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An International Journal of Systematic Entomology

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In Focus

The cover picture shows *Pampsilota dahomeyanus* Goergen, Koch & Liston, sp. n.

See paper of **Liston AD, Goergen G, Koch F** Revisions of the Afrotropical genera of Argidae and species of *Pampsilota* Konow, 1899 (Hymenoptera, Tenthredinoidea).

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Revisions of the Afrotropical genera of Argidae and species of *Pampsilota* Konow, 1899 (Hymenoptera, Tenthredinoidea)

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Abstract

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The Afrotropical fauna contains five genera of Argidae. These are keyed. New subjective synonyms, followed by the valid name in brackets, are *Calarge* Enslin, 1911 [*Arge* Schrank, 1802], *Calarge africana* Enslin, 1911 [*Arge congrua* Konow, 1907], *Clyparge* Pasteels, 1963 [*Scobina* Lepelletier & Serville, 1828], *Clyparge terminalis* Pasteels, 1963 [*Scobina poecila* (Klug, 1834)], and *Sterictophora* [sic] *afra* Pasteels, 1963 [*Sphacophilus afer* **comb. n.**, species inquirenda near *S. monjarasi* Smith & Morales-Reyes, 2015]. The type material of both *C. terminalis* and *S. afra* was probably collected in the New World, but labelled with the wrong locality “Kamerun”. An introduction of both species to Africa, not followed by long-term establishment, seems less likely. The removal of these taxa from the faunal list of the region is recommended. The nine known Afrotropical species of *Pampsilota* are revised, and an illustrated dichotomous identification key presented, with distribution maps for all species. Four species are here described as new to science: *P. dahomeyanus* Goergen, Koch & Liston, **sp. n.**, *P. nigeriae* Liston & Koch, **sp. n.**, *P. tsavoensis* Liston & Koch, **sp. n.**, and *P. zebra* Liston & Koch, **sp. n.** Lectotypes are designated for *Pampsilota afer* Konow, 1899, and *Cipdele africana* Mocsáry, 1909. The immature stages and host plant of only one species are known: *P. dahomeyanus* on *Lannea nigritana* (Anacardiaceae). Its larval morphology strongly resembles that of European and North American species of *Arge*. We provisionally retain *Pampsilota* as a valid genus, although it could justifiably be treated as comprising merely a species group, or groups, within *Arge*.

Introduction

Taeger et al. (2010) catalogued seven valid genera of Argidae as present in the Afrotropical Region. As a result of our studies, we concluded that only five valid genera can be considered to be present there: *Arge* Schrank, 1802, *Cibdela* Konow, 1899, *Pampsilota* Konow, 1899, *Sjoestedtia*, Konow, 1907 (Konow 1907a), and *Triarge* Forsius, 1931. With currently 127 valid species, *Arge* is by far the most species-rich sawfly genus in this biogeographic region (Koch et al. 2015). It is also well repre-

sented in the Holarctic and Oriental Regions, but makes up a much smaller proportion of the total sawfly fauna there. A total of about 350 valid species of *Arge* worldwide were catalogued by Taeger et al. (2010). The other four Afrotropical genera are comparatively small. Nine species of *Triarge* are known, all endemic to the winter rainfall zone of southern Africa (Koch et al. 2015). *Sjoestedtia* is only known from the Afrotropical Region, and contains two valid species (Taeger et al. 2010). *Cibdela*, not mentioned from the Afrotropics by Taeger et al. (2010), is represented there only because of the intro-

duction to Réunion, from Sumatra, of *C. janthina* (Klug, 1834) for control of invasive *Rubus alceifolius* JLM Poiret (Rosaceae) (Mathieu et al. 2014). The following revision of *Pampsilota* treats nine Afrotropical species:

- P. afer* Konow, 1899
- P. africanus* (Mocsáry, 1909)
- P. brandbergensis* Koch, 2006
- P. dahomeyanus* sp. n.
- P. leleupi* Pasteels, 1953
- P. luederitzensis* Koch, 2006
- P. nigeriae* sp. n.
- P. tsavoensis* sp. n.
- P. zebra* sp. n.

Taeger et al. (2010) listed three further *Pampsilota* species from the East Palaearctic and Oriental Regions: *P. cenchrus* Wei, 1997, *P. interstitialis* (Cameron, 1877), and *P. scutellis* Wei, 1997. They were described or re-described by Wei (1997) and Saini (2009), with illustrations of some body parts, and are not considered further here. No information on the hosts and immature stages of these species has been published. Recent combinations of some other species names with *Pampsilota* have been proposed, for example by Saini (2009), for several E. Palaearctic and Oriental species group taxa currently placed otherwise mostly in *Tanyphatnidea* Rohwer, 1912 (e.g. Wei 1997, Taeger et al. 2010).

The Afrotropical species of *Pampsilota* are highly heterogeneous in their appearance and morphology. For example, body length ranges from 5.3 mm to 15.3 mm, and whereas the ovipositor sheath is conspicuously compact in *P. afra* (Fig. 5) and *P. dahomeyanus* (Fig. 16), in *P. africanus* (Fig. 10) and *P. zebra* (Fig. 32) it is distinctly pincer-shaped. In other species the valvulae 3 of the ovipositor sheath more or less diverge towards their apices in dorsal view. This high morphological diversity was discussed by Pasteels (1955), who gave as examples the distally conspicuously laterally compressed metatibia and compact valvulae 3 of *P. afer*, compared to the distally cylindrical metatibia and pincer-shaped valvulae 3 of *P. africanus*. However, he concluded that a similarly wide range of character states also occurs in *Arge*, and that the high degree of heterogeneity in *Pampsilota* was therefore not remarkable. Additionally, we found such large interspecific differences in the morphology of the ovipositor itself, and sometimes of penis valves, that we have considerable doubts as to whether the genus is monophyletic as presently circumscribed. The treatment here of *Pampsilota* as distinct from *Arge* is justified on practical grounds, because it enables the easier identification of a number of species which could otherwise be mixed-up with species of the large and taxonomically difficult genus *Arge*.

Our study aims to render the rich Afrotropical fauna of Argidae more easily identifiable, using purely morphological methods, and thus make it accessible for further research.

Material and methods

Specimens were studied with Leica MZ12, Olympus SZX12, and Wild M8 binocular microscopes. Lancets and penis valves were examined with a Leitz Laborlux S transmitted-light microscope, and photographed through this with a Leica Wild MPS32 camera. The outlines for the illustrations of the dorsal and ventral parts of the male genital capsule, including the digitus and cuspis, were obtained using a Leo 1450VP scanning electron microscope. Details of the genitalia were filled in by hand while constantly cross-checking specimens through the microscope. Habitus photos of adults, and details of larvae, were mostly taken with a Leica DFC295 camera attached to an Olympus SZX12 microscope. Larvae were photographed immersed in ethanol, sometimes held in place with fine pellets of glass. Composite images with an extended depth of field were created using the software CombineZ5 (<http://hadleyweb.pwp.blueyonder.co.uk>).

Morphological terminology follows Viitasaari (2002).

Abbreviations used in the text

Material examined is deposited in the following institutions:

HNHM	Hungarian Natural History Museum, Budapest, Hungary.
IITAC	International Institute of Tropical Agriculture, Cotonou, Benin.
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain.
MFN	Museum für Naturkunde Berlin, Germany.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden.
NMKE	National Museum of Kenya, Nairobi, Kenya.
NNIC	Namibian National Insect Collection, Windhoek, Namibia.
OLML	Oberösterreichisches Landesmuseum, Linz, Austria.
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.
UZMT	Zoological Museum, University of Turku, Finland.
ZSM	Zoologische Staatssammlung, Munich, Germany.

Other abbreviations

HT	Holotype
LT	Lectotype
PT	Paratype

Results

The identity and status of *Calarge* Enslin, 1911, and its type species

Arge Schrank, 1802: 226–230. Type species: *Tenthredo enodis* Linnaeus, 1767, by subsequent designation of Rohwer (1911).

Calarge Enslin, 1911: 664. Type species: *Calarge africana* Enslin, 1911, by original designation. **Syn. n.**

Arge congrua Konow, 1907b: 309. Described: female (holotype, MNCN; 1 paratype, NHRM). Type locality: Africa occ., Kamerun [Cameroon]. Images of holotype and labels, by A. Taeger: see <http://dx.doi.org/10.6084/m9.figshare.757716>.

Calarge africana Enslin, 1911: 665. Described: female (holotype, MFN). Type locality: Bipindi, Süd-Kamerun [Cameroon]. **Syn. n.**

Enslin (1911) erected *Calarge* for a single female specimen collected in Cameroon. His main reason for considering this different from *Arge*, was the lack of pre-apical spurs on the metatibiae. We examined the holotype of *C. africana*, and found that it has a small pre-apical spur on the right metatibia, and no spur on the left. Pasteels (1953) had already noted this discrepancy, and concluded [translated from French] “It is therefore not possible to characterise this genus, until further specimens should be found”. In fact, apart from the anomalous development of only a single metatibial spur, the specimen is indistinguishable from *Arge congrua*. Notably, the two nominal taxa share the same distinctively shaped valvulae 3: in dorsal view with a conspicuous, subtriangular median depression; in lateral view wedge-shaped (Pasteels 1953; figs 9a, b). We based our opinion on *A. congrua* on the female paratype, which is the same specimen studied by Pasteels (1953), and the images of the holotype by A. Taeger.

The identity and status of *Clyparge* Pasteels, 1963, and its type species

Scobina Lepeletier & Serville, in Latreille et al., 1828: 574. Type species: *Hylotoma melanocephala* Lepeletier, 1823, by monotypy.

Clyparge Pasteels, 1963: 541–543. Type species: *Clyparge terminalis* Pasteels, 1963, by original designation. **Syn. n.**

Scobina poecila (Klug, 1834)

Hylotoma poecila Klug, 1834: 239. Described: male (holotype, MFN). Type locality: Mexiko [Mexico].

Clyparge terminalis Pasteels, 1963: 543–545. Described: female (holotype, MNCN; 1 paratype, MRAC), male (1 paratype, MNCN). Type locality: “Cameroun” (Cameroon). Images of holotype and labels, by A. Taeger: <http://dx.doi.org/10.6084/m9.figshare.775321>.

Syn. n. *Clyparge terminalis* Pasteels is a junior secondary homonym of *Scobina terminalis* (Klug, 1814).

The only species included in *Clyparge* is *C. terminalis* Pasteels, 1963, known just from the three specimens of the type series. The holotype is labelled “Kamerun 1898. 1899” (Taeger et al. 2014). The photographs made by A. Taeger made it possible to recognise *C. terminalis* as a *Scobina* species. Later, we examined the holotype of *C. terminalis*, which keys without problems in Smith (1992) to *S. poecila* (holotype examined). The sexual dimorphism described by Pasteels (1963) for *C. terminalis* exactly matches that described by Smith (1992) for *S. poecila*. This species is reliably known only from the Neotropical Region: Honduras, north into Mexico (Smith 1992). We suspect that the type material of *C. terminalis* may have been labelled with the wrong locality, as also the single known specimen of *S. afro* Pasteels, 1963, held by the same museum, and labelled in the same handwriting with the same locality name and nearly the same date (see below). We were informed by M. Paris (MNCN) that no details of the acquisition of these particular specimens can be traced in the museum’s records. A connection with the collector Leopold Conradt can be suspected, because he is known to have collected Hymenoptera, including sawflies, in Cameroon (Rohlfien 1975, Horn et al. 1990; but note that the latter work dates the Cameroon expedition to 1896, whereas contemporary publications and the specimen labels consistently give 1898–99), and many such specimens were acquired by the MNCN (M. Paris, personal communication). However, all specimens from Cameroon, leg. Conradt, in MNCN, as well as those in the SDEI, have a standard, printed label: see as an example image by A. Taeger <http://dx.doi.org/10.6084/m9.figshare.757716>. It is not clear who printed these labels. A large amount of material of various insect orders collected by Conradt in Venezuela, Cameroon and Togo was partly sold through the well-known firm of Staudinger (Horn et al. 1990), whereas further parts were received by Gustav Kraatz, founder of what is now the SDEI (Rohlfien 1975), and partly passed on to other individuals and institutions. Although the few characters on the hand-written labels of the type specimens in question do not provide an ideal basis for comparison, they seem not to be in the same hand as a letter in the SDEI archive, written by Conradt to Kraatz. If the four Pasteels’ type specimens really were collected by Conradt, then the complicated subsequent history of the material, which was perhaps at first largely unlabelled, would have increased the risk of a mistake in their labelling. Continuing to speculate that Conradt was the collector, then it is possible that they came from Venezuela, where he collected sometime before 1889 (Horn et al. 1990). Although L. Conradt did collect zoological specimens, including Hymenoptera, in Mexico (e.g. Milliron 1973), this was around 1910 (Beolens et al. 2011), several years after his visit to Cameroon, and as far as is known these specimens remained in collections in the New World. Mexico is therefore a less likely provenance. Of course, it cannot be excluded that both these species were introduced to Africa from the Neotropical Region, but did

not permanently establish themselves. *Sterictiphora afra*, if synonymous with *Sphacophilus monjarasi* (see below), is known to occur together with *Scobina poecila* in Chiapas Province, Mexico (Smith 1992). In view of the very imperfectly known ranges of many Neotropical sawflies, it is however easily possible that the range of *S. monjarasi* is much more extensive, and could extend to Guatemala. That the ranges of the two taxa overlap, offers little help in evaluating whether the Madrid types were obtained during the same collection event in Central America, or were introduced from there to Africa. In either case, because strong corroboratory evidence for their presence in the Afrotropical Region is lacking, we recommend that they should not be considered to currently occur there.

The identity and status of *Sterictiphora afra*

Sphacophilus afer (Pasteels, 1963), comb. n.

Sterictiphora [sic] *afra* Pasteels, 1963: 540–541. Described: male (holotype, MNCN). Type locality: “Cameroun” (Cameroon). Images of holotype and labels by A. Taeger: <http://dx.doi.org/10.6084/m9.figshare.746940>.

Notes. *Sterictiphora afra* Pasteels, 1963 has been regarded as the only Afrotropical species of *Sterictiphora*, an otherwise Holarctic and Oriental genus. The holotype

(examined) is the only known specimen of the species. It is labelled “Kamerun 1898”, in the same handwriting as on the label attached to the type of *Clyparge terminalis* (Taeger et al. 2014): see under that name above. In the keys by Koch (1988) and Smith (1971, 1992), *S. afra* runs without problem to *Sphacophilus* Provancher, 1888. This genus contains about 50 valid species, distributed in the Neotropical and Nearctic Regions. Species taxonomy of *Sphacophilus* is based mainly on females, and males of many species are unknown, or the association of the sexes is problematic (Smith 1992). We were unable to identify the holotype of *S. afra* to species level, using the keys by Smith (1971, 1992) and reference to several original descriptions. However, the colour pattern of the *S. afra* holotype is distinctive within this genus. Apart from the recently described *S. monjarasi* Smith & Morales-Reyes, 2015 (Monjarás-Barrera et al. 2015), no other known species has this combination of completely black head and thorax, including the entire legs, and an almost completely yellow abdomen. *Sphacophilus monjarasi* is unfortunately only known in the female sex. Its type locality is in Chiapas Province, Mexico. In view of the lack of any other evidence for its presence in the Afrotropics, we recommend that *Sphacophilus afer*, simultaneously the only representative of the Sterictiphorinae there, should be removed from the list of Afrotropical sawflies.

Key to genera of Afrotropical Argidae

- 1 Mesotibia and metatibia with preapical spine 2
- Meta- and mesotibia without preapical spine 3
- 2 Fore wing without crossvein 2r-m, and cells 1Rs and 2Rs fused, thus only three submarginal cells present, with the second very large; body usually entirely black..... *Triarge*
- Fore wing with crossvein 2r-m, and cells 1Rs and 2Rs present, thus four submarginal cells present, with the second not conspicuously larger; body usually bicoloured *Arge*
- 3 Body and legs entirely black, with blue metallic lustre .. *Cibdela* [only *C. janthina* (Klug, 1834) is present in the Afrotropics, by deliberate introduction to Réunion]
- Body extensively pale, with or without blue metallic lustre on black parts, or if entirely black at least tibiae pale marked 4
- 4 Interantennal area concave or plane, without interantennal carinae; fore wing with basal anal cell (1A) absent; especially in female head in dorsal view conspicuously narrow, about half as broad as thorax maximum width..... *Sjoestedtia*
- Interantennal area with two more or less conspicuously ridged interantennal carinae; fore wing with basal anal cell (1A) present; head in dorsal view not conspicuously narrow, about two thirds as broad as thorax maximum width... *Pampsilota*

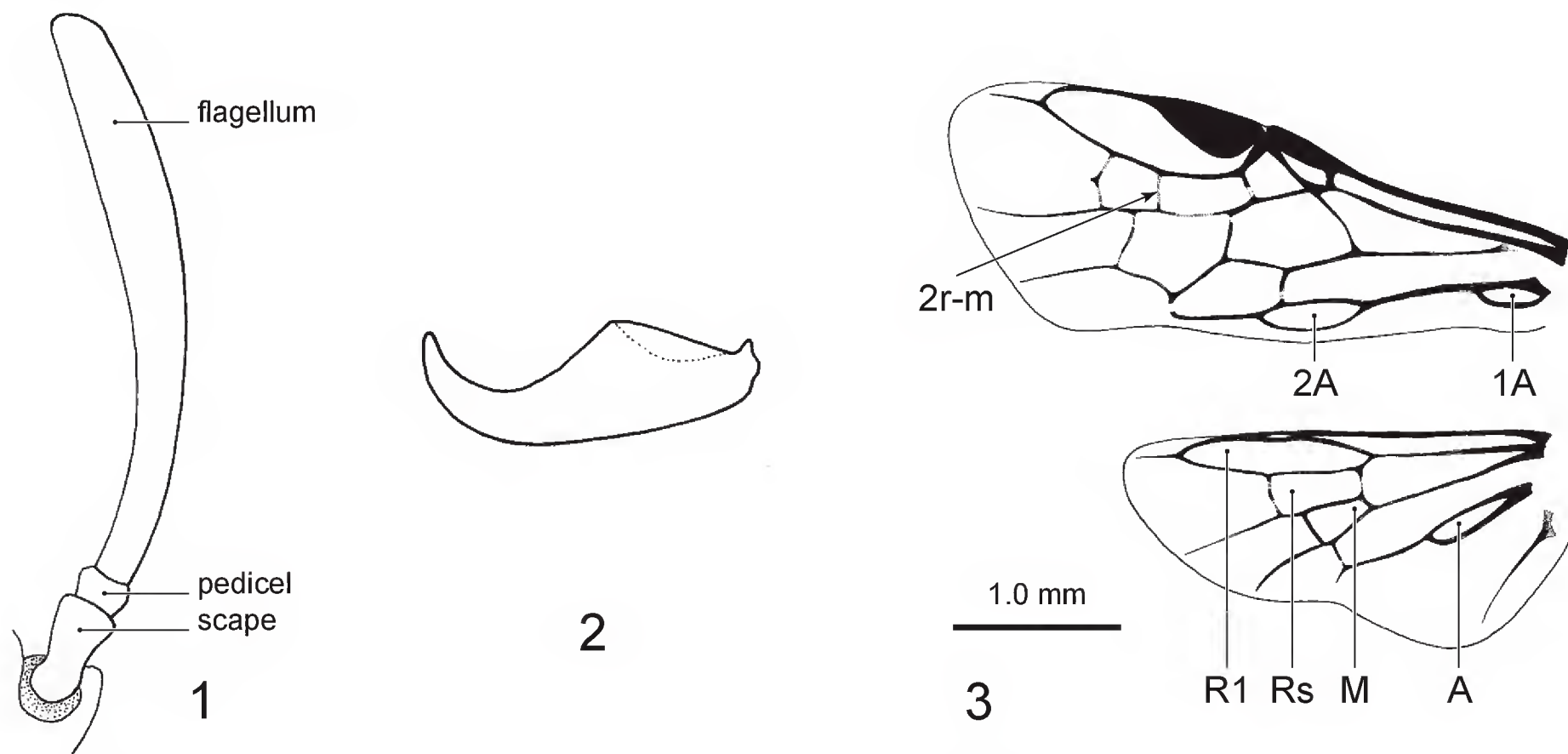
Revision of Afrotropical *Pampsilota* Konow, 1899

Pampsilota Konow, 1899: 76. Type species: *Pampsilota afer* Konow, 1899, designated by Rohwer, 1911. Additional images: <http://www.waspweb.org/Tenthredinoidea/Argidae/Athermantinae/Pampsilota/index.htm>

Description. Antenna has three articles (Fig. 1); scape and pedicel short, flagellum very long and undivided. Clypeus not clearly separated by an epistomal suture from the supraclypeal area, malar space conspicuously

present. Meso- and metatibia without preapical spine; tarsal claws simple (Fig. 2). Fore wing with radial crossvein (2r) absent and crossvein 2r-m present, with basal anal cell (1A) closed, and anal cell (2A) long petiolate (Fig. 3); radial cell of hind wing (R1) closed, with anal cell (A) and two middle cells (Rs and M) present (Fig. 3). Tergum 1 with a more or less narrow and deep median split.

Coloration black with more or less blue metallic lustre, and yellowish or yellow-orange markings. Body length from 5.3 to 15.3 mm.



Figures 1–3. *Pampsilota* sp.: 1. Antenna; 2. tarsal claw; 3. Fore wing (above), hind wing (below).

Host plants. *Lannea nigritana* (Anacardiaceae): only known for *P. dahomeyanus*.

Remarks. Taeger et al. (2010) catalogued three species of *Pampsilota* from the East Palaearctic and Oriental

Regions, as well as five valid species from the Afrotropical Region. Only the absence of the preapical spines on the meso- and metatibia distinguishes adults of *Pampsilota* from those of *Arge*.

Key to Afrotropical *Pampsilota* species

- 1 Abdomen entirely yellow or light brown (Figs 47–50, 64–67)..... 2
- Abdomen more or less bicoloured; yellow, orange and black, mostly with blue metallic lustre (Figs 38–46, 60–61, 68–71), or nearly entirely black (Figs 62–63)..... 4
- 2 Mesopleuron entirely yellow (Figs 48, 50, 65)..... 3
- Mesopleuron dorsally blackish (Fig. 67)..... *P. tsavoensis* sp. n.
- 3 Antenna partly yellow (Fig. 64); propleuron entirely yellow (Fig. 65), stigma conspicuously bicoloured, with basal half and anterior margin whitish, apical half blackish (Figs 64, 65)..... *P. nigeriae* sp. n.
- Antenna entirely black, propleuron dorsally and ventrally blackish margined, stigma unicoloured, black (Figs 47–50)...
..... *P. dahomeyanus* sp. n.
- 4 Fore legs black with at most small areas of tibia dark brown (Fig. 40); very large species, body length usually more than 10.0 mm..... *P. afer* Konow
- At least protibia light brown (Figs 42, 44, 46, 61, 63, 65); smaller species, body length rarely more than 10.0 mm ... 5
- 5 Thorax entirely black (Figs 60–63)..... 6
- At least lateral parts of pronotum pale (Figs 42–46, 64, 65)..... 7
- 6 All femora mostly black (Fig. 63)..... *P. luederitzensis* Koch
- Meso- and metafemur yellow (Fig. 61)..... *P. leleupi* Pasteels
- 7 Legs black without blue metallic lustre, only protibia light brown (Fig. 46)..... *P. brandbergensis* Koch
- Femora black with blue metallic lustre, tibiae predominantly yellow (Figs 44, 68)..... 8
- 8 Costa and subcosta blackish (Figs 68–71); metatarsus entirely black (Figs 69, 71); serrulae (Figs 33, 34); penis valve (Fig. 35)..... *P. zebra* sp. n.
- Costa and anterior of subcosta yellow (Figs 41–44); at least basitarsomere of metatarsus yellow (Figs 42, 44); serrulae (Figs 11, 12); penis valve (Fig. 13)..... *P. africanus* (Mocsáry)

***Pampsilota afer* Konow, 1899**

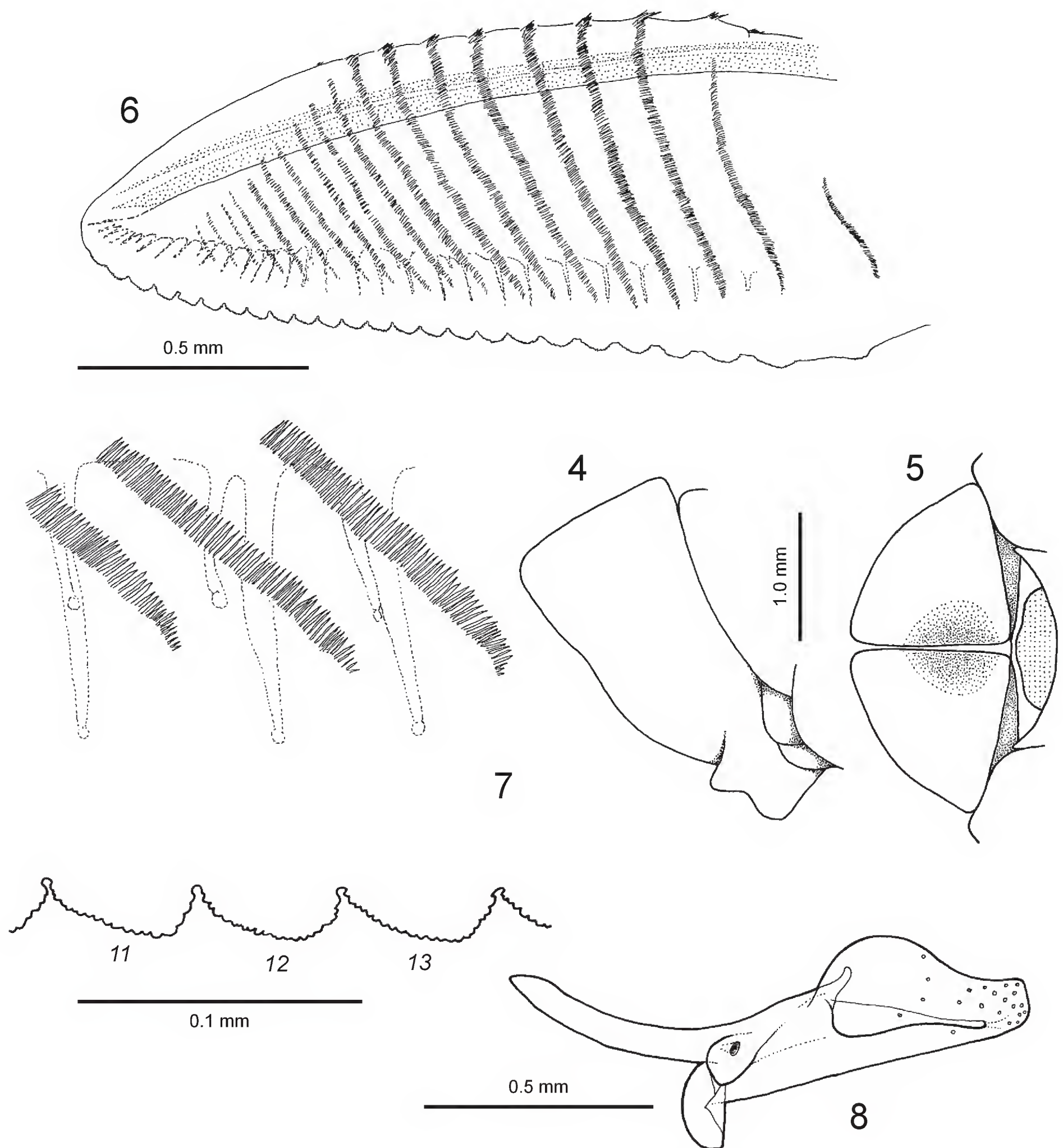
Pampsilota afer Konow, 1899: 76–77. Described: female [syntype females; lectotype designated below]. Type locality: Kamerun [Cameroon].

Pampsilota afer var. *maynéi* Forsius, 1928: 234. Described:

Female [holotype and paratype]. Type locality: Congo Belge [Democratic Republic of the Congo], Bena Bedi. Synonymy with *P. afer* by Pasteels (1953: 115–116).

Female. Figures 4–7, 38–40

Head, thorax and legs black with blue metallic lustre. Wings strongly infuscate, intercostal area fuscous;



Figures 4–8. *Pampsilota afer*: 4. Valvulae 3 (lateral aspect); 5. Valvulae 3 (dorsal aspect); 6. Lancet; 7. Serrulae 11–13; 8. Penis valve (left, lateral aspect).

substigmal spot inconspicuous; stigma, costa, subcosta and rest of venation black. Abdomen black with blue metallic lustre; at least terga 9/10 and ovipositor sheath yellow-orange.

Head enlarged behind eyes. Antenna 1.6× as long as maximum head width; flagellum enlarged towards apex, quadrangular in cross section, interior surface with sharply compressed longitudinal carina, other longitudinal carinae conspicuously more weakly compressed. Interior margins of eyes parallel-sided. Anterior margin of the clypeus circularly emarginate, supraclypeal

area gently rounded and protruding up to ventral limit of interantennal carinae. Interantennal carinae obtusely ridged, strongly converging below, extending to the level of ventral margin of torulus. Frons, supraclypeal area and clypeus rugosely sculptured or densely punctate, weakly shiny, vertex and gena sparsely micropunctate, shiny; pubescence light brown. Metatibia distally conspicuously laterally compressed. Mesoscutum nearly impunctate, shiny; pubescence similar to that on head. Abdomen smooth and shiny. Valvulae 3: Figs 4, 5. Lancet with about 24–25 serrulae: Figs 6, 7.

Length: 10.5–15.3 mm.

Male. Figure 8

Similarly coloured to female, only tergum 8 and sterna 6–9 yellow-orange. Head very slightly narrowed behind eyes. Antenna 1.8× as long as maximum head width; flagellum not enlarged towards apex, quadrangular in cross section, flattened apically, interior surface with sharply compressed longitudinal carina, other longitudinal carinae more weakly compressed. Supraclypeal area scarcely protruding up to base of interantennal carinae. Interantennal carinae extending about one quarter of way to clypeus. Other characters as for female. Penis valve: Fig. 8.

Length: 10.3 mm.

Type material examined. *Pampsilota afer*: Lectotype, hereby designated: ♀. Labels: “Type” (red); “Kamerun”; “Coll. Konow”; “Coll. DEI, Eberswalde”, “*Pampsilota afer* Knw., Kamerun”; “GBIF-GISHym, 2869”; “Lectotypus, *Pampsilota afer* Konow ♀, des.: F. Koch, 2016” (red) (SDEI). Paralectotype: 1 ♀. “Sierra Leone”, “Coll. Konow”, “Coll. DEI, Eberswalde”, “GBIF –GISHym, 2870” (SDEI).

Pampsilota afer var. *maynéi*: Paratype: 1 ♀. Democratic Republic of the Congo: Bena Bedi, V.[19]15, R. Mayné (UZMT).

Other material examined. 1 ♂, 7 ♀♀. Democratic Republic of the Congo: Luluabourg, P. Janssens (1 ♀) (RBINS); Sankuru, Komi, III.1930, J. Ghesquière (1 ♀); Eala, III.1936, J. Ghesquière (1 ♀) (MRAC); Kabwe, Luluabourg, 1937, R. R. Soeurs du Carmel (1 ♂) (MRAC); Fulubwe, sur herbes viv., E[lisabeth]’ Ville, 27.XII.[19]55 (1 ♀) (MRAC). Equatorial Guinea: Fernando-Po, 1901, L. Conradt (1 ♀) (MNCN); Makom, Alcu., Benitogbt., 16.–31.XII.[19]06, G. Tessmann (1 ♀) (MFN); Uelleburg, VI.–VIII.1908, G. Tessmann (1 ♀) (ZSM).

Distribution. Cameroon, Equatorial Guinea, Democratic Republic of the Congo, Sierra Leone (Fig. 36).

Diagnosis. By its large size and distinctive coloration (infusate wings; black body and legs, with only abdomen apically pale), *P. afer* is easily distinguished from all other *Pampsilota* species.

Remarks. The coloration of the abdomen varies from the described typical (darker) form to the apical half of the abdomen yellow-orange with terga 5/6 medially more or less black. In these pale specimens sterna 2–4 are basally yellow-orange. This form with a more or less entirely yellow-orange apical half of abdomen was described under the name *Pampsilota afer* var. *maynéi* Forsius, 1928. Other morphological differences to the nominate form are not detectable. The holotype (MRAC) of *Pampsilota afer* var. *maynéi* was not examined, but the paratype seems to have been collected on the same date and at the same place as the holotype, and there is no reason to doubt that the specimens are conspecific.

Pasteels (1953) first described the male of *P. afer* and misleadingly referred to the specimen as the allotype (MRAC).

***Pampsilota africanus* (Mocsáry, 1909)**

Cipdele [sic!] *africana* Mocsáry, 1909: 6. Described: female [unknown number of syntypes]. Type locality: Kilima-Ndjaru [Kilimanjaro, Tanzania].

Pampsilota africanus: Enslin 1913: 322–323.

Pampsilota africanus var. *interruptus* Forsius, 1928: 234–235. Described: female [holotype]. Type locality: Tanganyika [Tanzania], Tabora-Kigoma. Synonymy with *C. africana* by Pasteels 1955: 340.

Cipdele africana var. *interrupta*: Pasteels 1953: 119–120.

Female. Figures 9–12, 41–42

Head and thorax black with metallic lustre. Pronotum yellow with anterior margin and medial area black. Legs black with blue metallic lustre; pro- and mesotibia entirely yellow, metatibia yellow with narrow blackish apex, basitarsomeres yellow with apex of meso- and metabasitarsomere blackish. Wings including intercostal area flavescens-hyaline; substigmal spot small and fuscous; stigma black; costa and subcosta yellowish; rest of venation blackish. Abdomen yellow-orange; terga 1–6(7) broadly black with blue metallic lustre; terga 8/9 entirely black, sterna 5–7 more or less black; valvifers 2 of ovipositor sheath black.

Head very slightly enlarged behind eyes. Antenna 1.4× as long as maximum head width; flagellum enlarged towards apex, quadrangular in cross section, interior surface with sharply compressed longitudinal carina, other longitudinal carinae conspicuously weaker compressed. Eyes slightly converging towards clypeus. Anterior margin of the clypeus broadly, shallowly, circularly emarginate. Supraclypeal area gently rounded, protruding up to ventral limit of interantennal carinae. Interantennal carinae obtusely ridged, converging below, extending to about the level of ventral margin of torulus. Frons, vertex, supraclypeal area and clypeus densely punctate, dull. Postocellar area and gena moderately densely micropunctate, shiny; pubescence whitish. Metatibia not distally laterally compressed (nearly circular in cross section). Mesoscutum punctation similar to gena, shiny; pubescence similar to that on head. Abdomen smooth and shiny. Valvulae 3: Figs 9, 10. Lancet with about 17–18 serrulae: Figs 11, 12.

Length: 8.0–8.7 mm.

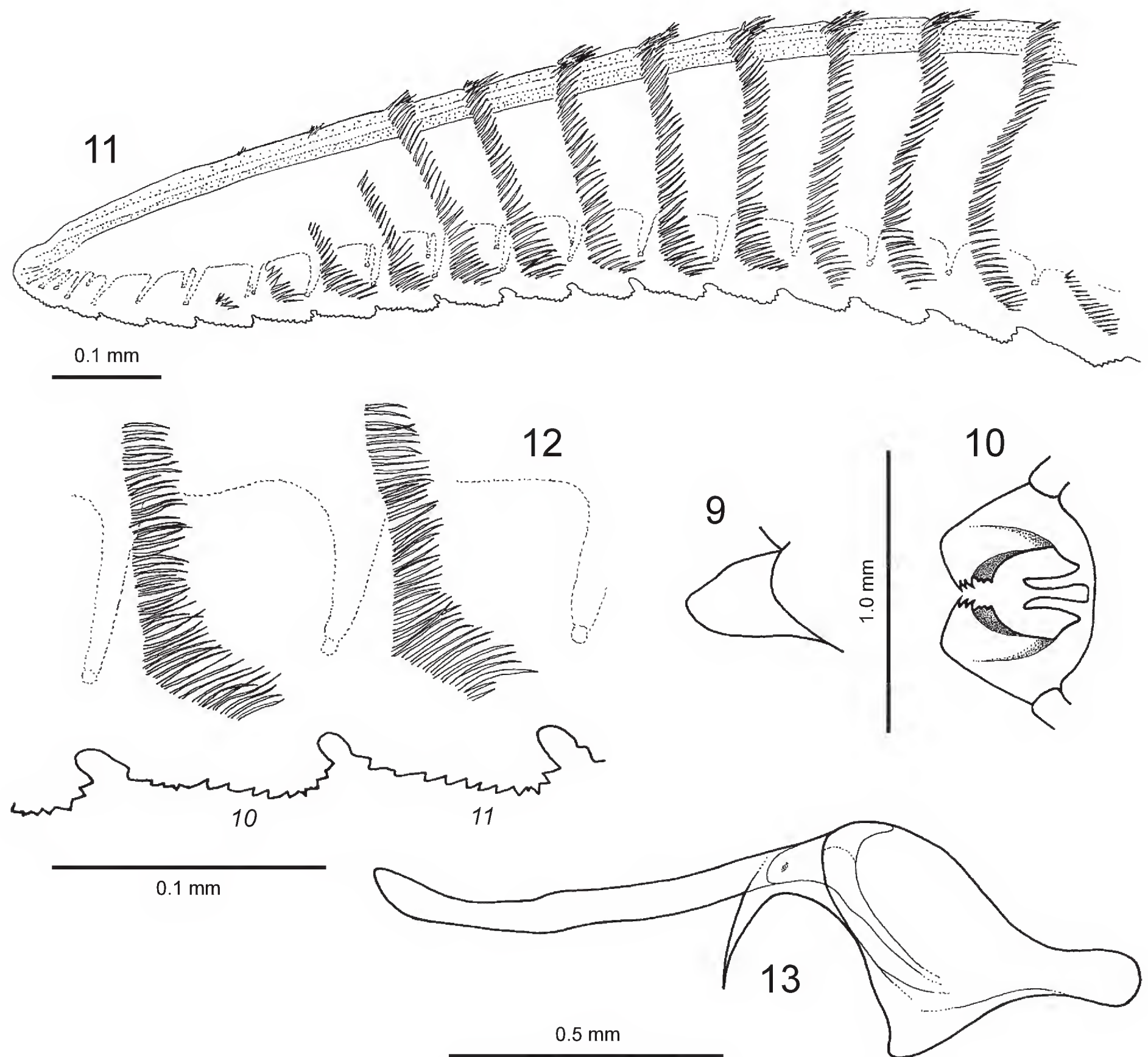
Male. Figures 13, 43–44

Similarly coloured to female, except narrow posterior margin of tergum 9 yellow, and tibiae entirely yellow.

Antenna 1.7× as long as maximum head width; flagellum not enlarged towards apex, about oval in cross section, interior surface with sharply compressed longitudinal carina, outer carina conspicuously more weakly compressed, other carinae negligible. Supraclypeal area gently rising up to ventral limit of interantennal carinae. Other characters as for female. Penis valve: Fig. 13.

Length: 7.3–8.3 mm.

Type material examined. *Cipdele africana*: Lectotype, hereby designated: ♀. Labels: “Kilimandjaro [Kilimanjaro], Bornemissza [Tanzania]”; “Africa, or.,



Figures 9–13. *Pampsilota africanus*: **9.** Valvulae 3 (lateral aspect); **10.** Valvulae 3 (dorsal aspect); **11.** Lancet; **12.** Serrulae 10–11; **13.** Penis valve (left, lateral aspect).

Arusha-Ju, 1906, Katona”; “Lectotype *Cipdele africana* Mocsáry, 1909 designated A. Liston 2015” (red); “GBIF GISHym 21276” (HNHM). Paralectotype: 1 ♀. Tanzania: same data as lectotype (HNHM).

Pampsilota africanus var. *interruptus*: Holotype: ♀. Labels: “E[ast] Tanganyika: Tabora-Kigoma, Lt. Stamp-er”; “*Pampsilota africanus* Mocs. var. *interruptus* n. ♀, type, R. Forsius det.”; “R. Dét. M, 1477”; “Type ♀” (red); “*Pampsilota africana* Mocs. (= *P. africana* M. var. *interrupta* Fors.)”; “DEI-GISHym. 21245”; “Holotypus, *Pampsilota africanus* var. *interruptus* Forsius ♀, teste: F. Koch, 2016” (red); “*Pampsilota africanus* (Mocsáry) ♀, det.: F. Koch, 2016” (MRAC).

Other material examined. 13 ♂♂, 17 ♀♀. Kenya: Stony Athi, Biol[ogical] Survey 5-40 (1♀) (NMKE); Eastern Katutu, Kihtioko, 27.XI.1999, M. Snižek

(5♂♂, 2♀♀); Taita, Mwatate, 30.XI.1997, M. Snižek (3♂♂, 8♀♀); 50km Namanga, Ilbisil env., 18.XI.1997, M. Snižek (1♀). Tanzania: (NE), W of Kiberashi, Kitwei plain, 16.III.2002, M. Snižek (5♂♂, 5♀♀) (MFN, OLML, SDEI, USNM).

Distribution. Tanzania, Kenya (Fig. 36).

Diagnosis. *Pampsilota africanus* resembles *P. zebra* in having pincer-shaped valvulae 3 (compact or diverging in all other species), metatibia distally nearly circular in cross section, and in the main colour characters (thorax black except for pronotum and sometimes tegulae, legs partly pale, and abdomen at least ventrally partly pale). *P. africanus* has a yellow costa and anterior of subcosta, whereas in *P. zebra* costa and subcosta are black. The tegulae of *P. africanus* are sometimes bicoloured, but in *P. zebra* always black. The hind tibia of *P. africanus* is nearly unicolorous

pale, and in *P. zebra* broadly ringed apically with blackish. The serrulae of these species are very differently shaped (Figs 12, 34), but their penis valves are quite similar (Figs 13, 35).

Remarks. *Pampsilota africanus* varies especially in the coloration of the abdomen. Sometimes the black on terga 2/3 is reduced to a small median spot, or as in *P. africanus* var. *interruptus* terga 2–4 are entirely yellow. No other morphological differences exist between the nominate form and var. *interruptus*, and their synonymy by Pasteels (1955) was justified.

Pampsilota brandbergensis Koch, 2006

Pampsilota brandbergensis Koch, 2006a: 120. Described: male [holotype and paratype]. Type locality: Brandberg Massif, Namibia.

Male. Figures 14, 45–46

Head black; flagellum dark brown. Thorax black; pronotum and tegula yellow. Legs black; anterior surface of protibia brownish yellow, posterior surface brown. Wings subhyaline including intercostal area; substigmal spot very small and slightly infuscate, costa and stigma light brown, subcosta and rest of venation brown. Dorsal surface of abdomen black with very slight metallic lustre; terga 3–5 yellow, tergum 5 medio-apically blackish spotted, terga 2/6 yellow laterally, sterna 3–6 yellow, sometimes with blackish markings medio-apically, sternum 9 with yellow apical half.

Head narrowed behind eyes. Antenna 2.0× as long as maximum head width; flagellum scarcely enlarged towards apex, triangular in cross section, somewhat flattened apically, interior surface with sharply compressed longitudinal carina, other longitudinal carinae more weakly compressed. Eyes slightly converging towards clypeus. Anterior margin of the clypeus shallowly circularly emarginate, supraclypeal area flatly rising up to base of interantennal carinae, interantennal carinae sharply ridged, scarcely converging below, extending about one third of way to clypeus. Vertex, frons and clypeus impunctate, shiny; gena with micropunctures, shiny; pubescence whitish. Mesoscutum nearly impunctate, shiny; pubescence similar to that on head. Abdomen shiny; terga 1–3 with irregular microsculpture, posterior margin of tergum 8 with large triangular membranous median depression. Penis valve: Fig. 14.

Length: 5.5–6.0 mm.

Female. Unknown.

Type material examined. Holotype: ♂. Labels: “Namibia, Brandberg, Mason Shelter, 21°04'39''S/14°05'43''E, 05.–14.III.2002, Malaise trap, river bed, A. H. Kirk-Spriggs & E. Marais”; “Holotypus, *Pampsilota brandbergensis* sp. n. ♂, det.: F. Koch, 2005” [red] (NNIC). Paratype: ♂: same data as holotype, except: below Wasserfläche, 21°10'43''S/14°32'51''E,

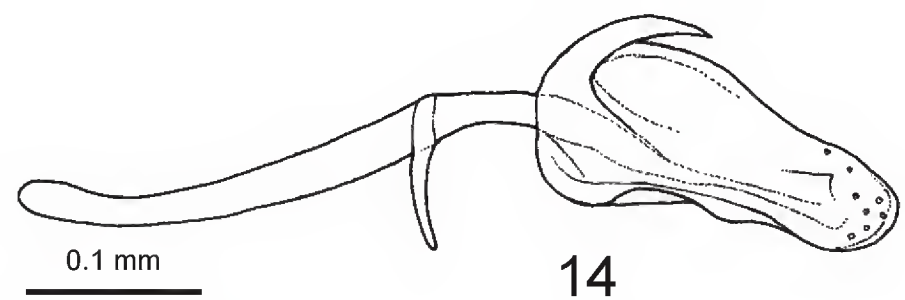


Figure 14. *Pampsilota brandbergensis*: Penis valve (left, lateral aspect).

18.–22.III.2001, Malaise trap, A. H. Kirk-Spriggs & E. Marais (MFN).

Distribution. Namibia (Fig. 36).

Diagnosis. Together with *P. luederitzensis*, also from southwest Africa, *P. brandbergensis* differs from other *Pampsilota* in its body length of maximally 6.0 mm (other species at least 7.0 mm long). The yellow pronotum and entirely black legs of *P. brandbergensis* distinguish it immediately from *P. luederitzensis*, with dark pronotum and largely pale tibia.

Remarks. Variability in colour pattern is scarcely noticeable in the two known specimens, except that tergum 5 as well as sterna 3–5 may be entirely yellow, and the pronotum may have a small ventro-lateral blackish spot.

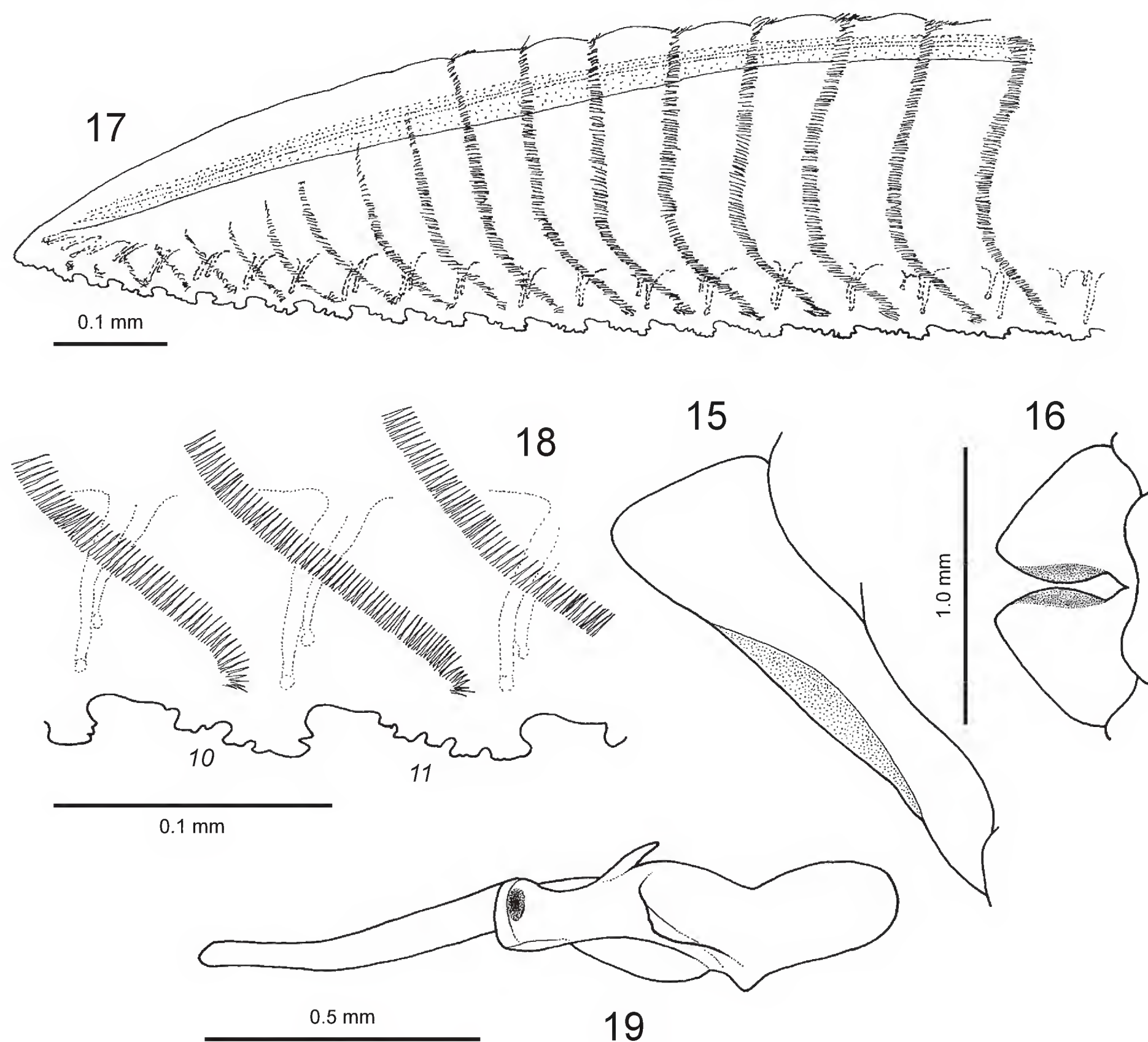
Pampsilota dahomeyanus Goergen, Koch & Liston, sp. n.

<http://zoobank.org/74BDE11B-8CA9-4566-8E73-9FEE395BD4BA>

Female. Figures 15–18, 47–48

Head black; labrum yellow. Thorax yellow with following black: mesoscutum except for a small lateral spot on lateral lobe adjacent to tegula; mesoscutellum and metanotum; dorsal and ventral margin of propleuron. Legs yellow; mesotibia very narrowly and metatibia broadly ringed blackish apically; mesotarsomeres with black apex, metatarsomeres black, with basal half of metabasitarsomere yellow. Wings bicoloured: basal half flavescens, apical half and intercostal area infuscate; substigmal spot fuscous and small; stigma, subcosta and venation in apical half black; costa and venation in basal half yellowish. Abdomen yellow.

Head parallel-sided behind eyes. Antenna 1.4× as long as maximum head width; flagellum enlarged towards apex, quadrangular in cross section, interior surface with sharply compressed longitudinal carina, other longitudinal carinae more weakly compressed. Eyes slightly converging towards clypeus. Anterior margin of the clypeus with shallow circular emargination, supraclypeal area slightly rounded, protruding up to base of interantennal carinae, interantennal carinae obtusely ridged, very slightly converging below, extending about to the level of ventral margin of torulus. Frons, supraclypeal area and clypeus moderately densely punctate, shiny; vertex and gena scattered micropunctate, shiny; pubescence yellowish. Anterior half of mesoscutum densely punctate, weakly shiny; posterior half nearly impunctate, shiny; pubescence similar to that



Figures 15–19. *Pampsilota dahomeyanus*: 15. Valvulae 3 (lateral aspect); 16. Valvulae 3 (dorsal aspect); 17. Lancet; 18. Serrulae 10–11; 19. Penis valve (left, lateral aspect).

on head. Abdomen smooth and shiny. Valvulae 3: Figs 15, 16. Lancet with about 19–20 serrulae: Figs 17, 18.

Length: 7.8–9.0 mm.

Male. Figures 19, 49–50

Coloration similar to female except for a more or less large yellowish patch on clypeus and supra-clypeal area. Sometimes mesoscutellum yellow only medially and on posterior half. Mesotibia entirely, mesotarsus nearly entirely yellow; metatarsomeres black ringed apically. Wings slightly infuscate throughout; stigma, subcosta and venation blackish, only costa yellowish.

Head slightly narrowed behind eyes. Antenna 1.9× as long as maximum head width; flagellum scarcely enlarged towards apex, scarcely flattened apically, slightly triangular in cross section; interior surface with sharply compressed longitudinal carina, other longitudinal carinae much more weakly compressed. Other characters as for female. Penis valve: Fig. 19.

Length: 7.3–7.7 mm.

Type material. Holotype: ♀. Labels: “Benin, Cotonou, on *Lannea nigritana*, 3.X.2014, leg.: G. Goergen”; “Holotype, *Pampsilota dahomeyanus* n. sp. ♀, det.: F. Koch, 2016” [red] (MFN). Paratypes [all from Benin, leg. G. Goergen]: 2 ♂♂; 4 ♀♀: same data as holotype (MFN, SDEI, USNM). 2 ♂♂; 1 ♀♀: Pobè-Forest, 6°57′46.7″N 2°40′26.7″E, on *Lannea nigritana*, 26.08.2016 (MFN). 2 ♀♀: Bohicon, 7°11′29.7″N 2°04′08.3″E, on *L. nigritana*, 07.2014 (MFN, SDEI). 2 ♂♂: Pahou, forest area, 05.07.2010 (MFN). 3 ♂♂, data as preceding, except 11.2014, on *L. nigritana* (MFN). 1 ♂ Womè, 11.2014 (MFN). 11 ♂♂; 9 ♀♀: Calavi IITA, ex larvae collected from and reared on *Lannea nigritana*, 11.2014, (IITAC). 14 ♂♂: Cotonou, 6°22′59.4″N 2°13′32.0″E, on *Lannea nigritana*, 05.10.2010 (IITAC). 3 ♂♂; 3 ♀♀: Cotonou, on *Lannea nigritana*, 05.10.2014 (IITAC).

Larva. Figures 51–55.

Individuals of two instars were examined in detail: GBIF GISHym 21229, total length 13mm, head capsule width 1.4mm; GBIF GISHym 21236, total length 6mm, head capsule width 0.9mm. Mature larvae reach a length of about 25 mm. All examined instars extremely similar in coloration except that the abdominal prolegs are pale in later instars (Fig. 51), and blackish in younger larvae (Fig. 52). The trunk is mainly green (Fig. 53). They possess the ground-plan characters of Argidae as given by Lorenz and Kraus (1957): one antennomere, abdominal segments 2–9 with 3 dorsal annulets, and tarsus of thoracic legs (Fig. 54) with large empodium.

Head with frons mainly dark, and extensive partly confluent black patches on parietal region and vertex (Figs 51, 55). Mandible with 2 setae. Maxillary palp with 6 setae on outer surface. Clypeus with 2 setae. Anterior edge of labrum with fringe of about 12 setae directed in same plane as labrum; two longer setae arise near the centre and are directed outwards. Frons with about 35 short setae, mostly shorter than diameter of antennomere. Rest of upper head moderately setose; setae mostly shorter than diameter of antennomere. All setae fine and pale. Labrum without central groove.

Thoracic legs with six articles (Fig. 54). Claw with strongly developed basal lobe. Coxa and trochanter black; distal articles brown. Cervical sclerite black. Thoracic subspiracular and surpedal lobes strongly projecting; black, including setae. Spiracular area of prothorax with three black markings.

Entire surface of trunk with numerous very short, fine, pale setae. On dark-pigmented areas of thorax and abdominal segments 1, 2 and 10, setae are darker and longer. All three dorsal annulets of meso- and metathorax and abdominal segments 1–2 with row of small, dark-pigmented glandubae (Fig. 52). Prothorax with fewer small glandubae, but paired medial black markings larger than on other segments (Fig. 52). Pigmentation of glandubae on abdominal segment 2 paler than on more anterior parts of dorsum. Pigmentation, size of glandubae on the abdominal dorsum and length of their setae diminish progressively towards the posterior (Fig. 52). Subspiracular lobe on abdominal segments 1–3(4) more or less marked with black, extent of black decreasing from segment to segment towards posterior.

Abdomen strongly tapering caudally, ventral surface appearing flat in live specimens. Prolegs very small; developed on abdominal segments 2–6 and 10 (Figs 51, 52), with numerous setae on exterior and interior surfaces; on segments 7–9 a minute scar-like vestige probably homologous with a proleg. Suranal lobe, dorsal and ventral surfaces of subanal lobe extensively black (Fig. 52). Posterior surface of anal prolegs dark-marked. Caudal edge of suranal lobe rounded (Fig. 51). Subanal lobe projecting beyond suranal lobe (Fig. 52). Setae on dorsal surface of subanal lobe particularly long and dense.

Prepupa and pupa. The trunk of the prepupa (Fig. 58) is darker than the larva, the head paler (mostly brown). The pattern of dark thoracic markings is retained. The

pupa (Fig. 59) is at first pale, darkening progressively as it nears eclosion.

Host plant. Larvae were found and reared by G. Goergen at the IITAC on *Lannea nigritana* (Scott-Elliot) Keay (Anacardiaceae), a small (height 3–6 m), deciduous, heliophilous tree species occurring from Senegal to Gabon, West and Central Africa.

Natural history. Flight period: June to December, peaking in July and October especially shortly after the annual flushing of individual trees of *Lannea nigritana*. During peak periods numerous adult sawflies were observed on the host plant. In early October 2014 host trees at the type locality were severely defoliated by *P. dahomeyanus*, and large numbers of larvae of all instars were found together with adults. Oviposition is generally on older leaves, with 1–3 eggs laid singly in slits cut into the leaf-blade, next to the midrib, at the base of a leaflet (Fig. 56). The female sits on the upperside of the leaf during oviposition. Larvae are gregarious (Fig. 53): a group of larvae occupies a whole compound leaf and feeds on plant tissues of all ages. As they mature, larvae turn from dull green to pale yellow. In the laboratory, maturation of the 33 larvae reared from field-collected eggs took about 12 days. When fully grown, the larvae drop onto the soil to spin cocoons. About half of the cohort reared in October 2014 made cocoons, sometimes stuck together, in the leaf litter near the soil surface. Cocoons of the remaining larvae were found at about 5 cm below the soil surface. The cocoon is elongate-oval, about 9 mm long, double-walled, with sand grains attached to the outside (Fig. 57). The outer wall is irregularly netted, the inner wall parchment-like separated from the first by a loose layer of silk strands. Whereas eclosion of the individuals which made cocoons above ground occurred already between 20–27 October 2014, i.e. 7–14 days after making their cocoons, adults emerged from cocoons made in the ground in the period 8–25 June of the following year, i.e. 207–224 days after entering the ground. In both instances, there was no obvious pattern in the emergence of male and female sawflies. It is concluded that *P. dahomeyanus* has a multivoltine life cycle with polymodal adult emergence. Parasitism: during larval peak periods imagines of an unidentified *Boethus* species (Hymenoptera, Ichneumonidae, Tryphoninae) were observed attaching eggs externally to the surface of the larvae. Members of the genus are known as koinobiont parasitoids of Argidae larvae. This is the first record of *Boethus* from West Africa.

Etymology. The new species name, a Latinised adjective, refers to the historical West African kingdom of Dahomey, the later Republic of Benin, in which the type locality is situated.

Distribution. Benin (Fig. 36).

Diagnosis. *Pampsilota dahomeyanus* adults resemble those of *P. nigeriae* and *P. tsavoensis* in the nearly entirely yellow colour of the abdomen and thorax underside. *Pampsilota nigeriae* is separated from *P. dahomeyanus* by its predominantly light brown to yellow antenna, entirely yellow propleuron, bicoloured stigma, and very

different penis valve (Fig. 26). *Pampsilota tsavoensis* differs from *P. dahomeyanus* in the blackish dorsal part of its mesepisternum, the shape of the serrulae (Figs 29, 30), and in the shape of the valvulae 3: conspicuously divergent in dorsal view, with distinct denticles on the interior surface (Fig. 28), whereas in *P. dahomeyanus* the ovipositor sheath is more compact, with the valvulae 3 not diverging distally, and without denticles (Fig. 16). The similarly coloured *P. nigeriae*, of which only a single male is known, differs from both species in the predominantly yellow antenna and the bicoloured stigma, and from *P. dahomeyanus* especially in the shape of the penis valve (Fig. 26).

Remarks. Especially males of *P. dahomeyanus* are highly variable in coloration. Four specimens have an entirely black mesonotum, metascutellum, black tegula, blackish markings on the pronotum and tergum 1, and terga (5)6–8 nearly entirely black. However, no accompanying differences in the shape of the penis valve were detected. Sometimes, in both sexes, the clypeus and the supraclypeal area are marked with dirty yellow. In the material studied, one male was found to have a very small subapical spine on one metatibia. We interpret this as a rare reversion to what may be the plesiomorphic character state.

General morphology of the larva is very similar to the Arginae species described by Lorenz and Kraus (1957; in that work represented only by larvae of *Arge*), and Smith (1989). Compared to Sterictiphorinae, *P. dahomeyanus* larvae share characters of *Arge*: thoracic leg with six articles (at most 5 in Sterictiphorinae), abdominal postspiracular lobes without raised or subcutaneous glands (present in Sterictiphorinae), subanal lobe without pseudocerci (present in Sterictiphorinae). There is no detailed published description of an Afrotropical argid larva with which to compare *P. dahomeyanus*.

Pampsilota leleupi Pasteels, 1953

Pampsilota leleupi Pasteels, 1953: 116–117. Described: male [holotype]. Type locality: Territoire de Sandoa, Kawanga, Congo belge [Democratic Republic of the Congo].

Male. Figures 20, 60–61

Head black with blue metallic lustre; antenna black. Thorax black with blue metallic lustre, except for yellow metapleuron. Legs dirty yellow to light brown with following black with more or less blue metallic lustre: coxae, trochanters, profemur, extreme apex of meso- and metatibia, protarsus, more or less distal tarsomeres of meso- and metatarsus. Wings strongly infuscate; intercostal area and small substigmal spot fuscous, stigma, costa, subcosta and rest of venation black. Abdomen yellow; terga 1/2 nearly entirely black, tergum 3 broadly black, tergum 4 blackish spotted medially.

Head very slightly enlarged behind eyes. Antenna 1.6× as long as maximum head width; flagellum not enlarged

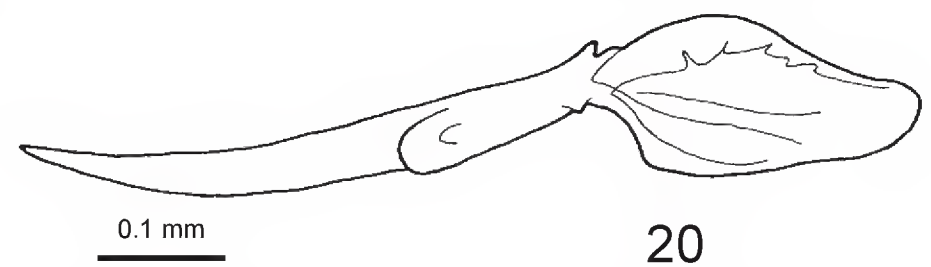


Figure 20. *Pampsilota leleupi*: Penis valve (left, lateral aspect).

towards apex, triangular in cross section, scarcely flattened apically, interior surface with sharply compressed longitudinal carina, other longitudinal carinae weakly compressed. Eyes slightly converging towards clypeus. Anterior margin of the clypeus shallowly circularly emarginate, supraclypeal area scarcely protruding up to ventral limit of interantennal carinae, interantennal carinae sharply ridged, conspicuously converging below, extending about one quarter of way to clypeus. Frons, supraclypeal area and clypeus moderately densely micropunctate, shiny, vertex and gena sparsely micropunctate, shiny; pubescence brownish. Mesoscutum sparsely micropunctate, shiny; pubescence similar to that on head. Abdomen irregularly microsculptured, with conspicuous dense pubescence. Penis valve: Fig. 20.

Length: 9.7 mm.

Female. Unknown.

Type material examined. Holotype: ♂. Labels: “Coll. Mus. Congo., Territ[oire] de Sandoa, Gal[erie] forest[ière] Kawanga, 20.XI.1948, N. Leleup”; “*Cipdela Leleupi* n. sp. ♂, J. Pasteels det. 1952”; “Holotype” (red); “Genit. ♂, H4-47”; “R. Det., 5967”; “DEI-GISHym 21244”; “Holotypus” (red); “Holotypus, *Pampsilota leleupi* Pasteels ♂, teste: F. Koch, 2016” (red); “*Pampsilota leleupi* Pasteels ♂, det.: F. Koch, 2016” (MRAC).

Distribution. Democratic Republic of the Congo (Fig. 37).

Diagnosis. *P. leleupi* resembles *P. afer* in its large body size, thorax without pale markings, and abdomen at least partly pale, but *P. leleupi* is easily recognised by its extensively pale legs (largely black in *P. afer*).

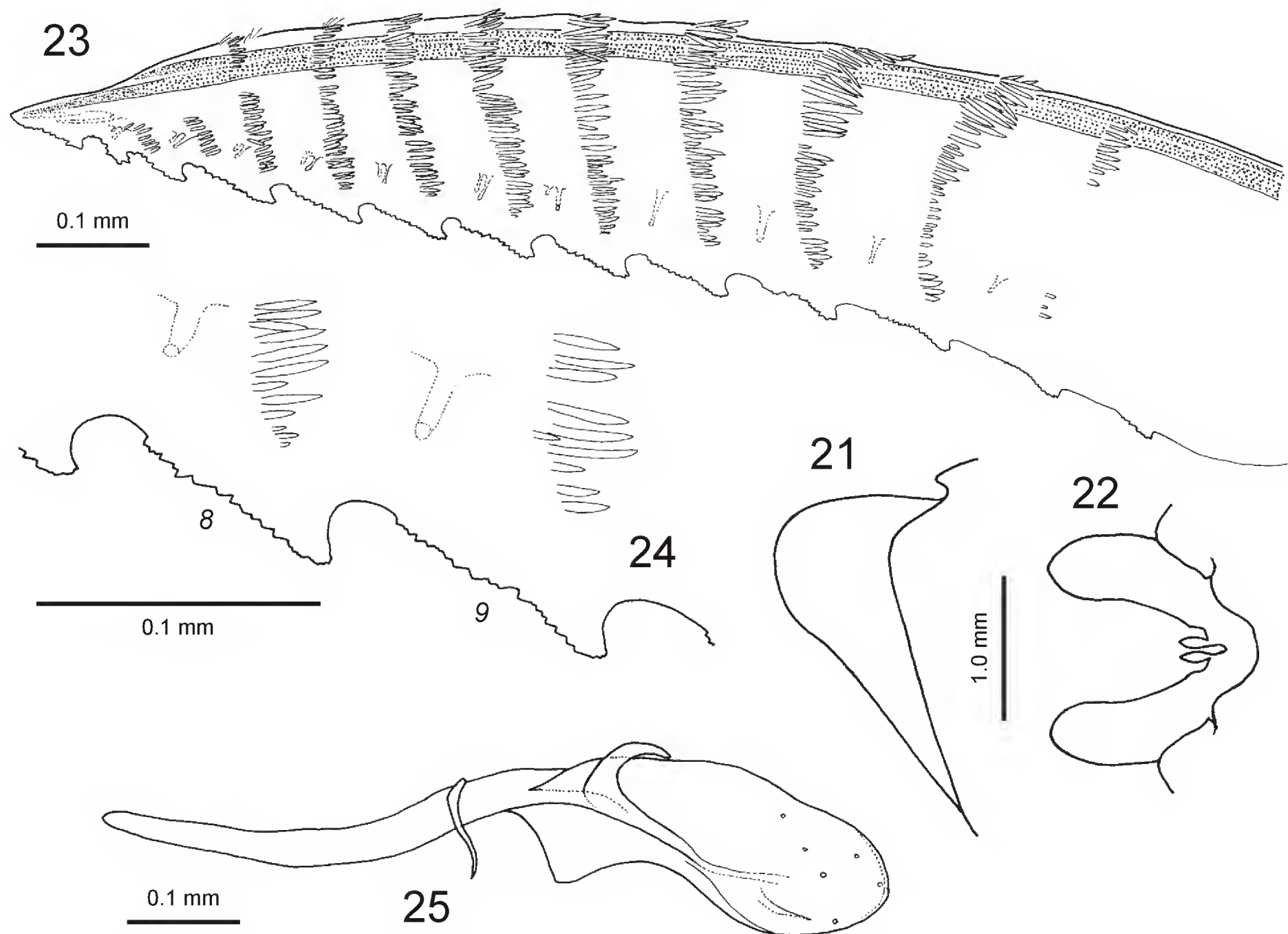
Remarks. The genitalia preparation mentioned above (“Genit. ♂, H4-47”) was not available (personal communication from Stephane Hanot, collection manager at MRAC, 26.02.2015). The illustration of the penis valve is therefore taken from Pasteels (1953).

Pampsilota luederitzensis Koch, 2006

Pampsilota luederitzensis Koch, 2006b: 224. Described: female [holotype], male [1 paratype]. Type locality: Namibia, Lüderitz, Scorpion Hill.

Female. Figures 21–24

Head black, including antenna. Thorax black. Legs black; tibiae whitish, apically slightly brownish, tarsi brownish. Wings hyaline with intercostal area slightly flavescence-hyaline; substigmal spot very small and slightly



Figures 21–25. *Pampsilota luederitzensis*: **21.** Valvulae 3 (lateral aspect); **22.** Valvulae 3 (dorsal aspect); **23.** Lancet; **24.** Serrulae 8–9; **25.** Penis valve (left, lateral aspect).

infusate; costa light brown with basal half white, stigma, subcosta and rest of venation light brown. Abdomen yellowish brown; terga 1,2 black, terga 3–5 with small light brown median spot, tergum 5 additionally with light brown posterior margin, terga 6/7 brown; ventral surface of abdomen brown with yellow longitudinal median stripe.

Head parallel-sided behind eyes. Antenna $1.6\times$ as long as maximum head width; flagellum scarcely enlarged towards apex, quadrangular in cross section, somewhat flattened towards apex, ventral surface with moderately compressed longitudinal carina, other longitudinal carinae more weakly compressed. Eyes slightly converging towards clypeus. Anterior margin of clypeus shallowly, circularly emarginated; supraclypeal area roundly protruding up to ventral limit of interantennal carinae; interantennal carinae sharply ridged between antennae, converging below, extending about one third of way to clypeus. Vertex, frons, gena, clypeus and supraclypeal area sparsely micropunctate, shiny; pubescence whitish. Mesoscutum nearly impunctate, shiny; pubescence similar to that on head; lateral lobe of mesoscutum with narrow glabrous stripe. Valvulae 3: Figs 21, 22. Lancet with about 13 serrulae: Figs 23, 24.

Length: 6.0 mm.

Male. Figures 25, 62–63

General coloration similar to that of female. Head and mesoscutum with slight metallic lustre; anterior margin of labrum brownish. Tarsi light brown. Costa almost entirely whitish. Abdomen blackish, tergum 3 yellowish with light brown median spot, terga 4/7 light brown, distal terga yellow; sterna 7/9 yellow.

Antenna $1.7\times$ as long as maximum head width; apex of flagellum flattened, interior surface with sharply compressed longitudinal carina. Other characters as for female. Penis valve: Fig. 25.

Length: 5.3 mm.

Type material examined. Holotype: ♀. Labels: “Namibia, Lüderitz, Scorpion Hill, $27^{\circ}49'S/16^{\circ}36'E$, 09.–12. VIII.1997, Malaise trap, Marais’s & Kirk-Spriggs”; “Holotypus, *Pampsilota luederitzensis* sp. n. ♀, det.: F. Koch, 2005” (red) (NNIC).

Paratype: 1 ♂: Namibia: Lüderitz Distr[ict], 10 km NW Rosh Pinah, $27^{\circ}54'S/16^{\circ}42'E$, 13.VIII.1990, C. Roberts & E. Marais (MFN).

Distribution. Namibia (Fig. 37).

Diagnosis. *Pampsilota luederitzensis* resembles *P. brandbergensis* in the body length not exceeding 6.0 mm (in other species at least 7.0 mm). The yellow pronotum and entirely black legs of the latter distinguish it immediately from *P. luederitzensis* with dark pronotum and largely pale tibia.

***Pampsilota nigeriae* Liston & Koch, sp. n.**

<http://zoobank.org/5C0DDF6E-9F09-4DD8-B683-308A3ACFBEE7>

Male. Figures 26, 64–65

Head black; labrum yellow; antenna light brown with blackish apex and sharply compressed longitudinal carina. Thorax yellow with following black: mesoscutum except for a small median spot between lateral lobes on posterior margin, mesoscutellum and metascutellum. Legs yellow; metatibia and metatarsomeres moderately broadly blackish-ringed apically, tarsomeres 3/4 nearly entirely black. Wings including intercostal area slightly infuscate; substigmal spot weakly developed, stigma bicoloured with dirty whitish base and blackish apical half, costa whitish, subcosta except for apex adjacent to stigma and rest of venation blackish. Abdomen yellow.

Head slightly narrowed behind eyes. Antenna 1.6× as long as maximum head width; flagellum very slightly enlarged towards apex, triangular in cross section, scarcely flattened apically, interior surface with sharply compressed longitudinal carina, other longitudinal carinae weakly compressed. Eyes very slightly converging towards clypeus. Anterior margin of clypeus semi-circularly emarginate over its entire width; supraclypeal area very slightly rounded, protruding up to ventral limit of interantennal carinae, interantennal carinae obtusely ridged, converging below, extending to a little below ventral margin of torulus. Frons, supraclypeal area and clypeus densely punctate, weakly shiny, vertex and gena scattered micropunctate, shiny; pubescence whitish. Mesoscutum moderately densely punctate, shiny; pubescence similar to that on head. Abdomen smooth and shiny. Penis valve: Fig. 26.

Length: 7.3 mm.

Female. Unknown.

Type material. Holotype: ♂. Labels: “Nigeria, 14.V.2011, 26 km SEE Abuja, N 09°06′/E07°45′, 400 m, J. Halada leg.”; “DEI-GISHym 21248”; “Holotype, *Pampsilota nigeriae* n. sp. ♂, det.: F. Koch, 2016” [red] (OLML).

Etymology. The new species is named after Nigeria, the country in which the holotype was collected.

Distribution. Nigeria (Fig. 37).

Diagnosis. *Pampsilota nigeriae* adults resemble those of *P. dahomeyanus* and *P. tsavoensis* in the mostly yellow colour of the abdomen and thorax underside, but differs from both in its predominantly yellow antenna and the bicoloured stigma. The penis valves of *P. dahomey-*

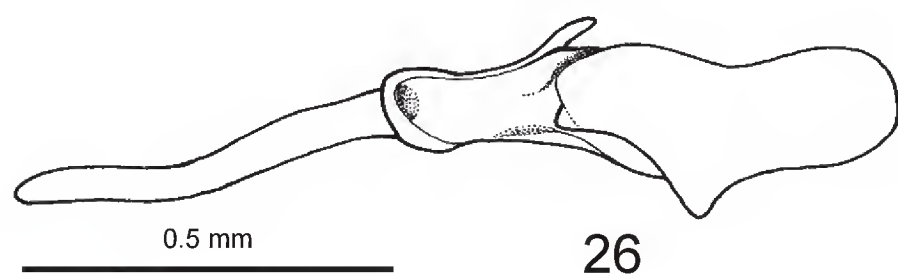


Figure 26. *Pampsilota nigeriae*: Penis valve (left, lateral aspect).

anus (Fig. 19) and *P. nigeriae* (Fig. 26) show differences. Additionally, the dorsal part of mesepisternum is blackish in *P. tsavoensis*, but yellow in *P. nigeriae*.

***Pampsilota tsavoensis* Liston & Koch, sp. n.**

<http://zoobank.org/F7FF2570-36FB-4A86-A8C1-F6D844104E9E>

Female. Figures 27–30, 66–67

Head black with following yellow: labrum, clypeus, supraclypeal area. Interantennal area light brown; antenna black with ventral surface brownish, base of scape yellow. Thorax yellow with following black: mesoscutum, metascutum, dorsal half of mesepisternum blackish. Legs yellow with following black: narrow apex of mesotibia, broad apex of metatibia, pro- and mesotarsomeres more or less blackish ringed apically, metabasitarsomere black ringed apically with following tarsomeres black. Wings slightly infuscate; intercostal area and very small substigmal spot infuscate; stigma, costa, subcosta and rest of venation blackish. Abdomen yellow.

Head parallel-sided behind eyes. Antenna 1.3× as long as maximum head width; flagellum conspicuously enlarged towards apex, quadrangular in cross section, interior surface with sharply compressed longitudinal carina, other longitudinal carinae conspicuously weakly compressed. Eyes very slightly converging towards clypeus. Anterior margin of the clypeus shallowly, circularly emarginated; supraclypeal area scarcely protruding up to ventral limit of interantennal carinae, interantennal carinae obtusely ridged, not converging below, extending about to level of ventral margin of torulus. Frons, supraclypeal area and clypeus sparsely micropunctate, shiny, vertex and gena densely micropunctate, subshiny; pubescence whitish. Mesoscutum irregularly microsculptured, subshiny; pubescence similar to that on head. Abdomen smooth and shiny. Valvulae 3: Figs 27–28. Lancet with about 16 serrulae: Figs 29–30.

Length: 7.0 mm.

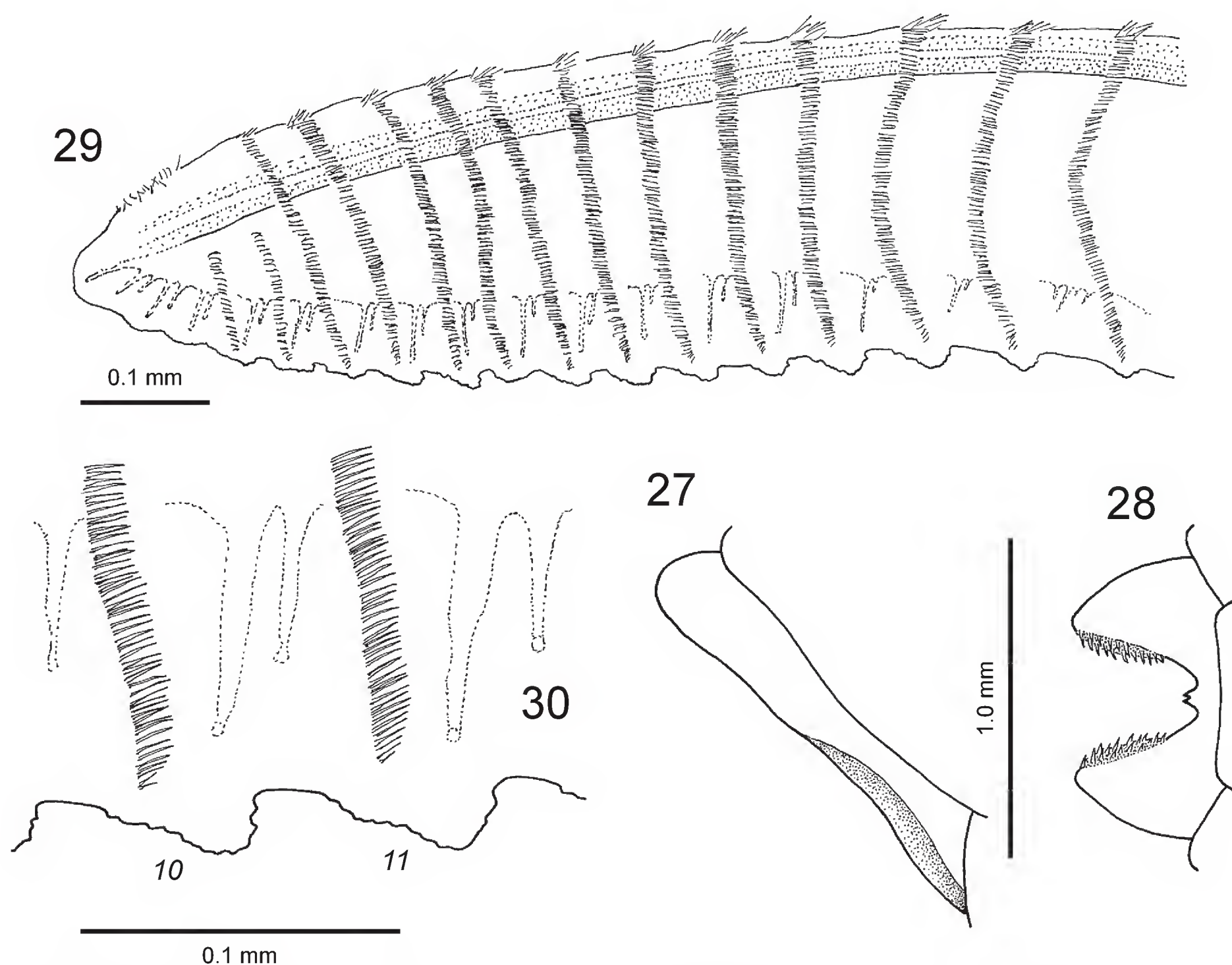
Male. Unknown.

Type material. Holotype: ♀. Labels: “Kenya S. E., Tsavo, Voi env[ironment], 15.IV.2004, M. Snižek leg.”; “DEI-GISHym 21247”; “Holotype, *Pampsilota tsavoensis* n. sp. ♀, det.: F. Koch, 2016” [red] (OLML).

Etymology. The species is named after its collection locality, Tsavo National Park in Kenya.

Distribution. Kenya (Fig. 37).

Diagnosis. *Pampsilota tsavoensis* adults resemble those of *P. dahomeyanus* and *P. nigeriae* in the mostly yellow colour of the abdomen and thorax underside, but differ from *P. dahomeyanus* in the blackish dorsal part of mesepisternum, shape of the serrulae (Figs 29, 30), and in the morphology of the valvulae 3, which in *P. tsavoensis* are conspicuously divergent in dorsal view, with distinct denticles on the interior surface (Fig. 28), whereas in *P. dahomeyanus* the valvulae 3 do not diverge distally, and are without denticles (Fig. 16). *P. nigeriae*, of which only a single male is known, differs from *P. tsavoensis* in its predominantly yellow antenna and the bicoloured stigma.



Figures 27–30. *Pampsilota tsavoensis*: **27.** Valvulae 3 (lateral aspect); **28.** Valvulae 3 (dorsal aspect); **29.** Lancelet; **30.** Serrulae 10–11.

***Pampsilota zebra* Liston & Koch, sp. n.**

<http://zoobank.org/D56CC835-6389-4FFB-91D5-8E4FB47936BE>

Female. Figures 31–34, 68–69

Head black with blue metallic lustre. Thorax black with metallic lustre; pronotum yellow with anterior margin and medially black. Legs black with blue metallic lustre; pro- and mesotibia entirely yellow, metatibia yellow with moderately broad blackish apex, probasitarsomere sometimes with yellow base. Wings including intercostal area subhyaline; substigmal spot strongly infuscate but small; stigma, costa, subcosta and rest of venation black. Abdomen yellow-orange; terga 1–6 broadly black with blue metallic lustre; terga 7–9 entirely black, sternum 5 with broad black posterior margin, sternum 6/7 entirely black; ovipositor sheath with black valvifers 2.

Head very slightly enlarged behind eyes. Antenna 1.4× as long as maximum head width; flagellum enlarged towards apex, quadrangular in cross section, interior surface with sharply compressed longitudinal carina, other longitudinal carinae conspicuously more weakly compressed. Eyes slightly converging towards clypeus. Anterior margin of the clypeus broadly, shallowly, tri-

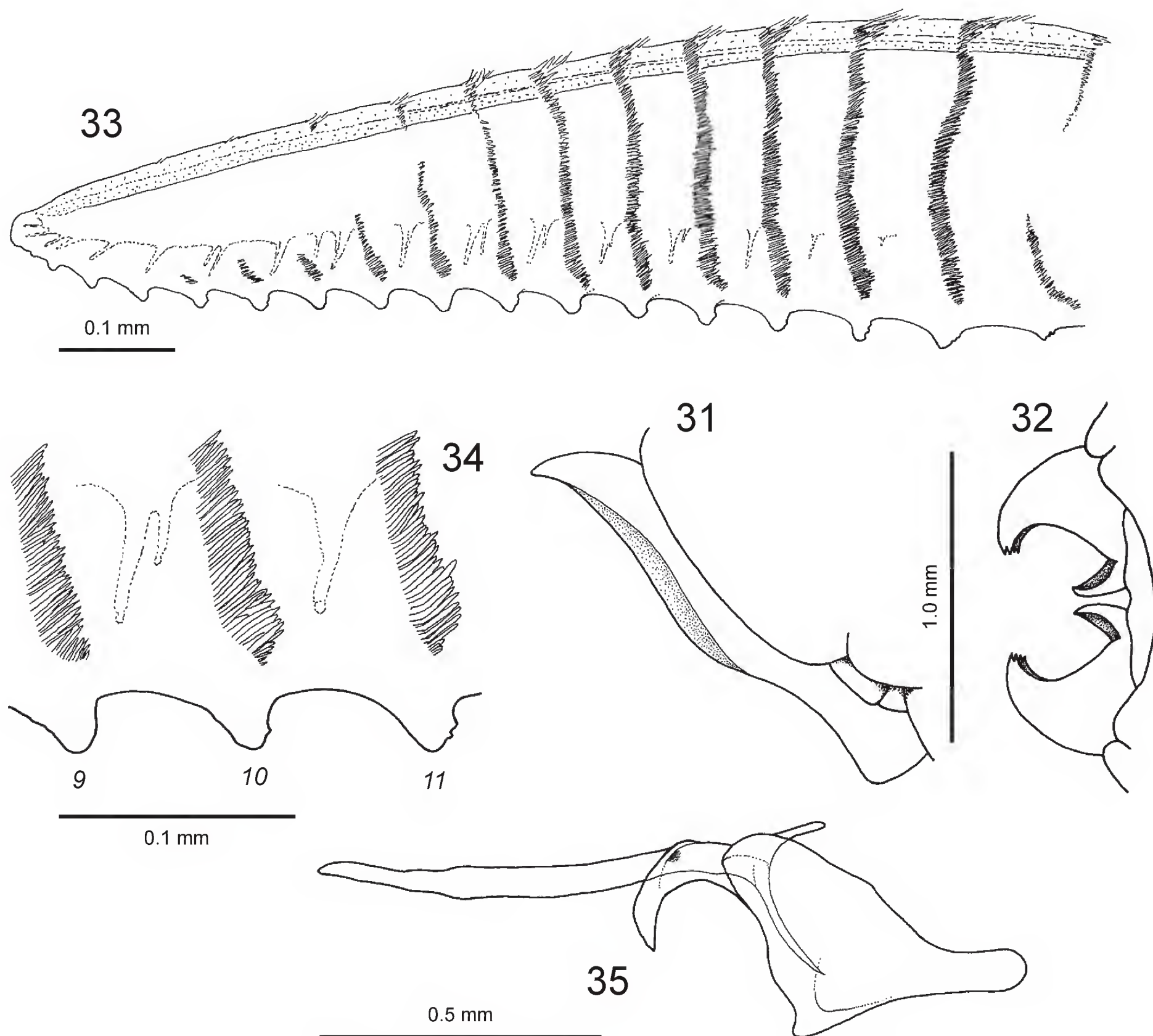
angularly emarginate; supraclypeal area nearly evenly rising up to base of interantennal carinae, interantennal carinae obtusely ridged, converging below, extending to about level of ventral margin of torulus. Frons, supraclypeal area and clypeus rugosely sculptured, dull, vertex densely punctate, dull, postocellar area and gena densely micropunctate, shiny; pubescence whitish. Mesoscutum moderately densely micropunctate, shiny; pubescence similar to that on head. Abdomen smooth and shiny. Valvulae 3: Figs 31, 32. Lancelet with about 16 serrulae: Figs 33, 34.

Length: 9.5 mm.

Male. Figures 35, 70–71.

General coloration similar to that of female. Metatibia entirely yellow, sometimes interior surface of apex slightly blackish, basal tarsomeres of fore and mid legs extensively yellow. Sternum 5–9 black with blue metallic lustre, sternum 9 broadly yellow apically.

Antenna 1.8× as long as maximum head width; flagellum slightly enlarged medially, scarcely flattened apically, approximately oval in cross section, interior surface with sharply compressed longitudinal carina, outer carina conspicuously more weakly compressed, other carinae not



Figures 31–35. *Pampsilota zebra*: **31.** Valvulae 3 (lateral aspect); **32.** Valvulae 3 (dorsal aspect); **33.** Lancet; **34.** Serrulae 9–11; **35.** Penis valve (left, lateral aspect).

developed. Other characters as for female. Penis valve: Fig. 35.

Length: 7.2–7.8 mm.

Type material. Holotype: ♀. Labels: “Tanzania CE, SE Nbuyuni Baobab vall[ey]. [ca. 7.54°S 36.62°E], NE Iringa [Iringa] 9.III.2002, M. Snižek”; “Holotype, *Pampsilota zebra* n. sp. ♀, det.: F. Koch, 2016” [red] (OLML). Paratypes: same data as holotype (5♂♂, 9♀♀) (MFN, OLML, SDEI, USNM).

Etymology. The new species name, a noun in apposition, refers to the well-known and widely distributed African ungulate, so named in several European languages.

Distribution. Tanzania. The only known locality lies on the edge of the Udzungwa Mountains National Park (Fig. 37).

Diagnosis. *Pampsilota zebra* resembles *P. africanus* in having pincer-shaped valvulae 3 (compact or diverging

in all other species), metatibia distally nearly circular in cross section, and in the main colour characters (thorax black except for pronotum and sometimes tegulae, legs partly pale, and abdomen at least ventrally partly pale). *Pampsilota zebra* differs from *P. africanus* especially in its black costa and subcosta (in the latter costa and anterior of subcosta bright yellow). The tegulae of *P. zebra* are always black, whereas in *P. africanus* they are sometimes bicoloured. Furthermore, the hind tibia of *P. zebra* is in contrast to *P. africanus* broadly ringed apically with blackish. The serrulae of these species are very differently shaped (Figs 12, 34), but their penis valves are quite similar (Figs 13, 35).

Remarks. Intraspecific variability is apparent in the coloration of the dorsum of the abdomen, where the black markings are medially more or less extensive, and the more or less extensively yellow coloured pro- and mesotarsi.

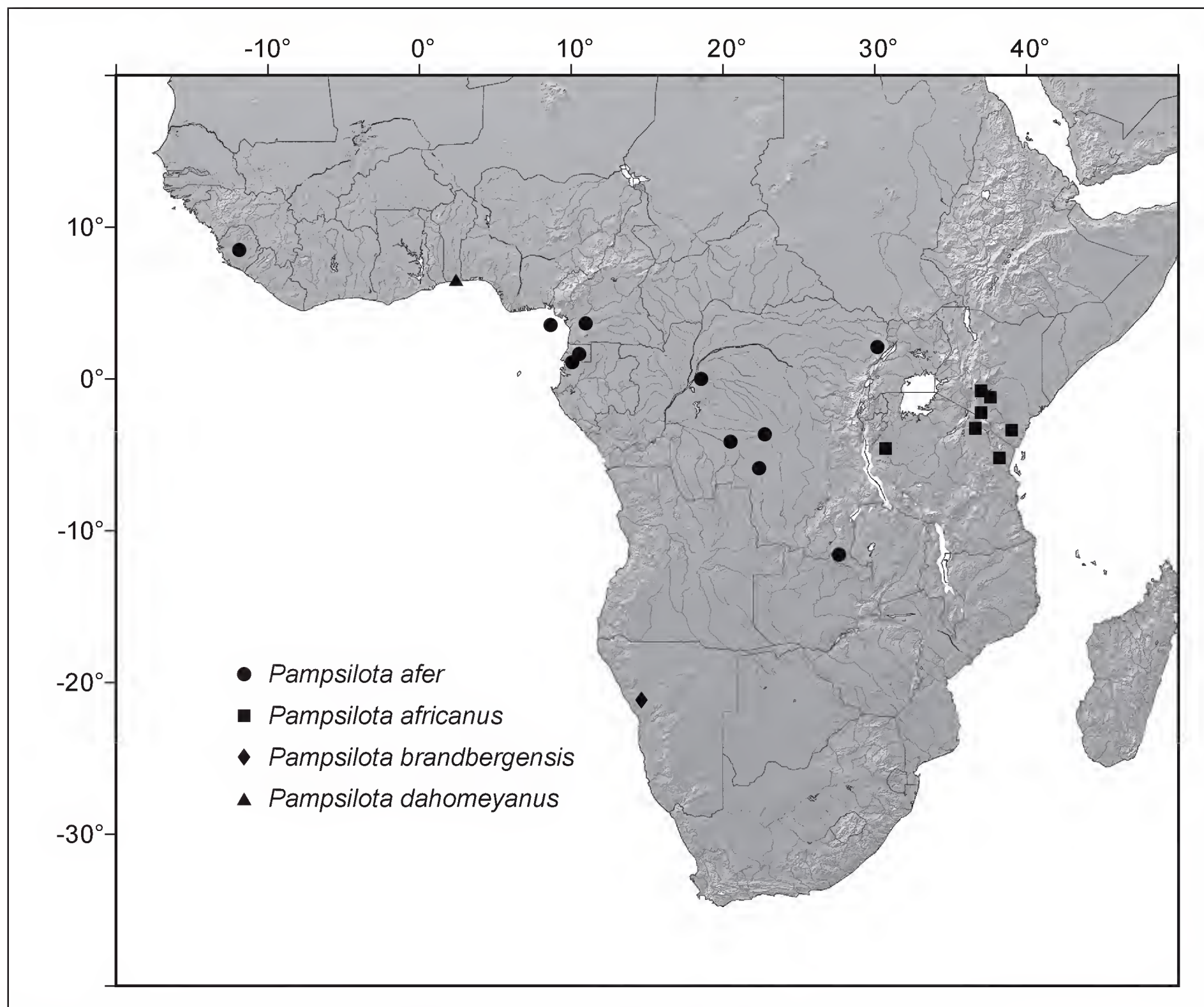


Figure 36. Distribution map for *Pampsilota afer*, *P. africanus*, *P. brandbergensis*, and *P. dahomeyanus*.

Discussion

The regrettable current lack of knowledge on the host plant associations of the majority of Afrotropical Tenthredinoidea, compared for example to the relatively large and partly corroborated data sets available for many regions in the Palearctic and Nearctic, has recently been highlighted by, for example, Koch et al. (2015) and Liston et al. (2015). This deficit makes it impossible to judge within a wider perspective the significance of the host plant record for the single *Pampsilota* species for which such data exists: *P. dahomeyanus* on *Lannea nigritana* (Anacardiaceae). This is currently one of very few records of an Afrotropical sawfly species using a native, woody host. We are not aware of other published records of leaf-eating African tenthredinoids reared, or otherwise unequivocally associated, with Anacardiaceae, although a few records associate Neotropical Pergidae and Nearctic Argidae with this plant family (e.g. McKay et al. 2009, Regas-Williams

and Habeck 1979). Among the other Afrotropical symphytan lineages, only Goulet (2014) recorded an association with a species of Anacardiaceae: *Afrotremex xylophagus* Goulet, 2014 (Siricidae) reared from wood of *Antrocaryon klaineinum* Pierre. The few host plants hitherto recorded for native Afrotropical tenthredinoids are, conspicuously, nearly all non-woody species, and very often those which are cultivated (Koch et al. 2015). By contrast, in the Holarctic many tenthredinoids, including most *Arge* species (Smith 1989, Liston 1995), use woody plants as hosts. Possibly the lack of data on sawflies of sub-Saharan Africa using native tree species as larval hosts might largely have been caused by various sampling biases, such as failure to employ effective collecting methods on trees at the right season, or perhaps even a widespread relative lack of interest in studying the insect fauna of native trees, compared to that of the crop plant species which are of more obvious importance to humans. Because the host of *P. dahomeyanus* is valued by humans for its fruit, and has a variety

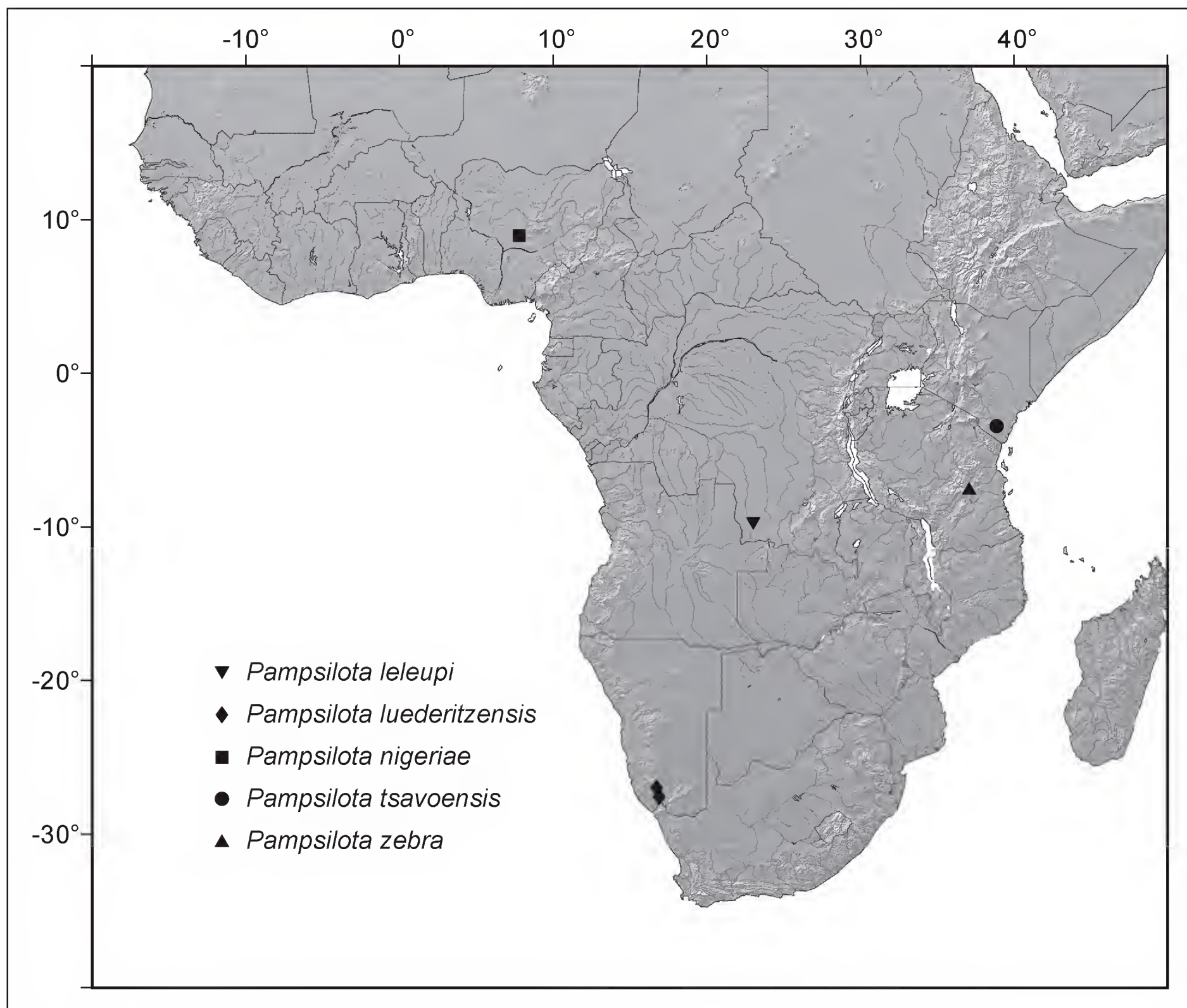


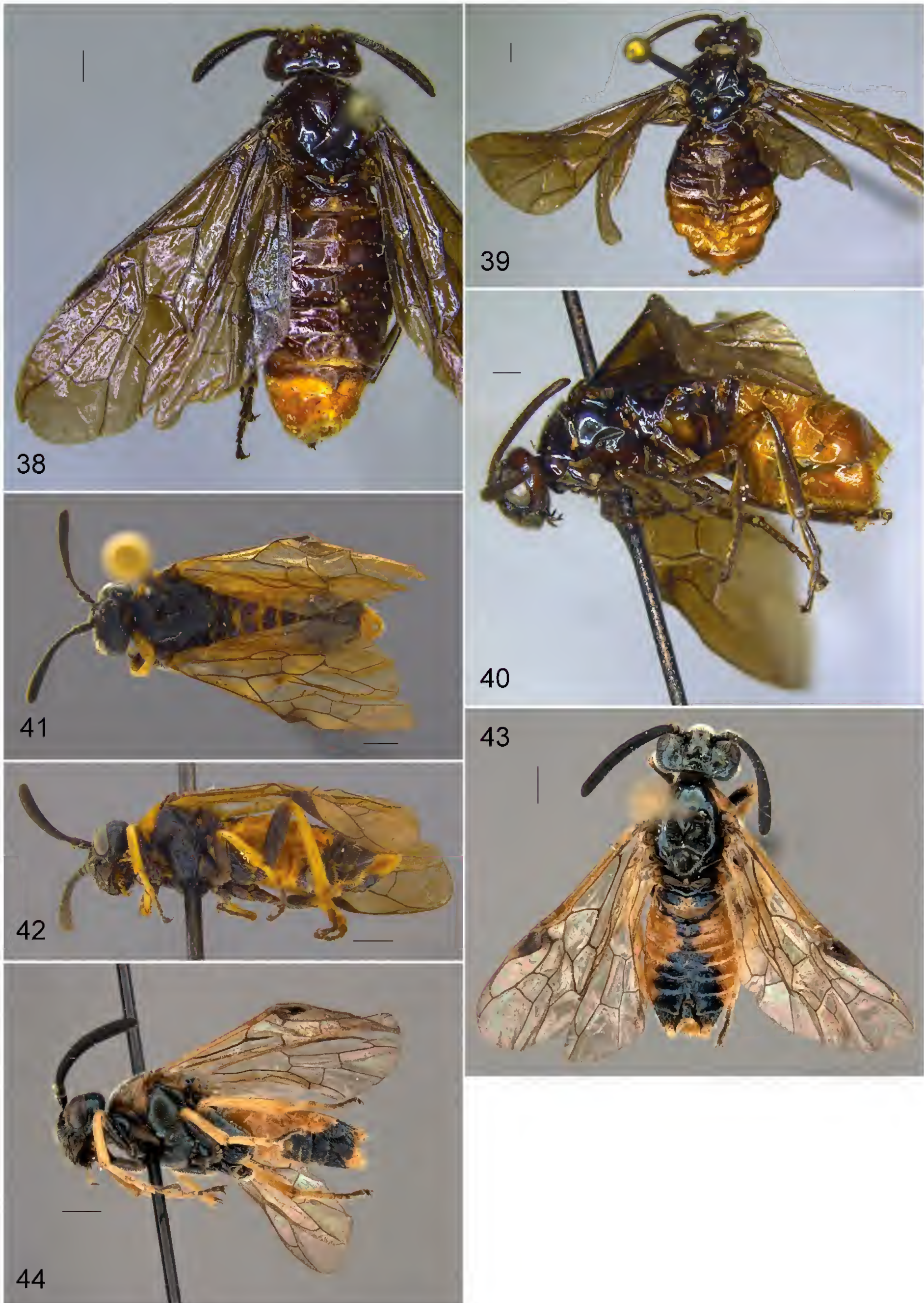
Figure 37. Distribution map for *Pampsilota leleupi*, *P. luederitzensis*, *P. nigeriae*, *P. tsavoensis*, and *P. zebra*.

of other uses, including medicinal, it is often planted in or near settlements (Burkhill 1985), and is thus a more conspicuous host than the many Afrotropical tree species found only in the rapidly diminishing areas of semi-natural forest.

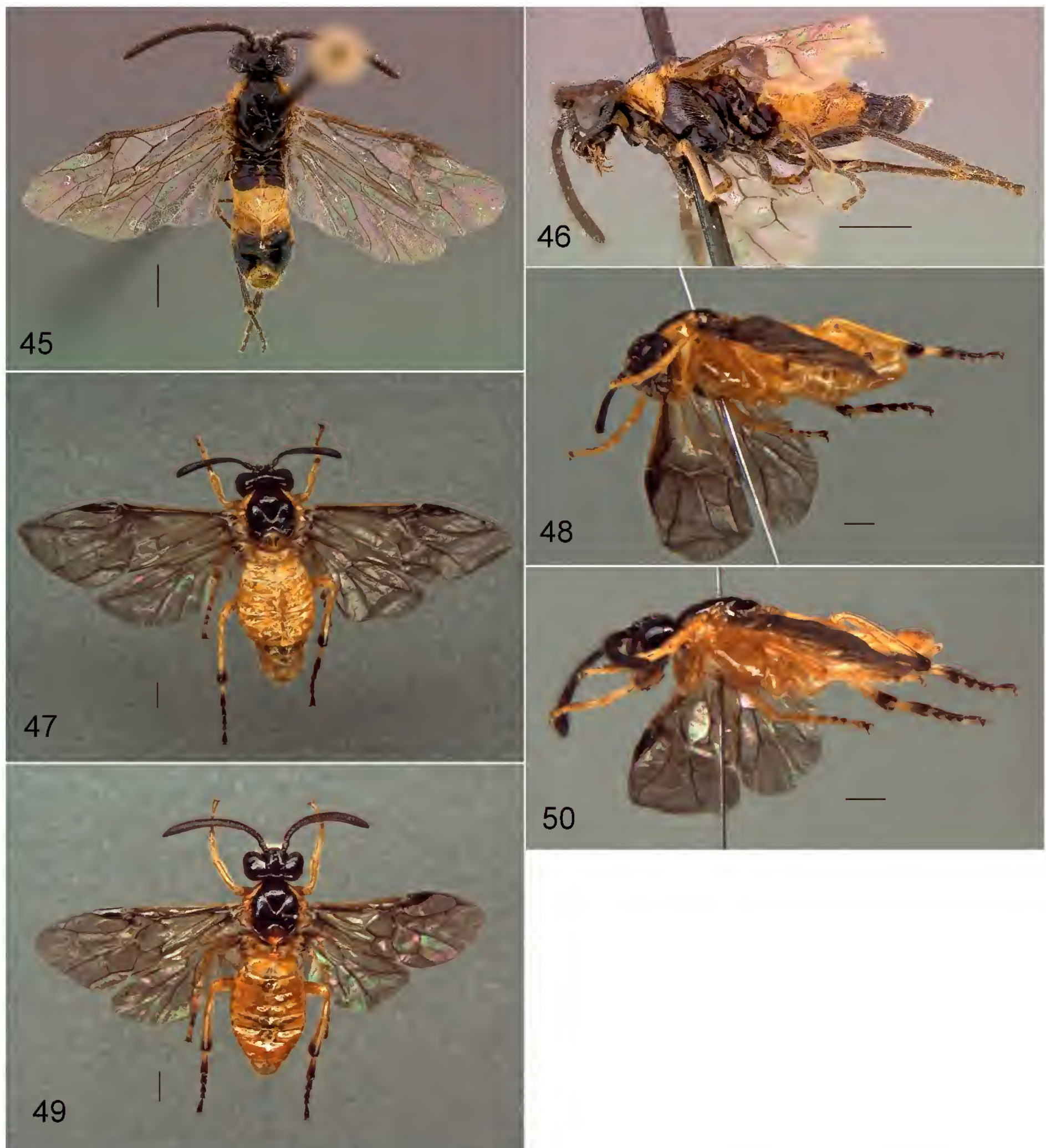
Our study aims to make possible the identification of part of the species-rich Afrotropical fauna of Argidae, and thus prepare the way for further research. The current lack of genetic data forced us to rely on morphological methods, but real progress in understanding the phylogeny of the twenty nominal argid genera worldwide that are currently placed in the Arginae (14) and Athermantinae (6) (Taeger et al. 2010), will probably only be possible when sufficient genetic data become available for a representative spectrum of these taxa. We are, however, a very long way from achieving this. The lack of fresh material of several Afrotropical taxa is a problem, well illustrated by the type species of *Pampsilota*, *P. afer*: at least six of the eleven specimens (one is without a date) which we were able to

examine were collected over one hundred years ago, with the most recent from 1955. The acquisition of gene sequence data for as many Afrotropical sawfly taxa as possible should nevertheless remain an objective, because, apart from its usefulness in phylogenetic analyses, it could also be used to accelerate the task of identifying larvae and host plants, by avoiding the need to rear the immature stages to adults. The latter technique, which is time-consuming and not always successful, will of course remain essential in the long term, if we desire to know more about the natural history of individual taxa.

The separation of the Arginae from the Athermantinae was first proposed by Benson (1938). He ascribed great importance to the character states “pre-apical spurs on meso- and metatibia present [Arginae] or absent [Athermantinae]”. This has become the only character used in more recent works, e.g. Koch et al. (2015), to distinguish members of the putative lineages. One might well question whether this single character of re-



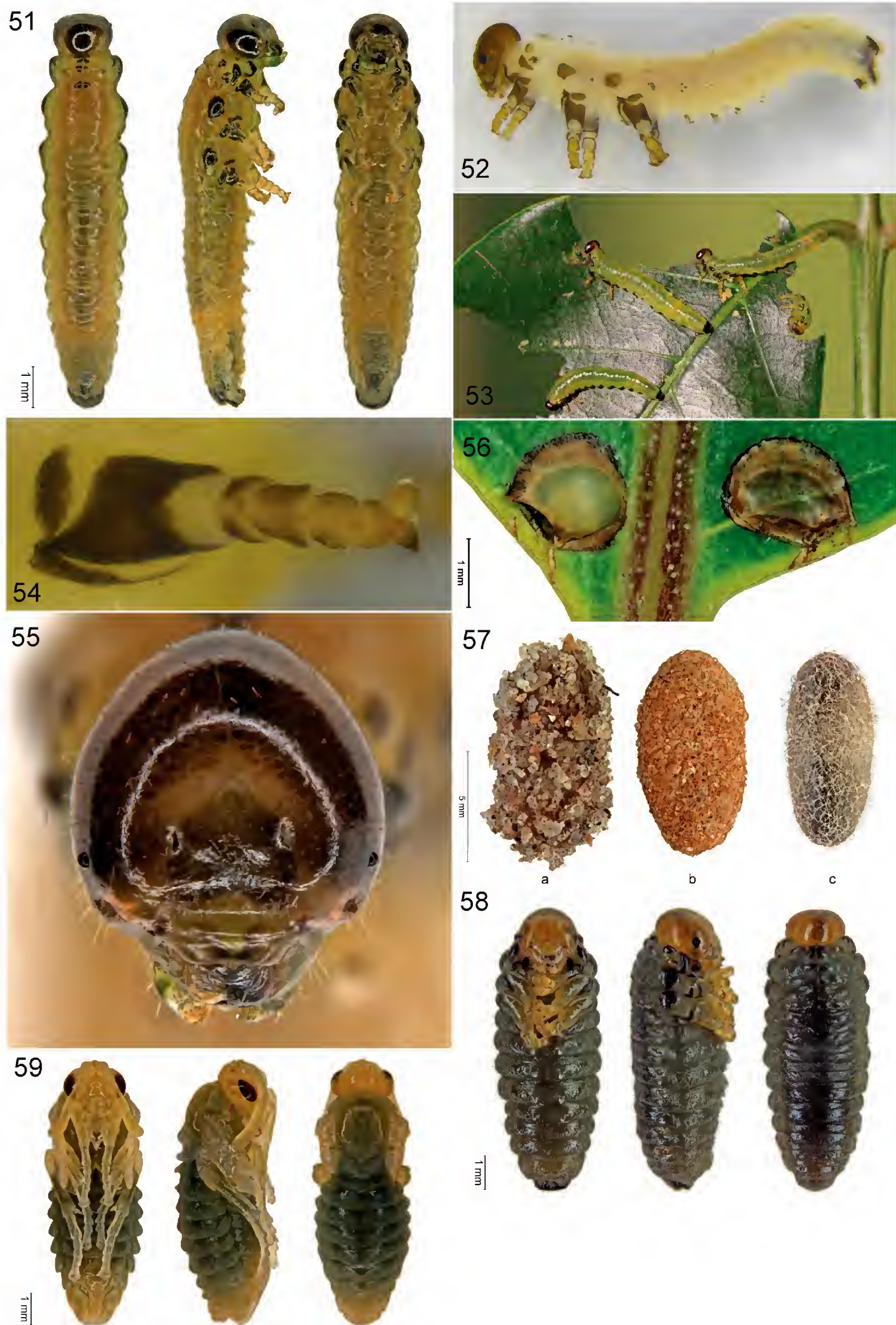
Figures 38–44. *Pampsilota afer* ♀: 38. Dark form, dorsal; 39–40. Pale form, dorsal / lateral. 41–44. *P. africanus*. 41–42. ♀ (LT), dorsal / lateral; 43–44. ♂, dorsal / lateral. Scale bars = 1 mm.



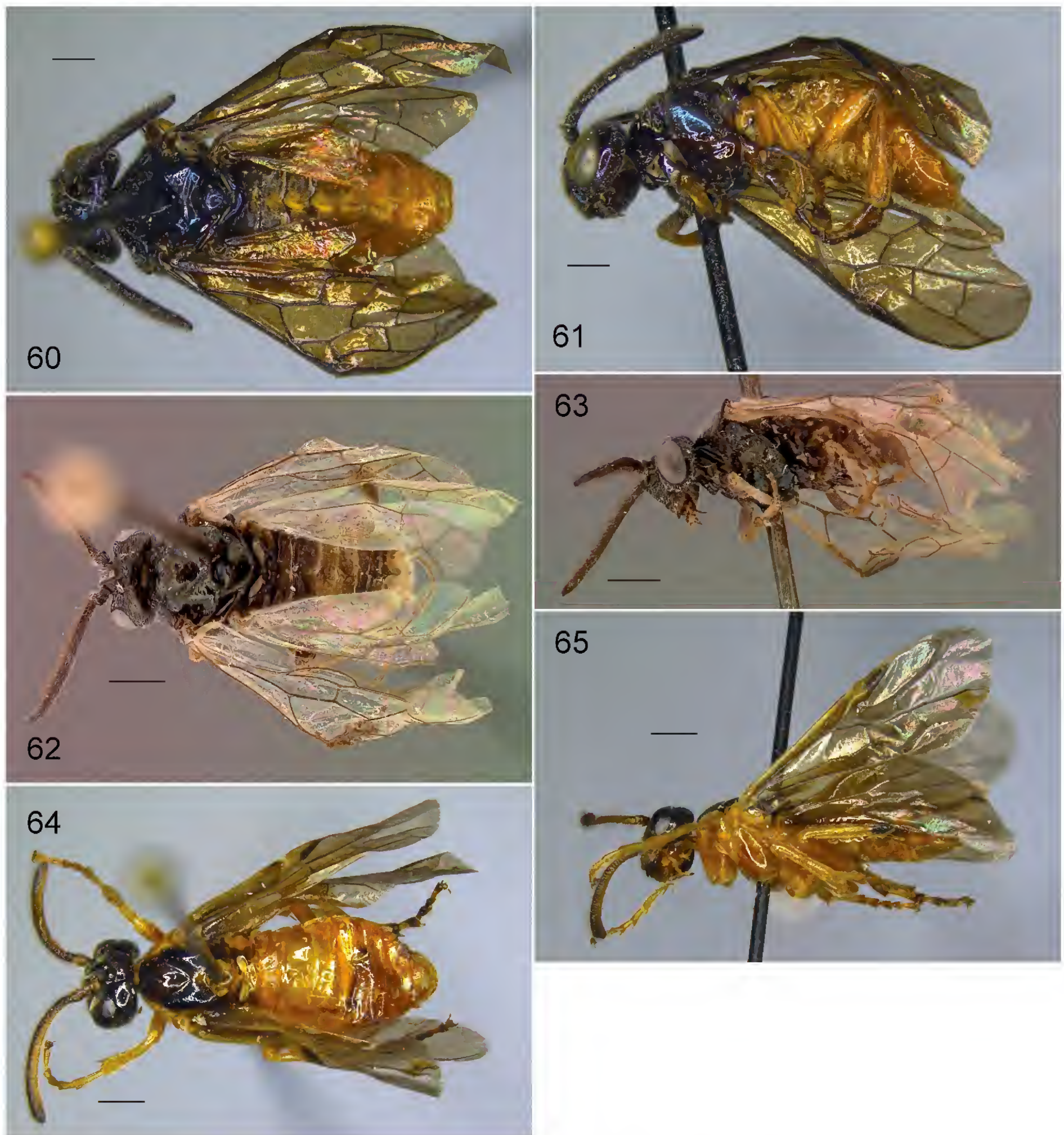
Figures 45–50. *P. brandbergensis* ♂ (PT), dorsal / lateral. **47–50.** *P. dahomeyanus*. **47–48.** ♀, dorsal / lateral; **49–50.** ♂, dorsal / lateral. Scale bars = 1 mm.

duction, which might have occurred or been reversed independently more than once within the Argidae, is really of such phylogenetic significance. On the other hand, of the very many Afrotropical argid specimens examined by the authors, only two specimens were found in which this character state was equivocal (the holotype of *Calarge africana*, and a single *Pampsilota dahomeyanus*). Therefore, we are of the opinion that the character is sufficiently stable at species level to be useful at least for identification.

The morphology of the larva of *P. dahomeyanus* does not differ in any notable way from known larvae of *Arge* species, as described for example by Lorenz and Kraus (1957), and Smith (1989). Given that at suprageneric level the larvae of exophytic sawfly taxa generally exhibit some clear apomorphies (Lorenz and Kraus 1957), this similarity supports the inclusion of *P. dahomeyanus* in the Arginae, rather than the Athermantinae, in which *Pampsilota*, *Sjoestedtia* and *Cipdela* have mostly been placed following Benson (1938) (e.g. Taeger et al. 2010).



Figures 51–59. *P. dahomeyanus*, immature stages: **51.** Mature larva, from L to R dorsal, lateral, ventral; **52.** Young larva, lateral (preserved in ethanol); **53.** Larvae on *Lannea nigritana*; **54.** Metathoracic leg; **55.** Head, frontal; **56.** Eggs in base of leaflet. **57.** Cocoons, from L to R with covering of sand, outer layer, inner layer; **58.** Prepupa, from L to R ventral, lateral, dorsal; **59.** Pupa, from L to R ventral, lateral, dorsal.

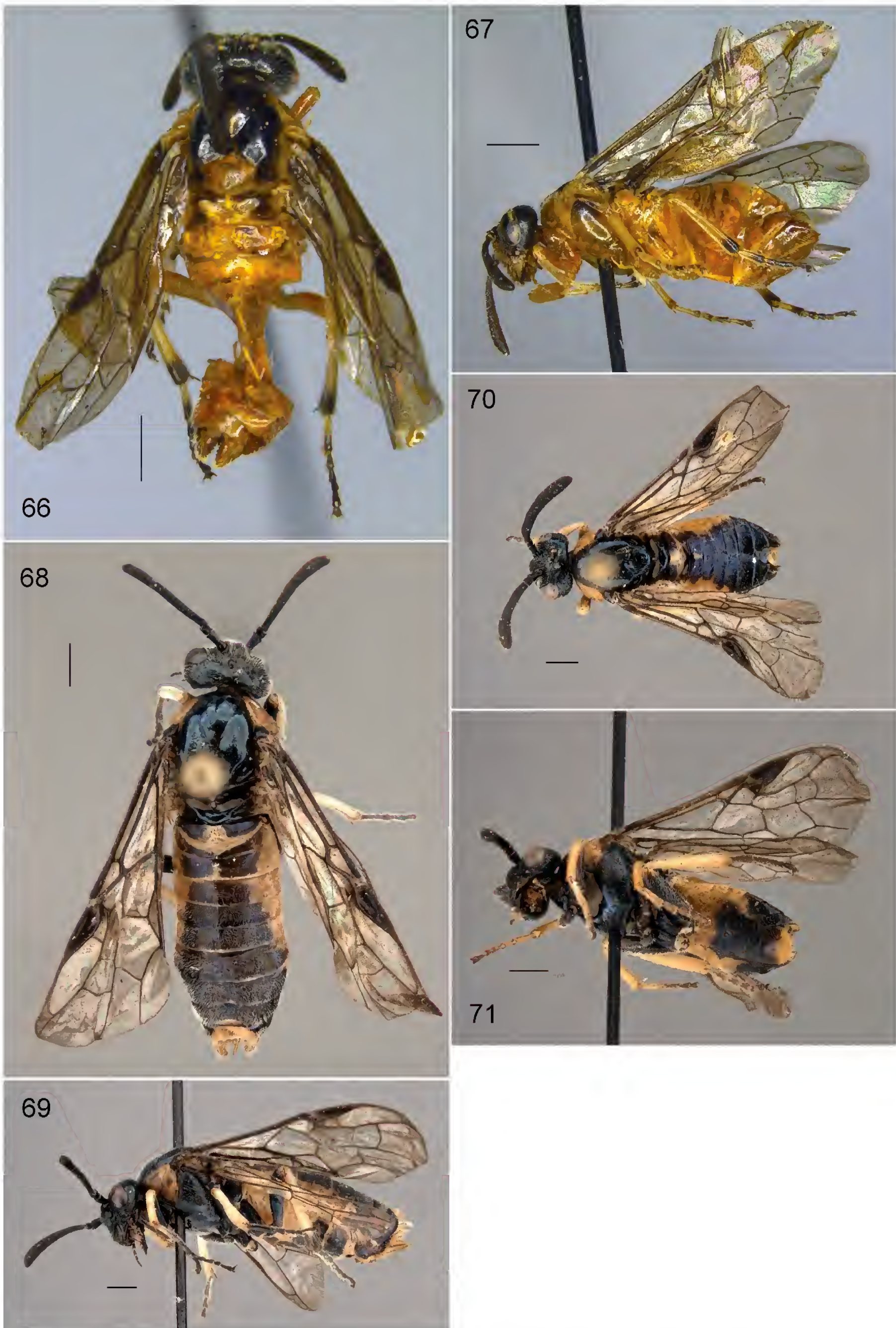


Figures 60–65. *P. leleupi* ♂ (HT), dorsal / lateral. **62–63.** *P. luederitzensis* ♂ (PT), dorsal / lateral. **64–65.** *P. nigeriae* ♂ (HT), dorsal / lateral. Scale bars = 1 mm.

However, it would be unwise to draw any conclusions from this assessment before gene sequences are acquired and larval morphology elucidated for the type species of *Pampsilota*, and as many other argine and athermantine species as possible worldwide. What is clear, is that after the exclusion of *Sphacophilus afer* and *Scobina poecila* from the Afrotropical fauna, and the synonymy of *Calarge* with *Arge*, the argid fauna of the sub-Saharan continent is by no means as diverse at higher taxonomic levels as previously believed.

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We are most grateful to S. M. Blank (SDEI), E. De Coninck and S. Hanot (MRAC), F. Gusenleitner (OLML), E. Marais (NNIC), M. Paris (MNCN), A. Taeger (SDEI), A. Teräs (UZMT), H. Vårdal (NHRS), S. Csösz, S. Vas, and L. Zombori (HNHM) for allowing us to examine the specimens in their care. Without their help, this study could not have been undertaken. M. Paris also sought information about the history of the *C. terminalis* and *S. afra* specimens. E. Schubert (SDEI) made available handwriting



Figures 66–71. *P. tsavoensis* ♀ (HT), dorsal / lateral. **68–71.** *P. zebra*. **68–69** ♀ (HT), dorsal / lateral; **70–71.** ♂ (PT), dorsal / lateral. Scale bars = 1 mm.

samples of L. Conradt, and D. R. Smith (USNM) kindly gave his opinion on our assessment of the status of *S. afra* and *C. terminalis*. Images for Figs 70–71 were kindly provided by B. Schurian (MFN). We thank the graphic designer E. Siebert (MFN) for her help with arranging and lettering the line drawings. The staff of the SDEI library have, over many years, made a great effort in obtaining and archiving potentially relevant literature. Particularly thanked for this by AL are K. Elgner, H. Framke, U. Kaczinski, and R. Riedelsheimer. We are also grateful to Aristide Adomou (Jardin Botanique et Herbarium National du Bénin, Université d'Abomey Calavi, Abomey-Calavi, Benin) for identifying the host plant of *P. dahomeyanus* and Hervé Houngoué, IITA Benin, for technical assistance in collecting and rearing the species. FK would like to express his gratitude to the International Bureau of the Federal Ministry of Education and Research (BMBF) at the Project Management Agency c/o German Aerospace Center (DLR) and the National Research Foundation (NRF), South Africa for a research grant. S. Monckton and S. van Noort reviewed the manuscript and suggested important improvements. Finally, the Museum für Naturkunde defrayed the cost of open access publication.

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Morphology of the larvae of three Central European *Strophosoma* Billberg, 1820 (Coleoptera, Curculionidae, Entiminae) species

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Abstract

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The larvae of *Strophosoma* (*Strophosoma*) *capitatum* (DeGeer, 1775), *S.* (*Strophosoma*) *melanogrammum* (Forster, 1771) and *S.* (*Neliocarus*) *sus* Stephens, 1831, are illustrated and re-described or described for the first time. The first larval instar, and the mature or an older larval instar, are illustrated, and a general description of the *Strophosoma* larva is given. The biological data obtained from breeding and field-collecting are compared and discussed in relation to the known life-cycle data.

Key Words

Weevil

Curculionoidea

taxonomy

chaetotaxy

immature stages

bionomics

European region

Introduction

The short-nosed weevil genus *Strophosoma* is represented in Southwest Europe (mainly Spain) and Northwest Africa (Morocco, Algeria) by more than 40 species (Pelletier 2013). Only a few species have a widespread distribution and are present in Southwestern Asia (two species) or Central Europe (five species), among them the parthenogenetic *Strophosoma melanogrammum* (Forster, 1771). Van Emden (1952) characterized the larvae of four species; in three, the description was based on L₁ larvae. Only in *S. faber* (Herbst, 1785) were higher stages also taken into account. This species was previously described by Urban (1913). Little additional information was added by Scherf (1964) on *Strophosoma* larvae. He included some brief information on the morphology of *S. melanogrammum*, but without any drawings. Only Willis

(1964) characterized the mature larva of *S. melanogrammum* in any detail, but this source, a thesis of the Queen's University Belfast, is not readily available.

In this paper the L₁ larvae of *S. capitatum* (DeGeer, 1775) and *S. melanogrammum* and the mature larva of *S. melanogrammum* are re-described, the mature larva of *S. capitatum* is described for the first time, and the young and an old larval instar of *Strophosoma sus* Stephens, 1831 (syn. *S. laterale* (Paykull, 1792)) are also described for the first time. Priority is given to the chaetotaxy of the described larvae.

Materials and methods

The older larvae on which these descriptions are based on, were collected in the field or – in a few cases – bred

Table 1. Measurements of characteristic body parts of the *Strophosoma* species studied. HW – head width; HW* head width with prominent eyes included; HL – head length; BL – body length; BH – body height; L1 – first instar larvae, LM – larvae of last instars. All measurements in millimeters [mm].

	L1								LM							
	HW.*		HL.		BL.		BW.		HW.		HL.		BL.		BW.	
	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.	min.	max.
<i>S. (Strophosoma) capitatum</i>	0.19	0.20	0.16	0.17	1.00	1.10	0.23	0.28	0.80	0.90	0.70	0.75	5.2	6.0	1.5	1.8
<i>S. (Strophosoma) melanogrammum</i>	0.21	0.23	0.19	0.20	0.87	1.03	0.22	0.26	0.90	1.00	0.80	0.90	5.0	6.5	1.5	2.0
<i>S. (Neliocarus) sus</i>	0.23	0.24	0.22	0.23	0.95	1.11	0.28	0.31	0.57	0.65	0.75	0.80	3.50	5.0	1.1	1.8

in flower-pots. L₁ larvae were obtained from adults kept in the laboratory. Larvae of the polyphagous species *Strophosoma capitatum* and *S. melanogrammum* were dug out of soil under possible host plants or, in the case of the monophagous *S. sus*, under *Calluna vulgaris* (L.) Hull, and fixed in 80% ethanol. The specimens were examined under an optical stereomicroscope (Olympus SZ 60). Measurements were made by using calibrated oculars; first larval instars and older larvae of each species were measured using a calibrated microscopic eyepiece: The measurements (body length (BL), body height (BH), width and length of the head capsule (HW, HL)). Measurements of all the species described are summarized in Table 1.

Drawings were made using a drawing tube installed on a stereomicroscope and processed by computer programmes (Corel Photo-Paint X7, Corel Draw X7). Photos were made using an Olympus BX63 microscope and processed by Olympus *cellSens Dimension* software. Names and abbreviations of body parts follow the terminology proposed by Scherf (1964), setae according to Anderson (1947) and May (1994), and mouthparts and antennae by Marvaldi (1997, 1998a). All specimens are deposited in the collection of the Department of Zoology, Maria Curie-Skłodowska University, in Lublin.

Strophosoma (Strophosoma) capitatum (Fig. 41)

L₁ larvae: 45 ex., 28.04.2012. Adults collected in Brelingen, north of Hannover (Germany), border of an oak forest, 80 m, 16.04.2012.

Mature larvae: 8 ex., 12.03.2016, Niedersachsen, Deister Mountains, Bredenbeck-Steinkrug, southwest of Hannover (Germany), 165 m (Fig. 40): 6 ex. between roots of young *Fagus sylvatica* L. and 2 ex. between roots of young *Picea abies* (L.) Karst. trees.

Strophosoma (Strophosoma) melanogrammum

L₁ larvae: 80 ex., 10.06.2012. Adults collected in Brelingen from a row of old oak trees and from broom (*Cytisus scoparius* (L.) Link) in a disused sand pit nearby, 70 m, 15.04.2012.

Mature larvae (9 ex.): 1 ex., 04.10.2013, climate chamber of the Julius-Kühn-Institute in Braunschweig, breeding in flower-pots with *Prunus laurocerasus* L.; 4 ex., 17.04.2015, Sachsen-Anhalt, National Park Harz, Harz Mountains, Schierke, Hohnekamm, nutrient-poor

grassland, 830 m; 1 ex., 30.03.2015, Sachsen-Anhalt, National Park Harz, Harz Mountains, Ilsenburg, Meineberg, pioneer forest with young birches (*Betula pendula* Roth), 340 m (Fig. 42); 2 ex., 06.07.2015, Niedersachsen, Brelingen, north of Hannover, disused sand pit, between roots of *Cytisus scoparius*, close to a row of old oak trees (*Quercus robur* L.), 70 m (Fig. 45); 1 ex., 30.12.2015, Niedersachsen, Hannover-Vahrenheide, Kugelfangtrift, nutrient-poor sandy grassland, 50 m, between roots of a mixed stand of *Geranium pusillum* L., *Erodium cicutarium* (L.) L'Hér. ex Aiton, grasses and a sedge species (*Agrostis capillaris* L., *Carex hirta* L., *Festuca rubra* L.), found together with pupae of *Phyllobius pyri* (Linnaeus) f. *vespertinus* (Fabricius).

Strophosoma (Neliocarus) sus

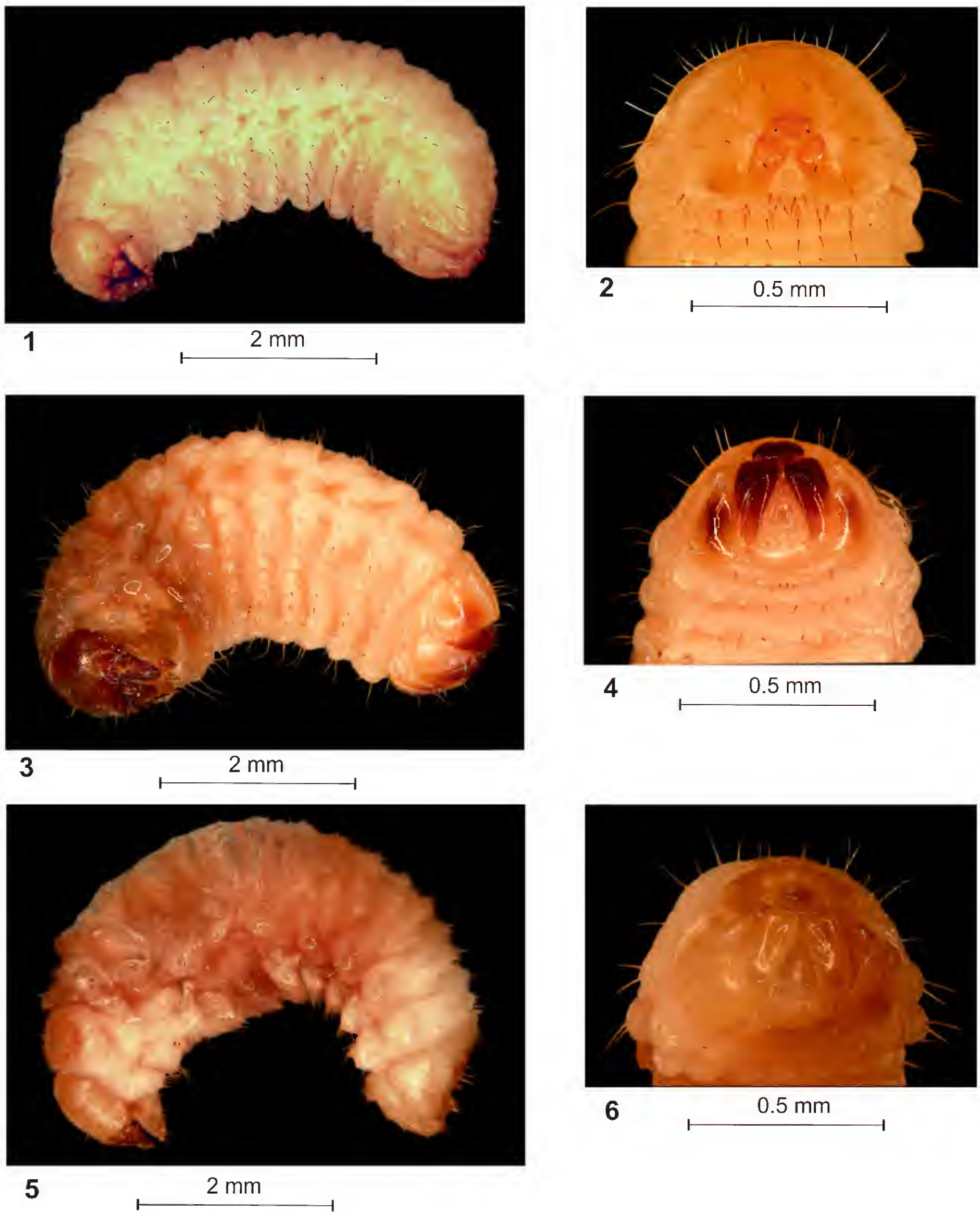
L₁ larvae: 6 ex., 23.05.2012. Adults collected in Berkhof, north of Hannover, heathland and light pine forest with *Calluna vulgaris*, 10.05.2012.

Old larvae (2 ex.): 1 ex., 25.07.2012, collected from under roots of *Calluna vulgaris* in Berkhof (Fig. 44); 1 ex. and 1 immature adult, 02.09.2012, from breeding in a flower-pot with *Calluna vulgaris* in Hannover, Curculio Institute (Fig. 43). In these cases it is not known, whether the larvae were in the last or the penultimate instar.

Results

Description of larvae - general diagnosis

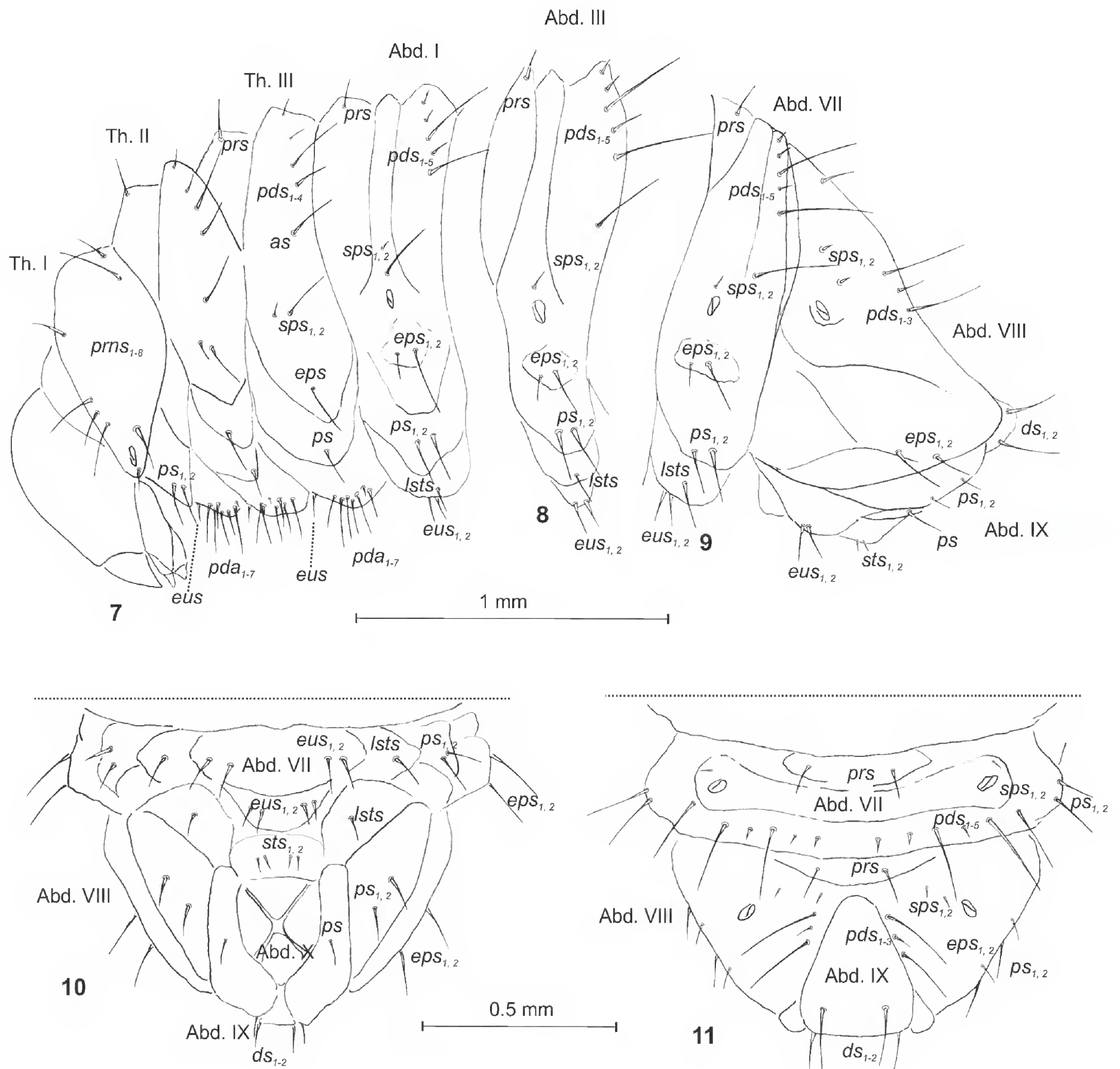
Body (Figs 1, 3, 5). Moderately slender, curved, rounded in cross section. Prothorax slightly smaller than mesothorax; metathorax as wide as mesothorax. Abdominal segments I–VII of almost equal length. Abdominal segment VIII wide, flattened posteriorly, with conical lateral lobes. Abdominal segment IX strongly reduced, consisting of four, well isolated lobes, distinctly smaller than previous segments. Abdominal segment X consists of four anal lobes of almost equal size. Anus located ventrally (Figs 2, 4, 6). Chaetotaxy well developed, setae capilliform, variable in length. Each side of prothorax with 8–11 *prns* (pronotal setae) of unequal length; 2 *ps* (pleural s.) and 1 *eus* (eusternal s.). Meso- and metathorax (Figs 7, 18, 29) on each side with 1 *prs* (prodorsal s.), 4 *pds*, variable in length (postdorsal s.), 1 long *as* (alar s.), 2 *ss* (spiracular s.), variable in length, 1 long *eps* (epipleural s.), 1 *ps* and



Figures 1–6. *Strophosoma capitatum*, 1, 2; *S. melanogrammum* 3, 4; *S. sus*, 5, 6; 1, 3, 5 - mature larva, lateral view; 2, 4, 6 - structure of last abdominal segments.

1 *eus*. Each pedal area of thoracic segments with 6–7 *pda* (pedal s.), variable in length. Abd. I–VII (Figs 7, 8, 18, 19, 29, 30) on each side with 1 medium-length *prs*, 5 *pds*, various in length and arranged along the posterior margin of each segment, 1 short and 1 long *ss*, 2 *eps* and 2 *ps*, 1 *lsts*

(laterosternal s.) and 2 short *eus*. Abd. VIII (Figs 9–11, 20–22, 31–33) on each side with 1 medium-sized *prs*, 3–4 *pds*, different in length and arranged along the posterior margin, 2 very short *ss*, paired *eps* and *ps*, 1 *lsts* and 2 short *eus*. Abd. IX (Figs 9–11, 20–22, 31–33) on each



Figures 7–11. *Strophosoma capitatum*, mature larva, chaetotaxy. **7** - thoracic segments and first abdominal segment, **8** - third abdominal segment, **9** - the 7th – 10th abdominal segments, **10** - ventral view of abdominal segments 7th – 10th, **11** - dorsal view of abdominal segments 7th – 10th. Abbreviations Th. I-III – thoracic segments, Abd. I-X – abdominal segments. Setae: *as* – alar, *ps* – pleural, *eps* – epipleural, *ds* – dorsal, *lsts* – laterosternal, *eus* – eusternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *sps* – spiracular, *sts* – sternal.

side with 2 *ds* (dorsal s.), medium in length, located close to the posterior margin of the segment, 1 medium *ps* and 2 short *sts* (sternal s.). Each vertical anal lobe (Abd. X) with a pair of minute setae, sometimes absent.

Head (Figs 12, 23, 34). Light yellow to dark brown, almost oval or suboval, frontal suture distinct, Y-shaped, endocarina absent. Setae on head capilliform. *Des*_{1, 2, 3, 5} (dorsal epicranial s.) usually equal in length; *des*₁ and *des*₂ located in the central part of epicranium, *des*₃ placed on frontal suture, *des*₅ located anterolaterally. *Fs*_{3, 4} (frontal s.) almost equal in length, *fs*₃ located anteromedially, *fs*₄ anterolaterally, close

to epistoma. *Les*₁ and *les*₂ (lateral s.) equal in length, slightly shorter than *des*₁. *Ves* (ventral s.) short, poorly developed. Postepicranial area with 4 very short *pes* (postepicranial s.). A pair of small stemmata (*st*) located anterolaterally on each side of head. Antenna (Figs 13, 24, 35) located at the end of frontal suture; antennal segment with sensorium, reniform, located medially; basal membranous article with 2-6 basiconic sensillae. Labrum (Figs 14, 25, 36) almost semicircular, anterior margin rounded or slightly sinuously emarginate; 3 pairs of *lrs* (labral s.) of different length, *lrs*₁ placed medially, *lrs*₂ anteromedially, *lrs*₃ anterolaterally; all

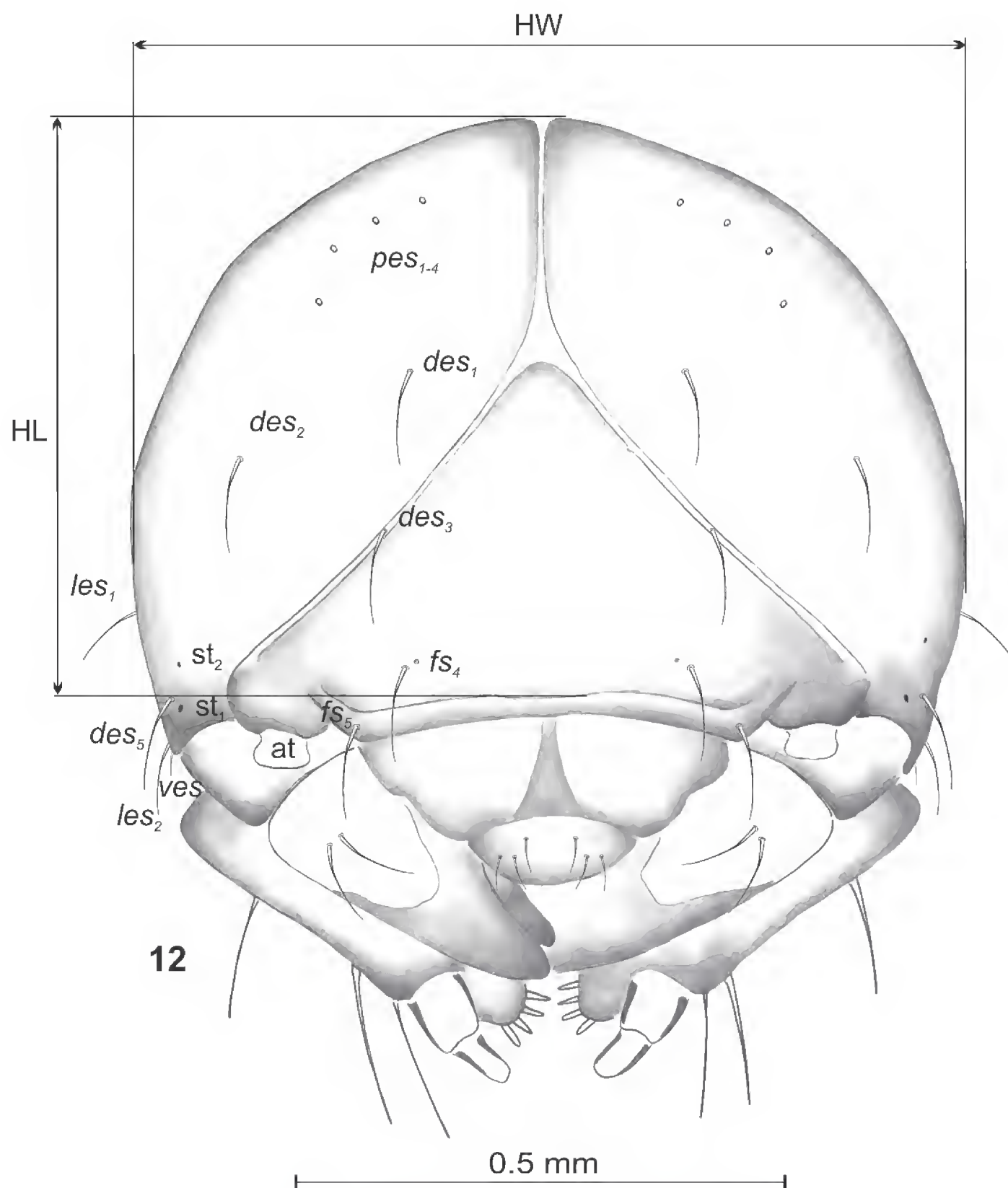
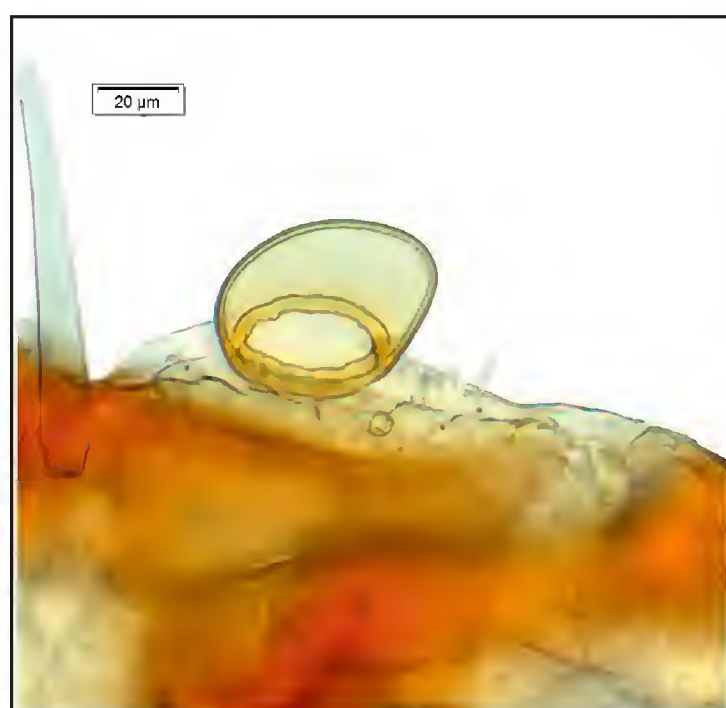


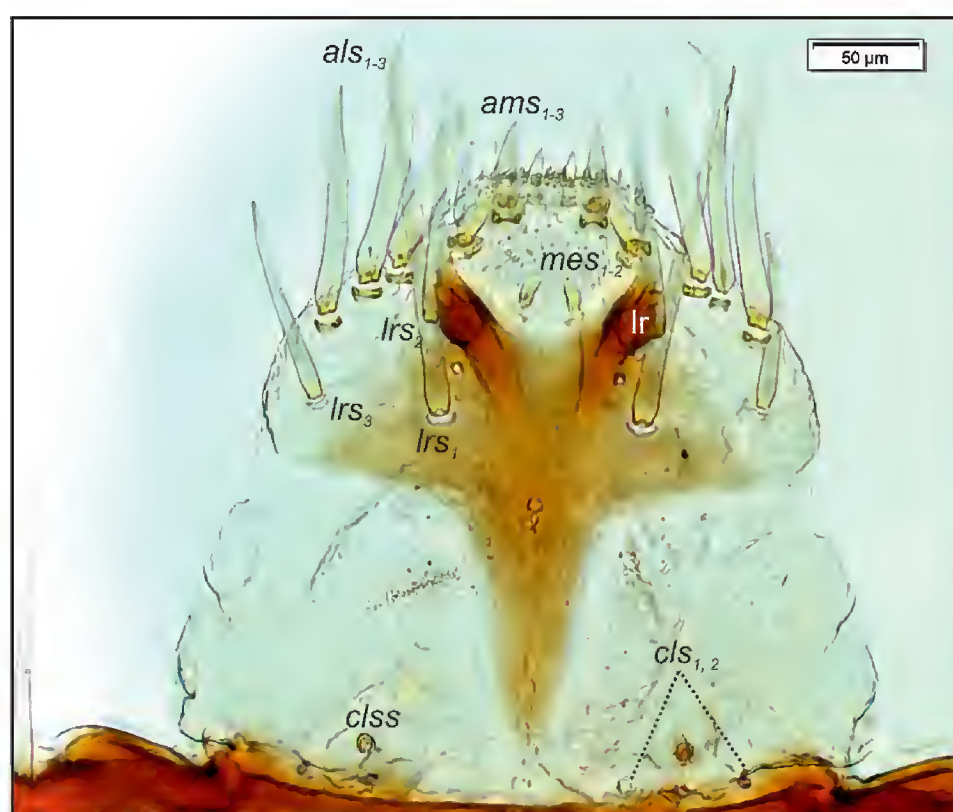
Figure 12. *Strophosoma capitatum*, mature larva, head. Abbreviations at – antenna, HL – head length, HW – head width, st – stemmata. Setae: *des* - dorsal epicranial, *fs* – frontal, *les* - lateral epicranial, *pes* – postepicranial, *ves* – ventral.

lrs without protuberances. Clypeus (Figs 14, 25, 36) of medium width, trapezium-shaped, lateral margins straight, anterior margin of clypeus straight or slightly concave; two pairs of *cls* (clypeal s.) reduced, vestigial, located posteromedially; *clss* (clypeal sensorium) clearly visible, placed medially between *cls*. Epipharynx (Figs 14, 25, 36) with 3 pairs of rod-shaped or capilliform *als* (anterolateral s.) of almost equal length; 3 pairs of *ams* (anteromedial s.): *ams*₁ very short, *ams*₂ half the length of *als*, *ams*₃ shorter than *ams*₂; 2 pairs of finger-like *mes* (medial s.), variable in length: first pair placed anteriorly, second pair medially. Anterior margin of epipharynx smooth or serrate, due to the presence of thorn-like cuticular processes placed between labral rods. Labral rods rather elongated, converging posteriorly. Mandibles (Figs 15, 26, 37) slightly curved, narrow, with divided apex (teeth different in length). There is a protruding additional tooth on the cutting edge between the apex and the middle of the

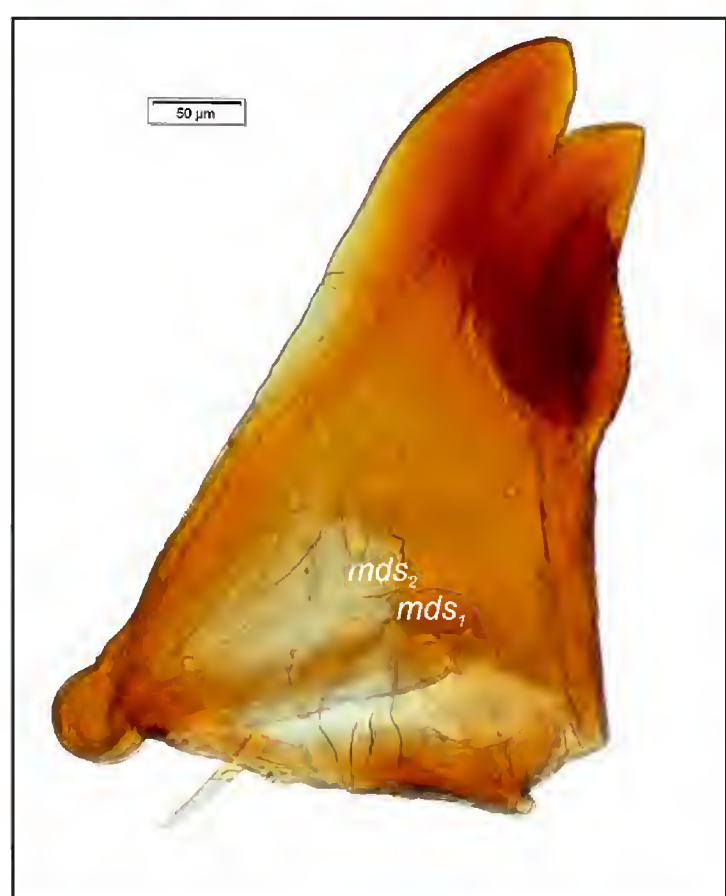
mandible; *mds*₁₋₂ capilliform, almost equal in length. Maxilla (Figs 17, 28, 39) with 1 *stps* (stipal s.) and 2 *pfs* (palpiferal s.) of equal length; mala with 8 finger-like or capilliform *dms* (dorsal malar s.), equal in size, and 4 *vms* (ventral malar s.); *vms* shorter than *dms*; *mbs* (malar basiventral s.) medium in length or short. Maxillary palpi with two palpomeres, basal with short *mxps* (maxillary palp s.); distal palpomere apically with a group of sensillae, each palpomere with a pore. Praelabium (Figs 16, 27, 38) almost rounded or heart-shaped with 1 long *plbs* (prelabial s.), located medially. Ligula with 1-2 capilliform *lgs* (ligular s.), variable in length. Premental sclerite clearly visible, Q-shaped. Labial palpi two-segmented; apex of distal palpomere with some sensillae; each palpomere with a pore. Postlabium (Figs 17, 28, 39) with 3 capilliform *pslbs* (postlabial s.), the first pair located anteromedially, the remaining two pairs laterally; *pslbs*₂ always distinctly longer than others.



13



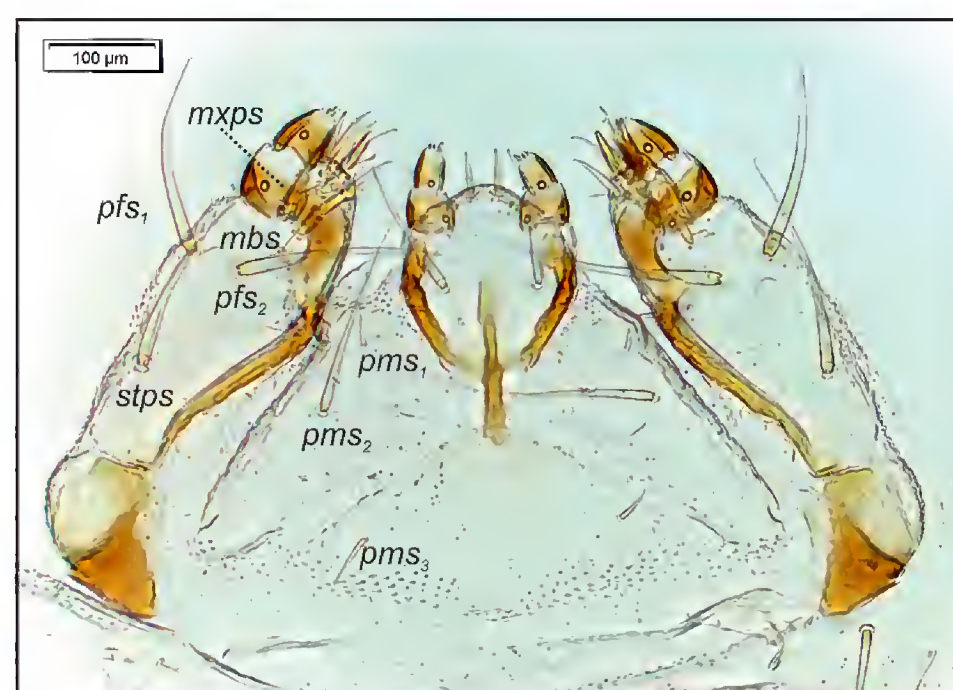
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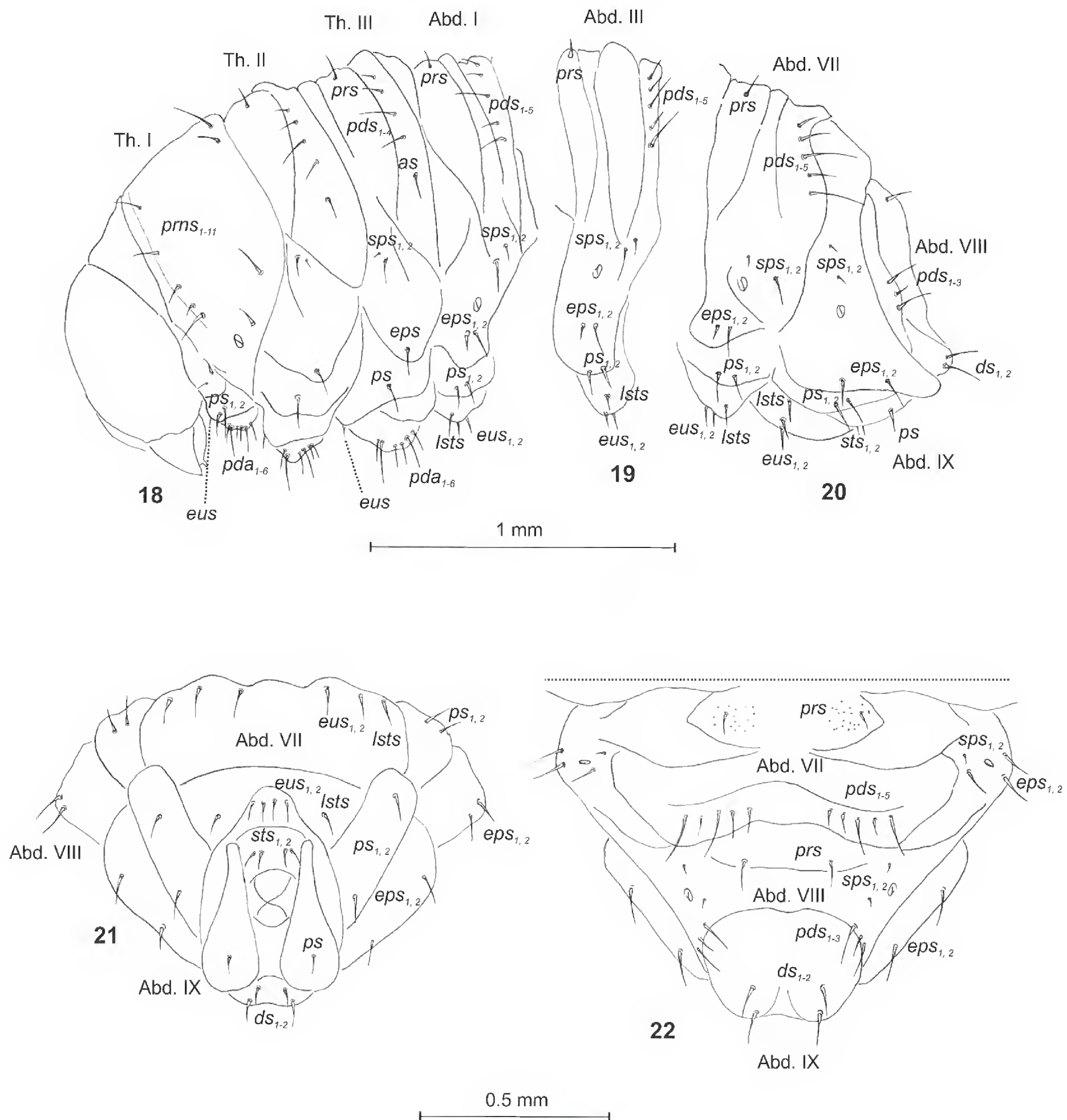


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17

Figures 13–17. *Strophosoma capitatum* mature larva, body parts. **13** - left antenna, **14** - clypeus, labrum and epipharynx, **15** - left mandible, **16** - praelabium, **17** - maxillolabial complex, ventral aspect. Lr – labral rods. Setae: *als* – anterolateral, *ams* – anteromedial, *cls* – clypeal, *clss* – clypeal sensorium, *dms* – dorsal malar, *ligs* – ligular, *lrs* – labral, *mbs* – malar basiventral, *mds* – mandibular, *mes* – median, *mxps* – maxillary palps, *pfs* – palpiferal, *plbs* – prelabial, *pslbs* – postlabial, *stps* – stival, *vms* – ventral malar.



Figures 18–22. *Strophosoma melanogrammum*, mature larva, chaetotaxy. **18** - thoracic segments and first abdominal segment, **19** - third abdominal segment, **20** - the 7th – 10th abdominal segments, **21** - ventral view of abdominal segments 7th – 10th, **22** - dorsal view of abdominal segments 7th – 10th. Abbreviations: Th. I-III – thoracic segments, Abd. I-X – abdominal segments. Setae: *as* – alar, *ps* – pleural, *eps* – epipleural, *ds* – dorsal, *lsts* – laterosternal, *eus* – eusternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *sps* – spiracular *sts* – sternal.

Diagnoses of the species

Strophosoma (Strophosoma) capitatum

Figs 1, 2, 7–17

Body. Rather elongate, white to yellowish, abdominal segment VIII dark yellow. Setae long to very short. Each side of prothorax (Fig. 7) with 8 *prns*, two setae placed close to spiracle. Meso- and metathorax (Fig. 7) each with 1 me-

dium long *prs* and 4 *pds*: first and second short, third very long; fourth medium. Each pedal area with 7 *pda*, variable in length. *Eps*₁ on abdominal segments I-VII almost twice as long as *eps*₂ (Fig. 8), on next segments almost equal in length (Fig. 9). Abd. segments I-VII each with 5 *pds*: first, second and fourth very short, third and fifth very long. Abd. VIII with 3 *pds* and 1 very short *ss* (Figs 9–11).

Head. Yellow, oval (Fig. 12). Antennal basal membranous article with 3 basiconic sensillae and a pore

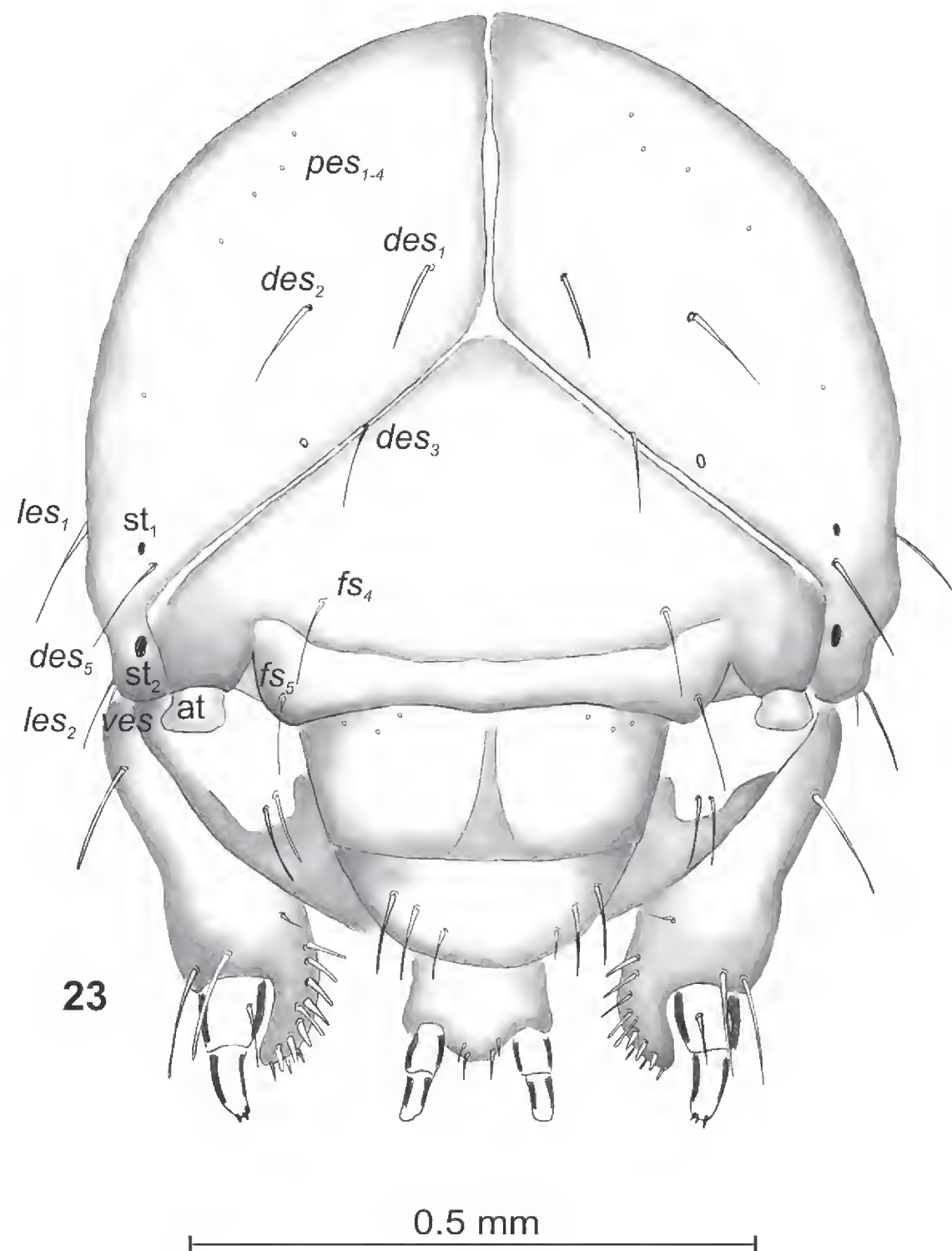


Figure 23. *Strophosoma melanogrammum*, mature larva, head. Abbreviations: at – antenna st – stemmata. Setae: *des* – dorsal epicranial, *fs* – frontal, *les* – lateral epicranial, *pes* – postepicranial, *ves* – ventral.

(Fig. 13). Labrum (Fig. 14) approximately 1.8 times as wide as long; anterior margin slightly sinuate, serrate due to some thorn-like cuticular processes located between *ams*; *als* capilliform. Surface of epipharynx between labral rods covered by very fine asperities. Labral rods of medium length. Clypeus (Fig. 14) 2.2 times as wide as long; anterior margin slightly convex. Mandible (Fig. 15) with a protruding cutting edge placed close to apex; *mbs* very long. Both maxillary palpomeres equal in length, but basal one wider than distal; maxilla with 8 *dms* and 4 *vms*, all capilliform (Figs 14, 16). Praelabium rounded, with a single pair of *ligs*; basal palpomere slightly longer and wider than distal; *pslb*₂ 6 times longer than remaining *pslb*.

Strophosoma (Strophosoma) melanogrammum

Figs 3, 4, 18–28, 45

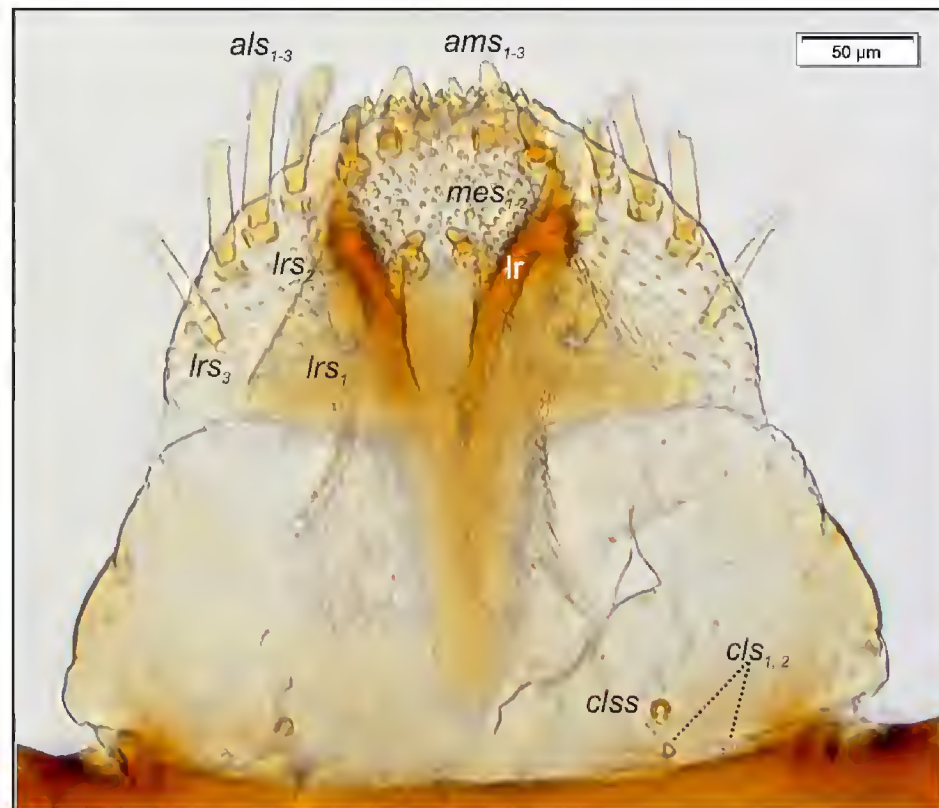
Body. Rather stout, yellowish, abdominal segment VIII dark brown. Setae medium-length to very short. Each

side of prothorax (Fig. 18) with 11 *prns*, two setae placed below spiracle. Meso- and metathorax (Fig. 18) each with one medium-sized *prns* and 4 *pds*: first very short, second short, third very long; fourth medium. Each pedal area with 6 *pda*, variable in length. *Eps*₁ on abdominal segments I–VII almost twice as long as *eps*₂ (Figs 19–20). Abd. segments I–VII each with 5 *pds*: first, second and fourth medium, third and fifth long. Abd. VIII with 3 *pds* and 2 very short *ss*_{1,2} (Figs 20–22).

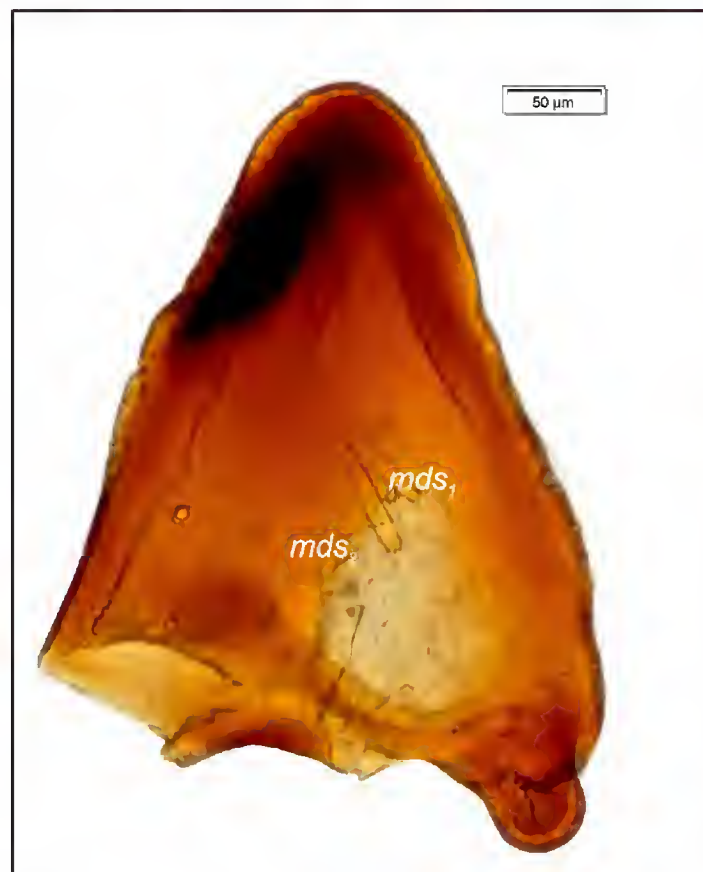
Head. Dark brown, almost circular (Fig. 23). Antennal basal membranous article with 6 basiconic sensillae (Fig. 24). Labrum (Fig. 25) approximately 1.7 times as wide as long; anterior margin rounded, serrate due to some thorn-like cuticular processes located between *ams*; *als* rod-shaped. Surface of epipharynx between labral rods densely covered by conical asperities. Labral rods relatively short. Clypeus (Fig. 25) 2.5 times as wide as long; anterior margin almost straight. Mandible (Fig. 26) conical, cutting edge poorly developed; *mbs* rather short. Both maxillary palpomeres equal in length, but basal one distinctly wider than distal; maxilla with



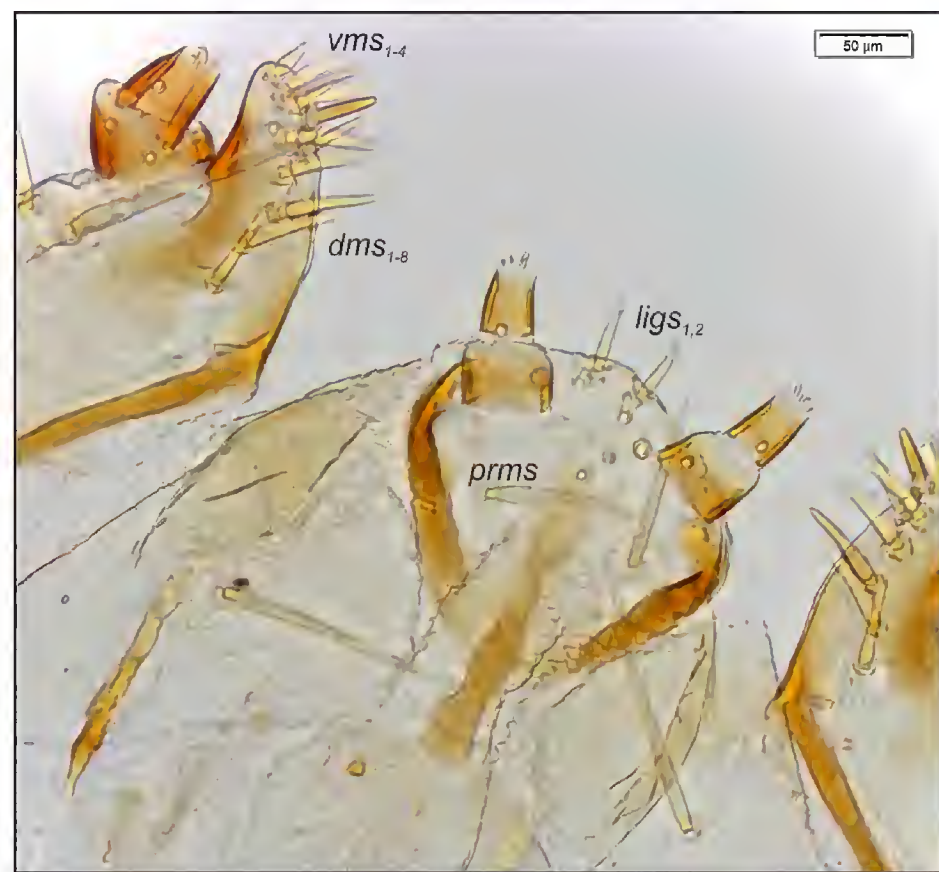
24



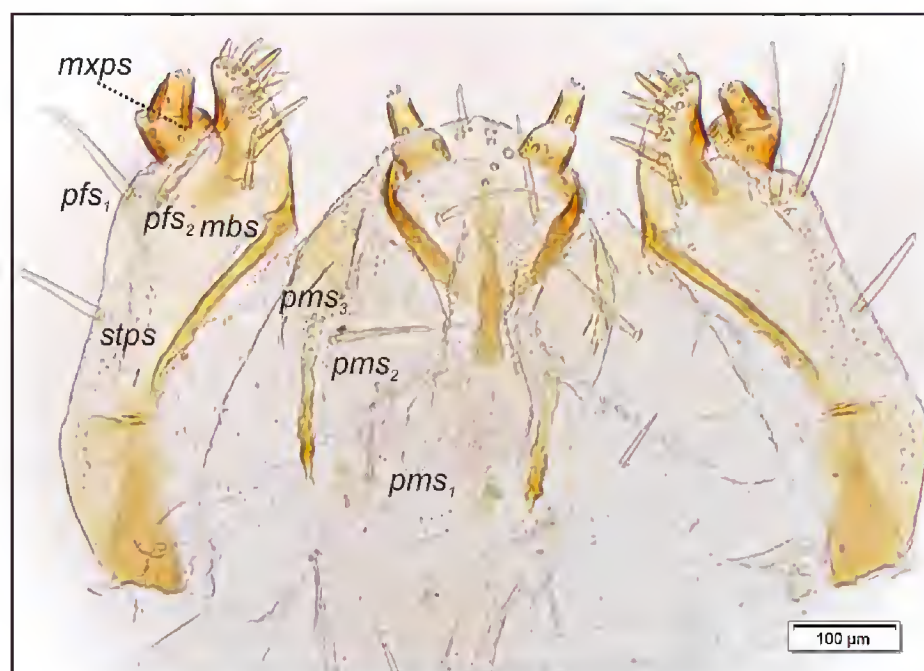
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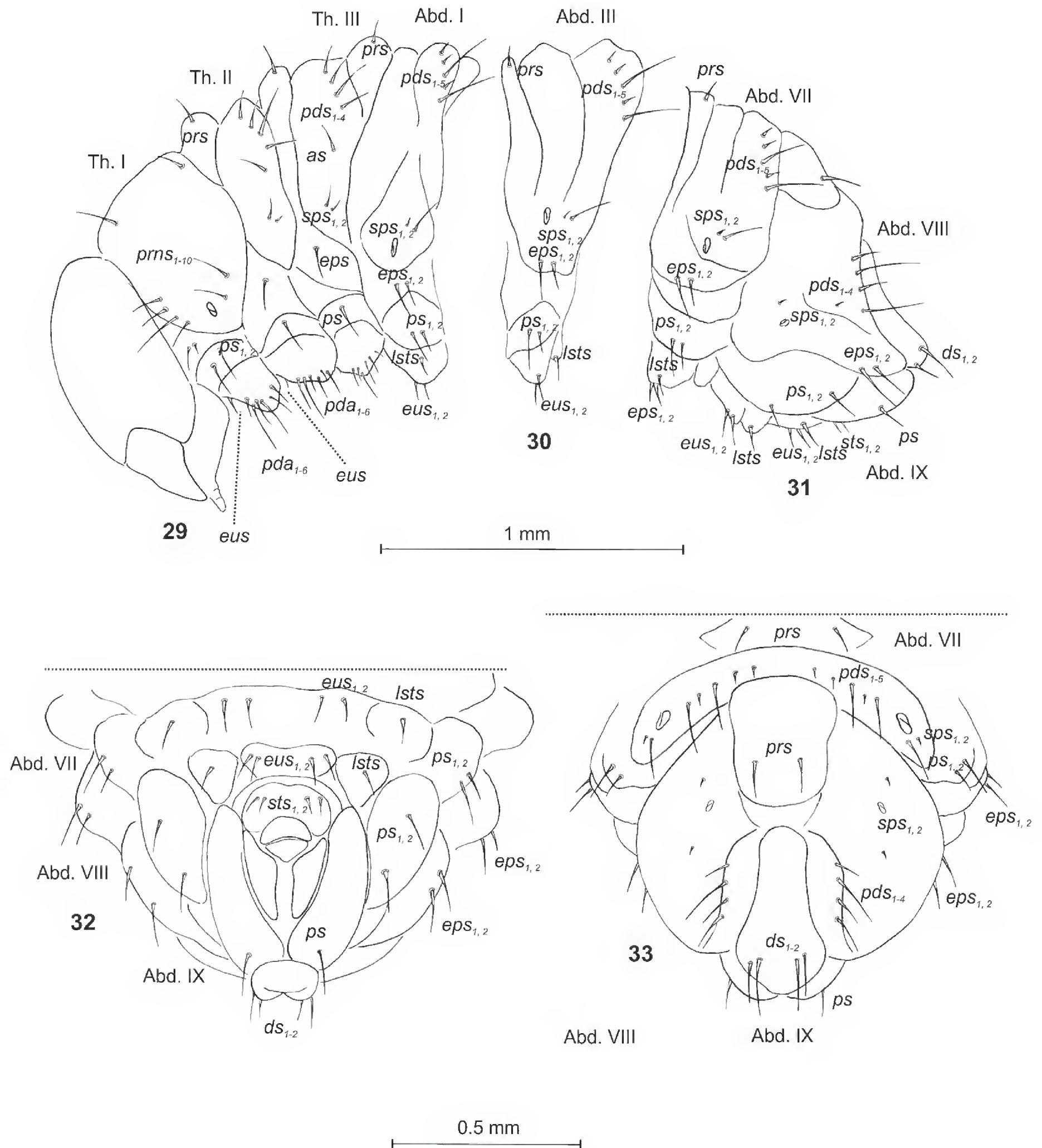


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Figures 24–28. *Strophosoma melanogrammum*, mature larva, body parts. 24 - left antenna, 25 - clypeus, labrum and epipharynx, 26 - left mandible, 27 - praelabium, 28 - maxillolabial complex, ventral aspect. Lr - labral rods. Setae: *als* - anterolateral, *ams* - anteromedial, *cls* - clypeal, *clss* - clypeal sensorium, *dms* - dorsal malar, *ligs* - ligular, *lrs* - labral, *mbs* - malar basiventral, *mds* - mandibular, *mes* - median, *mxps* - maxillary palps, *pfs* - palpiferal, *plbs* - prelabial, *pslbs* - postlabial, *stps* - stipal, *vms* - ventral malar.



Figures 29–33. *Strophosoma sus*, larva of high instar, chaetotaxy. **29** - thoracic segments and first abdominal segment, **30** - third abdominal segment, **31** - the 7th – 10th abdominal segments, **32** - ventral view of abdominal segments 7th – 10th, **33** - dorsal view of abdominal segments 7th – 10th. Abbreviations: Th. I-III – thoracic segments, Abd. I-X – abdominal segments. Setae: *as* – alar, *ps* – pleural, *eps* – epipleural, *ds* – dorsal, *lsts* – laterosternal, *eus* – eusternal, *pda* – pedal, *pds* – postdorsal, *prns* – pronotal, *prs* – prodorsal, *sps* – spiracular *sts* – sternal.

6 *dms* and 4 *vms*, all finger-like (Figs 27, 28). Praelabium heart-shaped, with two pairs of *ligs*, variable in length; basal palpomere slightly shorter and wider than distal; *pslb*₂ 3 times longer than remaining *pslb*.

Strophosoma (Neliocarus) sus

Figs 5, 6, 29–39, 43

Body. Elongated, yellowish, abdominal segment VIII dark yellow. Setae medium long to very short. Each side of prothorax (Fig. 29) with 10 *prns*, two setae placed below spiracle. Meso- and metathorax (Fig. 29) each

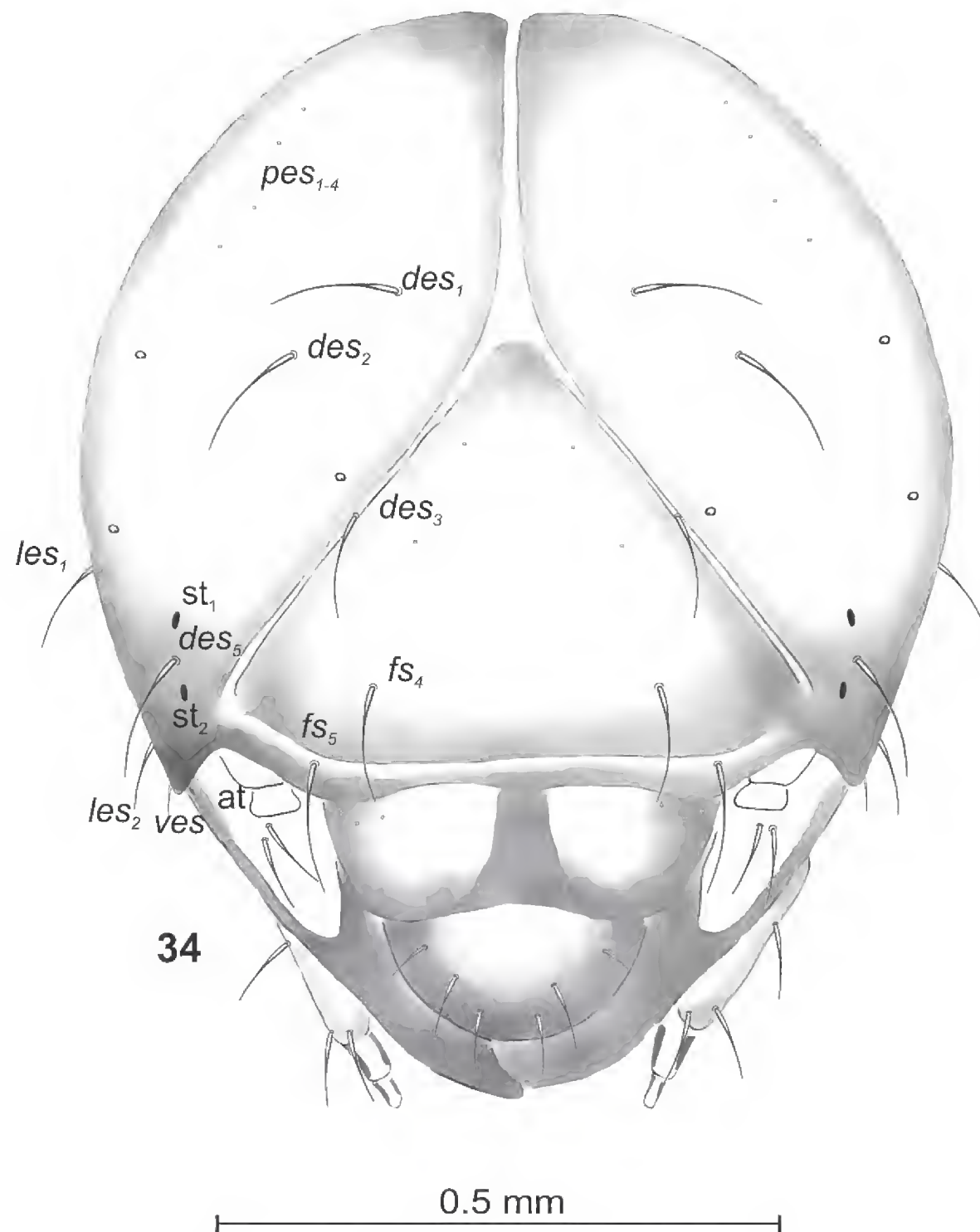


Figure 34. *Strophosoma sus*, larva of high instar, head. Abbreviations: at – antenna st – stemmata. Setae: *des* – dorsal epicranial, *fs* – frontal, *les* - lateral epicranial, *pes* – postepicranial, *ves* – ventral.

with one medium-length *prs* and 4 *pds*: first, second and fourth medium, third long. Each pedal area with 6 *pda*, variable in length. *Eps*_{1,2} on abdominal segments I-VII different in length (Figs 29–31). Abd. segments I-VII each with 5 *pds*: first, second and fourth short, third and fifth very long. Abd. VIII with 4 *pds* and 2 very short *ss*_{1,2} (Figs 31–33).

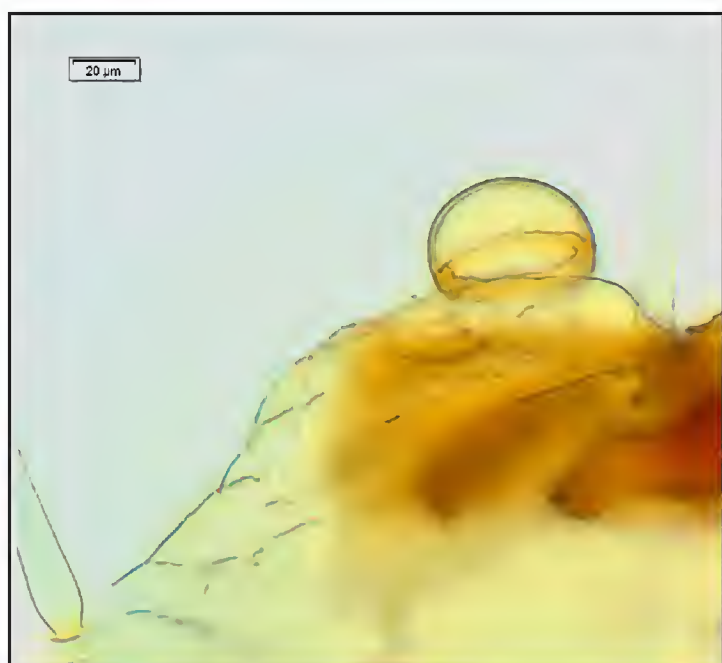
Head. Dark yellow to dark brown, slightly flattened bilaterally (Fig. 34). Antennal basal membranous article with two basiconic sensillae (Fig. 35). Labrum (Fig. 36) approximately twice as wide as long; anterior margin

slightly sinuate; *als* rod-shaped. Surface of epipharynx (between labral rods) densely covered by conical asperities. Labral rods strongly elongate. Clypeus (Fig. 35) 2.6 times as wide as long; anterior margin straight. Mandible (Fig. 37) with protruding cutting edge placed in the middle; *mbs* very short. Both maxillary palpomeres equal in length, but basal one wider than distal; maxilla with 6 *dms* and 4 *vms*, all capilliform (Fig. 39). Praelabium rounded, with a pair of relatively long *ligs*; basal and distal palpomeres almost equal in size and shape; *pslb*₂ 3 times longer than remaining *pslb*.

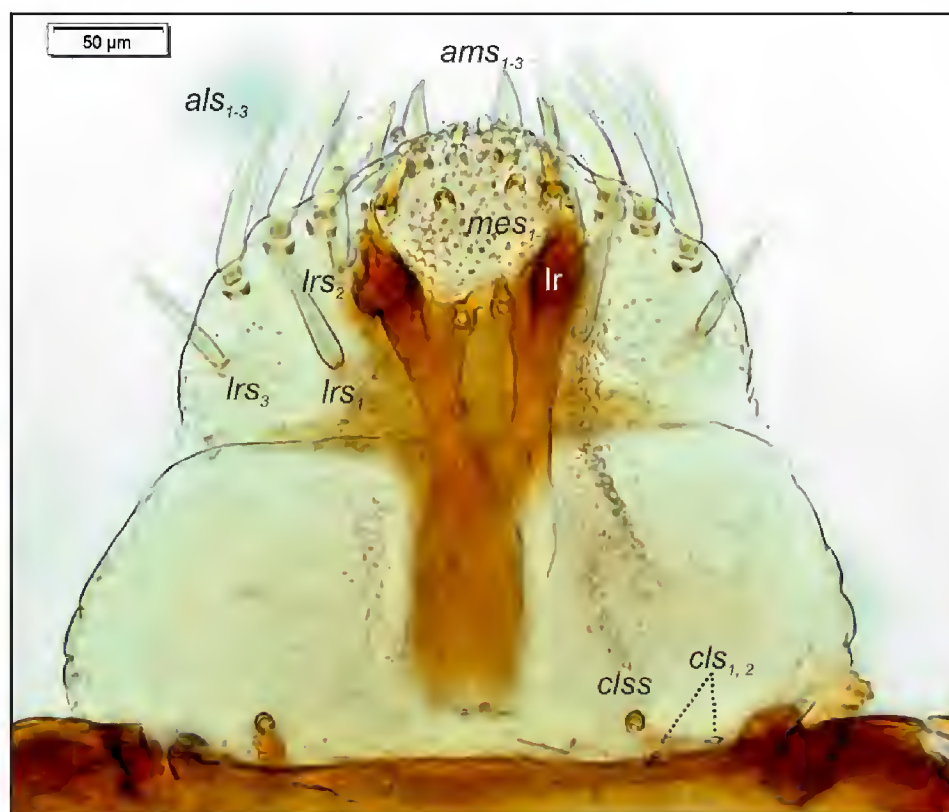
Key to mature larvae of selected *Strophosoma* subgenera and species

The larva of *Strophosoma (Neliocarus) faber* distinguished according to Van Emden (1952) and Scherf (1964), the remaining species as in the present work. In *S. sus* based on the last or penultimate instar.

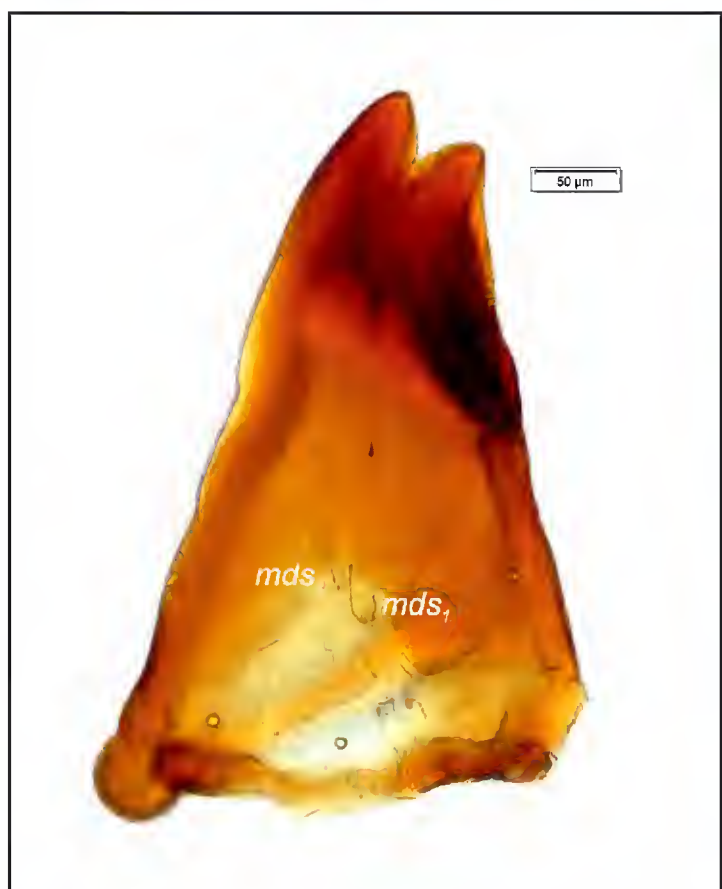
- 1 Abdominal segment VIII with 4 *pds*; anterior margin of epipharynx (between *ams*) almost smooth.....*Strophosoma (Neliocarus)*
- Abdominal segment VIII with 3 *pds*; anterior margin of epipharynx (between *ams*) distinctly serrate.....*Strophosoma (Strophosoma)*



35



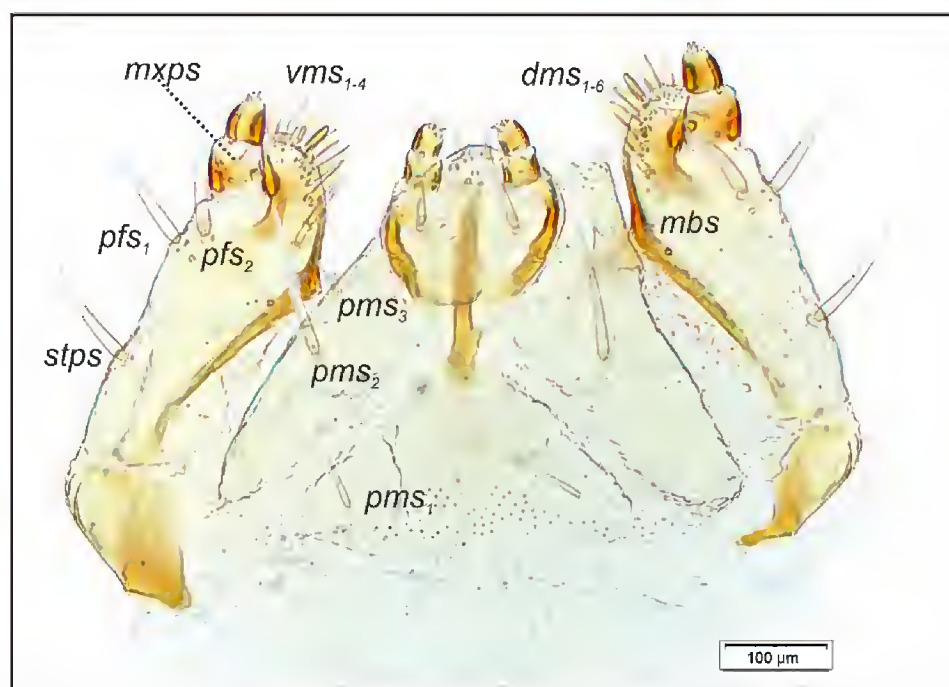
36



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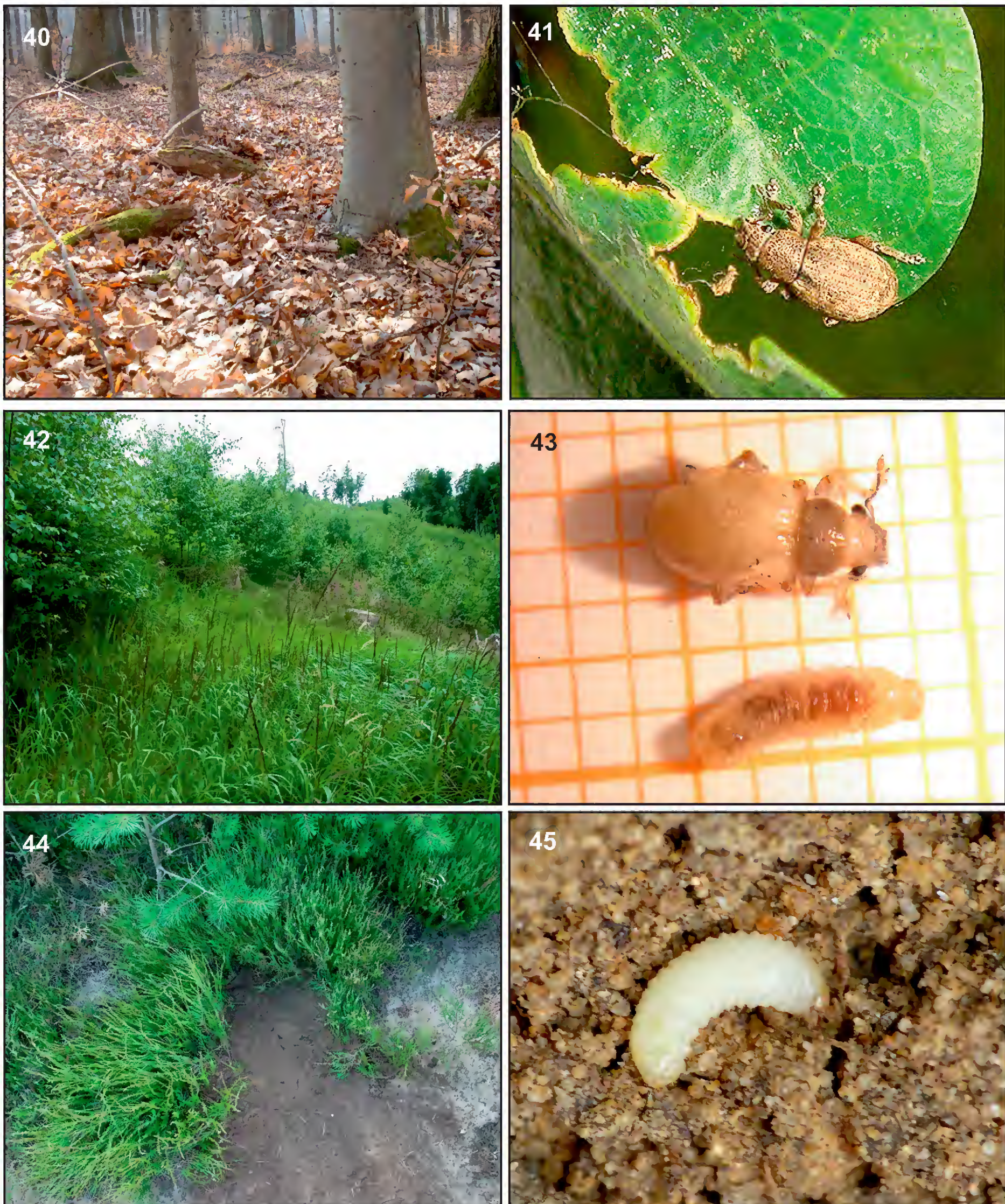


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Figures 35–39. *Strophosoma sus*, larva of high instar, body parts. **35** - left antenna, **36** - clypeus, labrum and epipharynx, **37** - left mandible, **38** - praelabium, **39** - maxillolabial complex, ventral aspect. Lr – labral rods. Setae: *als* – anterolateral, *ams* – anteromedial, *cls* – clypeal, *clss* – clypeal sensorium, *dms* - dorsal malar, *ligs* – ligular, *lrs* – labral, *mbs* – malar basiventral, *mds* – mandibular, *mes* – median, *mxps* – maxillary palps, *pfs* – palpiferal, *plbs* – prelabial, *pslbs* – postlabial, *stps* – stipal, *vms* – ventral malar.



Figures 40–45. Sampling sites, host plants, larvae, teneral and mature adults. **40** - sampling site of *Strophosoma capitatum* in a beech forest in the Deister Mountains southwest of Hannover, **41** - adult *S. capitatum* feeding on *Salix caprea* in a pine forest on the outskirts of Celle (Niedersachsen), **42** - habitat of *S. melanogrammum* near Ilsenburg (Sachsen-Anhalt) in the National Park Harz, a broken down spruce plantation, now containing a pioneer forest with young birch trees, **43** - mature larva and fresh adult of *S. sus* from breeding, **44** - searching site for immature stages of *S. sus* between the roots of *Calluna vulgaris* in the southern part of the Lower Saxonian heathland near Berkhof, **45** - mature larvae of *S. melanogrammum* found between the roots of *Cytisus scoparius* near Brelingen in the north of Hannover.

Subgenus *Neliocarus*

- 1 Stemmata absent; head capsule slightly flattened bilaterally; labral rods elongate *S. sus*
 – Stemmata (two pairs) present; head capsule rounded; labral rods short *S. faber*

Subgenus *Strophosoma*

- 1 Pleural lobes of Abd. VII narrow, elongate; anterior margin of labrum slightly sinuate, *a/s* capilliform; prelabium with 1 pair of *ligs*; antennal basal membranous article with three basiconic sensillae and a pore; prelabium rounded *S. capitatum*
 – Pleural lobes of Abd. VII wide, triangular; anterior margin of labrum rounded, *a/s* finger-like; prelabium with 2 pairs of *ligs*; antennal basal membranous article with 6 basiconic sensillae; prelabium heart-shaped *S. melanogrammum*

Conclusion

Remarks on the development of *Strophosoma* species

The data about the development of *Strophosoma melanogrammum* and *S. capitatum* (in part) have been mainly worked out and summarized by Grimm (1973) and Schauer mann (1973). According to these sources both species develop in the Solling Mountains in the southern part of Niedersachsen (Germany) very similarly, and over a period of more than one year. After overwintering adults start to feed and to lay eggs from May to first half of July. Dieckmann (1980) found females with eggs still in the abdomen in August. The eggs are usually laid in clusters in any kind of sheltered situations, e.g. in cracks of cork, between dry leaves of litter, in soil (probably in crevices), between leaf or flower buds of the host plant, on the ground in needles of pine shoots (Breese 1948; Grimm 1973) and, in the laboratory, between rolled or pleated absorbent paper or between paper and the substrate. The eggs are held together by a viscid fluid. This agrees with observations in the laboratory, documented by Sprick and Stüben (2012), who found bulks of eggs deposited between the layers of absorbent paper close to its edges, where these were laid by the female's ovipositor, and by the observations of Wolcott (1933) on neotropical Entiminae genera of the (same) former subfamily Brachyderinae. He had fixed double paper strips in the field on the top of stakes beneath cultivated young *Citrus* plants, and found many eggs deposited between the paper strips or sheets.

Larvae then develop in soil and feed mainly on fine roots until the third or last (fourth) instar and overwinter. In the following year the larvae complete their development and pupate, mainly in August. Adults of the new generation emerge from September to November and single specimens also in spring of the succeeding year. Adults climb for maturation feeding in tree crowns in spring, late summer and early autumn. They also feed in the herb layer and in leaf litter. Urban (1913) gave a strikingly different time of pupation for *S. faber*: the second half of May, producing a newly emerged weevil in June.

According to Schauer mann (1973) *S. melanogrammum* and *S. capitatum* have 4 larval instars. But there is no information about how these instars were differentiated. The method of Sprick and Gosik (2014) for the

determination of larval instars failed in these species, as the eyes are strongly protruding over the edge of the head in the pupae.

The breeding of *Strophosoma melanogrammum* and *S. capitatum* in the climate chamber, which was very successful in the case of *Otiorhynchus* larvae (Gosik et al. 2016), did not result in any *S. capitatum* larvae (two attempts) and only one larva of *S. melanogrammum* (four attempts), although host plants, the size of flower-pots and the soil substrate were varied. Also an addition of eggs bred before in keeping boxes was not successful. For these reasons no pupae could be obtained by breeding. Field-collecting was conducted only rarely in August, the main month of pupation.

The larval development of any other *Strophosoma* species is apparently unknown. Breeding of *Strophosoma sus* in two flower-pots with *Calluna vulgaris* and *Erica arborea* L. revealed the following data (but only in the pot with *Calluna*): egg-laying started in May (first adults being already active in April) and a newly emerged, weak, adult and a larva were obtained in the beginning of September; four further larvae were seen in the flower-pots, but a further check 3 or 4 weeks later did not reveal any larva, pupa or adult weevil. The reasons for the failure of the continuation of this breeding attempt are not known. Three pupae of *Strophosoma* cf. *sus* were found in the field at the heathland site near Berkhof with *Calluna vulgaris* and young *Pinus sylvestris* trees, where *S. sus*, *S. capitatum* and, rarely, also *S. fulvicorne* (Walton, 1846) were present (Gosik and Sprick 2013). Two pupae were found on 9th July and one on 2nd September, indicating an earlier start of pupation than in *S. capitatum* or *S. melanogrammum* from the Solling Mountains. This is not surprising, as the heathland near Berkhof with a population of *S. sus* is a warm and dry lowland area that allows earlier development. From this, it would be of interest to determine whether the development of *S. capitatum* or *S. melanogrammum* is also possible within one year at such warm sites, or whether larval overwintering and diapause are obligatory in these species.

General remarks about the morphology of *Strophosoma* larvae

Some basic information regarding the morphology of the larva of *Strophosoma (Neliocarus) faber* (Herbst, 1785),

with drawings of head, mouthparts and apex of abdomen, can be found in the work of Urban (1913). However, the main sources of information about morphology (and egg-laying habits) of *Strophosoma* larvae are studies of Van Emden (1950, 1952), containing descriptions of the first larval instar of *S. melanogrammum*, *S. capitatum* and *S. (Neliocarus) nebulosum* Stephens, 1831 (syn. *S. retusum* Marsham, 1802), as well as of the mature *S. faber* larva. Van Emden (1952) also specified a number of characters of taxonomic importance for the entire genus *Strophosoma*, such as the presence of 3 or 4 *pds* on Abd. VIII, the conspicuously sclerotized apex of the abdomen, the shape of the premental sclerite, the proportions of setae on the pedal lobes, and the *pds* proportions on Abd. VIII.

The presence of four ventral malar setae in larvae of the genus *Strophosoma* confirms the observations of Marvaldi (1998a) that this character, as well as the shape of the antennal sensorium (Marvaldi 1997, 2003), can be considered an additional apomorphic character for larvae of the subfamily Entiminae, while other Curculionidae, e.g. Cyclominae in the sense of Marvaldi (1998b, 2003), possess the plesiomorphic number of five *vms*.

Further information on the morphology of preimaginal stages of the genus *Strophosoma* was provided by Willis (1964), who presented a very detailed, but unfortunately sparsely illustrated, description of the mature larva of *S. melanogrammum*. In addition to valuable information on the biology of reproduction and the morphology of larval stages of selected Entiminae species (genera *Otiorynchus* Germar, 1822, *Barynotus* Germar, 1817, *Sciaphilus* Schönherr, 1823 and *Strophosoma*), Willis (1964) described a few general patterns valid for the morphology of weevils. Moreover, he observed changes in the proportions and relative lengths of setae when the larvae entered successive developmental stages. For this reason the key to the genus *Strophosoma* of Van Emden (1952), enabling identification of first-instar larvae to species level based on the proportions of setae, should be regarded – according to Willis (1964) – as at least inadequate for an identification of older larval instars. Changes in the proportions and shape of setae of weevil larvae when passing through successive developmental stages were also observed in later research on Entiminae (Gosik and Sprick 2012) and Hyperinae larvae (Skuhrovec 2004, 2006, 2007). Van Emden (1952) gave differences in the relative lengths of setae on pedal areas as the most important difference between *Strophosoma* sensu stricto and *Neliocarus*, but he did not mention the presence of four *pds* on the 8th abdominal segment in *Neliocarus* versus three *pds* in *Strophosoma*.

The differences in the number of setae and in the morphology of abdominal segments which are observed in the species treated in this paper (*S. capitatum*, *S. melanogrammum* and *S. sus*) as well as in the previously described larva of *S. faber* (Van Emden 1952; Scherf 1964) show that *Strophosoma* species can be easily recognized in both mature stages and in younger larvae. The differences between them (e.g. number of setae and presence or absence of asperities on the epipharynx) seem to sup-

port the existing division into subgenera (*Strophosoma* and *Neliocarus*). However, due to a lack of information about the morphology of the larvae of the remaining subgenera (*Morphostrophus* Flach, 1907, *Pelletierius* Alonso-Zarazaga & Lyal, 1999 and *Subcaulostrophus* Flach, 1907 according to Pelletier (2013)), a definitive evaluation of these characters will only be possible after further research.

8th abdominal segment: adaptation to the environment versus phylogenetic relationship

Because of the morphology of the eighth abdominal segment, especially the sclerotization and the dark colour, larvae of the genus *Strophosoma* are among the most easily recognized weevil larvae. Only the larvae of the genera *Philopodon* Schönherr, 1826, and *Tanymecus* Germar, 1817, are similar to *Strophosoma* larvae with respect to the morphology of this segment (Van Emden 1950). This leads to the question: are these genera more closely related to each other than to other Entiminae genera? Here we can state the following: Smreczyński (1966) placed the genus *Strophosoma* in a separate tribe, Strophosomini, in a close relationship with the tribe Cneorhinini Lacordaire, 1863, with the genus *Philopodon*, whereas *Tanymecus* was placed in another subfamily (Tanymecinae). Dieckmann (1980) did not use tribes, but he also placed *Philopodon* next to *Strophosoma* (and between them only *Cneorhinus* Schönherr, 1823 with unknown larvae). *Tanymecus* was again placed in another subfamily. Today all these genera are members of the subfamily Entiminae, but they are placed in three different tribes: Brachyderini with *Strophosoma* (Pelletier 2013), Cneorhinini with *Philopodon* (Alonso-Zarazaga 2013) and Tanymecini with *Tanymecus* (Li Ren et al. 2013). A carefully reconstructed phylogeny, combining molecular, morphological and biological data, is still lacking.

Even if we do not know anything about the function of this conspicuous abdominal structure, the possibility that this is an adaptation to the environment has to be taken into account. It is found in a few genera of Entiminae only, larvae of which develop in soil. But there is no information as to whether these larvae exhibit behaviour or habits that are different from those larvae without a sclerotized 8th abdominal segment.

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Taxonomy and phylogeny of the genera *Gymnocnemia* Schneider, 1845, and *Megistopus* Rambur, 1842, with remarks on the systematization of the tribe Nemoleontini (Neuroptera, Myrmeleontidae)

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Abstract

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The delineation of antlion genera has often been based on morphological characters not tested in a phylogenetic context, thus seriously impairing the study of systematics of the family Myrmeleontidae. Nebulous generic limits also impede the taxonomy and study of the affinities of closely related species. As a case study, the generic placement of *Megistopus mirabilis* Hölzel, 1980, was based on a single leg character. To test the position of this species, the reciprocal relationships of the members of the genera *Gymnocnemia* Schneider, 1845, and *Megistopus* Rambur, 1842 were investigated, using a morphology-based phylogenetic analysis. This approach demonstrated that *M. mirabilis* should actually be assigned to the genus *Gymnocnemia*, as *G. mirabilis* **comb. n.** This analysis also supports the subdivision of the tribe Nemoleontini in two subclades based on morphology of male and female genitalia. A new characterisation of these genera is provided, as well as a redescription of the very rare *G. mirabilis* and the poorly investigated *Megistopus lucasi* (Navás, 1912). An updated identification key to the members of the genera *Gymnocnemia* and *Megistopus* is presented.

Introduction

Myrmeleontidae, commonly known as antlions, are the most species-rich family of the order Neuroptera, including 1657 described species (Oswald 2016) that are distributed in all tropical and temperate regions of the world. The Western Palearctic, including the Arabian peninsula (following the boundaries of H. Aspöck et al. 2001), harbours a relatively rich fauna with at least 285 known species (H. Aspöck et al. 2001, Oswald 2016). Despite the notable diversity and wide distribution of this family, the phylogeny of antlions has been poorly investigated and few studies have dealt with this subject in a modern quantitative approach (Badano et al. 2017, Michel et al. 2017). Moreover, one of the main problems afflicting the systematics of Myrmeleontidae is the

poor characterisation of supraspecific taxa, thus making it difficult to trace the relationships among genera and to determine the placement of certain species. In fact, most genera are based on morphological characters that have not been tested in a phylogenetic context and have doubtful systematic value, as in the case of the commonly used wing markings and wing shape. An interesting case study is represented by two closely related genera, both restricted to the Western Palearctic: *Gymnocnemia* Schneider and *Megistopus* Rambur. As the name itself implies, *Gymnocnemia* (from Greek, “naked legs”) was distinguished from *Megistopus* by Schneider (1845) due to the absence of tibial spurs. In the beginning of the 20th century, during a period of intense taxonomic activity, the genus *Gymnocnemia* became an assemblage for a number of unrelated, usually long-legged, antlions from all

the main biogeographic regions that were only grouped together due to the lack of tibial spurs. In the following years, the exotic taxa were eventually excluded and assigned to other genera. Therefore, *Gymnocnemia* was long considered monotypic, including only *G. variegata*, a widespread but uncommon Holomediterranean species, until the description of a second species from the Moroccan Atlas Mountains, *G. editaerevayae* Michel, 2013. The diagnostic character proposed by Schneider (1845) remained the main criterion to distinguish *Gymnocnemia* from *Megistopus*, whose type species is the Holomediterranean *M. flavicornis* (Rossi, 1790). Hölzel (1980) placed a new species, *Megistopus mirabilis*, from the Sinai Peninsula in the latter genus due to the presence of spurs, following an almost one and a half century-old convention. Lastly, Güsten (2003) transferred *M. lucasi*, which was originally described by Navás (1912) as a member of the genus *Nelees* Navás, 1912 (now a synonym of *Neuroleon* Navás, 1909), to *Megistopus*, although its real affinities had already been hinted at by Banks (1913). Since the specimens from Italy, which were originally identified as *M. mirabilis*, actually belong to *M. lucasi* (Letardi and Pantaleoni 1996, Badano and Pantaleoni 2014), *M. mirabilis* was only known from the holotype. Based on a study of the collection of the late Herbert Hölzel, a foremost figure in the study of Palaearctic antlions, a series of undetermined specimens from Oman belonging to this taxon was brought to the attention of the authors. After careful examination of the morphology of this species, its generic placement was questioned, and the species was considered to have closer ties to *Gymnocnemia* thus challenging the value of certain morphological characters commonly used by specialists as diagnostic at the genus level. Therefore, we performed a morphology based quantitative phylogenetic analysis to test the affinities of the members of *Gymnocnemia* and *Megistopus* and to provide a solid phylogenetic argumentation for their delimitation. The aim of the present study is to re-describe these genera, discuss their affinities and detail the morphology of the inadequately known species.

Materials and methods

Examined specimens are deposited in the following collections: collection of Davide Badano, Taggia, Italy (DB); collection of Horst and Ulrike Aspöck, Vienna, Austria (HUAC); collection of Herbert Hölzel, Natural History Museum Vienna, Austria (NHMW) (Suppl. material 1).

Specimens were examined and measured with a Leica® MZ 9.5 stereomicroscope equipped with an optical micrometre and photographed with a Canon® EOS 600D digital camera with Canon® lens MP-E 65 mm; obtained images were stacked with the software Zerene® STACKER. Specimens were measured following the protocol of Pantaleoni and Badano (2012): body length was taken from vertex to abdomen tip; wing length was

measured longitudinally from base to apex, and wingwidth was taken as the maximum width perpendicular to the length measurement line. Genitalia were macerated in 10% KOH (potassium hydroxide) at room temperature, later rinsed in acetic acid and water and finally preserved in glycerol. Terminology mainly follows Stange (1970a) for body and wing morphology and U. Aspöck and H. Aspöck (2008) for genitalia.

The distribution map was made with Natural Earth, free vector and raster map data, available at www.naturalearthdata.com.

Abbreviations used in the text: Biogeogr, biogeography; Biol, biology; Cat, catalogue; Com, comment; Distr, distribution; Key, identification key; List, checklist; ODescr, original description; Syn, synonymy.

Phylogenetic analysis

Characters and states were coded for a set of antlion taxa illustrative of morphological variability across the family. *Palpares libelluloides* Linnaeus (Palparinae) was selected as the outgroup. A data matrix including 56 characters and 121 states was prepared in MESQUITE version 3.03 (Maddison and Maddison 2015) (Suppl. material 2). Inapplicable and unknown states were coded as ‘-’ and ‘?’ respectively. Cladistic parsimony analyses were conducted with TNT version 1.5 (Goloboff and Catalano 2016). The analyses were run under equal weights, selecting the ‘traditional search’ option with the following parameters: general RAM of 1000 Mbytes, memory set to hold 1,000,000 trees, setting 1000 replicates with tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Multistate characters were treated as unordered and zero-length branches were collapsed. Unambiguous character state changes were mapped on the most parsimonious trees using WINCLADA version 1.00.08 (Nixon 2002). Bremer support values were calculated in TNT from 10,000 trees up to 10 steps longer than the shortest trees obtained from a ‘traditional search’, using the ‘trees from RAM’ setting. Consistency and retention indices were calculated in MESQUITE version 3.03 (Maddison and Maddison 2015).

List of characters and character states used in the phylogenetic analysis

1. Labial palpus: (0) short and stout; (1) extremely long and thin. The labial palpus is extremely elongated, much longer than the head width in *Palpares Rambur*.
2. Labial palpus, sensory area (palpimacula): (0) rounded; (1) slit-like. The sensory area of the apical palpomere is slit-like in *Palpares libelluloides* (see also Stange 1994).
3. Pronotum: (0) wider than long; (1) as long as wide, (2) noticeably longer than wide. The proportions of pronotum widely vary across the family. In *Palpares* it is much wider than long, while in most antlions it is subquadrate and as long as wide. In

- Dendroleontini (*Dendroleon* Brauer, *Tricholeon* Esben-Petersen) and in *G. mirabilis* the pronotum is characteristically much longer than wide (see also Stange 1994) (Fig. 2E).
4. Thorax, outstanding setae: (0) absent; (1) present. In members of the genus *Gymnocnemia*, the thorax is covered with large and robust setae (Fig. 1B).
 5. Legs: (0) short and stout; (1) long and slender. Most myrmeleontids have relatively short and robust legs. Several species of Dendroleontini, such as *Dendroleon* and *Tricholeon*, and Nemoleontini, such as *Gymnocnemia*, *Megistopus* and *Nedroledon* Navás, have very long and slender legs, with the femur at least 7 times longer than wide (Fig. 1).
 6. Legs, colour pattern: (0) similar in all legs; (1) differing in each leg pair. In members of the genus *Gymnocnemia*, pro-, meso- and metathoracic legs have a strikingly different colour pattern.
 7. Tarsus, segments 1-4: (0) T1-T4 short, of the same size; (1) T1 much longer than the others, T2-T4 short; (2) T1-T3 elongated, of the same size. In *Palpares*, tarsomeres 1-4 are of similar length and equally short. In most genera of myrmeleontids, the basal tarsomere (T1) is much longer than tarsomeres 2-4, which are short; the basal tarsomere is usually as long as tarsomeres 2 and 3 together (T2+T3). In *Megistopus*, tarsomeres 1-3 are subequal in size, equally elongated while T4 is short (Fig. 1A).
 8. Tibial spurs: (0) absent; (1) present. Tibial spurs are absent in *G. variegata* and *G. editaerevayae*.
 9. Tibial spurs (if present), length: (0) long, at least 1/3 of tarsus length; (1) short, 1/4-1/5 of tarsus length; (2) minute, 1/6 of tarsus length. Tibial spurs are relatively long (at least one third of tarsus length) in most analysed taxa; however, they are relatively short, less than one fourth of tarsus length in *Cueta lineosa* (Rambur) and *Megistopus* (Fig. 1A). In *G. mirabilis*, tibial spurs are very small, much shorter than one sixth of tarsus length (Fig. 1C).
 10. Tarsal claws: (0) not opposable; (1) opposable. In some antlion genera, the tarsal claws can be folded against a brush of thickened setae on the distal tarsomere. Of the analysed species, this condition is found in members of the genera *Megistopus*, *Gymnocnemia* and *Nedroledon* (Fig. 1D).
 11. Prothoracic leg: (0) similar in length to meso- and metathoracic legs; (1) longer than meso- and metathoracic legs. In *Gymnocnemia* the prothoracic leg is much longer and thinner than the following pairs (Fig. 1B).
 12. Prothoracic leg femur, hair-like sensillum (femoral sense hair *sensu* Stange 1994): (0) absent; (1) present. The hair like sensillum is a synapomorphy of subfamily Myrmeleontinae (Stange 1994).
 13. Forewing, origin of Rs: (0) 1/4 of wing length or less; (1) 1/3 of wing length; (2) 1/2 of wing length. Rs arises near wing base (1/4 of wing length) in Dendroleontini (*Dendroleon* and *Tricholeon*), while it originates distally (around 1/3 of wing length) in all the other analysed taxa. In *G. mirabilis*, Rs arises at half wing length (Fig. 4A).
 14. Forewing, vein CuP: (0) long vein, running independently from 1A for its entire length; (1) short vein, parallel to 1A for a short distance and then merging with it, (2) crossvein-like. In *Palpares* and other Palparini, CuP is not fused with 1A, rather it is a distinct vein. In most other myrmeleontids, CuP is a very short vein fusing with 1A (Fig. 5A). In *Macronemurus* Costa, CuP is further reduced and is similar to a crossvein.
 15. Forewing, vein CuP+1A: (0) convergent with wing margin; (1) parallel to wing margin. The vein CuP+1A runs toward wing margin in almost all the analysed taxa, while it is parallel to wing margin in *Dendroleon*, *Tricholeon* and *Creoleon* Tillyard.
 16. Forewing, vein 2A: (0) gently curved; (1) close to 1A, then strongly bent toward to 3A. In *Palpares*, *Dendroleon*, *Tricholeon* and *Solter* Navás, vein 2A runs as a smooth curve. In *Cueta* Navás, *Myrmeleon* Linnaeus and in the members of Nemoleontini 2A is characteristically angled (Fig. 5A) (Stange 2004).
 17. Hind wing, presectoral area: (0) 1 crossvein; (1) more than 4 crossveins. The hind wing presectoral area is crossed by one crossvein in Dendroleontini (*Dendroleon*, *Tricholeon*) and Nemoleontini (*Nemoleon* Navás, *Distoleon* Banks, *Neuroleon*, *Macronemurus*, *Creoleon*) (Fig. 5B). In the other analysed taxa (*Palpares*, *Cueta*, *Solter*, *Myrmeleon*), the presectoral area is filled by numerous crossveins.
 18. *Pilula axillaris*: (0) absent; (1) present. Among the analysed taxa, the *pilula axillaris* is absent in *Cueta* and Nemoleontini (see Discussion).
 19. Male, abdomen length: (0) as long as the wings; (1) noticeably longer than the wings. The males of several antlion genera, such as *Cueta*, *Distoleon*, *Macronemurus*, *Creoleon* and *Nedroledon*, are characterized by elongated abdomens, much longer than wings.
 20. Male gonocoxites 9 and 11: (0) not fused; (1) fused into a tube-like structure. In *Palpares* and *Cueta* gonocoxites 9 and 11 are amalgamated into a tube-like structure.
 21. Male, gonocoxites 9, relative position to gonocoxites 11 (if not fused): (0) ventro-caudal to gonocoxites 11; (1) partly encircling gonocoxites 11. In *G. variegata* and *G. editaerevayae*, the proximal part of gonocoxites 9 characteristically curves upward, partly surrounding gonocoxites 11 in lateral view (Fig. 8B).
 22. Male, gonocoxites 9, shape: (0) plate-like; (1) fused in a Y-shaped structure; (2) fused in an upward hook-shaped structure. In ventro-caudal view, the apex of gonocoxites 9 appears as paired sclerotized plate-like structures in most myrmeleontid

- taxa. In several genera of Nemoleontini, including *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus*, *Creoleon*, gonocoxites 9 are fused into a structure resembling a “Y”, with a ventral projection and two processes curved upward (Fig. 8H). In *Cueta*, gonocoxites 9 are merged into a hook-like structure.
23. Male, gonocoxites 9 (if plate-like), relative position: (0) parallel; (1) oblique, converging apically. In ventro-caudal view, the plate-like apexes of gonocoxites 9 are parallel to each other in *Palpares*, *Solter* and *Gymnocnemia* (Fig. 8A). In contrast, in *Dendroleon*, *Tricholeon*, *Megistopus* and *Nedroledon* they converge apically (Fig. 8C, E, G). This character is not applicable to taxa with fused gonocoxites 9.
 24. Male, ectoproct, ventrocaudal projections: (0) absent; (1) present. In the males of several antlion genera, including *Palpares*, *Cueta*, *Macronemurus*, *Nedroledon*, and *Nemoleon*, the ectoproct is equipped with a posterior “clasper-like” processus (Fig. 8G, H).
 25. Male ectoproct, length of ventrocaudal projection (if present): (0) short, as long or slightly longer than ectoproct; (1) extremely long, much longer than ectoproct. The posterior projections of ectoproct are short in *Cueta*, while they are extremely long in *Palpares*, *Macronemurus* and *Nemoleon* (Fig. 8H). In *Nedroledon* both conditions are present: *N. anatolicus* Navás and *N. iranensis* Hölzel have short processes (Fig. 8G), while *N. striatus* Hölzel is characterized by a long and narrow processes.
 26. Female, process on segment 8: (0) absent; (1) present. In the female of several myrmeleontid genera, on the segment 8, proximal to gonocoxites 8 or at their base a pair of setiferous processes is present, usually termed “anterior gonapophyses” (e.g. Stange 1994). However, these processes are not homologous with the actual gonapophyses 8, and they are not as sclerotized as gonocoxites 8 (see also U. Aspöck and H. Aspöck 2008). Therefore, we presently term these structures as processes of segment 8 to distinguish them from the genital sclerites, gonocoxites or gonapophyses. Of the analysed taxa, they are present in *Dendroleon*, *Tricholeon* and *Myrmeleon*.
 27. Female, gonocoxite 7: (0) absent; (1) present. The gonocoxite 7 (praegenitale of authors, see Stange 1994) is absent in *Palpares libelluloides*, *Cueta lineosa* and the nemoleontine genera *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus* and *Creoleon*. This structure is present as a roughly triangular sclerite in *Myrmeleon*, *Dendroleon*, *Tricholeon*, *Gymnocnemia*, *Megistopus* and *Nedroledon* (Fig. 9).
 28. Female, gonocoxites 8: (0) not prominent; (1) short, 3-4 times longer than wide; (2) long, digitiform, over 5 times longer than wide. The gonocoxites 8 (posterior gonapophyses *sensu* Stange 1970a, 1994) are not prominent in *Palpares*, while they are longer than wide in all other analysed genera. Gonocoxites 8 are relatively short in *Cueta*, *Solter*, *Myrmeleon*, *Nemoleon*, *Distoleon*, *Neuroleon*, *Macronemurus* and *Creoleon*. In contrast, they are much longer than wide in *Dendroleon*, *Tricholeon*, *Gymnocnemia*, *Megistopus* and *Nedroledon* (Figs 7B, 9).
 29. Female, processes on segment 9: (0) absent; (1) present. Setiferous processes at base of gonocoxites 9 are present in the analysed species of *Cueta*, *Dendroleon* and *Tricholeon*.
 30. Female, gonocoxites 9, chaetotaxy: (0) only thin setae; (1) stout setae present. Gonocoxites 9 are only covered with thin setae in *Dendroleon* and *Tricholeon*, while the remaining analysed genera are characterised by the presence of stout digging setae. (Figs 7B, 9).
 31. Female, ectoproct, chaetotaxy: (0) only thin setae; (1) stout setae present. The female ectoprocts are only covered with thin setae in *Cueta*, *Solter*, *Dendroleon* and *Tricholeon*, while all other analysed genera are provided with stout digging setae.
 32. Larva, chaetotaxy of the dorsal side of the head capsule: (0) sensilla mainly bristle-like; (1) sensilla mainly dolichasters; (2) sensilla scale-like. See Badano et al. (2017).
 33. Larva, ocular tubercle, size: (0) large; (1) small. See Badano et al. (2017).
 34. Larva, upward bending of mandible: (0) not bent, i.e. straight; (1) bent upward. See Badano et al. (2017).
 35. Larva, fringe of extremely long setae on lateral side of the mandible: (0) absent; (1) present. See Badano et al. (2017).
 36. Larva, mesothoracic spiracle: (0) not raised; (1) raised. See Badano et al. (2017).
 37. Larva, metanotum tuft of setae: (0) absent; (1) present. See Badano et al. (2017).
 38. Larva, anterior mesothoracic setiferous process, type: (0) scolus-like; (1) small protuberance. See Badano et al. (2017).
 39. Larva, posterior mesothoracic setiferous process: (0) scolus-like; (1) tubercle-like. See Badano et al. (2017).
 40. Larva, anterior metathoracic setiferous process, type: (0) scolus-like; (1) tubercle-like; (2) small protuberance. See Badano et al. (2017).
 41. Larva, fringe of elongated setae on meso- and metathoracic legs: (0) absent; (1) present. See Badano et al. (2017).
 42. Larva, abdominal segment 9, shape: (0) longer than wide; (1) wider than long. See Badano et al. (2017).
 43. Larva, abdominal sternite 9, specialized digging setae on ventral surface: (0) absent; (1) present. See Badano et al. (2017).
 44. Larva, abdominal sternite 9, specialized digging setae (if present), number and pattern: (0) one line of 2-4 narrow digging setae at the base of rastra;

- (1) six stout digging setae arranged into a X-shaped pattern; (2) one or two transversal rows of stout digging setae. See Badano et al. (2017).
45. Larva, rastra: (0) absent; (1) present. See Badano et al. (2017).
46. Larva, rastra (if present), size: (0) very small, not prominent; (1) prominent and sclerotized.
47. Larva, rastra (if present), digging setae: (0) fused; (1) unfused. See Badano et al. (2017).
48. Larva, rastra (if present), relative dimensions of digging setae: (0) subequal in size; (1) medial pair distinctly smaller than lateral ones. See Badano et al. (2017).

Results

Phylogenetic analysis

The cladistic analysis yielded two most parsimonious trees with a tree length of 83 steps, a consistency index (CI) of 0.687 and a retention index (RI) of 0.752. One of the two most parsimonious trees was selected to map inferred character changes and is shown in Fig. 10. The two obtained trees uniquely differ in the reciprocal relationships among the species of *Gymnocnemia*. The strict consensus cladogram with Bremer support values is shown in Fig. 11. Two main clades, A and D, emerged from the analysis. Clade A was based on two nonhomoplasious apomorphies (31:0, chaetotaxy of female ectoproct as thin setae; 36:0, larva with mesothoracic spiracle not raised), obtaining a Bremer support value of 1. Within this clade, Dendroleontini (clade B), including *Dendroleon* and *Tricholeon*, were strongly supported as monophyletic based on six nonhomoplasious apomorphies (13:0, origin of forewing Rs at ¼ of wing length; 30:0, chaetotaxy of female ectoproct as thin setae; 37:1, larva with a tuft of setae on metanotum; 42:0, larva with abdominal segment 9 longer than wide; 43:0, larva with abdominal segment 9 devoid of specialized digging setae; 45:0, larva without rastra) and seven homoplasious apomorphies (3:2; 5:1; 15:1; 23:1; 26:1; 29:1; 34:1) and garnered a Bremer support value of 9. *Solter* (Myrmecaelurini *sensu* Stange 2004), *Cueta* (Nesoleontini) and *Myrmeleon* (Myrmeleontini) grouped in clade C, which relied on two nonhomoplasious apomorphies (33:1, larva with small ocular tubercles; 41:1, larva with a fringe of elongated setae on meso- and metathoracic legs) and received a Bremer support value of 1. Within the latter group, a sister relationship between *Cueta lineosa* and *Myrmeleon inconspicuus* Rambur was based on five nonhomoplasious apomorphies (32:0, larva with dorsal side of the head capsule covered with bristle-like sensilla; 35:1, larva with a fringe of very long setae on the lateral side of the mandible; 38:1, larva with the anterior mesothoracic setiferous process as a small protuberance; 40:2, larva with the anterior metathoracic setiferous process as a small protuberance; 48:0, larva with digging setae of ra-

stra subequal in size) and one homoplasious apomorphy (16:1) and obtained a Bremer support value of 1. Clade D, corresponding to the tribe Nemoleontini *sensu* Stange (2004) was reconstructed as monophyletic based on two homoplasious apomorphies (16:1; 18:0) and garnered a Bremer support value of 1. Nemoleontini were divided in two subclades E and G. Clade E was supported by one nonhomoplasious apomorphy (22:1, male gonocoxites 9 fused in a Y-shaped structure) and retrieved a Bremer support value of 1. The relationships within the latter group remained poorly resolved with a polytomy including *Distoleon tetragrammicus* (Fabricius), *Neuroleon arenarius* Navás and a group (clade F) formed by *Creoleon lugdunensis* (Villers) + (*Nemoleon notatus* (Rambur) + *Macronemurus appendiculatus* (Latreille)). The latter clade was corroborated by just one homoplasious apomorphy (19:1), and the sister relationship between *Nemoleon* and *Macronemurus* likewise relied on one homoplasious apomorphy (24:1).

Clade G was supported by one nonhomoplasious apomorphy (10:1, tarsal claws opposable) and one homoplasious apomorphy (5:1) with a Bremer support value of 1. Within the latter group, the genus *Megistopus* broke up as polyphyletic with “*Megistopus*” *mirabilis* forming a clade (clade H) with the members of the genus *Gymnocnemia*. The monophyly of this genus (“*M.*” *mirabilis* + (*G. variegata* + *G. editaerevayae*)), relied on three nonhomoplasious apomorphies (4:1, thorax with outstanding setae; 6:1, leg colour pattern differing in each leg pair; 11:1, prothoracic leg longer than meso- and metathoracic legs) and obtained a Bremer support value of 3. A sister relationship between *G. variegata* and *G. editaerevayae* was retrieved based on one nonhomoplasious apomorphy (8:0, tibial spurs absent). Clade I, composed by the species of *Megistopus* (exclusive of “*M.*” *mirabilis*) and *Nedroledon* was supported by just one homoplasious apomorphy (23:1) with a Bremer support value of 1. A clade composed by *M. flavicornis* and *M. lucasi* (clade J) was reconstructed as monophyletic based on one nonhomoplasious apomorphy (7:2, tarsomeres T1–T4 elongated, of the same size) and one homoplasious apomorphy (9:1) and garnered a Bremer support value of 2. The genus *Nedroledon* (clade K), whose monophyly was supported by one homoplasious apomorphy (24:1), received a Bremer support value of 1. *N. anatolicus* and *N. iranensis* were recovered as sister taxa based on one homoplasious apomorphy (25:0).

Systematics

The genus *Gymnocnemia* was recently revised by Michel (2013) on the occasion of the description of *G. editaerevayae*, while Badano and Pantaleoni (2014) detailed the larval morphology of *Gymnocnemia*, as well as *Megistopus* highlighting the importance of larval characters in systematics. Therefore, we focused on the species that are least known and on how they influence the delimitation of genera and recognition of species.

***Gymnocnemia* Schneider, 1845**

Gymnocnemia Schneider, 1845: 343.

Type species *Megistopus variegatus* Schneider, 1845.

Aplectrocnemus Costa, 1855: 18.

Type species *Aplectrocnemus multipunctatus* Costa, 1855 (Syn).

Comprised species. *G. variegata*, *G. editaerevayae*, and *G. mirabilis*.

Recognition. Thorax covered with robust, outstanding setae. Legs extremely long and thin. Prothoracic leg much longer and slender than meso- and metathoracic legs. Femora differing in pattern: prothoracic femur with small dark dots, mesothoracic femur with two parallel dark stripes, metathoracic femur with an apical dark marking. Tibial spurs absent (*G. variegata*, *G. editaerevayae*) or present (*G. mirabilis*). Tarsomeres 1-4 of prothoracic leg differentiated in size, with the first (basal) tarsomere at least as long as one and a half times the second tarsomere. Tarsal claws opposable, closing against a brush of thickened setae on the fifth tarsomere. Male (based on *G. variegata* and *G. editaerevayae*): ectoproct rounded, gonocoxites 11 arch-like, gonocoxites 9 partly encircling gonocoxites, 11 plate-like in shape. Female: gonocoxite 7 tooth-like, gonocoxites 8 digitiform, gonocoxites 9 covered with digging setae, ectoproct provided with digging setae.

Larval morphology (based on *G. variegata*). Mandible long and slender, provided with 3 teeth of which the apical and median are subequal in size. Ocular tubercle prominent. Mesothoracic spiracle raised on tubercle. Meso- and metathoracic setiferous processes scolus-like. Odontoid processes atrophied. Rastra with the internal pair of digging setae smaller than the others (Cesaroni et al. 2010, Badano and Pantaleoni 2014).

***Gymnocnemia variegata* (Schneider, 1845)**

Figs 1B, 2A–C, 3A, 4B, 8A–B, 9A–B

Diagnosis. Medium-sized antlion with a variegated habitus, with an alternating ochre and dark brown pattern. Forewing Rs at half the wing length with at least 8 crossveins. Thorax covered with outstanding black and white setae. Tibia without spurs. Tarsus shorter than tibia.

Variability. (Based on examination of 7 males and 8 females, see Suppl. material 1)

G. variegata is a widely distributed but exceedingly localized species ranging from the Mediterranean to Central Asia (H. Aspöck and Hölzel 1996, H. Aspöck et al. 2001, Stange, 2004, Krivokhatsky 2011, Michel, 2013, Monserrat and Acevedo, 2013, Badano and Pantaleoni 2014, U. Aspöck et al. 2015, Kral and Devetak 2016). Despite a recent and exhaustive re-description (Michel 2013), the variability of this myrmeleontid remains unstudied, potentially confusing its identification. Indeed, *G. variegata* is a highly variable species with distinct pale and dark morphs, differing in the dimension and

shape of body markings. The pale morph is characterized by a sand-like body colour with relatively small brown markings. In this form, the vertex has small paired dots, while the pronotum is characterized by two pale spots per side and brown lateral margin (Fig. 2A). On the contrary, the dark morph has a darker tinge and the markings are much more contrasted and developed, resulting in an overall dark habitus. In particular, the pronotal markings blend with each other forming one dark brown stripe per side, while the brown marking on the lateral margin is larger and more evident (Fig. 2B). In exceptionally dark specimens, the dark markings on the vertex are fused in a transversal band, while the pronotum appears mostly dark with a very large stripe per side (Fig. 2C). The body pattern of the closely related *G. editaerevayae* falls in the variability range of *G. variegata*, thus the two species are best set apart on wing and genital characters (Fig. 2D) (Michel 2013).

***Gymnocnemia mirabilis* (Hölzel, 1980) comb. n.**

Figs 1C–D, 2E, 3B, 4A, 6A, 7C–D

Megistopus mirabilis Hölzel, 1980 (ODescr): H. Aspöck and Hölzel 1996 (List), H. Aspöck et al. 2001 (Cat), Stange 2004 (Cat).

Diagnosis. Small-sized antlion with a variegated habitus, with an alternating ochre and dark brown pattern. Wing venation sparse. Forewing Rs at half the wing length, with few crossveins. Thorax and prothoracic leg covered with prominent white setae. Tarsus exceptionally elongated, longer than tibia.

Examined specimens. Oman 18.VIII.1988 / Wadi Bani Kharus / Al Misra / M.J. Ebejer, 1 ♀ (NHMW). Oman: JABAL SHAMS / 23°14'N, 57°14'E 1900M / 3Jul95 BSKule, 4 ♀, 1 ex. (NHMW); OMAN: Jabal Shams / Wadi Dar Sawda, 1865 m / 23°14'N, 57°12'E, 20.X.95 / to light, MD Gallagher, 1 ♀ (NHMW).

Redescription. Colouration. Vertex ochre dorsally and darker anteriorly. Frons dark brown. Clypeus dark brown with the ventral margin ochre. Labrum brown. Genae light brown. Maxillary and labial palpi ochre (Fig. 3B). Antennae light brown with dark brown scape and pedicel, basal antennomeres darker. Pronotum ochre, dorsal side with two dark brown stripes connected with the dark lateral margins (Fig. 2E). Mesonotum ochre medially, dark brown laterally; mesoscutellum with paired dark markings. Metanotum dark brown with a median, light brown stripe (Fig. 6A). Prothoracic leg ochre, femur and tibia dotted, tarsus ochre (Fig. 1C). Mesothoracic leg ochre, femur with parallel dark stripes, tibia dotted with the internal side dark brown. Metathoracic leg ochre, femur with a distal dark marking, tibia dotted. Wings hyaline, venation brown with alternating pale dashes. Pterostigma whitish, proximally with a faint brown marking. Forewing gradates with a faint dark marking. Cubital mark very faint (Fig. 4A). Abdomen with a variegated dark brown and

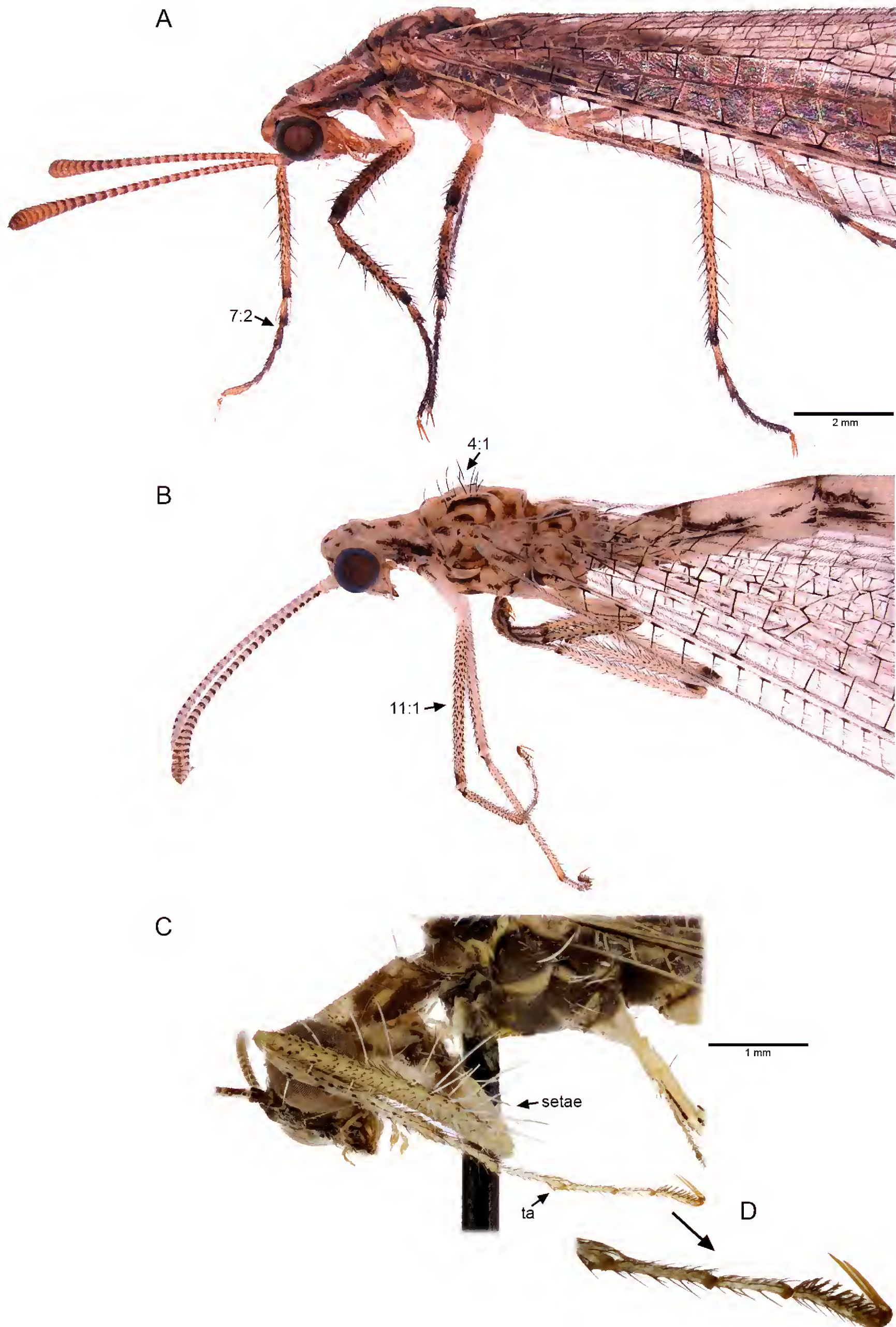


Figure 1. *Gymnocnemia* and *Megistopus*, habitus and details of thorax, lateral view. **A** *Megistopus lucasi* [Italy, Sardinia]; **B** *Gymnocnemia variegata* [Greece, Corfu]; **C–D** *Gymnocnemia mirabilis* [Oman, Jabal Shams], **C** thorax and prothoracic leg, **D** tarsus. Numbers indicate morphological characters of the data matrix and their state. Abbreviation: **ta** – tarsus.



Figure 2. Head and pronotum of *Gymnocnemia* and *Megistopus*, dorsal view. A–C *Gymnocnemia variegata*, variability, A Italy, Lazio, Rome [type locality], B Slovenia, C Italy, Sardinia; D *Gymnocnemia editaerevayae*, holotype [Morocco, High Atlas] (Photo: B. Michel, CBGP); E *Gymnocnemia mirabilis* [Oman, Jabal Shams]; F *Megistopus flavicornis* [France, Gard]; G *Megistopus lucasi* [Italy, Sardinia].

ochre pattern, tergites dark brown with a dorsal ochre marking, sternites brown.

Dimensions (based on 5 specimens). Average body length 14.62 mm (min-max 14.02-15.23); forewing length 18.06 mm (16.66-18.25), ratio width/length 0.23; hind wing length 17.05 mm (15.39-19.04), ratio width/length 0.21.

Head. Vertex with a slightly raised transversal ridge (Fig. 2E). Labial palpi with distal palpomere fusiform,

palpimacula elliptical. Antenna clavate. Antennal chaetotaxy constituted by short black setae.

Thorax. Pronotum slightly longer than wide. Pronotum and mesonotum covered with white outstanding setae (Fig. 2E). Legs very long and slender. Tarsus of pro-, meso- and metathoracic legs much longer than tibia (Fig. 1C). Tibial spur present, minute, less than half the length of first tarsomere. Femur and tibia of prothoracic

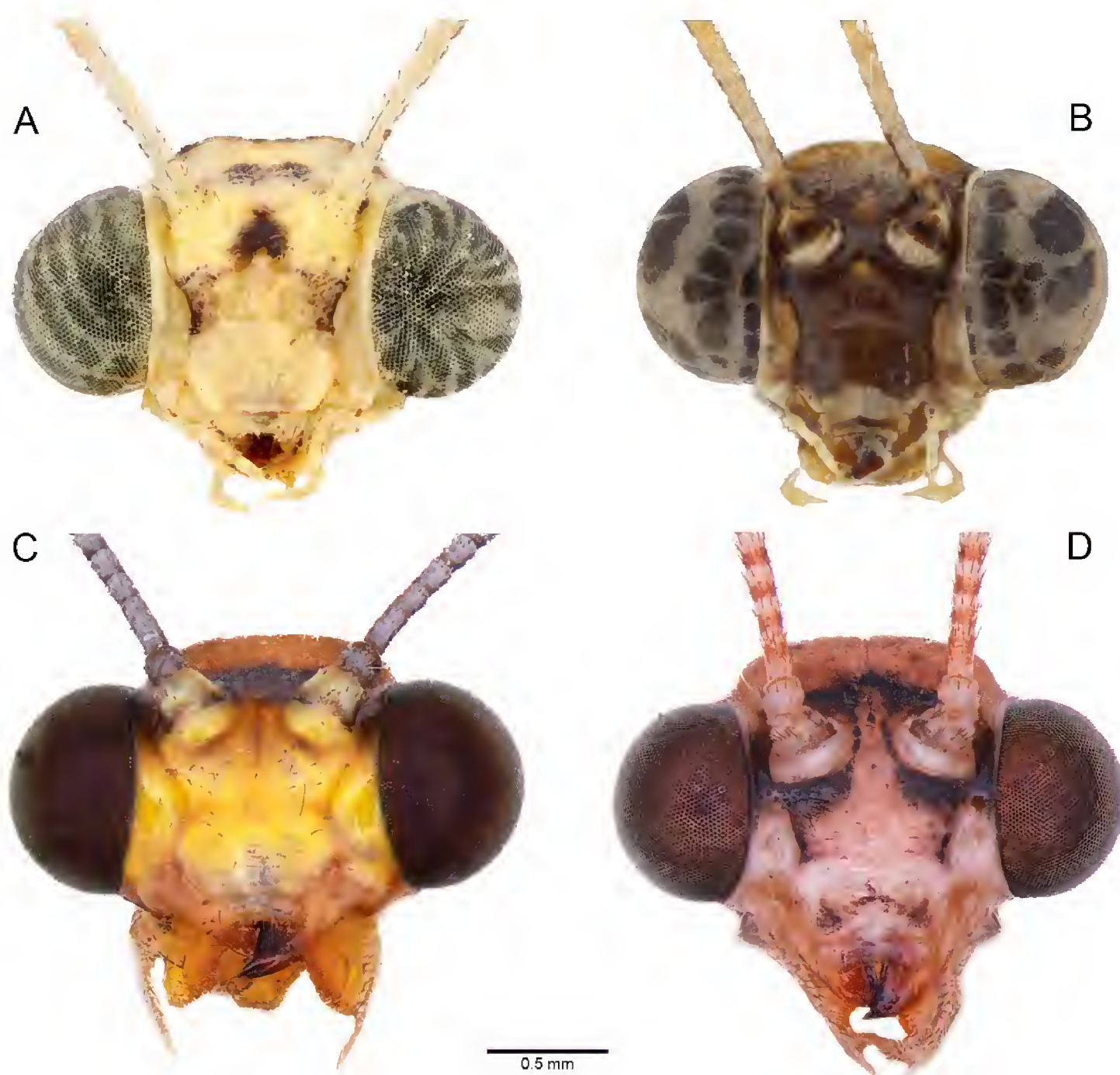


Figure 3. Head of *Gymnocrnemia* and *Megistopus*, frontal view. **A** *Gymnocrnemia variegata* [Italy, Sardinia]; **B** *Gymnocrnemia mirabilis* [Oman, Jabal Shams]; **C** *Megistopus flavicornis* [France, Gard]; **D** *Megistopus lucasi* [Italy, Sardinia].

leg covered with white outstanding setae, similar to those on thorax, arranged in a comb-like row (Fig. 1C). Tarsus of prothoracic leg, one and a half time as long as tibia.

Wings. Relatively narrow with an acute apex (Figs 4A, 6A). Venation relatively sparse. Forewing with 7–8 presectoral crossveins. Radius sector arising at half of forewing length, distinctly distal to Cubital fork. Rs with few, well-spaced crossveins (4–6). Branches of the Cubital fork divergent. CuP + 1A gently converging with wing margin but not abruptly. Hind wing with 1 presectoral crossvein (Figs 4A, 6A).

Female genitalia. As for genus. Gonocoxite 7 relatively large and sclerotized, tooth-like in shape. Gonocoxites 8 covered with thin black setae. Gonapophyses 8 narrow, ribbon-like. Ectoproct with a short ventrocaudal projection, ventral side covered with stout setae.

Male. Unknown.

Distribution. The species was originally described from a single specimen found in the Sinai Peninsula (Egypt). The examined specimens are the first records of this species from Oman and the Arabian Peninsula, which significantly expands the known area of distribution (Fig. 12).

Megistopus Rambur, 1842

Megistopus Rambur, 1842: 343. Type species *Megistopus bisignatus* Rambur, 1842, by monotypy.

Recognition. Legs long and slender, not abruptly differentiated in size. Tibial spurs as long as the first tarsomere. Tarsomeres 1–3 of prothoracic leg of similar size, tarsomere 4 shorter than the others. Tarsal claws opposable. Male: ectoproct rounded, gonocoxites 11 arch-like, gonocoxites 9 plate-like, converging apically. Female: gonocoxite 7 tooth-like, gonocoxites 8 digitiform, gonocoxites 9 provided with digging setae, ectoproct equipped with digging setae.

Larval diagnosis. Mandible relatively long, armed with 3 teeth. Ocular tubercle prominent. Mesothoracic spiracle raised on tubercle. Mesothoracic setiferous processes scolus-like, metathoracic processes tubercle-like. Odontoid processes atrophied or absent. Rastra with the internal pair of digging setae less than 1/4 the length of the others (Steffan 1965, Cesaroni et al. 2010, Badano and Pantaleoni 2014). The larva of *M. flavicornis* is characterized by prominent abdominal spiracles, while *M. lucasi* has sessile spiracles (Badano and Pantaleoni 2014).

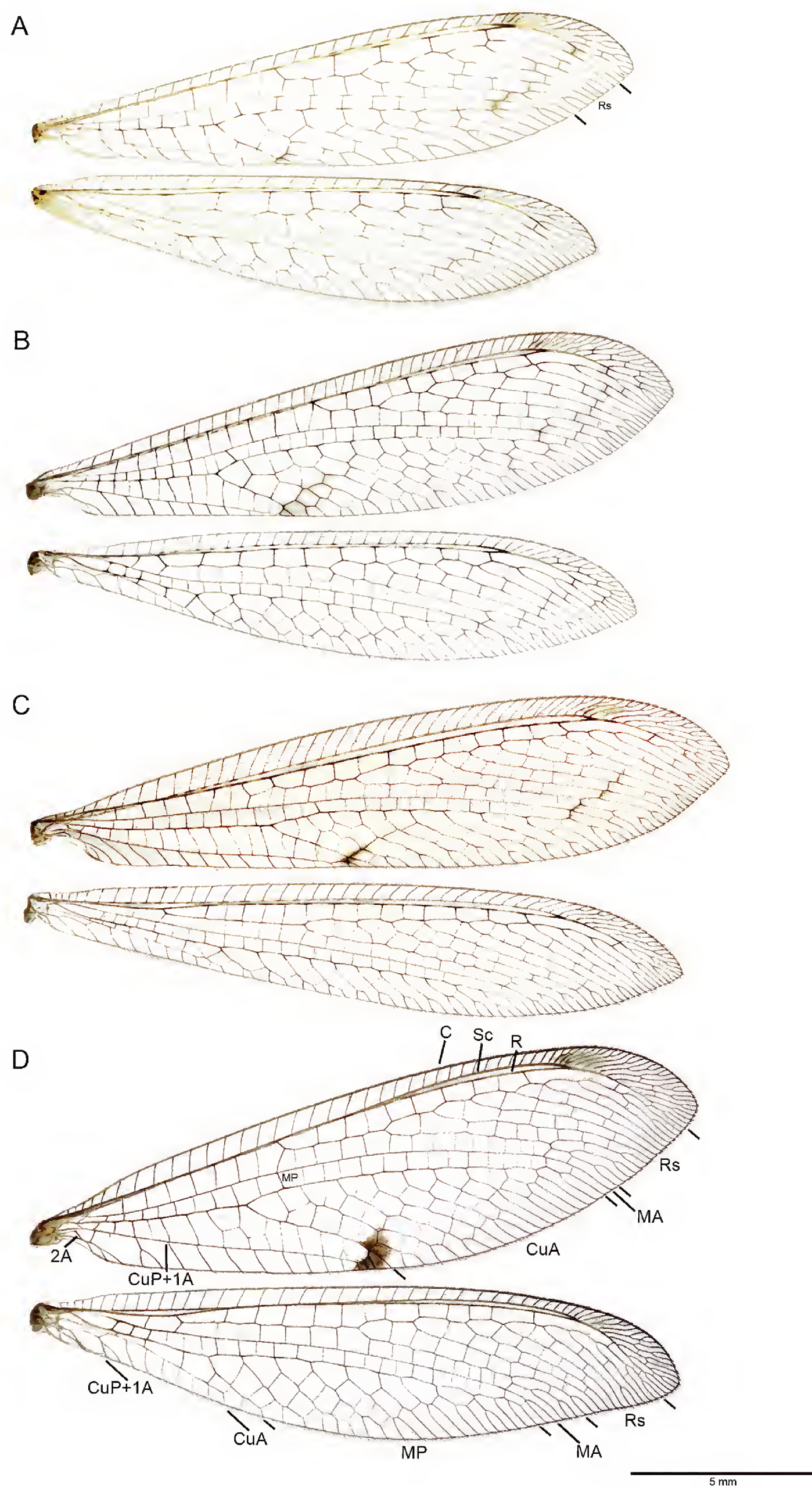


Figure 4. Wings of *Gymnocnemia* and *Megistopus*. **A** *Gymnocnemia mirabilis* [Oman, Jabal Shams]; **B** *Gymnocnemia variegata* [Italy, Lazio, Rome, type locality]; **C** *Megistopus lucasi* [Italy, Sardinia]; **D** *Megistopus flavicornis* [France, Gard]. Abbreviations: **C** – Costa, **Sc** – Subcosta, **R** – Radius, **Rs** – Radius sector, **MA** – Media anterior, **MP** – Media posterior, **CuA** – Cubitus anterior, **CuP** – Cubitus posterior, **A** – Anal vein.

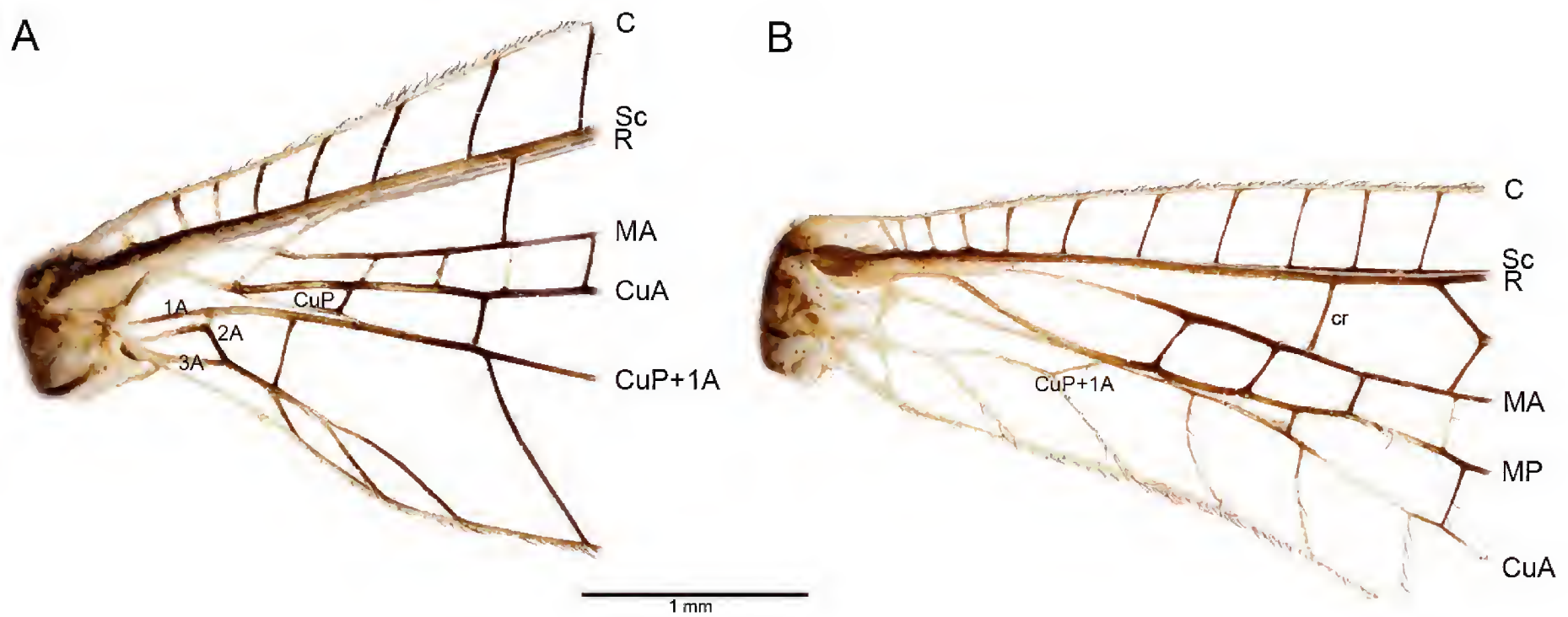


Figure 5. Base of fore- and hindwing of *Megistopus*, showing diagnostic wing characters of Nemoleontini. **A** forewing of *Megistopus flavicornis* [Italy, Liguria]; **B** hindwing of same specimen. Abbreviations: **C** – Costa, **Sc** – Subcosta, **R** – Radius, **Rs** – Radius sector, **MA** – Media anterior, **MP** – Media posterior, **CuA** – Cubitus anterior, **CuP** – Cubitus posterior, **A** – Anal vein, **cr** – presectoral crossvein.



Figure 6. *Gymnocnemia* spp., holotypes, dorsal view. **A** *Gymnocnemia mirabilis* [Sinai, Shreg]; **B** *Gymnocnemia editaerevayae* [Morocco, High Atlas, Oukaimeden] (Photo: B. Michel, CBGP).

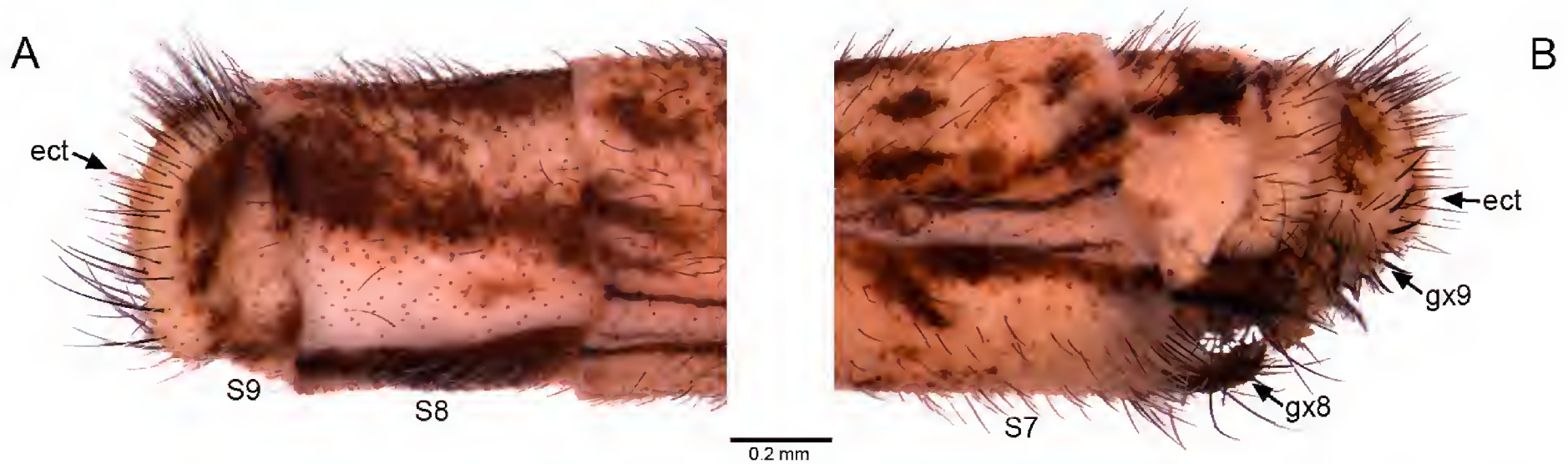


Figure 7. *Megistopus lucasi*: male and female terminalia, lateral view. **A** male [Italy, Sardinia]; **B** female [Italy, Sardinia]. Abbreviations: **ect** – ectoproct, **S9** – sternite 9, **gx9** – gonocoxite 9, **S8** – sternite 8, **gx8** – gonocoxite 8, **S7** – sternite 7.

Megistopus lucasi (Navás, 1912)

Figs 1A, 2G, 3D, 4C, 7, 8C–D

Nelees lucasi Navás, 1912 (ODescr): Banks 1913 (Com).

Neuroleon lucasi (Navás, 1912): H. Aspöck and Hölzel 1996 (Distr), H. Aspöck et al. 2001 (Cat), Stange 2004 (Cat).

Megistopus mirabilis Hölzel, 1980 (misidentification): [Bernardi] Iori et al. 1995 (List), Letardi and Pantaleoni 1996 (Distr), Letardi 1998 (Distr), Letardi 2006 (Distr), Popov and Letardi 2010 (Biogeogr), U. Aspöck et al. 2015 (List).

Megistopus lucasi (Navás, 1912): Güsten 2003 (Distr, Com), Badano and Pantaleoni 2014 (Biol), Letardi 2016 (Key), Badano et al. 2017 (photo).

Diagnosis. Medium-sized antlion with a mottled light and dark brown body pattern. Wings relatively narrow. Forewing Rs arising at the height of Cubital fork. Forewing gradates shaded with brown, cubital mark brown.

Examined specimens. Italy: Sardinia, Torre dei Corsari, 39°41,017'N 8°27,044'E, 28.V.2003, 50 m, H. and U. Aspöck and R.A. Pantaleoni leg, 3 ♀ (HUAC); Italy: Sardinia, Arbus (Oristano) / Torre dei Corsari, 39°41'23.09"N 8°27'14.50"E, coastal sand dunes /V.2010 D. Badano leg, 1 ♀ ex larva (DB); Italy: Sardinia, Arbus (Oristano)/ Torre dei Corsari, 39°41'23.09"N 8°27'14.50"E, coastal sand dunes /V.2011 D. Badano leg, 1 ♂ ex larva; Italy: Sardinia/ Chia (Cagliari), beach, XI.2011 (D. Badano), 1 ♂ ex larva (DB).

Redescription. Colouration. Vertex ochre with paired dark markings. Paired blackish markings extend from the anterior margin of the vertex to the lateral margins of the frons, surrounding the base of the antenna. Frons light brown, except the lateral margins. Clypeus light brown with suffused dark markings. Labrum brown. Genae, maxillary and labial palpi testaceous. Antennae light brown, scape with dark brown suffusions, antennomeres darker basally (Fig. 3D). Pronotum ochre, dorsal side with paired dark brown, variegated stripes connecting the dark brown anterior and posterior margins; lateral margins mottled (Fig. 2G). Mesothoracic proscutum light brown anteriorly, pos-

terior margins dark brown. Mesoscutum and mesoscutellum light brown with dark brown margins. Metathoracic proscutum brown with lighter margins. Metascutum and metascutellum with dark brown margins. Leg ochre, femur and tibia dotted (more thickly on the dorsal side) and with a dark marking near the articulation, tarsus ochre, darker near the articulation (Fig. 1A). Wings hyaline, venation brown with alternating pale dashes. Pterostigma whitish, with a faint brown proximal marking. Forewing gradates with a dark shade. Cubital mark elongated and clearly distinct (Fig. 4C). Abdomen mainly ochre, tergites with a darker median stripe on the anterior half and small darker spots on the margins. Abdomen covered with white and dark setae.

Dimensions (based on 2 specimens). Body length 20.31, 26.66 mm; forewing length 21.43, 26.61 mm, ratio width/length 0.24; hind wing length 20.8, 25.87 mm, ratio width/length 0.20.

Head. Vertex slightly inflated. Distal palpomere of labial palpi fusiform, relatively thin, palpimacula elliptical. Antennae clavate.

Thorax. Pronotum longer than wide (Fig. 2G). Thorax covered with short black setae. Legs extremely long and slender. Tibial spurs as long as the first tarsomere. Wings: relatively narrow with a rounded apex. Forewing costal area slightly wider at middle length. Forewing with ca. 6 presectoral crossveins. Origin of Radius sector at the same height of Cubital fork. Rs with more than ten crossveins. Branches of the Cubital fork divergent. CuP + 1A gently running toward the posterior wing margin but not abruptly. 2A gently curved before merging with 3A. Hind wing with 1 presectoral crossvein (Fig. 4C).

Male genitalia. As for genus. Gonocoxites 9 plate-like, converging apically (Fig. 8C). Ectoproct shell-like, ochre with a dark marking, covered with thin black setae (Fig. 7A).

Female genitalia. As for genus. Gonocoxites 8 dark brown, covered with thin black setae. Gonocoxites 9 and ectoproct covered with sparse stout setae (Fig. 7B).

Distribution. The species is only known from few coastal localities of Algeria, Tunisia and Italy (Lazio and Sardinia) (Letardi and Pantaleoni 1996 [*sub M. mirabilis*], Güsten 2003, Badano and Pantaleoni 2014) (Fig. 12).

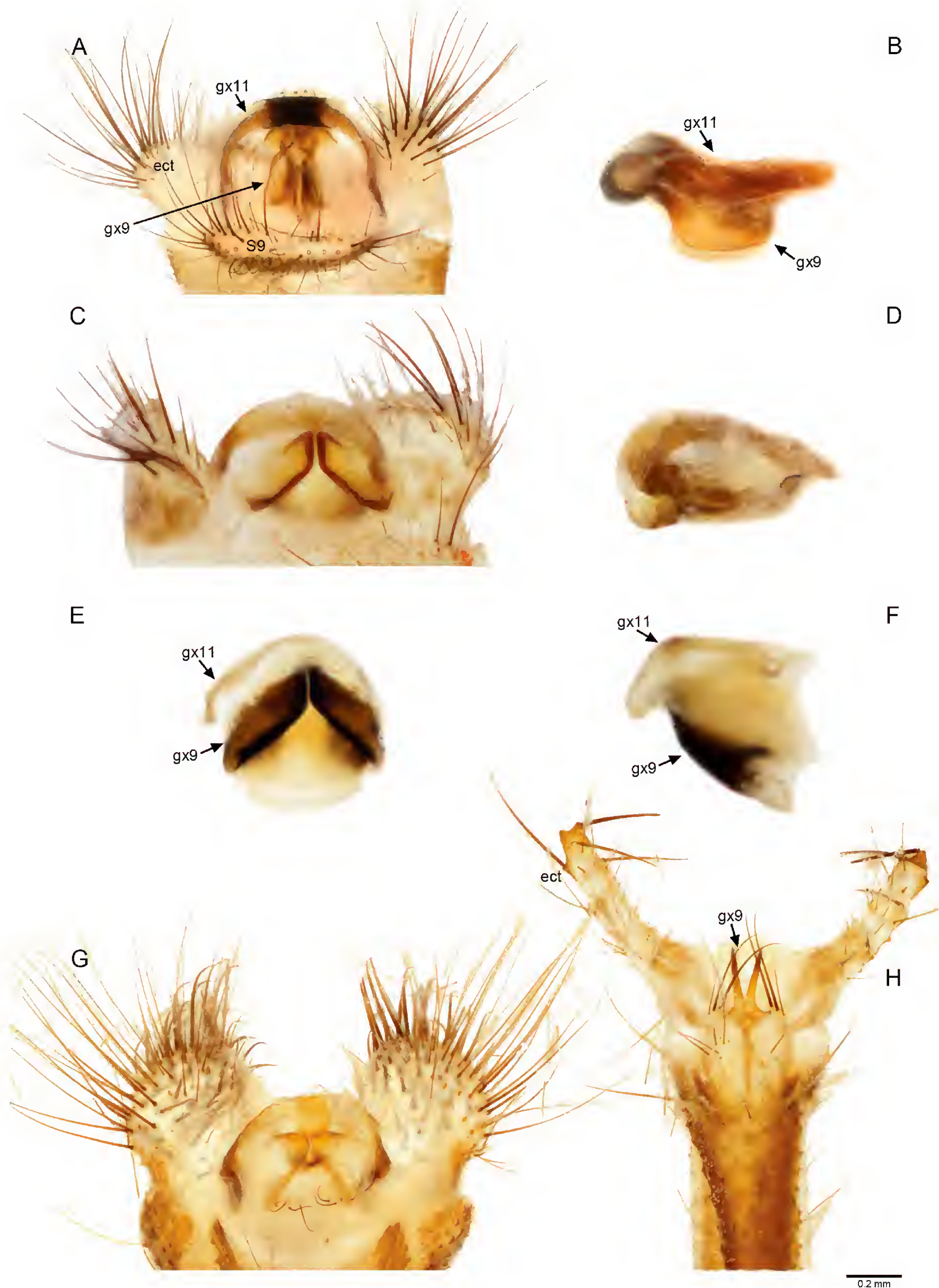


Figure 8. Male genitalia of Nemoleontini, complex of gonocoxites 9 + gonocoxites 11 *sensu* U. Aspöck and H. Aspöck (2008) (=gonarcus-parameres complex *sensu* H. Aspöck et al. 1980). **A–B** *Gymnocnemia variegata* [Greece, Corfu], **A** apex of abdomen, ventral view, **B** gx 9 + gx 11, lateral view; **C–D** *Megistopus lucasi* [Italy, Sardinia], **C** apex of abdomen, ventral view, **D** gx 9 + gx 11, lateral view; **E–F** *Megistopus flavicornis* [France, Gard], gx 9 + gx 11, **E** ventral view, **F** lateral view; **G** *Nedroledon iranensis* (Hölzel, 1972) [Iran], apex of abdomen, ventral view; **H** *Nemoleon notatus* [Italy, Sardinia], apex of abdomen, ventral view. Abbreviations: **ect** – ectoproct, **gx9** – gonocoxite 9, **gx11** – gonocoxite 11, **S9** – sternite 9.

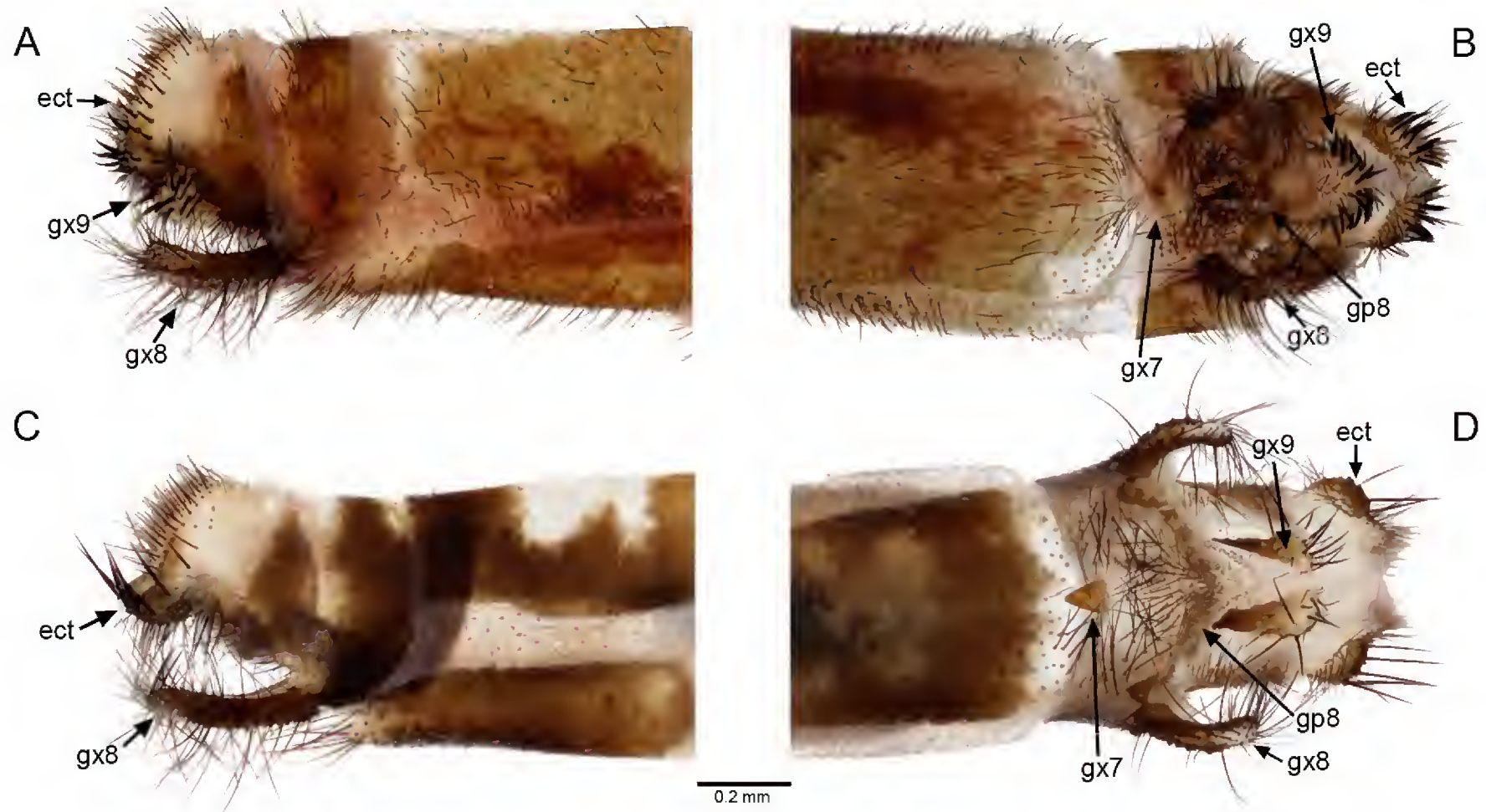


Figure 9. Female genitalia of *Gymnocnemia*. **A–B** *Gymnocnemia variegata* [Greece, Corfu], **A** lateral view, **B** ventral view; **C–D** *Gymnocnemia mirabilis* [Oman, Jabal Shams], **C** lateral view, **D** ventral view. Abbreviations: **ect** – ectoproct, **gp8** – gonapophysis 8, **gx7** – gonocoxites 7, **gx8** – gonocoxite 8, **gx9** – gonocoxite 9.

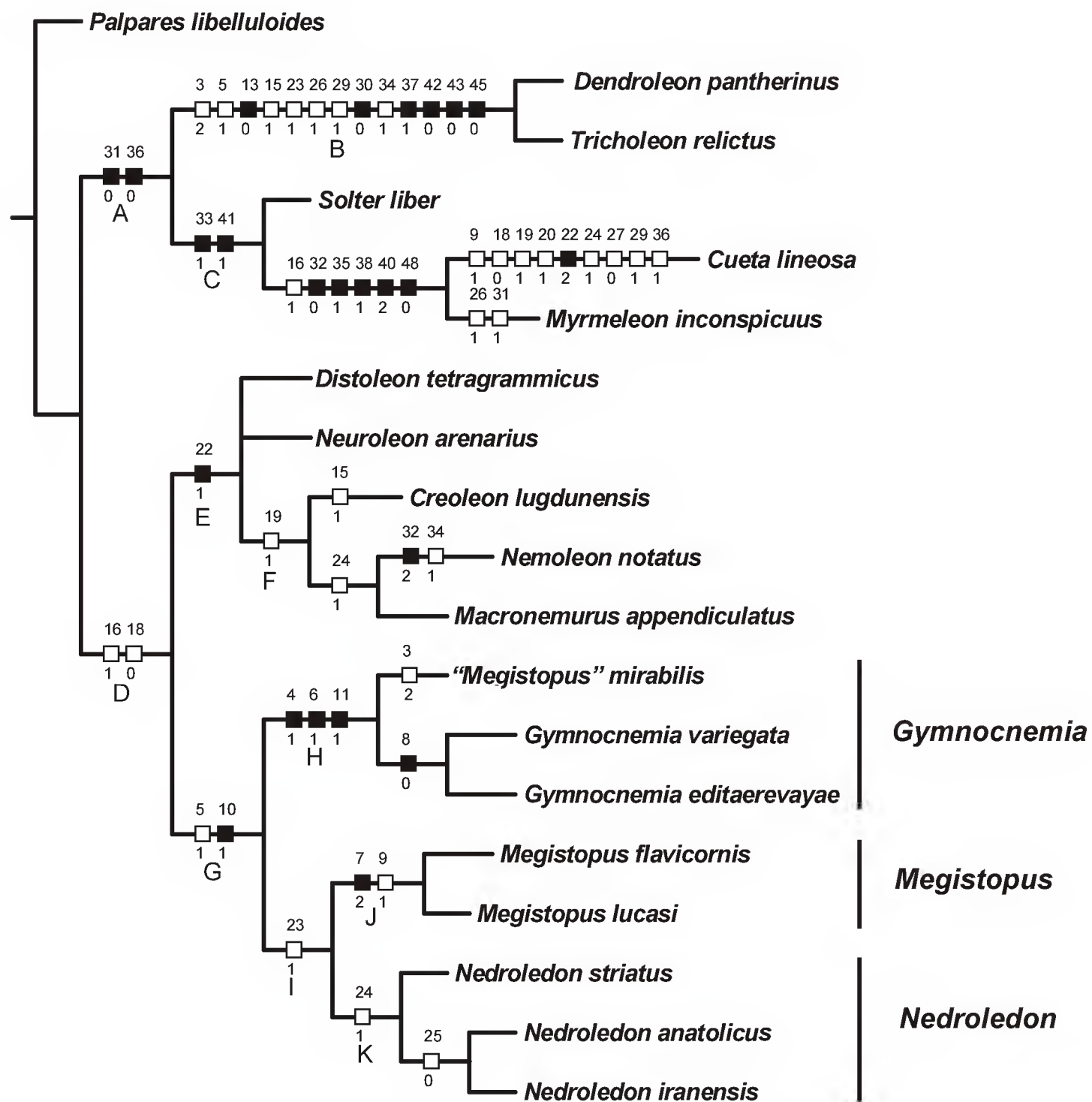


Figure 10. Preferred tree of the two most parsimonious trees (83 steps, C.I. 0.687) obtained in the analysis. Black squares indicate nonhomoplasious apomorphies, white squares homoplasious ones. Letters indicate clades discussed in the text.

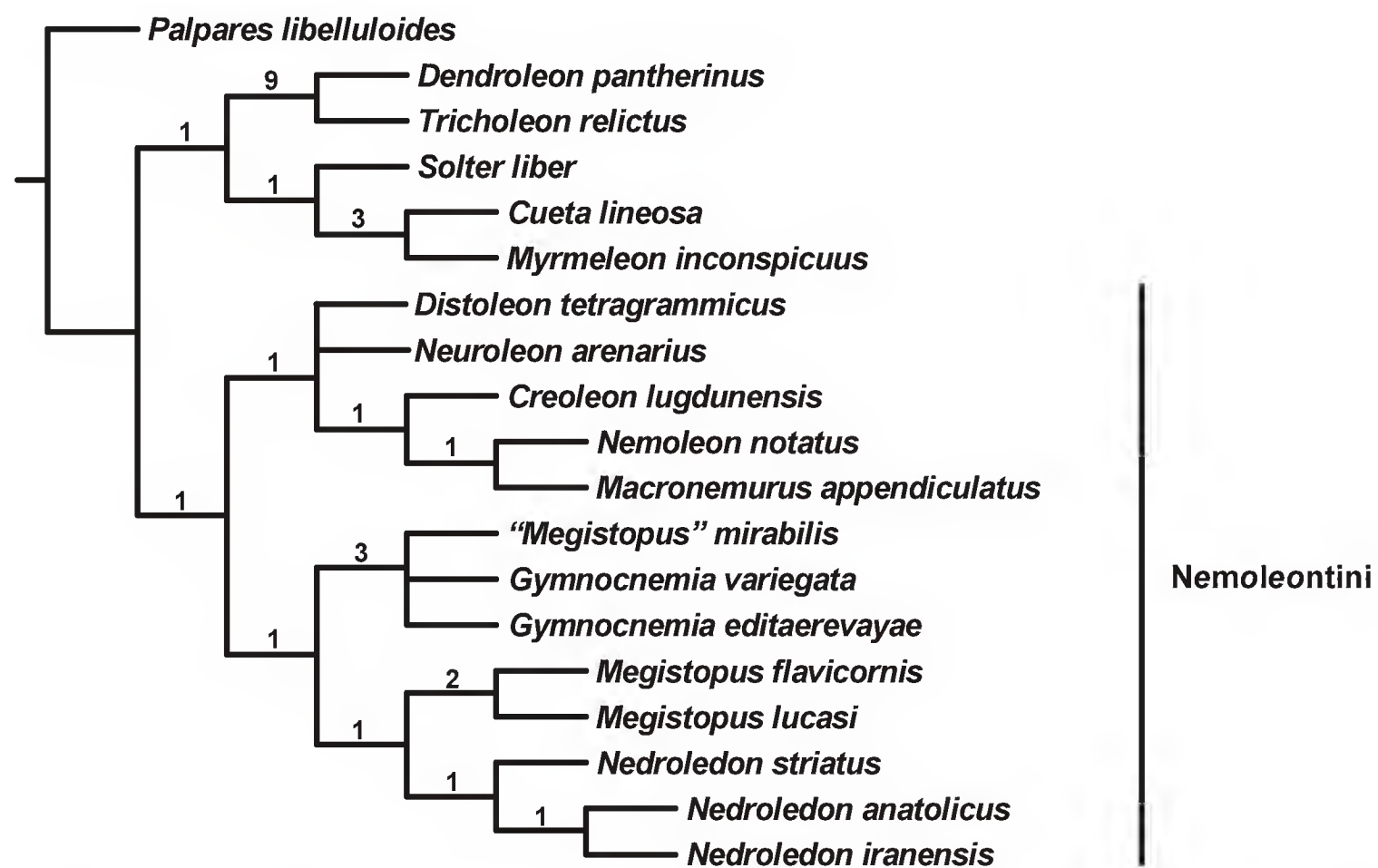


Figure 11. Strict consensus tree obtained from the two most-parsimonious trees with Bremer support values indicated above branches.

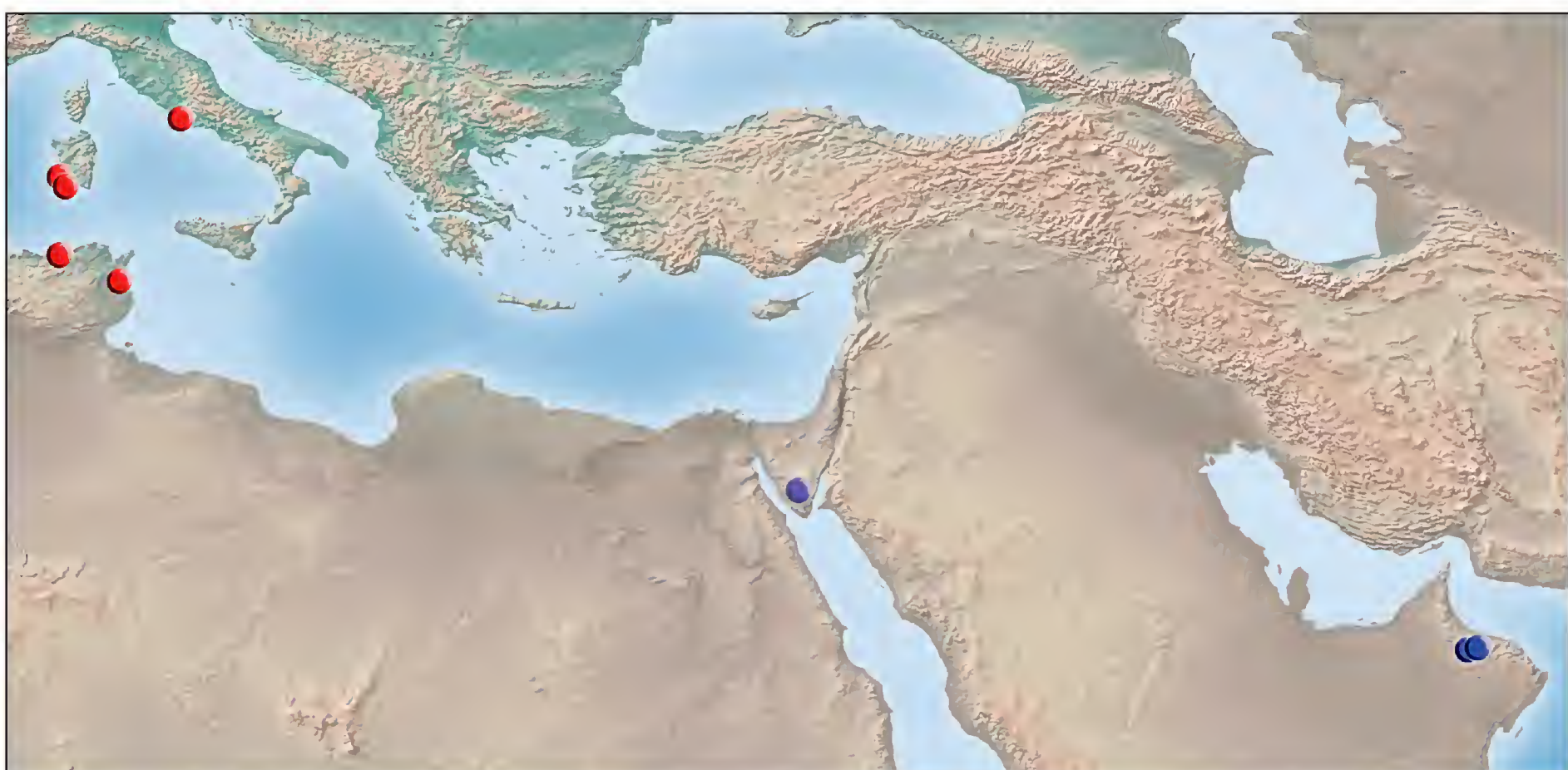


Figure 12. Distribution of *Gymnocnemia mirabilis* and *Megistopus lucasi*. Blue dots = *Gymnocnemia mirabilis*, red dots = *Megistopus lucasi*.

Ecology. *M. lucasi* is an extremely rare species and is exclusively known from well preserved coastal sand dunes and beaches with junipers. The unmistakable larva of this species (see Badano and Pantaleoni 2014) is an ambush hunter, dwelling at the base of junipers and amidst their

roots. The larva is parasitized by the generalist antlion parasitoid *Micomitra stupida* (Rossi) (Diptera, Bombyliidae) (Badano pers. obs.). This species of antlion is potentially endangered by human activities and exploitation of coastal sandy environments.

Identification key to the species of *Gymnocnemia* and *Megistopus* and the genus *Nedroledon*

- 1 Forewing vein Rs originating at or distal to cubital fork; forewing vein 2A strongly bent before merging with 3A (Fig. 5A); legs long and slender; tarsal claws folding against a brush of robust setae on fifth tarsomere (Fig. 1D) (Western Palaearctic)..... 2
- Other combination of characters other Myrmeleontidae

- 2 Thorax covered with outstanding, robust setae (Fig. 1B, 4:1); prothoracic leg much longer than the other legs (Fig. 1B, 11:1) 3...*Gymnocnemia*
- Thorax without outstanding setae; prothoracic leg as long as the other legs 5
- 3 Frons dark brown (Fig. 3B); wing venation sparse, forewing Rs with less than 8 crossveins (Fig. 4A); prothoracic femur with a fringe of long white setae (Fig. 1C); tibial spurs present, minute; tarsus much longer than tibia in all legs (Fig. 1C); pronotum Fig. 2E. *G. mirabilis*
- Frons light brown (Fig. 3A); wing venation dense; forewing Rs with 10 or more crossveins (Fig. 4B); prothoracic femur without a fringe of long white setae; tibial spurs absent; tarsus shorter than tibia 4
- 4 Wings relatively broad; forewing with cubital and gradate markings faint (Fig. 4B); pronotum Fig. 2A, B, C, head Fig. 3A..... *G. variegata*
- Wings relatively narrow; forewing with cubital and gradate markings dark, well evident (Fig. 6B); pronotum Fig. 2D
..... *G. editaerevayae*
- 5 Tarsomere 1 as long as T2 or slightly shorter (Fig. 1A); male: abdomen shorter than wings, ectoproct without ventrocaudal projections (Fig. 8C) 6...*Megistopus*
- Tarsomere 1 as long as T2+T3; male: abdomen longer than wings, ectoproct with ventrocaudal projections (Fig. 8G) ...
..... *Nedroledon*
- 6 Body pattern: blackish with pale areas in the abdomen; frons yellow (Fig. 3C); pronotum reddish with a pale median stripe (Fig. 2F); forewing with only a black cubital marking, forewing vein Rs originating distal to cubital fork (Fig. 4D); male genitalia (Fig. 8E, F) *M. flavicornis*
- Body pattern: ochre with dark brown markings; frons ochre with brown markings below the base of the antennae (Fig. 3D); pronotum ochre with paired darker stripes (Fig. 2G); forewing with faint cubital and gradate markings, forewing vein Rs originating at the same height or slightly proximally of cubital fork (Fig. 4C); male genitalia (Fig. 8C, D).... *M. lucasi*

Discussion

The phylogenetic analysis was conducted mainly to investigate the relationships among the species included in the genera *Gymnocnemia* and *Megistopus* and to test their respective monophyly. In addition, it is possible to draw some interesting, even if preliminary, observations on affinities at the tribal level. In agreement with Stange (1994, 2004), Nemoleontini was reconstructed as monophyletic, although it was only based on homoplasious apomorphies, thus obtaining only weak support. Michel et al. (2017) also retrieved this tribe as monophyletic in a phylogenetic analysis of the family based on molecular data. However, Badano et al. (2017), investigating the phylogeny of Myrmeleontiformia based on larval morphological characters, reconstructed Nemoleontini as paraphyletic with respect to Dendroleontini. Indeed, the members of these two tribes are characterised by strikingly similar larval morphology suggesting that further studies are necessary to clarify tribal level relationships. Stange (2004) noted that Nemoleontini is best delimited by a set of adult characters, such as the fusion of forewing veins 2A and 3A (16:1) and the absence of *pilula axillaris* in male forewing (18:0). The fusion of forewing anal veins also occurs in Nesoleontini and Myrmeleontini, while the *pilula axillaris* is probably an autapomorphy of Myrmeleontidae, which however, has been repeatedly and independently lost in several lineages at the tribal level (Acanthaclisini, Myrmecaelurini, Nesoleontini, Nemoleontini), generic level (e.g. *Dimares* Hagen, *Scotoleon* Banks) and species level (e.g. some *Brachynemurus* Hagen and *Myrmeleon* species) (Stange 1970a, 1994, 2004, Pantaleoni and Badano 2012). The retrieved subclades of Nemoleontini did not support the

subtribal level division into Nemoleontina and Neuroleontina as proposed by Stange (2004). In fact, *Nemoleon*, the only included member of Nemoleontina, was deeply nested within Neuroleontina. The presence of gonocoxites 9 fused in a Y-shaped structure (22:1) supported the monophyly of a clade (clade E) including *Distoleon*, *Neuroleon*, *Creoleon*, *Nemoleon* and *Macronemurus*. Further, subclade G was retrieved as monophyletic based on the presence of elongated legs (5:1) and opposable tarsal claws (10:1). The genera comprised in the latter group (i.e. *Gymnocnemia*, *Megistopus* and *Nedroledon*) were traditionally included in Glenurini (Markl 1954, Hölzel 1972, H. Aspöck et al. 2001). Markl (1954) distinguished Glenurini from Nemoleontini (which he divided into several tribes) based on the forked forewing vein 2A and simple 3A in the former tribe (vice versa in Nemoleontini). However, Stange (1970b) questioned the value of these characters, and Hölzel (1972) dismissed the importance of anal wing shape and bifurcations due to variability both among and within these tribes. Lastly, Stange and Miller (1990) synonymised Glenurini with Neuroleontina based on larval characters, thus including them within Nemoleontini. Krivokhatsky (2011) retained these groups as separate subfamilies, Nemoleontinae and Glenurinae, chiefly based on genital morphology. Our clade E corresponds to his characterisation of Nemoleontinae; however, we interpret the plate-like shape of the gonocoxites 9 (22:0) of the members of clade G as the plesiomorphic condition for Myrmeleontinae. This character is thus not warranted to delimit antlion taxa. A more extensive taxon sampling is necessary to test the relationships of “glenu-rines” with the other Nemoleontini.

Our analysis consistently recovered *Gymnocnemia mirabilis*, originally described as a member of *Megisto-*

pus, within the genus *Gymnocnemia*. The monophyly of this genus was well supported by elongated prothoracic legs, strikingly different pattern of leg pairs and the presence of robust, prominent thoracic setae. The characteristic shape of male gonocoxites 9, partly encircling gonocoxites 11, characterizes both *G. variegata* and *G. editaerevayae* (see also Michel 2013). Therefore, the discovery of the male of *G. mirabilis* is necessary to verify the value of this character to delimit the genus. The absence of tibial spurs, often used by antlion taxonomists to differentiate genera, is here re-interpreted as a weak homoplasious apomorphy that is not useful for systematic purposes questioning the importance of the character for generic delimitation. Furthermore, *Megistopus*, which now comprises only *M. flavicornis* and *M. lucasi*, is best distinguished by tarsomeres 1-4 being equally elongated and of similar size, while in other genera of Nemoleontini the first tarsomere is noticeably longer than the following articles (usually twice the length of the others).

The present analysis confirms the importance of a phylogenetic approach (i) to circumscribe genera as monophyletic groups in a family characterized by an overall homogeneous morphology, such as Myrmeleontidae, and (ii) to test the actual systematic value of commonly used diagnostic characters. A more inclusive taxon sampling and the integration of molecular data is advisable to delimit suprageneric taxa and to reconstruct the relationships within the family.

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Supplementary material 1

List of examined specimens

Authors: Davide Badano, Horst Aspöck, Ulrike Aspöck

Data type: RTF file

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Supplementary material 2

Data matrix for the phylogenetic analysis

Authors: Davide Badano, Horst Aspöck, Ulrike Aspöck

Data type: NEXUS file

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On the enigmatic *Sinonemestrius* Hong & Wang, 1990, with description of a new species based on a complete fossil fly (Diptera, Brachycera, Tabanomorpha, Heterostomidae)

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Abstract

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Key Words

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A new species of *Sinonemestrius* Hong & Wang, 1990 is described and illustrated based on a complete compression fossil of the fly. Currently placed in Rhagionemestriidae or Xylophagidae, the present study concludes that the morphology of the new find indicates that *Sinonemestrius* is a heterostomid genus within Tabanomorpha. The placement of *Ahirmoneura neimengguensis* K-y Zhang et al., 2008 is reassessed. It demonstrates close similarities in body structure and wing venation to those of *Sinonemestrius*, and can be provisionally transferred from Nemestrinidae to Heterostomidae: *Sinonemestriinae*.

Introduction

The Jehol biota (*sensu lato*) constitutes a suite of fossil plants and animals that lived during the Early Cretaceous in eastern- and north-eastern Asia (J-f Zhang 1992). As in the Lower Cretaceous Yixian Formation in Beipiao City of Liaoning Province, China (Ren and Guo 1995, Ren 1998), the order Diptera (true flies) is also well represented in the Lower Cretaceous of the Laiyang Formation in Laiyang City, Shandong Province, China. The suborder Brachycera is abundant. In the author's collection – about one half of the Diptera found is composed of Eremochaetidae (eremochaetid flies), Xylophagidae (awl-flies), Stratiomyidae (soldier flies), Nemestrinidae (tangle-veined flies), Tabanidae (horseflies), Athericidae (water snipe-flies), Rhagionidae (snipe flies), Empidi-

dae (dance flies), Protapioceridae (protapiocerid flies), Platypezidae (flat-footed flies) and Ironomyiidae (ironic flies), etc. Among them, only a few taxa have been described (J-f Zhang 1987, 2012, 2014, 2015, Hong and Wang 1988, 1990, J-f Zhang et al. 1993).

A rare and unusual nemestrinid-like brachyceran wing from the Laiyang Formation in the vicinity of Tuanwang Village, Laiyang, Shandong, China was described by Hong and Wang (1990) and named *Sinonemestrius tuanwangensis* Hong & Wang, 1990. The taxonomy and systematics of this enigmatic form have been much debated. It has a history of controversial taxonomy that has placed this nemestrinid taxon in up to four separate families (Hong and Wang 1990, Nagatomi and Yang 1998, Jarzembowski and Mostovski 2000, Mostovski and Martínez-Delclòs 2000, Nel 2010, Grimaldi 2016). This problem

is resolved here based on a new, complete compression of a sinonemestriid fly originating from the same fossil locality (Laiyang Formation in the vicinity of Tuanwang Village). In addition, the placement of another nemestrinid-like brachyceran, *Ahirmoneura neimengguensis* K-y Zhang et al., 2008, is reassessed. It could be related to Heterostomidae:Sinonemestriinae as it demonstrates close similarities in body structure and wing venation to those of *Sinonemestrius* Hong & Wang, 1990 rather than tangle-veined flies (see Remarks in Taxonomy below).

Material and methods

Material. The holotype of a shale fossil compression of a male sinonemestriid fly described herein is deposited in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), the Chinese Academy of Sciences, no. NIGP L91803. The fly-bearing sedimentary rocks of the Laiyang Formation are located near the village of Tuanwang, Laiyang City, Shandong Province, China.

Illustrations. Specimen descriptions, photomicrographs and line drawings were done with the application of glycerol to the surface of the specimens. The line drawings were produced with the aid of a camera lucida and the digital photomicrographs were taken using a stereomicroscope (Leica M205C).

Wing venation terminology here follows Wootton and Ennos (1989) and Shcherbakov et al. (1995). The cell traditionally named the anal cell is here considered to be the cubital cell. The following standard abbreviations are used: Sc, subcosta; R1, first radius; R2+3, second and third radius; R4, fourth radius; R4+5, fourth and fifth radius; bR4+5, basal section of R4+5; dR4+5, distal section of R4+5; R5, fifth radius; Rs, radial sector; M1, first media, M2, second media; M3, third media, M4, fourth media; CuA, cubitus anterior; CuP, cubitus posterior; r-m, crossvein between radius and media; m-m, crossvein between media; m-cu, crossvein between media and cubitus; bm, basal cell of media; br, basal cell of radius; cu, cubital cell; dc, discal cell.

Colour described here refers to that of the fossil, where patterning is preserved, not the hue of the live fly.

Taxonomy

Heterostomidae Nagatomi, 1977

Sinonemestriinae Nagatomi & Yang, 1998, stat. nov.

Sinonemestrius Hong & Wang, 1990

Type-species. *Sinonemestrius tuanwangensis* Hong & Wang, 1990

Included species. *Sinonemestrius akirai* Jarzembowski & Mostovski, 2000 and *Sinonemestrius completus* sp. n., besides the type species *Sinonemestrius tuanwangensis* Hong & Wang, 1990.

Diagnosis. Medium-sized flies with robust build; body covered with dense hairs but devoid of setae; head moderately large, semiglobose, shorter and narrower than thorax, comprised mostly of the eyes; eyes holoptic in male, hind margin with emargination; antenna short, corneous, with eight-segmented flagellum, first flagellomere swollen, stylus (or arista) absent; wing membrane with markings; R1 relatively short; R2+3 curved, relatively short, ending at, or near to, R1 tip; R4 usually sigmoidal; R5 nearly straight, aligned with stem of R4+5; crossvein r-m present; R5 or M1 ending at wing tip; M2 ending behind wing tip; cell cu (traditionally anal cell) open; metatibia with two very short spurs; empodium present.

Remarks. The original generic diagnosis was defined based on wing impressions (Hong and Wang 1990, Jarzembowski and Mostovski 2000). A revised and supplemented diagnosis including some critical structures of the body is proposed here based on a complete compression fossil of the fly.

Based on a single impression fossil of a nemestrinid-like fly from the Jurassic of the Daohugou biota in the vicinity of Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China, K-y Zhang et al. (2008) erected a new genus *Ahirmoneura* (type species: *Ahirmoneura neimengguensis* K-y Zhang et al., 2008). They classified this genus in Nemestrinidae. It certainly resembles representatives of the extinct nemestrinid subfamily Archinemestriinae and even some living tangle-veined flies in that R4, R5, M1 and M2 end near to the wing tip. Nevertheless, the clearly short R1 and the absence of the so-called diagonal vein exclude this genus from the Nemestrinidae. In many features (including body structures and wing venation), *Ahirmoneura* resembles *Sinonemestrius* (lack of setae on the body; hemispherical head; elongate-ovate abdomen covered with hairs; very short R1; R4, R5, M1 and M2 ending near to wing tip; and the so-called diagonal vein absent). It should be noted that the wing venation of *Ahirmoneura neimengguensis* demonstrates very close similarities to that of *Sinonemestrius akirai* (Figs 3C, D). The former species differs from the latter one only by the longer, straight R2+3, which ends at C far apart from the end of R1, M2 (instead of M1) ends just at the wing tip and r-m meets the anterior margin of the discal cell near to its base. Unfortunately, the crucial structure of the antenna of *Ahirmoneura neimengguensis* is unknown. Until a new find (including antenna) of this species is available, *Ahirmoneura* can only be provisionally assigned to Heterostomidae: Sinonemestriinae.

Sinonemestrius completus sp. n.

<http://zoobank.org/EC9ED5D1-18AF-4A69-9CF0-47E5A17709CB>

Figs 1–3

Diagnosis. Similar to *Sinonemestrius tuanwangensis*, but R2+3 smoothly curved downwards and parallel to R1, ending at C instead of R1 end; fork of R4+5 distinctly distad

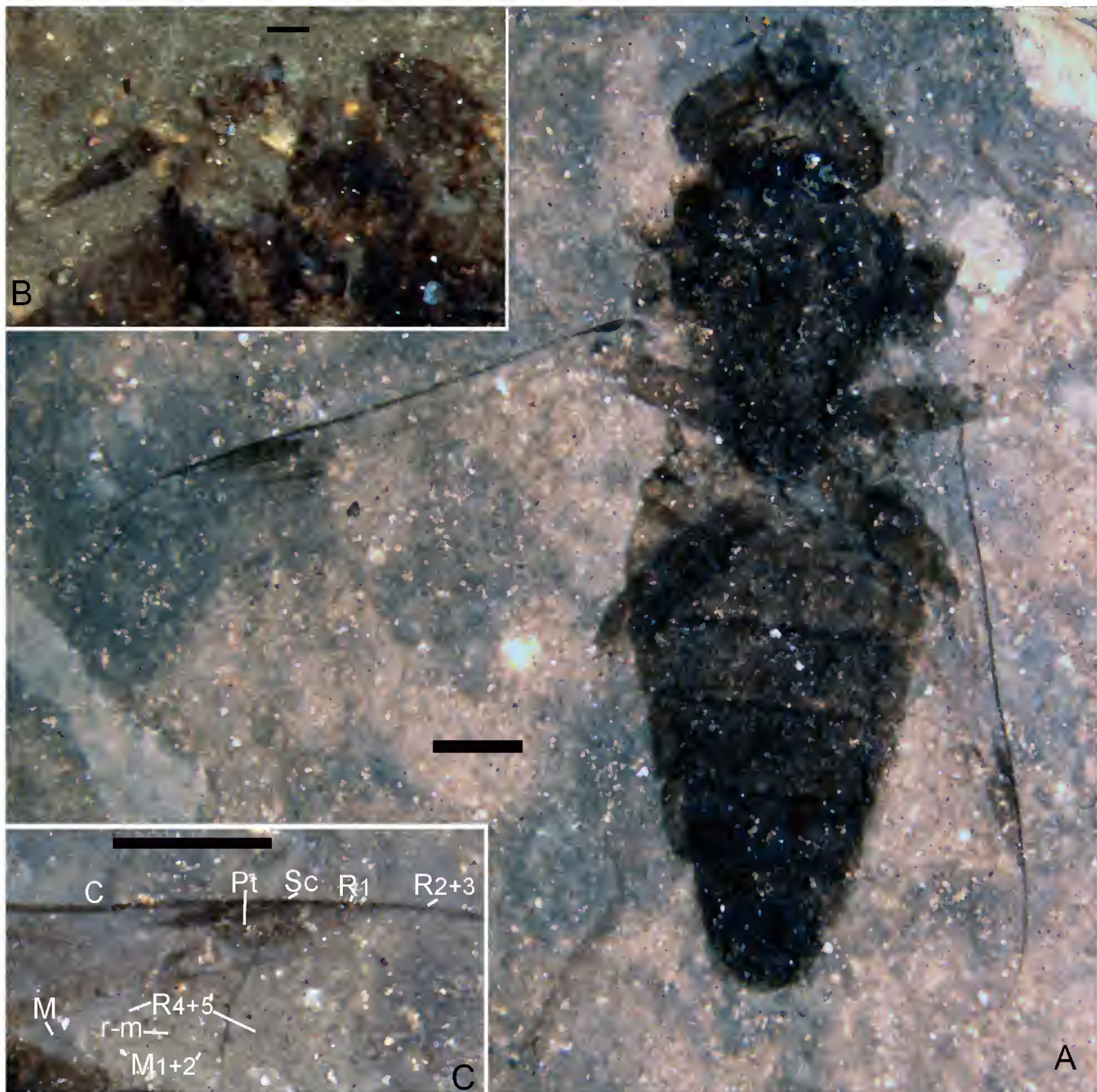


Figure 1. *Sinonemestrius completus* sp. n., no. NIGP L91803, holotype, photographs, male, dorsal view. **A** habitus, **B** antenna, **C** enlarged portions of right wing. Scale bars: 1 mm (**A**, **C**) and 0.1 mm (**B**).

to fork of M1+2; crossvein r-m meeting anterior margin of discal cell basad to its midlength; wing membrane with few markings (only limited to “Pt” and below it).

Description. Male medium-sized flies. Female unknown. Head moderately large, semiglobose, slightly narrower, but distinctly shorter, than thorax; vertex plus frons more or less flattened; eyes large, holoptic, covering almost entire head; antenna shorter than head, scape subquadrate, slightly wider than long, pedicel much shorter, less than one half of scape length, more than twice wider than long, first flagellomere extremely swollen, nearly pyriform, much longer and wider than scape and pedicel combined, less than twice as long as wide, other flagellomeres gradually tapering apically, about three times as long as first flagellomere (Figs 1B, 2B).

Thorax subovate, mesoscutum longer than wide, slightly wider than head; scutellum small, rounded apically, distinctly wider than long; wing nearly three times as long as wide; C thickened but thinned just at wing tip; R1 slightly curved smoothly, about three-fourths of wing length; Rs arising from R more or less late, about at one-third of wing length; R2+3 parallel to R1, ending at C; “Pt” well developed, another brown marking between R1 and R2+3 below base of “Pt” present (Figs 1A, C, 2C); Rs stem shorter than bR4+5, bR4+5 shorter than dR4+5, fork of R4+5 clearly distad to level of fork of M1+2; r-m meeting anterior margin of discal cell basad to its midlength, bM1+2 about one half of dM1+2 length; br cell nearly as long as, but obviously narrower than, bm cell; discal cell nearly pentagonal, relatively short, about

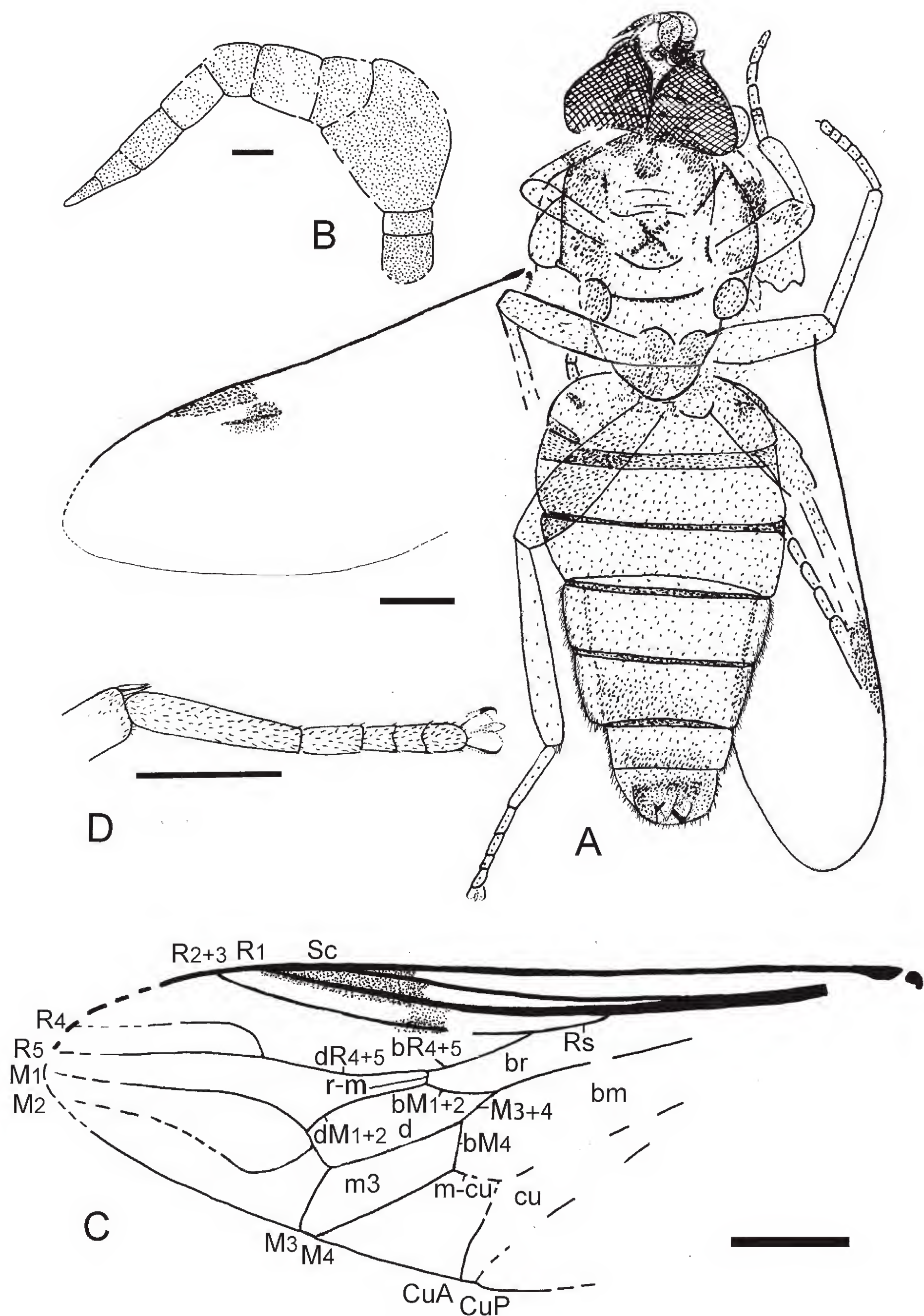


Figure 2. *Sinonemestrius completus* sp. n., no. NIGP L91803, line drawings of holotype. **A** habitus (wing venation omitted), **B** antenna, **C** left wing, **D** tarsus of left hindleg. Scale bars: 1 mm (A, C, D) and 0.1 mm (B).

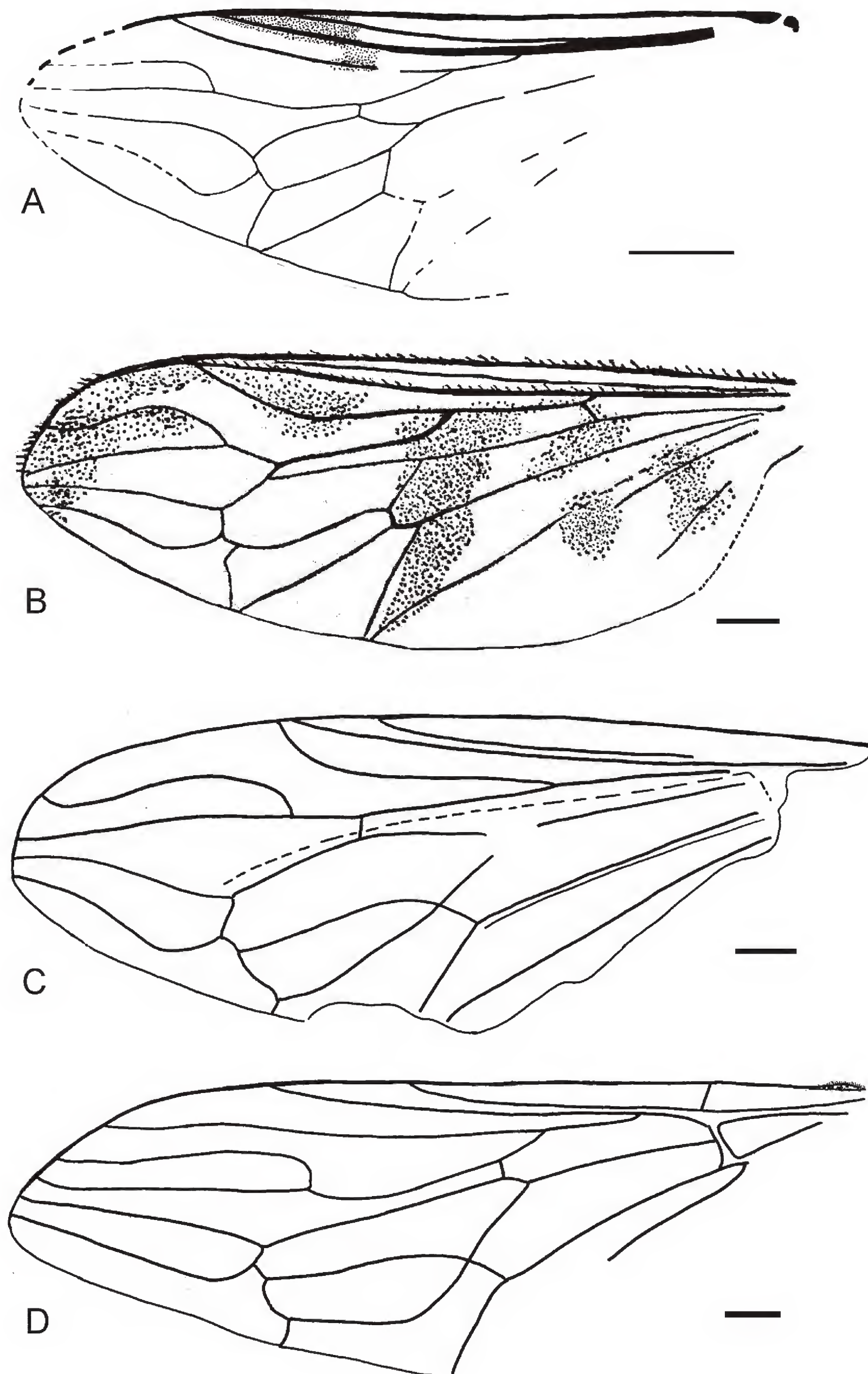


Figure 3. Difference and similarity between four sets of wings. Line drawings of holotypes. **A** *Sinonemestrius completus* sp. n., **B** *Sinonemestrius tuanwangensis* Hong & Wang, 1990 (after Hong and Wang 1990), **C** *Sinonemestrius akirai* Jarzembowski & Mostovski, 2000 (after Jarzembowski and Mostovski 2000), **D** *Ahirmoneura neimengguensis* K-y Zhang et al., 2008 (after K-y Zhang et al. 2008). Scale bars: 1 mm.

four times as long as wide; R4, R5, M1 and M2 slightly convergent, running towards wing tip (M1 ending just at wing tip); section of M3+4 slightly shorter than bM4; cell m3 nearly parallel quadrilateral but open apically; cell cu (traditionally anal cell) narrowly open. Legs with femora darkish brown, clavate, distinctly thicker than tibiae, tibiae and tarsi yellowish brown; femur of hindleg as long as, but twice as wide as, tibia, tibial spurs very short, distinctly less than tibial width, basitarsomere nearly as long as other tarsomeres combined, claw nearly as long as fifth tarsomere, empodium badly preserved, seemingly longer, but narrower, than pulvillus.

Abdomen ovate-oblong, with seven segments visible, clearly longer than head and thorax combined, with first segment longest, second segment widest, slightly wider than thorax; male genitalia longer than sixth segment with gonostylus (?) darkish brown, very narrow, strongly curved inwards.

Dimensions. Holotype: length of body 10.9 mm; head, 1.4 mm; thorax, 3.6 mm; abdomen 6.4 mm. Length of wing 7.4 mm, width of wing 2.9 mm.

Remarks. *Sinonemestrius completus* sp. n. differs from the type species *Sinonemestrius tuanwangensis* by the following features: R2+3 slightly curved, parallel to R1 and not meeting R1 end apically, fork of R4+5 distinctly distad to level of fork of M1+2, crossvein r-m meeting anterior margin of d cell basad to its midlength and wing membrane with a few markings (only limited to "Pt" and below it). On the other hand, this new species differs from *Sinonemestrius akirai* by Rs arising from R stem late (at about one-third of wing length vs near to wing base), the slightly curved R2+3 which runs parallel to R1 (vs R1 and R2+3 clearly convergent apically), fork of R4+5 distad (vs basad) to level of fork of M1+2 and cell m3 open (vs closed before hind margin of wing). Unfortunately, the body structures cannot be compared because the descriptions of the two known species are based on wing impressions.

Etymology. Latin, completus (complete), referring to the species erected based on a complete fly.

Holotype. No. NIGP L91803, a complete male fly, dorsoventral aspect, is held in the collection of NIGPAS.

Distribution. Type locality and horizon: Laiyang Formation, in the vicinity of Tuanwang, Laiyang, Shandong, China (Lower Cretaceous).

Repository. The Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Discussion

On the basis of a single wing of a fly from the Lower Cretaceous of the Laiyang Formation, Shandong, China, Hong and Wang (1990) erected the monotypic genus *Sinonemestrius*, which was originally placed in Nemestrinidae. Nagatomi and Yang (1998) erected a new monobasic family Sinonemestriidae for this genus. They considered it to be the sister group of Nemestrinidae. Judging from another find of a wing from the Lower Cretaceous of southern

England, Jarzembowski and Mostovski (2000) described a new species referring it to *Sinonemestrius* and retained Sinonemestriidae only as a tribe within Heterostominae, Xylophagidae; also, the diagnosis of *Sinonemestrius* was revised. Shortly after this study, Mostovski and Martínez-Delclòs (2000) transferred Heterostominae (including Sinonemestrine) into Rhagionemestriidae, another extinct family which is considered as a connecting link between Xylophagidae and Nemestrinidae. Nel (2010) agreed to the proposal (Mostovski and Martínez-Delclòs 2000) that *Sinonemestrius* belongs to Rhagionemestriidae. He moved the two modern genera (*i.e.* *Heterostomus* Bigot, 1857 and *Exeretoneura* Macquart, 1846) into Xylophagidae following Palmer and Yeates (2000) and Mostovski (2010 pers. comm.). Grimaldi (2016) also agreed with the placement proposed by Mostovski and Martínez-Delclòs (2000) that *Sinonemestrius* is a rhagionemestriid genus, but argued that Rhagionemestriidae is without question closely related to Acroceridae based on a distinct but very rare fly in late Cretaceous amber, while the modern genera *Heterostomus* and *Exeretoneura* appear to belong in the Tabanomorpha and Xylophagidae respectively, based on the studies of Coscarón et al. (2013) and Palmer and Yeates (2000).

The body structures and wing venation of *Sinonemestrius completus* sp. n. reveal that *Sinonemestrius* is very similar to the modern genus *Heterostomus*. This is based on the following synapomorphies: hemispherical head comprised mostly of the eyes; male holoptic; antennal flagellum with eight flagellomeres, stylus (or arista) absent; a pair of metatibial spurs present (although very small in *Sinonemestrius completus* sp. n.). In addition, there are close similarities in wing venation: wing membrane always with markings; C reaching wing tip, thinned behind wing tip; R2+3 ending close to R1 end; R4 sigmoidal; R5 aligned with stem of R4+5; R5 (or M1) ending at wing tip; crossvein r-m present; cell br very narrow, distinctly narrower than cell bm; discal cell usually narrow and long; cell m3 open (only closed in *Sinonemestrius akirai*); cell cu (traditionally anal cell) narrow and long (narrowly open in *Sinonemestrius*, closed in *Heterostomus*). For this reason, the proposal is supported here that *Sinonemestrius* could be related to heterostomid flies (Jarzembowski and Mostovski 2000, Mostovski and Martínez-Delclòs 2000). However, the placement of *Heterostomus* has been much debated. This genus includes only a single species, *Heterostomus curvipalpis* Bigot, 1857 from Chile. Lately, most works have classified it in Xylophagidae (Woodley 1989, Sinclair et al. 1994, Stuckenberg 2001, Kerr 2010); previously, it was included in various families within Tabanomorpha (Kröber 1930, Malloch 1932, Hennig 1972). Recently, the adult and pupa of *Heterostomus curvipalpis* were described and illustrated in detailed by Coscarón et al. (2013). They concluded that *Heterostomus curvipalpis* is related to Pelecorhynchidae within Tabanomorpha. Thus, it could be reasonable to retain Sinonemestriidae as a subfamily within Heterostomidae erected by Nagatomi (1977), and place these taxa in Tabanomorpha.

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Pseudochrysis Semenov, 1891 is the valid genus name for a group of cuckoo wasps frequently referred to as *Pseudospinolia* Linsenmaier, 1951 (Hymenoptera, Chrysididae)

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Abstract

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Key Words

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The cuckoo wasp genus *Pseudochrysis* Semenov, 1891 is currently treated by several authors as a junior subjective synonym of *Euchroeus* Latreille, 1809, due to a type species designation by O. W. Richards in 1935. In the original description of the genus *Pseudochrysis*, Semenov (1891) distinguished two subordinated taxa within the genus *Pseudochrysis*: the subgenus *Pseudochrysis* and the subgenus *Spintharis* (sensu Dahlbom 1854). Semenov included three species in the subgenus *Spintharis*, but failed to mention any species included in the nominal subgenus. He was the first author, however, who listed in a subsequent publication (Semenov 1892) eleven species to be included in the nominal subgenus. According to the International Code of Zoological Nomenclature (ICZN 1999, Art. 67.2.2), these eleven species are deemed to have been listed in the original description. One of these, *Chrysura humboldti* Dahlbom, 1845, was explicitly designated by Semenov (1892) as type species of *Pseudochrysis*. We therefore consider the designation of *Pseudochrysis (Spintharis) virgo* Semenov, 1891 as type species of *Pseudochrysis* by Richards (1935) as invalid. The currently widely used genus name *Pseudospinolia* Linsenmaier, 1951 (type species *Chrysis uniformis* Dahlbom, 1854) is consequently to be regarded as a junior subjective synonym of *Pseudochrysis*, given the current circumscription of the genus *Pseudospinolia* (including both *Pseudospinolia humboldti* and *Pseudospinolia uniformis*).

Introduction

Semenov¹ (1891: 444) described the genus *Pseudochrysis* at the end of a scientific article entitled “*Pseudochrysis (Spintharis) virgo*, sp. n.”, providing for it a short generic

diagnosis. Before this diagnosis, he announced the full description of the genus *Pseudochrysis* to be given in a forthcoming study on subfamilies, tribes, subtribes, genera, and subgenera of the family Chrysididae. The announced study was published a few months later (Semenov 1892).

In the original description of the genus *Pseudochrysis*, Semenov (1891: 443) subdivided his new genus into two subgenera: the nominal subgenus (*Pseudochrysis*) and the subgenus *Spintharis* sensu Dahlbom, 1854 (nec *Spintharis* Klug, 1845). Dahlbom’s (1854) interpretation of *Spintharis* differed from Klug’s (1845) original one,

¹ The family name of Andrey Petrovich Semenov-Tian-Shanskij (in Russian: Андрей Петрович Семёнов-Тянь-Шанский) was also spelled Semenow, Semenov-Tian-Shansky, Semenov-Tian-Shanskij in different publications on Chrysididae. The name Semenov is here standardised according to Kimsey and Bohart (1991).

possibly because Dahlbom did not know Klug's (1845) work, yet Semenov (1891) explicitly treated *Spintharis* in Dahlbom's sense. Thus, Semenov (1891) did not introduce (and consequently cannot be considered being author of) a new subgenus *Spintharis*.

Semenov (1891: 443) included three species in the subgenus *Spintharis*: *Pseudochrysis* (*Spintharis*) *virgo* Semenov, 1891, *P. (S.) limbata* (Dahlbom, 1854), and *P. (S.) singularis* (Spinola, 1838). However, he failed to name any species to be included in the nominal subgenus of his new genus *Pseudochrysis*. This information was provided in the announced second publication (Semenov 1892), in which eleven species were included in the subgenus *Pseudochrysis*. One of these, namely *Chrysura humboldti* Dahlbom, 1845, was explicitly designated as type species of *Pseudochrysis* (*Pseudochrysis*).

Despite Semenov's (1892) designation of *Chrysura humboldti* Dahlbom, 1845 as type species of *Pseudochrysis* (*Pseudochrysis*), Richards (1935) designated *Pseudochrysis* (*Spintharis*) *virgo* Semenov, 1891 as the type species of the genus *Pseudochrysis*. The genus *Pseudochrysis* was consequently considered by many authors as a junior subjective synonym of the genus *Euchroeus* Latreille, 1809, which currently includes (among others) the species *E. virgo* (Semenov, 1891), *E. limbatus* (Dahlbom, 1854), and *E. singularis* (Spinola, 1838). As a result of this, Linsenmaier (1951) described the new genus *Pseudospinolia* to name the group of species previously included by Semenov in his subgenus *Pseudochrysis*.

According to the 4th Edition of the International Code of Zoological Nomenclature (ICZN 1999, Art. 67.2.2), Semenov's (1892) designation of a type species of *Pseudochrysis* is valid and Richards' (1935) designation consequently is invalid. The valid type species of the genus *Pseudochrysis* is *Chrysura humboldti* Dahlbom, 1845. Moreover, despite the use of the genus name *Pseudospinolia* in the recent literature (especially by authors from Europe and the New World), a significant number of authors (especially from Russia) use the genus name *Pseudochrysis* instead. We therefore treat *Pseudochrysis* as a valid genus and consider *Pseudospinolia* as a junior subjective synonym of it.

Results and discussion

Article 43.1 of the ICZN (1999) [Statement of the Principle of Coordination applied to genus-group names] states: "A name established for a taxon at either rank in the genus group is deemed to have been simultaneously established by the same author for a nominal taxon at the other rank in the group; both nominal taxa have the same type species, whether it was fixed originally or subsequently." Thus, Semenov (1891: 444), when describing the nominal genus *Pseudochrysis*, is deemed to have described the nominal subgenus *Pseudochrysis* at the same time. Since all three species listed by Semenov (1891: 444) and included in the genus *Pseudochrysis* are unam-

biguously assigned to the subgenus *Spintharis*, the nominal subgenus *Pseudochrysis* was initially established with no species included.

Semenov (1891, 1892) treated *Euchroeus* Latreille, 1809, *Spintharis* Klug, 1845, *Spinolia* Dahlbom, 1854, *Brugmoia* Radoszkowski, 1877 as subgenera of his newly described genus *Pseudochrysis*, thus disregarding precedence of these genera upon *Pseudochrysis*. The way to treat the higher taxonomic ranks, such as "Tribus Chrysididae" and "Subtribus Pseudochrysidae" (Semenov 1892), appears unusual as well, considering current standards. It is to be stressed, however, that at the time Semenov published his studies, precisely codified nomenclatorial rules did not exist, and conventions and unwritten rules about it varied across disciplines, countries, and languages. At the 1st (Paris 1889) and 2nd (Moscow 1892) International Zoological Congresses, the need to establish common, widely accepted international rules for all branches of zoology was emphasized. The discussion resulted in the "International Rules on Zoological Nomenclature", first proposed at the 3rd International Congress for Zoology (Leiden 1895) and published in three languages (French, English, and German) in 1905.

In cases in which the description of a new genus or of a new subgenus does not include any species, Article 67.2.2 of the ICZN (1999) states: "If a nominal genus or subgenus was established before 1931 without included nominal species [Art. 12], the nominal species that were first subsequently and expressly included in it are deemed to be the only originally included nominal species". According to this statement, a nominal genus or subgenus before 1931 can have been validly established without any originally included nominal species. The nominal subgenus *Pseudochrysis* is therefore validly established, despite having no nominal species included in it, and the author and the date of publication of the nominal subgenus are Semenov, 1891.

Semenov (1892: 486), in the section "*Enumeratio specierum generis Pseudochrysis m.*", was the first author who explicitly stated what species were to be included in *Pseudochrysis* (*Pseudochrysis*). According to Article 67.2.2 of the ICZN (1999), the species originally included in the subgenus *Pseudochrysis* are those, and only those, listed by Semenov (1892). He included eleven species: *P. humboldti* (Dahlbom, 1845), *P. incrassata* (Spinola, 1838), *P. gratiosa* (Mocsáry, 1889), *P. coeruleiventris* (Abeille de Perrin, 1878), *P. transversa* (Dahlbom, 1854), *P. kohli* (Mocsáry, 1889), *P. marqueti* (du Buysson, 1887), *P. aureicollis* (Abeille de Perrin, 1878), *P. uniformis* (Dahlbom, 1854), *P. durnovi* (Radoszkowski, 1866) [incorrect subsequent spelling of *dournovii*], and *P. neglecta* (Shuckard, 1837).

Semenov (1892: 485) in his paragraph "*Tabula differentialis subgenerum generis Pseudochrysis m.*" provided a key to the subgenera of the genus *Pseudochrysis*, in which he also designated a type species of each subgenus: *Spintharina* Semenov, 1892 (type species: *Chrysis vagans* Radoszkowski, 1877); *Spintharis* Dahlbom, 1854 (type

species: *Pseudochrysis (Spintharis) virgo* Semenov, 1891); *Brugmoja* Radoszkowski, 1877 [incorrect subsequent spelling of *Brugmoia*] (type species: *Brugmoia pellucida* Radoszkowski, 1877); *Euchroeus* Latreille, 1809 (type species: *Chrysis purpurata* Fabricius, 1787); *Spinolia* Dahlbom, 1854 (type species: *Chrysis lamprosoma* Förster, 1853); *Pseudochrysis* Semenov, 1891 (type species: *Chrysura humboldti* Dahlbom, 1845); *Achrysis* Semenov, 1892 (type species: *Chrysis unicolor* Dahlbom, 1831).

Richards (1935: 158), dealing with the genus group names *Spintharis* Klug and *Pseudochrysis* Semenov, wrote: “*Pseudochrysis* Semenow [...] was erected for two species *Spintharis (P.) virgo* Semenow, 1891 and *Euchroeus limbatus* Dahlbom, 1854. *S. virgo* Sem. is here fixed as type”. This statement is in conflict with Semenov’s original description (1891) in at least two points: (1) Semenov (1891) described “*Pseudochrysis (Spintharis) virgo*, sp. n.” in the genus *Pseudochrysis* with *Spintharis* as subgenus, not in the genus *Spintharis* with *Pseudochrysis* as subgenus; (2) the number of species included by Semenov (1891) in the subgenus *Spintharis* are actually three: *Pseudochrysis (Spintharis) virgo*, *Pseudochrysis (Spintharis) limbata* (= *Euchroeus limbatus*), and *Spintharis singularis*.

It must be emphasized that Semenov (1891) unambiguously included the three species *P. virgo*, *P. limbatus*, and *P. singularis* in the subgenus *Spintharis*, not in the nominal subgenus *Pseudochrysis*, the latter being described with no species included. Richards’ (1935) designation is thus incompatible with Semenov’s intended classification. Semenov (1891), in the original description of the genus *Pseudochrysis*, did not include *P. virgo* in *Pseudochrysis (Pseudochrysis)*, but in *Pseudochrysis (Spintharis)*, and subsequently (1892) designated *P. (S.) virgo* as type species of the subgenus *Spintharis*. Given that Semenov (1892) had already designated *Chrysura humboldti* Dahlbom, 1845 as type species of *Pseudochrysis (Pseudochrysis)*, Richards’ (1935) designation of *P. virgo* as type species of *Pseudochrysis* was both invalid and unnecessary.

Linsenmaier (1951: 26) adopted Richards’ (1935) interpretation of the type species of the genus *Pseudochrysis*, which made *Pseudochrysis* a junior subjective synonym of the genus *Euchroeus*. He realized that there was no valid name available to refer to those species by Semenov (1891, 1892) included in his subgenus *Pseudochrysis*. Linsenmaier (1951: 31) consequently described *Pseudospinolia* as a new subgenus of *Euchroeus*, with *Chrysis uniformis* Dahlbom, 1854 as type species. *Pseudospinolia* was raised by Bohart and Kimsey (1980) to genus rank and synonymized by Kimsey (1983) with *Spinolia* Dahlbom, 1854. In the most recent generic revision of the family, Kimsey and Bohart (1991) granted *Pseudospinolia* the rank of the genus. However, both the names *Pseudospinolia* and *Pseudochrysis* as well as the taxonomic rank have been used heterogeneously by different authors.

We investigated the use of *Pseudospinolia* and *Pseudochrysis* in more than 1,300 publications, spanning

more than a century. Prior to Linsenmaier’s (1951) description of *Pseudospinolia*, *Pseudochrysis* Semenov was treated as a valid genus by the most important authors of that time. For example, Semenov’s (1892) classification was followed by Bischoff (1910, 1913, 1935), Hellén (1920, 1935), Maidl (1922), Noskiewicz (1922), Banzhaf (1930), Invrea (1930, 1933, 1935), Drogoszewski (1934), Špaček (1934, 1935), Bernard (1935), Molitor (1935), Crèvecoeur and Maréchal (1936, 1939), Grandi (1936), Berland and Bernard (1938), Atanassov (1940), Ceballos (1941); Giner Mari (1942), Balthasar (1946, 1948), Edney (1947), Cavro (1950), Enslin (1950), and Hammer (1950). Only du Buysson (1896) considered *Pseudochrysis* as a synonym of *Chrysis*. However, Trautmann and Trautmann (1919), and Trautmann (1922, 1926, 1927) deeply modified the original interpretation given by Semenov, including in *Pseudochrysis* several species belonging to different species groups of the genus *Chrysis* Linnaeus, 1761 (*C. amasina* Mocsáry, 1889; *C. bihamata* Spinola, 1838; *C. verna* Dahlbom, 1854; *C. pallidicornis* Spinola, 1838; *C. abeillei* Gribodo, 1879; *C. rufitarsis* Brullé, 1833), based on the combination of the following characters: “*mouth parts elongate over the mandible tip, forewing radial cell more or less open, apical margin of the third tergite full-rim to quadrangular. These species often resemble many species of the genus Chrysis in habitus*” (Trautmann 1927: 91).

Even after Linsenmaier’s (1951) description of *Pseudospinolia*, the name *Pseudochrysis* remained in use by a significant number of authors till today: Balthasar (1952, 1953, 1954a, 1954b), Invrea (1952, 1955), Tsuneki (1953), Semenov and Nikol’skaja (1954), Fahlander (1954), Zimmermann (1954), de Beaumont (1955), Haupt (1956), Kusdas (1956, 1958), Grandi (1957, 1962), Negru (1960), Móczár (1964, 1967), Hozak and Zeman (1966), Ressler (1966), Balthasar et al. (1967), Semenov (1967), Suárez (1969), Tumšs and Maršakovs (1970), Atanassov (1972), Banaszak (1975, 1980), Kofler (1975), Berland (1976), Nikol’skaya (1978), Skibinska (1982), Zvantsov (1988), Blagoveschenskaya (1990, 1994), Doronin (1996), Kuznetzova (1990), Buganin et al. (2000), Tarbinsky (2000, 2004), Krivonogova and Rudoiskatel (2004), Vinokurov (2004, 2005, 2006), Kalniņš et al. (2007), Rudoiskatel (2007, 2008, 2011), Kochetkov et al. (2008), Brustilo and Martinov (2008), and Kochetkov (2012). In total, we found that 49 authors used the name *Pseudochrysis* in 51 scientific articles, either as a valid genus or as a subgenus of *Spinolia*. On the other hand, we found that 99 authors used the name *Pseudospinolia* as either a valid genus or as a subgenus of *Euchroeus* in 114 scientific publications. Thus, the name *Pseudochrysis* has been used till today, although to a lesser extent than *Pseudospinolia*.

The relevant type specimens of *Chrysura humboldti* (see Rosa and Vårdal 2015), *Chrysis singularis* (see Rosa and Xu 2015) and *Pseudochrysis virgo* (Rosa, Belokobylskij and Fedorova, in litt.) have been studied. Only the type specimen of *Chrysis uniformis* remained unavailable. Dahlbom’s (1854) description of *Chrysis uniformis*

is based on a (single?) specimen from Loew's collection, collected in Asia Minor. The first author (P. R.) unsuccessfully searched for the type in the museum collections of Copenhagen, London, Lund, Stockholm, and Vienna, where Loew's specimens are supposedly deposited. The type of *Chrysis uniformis* is therefore currently thought to be lost. However, its unique morphology and coloration make *Pseudochrysis uniformis* an easily recognizable species. It is widespread, locally common (ranging from the Mediterranean region to Central Asia; Linsenmaier 1959; Semenov and Nikol'skaja 1954) and not known to be involved in any major taxonomic problem. We therefore currently consider a neotype designation as unnecessary.

We asked for the opinion of some current or former Commissioners on ICZN. Alberto Ballerio and the former presidents Alessandro Minelli and Denis Brothers fully support our nomenclatorial point of view; Douglas Yanega and Miguel A. Alonso Zarazaga conversely disagree on our interpretation, stating that *P. humboldti* was not listed in the first article (Semenov 1891) and consequently cannot be selected as type species of *Pseudochrysis*. It was also suggested that the chrysidologist community should find an agreement about the way to solve the case. We asked for the opinion of hymenopterists currently dealing with Chrysididae or other Hymenoptera. Michael Madl (Austria), Toshko Ljubomirov (Bulgaria), Zaifu Xu (China), David Baldock (England), Juho Paukkunen (Finland), Werner Arens and Christian Schmid-Egger (Germany), Afrouz Farhad (Iran), Gian Luca Agnoli, Guido Pagliano, Fabrizio Rigato and Marcello Romano (Italy), Eduardas Budrys and Svetlana Orlovskytė (Lithuania), Nico Schneider (Luxembourg), Frode Ødegaard (Norway), Bogdan Wiśniowski (Poland), Andrej Gogala (Slovenia), Leopoldo Castro (Spain), Alexander Berg and Mattias Forshage (Sweden), Marco Bernasconi (Switzerland), Erol Yıldırım (Turkey), and Kateryna Martynova (Ukraine) fully support our viewpoint, while Lynn S. Kimsey (U.S.A.) follows Yanega's opinion.

Conclusions

By applying Art. 67.2.2 (ICZN 1999) and in agreement with the majority of hymenopterologists working on cuckoo wasps, we recognize *Chrysurus humboldti* Dahlbom, 1845 as the type species of *Pseudochrysis* Semenov, 1891, and propose the following synonymy: *Pseudochrysis* Semenov, 1891 (type species: *Chrysurus humboldti* Dahlbom, 1845) = *Pseudospinolia* Linsenmaier, 1951 (type species: *Chrysis uniformis* Dahlbom, 1854) **syn. nov.** *Pseudospinolia* is a junior subjective synonym of *Pseudochrysis*.

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