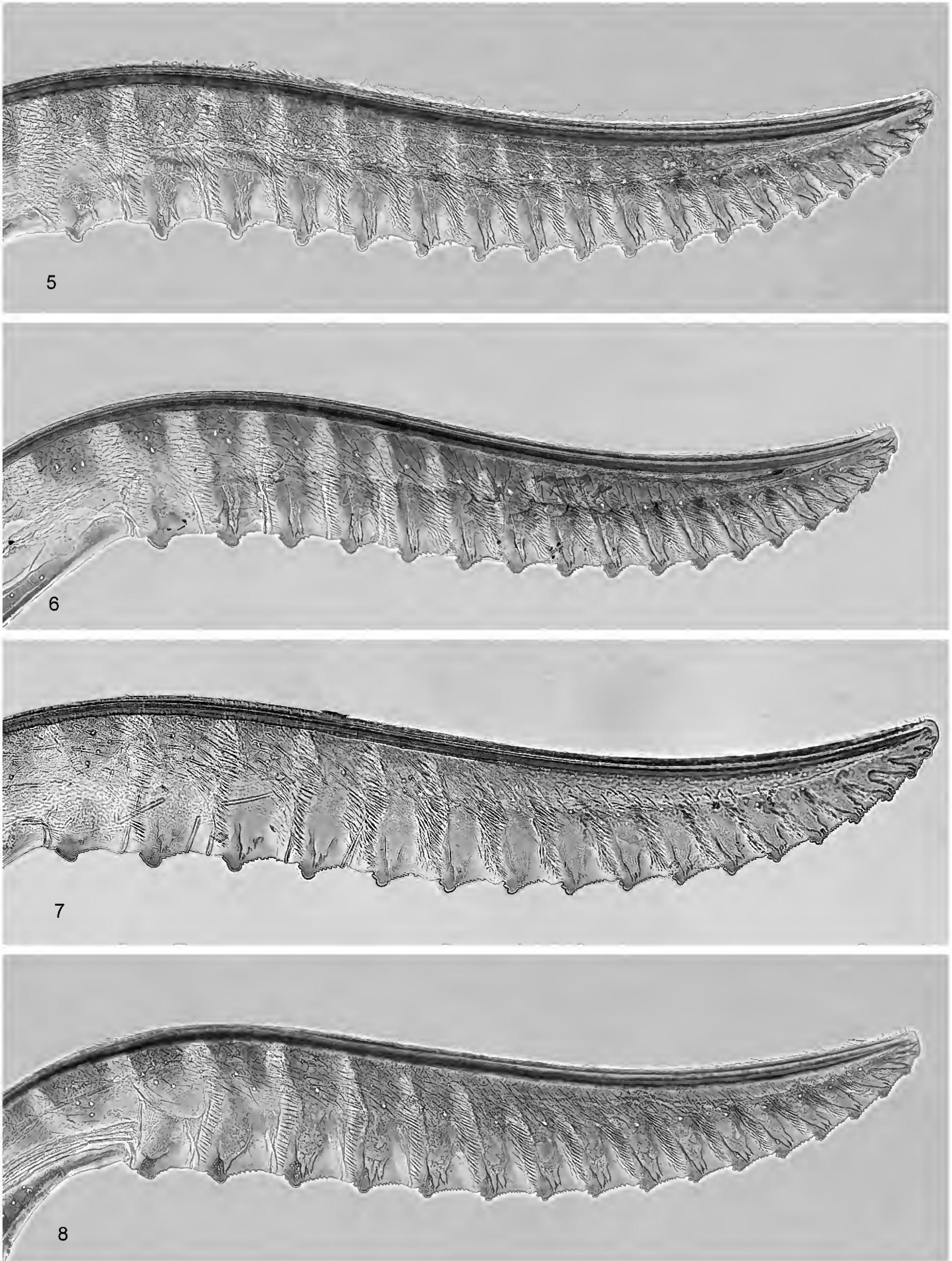
Figures 5–8. *Empria*, lancets, ♀. **5,** *E. archangelskii*, Crete. **6,** *E. archangelskii*, Crimea. **7,** *E. excisa*, France. **8,** *E. excisa*, Estonia.
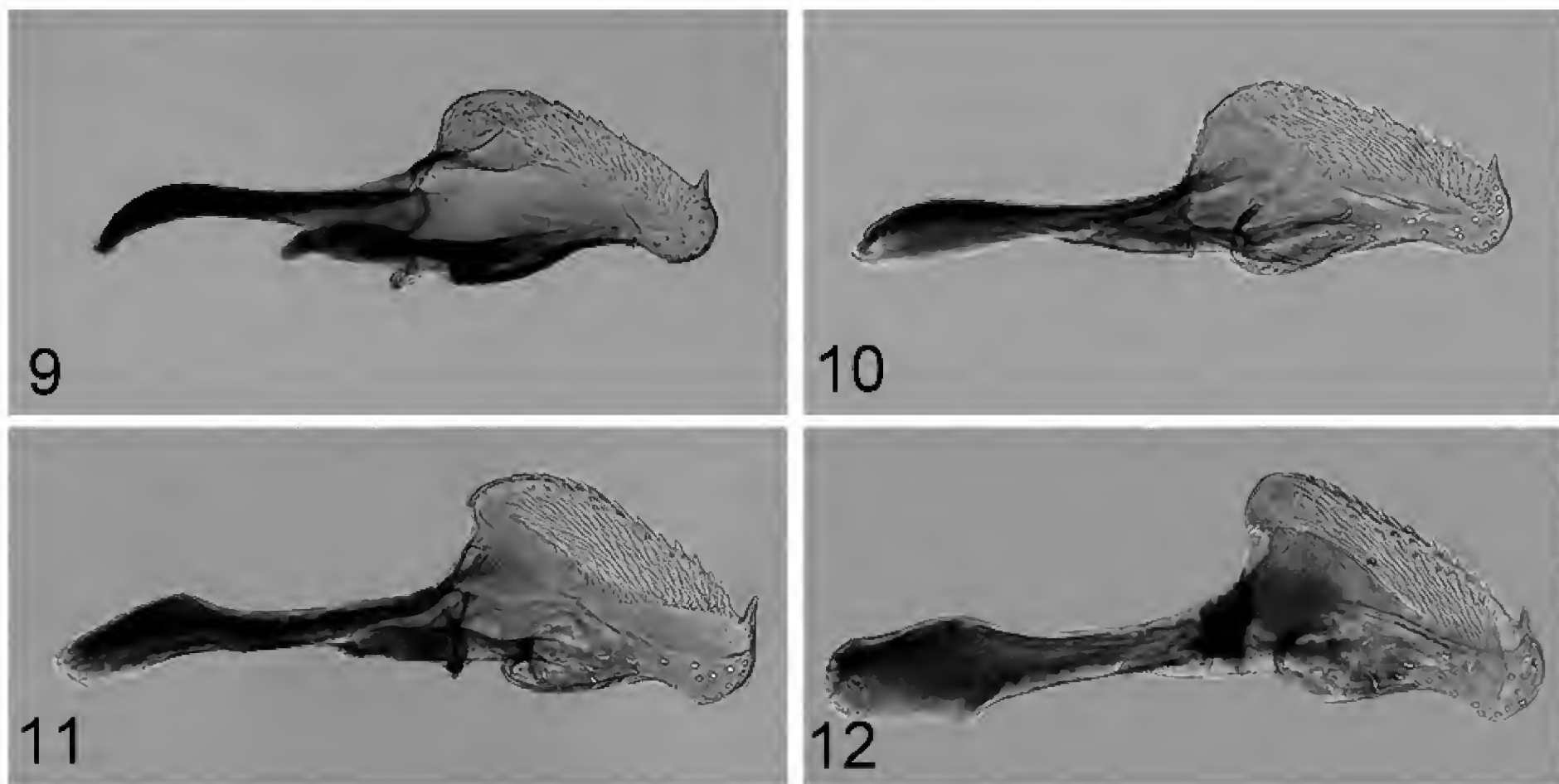
Figures 9–12. *Empria*, penis valves, ♂. **9,** *E. archangelskii*, Crete. **10,** *E. archangelskii*, Crimea. **11,** *E. excisa*, France. **12,** *E. excisa*, Estonia.

1♀, Drakona, 22.iv.2013. 4♀♀, Agia Irini, 26.iv.2013. 1♀, Samonas, 27.iv.2013. 1♀, Moni, 28.iv.2013.

†*Heterarthrus imbrosensis* Schedl, 1981

Material. Crete; 5♀♀, 7♂♂, Omalos, 25.iv.2013, swept from *Acer sempervirens*: the host (Schedl 1981).

Barcode data. the barcode of one specimen collected from *Acer sempervirens* from the Peloponnese and determined as *H. wuestneii* (Konow, 1905) (DEI-GISHym11102), diverges by 0.7% from two Lower Austrian specimens of *H. wuestneii* (BC ZSM HYM 04121, 04122). The minimum barcode divergence of the two barcoded Cretan *H. imbrosensis* (DEIGISHym20655, 20656) from the Peleponnesian *H. wuestneii* specimen is 1.8%.

Morphologically. *H. imbrosensis* closely resembles *H. wuestneii*. Specimens from Crete are darker than Central European (German and Austrian) *H. wuestneii*. The face may be entirely black in Cretan females, but usually there are at least small white patches on the inner orbits, whilst the tegula varies from entirely black to black with the posterior edge white. The *H. wuestneii* specimens from the Peloponnese are intermediate in coloration. According to Schedl (1981), *H. imbrosensis* is distinguished from similar species of the *aceris* group by the shape of the head behind the eyes in dorsal view. No such difference was found between the specimens of *H. wuestneii* and *H. imbrosensis* available to the authors. Furthermore, the apparently apically widened sawsheath of the holotype of *H. imbrosensis* [examined] as drawn by Schedl (1981) is the result of disruption of the valves of the sheath during extraction of the saw. As pointed out by Leppänen et al. (2012), the status of some of the *Acer*-feeding *Heterarthrus* needs further study, ideally including sequencing of nuclear DNA.
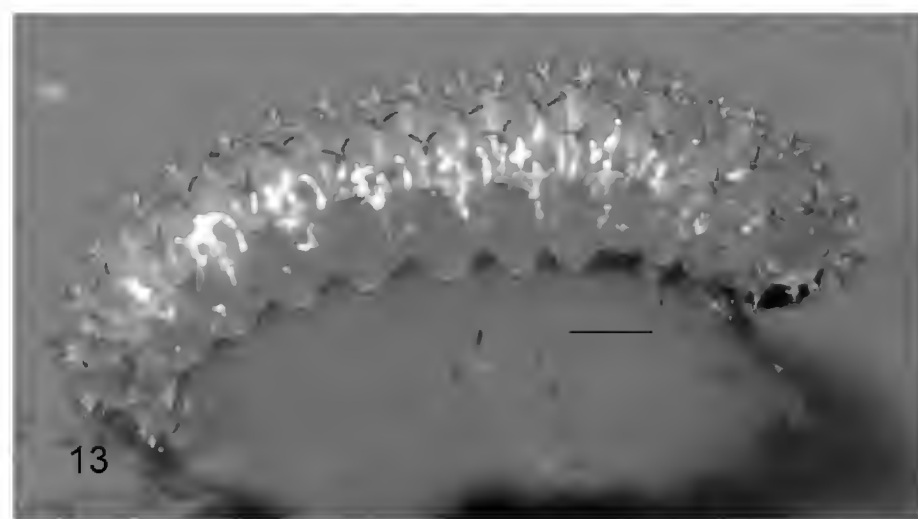
Figure 13. *Periclista cretica*, larva, Crete, scale = 1 mm.

†*Periclista cretica* (Schedl, 1981)

Material. Crete; 3♀♀, 32♂♂, Krasi, 27–28.iii.2013. 3♂♂, Livadia, 29.iii.2013. 2 larvae (Fig. 13) beaten from *Quercus coccifera*, Drakona 2, 22.iv.2013 (determined by barcode congruence of one larva with 2 adults).1♀, Askifou, 23.iv.2013. All specimens swept from, or netted near, upper branches of *Quercus coccifera* (plants 3–5 m tall).

The buds of the bushes and small trees of *Quercus coccifera* from which these were collected were swollen, but had not burst. Males were obtained mostly by netting them as they flew around the twigs in the upper crowns (at Krasi reached by standing on the many large boulders), and less so by sweeping around all accessible lower parts of the oaks. Sweeping yielded the only few females that we were able to obtain. The identification of the larvae allows us to state that *Q. coccifera* is the host plant. *P. cretica* was previously only known from the female holotype and a single male paratype (Schedl 1981), both of which we examined.

The taxonomy of this species will be dealt with in detail in a revision of West Palaearctic *Periclista* (A. Mol, in preparation).

Nematinae

*†*Cladius ordubadensis* **Konow, 1892**

Material. Crete; 1♀, Krasi, 28.iii.2013. 1♀, Agia Irini, 26.iv.2013. Swept from low vegetation containing *Sanguisorba minor*, which is possibly a host plant (Liston and Jacobs 2012).

†Cladius pectinicornis **(Geoffroy, 1785)**

Material. Crete; 1♀, 6♂♂, Topolia, 29.iv.2013, on *Rosa* sp.: the main hosts are *Rosa* spp. (Taeger et al. 1998).

Euura atra* **(Jurine, 1807)

Material. Crete; 2♀♀, 4♂♂, Moni Kato Preveli, 25.iii.2013, swept from *Salix alba*, one of the main hosts: Taeger et al. 1998.

Euura proxima **(Serville, 1823)**

Material. Crete; 3 galls in leaves of *Salix alba*, Meskla, 22.iv.2013. Galls very abundant (hundreds) on *Salix alba*, Agia, 29.iv.2013.

No adults were found by sweeping foliage of the three large trees at Agia. The majority of larvae were very small when about 200 galls were collected. Nevertheless, about 30 individuals had spun cocoons by 7.v.2013. Three females emerged in June 2013. Some others seemed to have entered prolonged diapause, but no adults were reared.

†Hoplocampa brevis **(Klug, 1818)**

Material. Crete; 1♀, Marathos, 24.iii.2013. 2♀♀, Pinakiano, 27.iii.2013. 2♀♀, Mesa Potami, 28.iii.2013. 1♀, Anogeia, 29.iii.2013. 2♀♀, Omalos, 25.iv.2013. Specimens mostly collected from inflorescences of *Pyrus* cultivars: the normal hosts are *Pyrus* spp. (Taeger et al. 1998).

†Hoplocampa chrysorrhoea* **(Klug, 1816)

Material. Crete; 4♀♀, Marathos, 24.iii.2013. 9♀♀, Pinakiano, 27.iii.2013. 7♀♀, Mesa Potami, 28.iii.2013. 1♀, Krasi, 28.iii.2013. 10♀♀, Anogeia, 29.iii.2013. 1♀, Omalos, 21.iv.2013. Most specimens were swept from *Crataegus monogyna* with unopened inflorescences, and some others from inflorescences of cultivated *Pyrus* growing near *Crataegus*.

At none of the localities were *Prunus* spp. seen, although these are usually considered to be the larval hosts of *H. chrysorrhoea* in northern parts of Central Europe (e.g. Taeger et al. 1998). Perhaps *Crataegus monogyna* is a host in Crete.

†Mesoneura opaca* **(Fabricius, 1804)

Material. Crete; 1♂, roadside between Kournas and Georgiopolis, 26.iii.2013. 1♀, Livadia, 29.iii.2013. Both specimens swept from freshly flushed *Quercus pubescens*: *Quercus* spp. are the known hosts (Liston 2012).

The depressed medial areas of the apical abdominal terga of the male are partly pale, unlike the completely dark terga of males so far examined from mainland Greece (see Liston 2012).

Pristiphora abbreviata **(Hartig, 1837)**

Material. Crete; 4 larvae on cultivated *Pyrus* sp., Fournes, 25.iv.2013. One larva, larger than the others, had spun a cocoon by 7.v.2013.

†Pristiphora cretica **Schedl, 1981**

Material. Crete; 7♂♂, Pinakiano, 27.iii.2013. 5♂♂, Mesa Lasithi, 28.iii.2013. 1♀, 8♂♂, Katharo Plateau, Kopraki, 30.iii.2013. 6♀♀, 8♂♂, Omalos, 21.iv.2013. 11♀♀, 19♂♂, Askifou, 23.iv.2013. 7♀♀, 16♂♂, Omalos, 25.iv.2013. 2♀♀, Agia Irini, 26.iv.2013. All specimens swept from *Acer sempervirens*: because all species of the *Pristiphora subbifida* group use *Acer* spp. as hosts (Liston and Späth 2008), *A. sempervirens* (the only *Acer* sp. occurring in Crete) is probably a host.

Barcode data. Minimum divergence of three Cretan *P. cretica* (DEIGISHym20657–20659) from two northern Greek *P. cretica* (DEIGISHym11052, 19646) is approximately 1.2%. Interspecific divergence from the next nearest species, *P. schedli* (Cyprus: DEIGISHym10980, 10981) is about 3.8%.

In Crete *Acer sempervirens* displays considerable infraspecific variability in the timing of bud burst. Although *Pristiphora cretica* occurred at some localities together with *P. tetrica* (Zaddach, 1883), it was observed that these species have strongly differing preferences for trees at different stages of leaf and flower development. *P. cretica* is found exclusively on trees whose buds have fully opened and which are already flowering, whereas *P. tetrica* is found on trees whose buds have not yet burst, or have just opened. The preference is so strong, that this phenomenon could be observed on trees standing beside each other which were at different stages of flushing (Fig. 14). The difference in habit is also reflected in the temporal distribution of collection data: a larger number of *P. cretica* and higher proportion of females were recorded during the second 2013 visit than during the first, whereas most specimens of *P. tetrica* were collected during the first visit.

The Cretan specimens listed above closely resemble the female holotype and male paratype (examined: Liston and Späth 2008), the only specimens previously known from Crete. Variability in the newly collected specimens affects the extent of pale coloration on the

Figure 14. *Acer sempervirens* at different stages of bud-break. On the tree at left only *Pristiphora cretica* adults were found and on tree at right only *P. tetrica*. Crete, Lasithi Pref., Pinakiano, late March 2013.

pronotum, outer orbits, clypeus and labrum in both sexes, and the extent of pale colour on the abdominal sternites. Specimens from the Vikos area, northern Greece (1♀, 7♂♂, Nom. Ioannina, Aristi, 16.4.2008, leg. Liston, SDEI) are very dark, with pronotum, abdominal sterna and metafemora nearly completely black. In a series (3♀♀, 3♂♂; SDEI) collected by S. M. Blank and C. Kutzscher in the western Peloponnese, the females are much paler than either the Cretan or Vikos specimens: abdomen including terga almost completely pale, in some specimens central part of mesepisternum pale. Colour of the Peleponnesian males falls within the range of variability seen in Cretan specimens. Some of the paler individuals of *P. cretica* could be mistaken for *P. tetrica* (Zaddach, 1883). Specimens of these species from the Mediterranean Region can be distinguished as follows:

– Metafemur at least with black stripes on anterior and posterior edges of dorsal face. Female with clypeus and labrum pale marked; male with at least labrum pale (brown). Abdominal terga largely black, rarely yellow (Peloponnesian ♀♀) and if so then tergum 1 also largely yellow. Female length 5–6 mm; male 4–5 mm..*P. cretica*
– Metafemur entirely yellow, except for black area on extreme base. Clypeus and labrum entirely black. Abdominal tergum 1 black; other terga yellow, except at most for small medial flecks on terga 2–3. Female length 4.0–4.5 mm; male 3.5–4.0 mm..........*P. tetrica*

Pristiphora pallidiventris (Fallén, 1808)

Material. Crete; 1♀, Daratsos, pool at hotel, 21.iv.2013. 1♀, Theriso-Drakona, 22.iv.2013.

These specimens are of the colour form with a very pale abdomen, which has sometimes been treated as a separate species, *P. denudata* Konow, 1902.

Pristiphora parnasia Konow, 1902

Material. Crete; 1♀, Krasi, 27.iii.2013. 1♀, Livadia, 29.iii.2013. Both specimens swept from *Quercus coccifera*.

†*Pristiphora* sp. [subbifida group]

Material. Crete; 1♂, Omalos, 21.iv.2013. Swept from *Acer sempervirens*, which is probably a host plant, because this is the only *Acer* sp. occurring in Crete and all species of the *Pristiphora subbifida* group use *Acer* spp. as hosts (Liston and Späth 2008).

Barcode data: the sequence of this specimen (DEI-GISHym20661) diverges by about 4.8% from its nearest neighbour, *P. tetrica* (Zaddach, 1883) from Sicily (DEI-GISHym10972). Divergence from two Cretan *P. tetrica* (see below) is approximately 5.3% and from *P. schedli* Liston and Späth, 2008 (Cyprus) approx. 8.6%.

Externally, the specimen differs from Cretan *Pristiphora tetrica* males only in the apex of the metatibia and most of metabasitarsomere being pale: Fig. 15 (largely black in *P. tetrica*: Fig. 19) and its slightly larger body length of 4.5 mm (*P. tetrica*: 3.5–4.0 mm). However, the penis valve of the unidentified species (Fig. 16) differs substantially from *P. tetrica* (Fig. 17), and resembles that of *P. schedli*: valvispina medially thickened and not strongly upcurved (in other *subbifida* group species not medially thickened, but strongly upcurved), apex of paravalva at base of valvispina not strongly expanded (other species: strongly expanded). On the other hand, the coloration of the head and thorax is much darker in *Pristiphora* sp. than in *P. schedli*, while the legs of the former are paler. Despite its morphological similarity to *P. schedli*, the very large barcode divergence of the single Cretan specimen suggests that it probably represents a previously unrecognized species. Possibly one of the two unidentified female *Pristiphora* specimens mentioned by Schedl (2011) belongs here. Further material should be obtained so that its status can be evaluated.

†Pristiphora tetrica (Zaddach, 1883)

= *Nematus tetricus* Zaddach in Brischke, 1883: 148–149; ♀, holotype. Type locality: Gumperda, Thüringen. Type probably destroyed (Liston and Späth 2008).
= *Nematus velatus* Zaddach in Brischke, 1883: 149; ♀, holotype. Type locality: Baiern [Bavaria]. Type should be in the Zoologische Staatssammlung, Munich, but was not located (Liston and Späth 2008).
= *Pristiphora tetrica*: Lacourt 1976, description of male.
= *Pristiphora nievesi* Haris, 2004: 164–165; ♀, holotype and paratypes [Museo Nacional de Ciencias Naturales, Madrid; examined]. Type locality: El Ventorillo, Madrid. **New synonym.**

Material. Crete; 7♀♀, 3♂♂, Pinakiano, 27.iii.2013. 2♀♀, 11♂♂, Mesa Lasithi, 28.iii.2013. 1♂, Livadia,
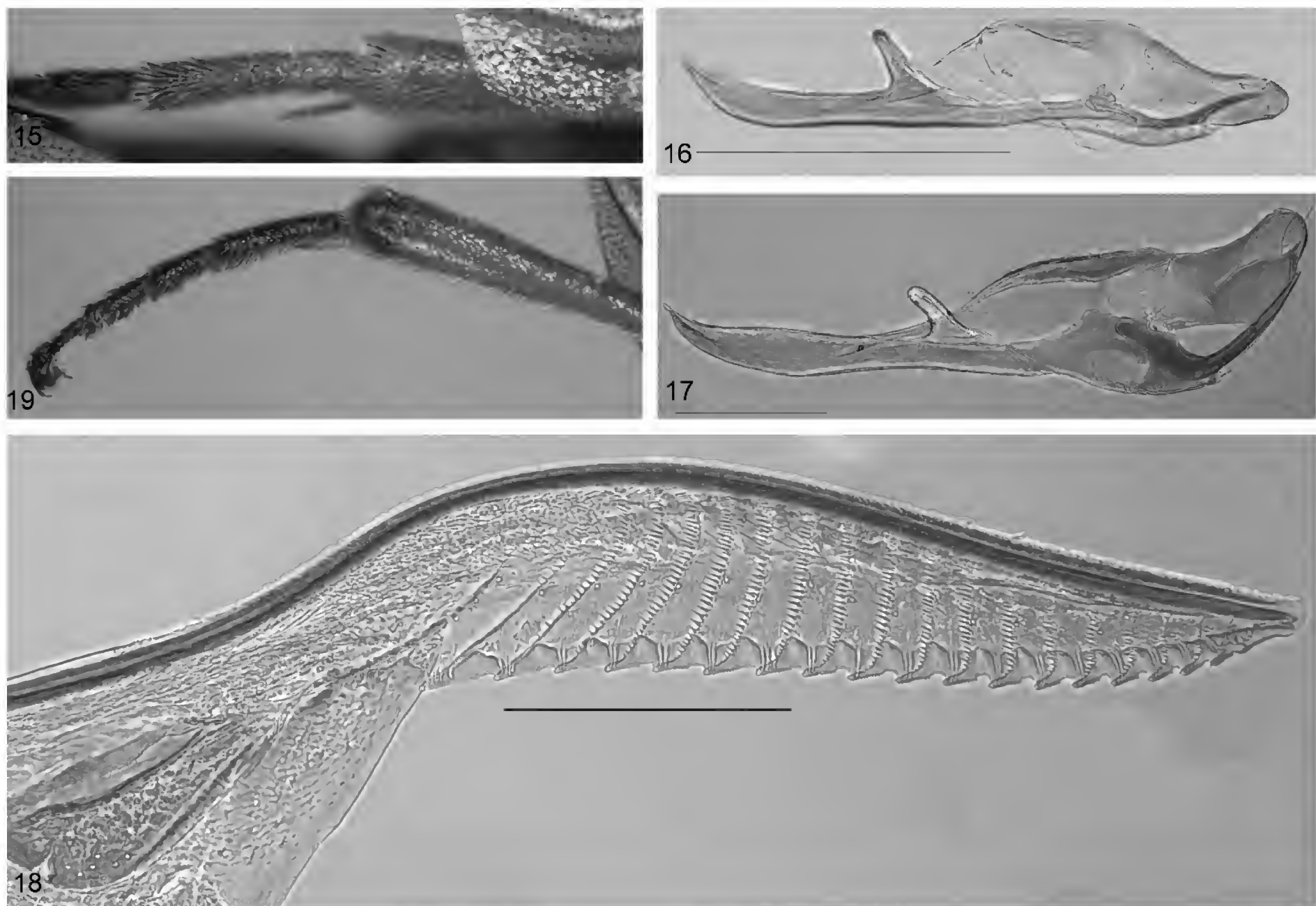
Figures 15–19. 15–16. *Pristiphora* [*subbifida* group], Crete, ♂. **15,** apex of metatibia and part of tarsus. **16,** penis valve, scale = 0.5 mm. **17–19.** *Pristiphora tetrica*, Crete. **17,** penis valve, ♂, scale = 0.2 mm. **18,** lancet, ♀, scale = 0.2 mm. **19,** metatarsus and apex of metatibia, ♂.

29.iii.2013. 1♀, 4♂♂, Anogeia, 29.iii.2013. 5♀♀, 5♂♂, Katharo Plateau, Kopraki, 30.iii.2013. 1♀, 1♂, Omalos, 21.iv.2013. 2♀♀, Omalos, 25.iv.2013. All specimens swept from *Acer sempervirens*: because all species of the *Pristiphora subbifida* group use *Acer* spp. as hosts (Liston and Späth 2008), *A. sempervirens* (the only *Acer* sp. occurring in Crete) is probably a host.

Barcode data: sequences have been obtained for five specimens that were previously identified as *P. nievesi*: one specimen each from France, DEIGISHym19640; Italy, Sicily, DEIGISHym10972; mainland Greece, DEIGISHym10965, and two from Crete (DEIGISHym20660, 20662). Nested within this cluster in the barcode similarity tree are three specimens of *P. tetrica* from Germany (BC ZSM HYM 09418, BC ZSM HYM 20222, DEIGISHym18864). Although the minimum sequence divergence of the Cretan specimens from the German ones is about 1.9%, the Sicilian specimen differed from the German ones by only 0.6%. This is a comparatively small barcode difference (Hebert et al. 2004).

P. tetrica and *P. nievesi* have been recognized as being morphologically the most similar *Pristiphora* species within the *Pristiphora subbifida* group (Haris 2004, Liston and Späth 2008); even the penis valves and lancets (Cretan specimens: Figs 17, 18) are indistinguishable. However, the phenotypes do display minor differences in colour and size:

– At least metafemur mainly yellow. Abdomen predominantly yellow; black are only tergum 1 and at most small medial flecks on terga 2–3. Wing membrane subhyaline. Female length 4.0–4.5 mm; male 3.5–4.0 mm ....*P. nievesi*
– Hind legs completely black. Abdomen usually with numerous terga medially and contiguously black. Wing membrane fuscous. Female length 5.0–6.5 mm; male 4.0–5.0 mm ....*P. tetrica*

Note. Occasional Central European specimens of *P. tetrica* occur that are unusually pale. They are larger than the types of *P. nievesi* but similarly coloured, apart from having black metafemora. One such individual is the type of *Nematus velatus*, described as having an almost completely yellow abdomen and less fuscous wings than typical *P. tetrica*. Specimens formerly identified as *P. nievesi* differ from each other in the colour pattern of the legs. The metatibia of the type specimens and the French specimen (Savina et al. 2014) is extensively or completely black. The base of the metatibia of the Sicilian and northern Greek specimens is obscurely paler. The Cretan specimens are paler than all of these, with the metatibia only apically black. For the following reasons, it seems best to regard the southern European *P. nievesi* as merely a series of relict populations of *P.*

tetrica, and to treat them all as conspecific: a continuous gradient of variability in colour and size occurs between Central European *P. tetrica* specimens and specimens which have recently been treated as *P. nievesi*; morphology of lancets and penis valves is identical; genetic data at present reveals no clear difference between these nominal species.

See comments on phenology and distinction of *P. tetrica* from *P. cretica*, under *P. cretica* (above). Colour variability in *P. tetrica* from Crete is in the extent of pale on the outer orbits, tegulae and posterior edges of the pronotum. These parts are usually partly pale, but are entirely black in the darkest individuals. Males tend to be darker than females. Occasionally in females, the mesepisternum is partly pale medially.

Selandriinae

†*Aneugmenus oertzeni* (Konow, 1887)

Material. Crete; 2♀♀, 2♂♂, Marathos, 24.iii.2013. 20♀♀, 23♂♂, Armeni, 25.iii.2013. 2♀♀, Lakki, 21.iv.2013. 7♀♀, 19♂♂, Sempronas, 21.iv.2013. 2♀♀, 5♂♂, Drakona, 22.iv.2013. 5♀♀, 4♂♂, Theriso-Drakona, 22.iv.2013. 7♀♀, 3♂♂, Strovles, 24.iv.2013. 7♀♀, 11♂♂, Agia Irini, 26.iv.2013. 2♀♀, 12♂♂, Topolia, 29.iv.2013. 1♀, 16♂♂, Agia, 29.iv.2013. All swept from, or netted near, *Pteridium aquilinum*, the only known host (Schedl 2011).

Barcode data. The barcodes of four sequenced Cretan specimens (DEIGISHym20637–206340: infraspecific variability about 0.7%) diverge by a minimum of 6.1% from the nearest neighbour *A. bibolinii* Zombori, 1979, represented by one male each from Corsica (first record from France: Ascu, 02.05.2004, leg. Liston, SDEI (DEIGISHym19725) and Sardinia (DEIGISHym19684): infraspecific variability about 0.7%. Minimum divergence of *A. oertzeni* to the next nearest species *A. padi* is 9.2% (many specimens from central and southern Europe, and Iran).

According to Benson (1968), *A. oertzeni* occurs not just in Crete (its type locality), but also in "Turkey and S. E. Europe". However, in the same publication Benson stated that he had never seen specimens of this species. His statement may have been influenced by Konow (1905), who gave the distribution as Crete, Asia Minor and Moscow. The occurrence of *A. oertzeni* outside Crete has not been confirmed.

Niu and Wei (2013) placed *Aneugmenus oertzeni* in *Atoposelandria* (type species *Selandria fuerstenbergensis* Konow, 1885), which they treated as a genus distinct from *Aneugmenus* (type species *Tenthredo coronata* Klug, 1818). *A. fuerstenbergensis* is indeed distinguished from the other West Palaearctic *Aneugmenus* species by several characters: see for example key by Blank (1998). Niu and Wei (2013) stated that "*Atoposelandria* differs from *Aneugmenus* in the clypeus roundly and deeply incised; the frontal wall very sharp; claw slender and weakly bent, without basal lobe, and the inner tooth ab-

sent". The depth and shape of the excision of the clypeus is by no means so different between *A. fuerstenbergensis* and other *Aneugmenus* as they suggest, and the development of the frontal wall shows considerable differences between the other W. Palaearctic species. On the other hand, *A. fuerstenbergensis* is unique amongst West Palaearctic species in the claws lacking an inner tooth, the densely transversely striated and matt abdominal terga and the lack of a sinus sexualis in the male. Nevertheless, at present there are no compelling arguments for the recognition of a separate genus, because insufficient phylogenetic evidence is available to support this, and because the practical value of the distinction is low: apart from *A. fuerstenbergensis* and *A. oertzeni*, Niu and Wei (2013) place only two other species, from the Oriental Region, in *Atoposelandria*. For the present, we point out that according to Niu and Wei's definition of *Atoposelandria*, *A. oertzeni* does not belong there, but shares the "generic" characters of other W. Palaearctic *Aneugmenus*. In particular, its claw has an inner tooth, at least half as long as the outer. The inner one is however easy to overlook, as in all *Aneugmenus* species, because it arises close to the base of the claw and is obscured by setae and other parts of the apical tarsomere. Schedl (1981), who examined the types of *Selandria oertzeni* in the SDEI observed that *A. oertzeni* resembles *A. coronatus* (Klug, 1818). This is closer to reality than the comments of Benson (1968), who wrote of *A. oertzeni*: "This species, which I have never seen, is distinguished from *A. padi* by its untoothed tarsal claws. From *A. fuerstenbergensis* it is distinguished in the ♂ by having the 6th tergite emarginate apically and a transverse groove (*sinus sexualis*) across the 7th tergite (as in *A. padi*) and the tergites yellow from the 3rd segment; and in both sexes by the shining surface of the tergites which in *A. fuerstenbergensis* are dull with transverse striations." On reading the original description of *S. oertzeni*, one sees how Benson was misled. Konow (1887) wrongly stated that *oertzeni* has simple claws and accordingly compared the taxon with the only other West Palaearctic *Aneugmenus* species that does have simple claws, namely *A. fuerstenbergensis*. Our examination of the types of *A. oertzeni* and the recently collected specimens revealed that this species is morphologically similar to *A. padi*. Externally, they can only be distinguished by colour characters and the larger inner tooth of the claw of *A. padi*. However, barcoding suggests a closer relationship of *A. oertzeni* to *A. bibolinii* than to *A. padi*. A revised key to West Palaearctic *Aneugmenus* species is in preparation.

**Dolerus puncticollis* Thomson, 1871

Material. Crete; 1♀, Katharo Plateau, Kopraki, 30.iii.2013.

As well as being the first record of a *Dolerus* species from Crete, this also seems to be the first published re-

cord of *D. puncticollis* from Greece. This is the most widespread *Dolerus* (*Poodolerus*) species in the Mediterranean Region, and the only member of the subgenus known in North Africa (Lacourt 1977).

†*Strongylogaster multifasciata* (Geoffroy, 1785)

Material. Crete; 6♂♂, Marathos, 24.iii.2013. 2♀♀, 4♂♂, Armeni, 25.iii.2013. 1♂, Lakki, 21.iv.2013. 3♂♂, 1♀, Sempronas, 21.iv.2013. 1♀, 13♂♂, Thériso-Drakona, 22.iv.2013. 2♀♀, 3♂♂, Drakona, 22.iv.2013. 9♀♀, 6♂♂, Strovles, 24.iv.2013. 3♀♀, 2♂♂, Agia Irini, 26.iv.2013. 3♀♀, 2♂♂, Agia Irini, 28.iv.2013. 1♂, Topolia, 29.iv.2013. 1♂, Agia, 29.iv.2013. All swept from, or netted near *Pteridium aquilinum*, which is the only known host in Crete: Schedl 1981, 1993, 2011.

Barcode data. The barcodes of three sequenced Cretan specimens (DEIGISHym20648–20650) are identical and diverge by a minimum of 3.2% from 24 specimens of *S. multifasciata* collected throughout Europe (from Scotland to the Peloponnese) and Iran (infraspecific variability about 0.5%).

The Cretan specimens all belong to the form described as *S. cretensis* Konow, 1887, which was regarded as an allopatric local population of *S. multifasciata* by Naito (1996) and Blank (2002). Alternatively, Schedl (2011) treated *S. cretensis* as a distinct species. The Cretan specimens differ from mainland ones in a number of characters:

– Postocellar area with sculpture similar to that of adjoining parts of the temples: punctures on postocellar area about as large as those on temples, with shiny unsculptured interspaces (Fig. 20). Terga 3–9 and all sterna entirely yellow (Fig. 21). Female metatibia basally white with apical two-thirds black; coxa mainly yellow..*S. cretensis*
– Postocellar area with denser sculpture than on adjoining parts of temples: average puncture diameter on postocellar area smaller than on temples, with interspaces matt (Fig. 22). Terga 2–8 in female mainly black, with pale apical margin (Fig. 23); male often with several terga black-marked. Female metatibia basally white with apical two-thirds red-brown; coxa entirely black ....*S. multifasciata*

Further studies, including sequencing of nuclear genes, are required to clarify the status of the Cretan taxon.

Cephidae

†*Calameuta haemorrhoidalis* (Fabricius, 1781)

Material. Crete; 7♀♀, 1♂, Nea Roumata, 21.iv.2013. 1♂, Fournes-Meskla, 22.iv.2013. 1♂, Drakona, 22.iv.2013. 1♂, Drakona 2, 22.iv.2013. 1♀, Askifou, 23.iv.2013. 1♀, Komitades, 23.iv.2013. 1♀, 3♂♂, Vrises, 23.iv.2013. 1♀, Kakopetros, 24.iv.2013. 1♂, Kandanos, 24.iv.2013. 2♂♂, Platanias, 24.iv.2013. 1♀, Strovles, 24.iv.2013. 1♀,
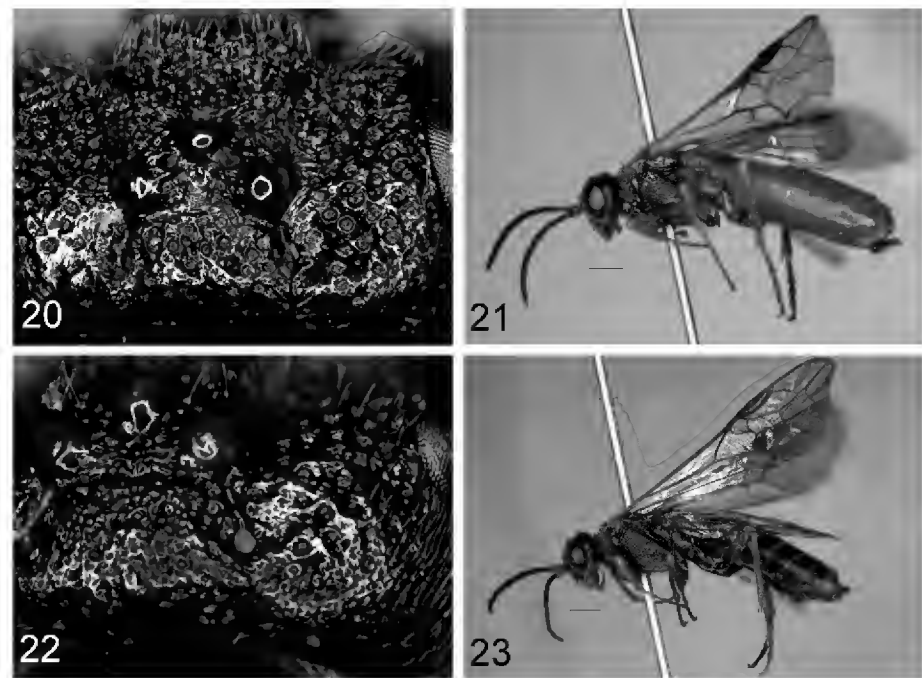
Figures 20–23. *Strongylogaster multifasciata*, ♀. **20,** head, Crete. **21,** habitus lateral, Crete, scale = 1 mm. **22,** head, Scotland. **23,** habitus lateral, Scotland, scale = 1 mm.

Fournes, 25.iv.2013. 2♂♂, Samonas, 27.iv.2013. 4♂♂, Agia Irini, 28.iv.2013. 1♂, Topolia, 29.iv.2013. 1♀, Lousakies, 29.iv.2013.

Calameuta idolon (Rossi, 1794)

Material. Crete; 1♂, Krasi, 28.iii.2013. 1♀, Samonas, 27.iv.2013. 2♂♂, Lousakies, 29.iv.2013. 1♂, Topolia, 29.iv.2013.

*†*Phylloecus faunus* Newman, 1838

Material. Crete; 1♀, Fournes-Meskla, 22.iv.2013.

A remarkable species because of its thelytoky, unusual in the Cephidae, and its mainly southern European distribution which extends north along the Atlantic coast to the French Department of the Manche (Chevin 1993; as *Hartigia albomaculata*), and possibly, at least historically, into southern England (Liston and Prous 2014).

†*Trachelus tabidus* (Fabricius, 1775)

Material. Crete; 7♀♀, 1♂, Moni, 28.iv.2013.

Discussion

Affinities of the Cretan sawfly fauna

Turrisi (2011) compared the richness and diversity of the sawfly fauna of the larger Mediterranean islands and pointed out that the fauna of Crete is most similar to that of Cyprus. This is hardly surprising, given that these are the two most easterly of the large islands, are at nearly the same latitude, share similar climatic conditions, and are roughly equal in size (Crete 8336 km^2; Cyprus 9251 km^2). Furthermore, a shared history of massive alteration of the natural vegetation by human activity, continued

over many thousands of years, has created similar habitats in both. Sometimes the resulting niches are occupied by the same sawfly species. These are species that occur, probably in many cases naturally, widely in the Mediterranean region (e.g. *Calameuta idolon*), or are attached to plants that have a long history of cultivation (*Hoplocampa brevis* and *Pristiphora abbreviata* on pear [*Pyrus*]) and/or were used as raw material for woven artefacts (*Euura atra* and *E. proxima* on *Salix alba*), a branch of technology already in use by c. 25000–22000 BCE (Soffer et al. 2000). Particularly sawflies that feed on plants important to humans can be suspected to have been introduced to regions outside their native ranges by human activity. Seaborne trade across the eastern Mediterranean is evident by Crete's Old Palace Period (c. 2000–1600 BCE), and Crete and Cyprus were important trade centres in the later 2nd millenium BCE (Wardle 1997, Pulak 1998). The use of common plants from the eastern Mediterranean shoreline as dunnage, or packing material, on ships of this period (Bass et al. 1967; Pulak 1998) represents another potential means of human-induced colonisation, involving sawfly species attached to plants which have no obvious direct use to humans. Long before recognisable trade patterns became evident, colonisation by humans using boats occurred, and the colonists can be assumed to have brought quantities of plant-derived material with them. It is therefore likely that some species of sawflies were already accidentally introduced to Crete and Cyprus long ago. Neither should the possibility be overlooked, that sawfly species may also have been transported in the other direction, but in general one would expect intraspecific genetic divergence between introduced island populations and populations in their area of origin to be less than between populations which are naturally present in Crete and their mainland counterparts, providing that in the latter case the populations have long been effectively isolated from each other. Unfortunately, we do not yet have sufficient genetic data to test this. The introduction of species to areas outside their natural range leads to homogenisation of faunas, obscuring biogeographic patterns (Poulakakis et al. 2014).

In contrast to the examples mentioned above, in rather more cases sawfly species of the same genera which feed on the same or closely related hosts belong to different species on each island. Examples are: on *Quercus* in Crete *Mesoneura opaca*, *Pristiphora parnasia*, *Periclista cretica* and possibly *Chevinia mediterranea* / on *Quercus* in Cyprus *Mesoneura lanigera* Benson, 1954, *Pristiphora calliprina* Liston & Jacobs, 2012 and *Periclista rufiventris* Zombori, 1979. On *Acer* in Crete *Heterarthrus imbrosensis*, *Pristiphora cretica*, *Pristiphora* sp. [*subbifida* group] and *P. tetrica* / on *Acer* in Cyprus *Heterarthrus cypricus* Schedl, 2005 and *Pristiphora schedli* Liston & Späth, 2008. We consider that these groups of species are assemblages which are naturally present on each island and that they illustrate a profound dissimilarity of their sawfly faunas, when these are compared at species level. On the other hand, six of the eight species mentioned above from Crete also occur in mainland Greece.

Age of the Cretan sawfly fauna: influenced by a high rate of extinction?

Both Crete and Cyprus have been separated from continental landmasses for at least 5 million years, and their degree of isolation since has sometimes been stated to be similar to that of today (Akin et al. 2010), although Ebmer (2014) drew attention to now vanished and still existing islands that could have functioned or might still function as "stepping stones" for winged insects to reach Crete. Poulakakis et al. (2014) reviewed the current state of knowledge of the phylogeography of animal taxa in the Aegean and surrounding areas and recognised four main patterns of colonisation. The first of these includes species present before the formation of the mid-Aegean Trench, more than 9 million years ago. The comparatively low degree of genetic divergence between mainland and island sawfly populations of the same or similar [morpho-] species, suggests that even the earliest species to have become established on Crete and Cyprus as part of the modern fauna arrived there considerably later than this, and probably even after the Messinian Salinity Crisis, 5–6 million years ago. That apparently no sawflies now use the Tertiary relict, endemic Cretan tree *Zelkova abelicea* as a host, is weakly indicative of a possible loss through extinction of ancient members of the Cretan sawfly fauna. Possibly much more important in its impact on the sawfly fauna was the change to the Mediterranean climate around 3.2 Ma (Fernández-Mazuecos and Vargas 2010).

Several other more recent events have at times been considered to be linked to a high rate of extinction in the Cretan flora and fauna, including for example the establishment of Neolithic culture 8400–7500 BP and the eruption of Santorini at around 3600 BP (Bottema and Sarpaki 2003). Recent studies do not support the hypothesis that the flora of Crete was devastated by ash deposition after the Santorini eruption (Bottema and Sarpaki 2003). On the contrary, a tendency noticeable in many recent works (e.g. Poulakakis et al. 2014) is to ascribe greater importance than previously to the shaping of the modern fauna and flora of Crete by human activities compared with natural events.

Cretan endemics

In many cases it is still impossible to state categorically whether a particular sawfly species is endemic to a Mediterranean island. This problem was discussed by Liston and Jacobs (2012) with reference to Cyprus. *Pristiphora cretica*, previously recorded only from Crete, is now known also to occur on the Greek mainland. Species which are probably endemic to Crete are *Allantus nigrolinearis*, *Aneugmenus oertzeni*, *Periclista cretica* and *Pristiphora* sp. [*subbifida* group]. The taxonomic status of *Heterarthrus imbrosensis* and *Strongylogaster cretensis* is equivocal: they could either be island endemic species, or are conspecific with taxa in mainland Europe. The Cretan sawfly fauna thus contains a higher proportion of endemic species than any other Mediterranean island, al-

though the number of endemics in Sicily, which has not been intensively investigated, may prove to be greater because the fauna is much richer (Turrisi 2011, Liston and Jacobs 2012, Liston et al. 2013). It is noteworthy that none of the single island endemic sawfly species known from the Mediterranean has so far been shown to have a single island endemic plant species as its larval host. On the contrary, for those of the endemic sawflies with known hosts, the plant species involved are rather widespread in the Mediterranean (e.g. *Pteridium aquilinum*, *Quercus coccifera*, *Acer sempervirens*) and the biology of the sawfly seems very similar to related mainland taxa. We suggest that this may be because most such sawflies are neoendemics, i.e. speciation has largely been driven by random genetic drift after isolation, rather than adaptive differentiation. If so, this situation contrasts strongly with that found in vascular plants. The endemic flora of Crete, comprising about 10% of the total, has a strongly relict character, although containing a not inconsiderable neoendemic element (Georghiou and Delepetrou 2010).

Niche specialisation of sawflies within the same plant host species

Three species of *Pristiphora* belonging to the same species group occur in Crete on the same host (*Acer sempervirens*) and partly at the same localities. It is remarkable that adults of two of these species were found on individual trees at different stages of vegetative development: *P. tetrica* on plants at a less advanced stage than those frequented by *P. cretica*. It would be interesting to know if the third species, *Pristiphora* sp. [*subbifida* group], also differs in this habit. Although a few examples of differing phenology between closely related species on the same host are known in other Tenthredinidae (e.g. *Parna apicalis* (Brischke, 1888) and *P. tenella* (Klug, 1816): leaf-miners on *Tilia*), *P. cretica* and *P. tetrica* are exceptional in that their adults can be found at the same locality on the same day, but on different trees. This is made possible by the very large variability in vegetative phenology of the host. Although the larva of *P. cretica* remains unknown, larvae of other species in the *subbifida* group are similar in appearance and behaviour: cryptically coloured, solitary, leaf-edge feeders. The rather low abundance of adults at any site, the small size of individuals, the [probably] solitary habits of the larvae and the abundance of the food resource (leaves) lead us to suppose that competition between the larvae of these species is negligible. It would be very interesting to know more about the apparently differing behavioural strategies of the Cretan *Acer*-feeding *Pristiphora*.

Conclusions

The quantitative similarity between the sawfly faunas of Crete and Cyprus identified by Turrisi (2011) still holds, with 42 species now known in Crete and 43 in Cyprus (Liston and Jacobs 2012), but the recent investigations on Cypriot sawflies and the present study on Crete revealed that the faunas are qualitatively more dissimilar than previously supposed, at least when compared at species level. The majority of characteristic species in Cyprus have an exclusively eastern Mediterranean distribution, that only extends in two cases (*Empria archangelskii*, *Mocsarya syriaca* Benson, 1936) as far West as Crete. Many more species are shared between the fauna of Crete and mainland Greece, than between the two islands.

Although the Cretan sawfly fauna is species poor, it is valuable and worthy of conservation not only because of its proportionately high number of endemic species and genetically distinctive populations, but also because of those which are elsewhere known only from the southern Balkan peninsula (*Pristiphora cretica*), or are isolated populations on the western edge of the species range (*Empria archangelskii*, *Mocsarya syriaca*).

Acknowledgements

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Appendix

Checklist of the Symphyta of Crete

Xyelidae
Xyela graeca (J. Stein, 1876)
Cephidae
Cephus pygmeus (Linnaeus, 1767)
Calameuta haemorrhoidalis (Fabricius, 1781)
Calameuta idolon (Rossi, 1794)
Phylloecus faunus Newman, 1838
Trachelus tabidus (Fabricius, 1775)
Trachelus troglodyta (Fabricius, 1787)
Argidae
Arge melanochra (Gmelin, 1790)
Arge ochropus (Gmelin, 1790)
Arge scita (Mocsáry, 1880)
Cimbicidae
Corynis krueperi (J. Stein, 1876)
Tenthredinidae
Allantinae
Allantus nigrolinearis (Zirngiebl, 1937)
Allantus viennensis (Schrank, 1781)
Ametastegia glabrata (Fallén, 1808)
Athalia ancilla Serville, 1823
Athalia circularis (Klug, 1815)
Athalia cordata Serville, 1823
Athalia rosae (Linnaeus, 1758)
Empria archangelskii Dovnar-Zapolskij, 1929
Blennocampinae
Chevinia mediterranea Lacourt, 2003
Heterarthrus imbrosensis Schedl, 1981
Periclista cretica (Schedl, 1981)
Silliana lhommei (Hering, 1934)
Halidamia affinis (Fallén, 1807)
Nematinae
Cladius ordubadensis Konow, 1892
Cladius pectinicornis (Geoffroy, 1785)
Hoplocampa brevis (Klug, 1816)
Hoplocampa chrysorrhoea (Klug, 1816)
Mesoneura opaca (Fabricius, 1775)
Euura atra (Jurine, 1807)
Euura proxima (Serville, 1823)
Pristiphora abbreviata (Hartig, 1837)
Pristiphora cretica Schedl, 1981
Pristiphora pallidiventris (Fallén, 1808)
Pristiphora parnasia Konow, 1902
Pristiphora sp. [*subbifida* group]
Pristiphora tetrica (Zaddach, 1883)
Selandriinae
Aneugmenus oertzeni (Konow, 1887)
Dolerus puncticollis Thomson, 1871
Strongylogaster multifasciata (Geoffroy, 1785)
Orussidae
Mocsarya syriaca Benson, 1936
Orussus morio Guiglia, 1954

museum für naturkunde

A revision of the genus *Chlorocryptus* Cameron (Hymenoptera, Ichneumonidae), with the first record of the genus from Japan

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Abstract

The genus *Chlorocryptus* is revised and two species are recognized: *Chlorocryptus purpuratus* (Smith, 1852) and *C. coreanus* (Szépligeti, 1916). *Cryptaulax metallicus* Szépligeti, 1916, which has been hitherto listed in catalogs as *Chlorocryptus fuscipennis* Townes et al., 1961, is shown as a new synonym of *Chlorocryptus purpuratus*. *Chlorocryptus purpuratus* and *C. coreanus* are redescribed and illustrated in detail and a key is provided. *Chlorocryptus purpuratus* is recorded from Japan and Vietnam for the first time and is considered to have recently been introduced into Japan.

Key Words

Introduction

Chlorocryptus Cameron, 1903 is a small genus presently comprising three species: *C. purpuratus* (Smith, 1852), *C. coreanus* (Szépligeti, 1916), and *C. fuscipennis* Townes et al., 1961. They are easily sighted because of their large body size (10–15 mm) and metallic blue, purple, or green luster throughout the body. *Chlorocryptus purpuratus* is widely distributed in the Oriental Region to northern China and is well known as a common parasitoid of limacodid moths, which are injurious to leaves of various trees, especially oil palms (Gauld 1987, Mariau 1999). *Chlorocryptus purpuratus* and *C. coreanus* are well recognized, particularly in China (Chu et al. 1978, He and Chen 2006, He et al. 1996, 2004, Sheng et al. 2013, Wang and Li 1987). However, difficulties in identification or taxonomic confusion still exist in other countries (Gauld 1987, Jonathan 2006). In contrast, *Cryptaulax metallicus* Szépligeti, 1916, for which Townes et al. (1961) proposed a new name *Chlorocryptus fuscipen-*

nis, is known only from the type series collected on Sulawesi and has not been studied in detail ever since its original description (Szépligeti 1916, Townes et al. 1961).

In 2010, one of us (RM) collected several specimens of *Chlorocryptus purpuratus* (Smith) at Isoshima in Osaka Prefecture. This finding was a surprise because *Chlorocryptus* species have never before been recorded from Japan, nor are any specimens collected in Japan known from older collections. However, specimens from other Southeast Asian countries are not rare in museum collections. Given the present known distribution of this species, it is presumed that it has recently been introduced into Japan.

Since this first discovery, we have collected additional specimens in Japan. Because its potential hosts, limacodid moths, are abundant in Japan (27 species from 19 genera are presently found; Owada et al. 2011), it is expected that the species can expand its distribution range into Japan.

Here, we study all three currently recognized species of the genus and revise their taxonomic status. We record

Chlorocryptus purpuratus from Japan as an alien species to provide the basis for monitoring the future expansion of the distribution range of this species.

Material and methods

Collection and field survey of *Chlorocryptus purpuratus* in Osaka and adjacent area were conducted by the second author (RM). Two immature specimens were collected from a cocoon of *Parasa consocia* Walker (Lepidoptera, Limacodidae). Cocoons of the moth are easily found clustered on the ground at the base of certain trees such as *Cerasus × yedoensis* (Matsum.) A.N.Vassiljeva, *Celtis sinensis* Pers., and *Salix* spp. in the study area. RM also conducted successful rearing experiments by supplying *C. purpuratus* females with *Parasa consocia* cocoon.

Morphological observations of *Chlorocryptus* specimens collected by RM and other colleagues and those from museum collections were conducted by the first author (TY). Specimen depositories are abbreviated as follows: Natural History Museum, London (BMNH), Hungarian Natural History Museum, Budapest (HNHM); Muséum national d'Histoire naturelle, Paris (MNHN); Osaka Museum of Natural History, Osaka (OMNH); Systematic Entomology, Graduate School of Agriculture, Hokkaido University, Sapporo (SEHU), Taiwan Agricultural Research Institute in Taichung (TARI).

A part of the specimens were dissected for detailed observations. Genitalia and other body parts were detached from the specimens that were previously macerated in hot water, and the detached body parts were further dissected in 80% ethanol. The dissected body parts were heated in 10% KOH solution at 60 °C for a sufficient period of time depending on the condition of the material to remove muscles from the exoskeleton. Cleaned parts were then washed in diluted acetic acid and distilled water and observed in 80% ethanol or pure glycerol.

Larval exuviae of the parasitoid were extracted from the host cocoon and their cephalic structures and spiracles were observed. They were macerated and stretched in 10% KOH solution and processed as body parts of adult specimens. One 5th instar larva collected in the field was killed to obtain DNA barcode sequences and subsequently treated as the exuviae in morphological observations.

Stereomicroscopes (Nikon SMZ-10 and Olympus SZ40), a light-microscope (Olympus BX40), and a field emission scanning electron microscope (SEM) (JEOL JSM-6301F, Tokyo, Japan) were used for morphological observations. Dissections and observations were carried out under the Olympus stereomicroscope, line drawings were made with a drawing tube attached to the Nikon stereomicroscope, and images of the wings and genitalia were taken using a Nikon Coolpix 4500 digital camera attached to the Olympus stereomicroscope. Images of larval exuviae were taken using the same digital camera attached to the light-microscope. Specimens for SEM analysis were not coated and were observed with an ac-

celerating voltage of 1.0 kV. Digital images were edited using Adobe Photoshop Elements® 6.0.

Terminology used for adult morphology follows Gauld (1991) and Harris (1979), whereas descriptions of immature stages follow Short (1978). OOL and POL refer to ocello-ocular line and postocellar line, respectively. Nervellar index is defined as in Gauld and Mitchell (1981), i.e., the relative length of the first abscissa of Cu1 to the length of cu-a of the hind wing (Fig. 22).

DNA barcoding was carried out by RM. The DNA barcode sequences of cytochrome *c* oxidase I (COI) were obtained from an adult and a larva collected in Japan. Amplification of COI was carried out using the primer set LCO1490 and HC02198 designed by Folmer et al. (1994). The PCR protocol consisted of an initial 5-min denaturation at 94 °C, followed by 40 cycles at 94 °C for 15 s, 46 °C for 15 s, and 72 °C for 15 s, and ending with a 10-min extension step at 72 °C. Gene regions were sequenced using the same primer set and a BigDye® Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). Cycle sequencing reactions were run on an ABI Prism 310 Genetic Analyzer (Applied Biosystems, USA).

Taxonomy

Genus *Chlorocryptus* Cameron

Chlorocryptus Cameron, 1903: 34. Type species: *Chlorocryptus metallicus* Cameron. Designated by Viereck (1914: 32).
Cochlidionostenus Uchida, 1936: 115. Type species: *Cryptaulax coreanus* Szépligeti. Original designation. Synonymized by Townes et al. (1961: 141).
Cryptaulaxoides Uchida, 1940: 121. Type species: *Cryptus purpuratus* Smith. Original designation. Synonymized under *Cochlidionostenus* by Townes (1957: 104).

Description. Large and stout species, fore wing length about 10–15 mm, with metallic blue, purple or greenish luster (Fig. 1). Frons deeply concave, with longitudinal ridge below median ocellus and laterally with transverse rugae and punctures (Figs 2, 13). Antennal scrobe glabrous and polished. Face distinctly convex medially, densely sculptured (Figs 2, 5, 13, 16). Clypeus large, 1.2–1.9 times as wide as high, flat to weakly convex (Figs 2, 13). Mandible short and stout, upper tooth longer than lower tooth (Figs 6, 17). Occipital carina joining hypostomal carina above mandibular base. Female flagellum with apical third flattened ventrally (Fig. 7), there densely covered with mixture of one type of sensilla chaetica and one type of sensilla basiconica (Figs 41, 42); apex round, not truncated, possessing a bundle of thick sensilla, which are widened apically, and whose sockets interrupted on one side (Figs 39, 40). Male flagellum not flattened ventrally; with 5 or 6 tyloids which can be on 13th–20th flagellomeres; apex of flagellum with thick sensilla as in female but fewer.

Epomia strong (Figs 9, 19). Notaulus absent (Figs 8, 18). Sternaulus distinct, about 0.7 as long as mesopleuron. Median part of postpectal carina represented by tubercle. Submetapleural carina distinct and complete. Metasternum with distinct flange immediately anterior to hind coxa (Fig. 10).

Legs slender, hind femur about 6–8 times as long as median width, and hind tibia about 9–11 times as long as apical width. Male hind tarsal claws sharply bent, apical part covered with scale-like sculpture (Fig. 45). Female hind tarsal claws not specialized unlike male (Fig. 43). Orbicula slender, flask-shaped in female (Fig. 44), parallel-sided in male (Fig. 46).

Wings infumate in various degrees (Figs 22–27). Fore wing with areolet small, quadrangular, 0.3–0.4 times as long as 2m-cu; 2m-cu joining behind middle of areola; cu-a a little distad of Rs&M. M+Cu of hind wing straight on apical 0.6; nervellar index less than 2.8; 2A curving toward anal margin.

First metasomal tergite with baso-lateral tooth (Figs 12, 21); petiole dorsally flat (Figs 11, 20), sparsely punctate; postpetiole (Figs 11, 12, 20, 21) parallel-sided in dorsal view, dorsal face weakly to moderately convex, densely with shallow, large punctures; median longitudinal carina weak, usually almost absent; lateral and ventral longitudinal carinae distinct. Second and 3rd tergites distinctly punctate, with narrow glabrous band on posterior rim. Fourth and following tergites with smaller, minute punctures. Female sterna heavily sclerotized; 2nd sternum posteriorly embraced by 3rd (Fig. 28). Ovipositor sheath 0.8–1.0 times as long as hind tibia, with terminal point (Fig. 47). Upper valve of ovipositor bearing apical ridges. Lower valve of ovipositor with distinct oblique teeth. Male sterna not evenly sclerotized; median part weakly sclerotized (Fig. 29). Gonosquama weakly tapered toward apex and apex rounded (Fig. 30). Apex of aedeagus round, gently curved in lateral view (Fig. 31), tapered in ventral view (Fig. 32).

Biology. Both *Chlorocryptus purpuratus* and *C. coreanus* are parasitoids of limacodid moths and are often reported in the context of biological control (Table 1). They are solitary ectoparasitoids that oviposit into the host cocoon. The possession of ridges on the upper valve of the ovipositor is considered to be an adaptation to penetrate the hard cocoons of limacodid moths because this character state is found in some other cryptine species such as *Lithochila nohirai* (Uchida, 1930) and *Paragambrus sapporoensis* (Uchida, 1930) that also attack the limacodid cocoons (Townes 1969).

Chlorocryptus purpuratus (Smith)

Figs 1–12, 22–25, 28–35, 39–58.

Cryptus purpuratus Smith, 1852: 33. Holotype: ♀, China, Hong-Kong (BMNH), mentioned "Ning-po-foo" in original description [examined].
Chlorocryptus metallicus Cameron, 1903: 35. Holotype: ♀,

India, Khasia Hill (BMNH) [examined]. Synonymized by Gauld (1987).
Chlorocryptus coeruleus Cameron, 1903: 36. Holotype: ♀, India, Khasia Hill (Oxford University Museum, UK). Synonymized by Gauld (1987).
Chlorocryptus reticulatus Cameron, 1907: 84. Holotype: ♂, India, Sikkim (BMNH) [examined]. Synonymized with *coeruleus* by Townes et al. (1961).
Cryptaulax cyaneus Szépligeti, 1916: 286. Lectotype: ♀, India, Sikkim (HNHM) designated by Townes et al. (1961) [examined]. Synonymized with *coeruleus* by Townes et al. (1961).
Cryptaulax metallicus Szépligeti, 1916: 287. Lectotype: ♀, designated by Townes et al. (1961), Celebes, Patunuang (HNHM) [examined]. **New synonym.**
Cryptaulaxoides purpuratus (Smith): Uchida 1940: 121.
Cryptaulaxoides metallicus (Cameron): Uchida 1940: 121.
Cochlidionostenus purpuratus (Smith): Townes 1957: 104.
Chlorocryptus fuscipennis Townes et al., 1961: 142. Replacement name for *Cryptaulax metallicus* Szépligeti, 1916.
Chlorocryptus purpuratus (Smith): Townes et al. 1961: 142.
Neodontocryptus hyalina Saxena, 1978: 216. Holotype: ♀, India, Manipur, Kanchipur (depository unknown; see "Remarks"). Synonymized with *coeruleus* by Gupta (1987).

References. Gonggrijp 1931: 8 (noted as parasitoid of *Thosea asigna*, photo); Kellogg 1938: 123 (*reticulatus*, listed); Uchida 1940: 121 (*Chryptaulaxoides purpuratus*, record), 122 (*Cryptaulaxoides metallicus*, in key); Wu 1941: 59 (*Cryptus purpuratus*, listed); Uchida 1952: 48 (*Cryptaulaxoides purpuratus*, record); Narayanan and Lal 1961: 257 (*coeruleus*, listed), 257 (*metallicus*, listed) 258 (*reticulatus*, listed); Townes et al. 1961: 141 (*coeruleus*, catalogued), 142 (*fuscipennis*, catalogued), 142 (*metallicus*, catalogued), 142 (*purpuratus*, catalogued); Townes et al. 1965: 167 (*coeruleus*, catalogued), 168 (*purpuratus*, catalogued); Chao 1976: 266 (*coeruleus*, listed, distribution), 267 (*purpuratus*, listed, distribution); Chu et al. 1978: 40 (description, figure, host, parasitism, distribution); Tiong 1979: 282 (*Chlorocryptus* sp. nr. *coeruleus*, noted as parasitoid of *Thosea asigna*); Yang and Wu 1981: 303 (listed); Tiong 1982: 535 (*Chlorocryptus* sp. nr. *coeruleus*, noted); Zhang 1983: 21 (diagnosis, host, biology); Xiao 1985: 25 (biological notes); He and Wang 1987: 379 (description, host, distribution); Wang and Li 1987: 1326 (in key, host, distribution, records); Gauld 1987: 130 (diagnosis, figure of fore wing, distribution, hosts, biology); Dang et al. 1990: 12 (description, figure, hosts, distribution); He et al. 1992: 1224 (description, figure, hosts, distribution); He and Tian 1993: 536 (description, figure, hosts, distribution); Wang and Yao 1993: 645 (records); Chen 1993: 138 (noted, figure); He et al. 1996: 511 (description, figure, hosts, distribution); Mariau 1999: 150 (table 1), 153 (listed and noted as a parasitoid of Limacodidae on palms); He et al. 2001: 721 (records); Lin 2003: 939 (catalogued); Wang 2003: 274 (*coeruleus*, description, distribution); He et al. 2004: 514

Figure 1. *Chlorocryptus purpuratus* female, ovipositing into a cocoon of *Parasa consocia* Walker.

(description, figure, hosts, records, distribution); Jonathan 2006: 191 (*coeruleus*, description, figures, records, distribution), 192 (*metallicus*, diagnosis, distribution); He and Chen 2006: 111 (description, figures, biology, hosts, distribution); Ding et al. 2009: 27 (record, hosts); Sheng and Sun 2009: 70 (description, photo, hosts, records, distribution); Sheng et al. 2013: 139 (description, photo, hosts, records, distribution).

Type specimens examined. Holotype of *Cryptus purpuratus* Smith: ♀, "56 113, Hong Kong", BMNH (ID 3b-572). Holotype of *Chlorocryptus reticulatus* Cameron: ♂, "Sikkim", BMNH (ID 3b-2013). Lectotype of *Cryptaulax cyaneus* Szépligeti: ♂, "India, Sikkim, ex coll. Fruhstorfer", HNHM (ID 115215). Lectotype of *Cryptaulax metallicus* Szépligeti: ♀, "S.-Celebes, Patunuang, Jan. 1896, H. Fruhstorfer", HNHM (ID 115222). One of the paralectotypes of *Cryptaulax metallicus* Szépligeti: ♀ same data as the lectotype, SEHU (Uchida collection).

Additional specimens. Japan. Yamadaike Park, Hirakata, Osaka Pref., 1 ♀, 6.viii.2011, Y. Mori, OMNH. Isoshima, Hirakata, Osaka Pref., 34.82683°N/ 135.6450°E, R. Matsumoto, OMNH: 1 ♂, 18.x.2010; 1 ♀, 29.x.2010; 1 ♀, 8.xi.2010; 1 ♀, 3.x.2010; 3 ♀, 2 ♂, 24.ix.2011; 1 ♀, emerged from a cocoon of *Parasa consocia* Walker collected on 15.i.2013, emerged in iii.2013. Offspring of females collected at Isoshima, bred on *Parasa consocia* Walker, OMNH: 1 ♂, laid on 1.xi.2010, emerged on 20.xii.2010; 1 ♂, laid on 4.xi.2010, emerged on 22.xii.2010; 1 ♂, laid on 10.xi.2010, emerged on 24.xii.2010; 1 ♂, laid on 9.xi.2010, emerged on 28.xii.2010; 1 ♂, laid on 4.xi.2010, emerged on 6.i.2011. Oka, Hirakata, Osaka Pref., 34.8178°N/135.6415°E, R. Matsumoto, OMNH:

1 ♂, 28.ix.2011; 1 ♀, 16 ♂, 24.ix.2011 [1 ♂ for DNA extraction: DNA-ICH-002]. Tawaraguchicho, Ikoma, Nara Pref., 34.7027°N/135.6795°E, 1 ♀, 19.viii.2012, R. Matsumoto, OMNH. Hitakatsu, Tsusima Is., Nagasaki Pref., 1 ♂, emerged from a cocoon of *Monema flavescens* Walker collected on 28.iii.2013, emerged in iv.2013, K. Sasaki, OMNH. **China**. Wutaihsien, Shanxi Prov., 1 ♀, 12.viii. SEHU. Chinkiang, Kiangsu [= Jiangsu Prov.], 1 ♀, 12.xi.1918, O. Piel, SEHU. Tchefou [= Yantai] Shandong Prov., 1 ♀, MNHN (coll. de Gaulle). Ningpo, Zhejiang Prov.: 3 ♀, P. Buch, 1924, MHNM; 2 ♀, MNHN (coll. de Gaulle). Moupin, Sichuan Prov., 1 ♀, 1899, Chasseurs indigènes, MNHN (coll. Oberthür). **Nepal**. Balaju, Kathmandu, 1 ♀, 11.ix.1987, H. Takizawa, SEHU. **Vietnam**. Chu Yang Sin National Park, 12°27'13.74"N/108°20'21.75"E, Krong Bong District, Dak Lak Province, 1 ♂, 12.iii.2013, K. Konishi. Cuc Phuong, Ha Son Binh Prov. (SEHU): 1 ♂, 28.iv.1996, Y. Okushima, OMNH; 1 ♂, 200–300m alt., 24.iv.1998, R. Matsumoto, OMNH. Ba Be National Park, Ba Be, 200m alt., 22.23°N/ 105.37°E, R. Matsumoto, OMNH: 1 ♂, 4.v.2006; 1 ♂, 1.v.2006. **Malaysia**. Klapa Bali, 3 ♀, 3 ♂, 10.vi.1949, MNHN. Klapa Bali, "ds cage de Setora nitens", "VI–VII 1949", P. Vayssuère: 11 ♀, 5 ♂, 10.vi.1949; 2 ♀, 1 ♂, 11.vi.1949. **Indonesia**. Semarang, Java, 1 ♀, E. Jacobson, 1906, MNHN. Malang, Java, 1 ♀, MNHN. Gunung Lompobattang, 1250–1350m, South Sulawesi, 1 ♀, 16.xii.2010, K. Takasuka, OMNH. **Unknown locality**. 2 ♂, "Sina", MNHN (coll. Sichel).

Immature stage. Fifth instar larva. 1 ex. Isoshima, Hirakata, Osaka Pref., in cocoon of *Parasa consocia* Walker, 24.ii.2012, R. Matsumoto [OMNH; DNA extraction: DNA-ICH-001].
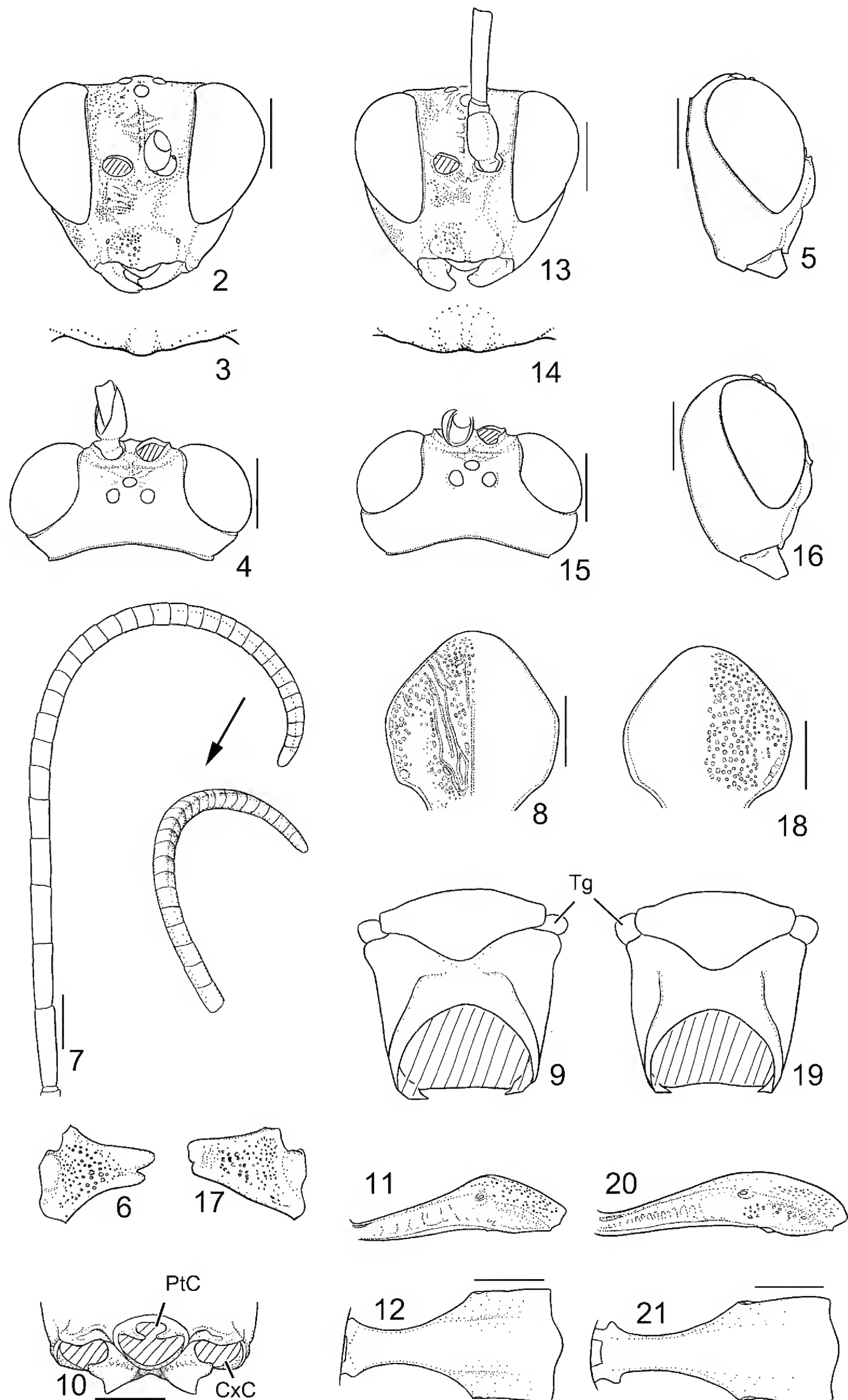
Figures 2–21. 2–12. *Chlorocryptus purpuratus*; **13–21.** *C. coreanus.* **2 & 13.** Head, frontal view (surfacial sculpture partly shown on right half); **3 & 14.** Apical margin of clypeus; **4 & 15.** Head, dorsal view; **5 & 16.** Head, lateral view; **6 & 17.** Mandible; **7.** Flagellum; **8 & 18.** Mesoscutum; **9 & 19.** Pronotum, anterior view, showing epomia; **10.** Metasternum, posterior view; **11 & 20.** First metasomal segment, lateral view; **12 & 21.** First lateral segment, dorsal view. **CxC** – coxal cavity; **PtC** – petiolar cavity; **Tg** – tegula. Scale lines: 1 mm.

Diagnosis. Punctation on head finer than *C. coreanus*. Temple flat and narrower, occupying 0.2–0.3 of length of head in dorsal view (Fig. 4). Face with transverse rugae in addition to punctures (Figs 2, 5). Clypeus with median obtuse tubercle on apical margin (Fig. 3). Mandibular teeth acute (Fig. 6). Female flagellum without white annulus and with apical third of flagellum ventrally distinctly flattened and widened (Fig. 7). Epomia turned abruptly horizontally toward mesal line of pronotum at midway to upper edge of pronotum (Fig. 9). Prepectus with a short vertical carina opposite lower corner of pronotum. Mesoscutum with longitudinal rugae in addition to punctures, and with moderate-sized glabrous area on lateral lobe (Fig. 8). Propodeum with posterior transverse carina. Nervellar index 1.9–2.8 (Figs 22–25). Postpetiole usually shorter, 0.7–0.9 times as long as wide in female (Fig. 12), 0.6–0.8 in male. Area between median longitudinal carinae of 1st metasomal tergite distinctly raised at beginning of postpetiole (Fig. 11). Subgenital plate (Figs 33–35) with postero-lateral corner gently curved, with posterior margin simply convex medially, and without white spot at base of its apodeme.

Description. Adult. ♀. Head 2.0–2.1 times as wide as long in dorsal view (Fig. 4). Temple flat and narrow, occupying only 0.2–0.3 of length of head in dorsal view (Fig. 4). POL/OOL=0.4–0.8. Vertex and gena densely punctate with shallow and small punctures; punctures smaller on gena than on vertex. Face 1.4–1.5 times as wide as high, distinctly convex medially, densely punctate with fine punctures and with some sublateral transverse rugae (Figs 2, 5). Clypeus with median obtuse protuberance on apical margin (Fig. 3); punctures sparser than on face and irregular with mixture of different sized punctures. Malar space 0.9–1.2 times as wide as mandible width. Mandible with acute teeth, its lower tooth about half length of upper one (Fig. 6). Antenna with 31–32 flagellomeres; apical third of flagellum weakly thickened and weakly flattened ventrally, weakly tapered to apex; first flagellomere 3.4–4.3 times as long as apical width, a little longer than 2nd flagellomere; fifth flagellomere 1.5–2.1 times as long as apical width (Fig. 7).

Epomia turns horizontally toward mesal line of pronotum at midway to upper edge of pronotum (Fig. 9). Prepectus with a short vertical carina opposite lower corner of pronotum. Mesoscutum densely punctate, with longitudinal to oblique rugae on median lobe, and with moderate-sized glabrous area on lateral lobe (Fig. 8). Scutellum with large punctures. Mesopleuron punctate to areolate-rugose on lower part to strigate on upper frontal part. Mesosternum punctate-reticulate. Metapleuron areolate-rugose. Upper division of metapleuron punctulate. Propodeum areolate rugose; posterior transverse carina distinct laterally, forming weak crest, with median portion merged in rugae and indistinct; anterior transverse carina and basal section of lateromedian longitudinal carina weakly marked; other carinae absent.

Legs slender. Hind femur 6.0–7.3 times as long as maximum width. Hind tibia 9.3–10.7 times as long as apical width.

Fore wing about 10–15 mm long. Nervellar index 1.8–2.8 (Figs 22–25).

First metasomal tergite 1.8–2.1 times as long as apical width, with postpetiole 0.6–0.9 times as long as apical width; area between median longitudinal carinae distinctly raised at proximal margin of postpetiole (Figs 11, 12). Ovipositor sheath 0.8–1.0 times as long as hind tibia.

Body with metallic luster in blue, purple or green. Flagellum entirely black, without white band. Fore and middle tibiae and all tarsi dark brown to black. Ovipositor sheath and ovipositor black. Wings infumate in variable degrees (Figs 22–25). Veins dark brown to black, strongly pigmented all over.

♂. Similar to female except as follows: face 1.2–1.3 times as wide as long; malar space 0.8–1.0 times as long as basal width of mandible; flagellum with 35–37 flagellomeres, with 5 or 6 tyloids which can be on 13th–20th flagellomeres; 1st flagellomere 2.7–3.3 times as long as apical width; 1st metasomal segment 1.6–2.1 times as long as apical width; hind femur 7.3–8.0 times as long as median depth; hind tibia 10.3–12.7 times as long as apical width; anterior side of fore femur, fore tibia and dorsal stripe of middle tibia light brown. Subgenital plate with posterior margin evenly convex and with postero-lateral corner gently rounded (Figs 33–35).

Immature stages. Mandible, labral sclerite, epistoma, hypostoma, and labial sclerite well sclerotized through larval development (Figs 48, 50). Pleurostoma less strongly sclerotized (Figs 48, 50). Mandible with minute teeth both on dorsal and ventral sides (ventral teeth difficult to discern under light microscope) (Figs 55, 56), except for 1st instar (Fig. 54). Labrum with five to seven conspicuous setae in a row on each side along labral sclerite. Clypeus with three pairs of setae on lower margin. Antenna of moderate size, conical, without papilla or obvious seta or sensilla (Fig. 51).

First instar larva (Fig. 48). Hypognathus. Hypostomal spur very weakly sclerotized. Stipital sclerite not developed. Mandible without teeth on blade (Fig. 54). Labrum with three setae on each side. Atrium of spiracle and closing apparatus not differentiated (Fig. 49).

Second instar larva. Prognathus. Narrow epistomal spur present. Two pairs of setae on labium of 1st instar remaining but upper most one situated just below salivary orifice present only as a hole. Spiracle with atrium differentiated.

Third and fourth instar larvae. Epistomal spur more developed than in 2nd instar and stipital sclerite present.

Final instar larva (Fig. 50). Dorsal part of epistoma not distinctly sclerotized and transparent, gradually evanescent. Clypeus slightly sclerotized but well delimited from surrounding area, without setae. Mid-dorsal part of labral sclerite weakly expanded and oval in form. Cardo very slightly sclerotized. Maxillary palp with two sensilla. Labial palp with two sensilla. Salivary orifice U-shaped. Closing apparatus of spiracle adjoining atrium (Figs 52, 53).

Biology. Several limacodid moths have been recorded as hosts. Some of the moths are serious pests of palm trees
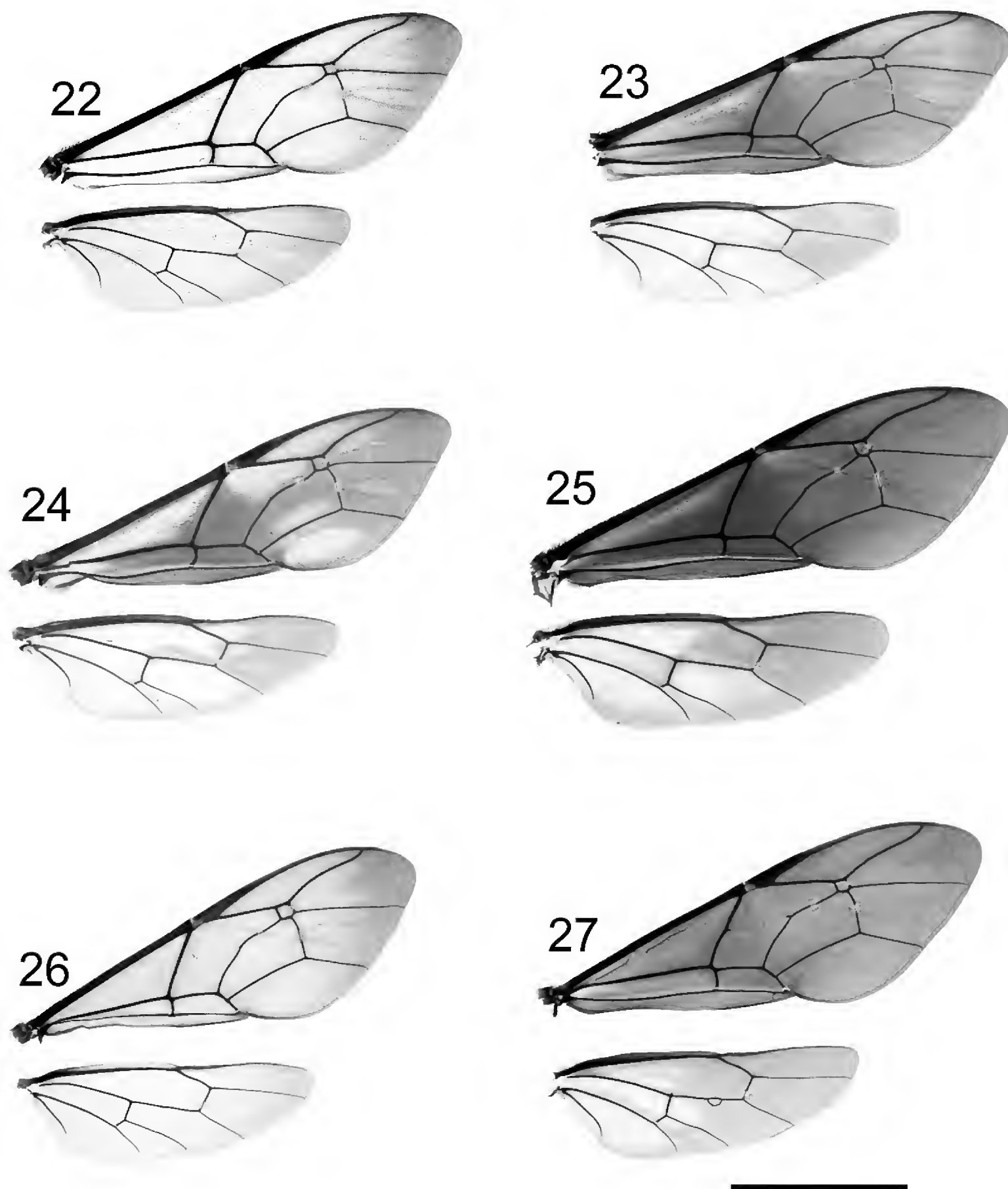
Figures 22–27. Wings. **22–25.** *Chlorocryptus purpuratus*; **26 & 27.** *C. coreanus.* **22.** ♂, Isoshima, Japan; **23.** ♀, Chinkiang, Jiangsu, China; **24.** ♀, Klapa Bali, Malaysia; **25.** ♀, Gunung Lompobattang, South Sulawesi, Indonesia; **26.** ♀, Keumsan, South Korea; **27.** ♀, Chulin, Taiwan, China. Scale line, 5 mm.

in the Oriental Region (Gauld 1987, Mariau 1999); hence, *C. purpuratus* is of economic importance as their natural enemy. The host records are summarized in Table 1.

In this study, we observed females collected in Osaka ovipositing into cocoons of *Parasa consocia* Walker (Fig. 1). They spent more than 30 min to penetrate the moth cocoons and to accomplish the oviposition.

Distribution (Figs 57, 58). Japan (new record): Honshu, Tsushima Is. China: Beijing (He and Wang 1987), Fujian (Chao 1976, Kellog 1938, Wang 2003), Guangxi (He et al. 1992), Guizhou (He et al. 1992, Wang and Yao 1993), Hebei (Wang and Yao 1993), Henan (Dang et al. 1991, Sheng and Sun 2009), Hong Kong (Smith 1852), Hubei (He and Chen 2006), Hunan (Dang et al. 1991), Jiangsu (Uchida 1940), Jiangxi (Chu et al. 1978, Ding et

al. 2009, Sheng et al. 2013), Shaanxi (Dang et al. 1991), Shandong (Chao 1976, He and Tian 1993), Shanghai (Chao 1976, Xiao 1985), Shanxi (Uchida 1952), Sichuan (He et al. 1992), Yunnan (Wang and Li 1987), Zhejiang (Chao 1976, He et al. 2001, 2004). Vietnam (new record). Malaysia: Sabah (Gauld 1987). Indonesia: Java (Gauld 1987, Saxena 1978), Sumatra (Gauld 1987), Sulawesi (Szépligeti 1916). India (Cameron 1903, Jonathan 2006, Saxena 1978, Szépligeti 1916). Nepal (Saxena 1978).

Remarks. Although this species shows a wide range of variation in density of the surface sculpture and setae, wing color (Figs 22–25), and shape of the subgenital plate (Figs 33–35), these variations are continuous. The specimens from Sulawesi, including the lectotype of *Cryptaulax metallicus* Szépligeti, have extensively dark

Table 1. Host records of *Chlorocryptus* spp. (modified from Gauld 1987). All hosts belong to Limacodidae.

Chlorocryptus	Host	Locality	References
C. coreanus	*Miresa inornata*	not mentioned	Uchida 1930a
	Monema flavescens	Taiwan	Uchida 1930b; Sun et al. 1982; Pan 1983; Yin and Zou 1987; Wang et al. 1991, 1993
C. purpuratus	*Birthamula chara*	Sumatra	Gauld 1987
	Birthosea bisura	Sumatra	Gauld 1987
	Darna sp.	Java	Gauld 1987
	Monema flavescens	Tsushima	Present study
	Parasa consocia	China, Osaka	Zhang 1983; Xiao 1985; present study
	Parasa lepida	China	Zhang 1983; Xiao 1985
	Setora nitens	Sumatra, Java	Gauld 1987
	Setothosea asigna	Indonesia, Sabah	Gonggrijp 1931; Tiong 1979, 1982; Gauld 1987
	Susica malayana	Indonesia	Gauld 1987
	Thosea lutea	Sumatra	Gauld 1987
	Thosea postornata	China	Zhang 1983; Xiao 1985
	Thosea sinensis	China	Zhang 1983; Xiao 1985
	Thosea vetusta	Indonesia	Gauld 1987
	Trichogyia semifascia	Sumatra	Gauld 1987
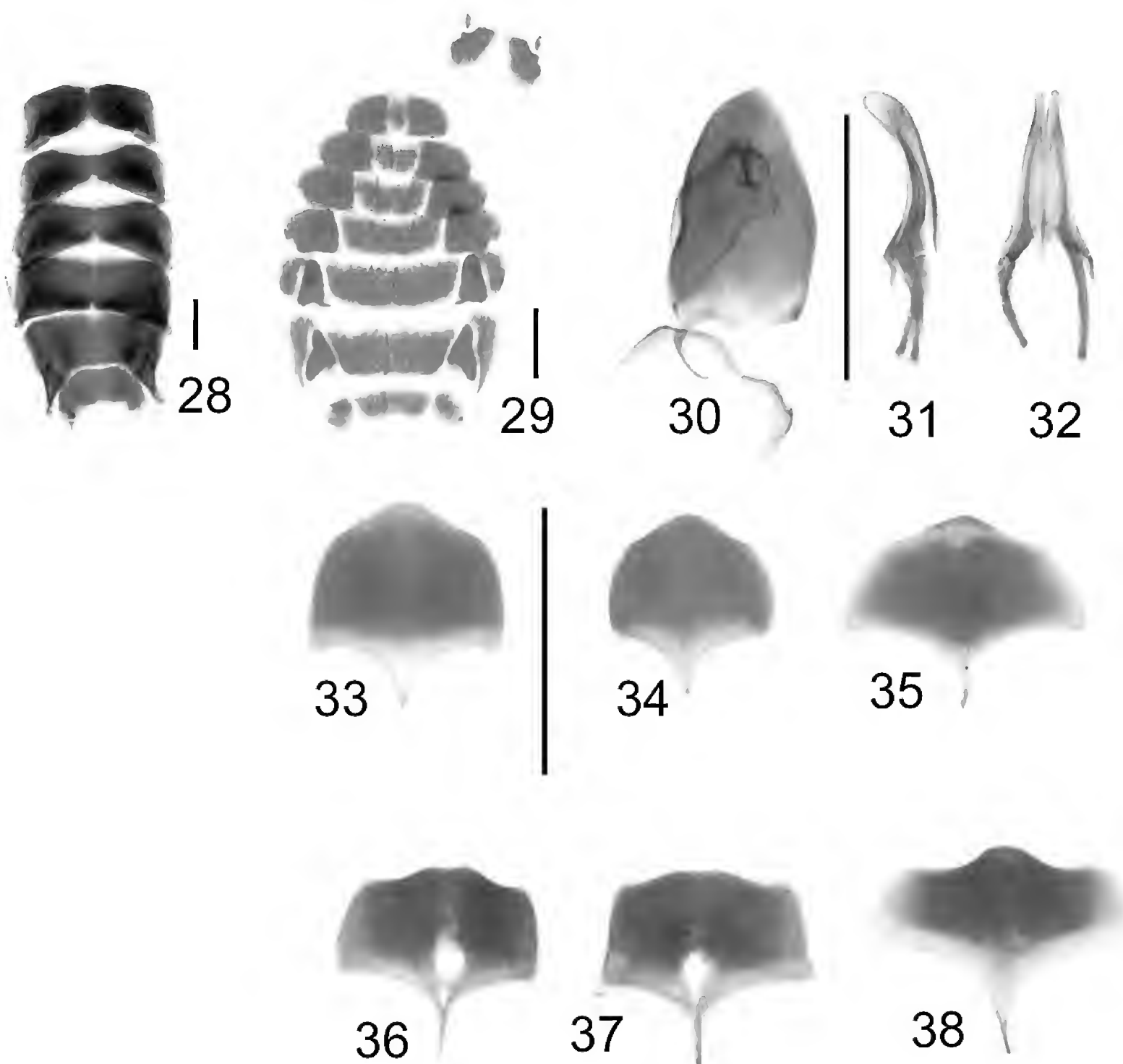
Figures 28–38. 28–35. *Chlorocryptus purpuratus.* **36–38.** *C. coreanus.* **28.** Second to seventh sterna (♀, Isoshima, Japan); **29.** Second to eight sterna and ninth tergites (♂, Isoshima); **30.** Gonosquama and basal ring (Isoshima); **31.** Aedeagus, lateral view (Isoshima); **32.** Aedeagus, ventral view (Isoshima); **33–38.** Subgenital plate (**33**. Isoshima; **34.** Cuc Phuong, Vietnam; **35.** Klapa Bali, Malaysia; **36.** Seonunsan, South Korea; **37.** Tieling, Liaoning, China; **38.** Keumsan, South Korea.).

wings (Fig. 25); however, we considered this an extreme end of the variation.

Jonathan (2006) treated *Chlorocryptus coeruleus* Cameron and *Chlorocryptus metallicus* Cameron as distinct species. However, given his descriptions, they fall within the variation of *Chlorocryptus purpuratus*.

Despite these large intraspecific variations, this species is clearly distinct from *Chlorocryptus coreanus* with the above given diagnostic characters.

The distribution of *Chlorocryptus purpuratus* extends further south than that of *C. coreanus* although the distributions of both species largely overlap in China (Figs 58, 59). We do not know what determines such a difference in the distribution and whether the species compete or segregate where they co-exist. The host and habitat preferences might be different between the species, which may also be of practical interest in the biological control of the notorious limacodids on various trees.

This is the first record of *Chlorocryptus purpuratus* from Japan and Vietnam. Considering that *C. purpuratus* has never before been collected in Japan, most probably the Japanese populations have been introduced recently. Its potential hosts, limacodid moths, are abundant and some of them have been well studied as pests in Japan, including their natural enemies (Kaji 1979, Koike 1985, 1998, Komeda and Hisamatsu 2006, Minamikawa 1962, Oda and Uezumi 1978, Togashi 1981, Togashi and Ishikawa 1994, 1995, 1996, Toyomura 1970, Yuasa 1934).

In 2012 and 2013, alongside the adults, we also collected two larvae in *Parasa consocia* cocoons in Osaka. This indicates that *C. purpuratus* has already been established in this area for two or three years.

One of the limacodid moths, *Parasa lepida* (Cramer), which had been originally distributed in South Asia, Southeast Asia, and southern China, invaded western Japan and became established in the late 1970's (Oda and Hattori 1981, Higa and Kishimoto 1984). It is probable that cocoons of *Parasa lepida* or other Limacodidae containing *C. purpuratus* were introduced accidentally in Japan with imported nursery trees.

The holotype of *Neodontocryptus hyalina* Saxena could not be located during the course of this study.

The holotype of the species was deposited in the V. K. Gupta collection, which was originally housed at the University of Delhi. Later, his collection was transferred to Florida, first to the University of Florida (Yu et al. 2012) and finally to FSCA (Virendra K. Gupta, personal communication). Therefore, we expected that the holotype of *N. hyalina* would be at FSCA; however, only one paratype was located, whereas the holotype was not found (Jim Wily, personal communication).

The lectotypes of *Cryptaulax cyaneus* Szépligeti and *C. metallicus* Szépligeti were designated by Townes et al. (1961). Five paralectotypes (two females and three males) of *C. cyaneus* and one paralectotype (female) of *C. metallicus* are preserved at HNHM together with their lectotypes (Gellért Puskás, personal communication). One female paralectotype of *C. metallicus*is preserved in the

Uchida collection at SEHU, which he obtained probably after visiting HNHM during his study trip to Europe and the United States from 1937 to 1939 (Uchida 1940).

DNA barcodes. INSD accession number: AB851419 for DNA-ICH-001 and AB851420 for DNA-ICH-002. Both have identical sequences.

### *Chlorocryptus coreanus* (Szépligeti)

Figs 13–21, 26–27, 36–38, 59

Cryptaulax coreanus Szépligeti, 1916: 287. Holotype: ♀, Korea, Seoul (HNHM) [examined].
Cryptus trirrhogmaniformis Sonan, 1929: 424. Lectotype: ♂, Formosa, Chikurin (TARI). Synonymized by Uchida (1930b).
Cochlidionostenus coreanus (Szépligeti): Uchida 1936: 116.
Chlorocryptus coreanus (Szépligeti): Townes et al. 1961: 141.

References. Uchida 1930a: 317 (*Cryptaulax*, records, host); Uchida 1930b: 360 (*Cryptaulax*, hosts); Uchida 1931: 177 (*Cryptaulax*, record, host); Matsumura 1931: 41 (*Cryptaulax*, diagnosis, figure, distribution); Uchida 1940: 122 (*Cochlidionostenus*, in key); Uchida 1942: 113 (*Cochlidionostenus*, records); Sonan 1944: 14 (*Cryptus trirrhogmaniformis*, listed); Uchida 1955: 114 (*Cochlidionostenus*, records); Kim 1955: 40 (*Cochleonosterus* (lapsus), record); Townes et al. 1961: 141 (catalogued); Chu et al. 1963: 750 (*Cryptaulax coteanus* (lapsus), as parasitoid of Limacodidae); Townes et al. 1965: 167 (catalogued); Yen 1973: 86 (*Cryptus trirrhogmaniformis*, listed, host); Chao 1976: 266 (listed, distribution, hosts); Chu et al. 1978: 40 (diagnosis, distribution, host); Yang and Wu 1981: 303 (listed, distribution, host); Sun et al. 1982: 46 (description, immature stages, host, biology); Pan 1983: 50 (*coevanus* (lapsus), description, figures, host, biology); Chiu et al. 1984: 17 (listed, distribution, hosts); Yin and Zou 1987: 11 (diagnosis, immature stages, biology, biological control effect on *Cnidocampa flavescens*); He and Wang 1987: 379 (diagnosis, host, distribution); Wang and Li 1987: 1326 (in key, record, host, distribution); Gauld 1987: 130 (taxonomic remarks); Wang et al. 1991: 30 (percentage of parasitism, biological control effect on *Cnidocampa flavescens*); Niu and Wang 1992: 1206 (description, figure, distribution, host, biology); Wang et al. 1993: 467 (rate of parasitism, life history, biological control effect); Wang and Huang 1993: 732 (description, figure, host, records, distribution); He et al. 1996: 510 (description, figure, host, distribution); Sheng et al. 1999: 374 (listed, records, distribution); He et al. 2001: 721 (listed, hosts, records, distribution); Lin 2003: 939 (listed, host, distribution); Wang 2003: 274 (description, figure, host, records, distribution); He et al. 2004: 514 (description, figures, host, records, distribution); He and Chen 2006: 110 (description, figures, biology, distribution); Chen et al. 2009: 70 (listed, distribution, records); Sheng and Sun 2009: 69 (description, photo, hosts, records, distribution); Sheng et al. 2013: 138 (description, photo, hosts, records, distribution).
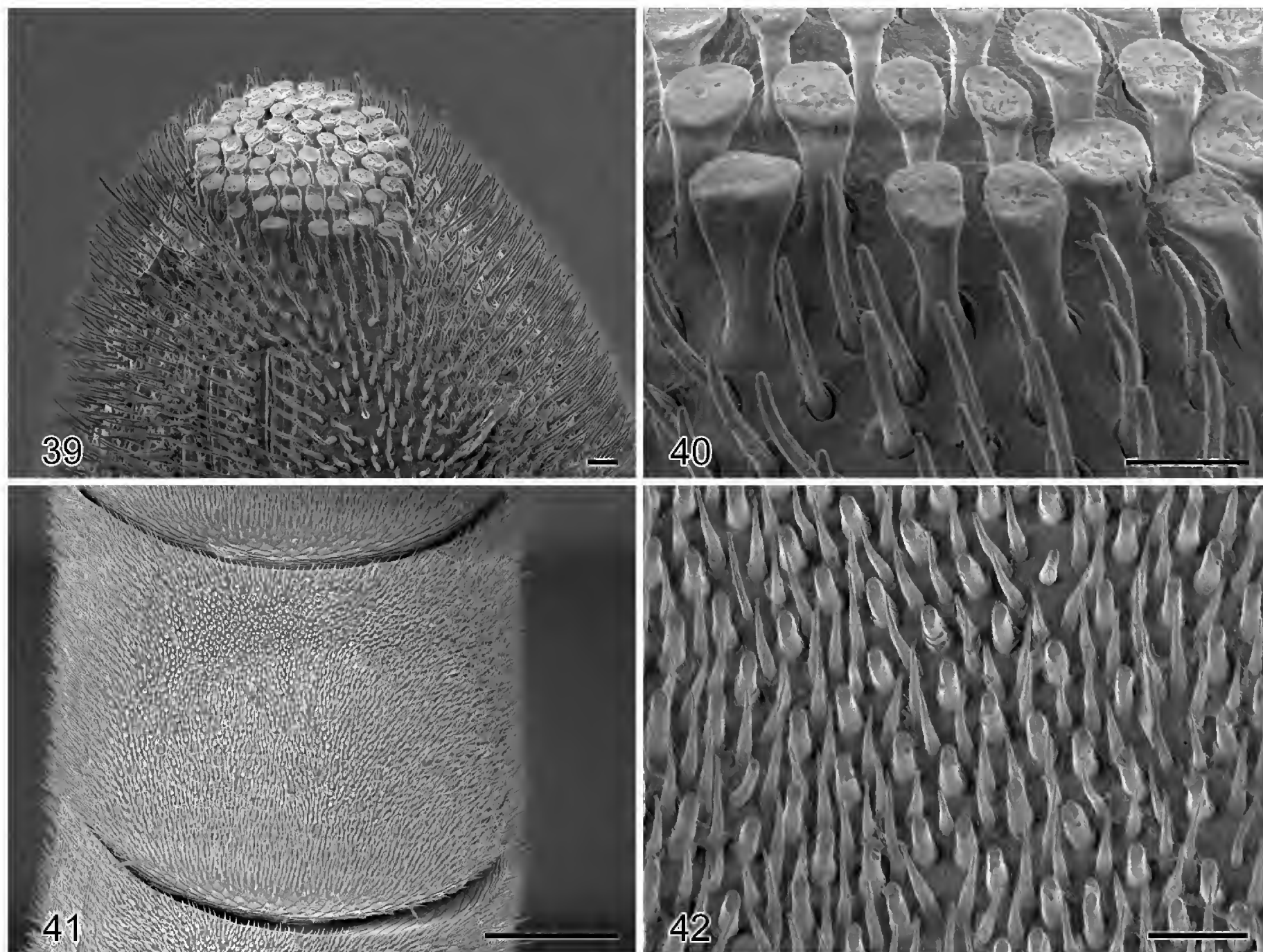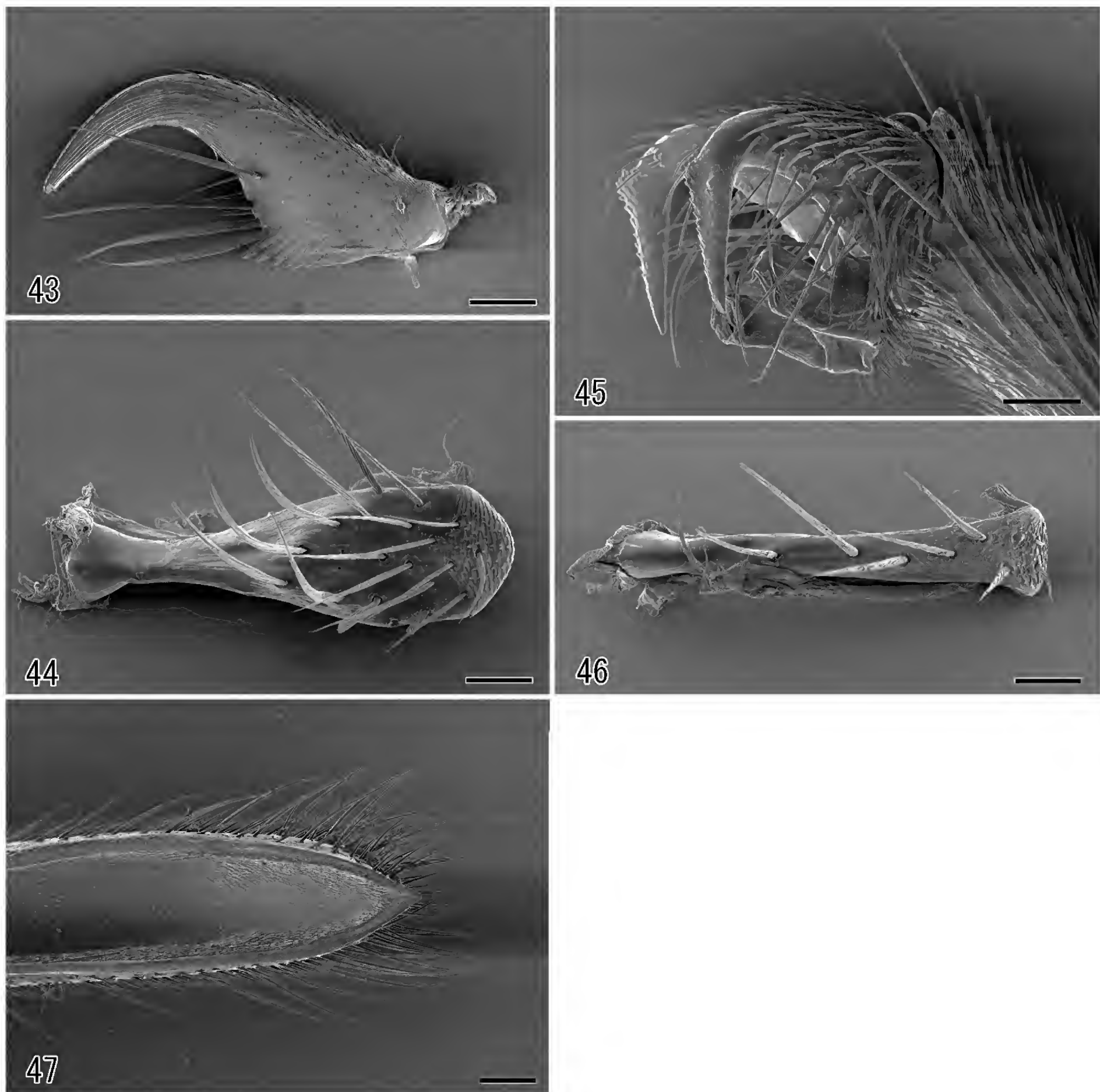
Figures 39–42. *Chlorocryptus purpuratus.* **39.** Apex of the female flagellum; **40.** Sensilla on the apex of the female flagellum; **41.** Ventral (flattened) face of the female flagellum (27th segment); **42.** Ditto, enlarged. Scale lines, 0.01 mm (Figs **39, 40, & 42**); 0.1 mm (Fig. **41**).

Type specimens examined. Holotype of *Cryptaulax coreanus* Szépligeti: ♀, "Korea, Sebul" ["Soeul" in the original description], HNHM (ID 115220). Paralectotype of *Cryptus trirrhogmaniformis* Sonan: ♂, "Shinchiku, Chikurin, ft. 3000" [= Chulin, Hsinchu], 10.ix.1928, J. Sonan, reared from a cocoon of *Monema* sp. on a cherry tree, SEHU.

Other specimens. South Korea. Poseoksa (N36°03.073'/E127°28.688'), Keumsan, Chungcheong-namdo, P. Tripotin, SEHU: 1 ♂, viii.1998; 1 ♀, 21.ix.2001. Seonunsan (N36°27'50"/E126°34'28"), Geochang, Jeollabuku-do, 1 ♂, 5.vi.2004, C. L. Young, SEHU. Suigen [= Suwon], Gyeonggi-do, K. Sato, SEHU: 1 ♂, 1925; 1 ♀, 4 ♂, 1.vi.1928; 1 ♀, 14.vi.1928. Shôyosan, Keikido [= Soyosan, Gyeonggi-do], SEHU: 1 ♀, 15.vi.1941; 2 ♂, 10.ix.1943; 2 ♂, 17.ix.1943. Homyeongsan, Cheongpyeong, 1 ♂, 4.v, SEHU. Godaesan, Gyeonggi-do, 1 ♂, 21.vi.1942, SEHU. **China.** Tetsurei, Manchoukuo, [= Tieling, Liaoning Prov.], 1 ♀, 1 ♂, 11.vi.1938, I. Okada, SEHU. Domonrei, Manchoukuo [= Tumenling, Jiutai, Jilin Prov.], 1 ♀, 1 ♂, 19.viii.1939, H. Kôno, SEHU. Kaigen, Manchoukuo, [= Kaiyuan, Liaoning Prov.], I. Okada, SEHU: 1 ♀, 15.ix.1935; 1 ♀, 1.vi.1938. Ryôsuiji, Dalian, 1 ♀, 23.vi.1929, SEHU. "Nord Pekin", 1 ♂, A. David, 1865, MNHN.

Diagnosis. Punctation on head coarser than *C. purpuratus*. Temple swollen and wide, occupying 0.3–0.4 of length of head in dorsal view (Fig. 15). Face without transverse rugae (Fig. 13). Clypeus usually with pair of weak tubercles on apical margin (Fig. 14). Mandibular teeth blunt (Fig. 17). Female flagellum with white annulus around mid-length and with apical third ventrally weakly flattened but not widened. Epomia not turned toward mesal line of pronotum (Fig. 19). Prepectus without a short vertical carina opposite lower corner of pronotum. Mesoscutum punctate, without rugae, and glabrous area on lateral lobe narrow (Fig. 18). Propodeum without posterior transverse carina. Nervellar index 1.3–1.8 (Figs 26, 27). Postpetiole long, 0.8–1.0 as long as wide in female, 0.7–1.0 in male (Fig. 21). Median longitudinal carina of 1st tergite not raised at all at beginning of postpetiole (Fig. 20). Subgenital plate (Figs 36, 37) with postero-lateral corner more angulated, with posterior margin weakly notched on median convexity, and with white spot at base of its apodeme.

Description. Adult. ♀. Head (Fig. 15) 1.7–1.8 times as wide as long in dorsal view. Temple swollen, occupying 0.3–0.4 of length of head in dorsal view (Fig. 15). POL/OOL=0.6–0.8. Vertex and gena densely with coarse punctures; punctures smaller and shallower on gena than

Figures 43–47. *Chlorocryptus purpuratus.* **43.** Female hind tarsal claw; **44.** Orbicular of female hind tarsus; **45.** Male hind tarsal claw; **46.** Orbicula of male hind tarsus; **47.** Apex of ovipositor sheath. Scale lines, 0.1 mm (Figs **43, 45, & 47**); 0.05 mm (Figs **44 & 46**).

on vertex. Face 1.4–1.5 times as wide as high, distinctly convex medially, punctate-reticulate (Figs 5, 13). Clypeus with pair of weak tubercles on apical margin, punctate-reticulate, punctures larger than on face (Fig. 14). Malar space 0.8–1.0 times as wide as mandible width. Mandible stout, with short and blunt teeth; upper tooth broad, a little longer than lower one (Fig. 17). Antenna with 32–34 flagellomeres. Apical third of flagellum weakly flattened ventrally but not thickened, weakly tapered to apex. First flagellomere 4.9–5.8 times as long as apical width, a little longer than 2nd flagellomere. Fifth flagellomere 2.3–2.5 times as long as apical width.

Epomia ends at midway to upper edge of pronotum without turning toward mesal line of pronotum (Fig. 19). Prepectus without a short vertical carina opposite

lower corner of pronotum. Mesoscutum and scutellum lacunose, without rugae, and with only narrow glabrous stripe on lateral lobe (Fig. 18). Mesopleuron punctate to areolate-rugose on lower part to transversely strigate on upper frontal part. Mesosternum densely punctate. Metapleuron areolate-rugose. Upper division of metapleuron punctulate. Propodeum areolate rugose; only anterior transverse carina present, other carinae absent.

Legs slender. Hind femur 6.0–7.7 times as long as maximum width. Hind tibia 8.5–9.5 times as long as apical width.

Fore wing about 11–14 mm long. Nervellar index 1.3–1.8 (Figs 26, 27).

First metasomal tergite 1.9–2.3 times as long as apical width, with postpetiole 0.7–1.0 times as long as apical
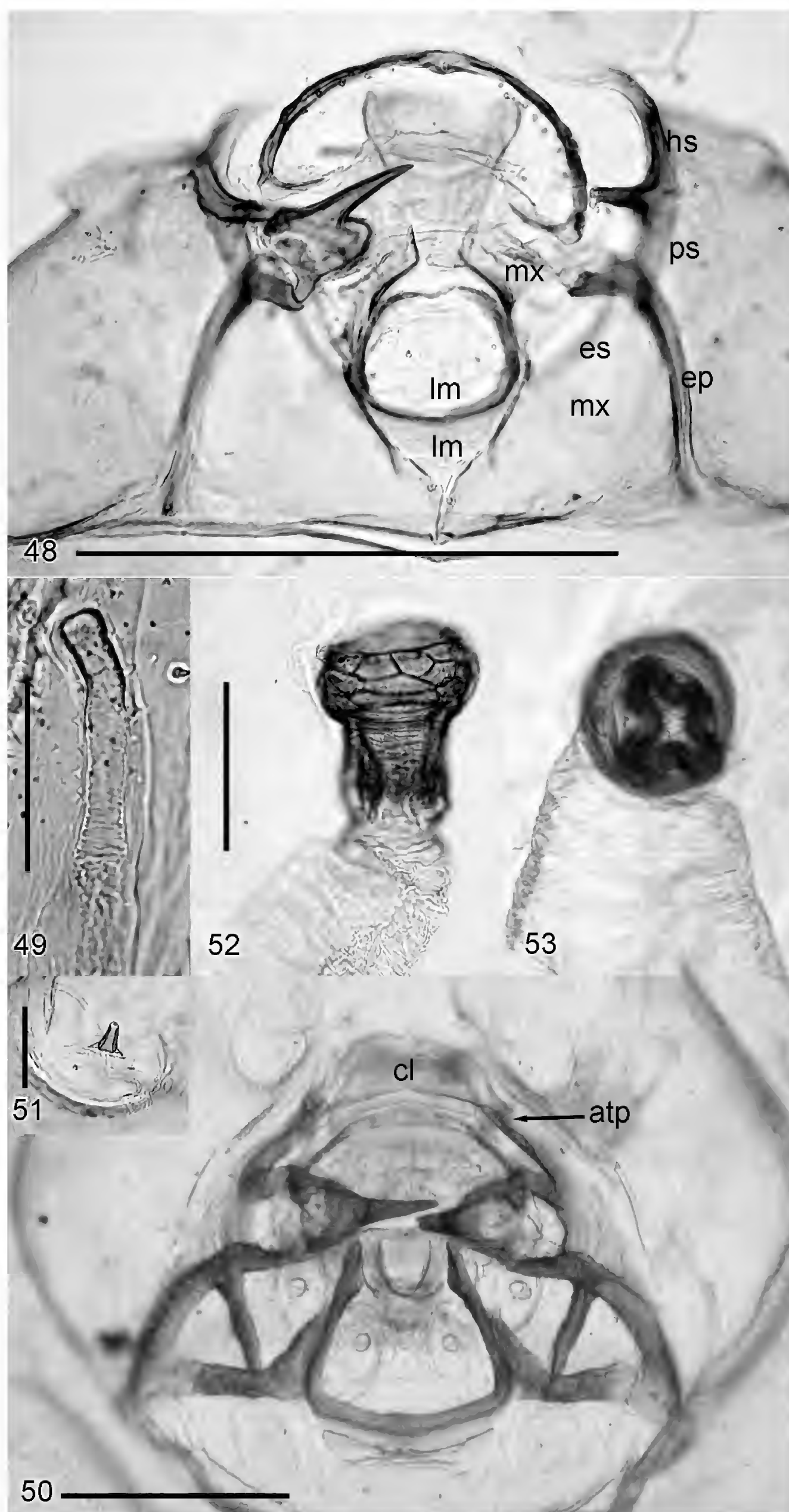
Figures 48–53. Larval morphology of *Chlorocryptus purpuratus*. **48.** Head capsule of 1st instar larva (left mandible is detached); **49.** Spiracle of 1st instar larva; **50.** Head capsule of 5th instar larva, antennae broken off; **51.** Antenna of 5th instar larva; **52 & 53.** Spiracle of 5th instar larva. **Atp** – anterior tentorial pit; **cl** – clypeus; **ep** – epistoma; **es** – epistomal spur; **hs** – hypostoma; **lm** – labrum; **mx** – maxilla; **ps** – pleurostoma. Scale lines, 0.5 mm (Fig. **48**); 0.05 mm (Fig. **49**); 0.5 mm (Fig. **50**); 0.1 mm (Fig. **51**); 0.2 mm (Figs **52 & 53**).
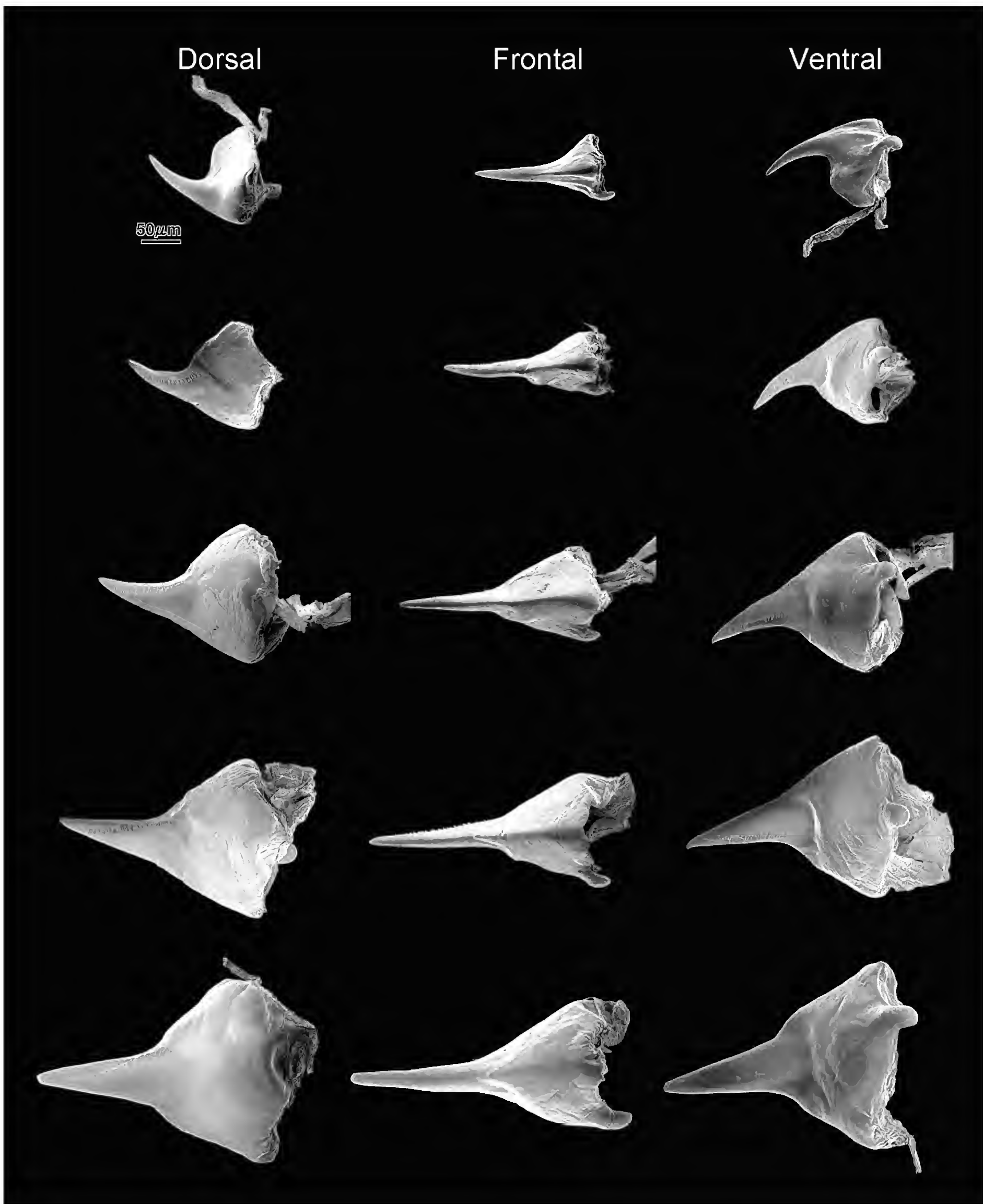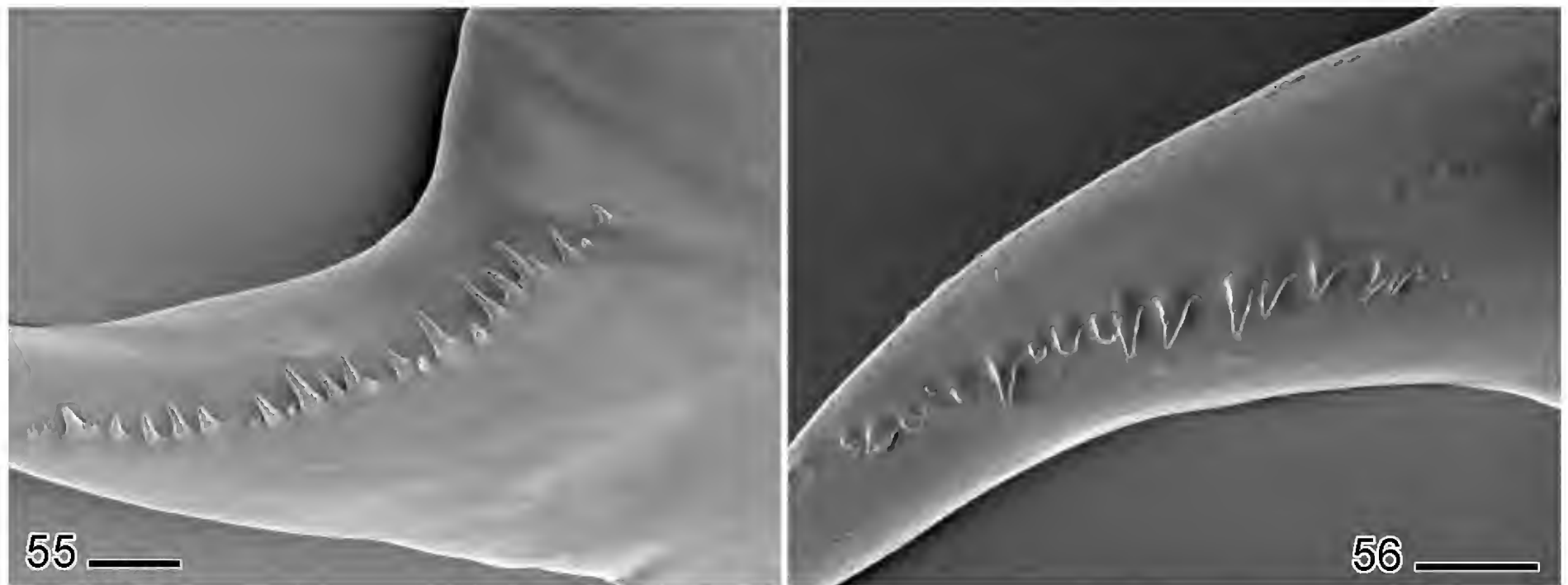
Figure 54. *Chlorocryptus purpuratus*, left mandibles of larva. The mandibular parts isolated from 1st to 5th larval exuviae of the same individual extracted from a host cocoon. From above to bottom, 1st to 5th instars.

width; dorsal face not distinctly raised; median longitudinal carina absent or very weak on its entire length (Figs 20, 21). Ovipositor sheath 0.9–1.0 times as long as hind tibia.

Body with metallic luster in blue, purple or green. Flagellum black with white band on 6th–9th flagellomeres. Fore and middle tibiae and all tarsi are dark brown to black. Ovipositor sheath and ovipositor black. Wings narrowly infumate apically (Fig. 26).

♂. Similar to female except as follows: face 1.0–1.2 times as wide as long; flagellum with 37–39 flagellomeres, with 5 or 6 tyloids which can be on 14th–20th flagellomeres; 1st flagellomere 2.8–3.3 times as long as

Figures 55, 56. Left mandible of 2nd larva of *Chlorocryptus purpuratus*. **55.** Dorsal side; **56.** Ventral side. Scale lines, 0.01 mm.
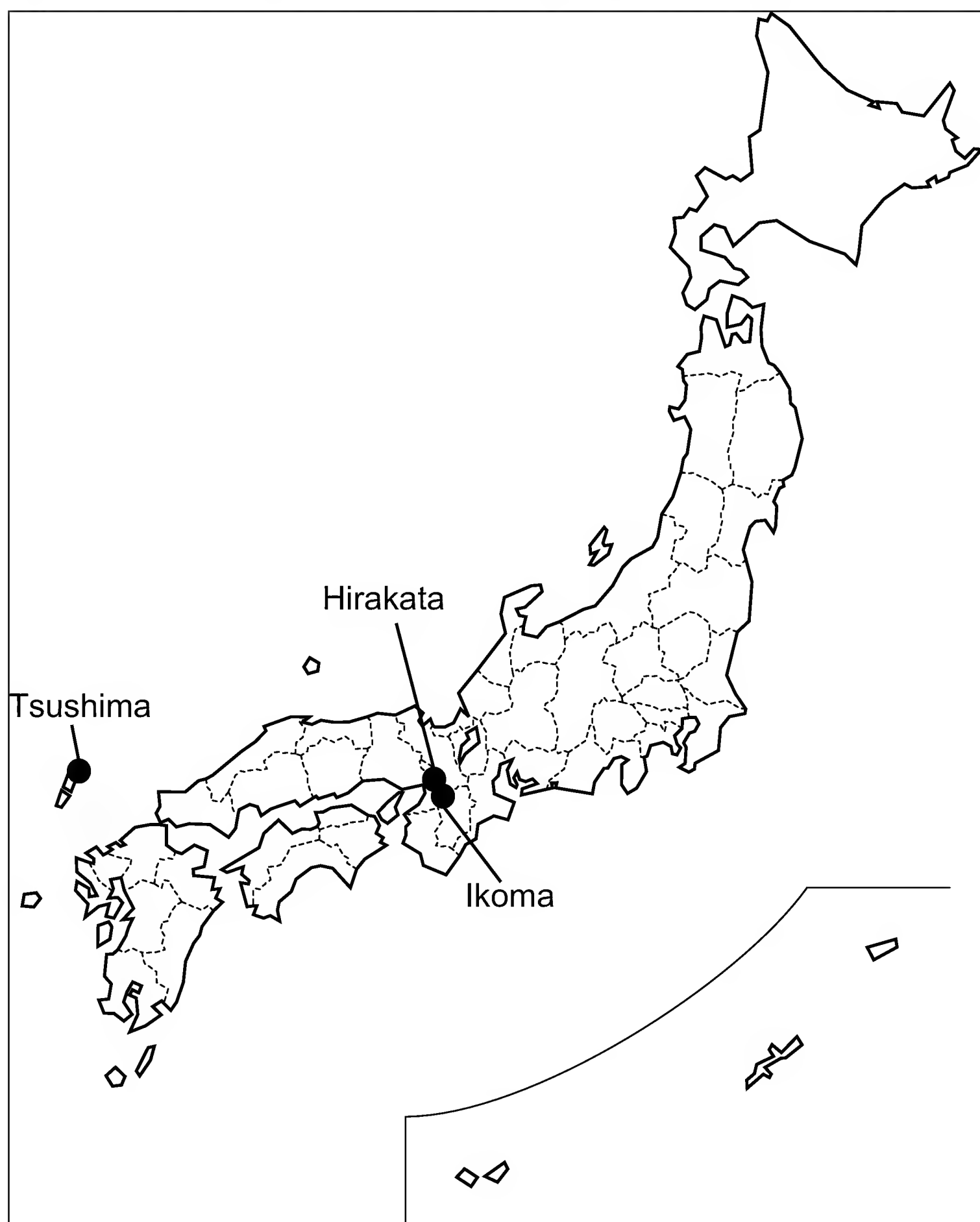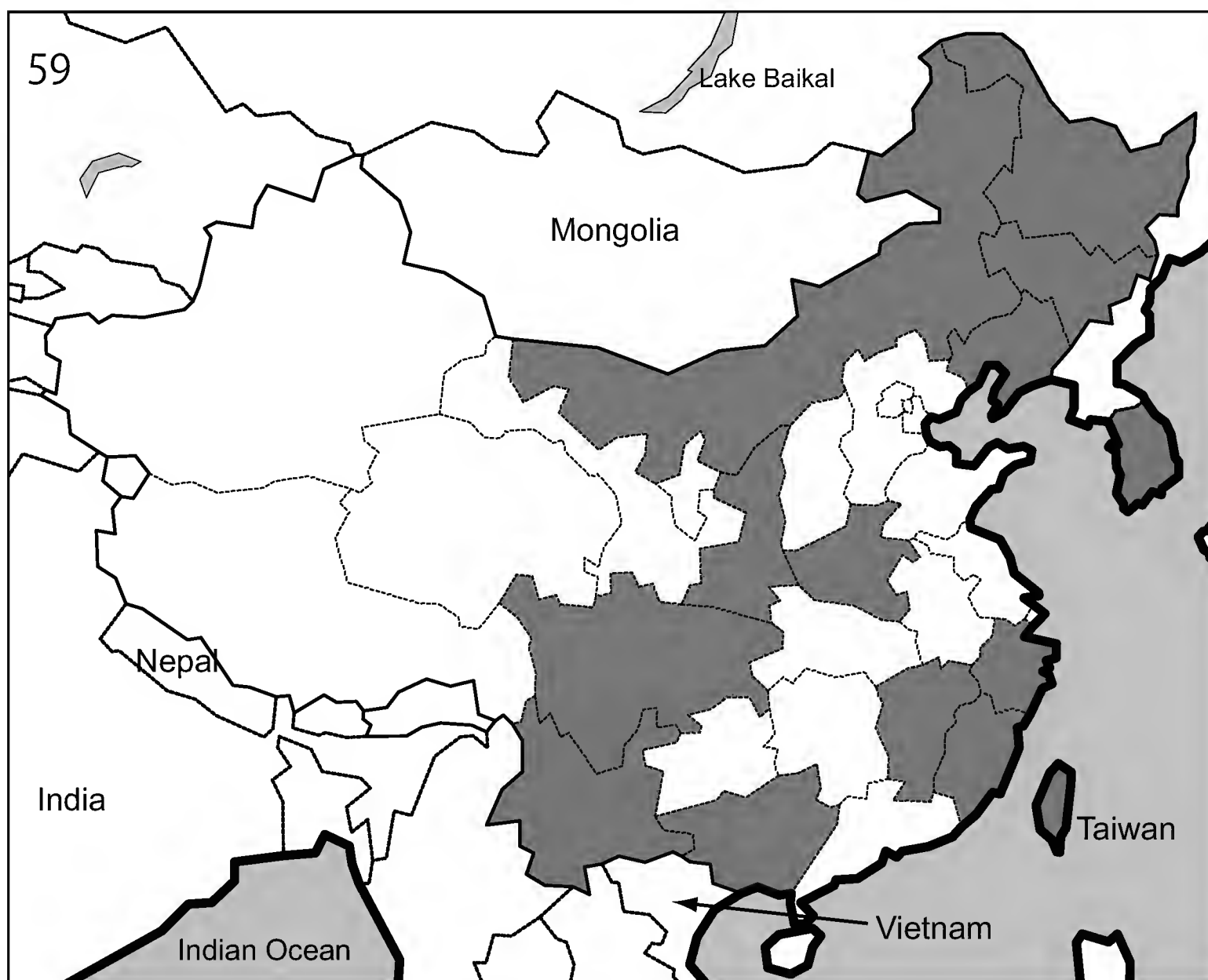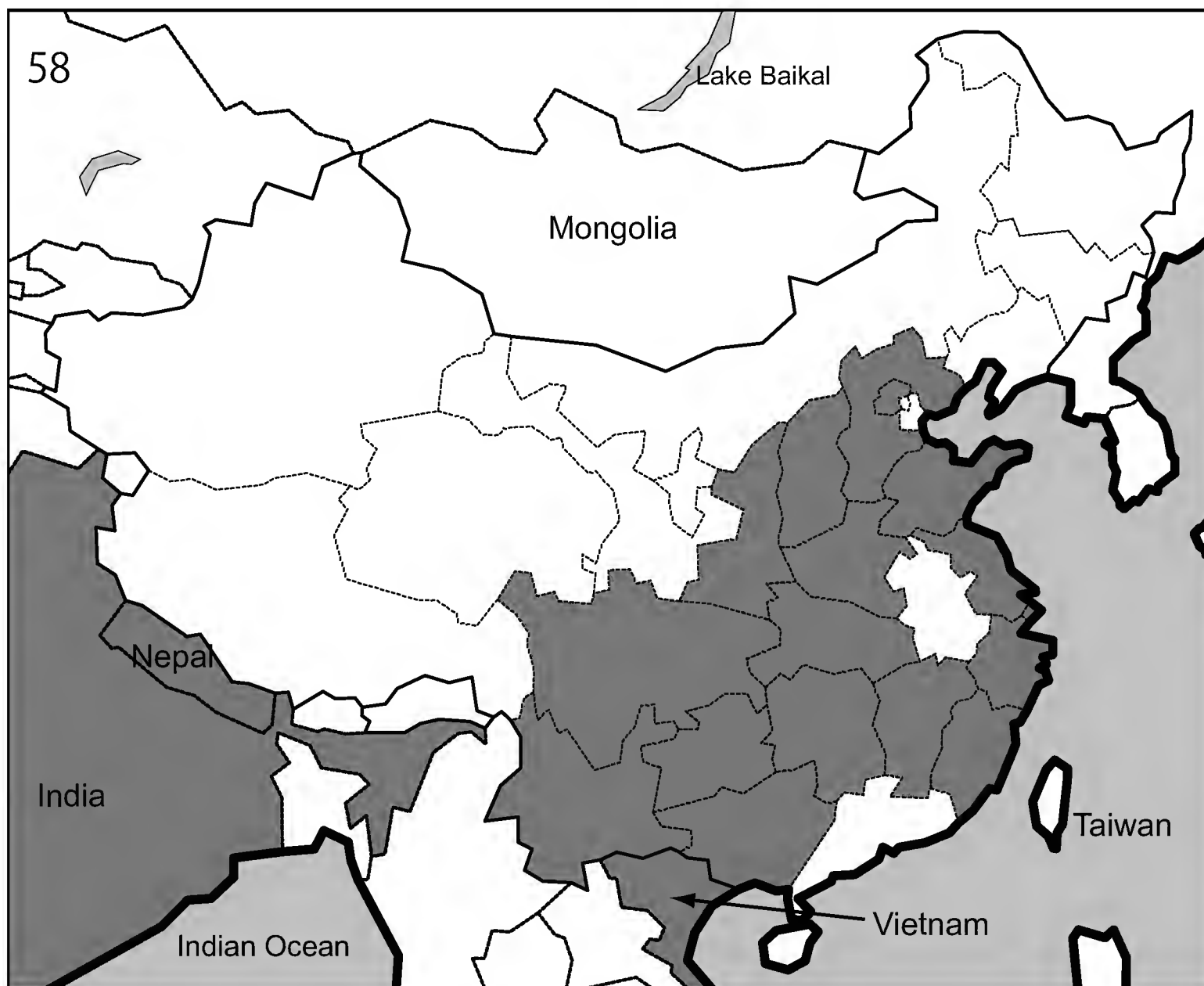

Figure 57. Distribution of *Chlorocryptus purpuratus* in Japan.

Figures 58, 59. Distributions of *Chlorocryptus purpuratus* and *C. coreanus* in China (by province) and in adjacent countries.

apical width; 1st metasomal segment 2.0–2.4 times as long as apical width; hind femur 7.0–8.5 times as long as median depth; hind tibia 9.3–10.0 times as long as apical width; stripe on anterior face of fore femur, fore tibia and dorsal stripe of middle tibia light brown. Subgenital plate with postero-lateral corner more angulated than in *C. purpuratus*, with posterior margin convex, with small concavity on middle of convexity (Figs 36, 37), but one aberrant specimen from Korea without concavity (Fig. 38); usually with white spot near base of apodeme. Wings narrowly infumate in specimens from Korea and North China, but Taiwanese specimens with extensively brown wings (Fig. 27).

Biology. *Monema flavescens* Walker (Uchida 1930b, Sun et al. 1982, Pan 1983, Yin and Zou 1987, Wang et al. 1991, 1993) and *Miresa inornata* Walker (Limacodidae) (Uchida 1930a) have been recorded as hosts.

Distribution. (Fig. 58). Korea (Szépligeti 1916, Uchida 1930a, 1955, Kim 1955). China: Fujian (Wang 2003, Wang and Huang 1993), Guangxi (Niu and Wang 1992), Heilongjiang (Niu and Wang 1992), Henan (Sheng et al. 1999, Sheng and Sun 2009), Jiangxi (Sheng et al. 2013), Jilin (Yin and Zou 1987), Liaoning (Uchida 1942, Sun et al. 1982, Pan 1983), Neimenggu (Niu and Wang 1992), Shaanxi (He and Chen 2006), Sichuan (Wang and Huang 1993), Yunnan (Wang and Li 1987), Zhejiang (He and Wang 1987, He et al. 2001). Taiwan (Sonan 1929, Uchida 1931).

Remarks. Similar to the preceding species, this species shows considerable intraspecific morphological variation. Only the Taiwanese specimens, namely the type series of *Cryptus trirrhogmaniformis*, have the fore wings entirely tinged with brown (Fig. 27) (according to the original description of *C. trirrhogmaniformis*, the lectotype has also brown wings), and all the other specimens examined have the fore wings darkened only apically (Fig. 26). One specimen from Korea (Fig. 38) has a differently shaped subgenital plate, which we considered to be aberrant.

In the description of *Cryptaulax coreanus*, Szépligeti (1916) did not originally designate the holotype nor mentioned the number of specimens he examined. The Szépligeti's collection at HNHM contains only one specimen of the species, which Townes et al. (1961) treated as the holotype fixed by monotypy.

Cryptus trirrhogmaniformis Sonan was described based on two male syntypes. One was deposited at TARI and the other was probably donated to Uchida at that time and now is located at SEHU. The TARI specimen was treated as "type" by Townes et al. (1961), which is considered a lectotype designation as it is evident that the authors cited the specimen to serve as the name-bearing type (ICZN 74.5).

Key to species

1 Temple swollen and wide, occupying 0.3–0.4 of length of head in dorsal view (Fig. 15). Face without transverse rugae (Fig. 13). Female flagellum with white annulus around mid-length and with apical third ventrally weakly flattened but not widened. Mesoscutum punctate, without rugae, and glabrous area on lateral lobe narrow (Fig. 18). Propodeum without posterior transverse carina .... *C. coreanus* (Szépligeti).

– Temple flat and narrower, occupying 0.2–0.3 of length of head in dorsal view (Fig. 4). Face with transverse rugae in addition to punctures (Fig. 2). Female flagellum without white annulus and with apical third of flagellum ventrally distinctly flattened and widened (Fig. 7). Mesoscutum with longitudinal rugae in addition to punctures, and with moderate-sized glabrous area on lateral lobe (Fig. 8). Propodeum with posterior transverse carina .... *C. purpuratus* (Smith).

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Contributions to the taxonomy of the ant genus *Echinopla* Smith, 1857 (Hymenoptera, Formicidae)

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Abstract

Sixteen species of *Echinopla* Smith, 1857 distributed west of Weber's Line are treated, including eight species described as new: *E. madli* **sp. n.** from southern Thailand and Borneo, *E. wardi* **sp. n.** from West Malaysia, *E. fisheri* **sp. n.**, *E. circulus* **sp. n.**, *E. mezgeri* **sp. n.**, and *E. subtilis* **sp. n.** from Borneo, *E. brevisetosa* **sp. n.** and *E. angustata* **sp. n.** from the Philippines. Lectotypes are designated for *E. lineata* Mayr, 1862 and *E. senilis* Mayr, 1862, **stat. rev.**, and differences between the two species are pointed out. New records are presented for *E. melanarctos* Smith, 1857 (West Malaysia, Sumatra, Borneo), *E. pallipes* Smith, 1857 (Borneo), *E. tritschleri* Forel, 1901 (West Malaysia, Borneo), *E. cherapunjiensis* Bharti & Gul, 2012 (Laos, West Malaysia), *E. lineata* Mayr, 1862 (Singapore, Borneo), *E.* cf. *pseudostriata* Donisthorpe, 1943 (Philippines), and *E.* cf. *vermiculata* Emery, 1898 (Philippines).

Introduction

Echinopla Smith, 1857 is among the small genera of camponotine ants. The 24 described species (Bolton 2015, plus *E. senilis* Mayr, 1862, stat.rev.) are distinguished by bizarre body structures and distributed from eastern India to Australia. Half of them (twelve species) live exclusively east of Weber's Line (Moluccas, New Guinea, Australia) and eleven species are restricted to the area west of Weber's Line (south-eastern Asia including north-eastern India and southern China, Nicobar Islands, Greater Sunda Islands, Philippines, and Sulawesi). A single polymorphic species, *Echinopla striata* Smith, 1857, is recorded from both sides in several subspecies, but it is possibly an assemblage of several similar species. Most species were described in

the 19ᵗʰ and the first half of the 20ᵗʰ century by short verbal notes, but one species was described recently (Bharti and Gul 2012). This poor taxonomic treatment is probably caused by the scarcity of individuals. The species of *Echinopla* typically inhabit the canopy of tropical forests. For this reason records are scarce and often based on single or few individuals caught by chance. Recently, some material was successfully obtained by tree fogging. In contrast to the relatively low species number, many structural characteristics are very variable among the species of *Echinopla* and make identification simple compared to the related genera *Camponotus* and *Polyrhachis*, each containing many sibling or cryptic species. The recent development of internet websites that grant access to large numbers of pictures of types and non-type specimens (e.g., Antbase 2015,

Antweb 2015, Discover Life 2015) makes the recognition of the described taxa more reliable than in the past.

This study aims to add knowledge of sixteen species (including eight new species) from west of Weber's Line, chiefly from the Asian mainland, from Borneo, and from the Philippine Islands. The taxonomy of *Echinopla striata* sensu lato is preliminarily excluded, because the treatment of this species (or species complex) should be based on larger samples to evaluate its geographic variation. In addition, taxonomic problems in two closely related species, *E. pseudostriata* Donisthorpe, 1943 (Philippines) and *E. vermiculata* Emery, 1898, are addressed.

Methods

Specimens were dry mounted on card squares or triangles. Examination of specimens was carried out with binocular microscopes; measurements were taken at magnifications up to 240×. Stacked digital images were taken with a Leica DFC camera attached to a Leica MZ16 binocular microscope with the help of Leica Application Suite V3, stacked with ZereneStacker 64-bit, and processed with Adobe Photoshop 7.0.

Acronyms of collections

CAS   California Academy of Sciences, San Francisco, U.S.A.
MCB   D. Mezger Collection, Balingen, Germany
NHMW   Natural History Museum Vienna, Austria
NMM   National Museum of the Philippines, Manila, the Philippines
UKL   University of Koblenz-Landau (Campus Landau), Germany
WCD   P.S. Ward Collection, Davis, California, U.S.A.
SCV   D.M. Sorger Collection, Vienna, Austria
ZCV   H. Zettel Collection, Vienna, Austria

Measurements (in millimetres) and indices

TL   Total length. Length of entire specimen measured in dorsal view with head stretched out, from anterior margin of mandible to apex of abdomen, or the added lengths of head (including mandibles), alitrunk, petiole, and gaster in specimens mounted otherwise.
HW_1 Head width. Maximum width of head in full-face view including eyes.
HW_2 Head width without eyes. Maximum width of head in full-face view excluding eyes.
HL   Head length. Maximum length of head in full-face view, excluding mandibles, measured from anterior-most point of clypeus to posterior-most point of head vertex, parallel to midline, including cuticular protrusions if present.
EL   Eye length. Maximum diameter of compound eye, measured in lateral view.

SL   Scape length. Maximum length of antennal scape in dorsal view excluding basal neck and condyle.
SW   Scape width. Maximum width of antennal scape, measured dorsally, usually within distal third of scape.
HaL   Hair length. Length of the longest standing hair on scape, measured from apex to base.
PML   Promesonotal length. Length of promesonotum, measured along midline dorsally from anterior-most point (excluding collar) to mesometanotal suture.
PMW   Promesonotal width. Maximum width of promesonotum measured dorsally, including spines or tubercles if present.
PpL   Propodeal length. Length of propodeum, measured dorsomedially from mesometanotal suture to posterior-most point.
PpW   Propodeal width. Maximum width of propodeum measured dorsally.
PH   Petiole height. Maximum height of the petiole in lateral view, measured from ventral-most point of petiolar sternum to dorsal apex, including spines or tubercles if present.
PL   Petiole length. Maximum length of petiole in lateral view, measured from inflexion point of anterior constriction to posterior margin, perpendicular to axis of maximum height.
PW   Petiole width. Maximum width of petiole in dorsal view, including spines or tubercles if present.
GL   Gastral length. Maximum length of first gastral tergite measured dorsally from anterior-most point of first gastral segment to its posterior-most point (further tergites not included if protruding).
GW   Gastral width. Maximum width of first gastral tergite measured dorsally, perpendicular to midline.
CI   Cephalic index. $HW_1 / HL \times 100$.
SI   Scape index. $SL / HW_1 \times 100$.
MI   Mesosoma index. $(PML + PpL) / PMW \times 100$.

Treatment of species

The species are ordered by similarity according to the following scheme:

Five new species that have a polyporous surface, i.e. multiple closely set pores in the integument (see Fig. 1).

Four described and one new species having "pedestals" on the mesonotum, i.e. socket-shaped protuberances of the integument bearing a long apical seta, surrounded by a subapical ring of short, horizontally projecting hairs (see Figs 22 and 23; also see Gnatzy and Maschwitz 2006 for detailed description).

Two new species with finely punctured gaster tergite 1, i.e. the dorsal gastral integument is matt with subtle sculpture, without pores, protuberances or rugae (see Figs 29 and 33).

Notes on four described species with predominantly striate surface structure, i.e. the integument bears a sculpture of longitudinal, often parallel lines (see Fig. 41).

Echinopla madli sp. n.

http://zoobank.org/938C50EB-DDD4-48C5-B744-1138ED2353ED
Figs 1–4

Type material. Holotype (worker, NHMW) from Thailand, Satun Province, Thale Ban National Park, 10–16. III.1993, leg. Michael Madl. Paratype (worker, CAS) from Borneo, Sabah, Danum Valley, Field Centre, 525 m a.s.l., 4.963056°N; 117.802806°E, 16–26.VIII.2010, rainforest, Ant Course 2010, unknown collector.

Non-type material. 3 workers (UKL, NHMW) from Borneo, Sabah, Poring Spring, lower montane mixed dipterocarp forest, > 650 m, *Aporusa* sp., fogging, 9–21. II.1993, leg. A. Floren (A50/F4, A51/F5).

Diagnosis (worker). Predominantly black, very small, stout species, TL = 3.9–4.6 mm. Surface polyporous, dorsal margins of mesosoma with sharp tubercles. Head wider than long (CI = 104–115). Mesosoma roughly one fourth longer than pronotal width (MI 120–131), with sharp and deep mesometanotal suture. Pronotum hardly wider than head, if eyes excluded. Propodeum shorter than promesonotum. Petiole dentate, with 1–2 sharp teeth and 0–2 smaller denticles laterally below lateral spine. Gaster tergite 1 with relatively small pores and wide, strongly shiny interspaces; on disk subcumbent pilosity very sparse. Standing setae on dorsal surface of trunk, on legs and scape relatively short. Setae on tibia abundant, surpassing base of distally following setae.

Description. Measurements of holotype worker: TL 4.3; HW_1 1.17; HW_2 1.10; HL 1.07; EL 0.23; SL 0.91; SW 0.12; HaL 0.15; PML 0.76; PMW 1.11; PpL 0.59; PpW 1.04; PH 0.45; PL 0.38; PW 1.03; GL 1.24; GW 1.22. Indices: CI 110; SI 78; MI 122.

Measurements of paratype worker: TL 3.9; HW_1 1.15; HW_2 1.07; HL 1.00; EL 0.22; SL 0.89; SW 0.12; HaL 0.18; PML 0.72; PMW 1.09; PpL 0.59; PpW 0.98; PH 0.45; PL 0.38; PW 0.96; GL 1.17; GW 1.15. Indices: CI 115; SI 77; MI 120.

Measurements of non-type workers: TL 4.4–4.6; HW_1 1.11–1.20; HW_2 1.00–1.11; HL 1.07–1.11; EL 0.22–0.25; SL 0.93–0.96; SW 0.13–0.14; HaL 0.11–0.13; PML 0.74–0.78; PMW 1.04–1.12; PpL 0.61–0.67; PpW 0.96–1.04; PH 0.46 (two measured); PL 0.36–0.38; PW 0.97–1.04; GL 1.26–1.37; GW 1.20–1.30. Indices: CI 104–108; SI 80–85; MI 129–131.

Structures: Head wider than long, subtrapezoidal, with slightly convex sides; dorsally and laterally polyporous, with closely set pores, posterolaterally with a few very small tubercles, matt; ventral surface smooth and shiny. Compound eye relatively small, moderately protruding, positioned slightly behind mid-length of head. Frons of type specimens with prominent median carina; frontal lobes chiefly horizontally oriented, completely covering antennal fossae in dorsal aspect, maximum distance of margins at mid-length, slightly greater than half of HW_2. Clypeus of type specimens with prominent median carina, anterior margin weakly convex. Mandibles striate, masti-

catory margin with five teeth. Antennal scape moderately long, weakly s-curved, steadily widened from base to apex; antennomeres 8–10 slightly wider than long.

Mesosoma stout, length only 1.2 times pronotum width in type specimens; propodeum shorter than promesonotum. Surface polyporous, with closely set pores, dorsal margins with sharp tubercles. Pronotum with strongly developed angles, about as wide as head excluding eyes. Promesonotal suture weak, indicated by a convex row of deeper pits. Mesometanotal suture sharp, narrow and deep. In dorsal aspect mesosoma with waist-like incision in front of propodeum. Legs moderately long; femora not much widened.

Petiole wide and stout, subtriangular in lateral, strongly transverse in dorsal aspect; surface structure as on mesosoma; sharp dorsal crest bearing four sharp teeth medially and another two pairs of small denticles laterally; lateral tooth strongly developed; below lateral tooth with two sharp teeth and 0–2 (asymmetrical) small denticles. Gaster tergite 1 as wide as long, strongly convex, and completely covering the following tergites; hind margin moderately convex, finely serrate; surface polyporous, interspaces smooth and shiny; distances of pores mostly slightly larger than their diameters.

Pilosity: Head (except ventral surface), mesosoma, and petiole with dense, appressed white pilosity and moderately long white standing setae. Gaster tergite 1 with very sparse appressed pilosity on disc, but relatively dense at sides; standing setae anteriorly much longer than posteriorly. White standing setae on scape about as long as the setae on head. Legs with fine appressed pilosity. Femora with some long standing setae on flexor side. Pilosity on tibiae and first tarsomeres oblique, relatively long and dense.

Colour: Trunk black, without metallic shimmer, appearing grey by whitish pilosity. Antenna with black scape and base of funiculus, distal part testaceous. Mandible basally black, distally testaceous; other mouthparts yellowish. Legs of type specimens testaceous, but forecoxa black, apices of femora, tibiae and first tarsomeres infuscated. Legs of non-type specimens predominantly blackish.

Comparative notes. *Echinopla madli* sp. n. and the following four new species belong to a peculiar species group that is characterized by small body size (except *E. fisheri* sp. n.), black colour (lack of metallic lustre), and polyporous surface structures that resemble the pores of coral rocks (see Stitz 1938). Other species groups can be defined by different surface structures, at least on head and mesonotum, either fine puncturation, or striations consisting of sharp rugae, or high, truncate tubercles ("pedestals") that give the specimens a spiny appearance. A peculiar character of *E. madli* sp. n. is gaster tergite 1 that is hardly longer than wide and has a shiny, weakly pilose and sparsely pitted disc. These characters distinguish it immediately from closely related species in the region (*E. wardi* sp. n., *E. brevisetosa* sp. n., and *E. angustata* sp. n.). A similarly structured tergite 1 is
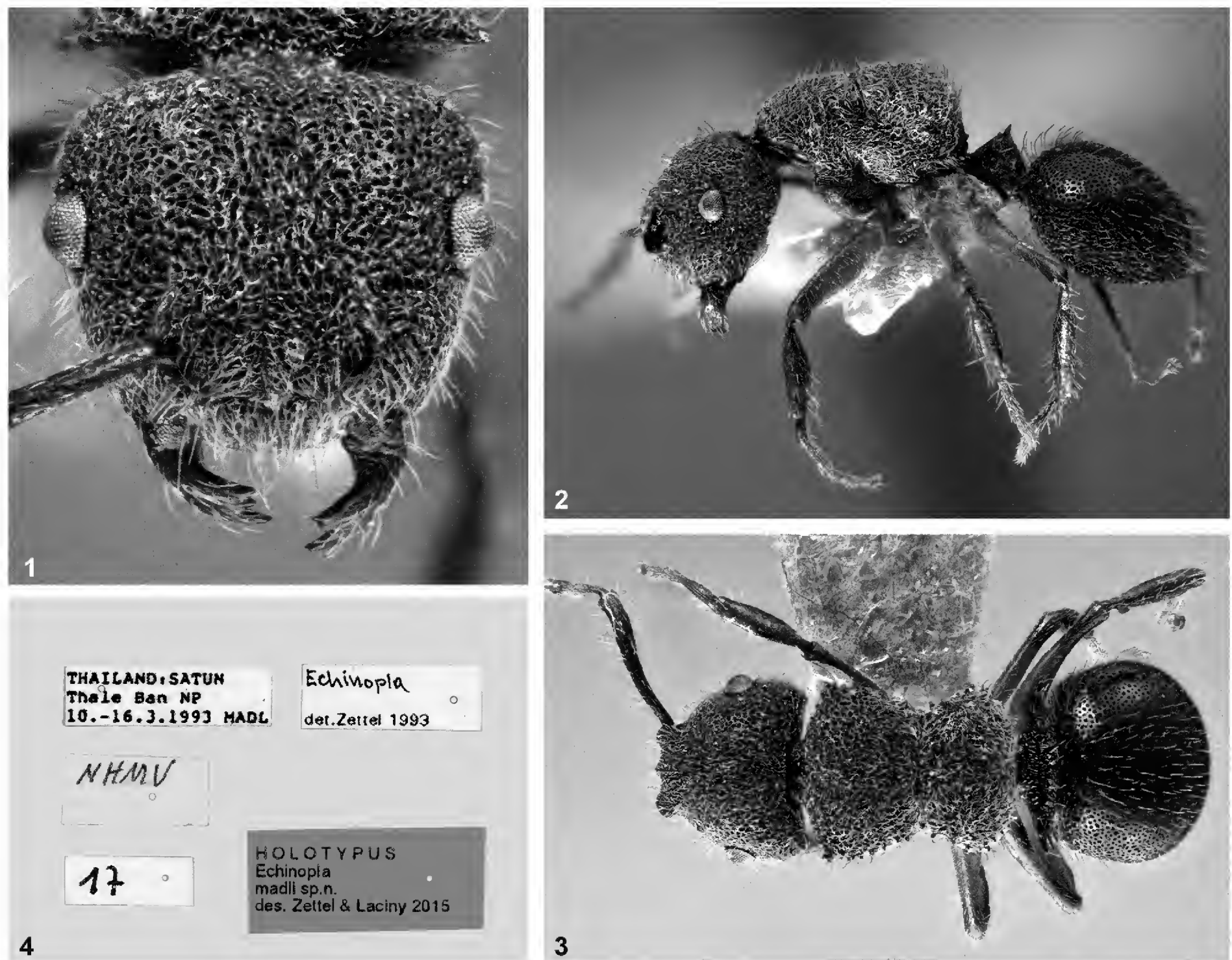
Figures 1–4. *Echinopla madli* sp. n., holotype: (**1**) Head, full face view. (**2**) Habitus, lateral view. (**3**) Habitus, dorsal view. (**4**) Labels.

found in *E. dubitata* Smith, 1862 from Sulawesi, but this is a slender species with black tarsi, weakly developed appressed pilosity and long black standing setae. Images of *E. dubitata* are presented by Antweb (2015).

We studied five workers of *E. madli* sp. n. from three localities and noted a high variability. Whereas the paratype from Danum Valley (Sabah) largely agrees with the holotype from southern Thailand, further Sabah specimens from Poring Spring differ by largely black legs (except one callow worker), reduced median carinae on frons and clypeus, and some morphometric data (e.g., higher SI, lower CI). The examination of more material would be necessary to clarify the status of this population.

Etymology. Dedicated to our colleague Michael Madl, Frauenkirchen, Austria, who collected the holotype specimen.

Echinopla wardi sp. n.

http://zoobank.org/044DDB4D-67C1-4A69-8FF8-677588D569F9

Figs 5–8

Type material. Holotype (worker, NHMW) from Malaysia, Johor, 13 km NE Kota Tinggi, 1°49'N; 103°50'E,

50 m a.s.l., 22.XI.1988, on low vegetation in second-growth rain forest, leg. Philip S. Ward (PSW09591-12; ANTWEB CASENT 0280337). Paratype (worker, ZCW) from West Malaysia, Pahang, 70 km SW Kuala Rompin, Endau Rompin National Park, Gunung Beremban, 600 m a.s.l., 13.IV.–3.V.2010, leg. Petr Čechovský.

Diagnosis (worker). Predominantly black, small species, TL = 3.8–4.3. Surface polyporous, dorsal margins of mesosoma with sharp tubercles. Head wider than long (CI = 110). Mesosoma roughly 1.25 times as long as pronotal width (MI 122–126), with sharp and deep incision in front of propodeum. Pronotal width equal to head width, if eyes excluded. Propodeum shorter than promesonotum. Petiole dentate, with three sharp teeth laterally below lateral spine. Gaster tergite 1 about one fourth longer than wide, anteriorly with relatively large pores and shiny interspaces; disk with dense subcumbent pilosity. Setae on dorsal surface, legs and scape relatively short. Setae on tibia reaching or surpassing base of distally following setae.

Description. Measurements of holotype worker: TL 3.8; HW_1 1.11; HW_2 1.02; HL 1.01; EL 0.23; SL 0.96; SW 0.12; HaL 0.16; PML 0.72; PMW 1.02; PpL 0.57; PpW 0.91; PH 0.45; PL 0.40; PW 0.91; GL 1.27; GW 1.11. Indices: CI 110; SI 80; MI 126.
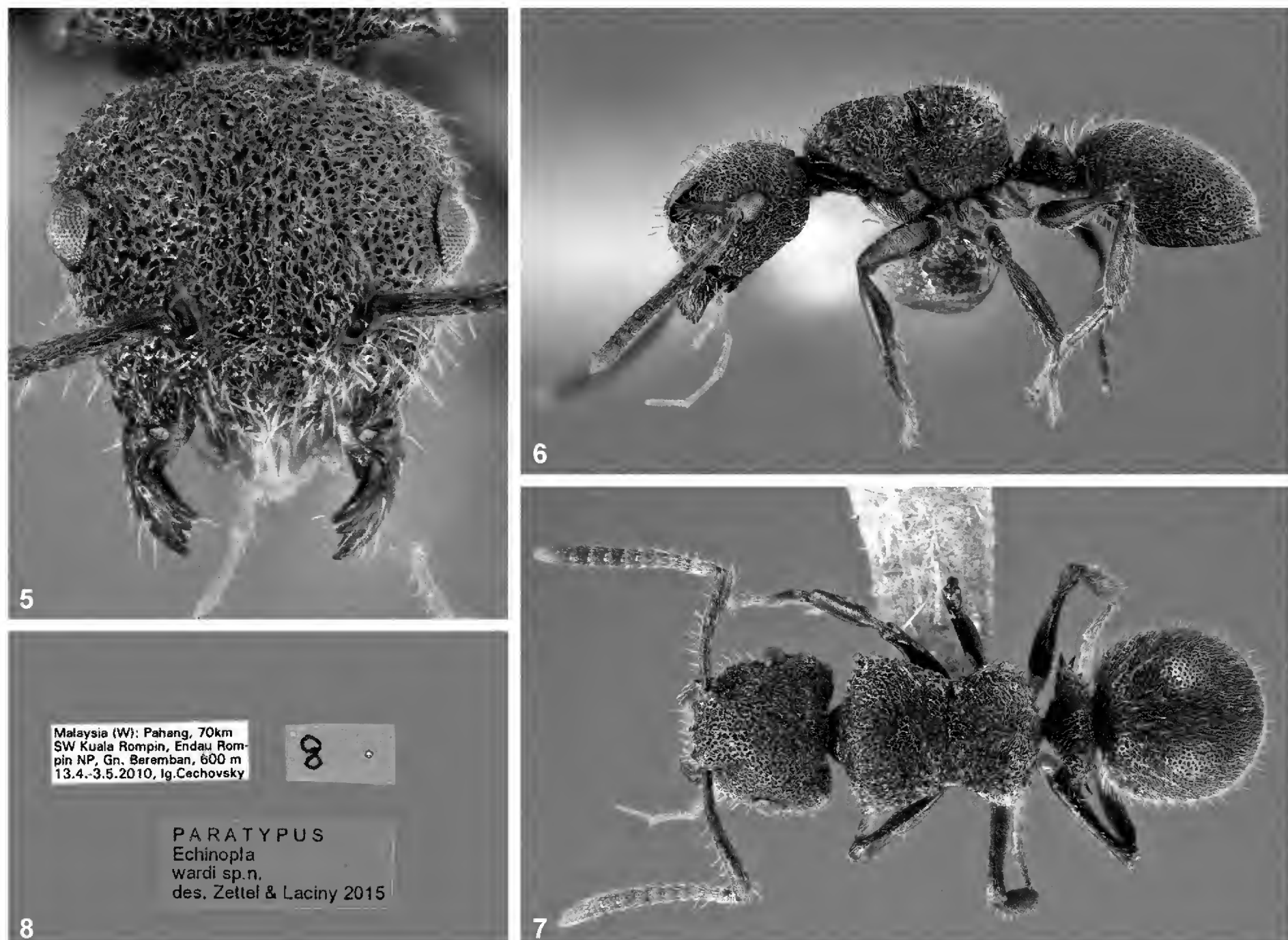
Figures 5–8. *Echinopla wardi* sp. n., paratype: (**5**) Head, full face view. (**6**) Habitus, lateral view. (**7**) Habitus, dorsal view. (**8**) Labels.

Measurements of paratype worker: TL 4.3; HW_1 1.17; HW_2 1.11; HL 1.07; EL 0.23; SL 0.96; SW 0.12; HaL 0.14; PML 0.76; PMW 1.11; PpL 0.59; PpW 1.00; PH 0.51; PL 0.38; PW 1.03; GL 1.37; GW 1.24. Indices: CI 110; SI 81; MI 122.

Structures: Head wider than long, subtrapezoidal, with slightly convex sides; dorsally and laterally polyporous, with closely set pores, posterolaterally with a few minute tubercles, matt; ventral surface smooth and shiny. Compound eye relatively small, moderately protruding, positioned slightly behind mid-length of head. Frons with prominent median carina; frontal lobes chiefly horizontally oriented, largely covering antennal fossae in dorsal aspect, maximum distance of margins slightly behind mid-length, as great as half of HW_2. Clypeus with distinct median carina, anterior margin almost straight. Mandibles striate, masticatory margin with five teeth. Antennal scape moderately long, weakly s-curved, steadily widened from base to apex; antennomeres 8–10 approximately as wide as long.

Mesosoma stout, length ca. 1.25 times pronotum width; propodeum shorter than promesonotum. Surface polyporous, with closely set pores, dorsal margins with sharp tubercles. Pronotum with distinct lateral angles, as wide as head excluding eyes. Promesonotal suture weak, indicated by a convex row of deeper pits. Mesometanotal

suture sharp and deep, medially narrow, laterally widened. In dorsal aspect mesosoma with waist-like incision in front of propodeum. Legs moderately long; femora not much widened.

Petiole wide and stout, subtriangular in lateral view, strongly transverse in dorsal aspect; surface structure as on mesosoma; sharp dorsal crest bearing four sharp teeth medially and one pair of small denticles laterally; lateral tooth strongly developed; below lateral tooth with one long and two short, sharp teeth. Gaster tergite 1 clearly longer than wide, completely covering the following tergites; hind margin moderately convex, finely serrate; surface polyporous, interspaces smooth and shiny; distances of pores mostly smaller than their diameters.

Pilosity: Entire trunk dorsally and laterally with dense, appressed white pilosity and moderately long white standing setae; only the standing setae on anterior part of gaster tergite 1 distinctly longer. White standing setae on scape about as long as the setae on head. Legs with fine appressed pilosity. Femora with some long standing setae on flexor side. Tibiae and first tarsomeres of middle and hind leg with rows of oblique white setae; their length as long as their distance.

Colour: Trunk black, without metallic shimmer, appearing grey by whitish pilosity. Antenna with black scape; funiculus basally black, becoming gradually paler

towards testaceous apex. Mandible basally black, distally brown; other mouthparts yellowish. Legs chiefly blackish, but coxae of middle and hind legs brown, all trochanters dark testaceous, and tarsi distally reddish testaceous.

Comparative notes. *Echinopla wardi* sp. n. is similar to *E. australis* Forel, 1901 from Australia, but this species has yellow legs and funiculus, relatively long pilosity, and pronotal width distinctly smaller than head width. Images of *E. australis* are presented by Antweb (2015). According to the original description (André 1892), *E. rugosa* André, 1892 from Borneo has similar structures of mesosoma and petiole, but differs by uniformly black colour with bronze shimmer and slightly smaller size. Unfortunately the holotype depository of this enigmatic species is unknown and no further specimen has become known. See also notes for *E. madli* sp. n. and *E. brevisetosa* sp. n.

Figures 5–8 are taken from the paratype whereas the holotype is illustrated by Antweb (2015) with specimen number CASENT 0280337.

Etymology. Dedicated to Phil S. Ward (University of California) who collected the holotype and kindly donated it to NHMW.

Echinopla brevisetosa sp. n.

http://zoobank.org/1AE042DE-C090-4D0F-973A-54112FA1C4E8
Figs 9–12

Type material. Holotype (worker, NMM) and paratype (worker, ZCW) from the Philippines, Mindanao Island, Bukidnon Province, Malaybalay City, Kaamulan site, 650 m a.s.l., 15–20.III.2000, leg. H. Zettel.

Diagnosis (worker). Predominantly black, small, stout species, TL = 4.0. Surface polyporous, dorsal margins of mesosoma with sharp tubercles. Head wider than long (CI = 106–109). Mesosoma roughly 1.3 times as long as pronotal width, with sharp and deep incision in front of propodeum. Pronotal width subequal to head width, if eyes excluded. Propodeum slightly shorter than promesonotum. Petiole dentate, with one long tooth and two small denticles laterally below lateral tooth. Gaster tergite 1 anteriorly with relatively fine pores and very narrow interspaces. Setae on dorsal surface, legs and scape relatively short. Short setae on tibia not reaching base of distally following setae.

Description. Measurements of holotype worker: TL 4.0; HW_1 1.09; HW_2 0.99; HL 1.02; EL 0.23; SL 0.87; SW 0.11; HaL 0.08; PML 0.67; PMW 0.97; PpL 0.61; PpW 0.88; PH 0.50; PL 0.37; PW 0.98; GL 1.20; GW 1.17. Indices: CI 106; SI 80; MI 133.

Measurements of paratype worker: TL 3.9; HW_1 1.11; HW_2 0.98; HL 1.02; EL 0.22; SL 0.91; SW 0.12; HaL 0.09; PML 0.65; PMW 1.02; PpL 0.63; PpW 0.91; PH 0.46; PL 0.36; PW 0.98; GL 1.22; GW 1.20. Indices: CI 109; SI 82; MI 126.

Structures: Head wider than long, subtrapezoidal, with slightly convex sides; dorsally and laterally polyporous, with closely set pores, posterolaterally with a few minute tubercles, matt; ventral surface smooth and shiny. Compound eye relatively small, moderately protruding, positioned almost at mid-length of head (very slightly behind). Frons with prominent median carina; frontal lobes chiefly horizontally oriented, in dorsal aspect covering antennal fossae only in part, maximum distance of margins clearly behind mid-length, slightly greater than half of HW_2. Clypeus with distinct median carina, anterior margin almost straight. Mandibles striate, masticatory margin with five teeth. Antennal scape moderately long, almost straight, steadily widened from base to apex; antennomeres 8–10 approximately as wide as long.

Mesosoma stout, length roughly 1.3 times pronotum width; propodeum slightly shorter than promesonotum. Surface polyporous, with closely set pores, dorsal margins with sharp tubercles. Pronotum with distinct lateral angles, approximately as wide as head excluding eyes. Promesonotal suture very weak, indicated by a few deeper pits. Mesometanotal suture sharp, narrow and deep. In dorsal aspect mesosoma with waist-like incision in front of propodeum. Legs moderately long; femora not much widened.

Petiole wide and stout, subtriangular in lateral, strongly transverse in dorsal aspect; surface structure as on mesosoma; sharp dorsal crest bearing six sharp teeth of slightly varying length; lateral tooth strongly developed; below lateral tooth with one long tooth and two small denticles. Gaster tergite 1 slightly longer than wide, completely covering the following tergites; hind margin convex, finely serrate; surface polyporous, interspaces smooth and shiny; distances of pores everywhere clearly smaller than their diameters.

Pilosity: Entire trunk dorsally and laterally with dense, appressed white pilosity and moderately long white standing setae; standing setae on anterior part of gaster tergite 1 slightly longer. White standing setae on scape about as long as the setae on head. Legs with fine appressed pilosity. Femora with only 0–3 standing setae on flexor side. Tibiae and first tarsomeres of middle and hind leg with relatively few oblique white setae; on tibiae their length smaller than their distance.

Colour: Trunk black, without metallic shimmer, appearing grey by whitish pilosity. Antenna with black scape; funiculus reddish dark brown, paler towards apex. Mandible basally black, distally pale brown; other mouthparts yellowish. Legs: forecoxa black; middle and hind coxa and all trochanters pale testaceous; femora and hind tibia blackish brown; other tibiae and tarsi brown, paler towards apical tarsomeres.

Comparative notes. *Echinopla brevisetosa* sp. n. is similar to *E. wardi* sp. n. from West Malaysia, but has a more slender mesosoma, a relatively longer propodeum and a differently structured petiole that bears one slender tooth and two small denticles below the lateral spine whereas the petiole of *E. wardi* sp. n. has three relatively strong teeth. *Echinopla brevisetosa* sp. n. differs distinctly from *E. wardi* sp. n. and *E. madli* sp. n. by the very short tibial setae.
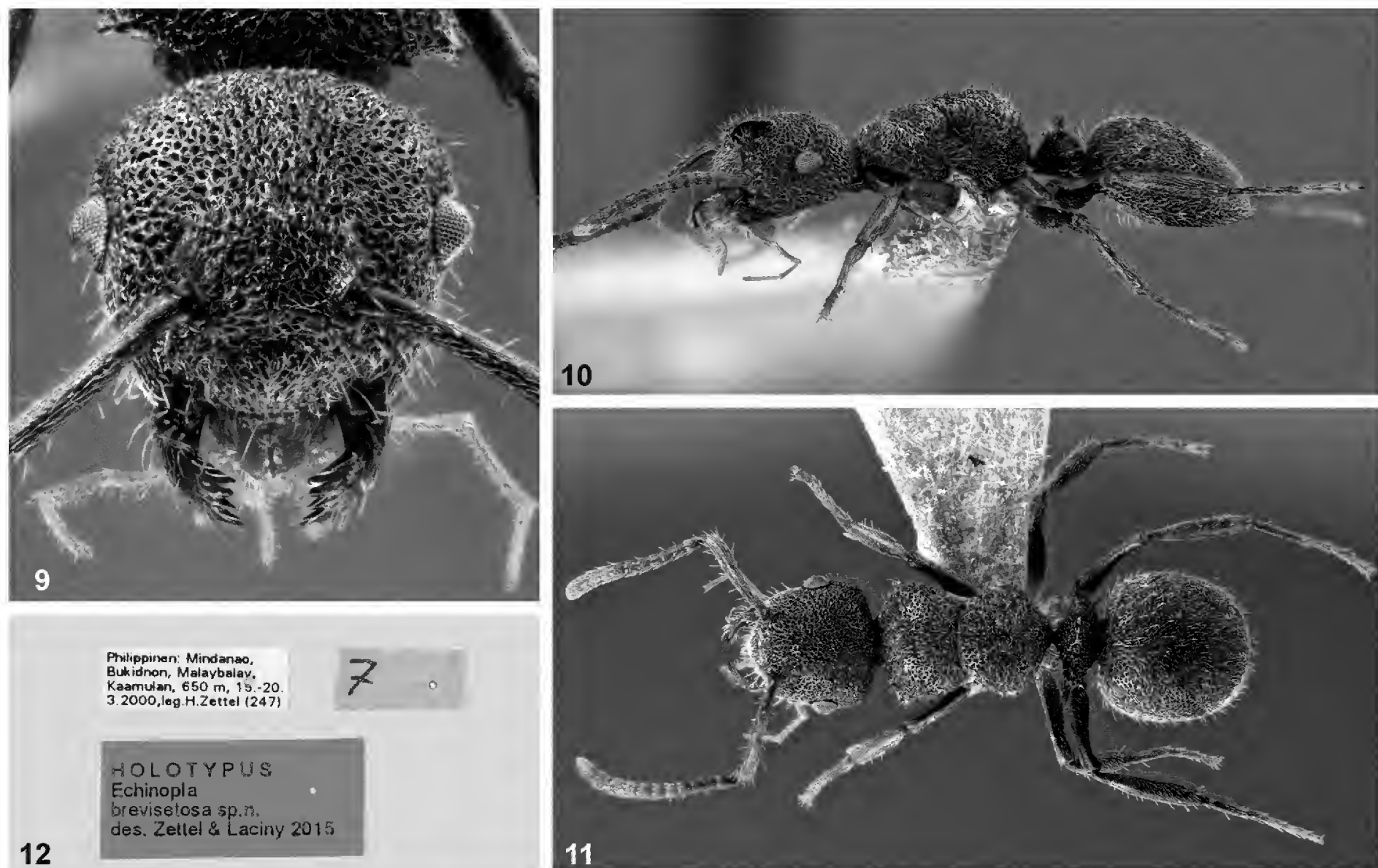
Figures 9–12. *Echinopla brevisetosa* sp. n., holotype: (**9**) Head, full face view. (**10**) Habitus, lateral view. (**11**) Habitus, dorsal view. (**12**) Labels.

Etymology. From Latin adjectives *brevis* meaning short and *setosus* meaning bristly, and referring to the short pilosity of trunk, scape and legs.

Echinopla angustata sp. n.

http://zoobank.org/0F71F455-B740-46A3-BD07-1BA2B0A63E4F

Figs 13–16

Type material. Holotype (worker, NMM) from the Philippines, Negros Island, Negros Oriental Province, Valencia, Apolong, Casaroro Falls, slopes of Cuernos de Negros, 9–13.III.2005, leg. H. Zettel (420), in the National Museum of the Philippines, Manila; two paratypes (workers, ZCW) from the same locality, 3–4.III.2008, leg. H. Zettel (513).

Diagnosis (worker). Predominantly black, small, slender species, TL = 4.6–4.8. Surface polyporous, pronotum with one pair of sharp tubercles, otherwise tubercles on mesosoma hardly developed. Head longer than wide (CI = 93–94). Mesosoma almost twice as long as pronotal width, with sharp, narrow mesometanotal suture. Pronotal width distinctly smaller than head width, if eyes excluded. Propodeum slightly shorter than promesonotum. Petiole with one pair of dorsal spines, without dentition below prominent lateral spines. Gaster tergite 1 anteriorly with relatively large pores and very narrow interspaces. Setae on dorsal surface, legs and scape relatively short. Short setae on tibia not reaching base of distally following setae.

Description. Measurements of holotype worker: TL 4.6; HW_1 1.10; HW_2 0.93; HL 1.17; EL 0.23; SL 1.04; SW 0.13; HaL 0.11; PML 0.87; PMW 0.83; PpL 0.72; PpW 0.73; PH 0.50; PL 0.41; PW 0.83; GL 1.41; GW 1.15. Indices: CI 94; SI 95; MI 192.

Measurements of paratype workers: TL 4.8, 4.8; HW_1 1.13, 1.16; HW_2 0.98, 1.00; HL 1.22, 1.24; EL 0.25, 0.24; SL 1.11, 1.11; SW 0.14, 0.13; HaL 0.13, 0.10; PML 0.93, 0.93; PMW 0.87, 0.91; PpL 0.76, 0.76; PpW 0.76, 0.80; PH 0.55, 0.56; PL 0.42, 0.44; PW 0.87, 0.91; GL 1.54, 1.50; GW 1.24, 1.25. Indices: CI 93, 94; SI 98, 95; MI 195, 186.

Structures: Head longer than wide, subovate, with convex sides; dorsally and laterally polyporous, with closely set, relatively large pores, posterolaterally with a very few indistinct tubercles, matt; ventral surface smooth and shiny. Compound eye relatively small, strongly protruding, positioned slightly behind mid-length of head. Frons with prominent median carina; frontal lobes chiefly horizontally oriented, in dorsal aspect covering antennal fossae only in part, maximum distance of margins clearly behind mid-length, slightly greater than half of HW_2. Clypeus with short, angularly elevated median carina, anterior margin straight. Mandibles striate, masticatory margin with five teeth. Antennal scape moderately long, almost straight, steadily widened from base to apex; antennomeres 8–10 approximately as wide as long.

Mesosoma slender, length roughly 1.9 times pronotum width; propodeum much shorter than promesonotum.
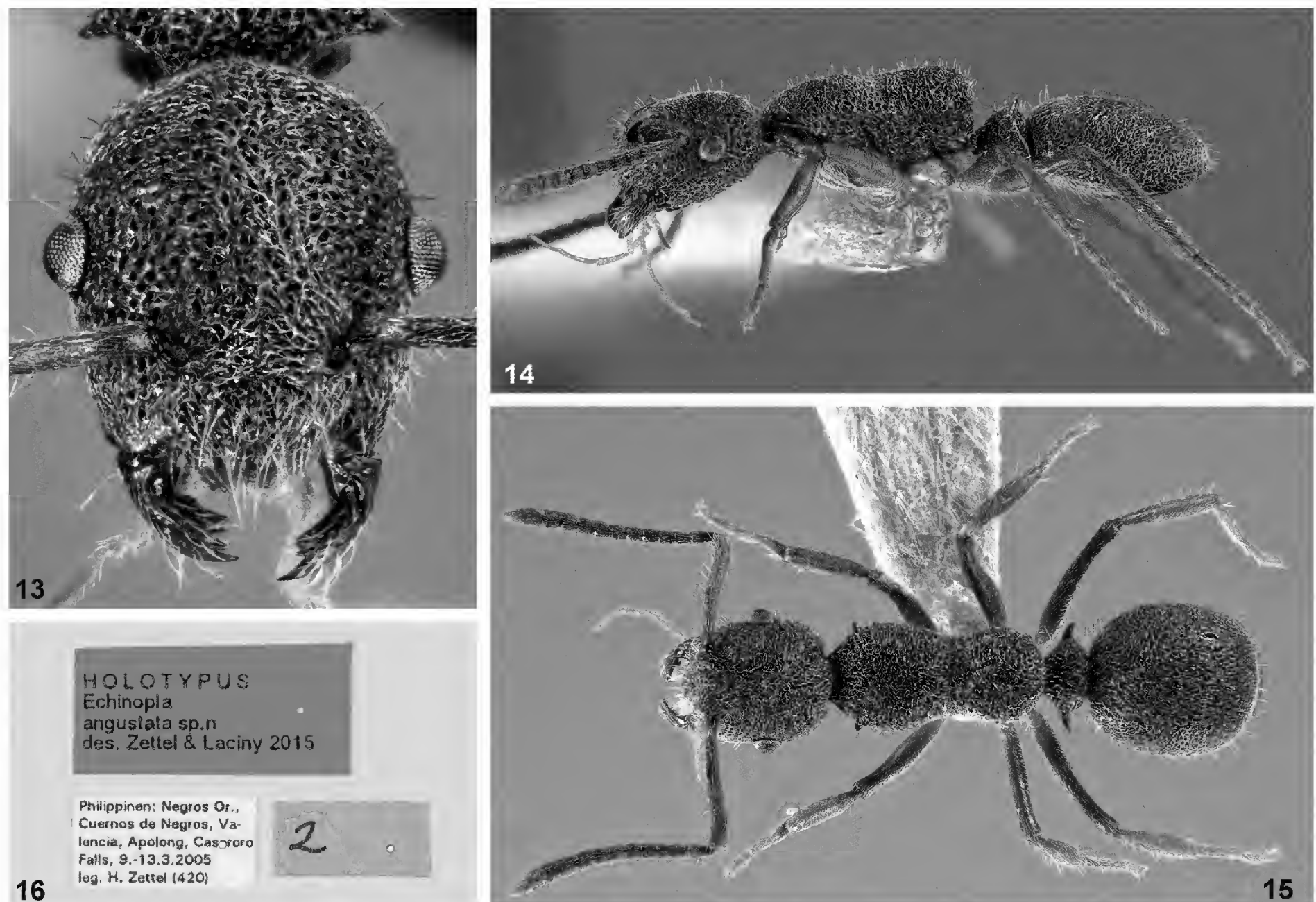
Figures 13–16. *Echinopla angustata* sp. n., holotype: (**13**) Head, full face view. (**14**) Habitus, lateral view. (**15**) Habitus, dorsal view. (**16**) Labels.

Surface polyporous, with closely set, relatively large pores, dorsal margins with very few small tubercles. Pronotum rounded, but with distinct lateral teeth, distinctly narrower than head excluding eyes. Promesonotal suture absent. Mesometanotal suture sharp, narrow and deep. "Waist" in front of propodeum weakly developed. Legs moderately long, relatively slender.

Petiole stout, moderately wide, subtriangular in lateral, transverse in dorsal aspect; surface structure as on mesosoma; dorsal apex not sharply crested, bearing one pair of sharp, rather long teeth and occasionally a small medial denticle; below strongly developed lateral teeth without further dentition. Gaster tergite 1 considerably longer than wide, completely covering the following tergites; hind margin convex, serration blunt, in one paratype almost absent; surface polyporous, interspaces smooth and shiny; distances of pores everywhere clearly smaller than their relatively large diameters.

Pilosity: Entire trunk dorsally and laterally with dense, appressed white pilosity and moderately long white and grey standing setae; some standing setae on clypeus and on anterior declivity of gaster tergite 1 longer. White standing setae on scape about as long as the setae on head. Legs with fine appressed pilosity. Femora with only 0–2 standing setae on flexor side. Tibiae and first tarsomeres of middle and hind leg with oblique white setae; on tibiae their length greater than their distance.

Colour: Trunk black, without metallic shimmer, appearing grey by whitish pilosity. Antenna black or very dark brown, funiculus slightly paler towards apex. Mandible basally black, distally brown; other mouthparts yellowish. Legs chiefly black to dark brown; middle and hind coxa, all trochanters, and bases of femora yellowish to pale testaceous; tarsi towards apical tarsomeres reddish brown.

Comparative notes. *Echinopla angustata* sp. n. differs from the previous three species by the much more slender body. The tubercles on the mesosomal sides are poorly developed except for one prominent pair on the pronotum. The petiole has no teeth below the lateral spines, and the pits on gaster tergite 1 are relatively coarse.

**Etymology.** From the Latin adjective *angustatus* meaning narrow and referring to the slender body.

Echinopla fisheri sp. n.

http://zoobank.org/E313BDB6-7658-4234-AFAB-E1BFE30CD60B
Figs 17–20

Type material. Holotype (worker, CAS, CASENT 0214564-D01) from Malaysia, Sabah, Danum Valley, Nature Trail, 180 m a.s.l., 4.96072°N; 117.80014°E, in rainforest, 24.VII.2010, leg. B.L. Fisher.

Diagnosis (worker). Predominantly black, medium-sized, slender species, TL = 6.3. Surface polyporous, prono-
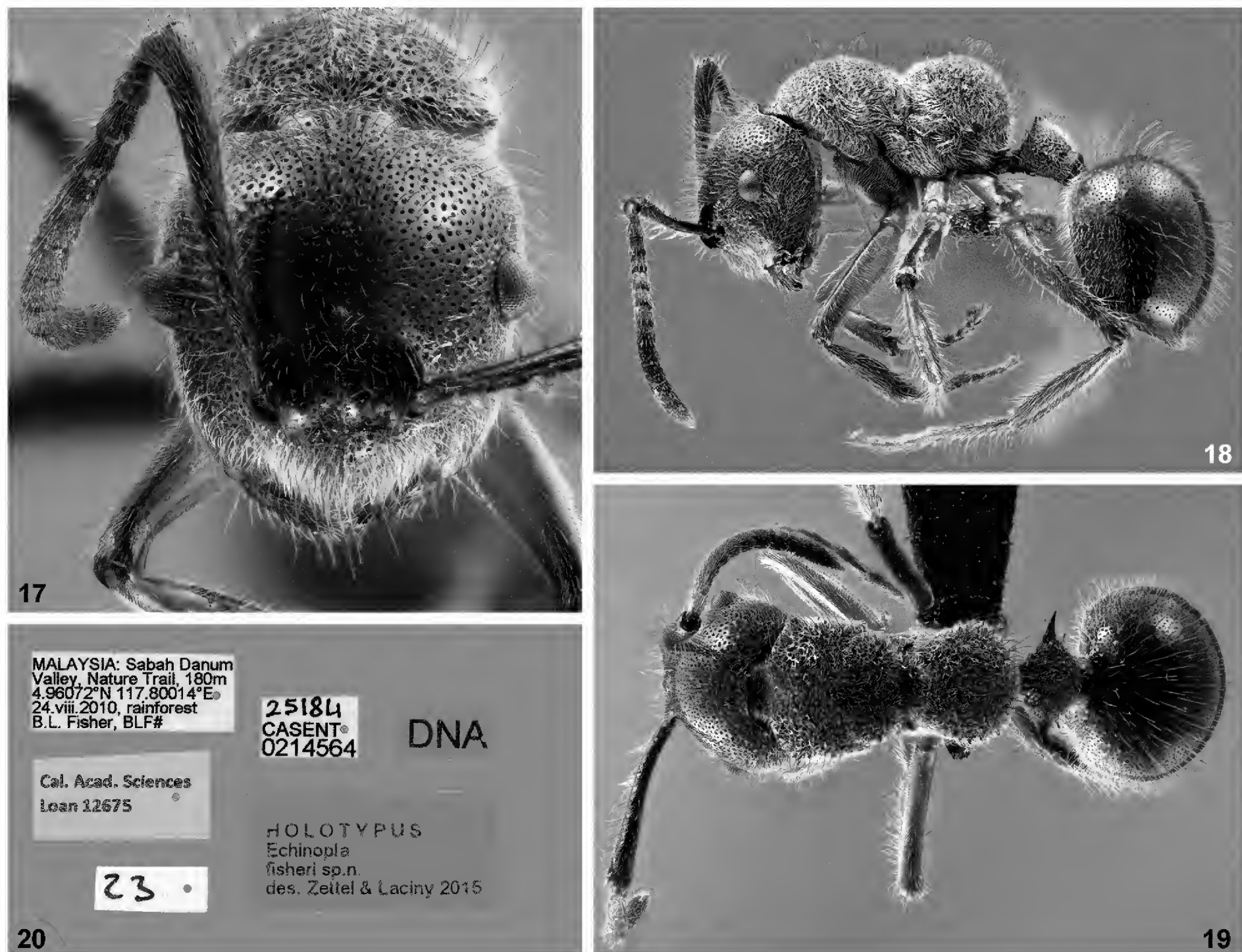
Figures 17–20. *Echinopla fisheri* sp. n., holotype: (**17**) Head, full face view. (**18**) Habitus, lateral view.(**19**) Habitus, dorsal view. (**20**) Labels.

tum with one pair of sharp tubercles, otherwise tubercles on mesosoma hardly developed. Head very large, about as wide as long (CI = 101). Mesosoma about two thirds longer than wide (MI = 166), with sharp and very deep mesometanotal suture. Pronotal width much smaller than head width. Propodeum much shorter than promesonotum. Petiole longer than high, with three pairs of dorsal spines and three spines below the prominent lateral spines. Gaster tergite 1 with very fine, sparsely distributed pores, along hind margin with transverse impression. Setae on dorsal surface, legs and scape very long, mostly brown.

Description. Measurements of holotype worker: TL 6.3; HW_1 1.58; HW_2 1.41; HL 1.57; EL 0.27; SL 1.53; SW 0.18; HaL 0.27; PML 1.20; PMW 1.28; PpL 0.93; PpW 1.04; PH 0.54; PL 0.63; PW 1.17; GL 1.87; GW 1.61. Indices: CI 101; SI 97; MI 166.

Structures: Head very large compared to mesosoma, as long as wide, with convex sides and almost straight hind margin bearing a small medial lobe; dorsally and laterally polyporous, unevenly large pores, posteriorly and laterally larger and denser than in centre, shiny; ventral surface smooth and shiny. Compound eye small, slightly protruding, positioned near mid-length of head (slightly posteriorly). Frons with two short sections of a median

carina; frontal lobes chiefly horizontally oriented, in full-face view covering antennal fossae only in part, maximum distance of margins near posterior end, smaller than half of HW_2. Clypeus with median carina, anterior margin emarginated at middle. Mandibles striate, masticatory margin with five teeth. Antennal scape moderately long, almost straight, steadily widened from base to apex; all antennomeres longer than wide.

Mesosoma slender, length roughly 1.7 times pronotum width; propodeum much shorter than promesonotum. Dorsal outline of both promesonotum and propodeum strongly convex, meeting at the deep incision of a sharp metanotal groove. Promesonotal suture only laterally indicated. Surface polyporous, with closely set, relatively large pores, dorsal margins with few small tubercles, on propodeum more numerous than on promesonotum. Pronotum angular, much narrower than head. "Waist" in front of propodeum well developed in dorsal aspect. Legs comparatively long and slender.

Petiole moderately wide, slender subtriangular in lateral, slightly transverse in dorsal aspect; surface sculpture on node as on the mesosoma, a broad posterior rim smooth; dorsal apex crested with three pairs of sharp, rather long teeth; each side bearing three teeth below a

strongly developed lateral tooth. Gaster tergite 1 considerably longer than wide, completely covering the following tergites; hind margin convex, with indistinct serration and with shallow emargination at middle; along posterior margin a shallow but rather wide impression; surface polyporous, but pores extremely fine and sparse; interspaces smooth and shiny; distances of pores everywhere several times larger than their diameters.

Pilosity: Trunk dorsally and laterally with dense, appressed white pilosity, lacking only on centre of face and gaster tergite 1. Dorsal surface with very long brown standing setae. Standing setae on scape, femora, tibiae, and first tarsomeres also very long, brown or grey.

Colour: Trunk black, without metallic shimmer, mesosoma appearing grey by whitish pilosity. Antenna black. Mandible black, teeth dark reddish brown; other mouthparts pale yellowish. Legs chiefly black; middle and hind coxa, all trochanters, and femora except their apices reddish.

Comparative notes. *Echinopla fisheri* sp. n. differs strongly from other species with polyporous surface structure by a very long, dark pilosity of the trunk, a deep metanotal suture that separates the strongly convex promesonotum and propodeum (Fig. 18), and very fine and sparsely distributed pores on gaster tergite 1 (Fig. 19). It is conspicuously larger than the preceding species and it has a distinctly emarginated clypeus margin (straight to convex in the other species) and a petiole that is longer than high (higher than long in the other species).

Notes. Antweb (2015) states that the holotype specimen was sent for barcoding (Guelph CCDB-016889).

Etymology. Dedicated to Brian L. Fisher (California Academy of Sciences) who discovered this extraordinary species.

Echinopla melanarctos Smith, 1857

Material examined. 1 worker (NHMW) from Indonesia, Sumatra, Aceh Province, Gunung Leuser National Park, Ketambe, 22.II.1990, leg. H. Schillhammer; 1 worker (NHMW) from West Malaysia, Kedah, Gunung Jerai, north of Sungai Petani, 700 m a.s.l., leg. M.A. Jäch; 15 workers, 2 dealate gynes (ZCW, NHMW) from West Malaysia, Kelantan, 30 km NW Gua Musang, Ulu Lalat, Kampong Sungai Om, 800–1000 m a.s.l., 21.VI.–14.VII.2010, leg. Petr Čechovský; 1 gyne (MCB) from Sabah, Danum Valley, Western Trail, 04°58'N; 117°48'E, 4.VI.2004, leg. D. Mezger (C 00619); 1 worker (UKL) from Borneo, Sabah, Deramakot Forest Reserve, Plot H196, ca. 5°27'N; 117°25'E, ca. 85 m, disturbed logged-over forest, 1998, leg. M. Gossner; 1 gyne (UKL) from Borneo, Sarawak, Gunung Mulu National Park, 04°08'N; 114°54'E, leg. D. Mezger (KE91).

Notes. *Echinopla melanarctos* is the type species of *Echinopla*. It can be easily recognized by its relatively large size (in workers TL ca. 6.5–8.2 mm, HW_1 ca. 2.05–2.44 mm), very spiny appearance, long black hair, and entirely black colour (except palpi). The "spines" are

slender, socket-shaped protuberances ("pedestals") of the integument, their apex is truncate and bears a long seta, surrounded by a subapical ring of short, horizontally projecting hairs (bearing resemblance to the pappus of a dandelion seed). They are typical for a group of species also containing *E. pallipes*, *E. circulus* sp. n., *E. tritschleri*, and *E. cherapunjiensis*. In *E. tritschleri*, however, the ring of short setae is not horizontally projecting but oblique, therefore the pilosity is less obvious.

Due to the scarcity of specimens, hitherto little is known about the differences between workers and gynes in *Echinopla*. We were able to study both castes of *E. melanarctos* and noted the following differences: body of gynes larger (TL 8.8–9.7 vs. 6.5–8.2; HW_1 2.41–2.70 vs. 2.05–2.44); eyes slightly larger; ocelli present; pedestals lower than in worker, on scutum and scutellum reduced to low tubercles; these parts with coarse, irregular rugae, scutum anteriorly with distinct, long median carina; short pilosity of dorsum less obvious; thoracic structures as typical for winged ant gynes (all examined specimens with wings broken off); scutellum laterally with a short lobe (not with a sharp projection as in some congeners).

Echinopla melanarctos was described from Singapore (Smith 1857) and recorded from Sumatra (Mayr 1872, Emery 1900) and Sipora Island of the Mentawai group (Emery 1900) in Indonesia. A worker from "Banka" deposited in the Zoological State Collection, Munich, and illustrated by Antbase (2015) originates probably from Bangka Island offshore Sumatra. Antweb (2015) records specimens from Borneo (Sabah and Kalimantan). Examined specimens from West Malaysia, Sumatra, and Borneo (Sabah and Sarawak) fully agree with illustrations of a Sabah specimen in Antweb (2015).

Echinopla pallipes Smith, 1857

Fig. 26

Material examined. 2 workers (syntypes?; NHMW) from unknown locality, G. Mayr Collection (see Notes); 1 worker (SCW) from Borneo, Sarawak, Gunung Mulu National Park, dipterocarp forest, 4°02'30"N; 114°52'15"E, 23–26.X.2009, leg. D.M. Sorger; 1 worker (MCB) from the same area, Camp 1, 4°02'29"N; 114°49'08"E, 3.VI.2006, leg. D. Mezger (C 001862); 1 worker (UKL) from Sabah, Poring Spring, lower montane mixed dipterocarp forest, > 650 m as.l., on *Aporusa* sp., 20.V.1992, fogging, leg. A. Floren; 1 worker (NHMW) from Sabah, Poring Spring, lower montane mixed dipterocarp forest, > 650 m a.s.l., on *Xanthophyllum affinis*, 21.V.1992, fogging, leg. A. Floren; 1 worker (UKL) from Borneo, Sabah, Poring Hot Spring, leg. A. Malsch.

Notes. *Echinopla pallipes* is similar to *E. melanarctos*, but smaller (TL ca. 6 mm), and has pale legs, lower tubercles on head and mesosoma and strongly reduced tubercles on gaster tergite 1 (only anteriorly present). It differs from *E. tritschleri* and *E. cherapunjiensis* by the posterior position of the eyes, and from *E. circulus* sp. n.

by the sculpture of the gaster tergite 1 (comp. Figs 24 and 26). See also notes for *E. circulus* sp. n.

Smith (1857) described *Echinopla pallipes* from Sarawak, Borneo. One type specimen (holotype?) is in the Oxford University Museum and has been illustrated in Antweb (2015). Mayr (1862) published some descriptive notes on two specimens (now in NHMW) that he had received from Frederick Smith. Their locality is unclear, but considering the rareness of collections from Borneo in the 19th century they could be syntypes. These three specimens and the two examined specimens from Poring, Sabah, clearly belong to the same species. One further specimen collected by Miss D.M. Sorger in Sarawak is slightly larger and has longer lateral spines on the petiole, but otherwise agrees fairly well in the sculptural details.

Besides the examined specimens from Sarawak, the specimen from Kalimantan Barat in the Indonesian part of Borneo, illustrated by Antweb (2015) and a worker from the Gunung Mulu National Park in northern Sarawak, illustrated by Antbase (2015) and deposited in the Natural History Museum London, can be safely identified as *E. pallipes*. However, *E. pallipes* is apparently not restricted to Borneo. General and Alpert (2012) report and illustrate a specimen from Luzon, the Philippines, which agrees well with the type in structural details. A record from Sulawesi ("Celebes") by Smith (1862) remains unconfirmed.

Echinopla circulus sp. n.

http://zoobank.org/D944FB8D-F02E-485C-8ACC-90F7E1D9AE30
Figs 21–25

Type material. Holotype (worker, NHMW) from Borneo, Sarawak, Kelabit Highlands, Bareo – Arur Dalam, ca. 1000 m a.s.l., 26.II.1993, leg. M.A. Jäch (14); 4 paratypes (workers, NHMW, ZCW) same locality, leg. H. Zettel (11); 1 paratype (worker, NHMW) from Borneo, Sabah, Crocker Range National Park, Mawer Waterfall area, undergrowth, 17.VI.1996, unknown collector; 2 paratypes (workers, UKL) from Borneo, Sabah, Poring Hot Spring, 7.I.1998, leg. A. Malsch (8257).

Diagnosis (worker). Predominantly black species with yellowish legs (but tarsi black); relatively large, TL = 6.4–7.6 mm. Surface of head and mesosoma with numerous pedestals, each bearing one long standing black seta and a ring of short pale hairs directed horizontally. Gaster tergite 1 with similar pedestals at base, but their height strongly reduced towards posterior margin, so that they appear as low dimples; additionally with strong, circular ridges (Fig. 24). Head wider than long (CI = 115–124). Mesosoma about one fourth longer than pronotal width (MI 124–132), with narrow, sharp and deep incision in front of propodeum. Pronotal width slightly less than head width, if eyes excluded. Propodeum slightly shorter than promesonotum. Petiole node almost smooth, anteriorly with transverse ridge, dorsally with four small teeth between the lateral spines, without teeth laterally below lateral spine. Setae on dorsal surface, legs and scape abundant, long and mostly black.

Description. Measurements of holotype worker: TL 7.6; HW_1 2.29; HW_2 2.07; HL 1.89; EL 0.31; SL 1.78; SW 0.20; HaL 0.55; PML 1.30; PMW 1.98; PpL 1.2; PpW 1.63; PH 0.63; PL 0.53; PW 1.11; GL 2,28; GW 2.38. Indices: CI 121; SI 78; MI 126.

Measurements of paratype workers: TL 6.4–7.8; HW_1 2.04–2.23; HW_2 1.80–2.07; HL 1.67–1.93; EL 0.29–0.31; SL 1.57–1.83; SW 0.18–0.21; HaL 0.46–0.58; PML 1.09–1.47; PMW 1.63–1.98; PpL 0.96–1.15; PpW 1.41–1.65; PH 0.55–0.62; PL 0.45–0.51; PW 0.90–1.06; GL 1.96–2.41; GW 2.12–2.32. Indices: CI 116–124; SI 77–84; MI 124–132.

Structures: Head wider than long, roundish, with convex sides; frons, vertex and tempora rugose-tuberculate, the high "pedestals" connected by low ridges; antennal scrobes, part of genae, and clypeus longitudinally rugose; ventral surface smooth and shiny. Ventrolateral ridge forming a distinct angle below eye. Compound eye small, but strongly protruding, positioned distinctly behind midlength of head on a small socket. Frons with long median carina; frontal lobes obliquely elevated, completely covering antennal fossae in dorsal aspect; margins anteriorly slightly converging, their maximum distance near posterior end, distinctly greater than half of HW_2. Clypeus subapically with transverse carina; median carina indistinct among longitudinal rugae. Mandibles striate, masticatory margin with five teeth. Antennal scape moderately long, weakly s-curved, steadily widened from base to apex; antennomeres 8–10 slightly longer than wide.

Mesosoma very stout, length roughly 1.3 times pronotum width, dorsal outline regularly convex; propodeum distinctly shorter than promesonotum. Dorsal surface rugose-tuberculate as on vertex; sides irregularly rugose; posterior-most part of propodeum smooth and shiny. Pronotum rounded, distinctly narrower than head excluding eyes. Promesonotal and mesometanotal suture sharp, narrow and (laterally) deep, but both inconspicuous between "pedestals"; promesonotal suture evanescent in medial third. "Waist" in front of propodeum hardly developed. Legs moderately long; femora basally stout, strongly narrowed towards apex.

Petiole small, node square, without dorsal crest; surface smooth; lateral teeth moderately long, directed straight towards sides; dorsally between lateral teeth with two pairs of small denticles; anterior face of node separated from dorsal summit by a fine ridge that is medially evanescent; below strongly developed lateral teeth without further dentition. Gaster tergite 1 wider than long, completely covering the following tergites; hind margin convex, without serration; surface anteriorly with pedestals that are basally almost as high as those on mesosoma, but gradually becoming lower towards hind margin where they are only low tubercles; between these structures with coarse rugae that are more or less arranged in circles.

Pilosity: Trunk dorsally with very long, mostly black, but in some areas pale, standing setae that arise from the apices of tubercles. Short, pale pilosity rather inconspicuous (more conspicuous only on dorsum of mesosoma), often arranged in subapical rings of horizontally projecting
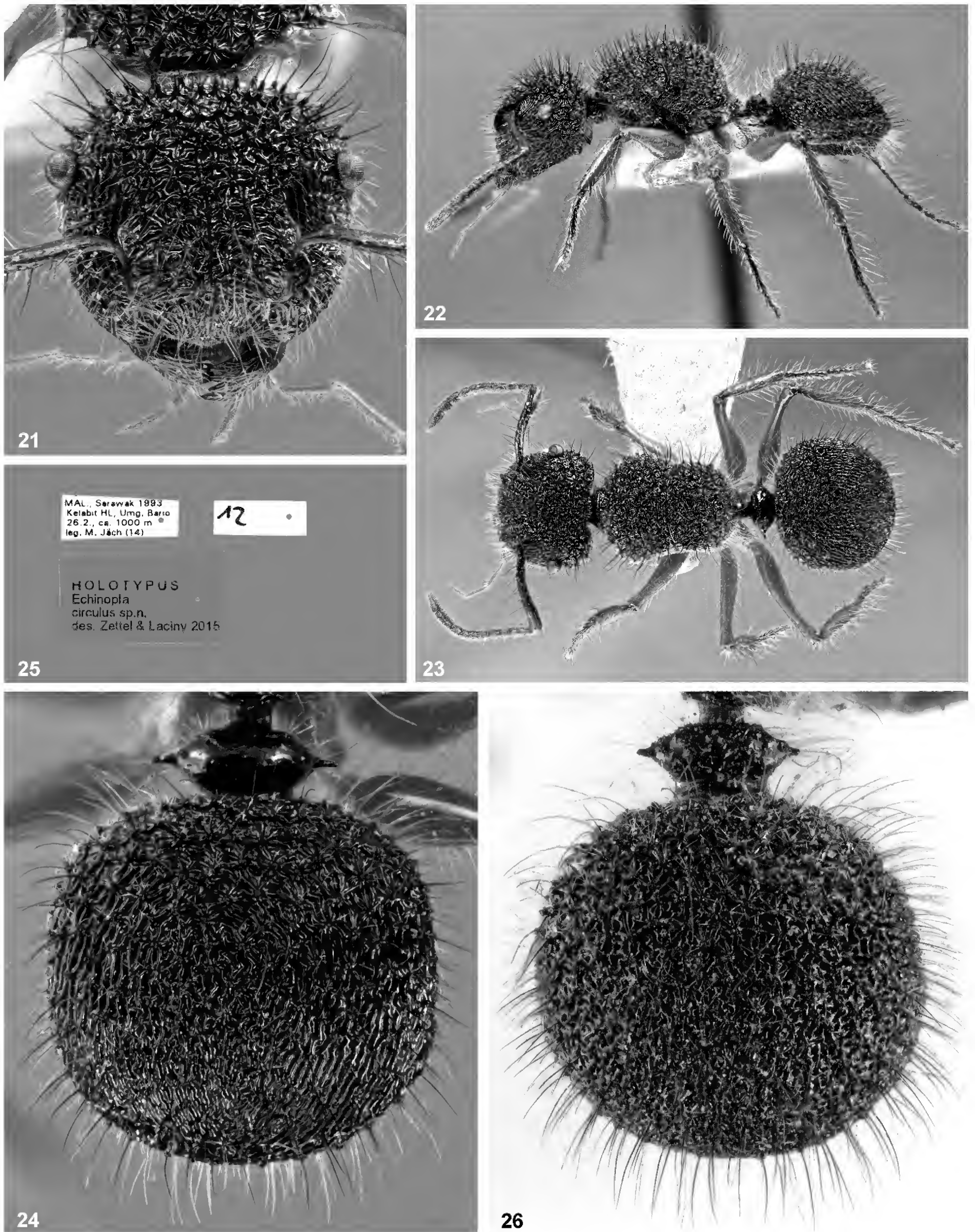
Figures 21–26. (**21–25**) *Echinopla circulus* sp. n., holotype: (**21**) Head, full face view. (**22**) Habitus, lateral view. (**23**) Habitus, dorsal view. (**24**) Dorsal aspect of gaster tergite 1. (**25**) Labels. (**26**) *Echinopla pallipes*, dorsal aspect of gaster tergite 1.

hairs on pedestals. Scape also with very long standing setae. Legs without appressed pilosity, but all parts with numerous, black or white, oblique setae of varying length. Femora with rows of setae on flexor and extensor sides.

Longest setae on middle and hind tibiae as long as those on scape.

Colour: Trunk black, without metallic shimmer; apex of abdomen testaceous. Antenna black or very dark brown,

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extreme base of scape and apex of last antennomere pale. Mandible basally black, distally brown; other mouthparts yellowish to testaceous. Legs chiefly testaceous; forecoxa black (but anteriorly testaceous in the specimen from the Crocker Range); tarsi partly infuscated.

Notes. *Echinopla circulus* sp. n. is very similar to *E. pallipes*, but clearly differs in the structure of gaster tergite 1 (compare Figs 24 and 26). A less conspicuous difference is found in the frontal lobes that are parallel in *E. pallipes*, but anteriorly slightly converging in *E. circulus* sp. n. (Fig. 21). On average *E. circulus* sp. n. is larger than *E. pallipes* (HW_1 2.04–2.29 in *E. circulus* sp. n., 1.85–2.02 in *E. pallipes* including the aberrantly large worker from Gunung Mulu).

Etymology. From the Latin *circulus* for a small circle and referring to the concentric rugae on gaster tergite 1; used as a noun in apposition.

Echinopla tritschleri Forel, 1901

Material examined. 9 workers and 1 dealate gyne (ZCW, NHMW) from West Malaysia, Kelantan, 30 km NW Gua Musang, Ulu Lalat, Kampong Sungai Om, 800–1000 m a.s.l., 21.VI.–14.VII.2010, leg. Petr Čechovský; 2 dealate gynes (NHMW) from Borneo, Sabah, Crocker Range National Park, Gunung Emas Highland Resort, 1500–1700 m a.s.l., 6–18.VI.1998, unknown collector (2a); 3 workers (CAS, CASENT0202195–97) from Borneo, Sabah, Danum Valley, nature trail, 180 m a.s.l., 4.96072°N; 117.80014°E, 25.VIII.2010, rainforest, leg. B.L. Fisher; 1 worker (CAS) from the same locality, 16–26.VIII.2010, Ant Course 2010, unknown collector.

Notes. *Echinopla tritschleri* differs from the previous three species by the position of the eyes that are close to the mid-length of the head. The short hair of the mesosoma is less conspicuous than in *E. pallipes* and *E. circulus* sp. n. The sculpture of gaster tergite 1 is very characteristic: anteriorly with a few tubercles, sides and disc with punctures that flow together to form longitudinal lines, and posteriorly with punctures that flow together into transverse lines.

Gynes similar to workers but differing by the following characters: body much larger (TL 8.4–8.7 vs. 6.1–6.8; HW_1 2.12–2.19 vs. 1.58–1.86); eyes slightly larger; ocelli present; scape wider; pedestals comparatively low and restricted to posterior of head, pronotum, propodeum, and base of gaster tergite 1; scutum and scutellum with coarse, irregular rugae, scutum anteriorly with short median carina; short pilosity of dorsum less obvious; thoracic structures as typical for winged ant gynes (all examined specimens with wings broken off); scutellum laterally with a short lobe.

Forel (1901) described the worker of *E. tritschleri* from Sumatra and added a gyne from southeastern Borneo. From Sabah, northern Borneo, we have studied the worker specimens listed by Antweb (2015) and deposited in CAS, and two gynes in NHMW. The specimens from West Malaysia represent the first record from the Asian mainland.

Echinopla cherapunjiensis Bharti & Gul, 2012

Material examined. 2 workers (NHMW) from Laos, Luang Nam Tha Province, ca. 25 km SE Muang Sing, 900 m a.s.l., 14–15., 20–22.VI.1996, leg. H. Schillhammer (27, 34); 1 worker (ZCW) from West Malaysia, Perak. 40 km SE of Ipoh, Banjaran Titi Wangsa, Ringlet, 900 m a.s.l., 29.III.–15.IV.2004, leg. Petr Čechovský.

Notes. This species can be characterized by tuberculate sculpture of head and mesosoma, whereas the gaster tergite 1 is polyporous, by black trunk with yellowish legs, scape, and mouthparts, and by white pilosity. It shares the position of eyes with *E. tritschleri* but can be easily distinguished from this species by relatively low pedestals on head and mesosoma, the polyporous sculpture of tergite 1, the almost vertically positioned frontal lobes, and a longer and lower, polyporous petiolar node. Bharti and Gul (2012) stated that the mesometanotal suture is obsolete in the holotype of *E. cherapunjiensis*. However, a re-examination of the type by Professor Himender Bharti revealed the presence of a narrow suture covered by the dense hair (Bharti, in litteris), as in our specimens from Laos and Malaysia, and as in *E. tritschleri*.

Bharti and Gul (2012) described *E. cherapunjiensis* based on a single worker from Meghalaya, northeastern India. Liu et al. (2015) published a new record from Yunnan, China. Antweb (2015) illustrated the holotype and an *"Echinopla* cn01" specimen from Guanxi, China, that apparently belongs to this species. Our first records from Laos and West Malaysia are a considerable extension of the known distribution of *E. cherapunjiensis*.

Echinopla mezgeri sp. n.

http://zoobank.org/E621C191-5568-4274-9AB8-8D556D73D444
Figs 27–30

Type material. Holotype (worker, NHMW) from Sabah, Danum Valley, Western Trail, T#33, 04°58'N; 117°48'E, 21.VII.2004, leg. D. Mezger (C 003604).

Diagnosis (worker). Predominantly black species with partly yellowish legs; slender and rather small, TL = 5.3 mm. Trunk with extremely fine sculpture, only meso- and metapleura with coarse punctures. Head much longer than wide (CI = 86). Palp formula 5, 3. Mesosoma about twice as long as pronotal width (MI 205), with sharp, but shallow incision in front of propodeum. Pronotal width smaller than head width, if eyes excluded, with tooth-like lateral corners. Propodeum clearly shorter than promesonotum. Petiolar node stocky, without teeth, with obtuse lateral corners. Gaster tergite 1 much longer than wide, with very dense, extremely fine and shallow puncturation. Body almost without standing setae (some on clypeus and abdominal segments 5 and 6), but with dense, very short, appressed pubescence that gives the species a dull appearance.

Description. Measurements of holotype worker: TL 5.3; HW_1 1.09; HW_2 0.98; HL 1.28; EL 0.36; SL 1.11; SW 0.16; HaL not applicable; PML 0.98; PMW 0.89;

Figures 27–30. *Echinopla mezgeri* sp. n., holotype: (**27**) Head, full face view. (**28**) Habitus, lateral view. (**29**) Habitus, dorsal view. (**30**) Labels.

PpL 0.85; PpW 0.76; PH 0.55; PL 0.51; PW 0.79; GL 1.50; GW 1.22. Indices: CI 86; SI 102; MI 205.

Structures: Head much long than wide, roundish, with convex sides, with inconspicuous lobe at middle of posterior margin; dorsally and laterally with fine punctures that are evanescent close to the midline, and larger only between antennal fossae and eyes; ventral surface smooth and shiny. Compound eye small, weakly protruding, positioned at mid-length of head. Frons with fine median carina; frontal lobes horizontal, partly covering antennal fossae in dorsal aspect, maximum distance near posterior end equalling half of HW_2. Clypeus with median tumescence. Mandibles striate, masticatory margin with five teeth. Palp formula 5, 3. Antennal scape long, weakly s-curved, steadily widened from base to apex; antennomeres 8–10 approximately as long as wide.

Mesosoma very elongated and subcylindrical, length roughly twice pronotum width; dorsal outline shaped as two weakly convex curves separated by a weakly impressed mesometanotal suture. Propodeum abruptly declivitous and distinctly shorter than promesonotum. Dorsal surface smooth on major part of pronotum, relatively finely punctured on posterior parts; meso- and metapleura with coarse punctures. Pronotum with tooth-like angles, narrower than head excluding eyes. Promesonotal suture laterally indicated by a short row of punctures; mesometanotal suture narrow and shallow; metanotum recognizable as a narrow ovate depression. "Waist" in front of propodeum weakly developed. Legs long; femora slender.

Petiole relatively large and stout, with a distinct peduncle; node subtriangular in lateral view, spindle-shaped in dorsal view; surface punctured; lateral teeth obtuse, no further dentition. Gaster tergite 1 much longer than wide, completely covering the following tergites in dorsal aspect, very finely and densely punctured; hind margin convex, slightly depressed, without serration.

Pilosity: Body with dense, very short, appressed pubescence giving the species a dull appearance; long standing

setae restricted to clypeus and abdominal segments 6 and 7; a few short oblique setae on other abdominal sternites.

Colour: Trunk dull black, without metallic shimmer; apex of abdomen testaceous. Antenna blackish brown, apex of scape and distal flagellomeres orange brown. Mandible basally black, distally reddish brown; palpi pale yellow. Legs black, but coxae and trochanters yellow, tarsi pale brownish towards apex.

Comparative notes. *Echinopla mezgeri* sp. n. is a very peculiar species that resembles *E. mistura* (Smith, 1860). *Echinopla mistura* was described by a worker from Bacan Island ("Bachian"), Moluccas, in a new genus *Mesoxena* in the subfamily Ponerinae (Smith 1860), and indeed the strange cylindrical mesosoma and petiole of the specimen have superficial similarities to some ponerines. Donisthorpe (1936) gave a redescription of the type and confirmed its placement in Formicinae, and Brown (1973) synonymized *Mesoxena* with *Echinopla*. The damaged type is illustrated by Antweb (2015). Both *E. mistura* and *E. mezgeri* sp. n. have an elongated mesosoma and very fine body sculpture, and – in contrast to all congeners – they lack standing setae. However, there are important differences between the two species and it is presently not certain whether they are closely related. The antennal fossae are fully exposed in *E. mistura*, whereas they are largely covered by the horizontal frontal carinae in *E. mezgeri* sp. n. The petiole of *E. mistura* is square in lateral and dorsal aspect, whereas in *E. mezgeri* sp. n. it is subtriangular in lateral aspect and spindle-shaped in dorsal aspect. In *E. mistura* the posteriorly flat gaster tergite 1 does not fully cover the following tergites, whereas in *E. mezgeri* sp. n. it has a downcurved posterior margin and the following segments protrude ventrally. In addition, there are many differences in sculpture, colour of antenna, armature of the pronotum, presence of a metanotal suture, etc. *Echinopla mezgeri* sp. n. has a palp formula of 5, 3 in contrast to any other species treated here that all have 6, 4, and to *E. mistura* that has according to Smith (1860) six-segmented maxillary palpi (now lacking in the type).

Etymology. We dedicate this extraordinary species to Dirk Mezger (Balingen, Germany) who discovered it.

Echinopla subtilis sp. n.

http://zoobank.org/4F3F5D00-69A2-433B-A11F-075DBBF02485
Figs 31–34

Type material. Holotype (worker, NHMW) from Sabah, Poring Spring, lower montane mixed dipterocarp forest, > 650 m a.s.l., on *Aporusa* sp., 13.IV.1992, fogging, leg. A. Floren (A62/F1); paratype (worker, NHMW), same locality and collection data, except 9.II.1993, leg. A. Floren (A51/F5).

Diagnosis (worker). Predominantly black, medium-sized, slender species, TL = 6.1–6.8. Dorsal surface of head and mesonotum with irregularly winding deep impressions, laterally with smaller fractions, tending to become polyporous. Head wider than long

(CI = 106–115). Maxillary palpi exceptionally long. Mesosoma about one half longer than wide (MI = 151–156). Pronotum much narrower than head, laterally rounded. Propodeum much shorter than promesonotum; promesonotal suture distinct, medially forming an angle; metanotal suture straight, sharp and deep. Petiole polyporous, longer than high, with irregularly tuberculated dorsal crest and 1–2 teeth below prominent lateral spines. Gaster tergite 1 and visible hind margins of the following tergites 2–4 with very fine, dense puncturation, appearing matt. Setae on dorsal surface white, relatively short.

Description. Measurements of holotype worker: TL 6.1; HW_1 1.52; HW_2 1.41; HL 1.33; EL 0.36; SL 1.45; SW 0.17; HaL 0.17; PML 1.04; PMW 1.20; PpL 0.76; PpW 0.91; PH 0.49; PL 0.55; PW 1.00; GL 1.72; GW 1.61. Indices: CI 115; SI 95; MI 151.

Measurements of paratype worker: TL 6.8; HW_1 1.65; HW_2 1.57; HL 1.57; EL 0.38; SL 1.52; SW 0.18; HaL 0.17; PML 1.13; PMW 1.28; PpL 0.87; PpW 1.00; PH 0.50; PL 0.62; PW 1.08; GL 1.72; GW 1.63. Indices: CI 106; SI 92; MI 156.

Structures: Head slightly wider than long, with convex sides and almost straight hind margin; dorsally with irregularly winding deep impressions, laterally and on clypeus with smaller fractions, tending to become polyporous; ventral surface smooth and shiny. Compound eye slightly protruding, positioned behind midlength of head. Frons with low median carina subdivided by a narrow impression; frontal lobes chiefly horizontally oriented, in full-face view covering most of antennal fossae, maximum distance of margins clearly smaller than half of HW_2. Clypeus with low median carina, anterior almost straight (weakly convex). Mandibles striate, masticatory margin with five teeth. Palpi very long. Antennal scape relatively long, weakly s-curved, steadily widened from base to apex; all antennomeres longer than wide.

Mesosoma moderately slender, length slightly more than 1.5 times pronotum width; propodeum much shorter than promesonotum. Dorsal outline of promesonotum and propodeum almost forming a straight line (anteriorly and posteriorly slightly downcurved), interrupted by the incision of a sharp, narrow metanotal groove. Promesonotal suture complete medially forming a blunt angle. Surface as on head, but less conspicuous due to dense pilosity. Few small tubercles along dorsal margins, almost absent from mesonotum. Pronotum anterolaterally rounded, much narrower than head. "Waist" in front of propodeum well developed in dorsal aspect. Legs comparatively long and slender.

Petiole, longer than high, slender subtriangular in lateral, slightly transverse in dorsal aspect; surface sculpture polyporous; dorsal apex bluntly crested, with irregularly set tubercles; below moderately long, apically blunt lateral teeth with one or two smaller teeth. Gaster tergite 1 and visible hind margins of the following tergites 2–4 with very fine, dense puncturation, appearing mat. Gaster tergite 1 slightly longer than wide, with evenly convex,
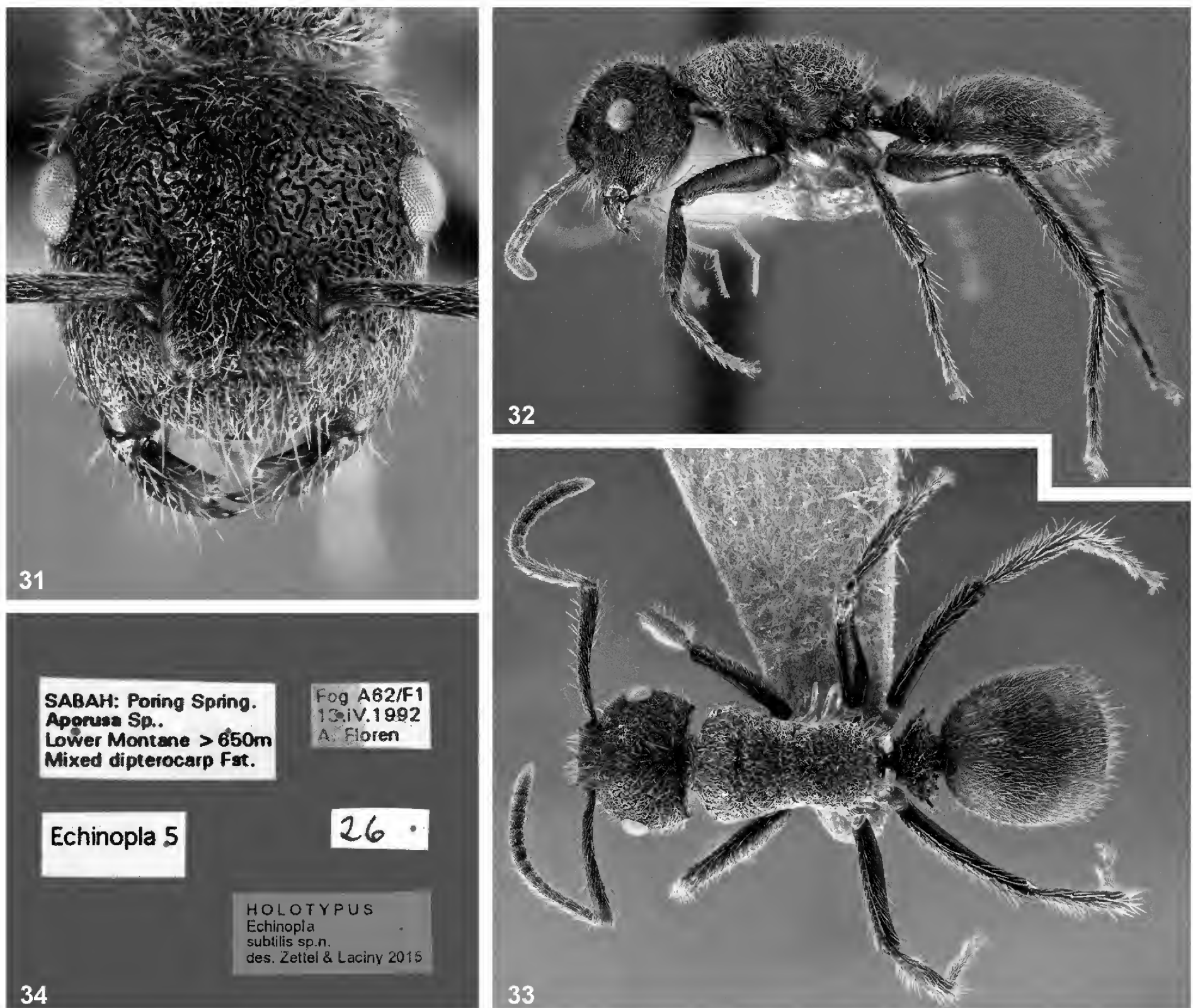
Figures 31–34. *Echinopla subtilis* sp. n., holotype: (**31**) Head, full face view. (**32**) Habitus, lateral view. (**33**) Habitus, dorsal view. (**34**) Labels.

unmodified hind margin; insertions of setae appearing as small punctures.

Pilosity: Trunk dorsally and laterally with very dense, appressed white pilosity, but almost absent from centre of face. Dorsal surface with relatively short whitish standing setae, slightly longer on clypeus, propodeum and anterior part of gaster tergite 1. White standing setae on scape, femora, tibiae, and first tarsomeres relatively long.

Colour: Black, without metallic shimmer, mesosoma appearing grey by whitish pilosity. Gaster of holotype dark brown. Gaster tergites 2–4 with narrow whitish hind margin. Mandible basally black, distally reddish. Other mouthparts pale yellow. Apex of last antennomere, apices of middle and hind coxa, trochanters, and distal parts of tarsi orange coloured.

Comparative notes. *Echinopla subtilis* sp. n. strongly differs from all hitherto described congeners by its sculpture. The dorsal surface of the head and mesosoma has irregularly winding deep impressions; they are best seen in the centre of the face where the pilosity is reduced (Fig. 31). The gaster tergite 1 appears dull due to a very

fine and dense puncturation and a relatively dense, appressed pilosity. In contrast to all aforementioned species it does not fully cover the following tergites; this character is shared with the following species that are related to *E. lineata* and *E. striata*.

Etymology. The Latin adjective *subtilis* (= fine, subtle) refers to the fine sculpture of gaster tergite 1.

Echinopla lineata Mayr, 1862

Figs 35–38, 43

Type material examined. Lectotype (worker, present designation, NHMW) from "Batavia (Novara)" (Mayr 1862); labels see Figure 26. Paralectotypes (2 workers, NHMW), from the same locality.

Additional material examined. 1 worker (NHMW) of unknown origin, leg. Ida Pfeiffer, det. G. Mayr; 1 worker (NHMW) from Java, leg. Vollenhoven, det. G. Mayr; 5 workers (ZCW) from Singapore, Singapore Zoo, 2.XI.2003, leg. H. Zettel; 8 workers (SCV, ZCW)
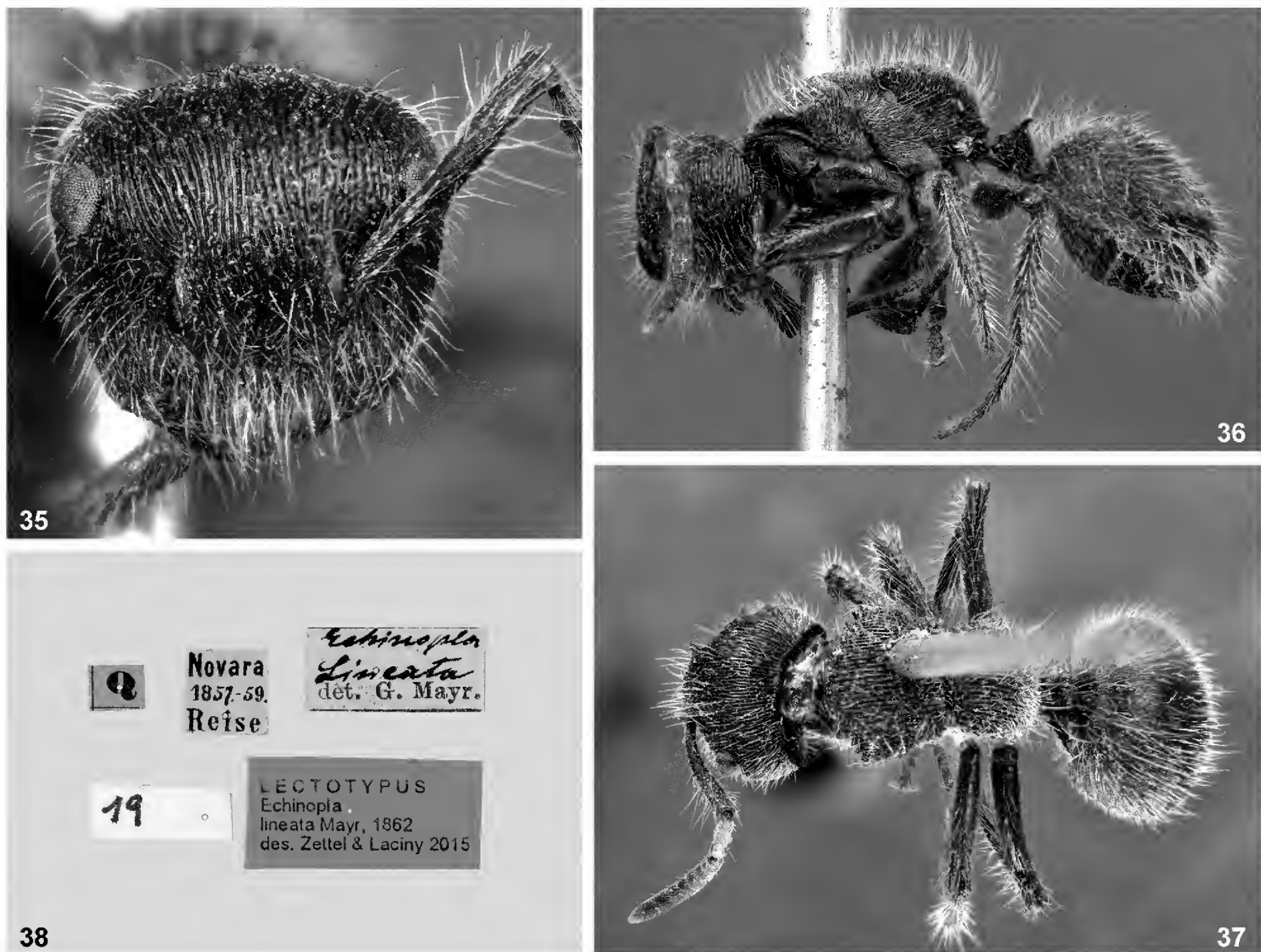
Figures 35–38. *Echinopla lineata*, lectotype: (**35**) Head, full face view. (**36**) Habitus, lateral view. (**37**) Habitus, dorsal view. (**38**) Labels.

from Borneo, Sarawak, Mulu National Park, Kerangas Forest behind Mulu Airport, 21.VII.2010, leg. D.M. Sorger; 1 worker (WCD) from Borneo, Sabah, Danum Valley Field Centre, 4.96462°N; 117.804000°E ± 70 m, 180 m a.s.l., 24.VIII.2010, leg. P.S. Ward (#16476); 5 workers (CAS), from same locality, 525 m a.s.l., 4.965611°N; 117.799806°E, 16–26.VIII.2010, rainforest, Ant Course 2010, various collectors; 1 workers (CAS), from same area, Danum Valley, West Trail, 225 m a.s.l., 4.963056°N; 117.802806°E, 16–26.VIII.2010, rainforest, Ant Course 2010, unknown collector.

Measurements of the lectotype. TL 6.3; HW_1 1.66; HW_2 1.58; HL 1.57; EL 0.36; SL 1.39; SW 0.18; HaL 0.48; PML 1.17; PMW 1.50; PpL 1.04; PpW 1.20; PH 0.47; PL 0.51; PW 1.23; GL 1.65; GW 1.80. Indices: CI 106; SI 84; MI 148.

Notes. *Echinopla lineata* has some similarities with *E. striata*, especially in sculpture, but can be recognized by the combination of black colour (without metallic lustre), coarse longitudinal striation on head and mesosoma, fine longitudinal striation on gaster, long white setae, and relatively abundant short appressed hair that gives the specimens a dull appearance. See also notes on the similar *E. senilis*.

The collection of NHMW contains five historical specimens of *E. lineata*, one of which was erroneously labelled as *E. senilis*. Three specimens are considered as types, whereas one gyne from Java (see Mayr 1872) and one worker collected by Ida Pfeiffer from an unknown locality are non-type specimens. The worker (paralectotype) labelled "Batavia" (now Jakarta, Java, Indonesia) is missing its head. One worker (paralectotype) bears the same locality code label Q and the same Novara expedition label as the lectotype (see Fig. 38), but a determination label "*Echinopla senilis* det. G. Mayr" (in Anton Handlirsch's handwriting!) which is probably a curatorial error (see notes for *E. senilis*). This slightly damaged specimen clearly belongs to *E. lineata*. The third type specimen, which is in a very good condition (see Figs 35–37), was selected as the lectotype.

The species was originally described from Java (Mayr 1862). This first description is very short, but Mayr (1865) presents illustrations (Fig. 43) and a much more detailed description. Emery (1900) recorded *E. lineata* from Sumatra. *Echinopla sucki* was described by Forel (1901) from Sarawak, Borneo, and synonymised by Emery (1925). After having studied the pictures of a syntype of *E. sucki* in Antweb (2015) and non-type specimens from Sarawak,
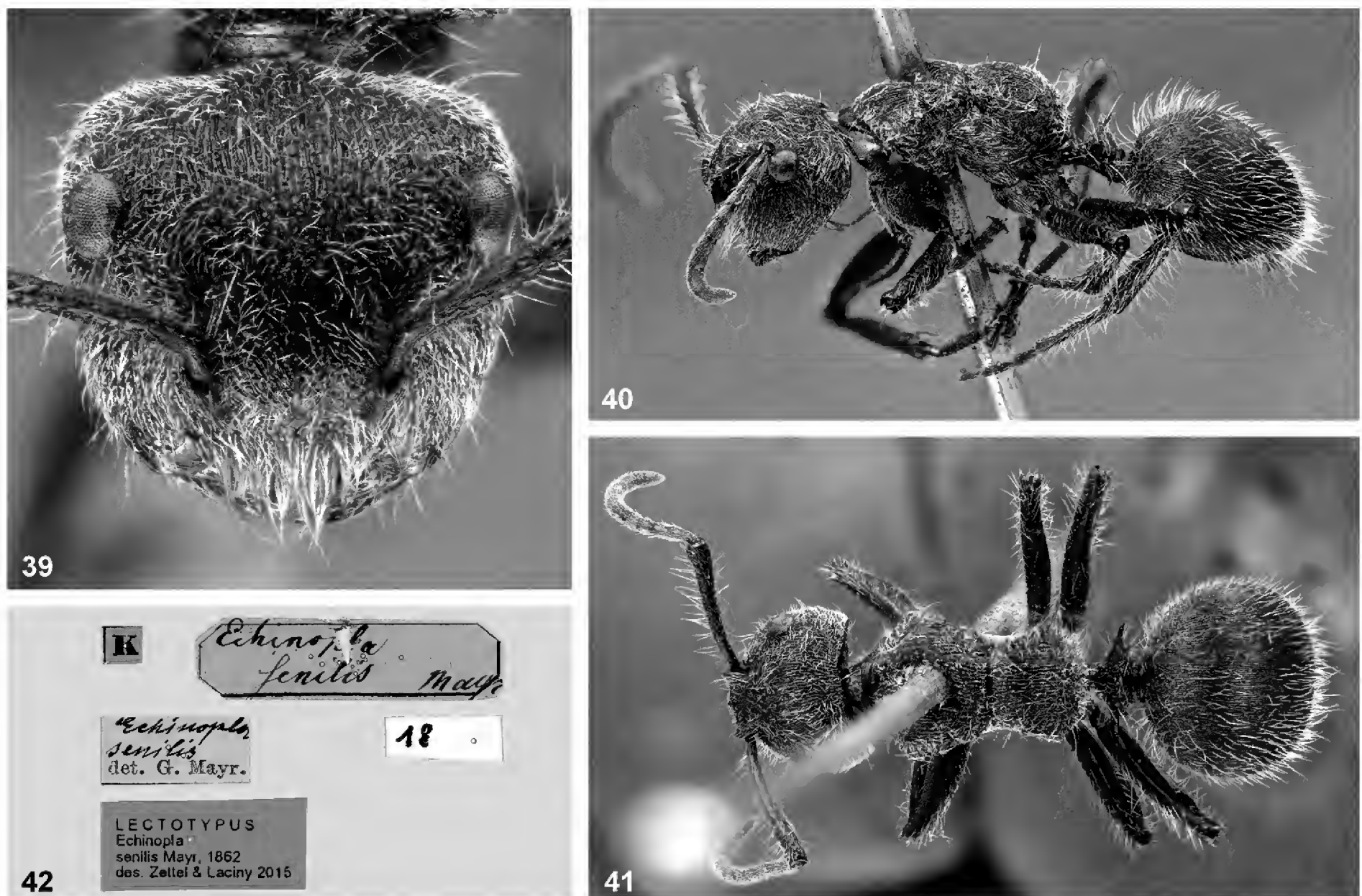
Figures 39–42. *Echinopla senilis*, lectotype: (**39**) Head, full face view. (**40**) Habitus, lateral view. (**41**) Habitus, dorsal view. (**42**) Labels.

we affirm this synonymy. We also confirm the presence of *E. lineata* in Sabah, northern Borneo, based on examined worker specimens in the P.S. Ward Collection and in the California Academy of Sciences. Antweb (2015) records two specimens from Sabah (not examined), but the illustrated one from the Maliau Basin is not *E. lineata*, because it differs strongly by a fine sculpture of head and thoracic nota, by long black pilosity and the almost absent short hair on the thoracic nota; except for its non-metallic colour it resembles *E. striata*. Also the Antweb (2015) record of *E. lineata* in Singapore can be confirmed after having studied the illustrations of this specimen and additionally collected specimens. Antbase (2015) illustrates a correctly identified worker from Kuala Lumpur, West Malaysia, in the Natural History Museum in London.

Echinopla senilis Mayr, 1862, stat. rev.

Figs 39–43

Type material examined. Lectotype (worker, present designation) from "Sambelong" (Mayr 1862); labels see Figure 42.

Measurements of the lectotype. TL 7.2; HW_1 1.85; HW_2 1.80; HL 1.67; EL 0.37; SL 1.72; SW 0.20; HaL 0.36; PML 1.30; PMW 1.63; PpL 1.13; PpW 1.28; PH 0.50; PL 0.55; PW 1.28; GL 1.96; GW 2.15. Indices: CI 110; SI 93; MI 149.

Notes. Although the collection of NHMW contains two specimens labelled as *E. senilis*, only one specimen fairly agrees with Mayr's (1862) original description and is designated as the lectotype. This lectotype does not bear a locality label and we do not know about records that connect the code letter K (Fig. 42) with a specific locality of the Novara expedition. We trust Mayr (1862) that the type was collected in "Sambelong", a name for the Southern Group of the Nicobar Islands. The second specimen in NHMW was probably mislabelled by the former curator Anton Handlirsch (1865–1935) when he integrated Mayr's collection into the museum's main collection. It is a typical specimen of *E. lineata* and bears the same code letter Q as the lectotype of *E. lineata* (see notes of this species).

Echinopla senilis is very similar to *E. lineata*. It was treated as a variety of *E. lineata* by Emery (1896) and as a subspecies by Emery (1900). It is currently catalogued as a subspecies by Bolton (2015). With more specimens of *E. lineata* available, some differences given by Mayr (1862) and subsequently by Mayr (1865) are not diagnostic. In fresh specimens of *E. lineata* the appressed hair is as abundant as in *E. senilis*, and the shape of the petiole (comp. Mayr 1865: tab. II, Figs 12c and 13c; see Fig. 43) is rather variable. A bluish black colour of the body ("blauschwarz" in Mayr 1862, "dunkelblau" in Mayr 1865) can hardly be recognized in the lectotype of *E. senilis* (Figs 39–41). However, the sculptural differ-

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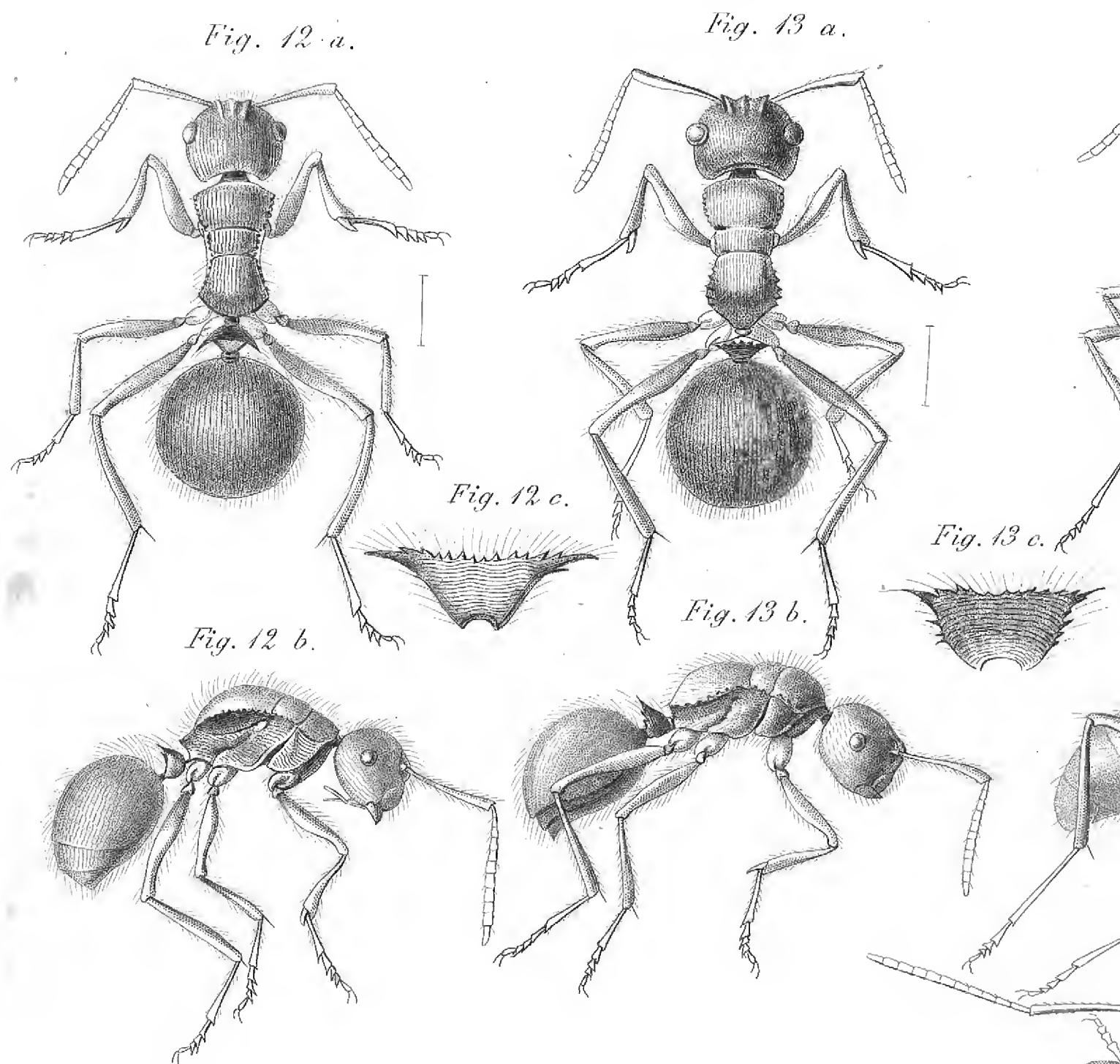
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Figure 43. Part of plate II in Mayr (1865) showing *Echinopla lineata* (fig. 12) and *Echinopla senilis* (fig. 13).

ences are rather strong and were clearly pointed out by Gustav Mayr (1862, 1865): On the clypeus and on the sides of the mesosoma the striation is regularly striate in *E. lineata* whereas it is intermixed with punctures in *E. senilis;* at the hind margin of the propodeum and on the posterior face of the petiole, the sculpture consists of transverse striae in *E. lineata* whereas it is irregular and fine in *E. senilis*. Moreover the propodeum is anteriorly more strongly, more roundly constricted in *E. senilis*. We conclude that *E. senilis* should better be regarded as a distinct species.

Echinopla cf. *pseudostriata* Donisthorpe, 1943

Material examined. 5 workers (ZCW) from the Philippines, Cebu Province, Cebu Island, Dalaguete, Mantalungon, 19.II.2012, leg. C. V. Pangantihon (CP406).

Notes. Donisthorpe (1943) described *E. pseudostriata* based on two syntype workers, one from Sulawesi, Indonesia, and one from Luzon, the Philippines. The studied specimens from Cebu Island differ considerably from the Sulawesi syntype illustrated by Antweb (2015), especially by the more regularly and finely striate sculpture of the mesosoma. Nevertheless we preliminarily identify them as *E.* cf. *pseudostriata*, because the species identity and type locality should be fixed by the designation of a lectotype, and the sculptural variability should be examined in more specimens.

Echinopla cf. *vermiculata* Emery, 1898

Material examined (all from the Philippines). 1 worker (CAS, CASENT0267357) from Luzon, Mt. Banahaw de Lucban, 747 m a.s.l., 14°05.859'N; 121°31.071'E, 14–22.V.2011, forest, PH0009, leg. H Wood et al.; 1 worker (NHMW) from Luzon, Nueva Viscaya Province, Santa Fe, Imugan, 1100–1200 m a.s.l., 10.XI.2002, leg. H. Zettel; 1 worker (ZCW) from Luzon, Quezon Province, Atimonan, near Old Zigzag Road, 24–30.III.1998, leg. Zettel (165); 1 worker (ZCW) from Luzon, Laguna Province, Los Baños, Mt. Makiling, 400–800 m, 27.XI.1999, leg. H. Zettel (211); 1 worker (ZCW) from Luzon, Camarines Norte Province, south of Daet, Basud, Nalisan, 13.III.2006, leg. H. Zettel, R. Gille & L. S. Vichozo (446); 1 worker (ZCW) from Luzon, Pampanga, Arayat, Mt. Arayat, 19–20.IV.2014, leg. C. V. Pangantihon (P506);

1 worker (ZCW) from Mindoro, Mindoro Oriental Province, Roxas, San Vicente, Taugad Diit, Taugad Daka Forest, 27.IX.2014, leg. C. V. Pangantihon (P513); 2 workers (ZCW) from Cebu Province, Cebu Island, Dalaguete, Mantalungon, 29–30.VIII.2010 and 19.II.2012, leg. C. V. Pangantihon (P361, CP406).

Notes. The identity of this species is presently unclear. Emery (1898) described a queen from Sulawesi and later he (Emery 1900) described workers from two localities on Sipora, an island of the Mentawai group. The type and one worker specimen from Sipora were imaged by Antweb (2015), but their conspecificity needs confirmation. General and Alpert (2012) report *E. vermiculata* from the Philippines (Luzon) for the first time; one specimen was illustrated on the Discover Life (2015) website. Examined specimens from the islands of Luzon, Mindoro and Cebu perfectly agree with this illustration in structural details. However, all Philippine workers considerably differ from Indonesian specimens by a very coarse, irregularly vermiculate rugosity on mesonotum and propodeum and may in fact represent an undescribed species. The worker specimen in the California Academy of Sciences was listed by Antweb (2015) as *Echinopla* ph01 and sent for barcoding (Guelph CCDB-14532).

Acknowledgements

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