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- Discussion
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In Focus

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See paper of **Aspöck H et al.** Anthropogenic dispersal of a snakefly (Insecta, Neuropterida) – a singular phenomenon or a model case in Raphidioptera?

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160 years of D.E.Z. – what is the recipe for thy long life?

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This year we look back at 160 years of entomological research published in the DEZ. Believe it or not, our journal is the third oldest of all still existing entomological periodicals worldwide! A concatenation of favourable circumstances? At first glance, the first decades were rather tough ones, involving personal controversies, splitting of the society behind the journal and the journal itself, and later reunion (Wessel 2007). However, at the second glance, this period seems to have been an excellent one at the same time, as the young and dedicated visionary, Gustav Kraatz, the first editor of the DEZ, guided the journal throughout these troublesome waters for the first 50 years. What makes him visionary? Already 160 years ago, he promoted high standards in taxonomical publications such as the description of both sexes when erecting new genera, the publication of comprehensive revisions instead of single species descriptions and the exploration of new diagnostic characters (Wessel 2007) – not much to add 160 years later! More than this, under his editorship the DEZ was at the forefront of the development and establishing of internationally recognized nomenclatorial rules in entomology, regulating foremost issues of priority (Wessel 2007). Still today, nomenclatorial issues constitute a hot topic in entomological publishing.

Finally, Gustav Kraatz was driven by the urge to combine collections and libraries of all German entomologists, so that scientists could have free access (Wessel 2007).

In 1886, he founded an Entomological National Museum that still exists and is nowadays known as DEI – Deutsches Entomologisches Institut. It would have certainly pleased Gustav Kraatz that since the transfer of the DEZ from Wiley to Pensoft in 2014 all articles are published under an open access policy, likewise facilitating the access to knowledge.

The incredible number of 22.613 species descriptions published in the last 160 years in the DEZ (Stelbrink and Wessel 2008; numbers updated) are a substantial contribution to our knowledge of the insects on this planet. The vision of Gustav Kraatz and the commitment of many following editors and authors have made the success of the DEZ possible.

Together let's do our best to continue this line to the future!

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- Wessel A (2007) D.E.Z. – A history. 150 years of scientific publishing in entomology. *Deutsche Entomologische Zeitschrift* 54: 157–167. <https://doi.org/10.1002/mmnd.200700016>

The Nevrorthisidae, mistaken at all times: phylogeny and review of present knowledge (Holometabola, Neuropterida, Neuroptera)

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Abstract

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This monographic review of the Nevrorthisidae Nakahara, 1915, covers all 19 validly described, extant species worldwide that belong to one of the smallest families of the order Neuroptera. The family embraces four genera: *Nevrorthis* Costa, 1863 (with five species occurring in the Mediterranean region), *Austronevrorthis* Nakahara, 1958 (with two species restricted to eastern Australia), *Nipponevrorthis* Nakahara, 1958 (with 11 species from eastern Asia: Japanese islands, mainland China, Taiwan), and *Sinonevrorthis* Liu, H. Aspöck & U. Aspöck, 2012 (with one species recorded from mainland China). A comprehensive taxonomical treatment of all extant taxa is presented, including the scant available biological data. Distribution maps for all species are provided. A phylogenetic analysis based on morphological data from both extant and extinct taxa was performed. *Austronevrorthis*, together with *Nevrorthis* and some Eocene Baltic amber genera, form a monophylum. The disjunct distribution of modern nevrorthisid genera demonstrates the relictual nature of the family and points to a historical biogeography that could have led to the formation of the present distribution pattern. Future discovery of fossil material might substantiate these claims.

Sonnet for a Vulnerable Creature

Is the Climate still fine?

Still clean, the Riverine?

Ruined rivulets run dry,

Fossils – tho' living – may Die.

Introduction

The family Nevrorthisidae comprises only 19 described extant species assigned to four genera – with an extremely disjunct distribution (U. Aspöck and H. Aspöck 1994, 2007, Liu et al. 2012, 2014) – and nine described fossil species assigned to five genera from the Eocene Baltic amber (Wichard 2016). In addition, there is record of an undescribed putative nevrorthisid from the mid-Cretaceous Burmese amber (mentioned in Makarkin 2016, based on a photograph in Xia et al. 2015).

The eidonomically inconspicuous adults are nonetheless impressive due to their excessively shaped male genital sclerites that are of high phylogenetic relevance. The aquatic larvae are equipped with a complex joint (“Rollen-gelenk”) between head and pronotum (Zwick 1967), and the archaic head capsule has played a key role in understanding the phylogeny of Neuroptera. The aquatic pupa (Malicky 1984) is unique among Neuroptera and Neuropterida. The phylogenetic position of Nevrorthisidae is controversial (Wang et al. 2016). The aim of the present paper is to summarize the accumulated knowledge

on Nevrorthidae and to hypothesize on phylogenetic relationships of the family internally and within the order Neuroptera.

Historical overview

The odyssey of Nevrorthidae from nowhere to a phylogenetic key position in the context of landmarks in neuropterology (U. Aspöck and H. Aspöck 2010b) follows a unique pathway – though “mistaken at all times” – as addressed in the title. *Mucropalpus fallax* Rambur, 1842, the first described nevrorthid, was originally placed in Hemerobiidae (Rambur 1842). Costa (1863) established the genus *Nevrorthus* and – in describing *N. iridipennis* – provided the first (and quite wondrous) illustration of a nevrorthid (Fig. 1). In the opus magnum of Anton Handlirsch “Die fossilen Insekten und die Phylogenie der rezenten Formen” (1906–1908), Nevrorthidae were still cryptic and hidden within Sisyridae (as *Sisyra (Rophalis) relicta* Hagen, 1856).

Krüger (1923) treated the genera *Rhophalis* (sic) Erichson (sic) and *Neurorthus* (sic) Costa again as belonging to Sisyridae. They remained hidden in the phylogenetic tree of the Neuroptera by Withycombe (1925). In the meantime Nakahara (1915) erected the tribe Neurorhini, yet placed it in the Hemerobiidae: Hemerobiinae. Forty years later he raised Neurorhini to the subfamily level (Nakahara 1958), yet retained them within Sisyridae.

Zwick (1967) finally awarded family status to Neurorhinae Nakahara: Neurorhidae Nakahara, 1915, and discussed a sister group relationship of Neurorhidae with Osmylidae. Oswald and Penny (1991) re-established *Nevrorthus* Costa, 1863, as the clear intention of Costa and identified *Neurorthus* as a misspelling.

In two small and inconspicuous papers (U. Aspöck 1992, 1993), Nevrorthidae received special phylogenetic attention and the following hypothesis was proposed: The Nevrorthidae do not belong to the Hemerobiformia as hitherto assumed but are interpreted as the sister group of the Myrmeleontiformia with a special head cervix articulation serving as a larval synapomorphy.

In the first computerized analysis of the Neuropterida (U. Aspöck et al. 2001), the Nevrorthiformia emerged as sister group of Hemerobiformia + Myrmeleontiformia (with larval cryptonephry as a synapomorphy). The com-

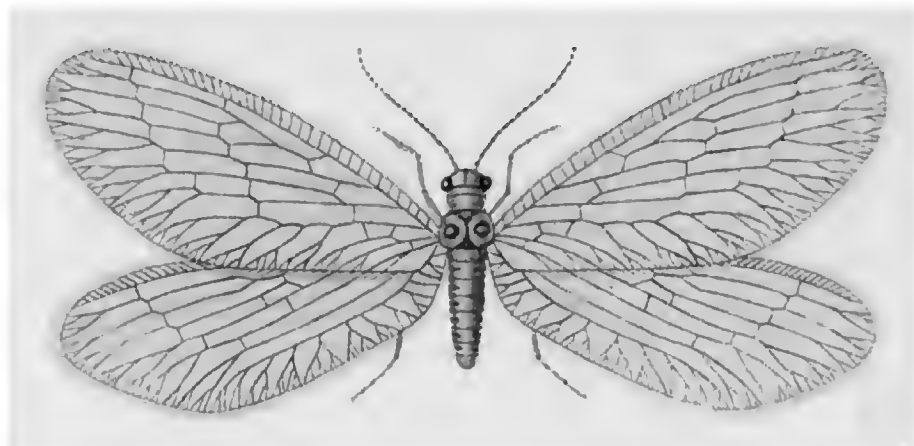


Figure 1. *Nevrorthus iridipennis* Costa. Italy: Calabria. From Costa (1863), who published the first illustration of a nevrorthid.

compact larval head capsule of Nevrorthiformia represents a basic pattern, the compact head capsule is retained in Myrmeleontiformia, where however, it is strongly modified, as emphasized in U. Aspöck (2002).

In the first molecular analysis of Neuropterida (Haring and U. Aspöck 2004), Nevrorthidae held their position as sister group of all other families, however, the Hemerobiformia were disrupted.

To escape the conflicting results, the phylogenetic relevance of the genital sclerites was tested on the basis of the gonocoxite concept put forward by U. Aspöck and H. Aspöck (2008a). In this analysis Nevrorthidae retained their position as sister group to all other families.

In the course of further molecular analyses, mentioned above, Nevrorthidae was retrieved either as a sister group to Sisyridae and Osmylidae and all three constituted a monophylum (Winterton et al. 2010), or Nevrorthidae and Sisyridae alone constituted the sister group to the rest of Neuroptera except Coniopterygidae (Wang et al. 2016).

In context of a microcomputer analysis of the larval head of *Nevrorthus* (Beutel et al. 2010), the sister group relationship of Megaloptera + Neuroptera was corroborated, and Nevrorthidae was confirmed as sister group of Myrmeleontiformia + (the reinstated) Hemerobiformia. In the context of that analysis, three-dimensional reconstructions of the larval head not only of *Nevrorthus* but also previous ones concerning Raphidioptera (Beutel and Ge 2008) and Megaloptera (Beutel and Friedrich 2008) became essential for better understanding the evolution of the characters. A special focus on the head morphology of adult Neuroptera by Zimmermann et al. (2011) and Randolph et al. (2013, 2014) ended up with Sisyridae as sistergroup of all other Neuroptera, followed by Nevrorthidae as sistergroup of the remaining families. The discovery of the mouthpart muscle *M. stipitalis transversalis* and a hypopharyngeal transverse ligament found in the head of *N. apatelios* was newly discovered for Neuroptera and herewith for the first time in Endopterygota by Randolph et al. (2014). In addition a submental gland with multiporous opening – apparently unique among insects – was described for Nevrorthidae and Osmylidae (Randolph et al. 2014). The phylogenetic relevance of the adult head in Nevrorthidae is obvious.

Biology

The unique aquatic larva of *Nevrorthus fallax* was discovered and described in detail by Zwick (1967). The first description of a nevrorthid larva, however, is much older (Takahashi 1942), but it was subordinated under Dilariidae. Larvae are carnivorous and live in the coarsely granular sands of clear, clean rivulets. Pupation takes place in the water on the undersides of stones. The silky cocoon spun by the larva comprises two layers (Malicky 1984). An aquatic pupa is unique among Neuroptera and Neuropterida. The length of development has not been adequately investigated. Probably, it takes one year. Nothing is known on the number of eggs laid by a female.

Adults (Fig. 2) are found on leaves of overhanging tree branches and on bushes and low vegetation close to the water. They are active in the day-time and are rarely attracted by artificial light.

Malicky (1984) found adults on sticky leaves and assumed honeydew to be an important part of the diet. The adaptations of the mouthparts, namely paraglossae that are folded onto the ligula thus forming a secondary prolongation of the salivary opening to the tip of the ligula (Randolf et al. 2013, 2014) are interpreted as adaptations to feeding not only on liquid but also on desiccated honeydew. A further indication for glycophagous feeding habit has been studied already by Kokubu and Duelli (1983). Monserrat (2005) found fungal spores in the digestive tract of *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, 1977, and *Nipponeurorthus fasciatus* Nakahara, 1958. Randolf et al. (2014) described the mouthparts of *Nevrorthus apatelios* as instruments with strongly sclerotized asymmetrical mandibles with apical incisors which indicate a carnivorous feeding habit (Stelzl 1992).

Fossil taxa

At present, fossil Nevrorthidae have been found in Eocene Baltic amber (about 45 million years BP) and in mid-Cretaceous Burmese amber (about 100 million years BP, species with familial placement not confirmed and undescribed).

As concerns fossil Nevrorthidae, all available knowledge of material from the Baltic amber has been summarized recently (Wichard 2016). The excellent preservation especially of the genital sclerites of most species allows homologisation with extant species, which is fascinating. However, the Baltic amber material is too young to interpret deeper phylogeny. This may also be the case with the much older Burmese amber (Grimaldi et al. 2002, Xia et al. 2015), from which more surprising findings are to be expected.

Further information on fossil Nevrorthidae can be found in Berendt (1845-1856), Nel and Jarzembowski (1997), Makarkin and Perkovsky (2009), Wichard et al. (2009, 2010), Wedmann et al. (2013), Wichard (2014, 2016), Makarkin (2016).

Material and methods

List of taxa examined

Nevrorthus apatelios H. Aspöck, U. Aspöck & Hölzel, 1977
Nevrorthus fallax (Rambur, 1842)
Nevrorthus hannibal U. Aspöck & H. Aspöck, 1983
Nevrorthus iridipennis Costa, 1863
Austroneurorthus brunneipennis (Esben-Petersen, 1929)
Austroneurorthus horstaspoecki U. Aspöck, 2004

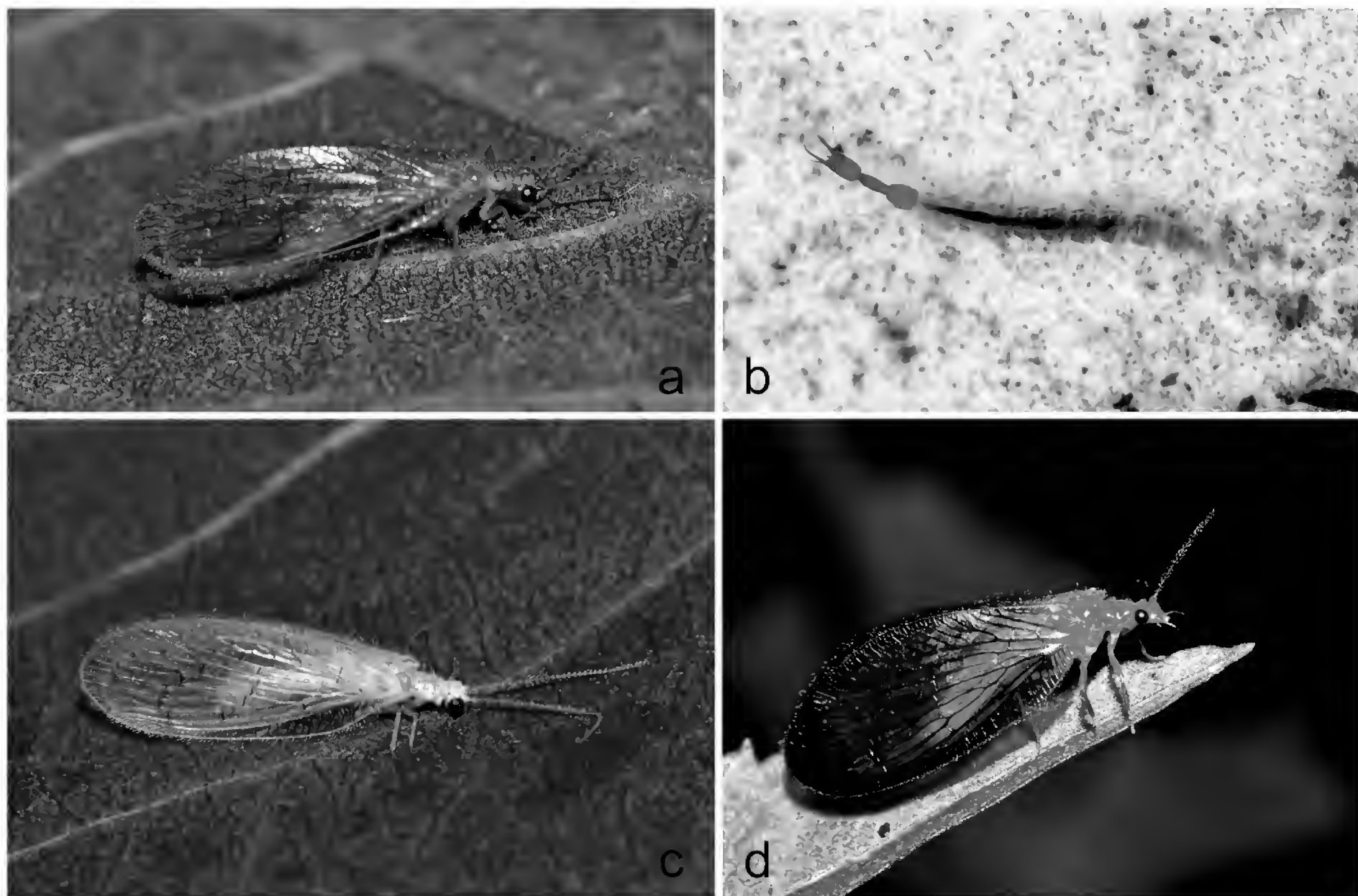


Figure 2. Photographs of living nevrorthids. **a** *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, female, Italy: Friuli (Photo P. Sehnal) **b** *Nevrorthus apatelios*, larva, Italy: Friuli (Photo F. Denner (former Anderle) **c** *Nipponeurorthus fuscinervis* (Nakahara), female, Japan, Hokkaido (Photo X. Liu) **d** *Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, female holotype, China, Yunnan (Photo H. Li).

Nipponeurorthus damingshanicus Liu, U. Aspöck & U. Aspöck

Nipponeurorthus fasciatus Nakahara, 1958

Nipponeurorthus flinti U. Aspöck & H. Aspöck, 2008

Nipponeurorthus furcatus Liu, H. Aspöck & U. Aspöck, 2014

Nipponeurorthus fuscinervis (Nakahara, 1915)

Nipponeurorthus multilineatus Nakahara, 1966

Nipponeurorthus pallidinervis Nakahara, 1958

Nipponeurorthus punctatus (Nakahara, 1915)

Nipponeurorthus tinctipennis Nakahara, 1958

Sinoneurorthus yunnanicus Liu, H. Aspöck & U. Aspöck, 2012

Laboratory techniques

Photographs of living adults were made with a Nikon D300 or D90 with a Nikon AF Micro-NIKKOR 105mm f/2.8D lens and Nikon macro flash -Kit R1 (Figs 1a, c, d). The photograph of the larva was made with a Canon EOS 350D (Fig. 1b).

Stacked digital images (Figs 1, 3, 4a, f–h) were taken with a Leica DFC camera attached to a Leica MZ16 binocular microscope and processed with the help of Leica Application Suite. They were then stacked with Zerene Stacker 64-bit and processed with Adobe Photoshop Elements 8. Other images (Figs 4b–e, i–k) were made with a Nikon D800 attached with a Nikon AF Micro-NIKKOR 105mm f/2.8D lens.

Illustrations

Genitalic preparations in connection with redescrptions were made by clearing the apex of the abdomen in a cold saturated KOH solution for 3 h. After rinsing the KOH with acetic acid and water, the apex of the abdomen was transferred to glycerine for further dissection and examination. Drawings of the genitalia were made with a camera lucida of a Leica WILD M 10 at the NHMW and with a Leica S8 APO at the CAU. The genital structures were interpreted and labelled on the basis of the gonocoxite-concept hypothesized by U. Aspöck and H. Aspöck (2008a, b).

Distribution maps were provided with ArcMap ver. 10.3.1.4959 based on the distribution records provided in the Supplementary material 1. Source of the maps: National Geographic-Weltkarte – Content may not reflect National Geographic's current map policy. Sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.

Redescrptions

In the redescrptions of the species the homology hypotheses and the terminology of the genital sclerites developed by U. Aspöck and H. Aspöck (2008a, b) are applied.

Character description and phylogenetic analysis

The present phylogenetic analysis aimed to reconstruct the intergeneric phylogeny of Nevrorthidae. Morphological characters were used for the phylogenetic inference. Thirty-one characters were coded with 27 binary and four multistate (see Supplementary material 2). The character matrix can be found in Supplementary material 3. All characters were treated as unordered and with equal weight. The multistate characters were treated as additive. *Italoraphidia solariana* (Navás, 1928) (Raphidioptera: Raphidiidae) and *Megalomus tortricoides* Rambur, 1842 (Neuroptera: Hemerobiidae) were selected as the outgroup taxa. The ingroup taxa include all extant and fossil species of Nevrorthidae previously described. However, two species of *Nipponeurorthus* (i.e., *Ni. qinicus* and *Ni. tinctipennis*) and one species of *Proberotha* (i.e., *P. dichotoma*), which lack a large amount of data, were excluded for an additional analysis. Analyses were performed using NONA ver. 2.0 (Goloboff 1993) with a heuristic search. Maximum number of trees to keep was set to 10000 and the number of replications to 100. The bootstrap branch support values were calculated in NONA ver. 2.0. Character states were mapped on the strict consensus tree using WinClada ver. 1.00.08 (Nixon 2002), showing only unambiguous changes.

Results

Taxonomy

List of abbreviations

anat (anatomy), annotcat (annotated catalogue), biogeogr (biogeography), biol (biology), cat (catalogue), charact (characteristics), com (comment), compmorphol (comparative morphology), descr (description), distr (distribution), distrmap (distribution map or maps), ecol (ecology), fig (figure), gs (genital segments), key (identification key), la (larvae), list (listed or mentioned), mon (monograph), nom (nomenclature), odescr (original description), overv (overview), phyl (phylogeny), pu (pupae), rec (record), syn (synonymisation), syst (systematics), tax (taxonomy).

Acronyms of institutions

Entomological Museum, China Agricultural University, Beijing, China (CAU); National Science Museum, Tokyo, Japan (NSMT); Australian Museum, Sydney, Australia (AMS); Australian National Insect Collection, Canberra, Australia (CSIRO); Smithsonian Institution, National Museum of Natural History, Washington D.C., USA (NMNH); Texas A & M University, College Station, Texas, USA (TAM); Zoologisk Museum, Copenhagen, Denmark (ZMC); Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany

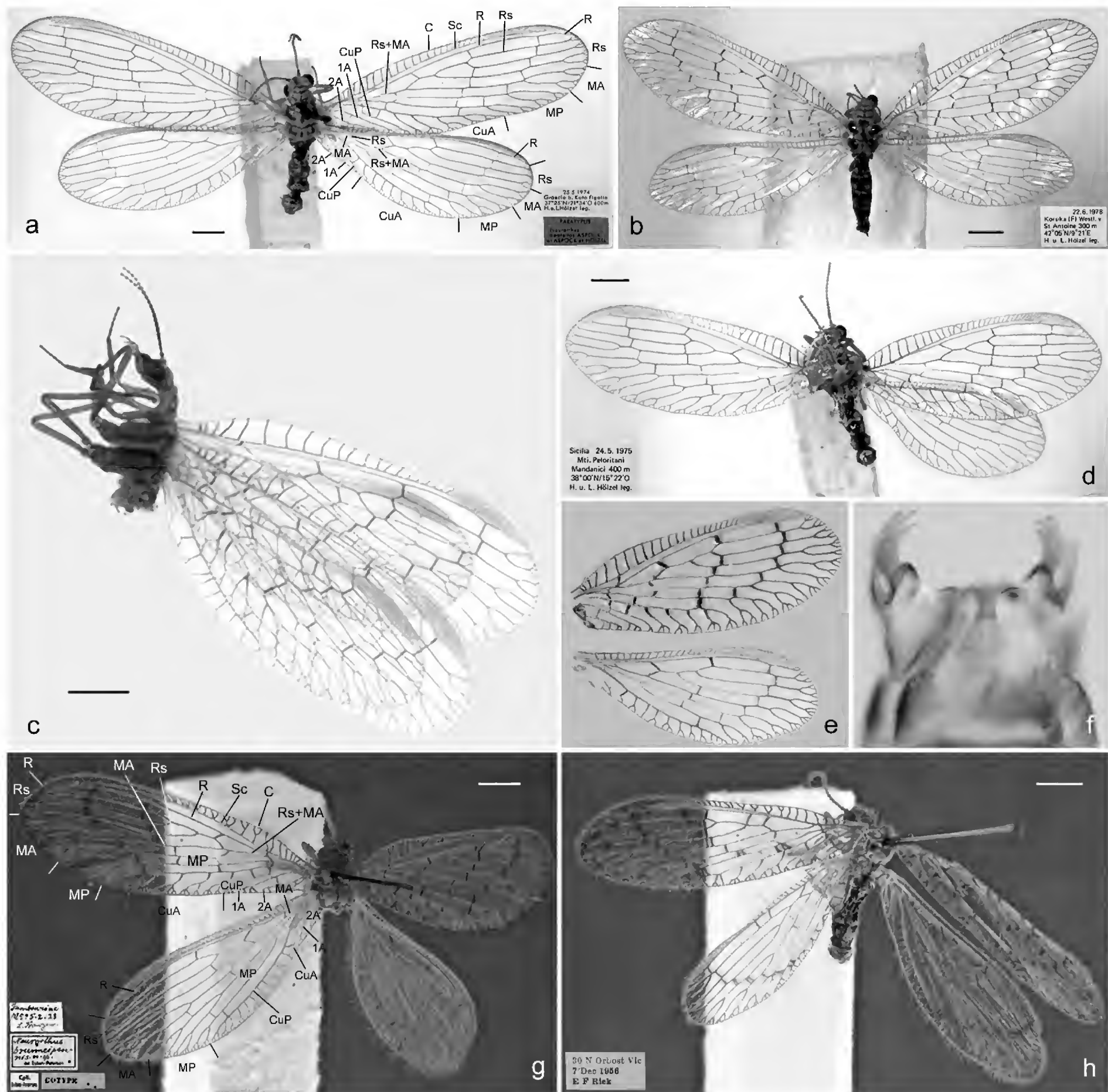


Figure 3. Wings and genital segments of representatives of the genera *Nevrorthus* Costa and *Austroneurorthus* Nakahara. **a** *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, male paratype, Greece: Peloponnesus/Peloponnese (Photo H. Bruckner) **b** *Nevrorthus fallax* (Rambur), female, Italy: Sardinia (Photo H. Bruckner) **c** *Nevrorthus hannibal* U. Aspöck & H. Aspöck, male holotype, Tunisia: S Ain Draham (Photo H. Bruckner) **d** *Nevrorthus iridipennis* Costa, male, Italy: Sicilia (Photo H. Bruckner) **e–f** *Nevrorthus reconditus* Monserrat & Gavira **e** right fore- and hindwing **f** male genital segments, ventral, Spain: Malaga (adapted from Monserrat and Gavira 2014) **g** *Austroneurorthus brunneipennis* (Esben-Petersen), male paratype, Australia: Tambourine Mt. (Photo H. Bruckner) **h** *Austroneurorthus horstaspoECKi* U. Aspöck, male, Australia: Victoria (Photo H. Bruckner). **Abbreviations.** A – Analis; C – Costa; CuA – Cubitus anterior; CuP – Cubitus posterior; MA – Media anterior; MP – Media posterior; R – Radius; Rs – Radial sector; Sc – Subcosta. Scale bar: 1.0 mm.

(MFN); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); Museo Zoologico dell'Università di Napoli Federico II, Naples, Italy (MZUN); Collection of Horst & Ulrike Aspöck, Vienna, Austria (HUAC); Collection of Victor Monserrat, Madrid, Spain (VM); Collection of Fumio Hayashi, Tokyo, Japan (HFC).

Neurorthidae Nakahara, 1915

Neurorthini Nakahara, 1915: 14 (nom).

Neurorthinae Nakahara: Nakahara 1958 (mon, nom).

Neurorthidae Nakahara: Zwick 1967 (la, compmorphol, syst); Gaumont 1968 (compmorphol la); Riek 1970

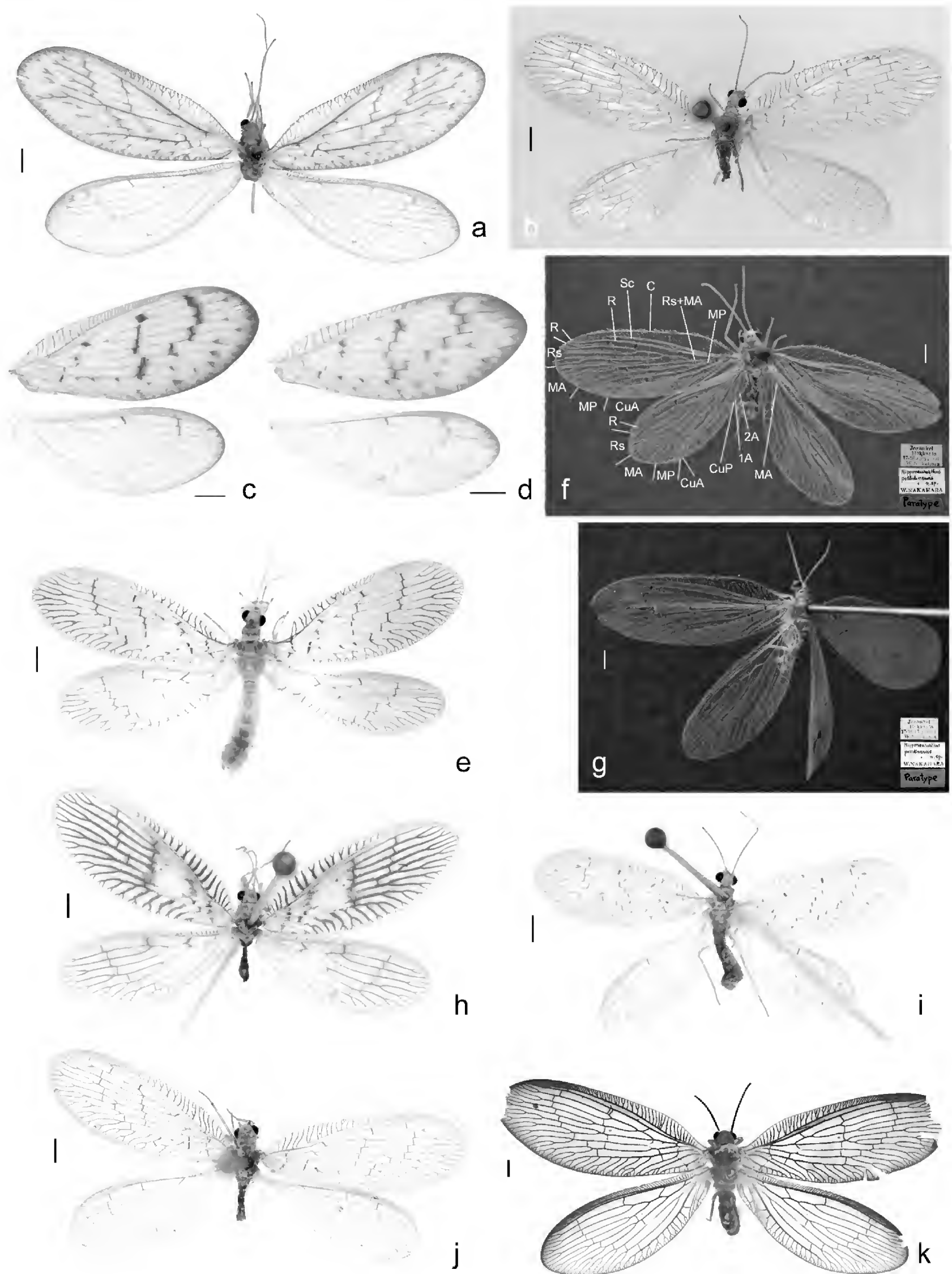


Figure 4. Wings of representatives of the genera *Nipponeurorthus* Nakahara and *Sinoneurorthus* Liu, H. Aspöck & U. Aspöck. **a.** *Nipponeurorthus fasciatus* Nakahara, male, Taiwan: Nantou (Photo H. Bruckner); **b.** *Nipponeurorthus fuscinervis* (Nakahara), Japan: Aomori (Photo X. Liu); **c.** *Nipponeurorthus damingshanicus* Liu, H. Aspöck & U. Aspöck, female paratype, China: Guangxi (Photo X. Liu); **d.** *Nipponeurorthus furcatus* Liu, H. Aspöck & U. Aspöck, male paratype, China: Yunnan (Photo X. Liu); **e.** *Nipponeurorthus flinti* U. Aspöck & H. Aspöck, male, Japan: Amamioshima (Photo X. Liu); **f-g.** *Nipponeurorthus pallidinervis* Nakahara, **f.** male paratype, **g.** female paratype, Japan: Hokkaido (Photo H. Bruckner); **h.** *Nipponeurorthus multilineatus* Nakahara, male, Taiwan (Photo H. Bruckner); **i.** *Nipponeurorthus punctatus* (Nakahara), male, Japan (Photo X. Liu); **j.** *Nipponeurorthus tinctipennis* Nakahara, male, Japan: Yakushima Island (Photo X. Liu); **k.** *Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, female holotype, China: Yunnan (Photo X. Liu). **Abbreviations.** **A** – Analis; **C** – Costa; **CuA** – Cubitus anterior; **CuP** – Cubitus posterior; **MA** – Media anterior; **MP** – Media posterior; **R** – Radius; **Rs** – Radial sector; **Sc** – Subcosta. Scale bars: 1.0 mm.

(charact); Gaumont 1976 (compmorphol la); Monserrat 1977 (nom, list); H. Aspöck et al. 1978 (charact); New 1978 (ecol la); H. Aspöck et al. 1980 (mon); Henry 1982 (charact); Gepp 1984 (tax la); Malicky 1984 (biol, ecol); New 1986 (charact, biol), 1989 (tax), 1991 (charact, tax, tax la); U. Aspöck 1995 (phyl); Güsten 1996 (compmorphol); New 1996 (cat: Australia); Wachmann and Saure 1997 (tax, tax la).

Nevrorthidae Nakahara: Oswald and Penny 1991 (list, nom); U. Aspöck 1995 (phyl); H. Aspöck and Hölzel 1996 (overv); U. Aspöck and H. Aspöck 1999 (overv); H. Aspöck et al. 2001 (annotcat); U. Aspöck et al. 2001 (phyl); U. Aspöck and H. Aspöck 2007 (biogeogr, distrmap, figs: gs males); Monserrat and Gavira 2014 (distrmap).

Remarks. The Nevorthidae are a species-poor relic family with an extremely vicariant distribution pattern (Fig. 17) of its four extant and five extinct genera: *Nevorthus* Costa, 1863, comprising five disjunctively scattered Mediterranean species: *N. iridipennis* Costa, 1863 (Italy: Calabria, Sicily), *N. apatlios* H. Aspöck, U. Aspöck & Hölzel, 1977 (Balkan Peninsula, Romania, northern Italy: Friuli, and Slovenia), *N. fallax* (Rambur, 1842) (France: Corsica, Italy: Sardinia), *N. hannibal* U. Aspöck & H. Aspöck, 1983 (Algeria, Tunisia), *N. reconditus* Monserrat & Gavira, 2014 (Spain: Malaga); *Austroneurorthus* Nakahara, 1958, comprising two species, restricted to southeastern parts of Australia: *A. brunneipennis* (Esben-Petersen, 1929) (southeastern Queensland, New South Wales), *A. horstaspoeki* (U. Aspöck, 2004) (Victoria, New South Wales); *Nipponneurorthus* Nakahara, 1958, comprising eleven species, distributed in China and Japan: *Ni. damingshanicus* Liu, H. Aspöck & U. Aspöck, 2014 (China: Guangxi), *Ni. fasciatus* Nakahara, 1958 (China: Taiwan), *Ni. flinti* U. Aspöck & H. Aspöck, 2008 (Japan: Okinawa, Amamiyoshima), *Ni. furcatus* Liu, H. Aspöck & U. Aspöck, 2014 (China: Yunnan), *Ni. fuscinervis* (Nakahara, 1915) (Japan: Hokkaido, Honshu), *Ni. multilineatus* Nakahara, 1966, (China: Taiwan), *Ni. pallidinervis* Nakahara, 1958 (Japan: Hokkaido, Honshu, Kyushu, Tsushima Island), *Ni. punctatus* (Nakahara, 1915) (Japan: Honshu, Hokkaido, Kyushu, Yakushima), *Ni. qinicus* Yang in Chen, 1998 (China: Shaanxi), *Ni. tianmushanus* Yang & Gao, 2001 (China: Zhejiang), *Ni. tinctipennis* Nakahara, 1958 (Japan: Yakushima); *Sinoneurorthus* Liu, H. Aspöck & U. Aspöck, 2012, so far comprising only one described species, *S. yunnanicus* Liu, H. Aspöck & U. Aspöck, 2012 (China: Yunnan).

Extinct taxa from the Eocene Baltic amber are assigned to the monotypic genus *Rophalis* Hagen, 1856, with *R. relictata* (Hagen in Berendt, 1845-1856), *Electroneurorthus* Wichard, Buder & Caruso, 2010, comprising *E. malickyi* Wichard, Buder & Caruso, 2010, *Palaeoneurorthus* Wichard, 2009, comprising *P. bifurcatus* Wichard, 2009, *P. hof-feinsorum* Wichard, 2009, *P. groehni* Wichard, Buder & Caruso, 2010, *P. eocaemus* Wichard, 2016, *Balticoneurorthus* Wichard, 2016, with *B. elegans* Wichard, 2016, and *Proberotha* Krüger, 1923, comprising *Pr. prisca* Krüger, 1923, and *Pr. dichotoma* Wichard, 2016.

Nevorthidae are alternately addressed as enigmatic or mysterious – but why? The adults look rather inconspicuous and may even be frequent if one searches for them at the right place and at the right time. Even the cryptic larvae, which inhabit sandy and stony grounds of rivulets may be frequent if one searches for them at the right place and at the right time. The aquatic pupae are certainly unique among Neuropterida, but neither enigmatic nor mysterious. The secret around the mystery concerning Nevorthidae may be their isolated existence in hidden mountainous rivulets and the hypothesis that there are hitherto undiscovered remote relic places harbouring populations of known or still unknown species.

Genus *Nevorthus* Costa, 1863

Nevorthus Costa, 1863: 32 (odescr) [Type species: *Mucropalpus fallax* Rambur, 1842, by subsequent designation]:

Leraut 1981 (nom); Oswald and Penny 1991 (nom); H. Aspöck et al. 2001 (annotcat); U. Aspöck and H. Aspöck 2007 (biogeogr, distrmap); U. Aspöck and H. Aspöck 2008a (compmorphol, figs: gs female); U. Aspöck and H. Aspöck 2010a (overview, biogeogr, fig: distrmap); Gavira et al. 2012 (com); Monserrat and Trivino 2013 (com); Monserrat and Gavira 2014 (distrmap).

Neurorthus Costa (unjustified emendation): McLachlan 1881 (nom); Nakahara 1915 (charact); Klapálek 1917 (descr); Navás 1935 (mon); Parfin and Gurney 1956 (mon); Nakahara 1958 (charact); Zwick 1967 (fig: la, compmorphol, syst); Tjeder 1979 (compmorphol); H. Aspöck et al. 1980 (mon); Malicky 1984 (biol, ecol, distr); Oswald and Penny 1991 (nom); Wichard et al. 1995 (fig pu); Wachmann and Saure 1997 (key).

Sartena Hagen, 1864: 41 (odescr) [Type species: *Sartena amaena* Hagen, 1864, by monotypy]: McLachlan 1881 (nom); H. Aspöck et al. 1980 (syn); Oswald and Penny 1991 (nom).

Diagnosis. Adults of small body size; male forewing length 6–8 mm. Body coloration greyish-brownish. Forewings transparent to pale yellowish, crossveins sometimes dark and shaded. Costal cross veins of forewings not forked. Hindwing MA and anterior branch of MP forked distal to outer series of gradate cross veins. Male: Abdominal segment 7 enlarged. A ring-like zone of glands present between male abdominal segments 7 and 8. Abdominal eversible sacks present between segments 6 and 7. Male sternite 9 long, strongly extending posteriad; gonocoxites 9 as huge plates with digitiform gonostyli 9 and processus-like gonapophyses; complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally; gonocoxites 11 fused into a bow-like bridge. Female: Fused gonocoxites 8 forming a broad trapezoid sclerite; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Distribution. Mediterranean region.

***Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, 1977**

Figs 2a–b; 3a; 5a–e; 6c; 14

Nevrorthus iridipennis auct. nec Costa (misidentification): Klapálek 1917 (syst, distr); Pongracz 1923 (distr); Zelený 1964 (rec); 1971 (rec).

Nevrorthus apatelios H. Aspöck, U. Aspöck & Hölzel, 1977: 54 (odescr, figs: gs male); H. Aspöck et al. 1978 (distr); H. Aspöck et al. 1980 (mon); U. Aspöck and H. Aspöck 1983 (distr); Malicky 1984 (ecol, distr); Saure 1989 (distr); Popov 1990 (distr); 1991 (rec); 1992 (distr); Devetak 1992 (distr); Popov 1993 (distr);

Nevrorthus apatelios: H. Aspöck and Hölzel 1996 (distr); U. Aspöck and H. Aspöck 1999 (fig); H. Aspöck et al. 2001 (annotcat); Devetak and Jakšič 2003 (distr); Letardi et al. 2006 (distr, biol); U. Aspöck and H. Aspöck 2007 (figs: adult, distrmap); Popov 2007 (distr, biol); U. Aspöck and H. Aspöck 2008a (compmorphol, fig: gs female); Sziráki 2008 (rec, distr); Jones and Devetak 2009 (distr); U. Aspöck and H. Aspöck 2010a (biogeogr, fig: distrmap); Monserrat and Gavira 2014 (figs: gs, head, thorax); Devetak and Klokočovník 2016 (biol).

Type locality. Greece (Euboea: S Prokopion).

Male. Body length 2.2 mm; forewing length 6.0–7.5 mm, hindwing length 5.5–6.5 mm.

Head yellowish. Antennae pale yellow, scapus and pedicellus brownish. Mouthparts yellow.

Prothorax yellow; meso- and metathorax darker. Legs yellow. Wings hyaline, membrane uncoloured; forewing veins yellowish; hindwing veins pale yellow, paler than in forewing.

Abdomen dorsally dark brown with yellow pattern, ventrally yellowish. Gonocoxites 9 as huge plates, gonostyli 9 digitiform, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally, terminally rounded. Gonocoxites 11 fused into a bow-like bridge.

Female. Body length 2.4 mm; forewing length 7.4–7.9 mm, hindwing length 7.6–7.8 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; fused gonapophyses 8 triangular; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): “Griechenland, Euboea, S von Prokopion, 38°42’N / 23°30’E, 250 m, 24.5.1974, H. Malicky leg.” (HUAC).

Biology and ecology. Adults have been taken from May to October, most specimens were collected in June and July. The known vertical distribution is 90–1400 m. The larva is found in mountain rivers (the temperature of inhabited brooks varied from 11.9–21.5°C).

Distribution. Albania, Bosnia-Herzegovina, Bulgaria, Greece, Italy, Kosovo, Macedonia, Romania, Serbia, Slovenia.

***Nevrorthus fallax* (Rambur, 1842)**

Figs 3b; 6a, f–g; 14

Mucropalpus fallax Rambur, 1842: 422 (odescr).

Sartena amaena Hagen, 1864: 41 (odescr). McLachlan 1881 (nom).

Nevrorthus fallax (Rambur): McLachlan 1881 (nom); 1898 (com); Klapálek 1917 (descri, distr, figs: wings, gs male); Esben-Petersen 1913 (distr); Lestage 1924 (syst); Kimmins 1930 (distr); Nakahara 1958 (character, figs wings, gs male, female); Zwick 1967 (ecol, compmorphol, syst, figs: gs male, la); Gaumont 1976 (anat); H. Aspöck et al. 1977 (tax); Tjeder 1979 (tax); H. Aspöck et al. 1980 (mon); U. Aspöck and H. Aspöck 1983 (distr); Malicky 1984 (ecol, distr, tax, figs: la); Letardi 1994 (distr).

Nevrorthus fallax (Rambur): Leraut 1981 (distr); Pantaleoni 1994 (distr); Iori et al. 1995 (distr); H. Aspöck and Hölzel 1996 (distr); U. Aspöck and H. Aspöck 1999 (fig: la); H. Aspöck et al. 2001 (annotcat); U. Aspöck and H. Aspöck 2007 (fig: distrmap); Letardi et al. 2008 (rec); U. Aspöck and H. Aspöck 2010a (biogeogr, fig: distrmap); Monserrat and Gavira 2014 (figs: gs, adult).

Type locality. Italy (Sardinia).

Male. Body length 2.2 mm; forewing length 6.0–8.0 mm, hindwing length 5.5–6.5 mm.

Head yellowish, dark brown line at middle. Antennae pale yellow, scapus and pedicellus brownish. Mouthparts yellow.

Prothorax yellow; meso- and metathorax darker. Legs yellow. Wings hyaline, membrane uncoloured; forewing veins yellowish; hindwing veins pale yellow, paler than in forewing.

Abdomen dorsally dark brown with yellow pattern, ventrally brown. Gonocoxites 9 as huge plates, gonostyli 9 digitiform, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally, terminally sinuated. Gonocoxites 11 fused into a bow-like bridge.

Female. Body length 2.4 mm; forewing length 7.4–7.9 mm, hindwing length 7.6–7.8 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; fused gonapophyses 8 triangular; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Specimens examined and records published. Supplementary material 1. Original type(s) lost. Herewith, a male is designated as neotype: “6.6.–11.6. 1978, Sardinien (I) Monti di Gennargentu 700m 40°06’N / 9°32’E, H.u.L. Hölzel leg.” (NHMW).

Biology and ecology. Adults have been taken from March–October, most specimens were collected in June. The known vertical distribution is 70–1050 m. The larva is known and has been described (Zwick 1967). Larvae inhabit the stony bottom of cold (5–10°C) swiftly running

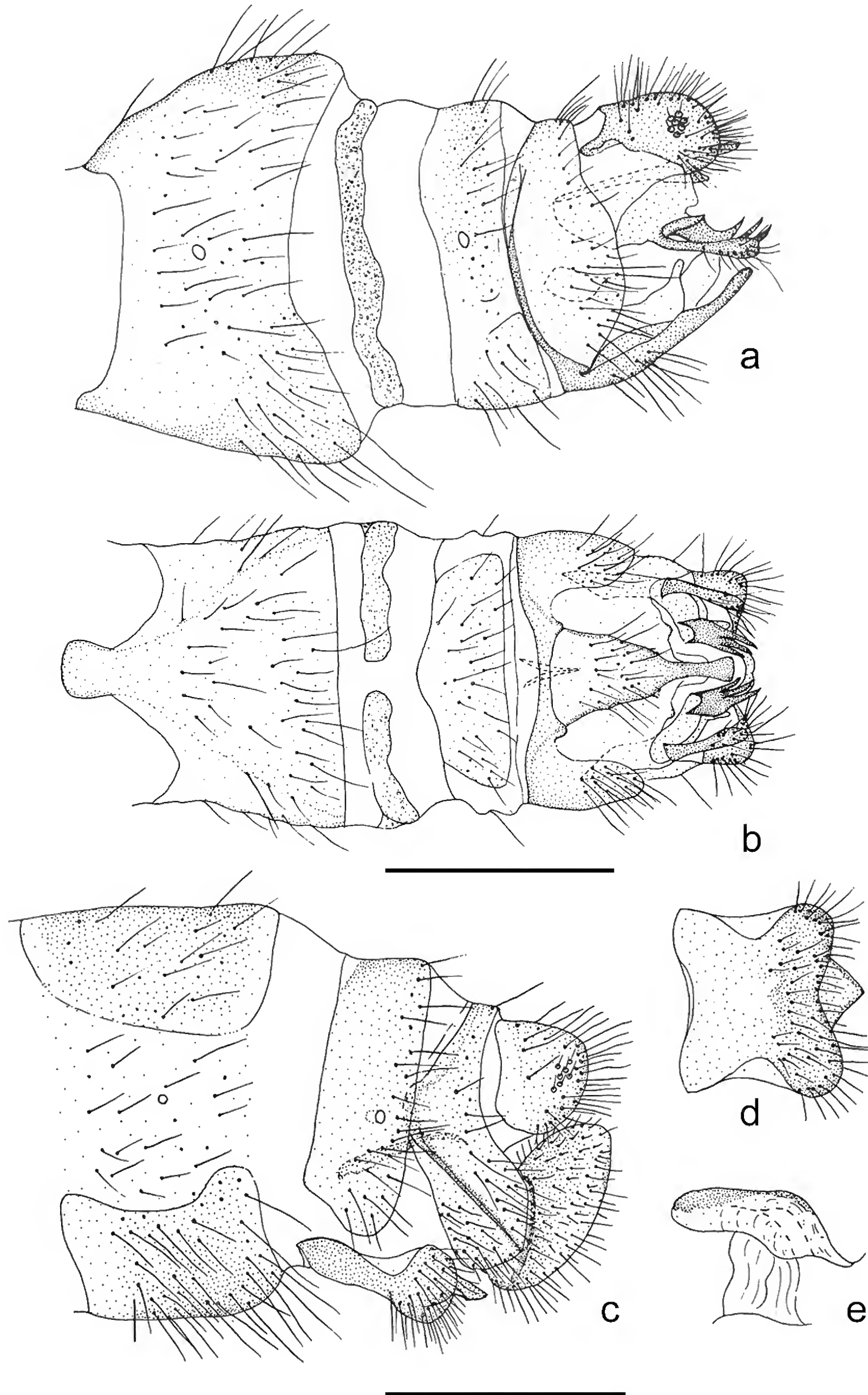


Figure 5. *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel. **a.** Male, genital segments, lateral; **b.** Same, ventral; **c.** Female, genital segments, lateral; **d.** Gonocoxites 8 and gonapophyses 8, ventral; **e.** Bursa copulatrix, lateral. Scale bars: 0.5 mm.

mountain brooks (Zwick 1967). We have, however, found the species in Sardinia also at the estuary of a river a few meters above sea level. Malicky (1984) reports findings of larvae in waters with temperature 10.7–20.1°C (Sardinia) and 8.6–21.4°C (Corsica).

Distribution. Italy (Sardinia), France (Corsica).

Nevrothus hannibal U. Aspöck & H. Aspöck, 1983

Figs 3c; 6d–e; 6h–i; 14

Neurothus fallax McLachlan nec Rambur (misidentification: McLachlan 1898 (com))

Neurothus iridipennis Klapálek nec Costa: Klapálek 1917 (com).

Neurothus hannibal U. Aspöck & H. Aspöck, 1983 (odescr, figs: gs male, female, distrmap); Malicky 1984 (rec, ecol).

Neurothus hannibal: H. Aspöck and Hölzel 1996 (distr); H. Aspöck et al. 2001 (annotcat); U. Aspöck and H. Aspöck 2007 (fig: distrmap); U. Aspöck and H. Aspöck 2010a (biogeogr, fig: distrmap); Monserrat and Gavira 2014 (figs: gs, forewing, head and thorax).

Type locality. Tunisia (S Ain Drahem).

Male. Body length 2.2 mm; forewing length 7.0–8.0 mm, hindwing length 5.5–6.5 mm.

Head yellowish, vertex caudally darker. Antennae pale yellow, scapus and pedicellus brownish. Mouthparts yellow.

Prothorax yellow; meso- and metathorax darker. Legs yellow. Wings hyaline, membrane uncoloured; forewing veins yellowish; hindwing, veins pale yellow, paler than in forewing.

Abdomen dorsally brown with yellow pattern, ventrally yellowish with only a few brownish spots. Gonocoxites 9 as huge plates, gonostyli 9 digitiform, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally, terminally with short incision. Gonocoxites 11 fused into a bow-like bridge.

Female. Body length 2.4 mm; forewing length 7.2–8.2 mm, hindwing length 7.6–7.8 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; fused gonapophyses 8 triangular; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): “Tunesien, 4 km S Ain Drahem, 36°43’N / 8°40’E, 530 m, 17.–18.V.1982 (T6), H. Malicky leg.” (HUAC).

Biology and ecology. Adults have been taken from April–June; most specimens were collected in May. The known vertical distribution is 336–530 m. Larvae were found in small brooks. Temperature of inhabited brooks varied from 13.6–15.7°C (Malicky 1984).

Distribution. Tunisia, Algeria.

Nevrothus iridipennis Costa, 1863

Figs 1; 3d; 6b; 14

Neurothus iridipennis Costa, 1863: 33 (odescr, fig: wings); Iori et al. 1995 (distr); H. Aspöck and Hölzel 1996 (distr); Letardi and Pantaleoni 1996 (distr); Pantaleoni 1999 (lectotype); H. Aspöck et al. 2001 (annotcat); Pantaleoni 2005 (com); U. Aspöck and H. Aspöck 2007 (fig: distrmap); U. Aspöck and H. Aspöck 2010a (fig: distrmap); Nicoli Aldini et al. 2012 (com); Monserrat and Gavira 2014 (figs: gs, head, thorax).

Neurothus iridipennis Costa: McLachlan 1881 (nom); 1898 (com); Klapálek 1917 (descr, distr, figs: gs male, female); Lestage 1924 (sys); Nakahara 1958 (com); Principi 1966 (distr, rec); H. Aspöck et al. 1977 (tax); H. Aspöck et al. 1980 (mon); U. Aspöck and H. Aspöck 1983 (distr); Malicky 1984 (ecol, biol, distr, rec; figs: cocoon, pu); Monserrat 1985 (nom); Letardi 1994 (distr); Wichard et al. 1995 (fig: pu); Nicoli Aldini et al. 2012 (rec).

Type locality. Italy (Calabria).

Male. Body length 2.25 mm; forewing length 6.5 mm, hindwing length 5.5–6.5 mm.

Head yellowish, vertex caudally darker. Antennae pale yellow, scapus and pedicellus brownish. Mouthparts yellow.

Prothorax yellow; meso- and metathorax darker. Legs yellow. Wings hyaline, membrane uncoloured; forewing veins yellowish; hindwing veins pale yellow, paler than in forewing.

Abdomen dorsally brown with yellow pattern, ventrally yellowish with only a few brownish spots. Gonocoxites 9 as huge plates, gonostyli 9 digitiform, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally, terminally deeply forked. Gonocoxites 11 fused into a bow-like bridge.

Female. Body length 2.4 mm; forewing length 7.2–8.2 mm, hindwing length 7.6–7.8 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; fused gonapophyses 8 triangular; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Specimens examined and records published. Supplementary material 1. Lectotype female (by explicit designation): Calabria, Reggio Calabria “Valli di Aspromonte” (MZUN), Pantaleoni (designated 1993, published 1999).

Biology and ecology. Adults have been taken from May–July; most specimens were collected in May. The known vertical distribution is 354–1350 m. The larva is known and has been described (Malicky 1984), the temperature of inhabited brooks measured varied from 7.9–23.8°C.

Distribution. Italy (Calabria, Sicily).

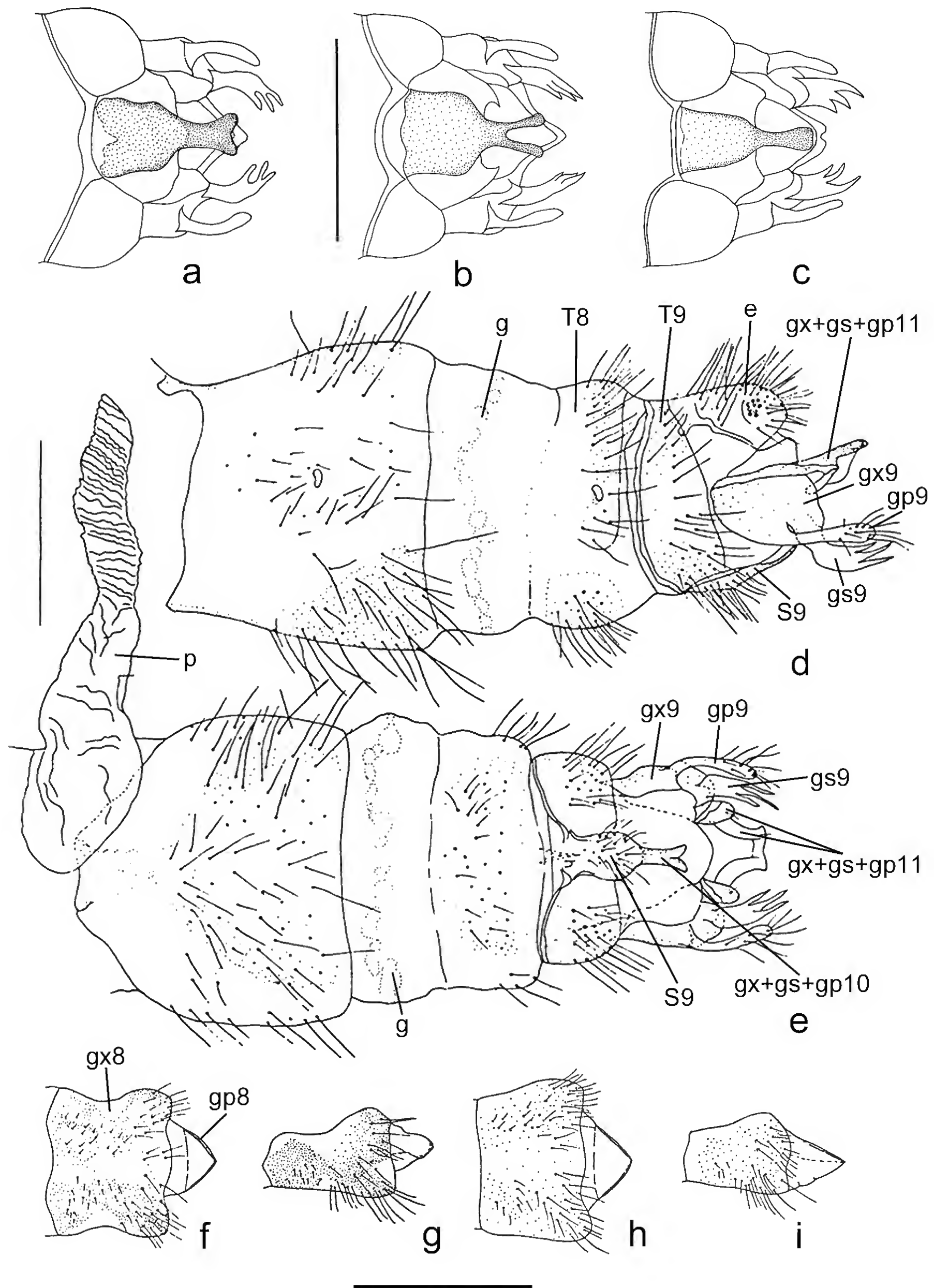


Figure 6. Male genital segments of *Nevrorthus* spp. **a** *Nevrorthus fallax* (Rambur), ventral **b** *Nevrorthus iridipennis* Costa, ventral **c** *Nevrorthus apatlios* H. Aspöck, U. Aspöck & Hölzel, ventral **d–e** *Nevrorthus hannibal* U. Aspöck & H. Aspöck, male holotype: **d** lateral **e** ventral **f–g** *Nevrorthus fallax* (Rambur), female: **f** gonocoxites 8 and gonapophyses 8, ventral **g** lateral **h–i** *Nevrorthus hannibal* U. Aspöck & H. Aspöck, female: **h** gonocoxites 8 and gonapophyses 8, ventral **i** lateral. **Abbreviations.** **e** – ectoproct; **g** – ring of glands; **gp** – gonapophysis; **gs** – gonostylus; **gx** – gonocoxite; **p** – pleuriticava; **S** – sternite; **T** – tergite. Scale bars: 0.5 mm.

***Nevrorthus reconditus* Monserrat & Gavira, 2014**

Figs 3e–f; 14

Nevrorthus reconditus Monserrat & Gavira, 2014: 352 (odescr, figs: wings, gs male, la, distrmap).**Type locality.** Spain (Malaga: Coín, Sierra Alpujata).**Male.** Forewing length 6.1 mm, hindwing length 5.1 mm.

Head very pale brown. Antennae pale yellow, scapus and pedicellus brownish, basal two thirds of flagellum pale brownish, apically darker. Mouthparts brownish.

Pronotum pale brownish, with irregular darker pattern; meso-metanotum pale brownish with dark brown patches. Legs brownish. Wings hyaline, membrane uncoloured; forewing veins brownish, crossveins very dark and with dark shadows; hindwing veins brownish, crossveins partly with shadow.

Abdomen with tergites and sternites irregularly brownish pigmented. Gonocoxites 9 as huge plates, gonostyli 9 digitiform, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally, terminally sinuate. Gonocoxites 11 fused into a bow-like bridge.

Female. Forewing length 6.4–6.7 mm, hindwing length 5.8–6.0 mm.

Text adapted from Monserrat and Gavira (2014): Tergite 9 with a small circular emargination on the caudal margin. Fused gonocoxites 8 forming a broad sclerite with external margins straight; gonocoxites 9 narrow and digitiform.

Specimens examined by Monserrat and Gavira (2014), see there and Supplementary material 1. Holotype male (by original designation): “Spain, Malaga, Coín, Sierra Alpujata, Arroyo del Manzano, 30SUF35 (WGS84), 450 m, 13.V.2013, captured with a light trap in perennial stream covered by bushy willow gallery forest, T. Herrera, P. Carrasco & O. Gavira leg.” (VM).

Biology and ecology. Adults have been taken from April–May. The known vertical distribution is 150–450 m. The larva is known and has been described (Monserrat and Gavira 2014).**Distribution.** Spain (Malaga).**Genus *Austroneurorthus* Nakahara, 1958***Austroneurorthus* Nakahara, 1958: 29 (odescr) [Type species: *Neurorthus brunneipennis* Esben-Petersen, 1929, by original designation].*Austroneurorthus* Nakahara, 1958: New 1978 (com); U. Aspöck 2004 (distr); U. Aspöck and H. Aspöck 2007 (fig: distrmap); U. Aspöck and H. Aspöck 2010a (fig: distrmap).**Diagnosis.** Adults of small body size; male forewing length 6.0–8.0 mm, hindwing length 6.0–7.0 mm, female forewing length 7.8–9.0 mm, hindwing length 6.8–8.0 mm. Body coloration yellowish, with dark pattern or brownish. Forewings transparent, crossveins partly dark and shaded.

Costal crossveins of forewings partly forked. Hindwing MA and anterior branch of MP forked proximal to outer series of gradate crossveins. Male abdominal segment 7 not enlarged. A ring-like zone of glands present between male abdominal segments 8 and 9. Abdominal eversible sacks absent. Male sternite 9 long, strongly extending posteriad; gonocoxites 9 as huge plates without articulated gonostyli; gonapophyses 9 forming lobes; complex of gonocoxites + gonostyli + gonapophyses 10 amalgamated with sternite 9, forming a pseudoapex of the latter and framing it laterally; gonocoxites 11 fused into a broad sclerite. Fused female gonocoxites 8 forming a rectangular sclerite; gonocoxites 9 club-shaped, without distinct gonostyli; bursa copulatrix comprising a sclerotized structure.

Distribution. Australia.***Austroneurorthus brunneipennis* (Esben-Petersen, 1929)**

Figs 3g; 7a–c; 15

Neurorthus brunneipennis Esben-Petersen, 1929: 33 (odescr, fig: wings).*Austroneurorthus brunneipennis* (Esben-Petersen, 1929): Nakahara 1958 (nom, charact, figs: wings, gs male, female); U. Aspöck and H. Aspöck 2007 (Fig: distrmap).**Type locality.** Australia (Queensland: Tamborine Mt.).**Male.** Forewing length 7.0–8.0 mm, hindwing length 6.0–7.0 mm.

Head yellowish. Antennae and mouthparts yellowish.

Pronotum yellowish; meso-metanotum ochre. Legs yellowish. Wing membrane hyaline, in the original description it is characterised as “yellowish tinged; but the apical margin narrowly brownish shaded” (available material was, however, rather faded); forewing longitudinal veins brownish yellow, crossveins brownish, slightly shaded; hindwing paler than forewing, veins pale yellow.

Abdomen dorsally dark brown with yellow pattern, ventrally yellowish. Male: Gonocoxites 9 as huge plates, apically rounded, gonostyli 9 not discernible, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxites + gonostyli + gonapophyses 10 partly amalgamated with sternite 9, forming i) a pseudoapex of the latter which is deeply forked and ii) a paired hook. Gonocoxites 11 fused into a broad plate with a big median tooth.

Female. Forewing length 8.5 mm, hindwing length 8 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; gonocoxites 9 club-shaped, without distinct gonostyli.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): Australia: Queensland, “Tambourine Mt. 5/11/1928 (L. Franzen leg.)” (CSIRO).**Biology and ecology.** Adults have been taken from November–February. There is no data concerning the vertical distribution. The larva of *A. brunneipennis* is possibly known, however, it cannot be differentiated from that of *A. horstaspoecki* (see *Austroneurorthus* sp. in Fig. 15).**Distribution.** Australia (NSW, Queensland).

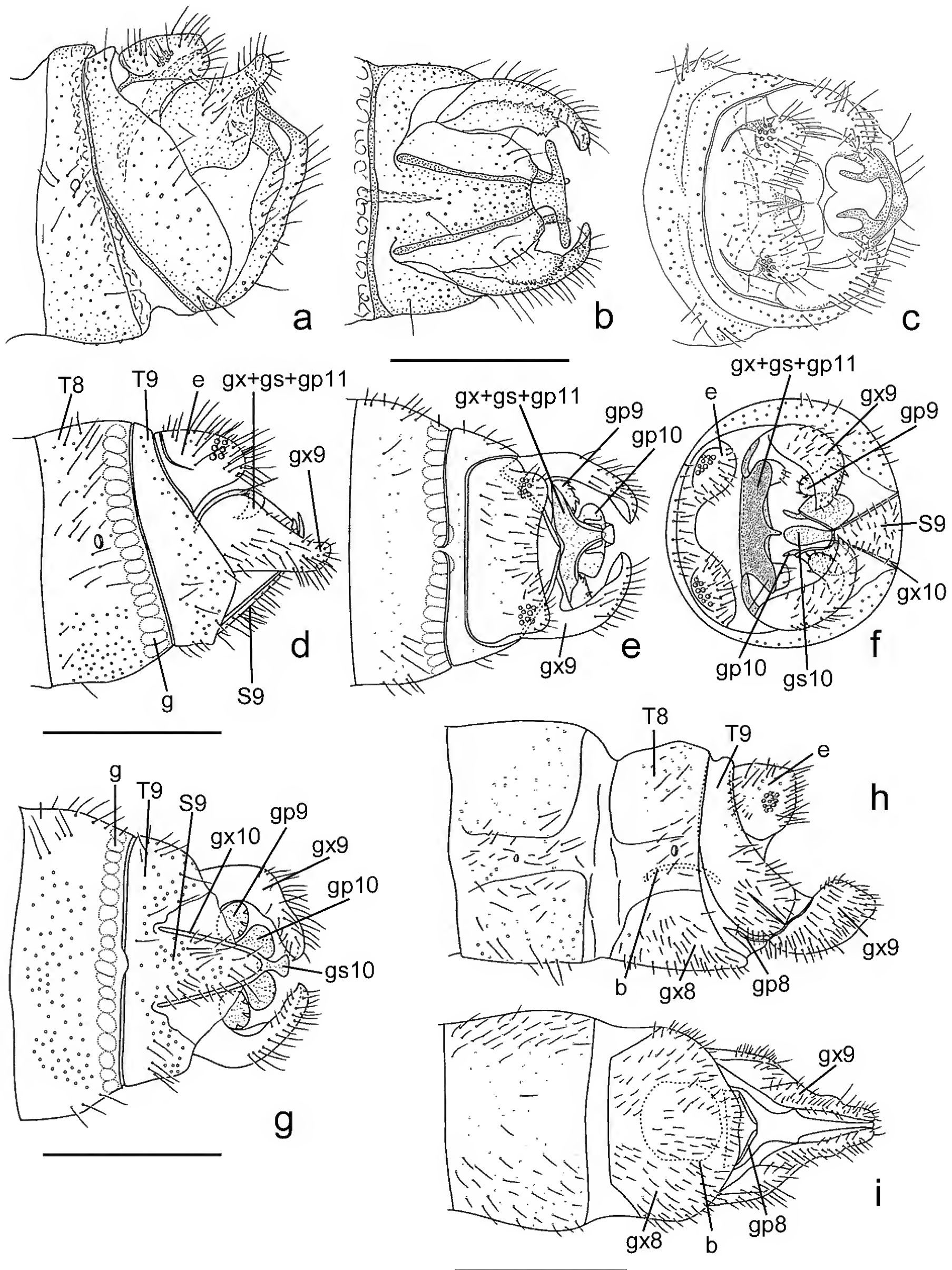


Figure 7. Genital segments of *Austroneurorthus* spp. **a–c** *Austroneurorthus brunneipennis* (Esben-Petersen), male paratype: **a** lateral **b** ventral **c** caudal **d–g** *Austroneurorthus horstaspoecki* U. Aspöck, male holotype, genital segments: **d** lateral **e** dorsal **f** caudal **g** ventral **h–i** *Austroneurorthus horstaspoecki* U. Aspöck, female paratype, genital segments: **h** lateral **i** ventral. **Abbreviations.** **b** – bursa copulatrix; **e** – ectoproct; **g** – ring of glands; **gp** – gonapophysis; **gs** – gonostylus; **gx** – gonocoxite; **S** – sternite; **T** – tergite. Scale bars: 0.5 mm.

***Austroneurorthus horstaspoecki* U. Aspöck, 2004**

Figs 3h; 7d–i; 15

Austroneurorthus horstaspoecki U. Aspöck, 2004: 177 (odescr); U. Aspöck and H. Aspöck 2008a (compmorphol, figs: gs male).

Type locality. Australia (Victoria: Aucheron R.).

Male. Forewing length 6.5–7.0 mm, hindwing length 5.5–6.0 mm.

Head yellowish. Antennae and mouthparts yellowish.

Pronotum yellowish; meso-metanotum ochre. Legs yellowish, femora on inner side with dark ovoid plate with smooth surface. Wing membrane hyaline, slightly smoky; forewing longitudinal veins yellowish, crossveins brownish, partly “shaded”. Hindwing paler than forewing, crossveins brownish.

Abdomen dorsally dark brown with yellow pattern, ventrally yellowish. Male: Gonocoxites 9 as huge plates, apically rounded, gonostyli 9 not discernible, gonapophyses 9 processus-like; ectoproct broadly rounded. Complex of gonocoxite + gonostylus + gonapophysis 10 partly amalgamated with sternite 9, forming i) a pseudoapex of the latter which is deeply forked and ii) a paired hook. Gonocoxites 11 fused into a broad plate with a large median tooth (fused gonostyli 11?).

Female. Forewing length 7.8–9.0 mm, hindwing length 6.8–8.0 mm.

Fused gonocoxites 8 forming a broad trapezoid sclerite; gonapophyses 8 fused to triangular sclerite; gonocoxites 9 club-shaped, without distinct gonostylus.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): “Australia, Vic. Aucheron R. Feb.1987 Zwick” (CSIRO).

Biology and ecology. Adults have been taken from December–February, with most specimens collected in February. There is no data concerning the vertical distribution. The larva of *A. horstaspoecki* is possibly known, however, it cannot be differentiated from that of *A. brunneipennis* (see the distribution of *Austroneurorthus* sp. in Fig. 15).

Distribution. Australia (Victoria, NSW).

Genus *Nipponeurorthus* Nakahara, 1958

Nipponeurorthus Nakahara, 1958: 25 (odescr) [Type species: *Nipponeurorthus pallidinervis* Nakahara, 1958: 25, by original designation].

Nipponeurorthus Nakahara: Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2007 (fig: distrmap); U. Aspöck and H. Aspöck 2010a (fig: distrmap); Liu et al. 2014 (overview, fig: distrmap).

Diagnosis. Adults of small body-size; male forewing length 6–10 mm. Body coloration generally yellow. Fore-

wings transparent to pale yellowish brown, sometimes with brown markings, sometimes with spectacular colour pattern. Costal crossveins of forewings at least partially forked in most species. Hindwing MA and anterior branch of MP forked distal to outer series of gradate crossveins in most species. Male abdominal segment 7 sometimes enlarged. A ring-like zone of glands sometimes present between male abdominal segments 8 and 9. Abdominal eversible sacks – as e.g. in *Nevrorthus* – are so far found only in *Nipponeurorthus fasciatus* (between segments 8 and 9). Male sternite 9 short, not strongly extending posteriorly; gonocoxites 9 present as a pair of robust claspers, terminally with gonostyli 9; complex of gonocoxites + gonostyli + gonapophyses 10 present as a pair of discrete sclerites with long blade-like, spinous, or claw-like distal lobes, free or more or less attached (or amalgamated respectively) with sternite 9, as lateral “frame” and terminal sclerites (appearing as a pseudoapex of sternite 9); gonocoxites 11 reduced to sclerite claspers which might represent the gonostyli 11, located between bases of gonocoxites 9. Fused female gonocoxites 8 broad, nearly twice as long as tergite 8; gonocoxites 9 foliate or club-shaped; bursa copulatrix comprising a sclerotized structure.

Distribution. China, Japan.

***Nipponeurorthus damingshanicus* Liu, H. Aspöck & U. Aspöck, 2014**

Figs 4c; 8a–f; 16

Nipponeurorthus damingshanicus Liu, H. Aspöck & U. Aspöck, 2014: 225 (odescr, key, figs: wings, gs male, female, distrmap).

Type locality. China (Guangxi: Mt. Damingshan).

Male. Body length 4.5 mm; forewing length 7.7 mm, hindwing length 7.1 mm.

Head pale yellow. Antennae pale yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow. Legs yellow; coxae, trochanter and femora slightly paler. Wings slightly yellowish brown, with pterostigmatic areas creamy yellow; forewing with distal margin brown and with distinct brown markings on gradate crossveins as well as on 1r-rs; other less distinct brown markings present on distal branching points of most longitudinal veins. Veins yellowish brown except for those in dark markings brown. Hindwing much paler than forewing, with distal dark edging much shorter and paler than that on forewing. Veins pale yellow, with 1r-rs and 2r-rs brown.

Abdomen yellow, dorsally largely tinged with pale reddish brown. Gonocoxite 9 robust on proximal half and strongly incurved on distal half, with a small hairy tubercle on inner surface; gonostylus 9 terminally flattened and bearing a spinous lobe. Ectoproct broad, directed posteroventrad, and concaved medially on posterior margin, with median portion slightly domed dorsad in lateral view, and with posterolateral corner protruding into a digitiform process. Complex of gonocoxites + gonostyli

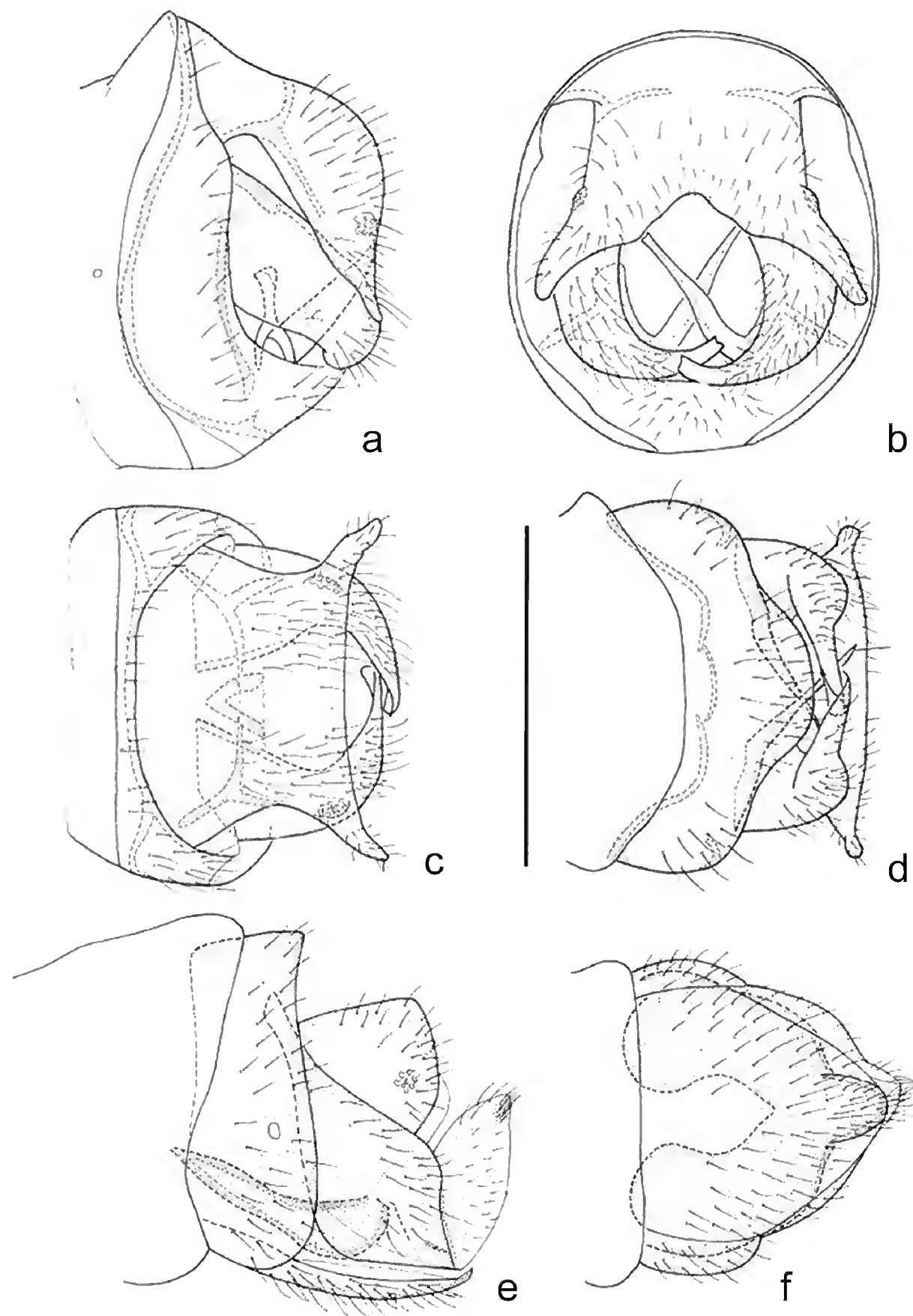


Figure 8. Genital segments of *Niponeurorthus damingshanicus* Liu, H. Aspöck & U. Aspöck. **a–d** Male holotype: **a** lateral **b** caudal **c** dorsal **d** ventral **e–f** Female paratype: **e** genital segments, lateral **f** ventral. Scale bar: 0.5 mm.

+ gonapophyses 10 proximally broad, bearing a roundly tapered dorsal lobe and slender ventral lobe, distally with a long and blade-like projection; distal projections crossing each other at mid-length. Gonocoxite 11 not visible; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Body length 5.3–5.6 mm; forewing length 8.1–8.2 mm, hindwing length 7.1–7.3 mm.

Fused gonocoxites 8 about twice as long as tergite 8, flatly and roundly plate-like, with posterior portion feebly sclerotized. Gonapophyses 8 subtriangular, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix comprising a large and arcuate sclerotized sclerite, which is nearly as long as gonocoxite 8.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): “CHINA, Guangxi, Wuming, Mt. Damingshan

[23°29’N, 108°26’E, 1257 m], 25.V.2011, Tingting Zhang” (CAU).

Biology and ecology. Adults have been taken in May. The known vertical distribution is 1257 m. The larva is unknown.

Distribution. China (Guangxi).

Niponeurorthus fasciatus Nakahara, 1958

Figs 4a; 9a–f, 16

Niponeurorthus fasciatus Nakahara, 1958: 28 (odescr, figs: wings, gs male); Nakahara 1966 (distr); Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2007 (fig: distrmap); U. Aspöck and H. Aspöck 2008b (distrmap); Liu et al. 2014 (key, fig: distrmap).

Type locality. China (Taiwan: Urai).

Male. Forewing length 7.6–7.7 mm, hindwing length 6.7–7.2 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow; pronotum with lateral margins slightly darker; meso- and metanota laterally with a pair of broad brown markings. Legs yellow, with 5th tarsomere slightly darker. Wings slightly yellowish brown, with pterostigmatic areas pale brown; forewing with distal and posterior margins almost brown and with pale brown markings on gradate crossveins as well as on 1r-rs; other pale brown markings present on branching points of most longitudinal veins. Veins yellowish brown except for those in dark markings brown. Hindwing much paler than forewing, with distal margin brown. Veins pale yellowish brown, with 1r-rs, 2r-rs, and gradate crossveins brown.

Abdomen yellow, dorsally largely tinged with pale reddish brown. Gonocoxite 9 robust on proximal half, with a small hairy tubercle on inner surface; distal half strongly incurved, with an obtuse ventral lobe; gonostylus 9 spinous with a feebly produced subdistal projection. Ectoproct broad, directed posteroventrad, and slightly concaved medially on posterior margin. Complex of gonocoxites + gonostyli + gonapophyses 10 rather small; lateral arms much longer than distal projections, which are slenderly digitiform and parallelly directed dorsad. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 11.7 mm, hindwing length 10.8 mm.

Fused gonocoxites 8 about 1.5 times as long as tergite 8, flatly plate-like. Gonapophyses 8 subtrapezoidal, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix comprising a generally subglobal sac-like structure, which is nearly as long as tergite 8; proximal portion moderately sclerotized, lateral portion protruding into a pair of ovoid membranous lobes, which are acutely pointed dorsad.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): China, “Urai Formosa, June 20, 1922 (Dr. Kichizo Takeuchi)” (NSMT).

Biology and ecology. Adults have been taken from April–June. The known vertical distribution is 1100 m.

Distribution. China (Taiwan).

Nipponeurorthus flinti U. Aspöck & H. Aspöck, 2008

Figs 4e; 9g–i; 16

Nipponeurorthus flinti U. Aspöck & H. Aspöck, 2008b: 818 (odescr, figs: wings, gs male, distrmap); Liu et al. 2014 (key, fig: distrmap).

In the heading of the original description (U. Aspöck and H. Aspöck 2008b: page 818) it is erroneously written “*Austroneurorthus flinti*”. This is a lapsus calami.

Type locality. Japan (Okinawa: Yonagawa, Yona).

Male. Body length 5.0–5.3 mm; forewing length 6.5–8.5 mm, hindwing length 6.0–6.6 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow. Legs yellow. Wings transparent, immaculate, with pterostigmatic areas dark yellow. Veins yellow, with costal crossveins slightly darker.

Abdomen yellow. Gonocoxite 9 robust on proximal half, with a small hairy tubercle on inner surface; distal half strongly incurved, with an obtuse ventral lobe; gonostylus 9 spinous and forked at tip. Ectoproct broad, directed posteriorly. Complex of gonocoxites + gonostyli + gonapophyses 10 rather small; lateral arms much longer than distal projections, strongly sinuate, and distinctly widened posteriorly; distal projections slenderly digitiform, rather close to each other, each projection laterally with a feebly sclerotized flat lobe. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 as posteriorly bifurcated sclerite.

Female. Unknown.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): Japan, “Okinawa: Kunigami-gun upper Yonagawa, Yona 26°45.0’N, 12°8’13.3’E, 25 March 1997 O.S. Flint, Jr.” (NMNH).

Biology and ecology. Adults have been taken in March and May. No data concerning vertical distribution are available.

Distribution. Japan (Okinawa, Amamiyoshima).

Nipponeurorthus furcatus Liu, H. Aspöck & U. Aspöck, 2014

Figs 4d; 10a–c; 16

Nipponeurorthus furcatus Liu, H. Aspöck & U. Aspöck, 2014: 229 (odescr, key, figs: wings, gs male, distrmap).

Type locality. China (Yunnan: Lvchun).

Male. Body length 4.0 mm; forewing length 7.1–7.4 mm, hindwing length 6.5–6.9 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow, with yellowish setae. Legs yellow throughout, with yellowish setae. Wings slightly yellowish brown, with pterostigmatic areas yellowish brown; forewing with distal margin brown, and with distinct brown markings on gradate crossveins as well as on 1r-rs; other less distinct brown markings present on distal branching points of most longitudinal veins; veins yellowish brown except for those in dark markings brown; hindwing much paler than forewing, with distal dark edging much shorter and paler than that on forewing; veins pale yellow, with 1r-rs and 2r-rs brown.

Abdomen yellow. Gonocoxite 9 robust on proximal half and strongly incurved on distal half, ventrally with

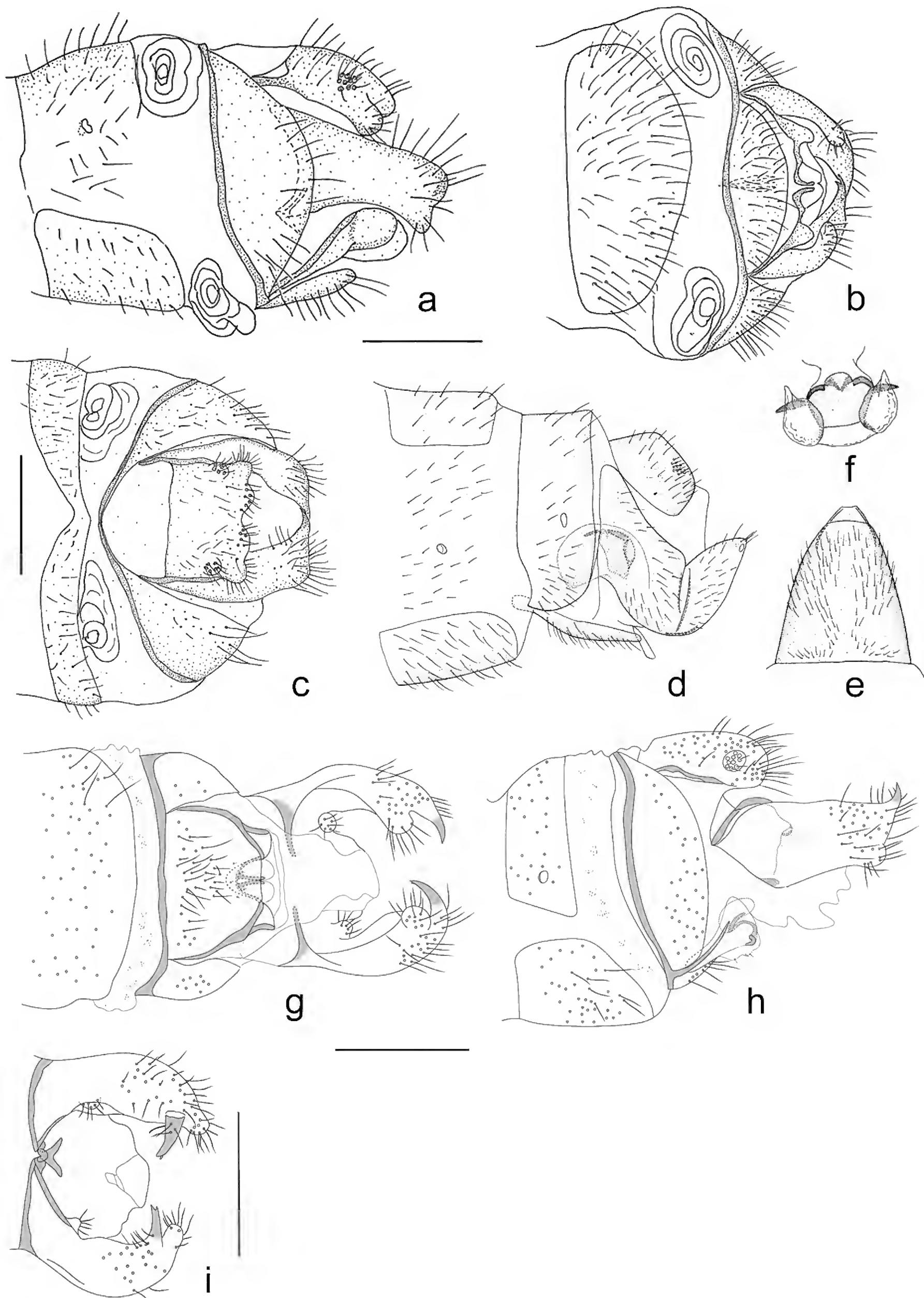


Figure 9. Genital segments of *Niponeurorthus* spp. **a–f** *Niponeurorthus fasciatus* Nakahara, **a–c** male: **a** lateral **b** ventral **c** dorsal **d–f** female: **d** lateral **e** gonocoxites 8 and gonapophyses 8, ventral **f** bursa copulatrix **g–i** *Niponeurorthus flinti* U. Aspöck & H. Aspöck, male holotype: **g** ventral **h** lateral **i** dorsal. Scale bars: 0.5 mm.

an upcurved short lobe separated from the main body of gonocoxite 9; inner surface with a small hairy tubercle; gonostylus 9 terminally rounded and bearing a spinous lobe. Ectoproct broad, directed posteriad, and subtrapezoidal and slightly concaved on posterior margin in dorsal view. Complex of gonocoxites + gonostyli + gonapophyses 10 proximally robust, distally with a slenderly spinous projection, which laterally bears a feebly sclerotized flat lobe. Gonocoxite 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as a posteriorly bifurcated sclerite. Hypandrium internum not visible.

Female. Unknown.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): “CHINA, Yunnan, Lvchun, Qimaba, Dapingzhang [22°50’N, 102°13’E], 1600 m, 21.VII.2013, Yang Zhao” (CAU).

Biology and ecology. Adults have been taken in July. The known vertical distribution is 1600 m. The larva is unknown.

Distribution. China (Yunnan).

Nipponeurorthus fuscineris (Nakahara, 1915)

Figs 2c; 10d–h; 16

Neurorthus fuscineris Nakahara, 1915: 16 (odescr, figs: gs female).

Nipponeurorthus fuscineris: Nakahara 1958 (charact, figs: wing, gs male, female); Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2008b (fig: distrmap); Liu et al. 2014 (key, fig: distrmap).

Type locality. Japan (Kyoto: Mt. Atago).

Male. Forewing length 8.9–9.3 mm, hindwing length 7.5–7.8 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow. Legs yellow. Wings transparent, immaculate, with pterostigmatic areas yellow; longitudinal veins mostly yellow, except for those posterior to 2nd gradate crossveins brown; crossveins mostly brown, except for those on pterostigmatic areas yellow.

Abdomen yellow, dorsally much darker. Gonocoxite 9 robust on proximal half, with a small hairy tubercle on inner surface; distal half strongly incurved and sinuate, ventrally with two obtuse lobes, one directed outward and bald, the other directed inward and setose; gonostylus 9 acutely pointed but unforked. Ectoproct broad, directed posteroventrad, with posterior margin slightly concave. Complex of gonocoxites + gonostyli + gonapophyses 10 with lateral arms much longer than distal projections, straightly directed; distal projections digitiform, acutely pointed at tip, widely separated and parallelly directed with each other. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 8.8 mm, hindwing length 7.6 mm.

Fused gonocoxites 8 about 2.0 times as long as tergite 8, flatly plate-like. Gonapophyses 8 subtrapezoidal, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix sac-like, nearly hexagonal in ventral view, slightly longer than tergite 8; distal portion internally with an ovoid sclerotized area, terminally curved dorsad in lateral view.

Specimens examined and records published. Supplementary material 1. Syntypes: “Mt. Atago near Kyoto on July 2, ’14” [A lectotype should be designated, however, the syntypes are currently unavailable and possibly even lost].

Biology and ecology. Adults have been taken from July–August. The known vertical distribution is 235–1000 m.

Distribution. Japan (Hokkaido, Honshu).

Nipponeurorthus multilineatus Nakahara, 1966

Figs 4h; 11a–f; 16

Nipponeurorthus multilineatus Nakahara, 1966: 204 (odescr, figs: wing, gs male, female); U. Aspöck and H. Aspöck 2008b (fig: distrmap); Liu et al. 2014 (key, fig: distrmap).

Type locality. China (Taiwan: Ilan).

Male. Forewing length 8.3–8.9 mm, hindwing length 7.2–7.6 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Prothorax yellow, meso- and metathorax pale brown. Legs yellow. Wings transparent, with pterostigmatic areas pale yellow. Forewing with brown stripes along longitudinal veins posterior to 1st gradate crossveins and branches of CuA, CuP and 1A, and also with brown stripes on most crossveins except for those on pterostigmatic areas. Hindwing only with brownish stripes on 1r-rs and 2r-rs. Veins blackish brown on forewings and pale brown on hindwings, but costal crossveins on pterostigmatic areas and longitudinal veins on proximal half yellow.

Abdomen yellow, dorsally purplish brown. Gonocoxite 9 robust on proximal half, with a small hairy tubercle on inner surface; distal half strongly incurved, ventrally with a subtriangular lobe; gonostylus 9 spinous and unforked. Ectoproct broad, directed posteroventrad, with posterior margin slightly concave. Complex of gonocoxites + gonostyli + gonapophyses 10 present as a pair of slender straight lobes, which are directed posterodorsally. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 9.7–9.9 mm, hindwing length 8.3–8.8 mm.

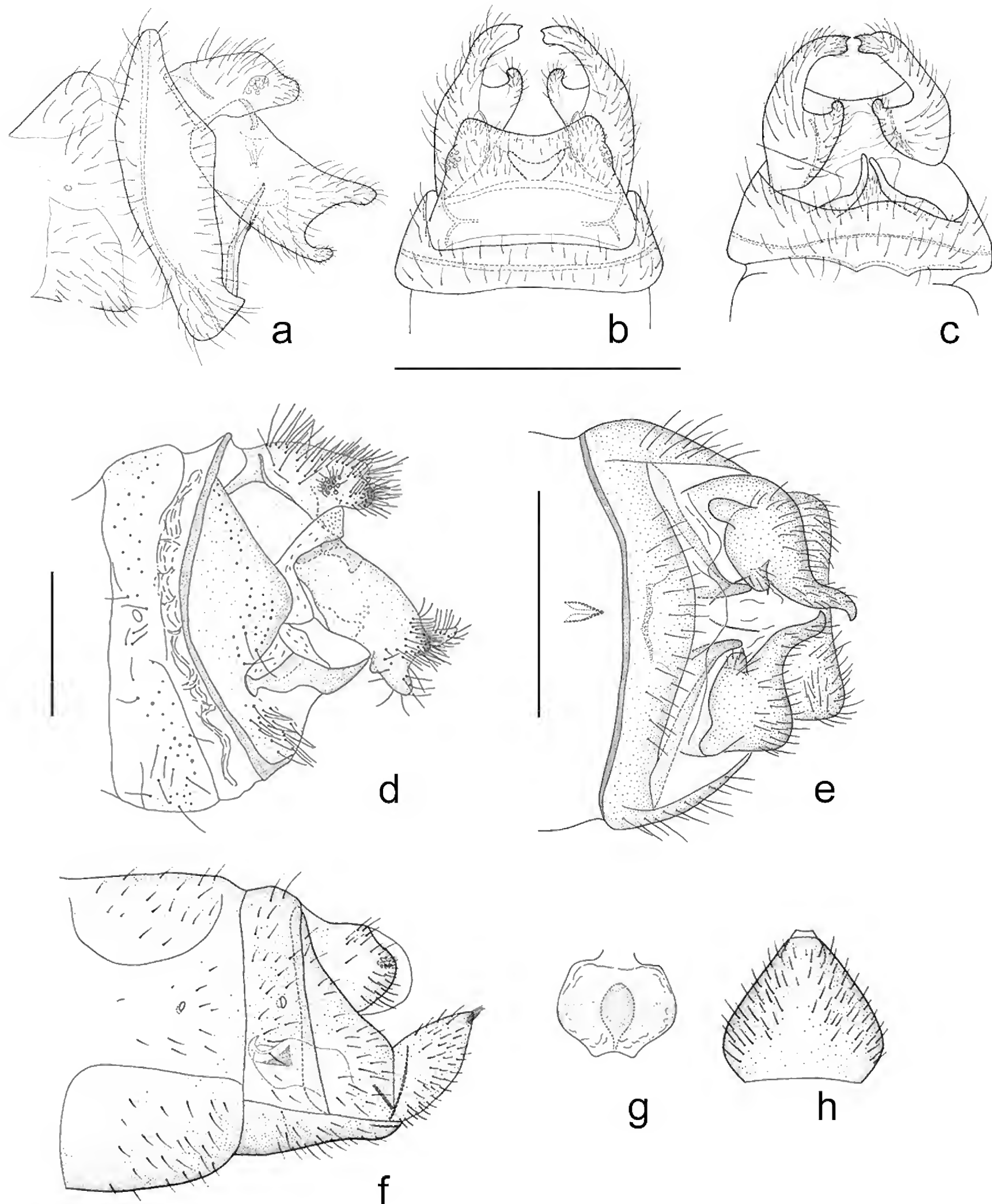


Figure 10. Genital segments of *Nipponeurorthus* spp. **a–c.** *Nipponeurorthus furcatus* Liu, H. Aspöck & U. Aspöck, male holotype, **a:** lateral; **b:** dorsal; **c:** ventral; **d–h.** *Nipponeurorthus fuscinervis* (Nakahara), **d–e:** male, **d:** lateral, **e:** ventral, **f–h:** female, **f:** lateral; **g:** bursa copulatrix; **h:** gonocoxites 8 and gonapophyses 8, ventral. Scale bars: 0.5 mm.

Fused gonocoxites 8 about 1.5 times as long as tergite 8, flatly plate-like. Gonapophyses 8 subtriangular, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix sac-like, subquadrate in ventral view, nearly as long as tergite 8; distal portion internally with an ovoid sclerotized area, terminally curved dorsad in lateral view.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): China, “Ilan, Taipei Hsien, Formosa, April 16 1965 (Hirashima)” (NSMT).

Biology and ecology. Adults have been taken in April. No data concerning the vertical distribution are available. The larva is unknown.

Distribution. China (Taiwan).

***Niponeurorthus pallidinervis* Nakahara, 1958**

Figs 4f–g; 11g–k; 16

Niponeurorthus pallidinervis Nakahara, 1958: 25 (odescr, figs: wing, gs male, female); Kuwayama 1962 (fig. body, wings); Zwick 1967 (figs: gs female); Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2008a (compmorphol, figs: gs male); U. Aspöck and H. Aspöck 2008b (fig: distrmap); Liu et al. 2014 (key, fig: distrmap).

Type locality. Japan (Hokkaido: Jozankei).

Male. Forewing length 8.8–9.8 mm, hindwing length 7.4–8.6 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow. Legs yellow. Wings transparent, immaculate, with pterostigmatic areas yellow; longitudinal veins yellow; crossveins mostly dark brown, except for those on pterostigmatic areas yellow.

Abdomen yellow, dorsally purplish brown. Gonocoxite 9 robust on proximal half, with a small hairy tubercle on inner surface; distal half strongly incurved; gonostylus 9 spinous and unforked. Ectoproct broad, directed posteroventrad, with posterior margin slightly concaved, and with a pair of subtriangular ventral projection. Complex of gonocoxites + gonostyli + gonapophyses 10 transversely broad; lateral arms nearly as long as distal projections, arcuate, medially with a pair of projections, which are straightly directed dorsad and widened on distal half; distal projections digitiform, straightly and parallelly directed dorsad with each other. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 9.1–11.4 mm, hindwing length 8.0–9.9 mm.

Fused gonocoxites 8 about 2.0 times as long as tergite 8, flatly plate-like. Gonapophyses 8 subtriangular, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix sac-like, suboval, slightly longer than tergite 8, with distal portion laterally expanded in ventral view, marginally and internally with several sclerotized bands.

Specimens examined and records published. Supplementary material 1. Holotype male (by original designation): Japan, “Jozankei, Hokkaido, July 17–18, 1956, Waro Nakahara” (NSMT).

Biology and ecology. Adults have been taken from May–July, most specimens were collected in July. No data concerning the vertical distribution are available. The larva is unknown, however, Nakahara (1958) hypothesized an aquatic life style of the larva due to the findings of adults along rivers and brooks.

Distribution. Japan (Hokkaido, Honshu, Kyushu, Tsushima Island).

***Niponeurorthus punctatus* (Nakahara, 1915)**

(Figs 4i; 12a–e; 16)

Neurorthus punctatus Nakahara, 1915: 15 (odescr, figs wings); Navás 1935 (mon, fig: wing).

Niponeurorthus punctatus (Nakahara, 1915): Okamoto and Kuwayama 1932 (fig. body, wings); Nakahara 1958 (figs: wings, gs male, female); Zwick 1967 (figs: gs female); Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2008b (fig: distrmap); Liu et al. 2014 (key, fig: distrmap).

Type locality. Japan (Honshu: Tottori, or Kyoto: Mt. Atago, or Osaka: Mt. Minomo) [A lectotype should be designated, however, the syntypes (from the above mentioned localities) are unavailable presently].

Male. Forewing length 7.1–7.4 mm, hindwing length 6.2–6.5 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow. Legs yellow. Wings transparent, with pterostigmatic areas pale yellow; forewing with brownish stripes on most crossveins except for costal crossveins and with brownish spots on distal branching points of most longitudinal vein; hindwing with brownish spots on distal branching points of Rs, MA and MP; veins mostly yellow, except for those on dark markings brown; costal crossveins on proximal half of forewing costal areas pale brown.

Abdomen yellow, dorsally slightly darker. Gonocoxite 9 robust on proximal half; distal half strongly incurved, ventrally with a short digitiform projection, which bears several spines; gonostylus 9 spinous and forked into a triangular subdistal projection. Ectoproct broad, directed posteroventrad. Complex of gonocoxites + gonostyli + gonapophyses 10 with sinuate lateral arms, which are inflated posterolaterally; distal projections slenderly digitiformed, straightly directed posteriad. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 7.7–8.9 mm, hindwing length 7.2–7.9 mm.

Fused gonocoxites 8 about 2.0 times as long as tergite 8, flatly plate-like. Gonapophyses 8 subtriangular, largely covered by gonocoxite 8, lateral margins distinctly sclerotized. Bursa copulatrix sac-like, suboval, much longer than tergite 8; proximal portion with a pair of broad sclerotized areas, median portion ventrally with a pair of sclerotized holes, distal portion marginally sclerotized and terminally curved dorsad in lateral view.

Specimens examined and records published. Supplementary material 1. Lectotype designation presently not possible (see above).

Biology and ecology. Adults have been taken from July–August, most specimens were collected in July. No data concerning the vertical distribution are available. The larva is unknown.

Distribution. Japan (Honshu, Hokkaido, Kyushu).

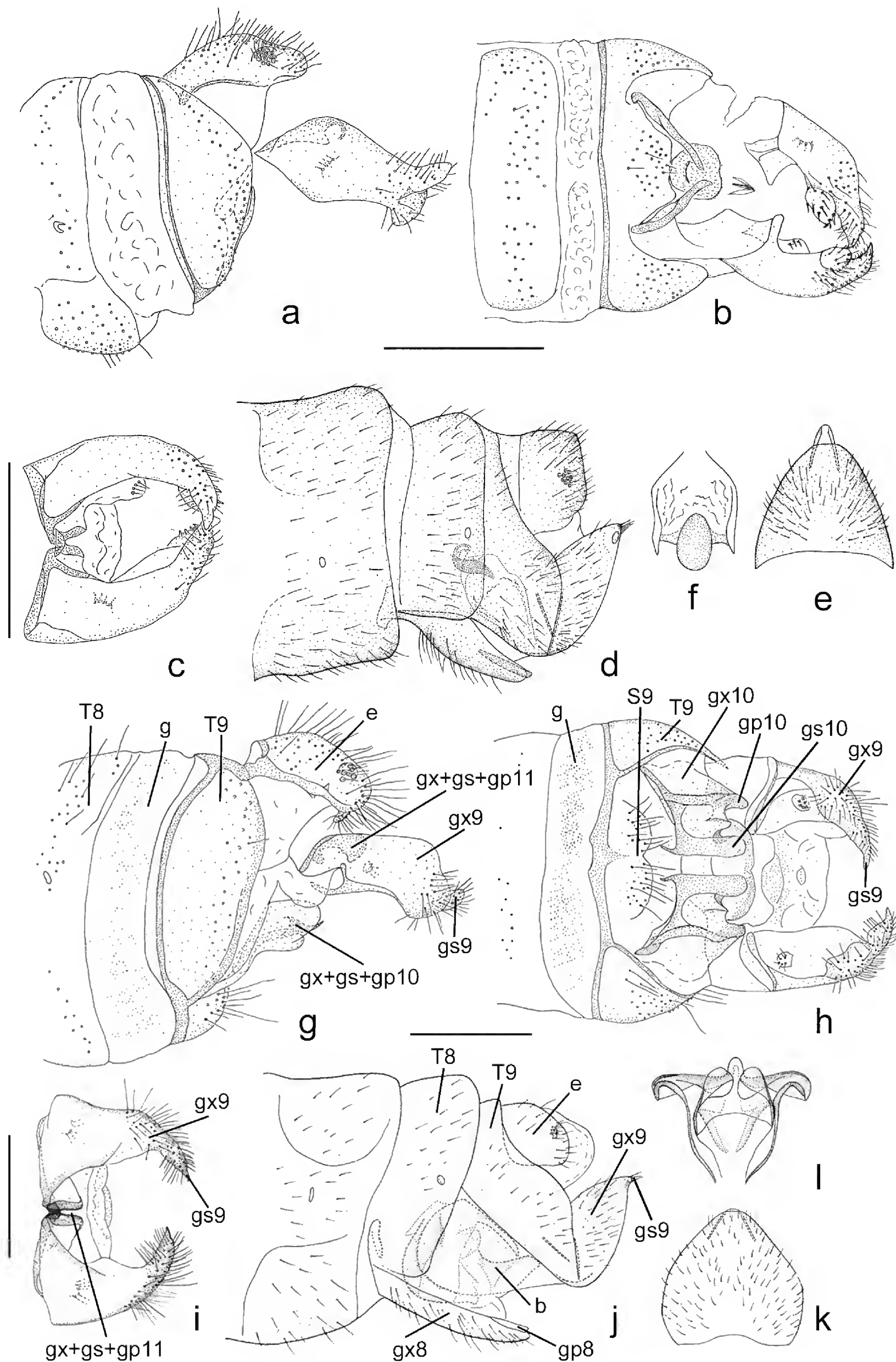


Figure 11. Genital segments of *Nipponeurorthus* spp. **a–f** *Nipponeurorthus multilineatus* Nakahara **a–c** male: **a** lateral **b** ventral **c** dorsal **d–f** female: **d** lateral **e** gonocoxites 8 and gonapophyses 8, ventral **f** bursa copulatrix, ventral **g–j** *Nipponeurorthus pallidinerbis* Nakahara **g–i** male paratype: **g** lateral **h** ventral **i** dorsocaudal **j–l** female paratype: **j** lateral **k** gonocoxites 8 and gonapophyses 8, ventral **l** bursa copulatrix. **Abbreviations.** **b** – bursa copulatrix; **e** – ectoproct; **g** – ring of glands; **gp** – gonapophysis; **gs** – gonostylus; **gx** – gonocoxite; **S** – sternite; **T** – tergite. Scale bars: 0.5 mm.

***Nipponeurorthus qinicus* Yang in Chen, 1998**

Figs 12f, 16

Nipponeurorthus qinicus Yang in Chen, 1998: 105 (odescr, figs: habitus); Liu et al. 2014 (key, fig: distrmap).**Type locality.** China (Shaanxi: Ankang).**Male.** Body length 7.0 mm; forewing length 9.5 mm, hindwing length 8.0 mm.

Head yellow. Antennae yellow but gradually darkened toward apex.

Thorax yellow. Legs yellow. Wings transparent, immaculate; veins mostly pale brown on forewings, except for veins on wing base and proximal half of anterior branch of MP yellow; veins mostly pale brown on hindwings, except for veins on wing base yellow.

Abdomen yellow. Gonocoxite 9 strongly curved distad. Ectoproct broad, slightly concaved on posterior margin. Complex of gonocoxites + gonostyli + gonapophyses 10 present as a pair of hook-like lobes. Gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Unknown.**Specimens examined and records published.** Supplementary material 1. Holotype (by implicit monotypy) male: China, “Shaanxi, Ankang” (CAU). So far, the holotype has not been found in the entomological collection of CAU. There is a possibility that the primary type is lost or damaged. However, due to the lack of additional specimens of this species, we cannot designate a neotype.**Biology and ecology.** No data are available. The larva is unknown.**Distribution.** China (Shaanxi).***Nipponeurorthus tianmushanus* Yang & Gao, 2001**

Figs 12g–i, 16

Nipponeurorthus tianmushanus Yang & Gao, 2001: 308 (odescr, figs: wings, gs male); Liu et al. 2014 (key, fig: distrmap).**Type locality.** China (Zhejiang: Tianmushan).**Male.** Body length 7.0 mm; forewing length 8.0 mm, hindwing length 7.0 mm.

Head yellow. Antennae yellowish brown, with several terminal flagellomeres dark brown.

Wings slightly yellowish brown, with pterostigmatic areas pale brown; forewing with distal margin brown and with brownish markings on most crossveins except for costal crossveins; hindwing similarly patterned; veins pale brown.

Gonocoxite 9 robust on proximal half and strongly incurved on distal half. Ectoproct broad, directed posteroventrad, and strongly concaved on posterior margin. Complex of gonocoxites + gonostyli + gonapophyses 10 present as a pair of slender lobes, which are rather close to each other at the tip.

Female. Unknown.**Specimens examined and records published.** Supplementary material 1. Holotype (by original designation), male, China, “Zhejiang, Tianmushan, 22.VII.1963, Io Chou” (CAU). Thus far, the holotype has not been found in the entomological collection of CAU. There is a possibility that the primary type is lost or damaged. However, due to a lack of any additional specimens of this species, we cannot designate a neotype.**Biology and ecology.** No data available. The larva is unknown.**Distribution.** China (Zhejiang).***Nipponeurorthus tinctipennis* Nakahara, 1958**

Figs 4j, 12j–m, 16

Nipponeurorthus tinctipennis Nakahara, 1958: 27 (odescr, figs: wing, gs male, female); Hayashi 2005 (list, distr, figs); U. Aspöck and H. Aspöck 2008b (fig: distrmap); Liu et al. 2014 (key, fig: distrmap).**Type locality.** Japan (Yakushima Island: Hananoegou and Muromidake).**Male.** Forewing length 9.1 mm, hindwing length 8.0 mm.

Head yellow. Antennae yellow. Mouthparts yellow; mandibles with brownish tips.

Thorax yellow; meso- and metanota laterally much darker. Legs yellow. Wings transparent, immaculate, with pterostigmatic areas pale yellow; veins mostly yellowish brown, with crossveins much darker, and with C, Sc and R pale yellow on forewings; veins mostly pale yellow, with longitudinal veins of distal half and some crossveins (i.e. 1r-rs, 2r-rs, and gradate crossveins) pale brown on hindwings.

Abdomen yellow, dorsally purplish brown. Gonocoxite 9 robust on proximal half, distal half strongly incurved; gonostylus 9 spinous. Complex of gonocoxites + gonostyli + gonapophyses 10 present as a pair of slender lobes, which are inflated distad and bear a tooth-like process. Gonocoxites 11 present as a simple, transverse, sclerotized band; gonostyli 11 present as posteriorly bifurcated sclerite.

Female. Forewing length 10.0 mm, hindwing length 9.0 mm.

Fused gonocoxites 8 flatly plate-like. Gonapophyses 8 subtriangular, largely covered by gonocoxite 8, lateral margins distinctly sclerotized.

Specimens examined and records published. Supplementary material 1. Holotype male (by original description), Japan, “Hananoegou, Yakushima, 12 July 1954, Yosihiko Kurosawa” (NSMT).**Biology and ecology.** The adult has been taken in July. The known vertical distribution is 1800 m. The larva is unknown.**Distribution.** Japan (Yakushima Island).

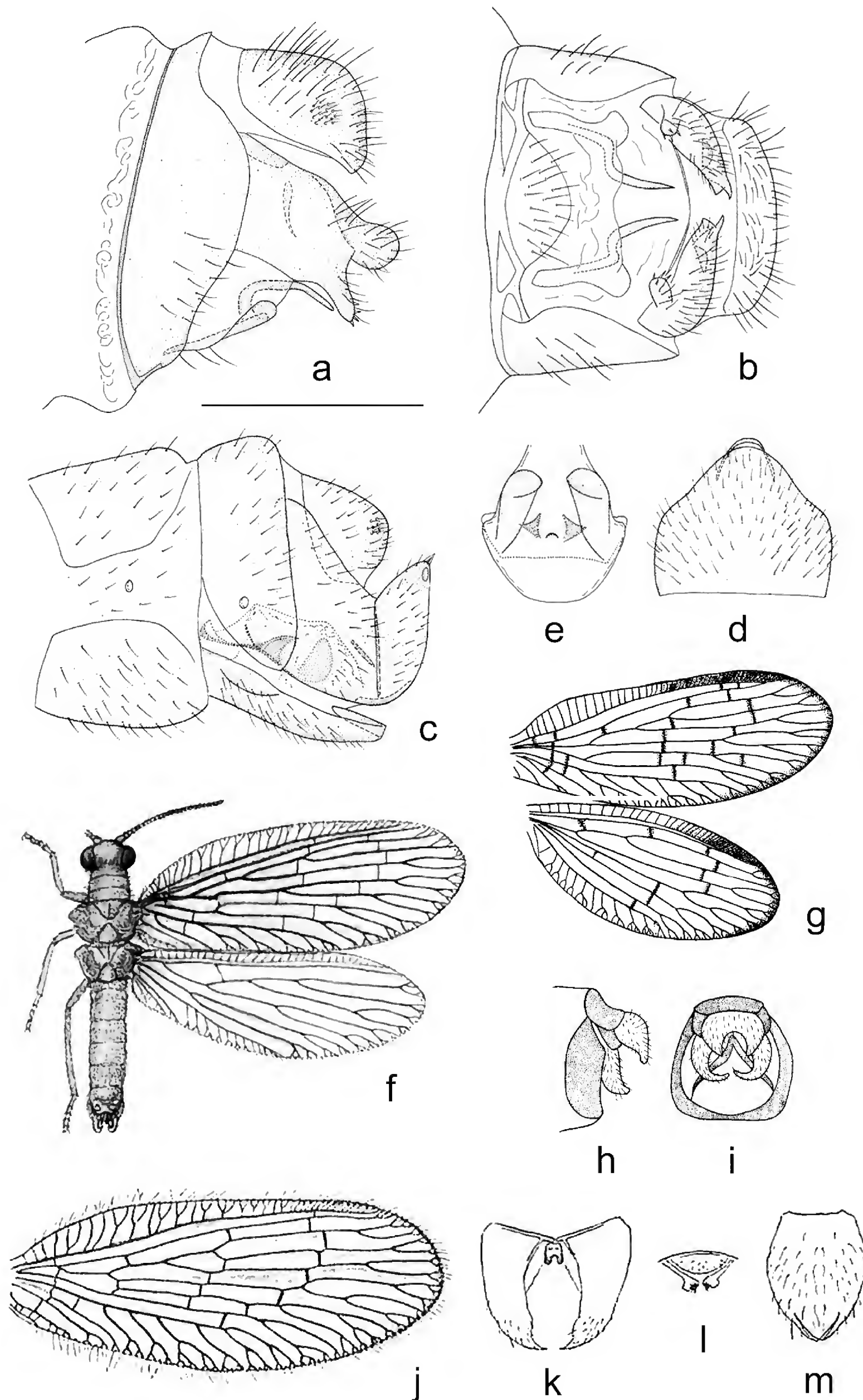


Figure 12. *Niponeurorthus* spp. **a–e** *Niponeurorthus punctatus* (Nakahara) **a–b** male genital segments: **a** lateral **b** ventral **c–e** female genital segments: **c** lateral **d** gonocoxites 8 and gonapophyses 8, ventral **e** bursa copulatrix **f** *Niponeurorthus qinicus* Yang in Chen, male holotype, habitus drawing (adapted from Yang in Chen 1998) **g–i** *Niponeurorthus tianmushanus* Yang & Gao, male: **g** wings **h** genital segments, lateral **i** caudal (adapted from Yang and Gao 2001) **j–m** *Niponeurorthus tinctipennis* Nakahara, male: **j** forewing **k–m** genital sclerites (adapted from Nakahara 1958). Scale bar: 0.5 mm (**a–e**).

Genus *Sinoneurorthus* Liu, H. Aspöck & U. Aspöck, 2012

Sinoneurorthus Liu, H. Aspöck & U. Aspöck, 2012: 132 (odescr) [Type species: *Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, 2012: 133, by original designation].

Diagnosis. Adults of medium body size; female forewing length 12–13 mm. Body coloration reddish orange. Wings slightly leathery, smoky brown. Longitudinal veins with dense branches, leaving small bifurcated or trifurcated forks marginally. Female fused gonocoxite 8 flatly and roundly plate-like; gonocoxites 9 narrowly foliate, with ovoid gonostyli; bursa copulatrix distinctly shaped and sclerotized.

Distribution. China.

***Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, 2012**

Figs 2d; 4k; 13a–e; 16

Sinoneurorthus yunnanicus Liu, H. Aspöck & U. Aspöck, 2012: 133 (odescr, figs: adult, wings, gs female, distrmap).

Type locality. China (Yunnan: Xiaocaoba).

Female. Body length 6.9 mm; forewing length 12.6 mm, hindwing length 11.0 mm.

Head reddish orange, slightly shiny. Antennae blackish brown, with scape and pedicel pale yellowish brown, and with proximal two segments of flagellum orange. Mouthparts orange.

Thorax reddish orange, slightly shiny. Legs orange. Wings smoky brown, with slightly leathery membrane; veins blackish brown, with proximal half of C and extreme bases of other longitudinal veins much paler.

Pterostigmatic areas very dark, with their crossveins rather weak and obscure; Rs proximally 2-branched, both branches deeply bifurcated, with bifurcation nearly 1/2 as long as whole wing; all main branches having additional branching, terminally leaving 8–10 small bifurcate or trifurcate forks; MA completely fused with Rs proximally in forewing, but visible as an independent vein at base of hindwing; medially bifurcated, with both branches having additional branching, terminally leaving 8 small bifurcated or trifurcated forks; MP proximally 2-branched, each branch bifurcated at distal 1/3 in forewing and at distal 1/4 in hindwing, terminally leaving 8–10 small bifurcate or trifurcate forks; CuA 7 to 8-branched in forewings, terminally leaving ca. 10 small bifurcate or trifurcate forks, and 11 to 13-branched in hindwings, with proximal branches vertical to stem of CuA, terminally leaving 14–15 small bifurcate or trifurcate forks; CuP with a small bifurcate fork terminally; 1A terminally 4 to 5-branched in forewings and 3-branched in hindwings; 2A 7-branched in forewings and 6 or 8-branched in hindwings; 3A simple.

Abdomen reddish orange. Fused gonocoxites 8 about twice as long as tergite 8, flatly and roundly plate-like. Gonapophyses 8 subtrapezoidal, proximal half covered by gonocoxites 8, lateral margins distinctly sclerotized. Bursa copulatrix comprising an ovoid sclerotized sclerite, with a pair of cone-shaped hollow processes directed ventrad.

Male. Unknown.

Specimens examined and records published. Supplementary material 1. Holotype female (by original designation): “CHINA: Yunnan Province, Zhaotong City, Yiliang County, Xiaocaoba, 27°50.079N, 104°17.554E, 1715 m, 2009.V.28, Liangming Cao leg.” (CAU).

Biology and ecology. The only adult has been taken in May in the vicinity of a waterfall. The known vertical distribution is 1715 m. The larva is unknown.

Distribution. China (Yunnan).

Key to extant genera of Nevrorthidae

- 1 Wing membrane slightly leathery (only female known) (Fig. 2d)..... *Sinoneurorthus*
- Wing membrane soft 2
- 2 Males: Segment 7 enlarged (Figs 6d, e), distribution restricted to Mediterranean (and submediterranean) regions *Nevrorthus*
- Males: Segment 7 not enlarged 3
- 3 Males: Complex of gonocoxites, gonostyli, gonapophyses 11 forming a transverse sclerite (Fig. 7e), distribution restricted to Australia..... *Austroneurorthus*
- Males: Complex of gonocoxites, gonostyli, gonapophyses 11 with a small median fork (Fig. 11i), distribution restricted to Eastern Asia *Nipponeurorthus*

Key to extinct genera of Nevrorthidae (all from the Eocene Baltic amber) (see Wichard 2016).

Key to species of *Nevrorthus* (males)

- 4 Forewing without shadows on cross veins (Figs 3a, d) 2
- Forewing with shadows on cross veins (Figs 3b, e)..... 3
- 5 Scapus and pedicellus yellowish, pseudoapex of sternite 9 deeply forked (Fig. 6b)..... *N. iridipennis*
- Scapus and pedicellus dark brown, pseudoapex of sternite 9 unforked (Fig. 6c)..... *N. apatelios*

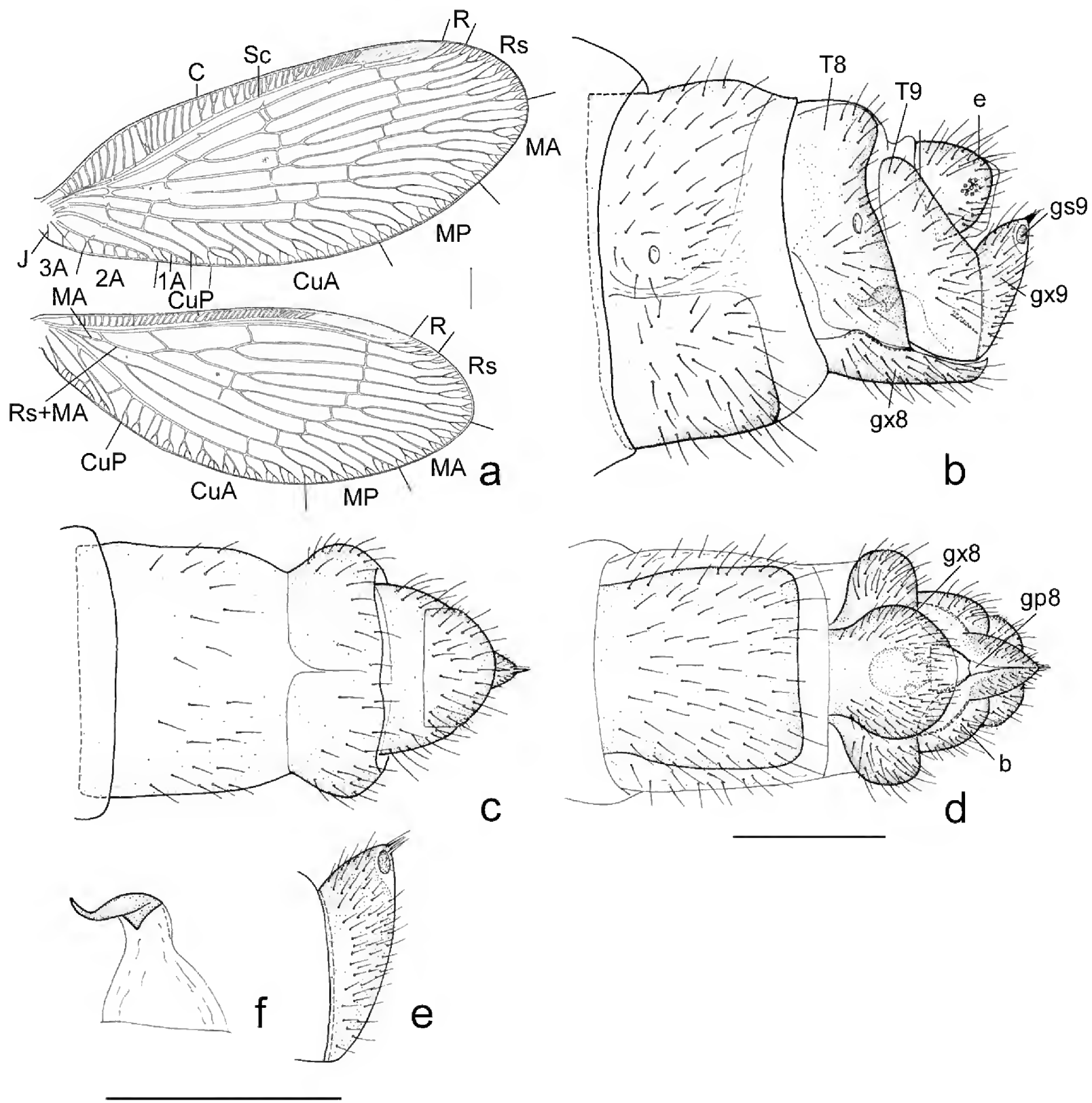


Figure 13. *Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, female holotype **a** wings **b** genital segments, lateral **c** same, dorsal **d** same, ventral **e** gonocoxites 9, lateral **f** bursa copulatrix, lateral. **Abbreviations.** A – Analis; –: Costa; **CuA** – Cubitus anterior; **CuP** – Cubitus posterior; **J** – Jugal vein; **MA** – Media anterior; **MP** – Media posterior; **R** – Radius; **Rs** – Radial sector; **Sc** – Subcosta. **b** – bursa copulatrix; **e** – ectoproct; **gp** – gonapophysis; **gs** – gonostylus; **gx** – gonocoxite; **S** – sternite; **T** – tergite. Scale bar: 1.0 mm (a) and 0.5 mm (b–f).

- 6 Flagellum of antennae uniformly yellowish brownish, pseudoapex of sternite 9 deeply grooved (Figs 6a, e) 4
- Flagellum of antennae slightly darker in distal third, pseudoapex of sternite 9 distally sinuate (Fig. 3f) *N. reconditus*
- 7 Gonocoxites 11 forming a triangle (Fig. 6a).....*N. fallax*
- Gonocoxites 11 forming a bar (Fig. 6e).....*N. hannibal*

Key to species of *Austroneurorthus* (males)

- 1 Forewing with intensive shadows around crossveins (Fig. 3h), femora of all three legs in males with dark orange coloured oval sclerite; pseudoapex of sternite 9 rounded (Fig. 7f)*A. horstaspoecki*
- Forewing without shadows around crossveins (Fig. 3g), femora of males without dark orange sclerites; pseudoapex of sternite 9 deeply forked (Fig. 7b).....*A. brunneipennis*

Key to species of *Nipponneurorthus*

See Liu et al. (2014)

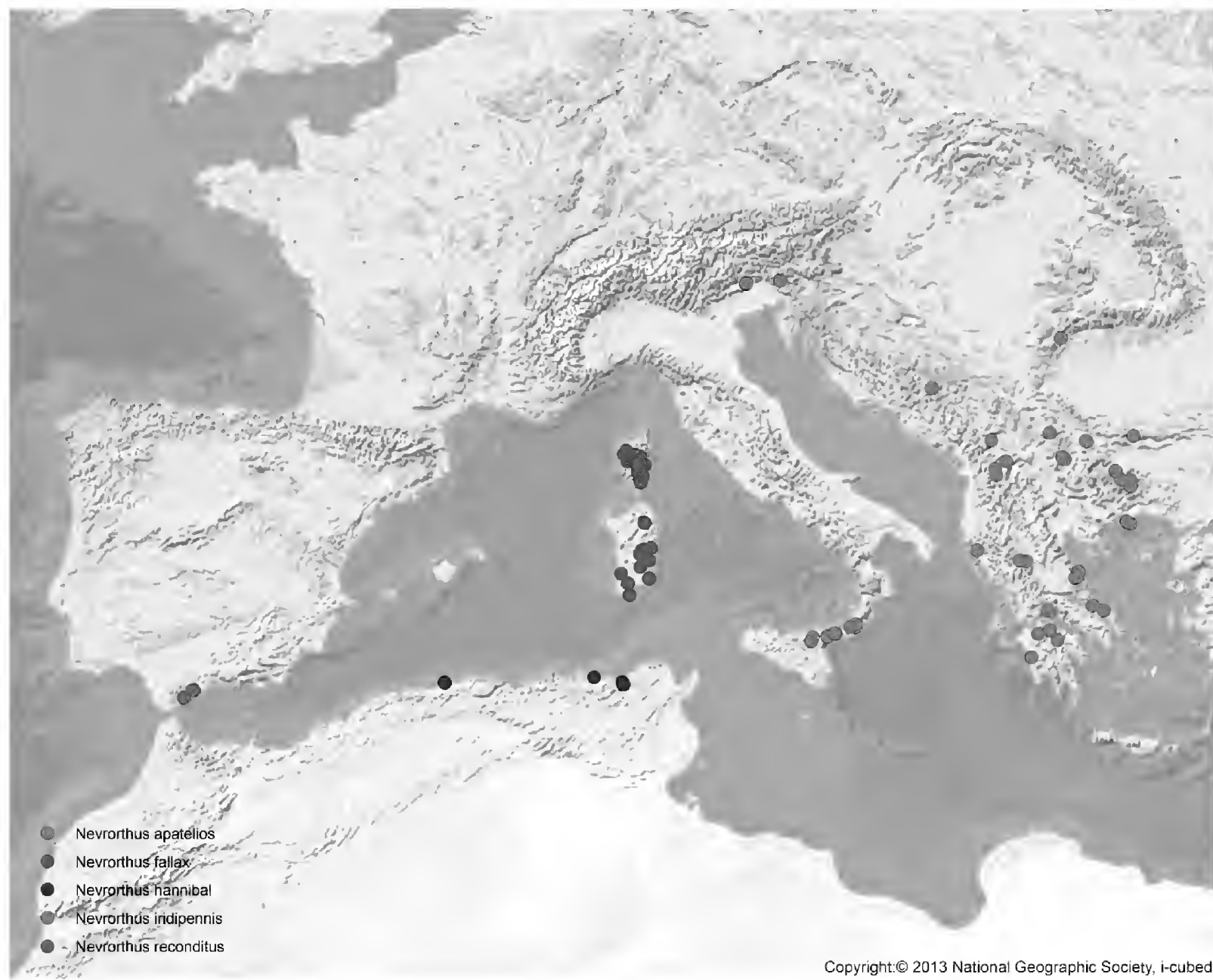


Figure 14. Distribution map of the species of *Nevrorthis*.

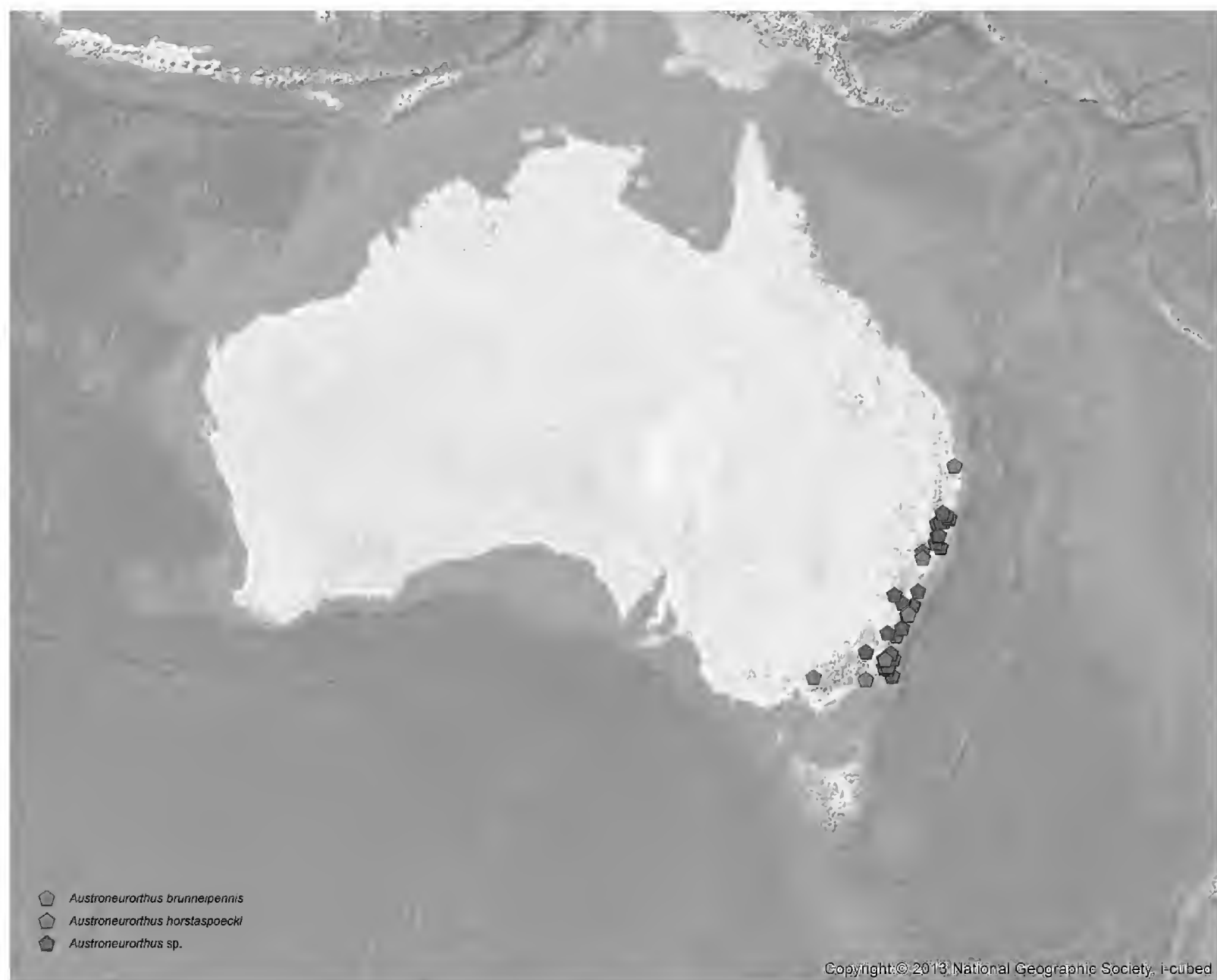


Figure 15. Distribution map of the species of *Austroneurorthus*.

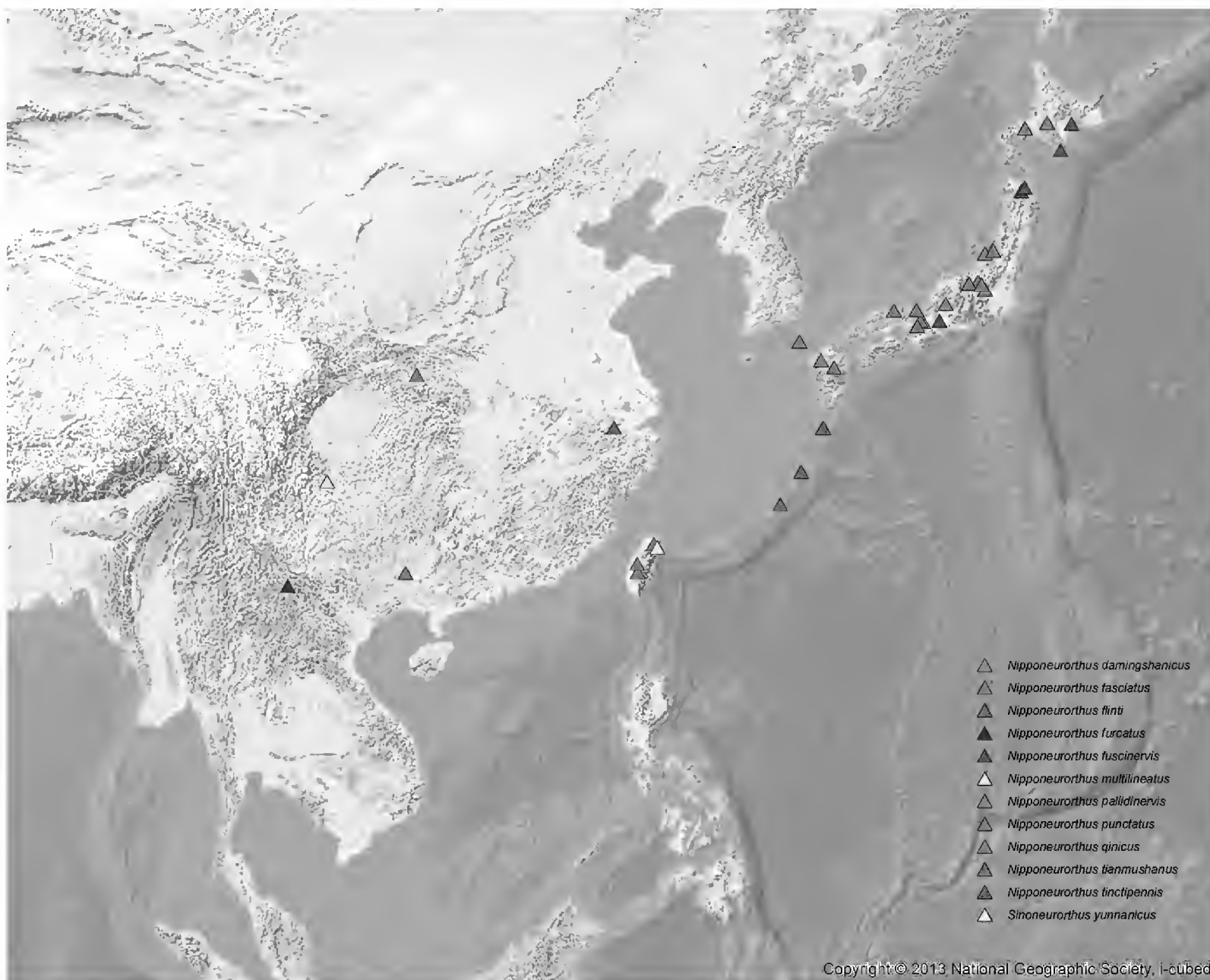


Figure 16. Distribution map of the species of *Nipponeurorthus* and *Sinoneurorthus*.

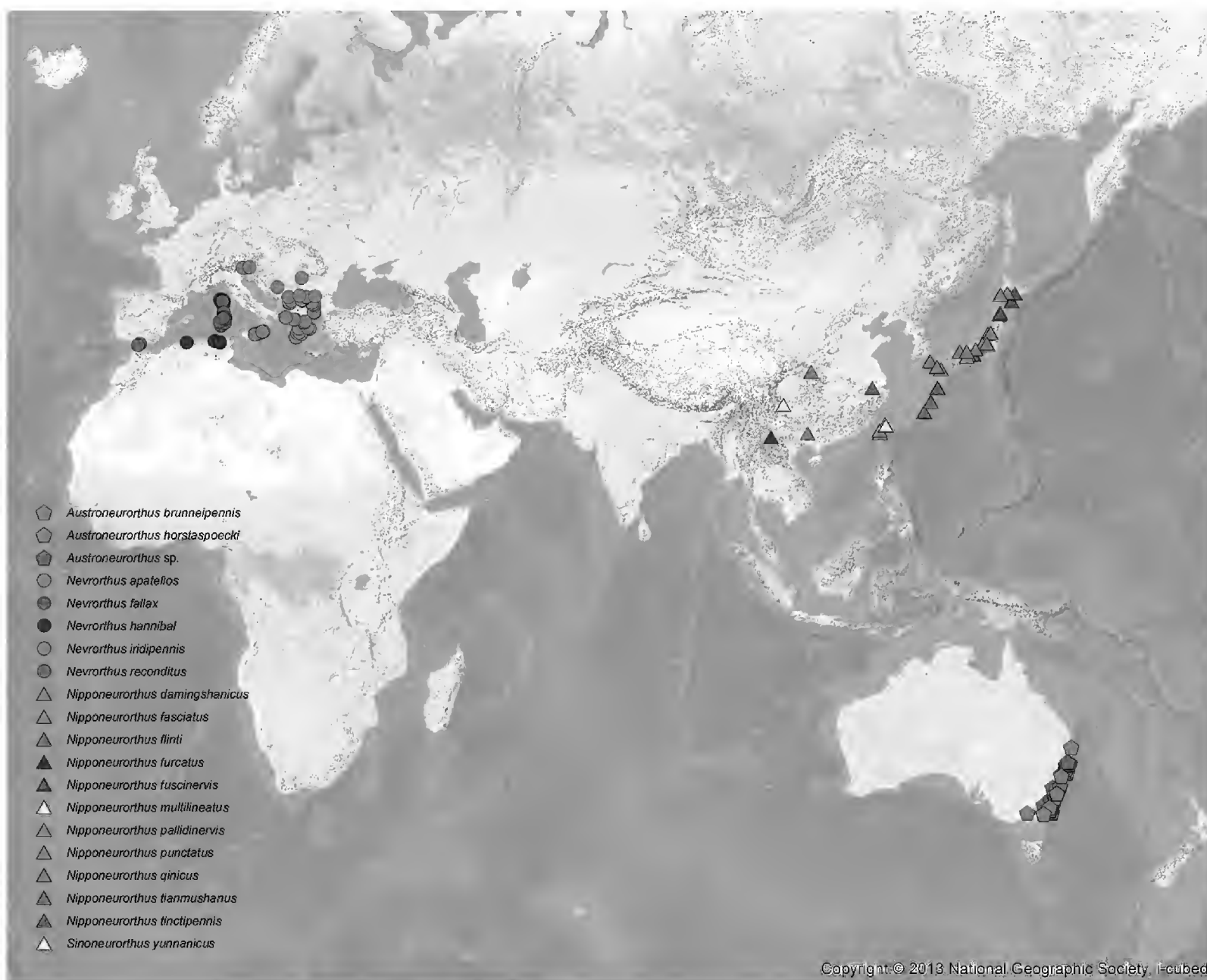


Figure 17. Distribution map of the family Nevrorthisidae.

Phylogenetic analysis

The parsimony analysis of the primary matrix including all species of Nevrothidae yielded 7712 most parsimonious trees (MPT) (length = 49, consistency index = 73, retention index = 93) and the strict consensus tree is shown in Supplementary material 4. The phylogeny was poorly resolved probably due to the inclusion of several ingroup taxa with a large number of missing data. The monophyly of only three genera with more than one species was recovered, including *Austroneurothus*, *Nevrothus* and *Palaeoneurothus*. The latter two genera formed a sister group, and together with *Rophalis* they formed a monophylum.

The parsimony analysis of the refined dataset with deletion of two species of *Nipponeurothus* (i.e., *Ni. qinicus* and *Ni. tinctipennis*) and one species of *Proberotha* (i.e., *P. dichotoma*) yielded 40 most parsimonious trees (MPT) (length = 49, consistency index = 73, retention index = 92) and the strict consensus tree is shown in Figure 18. Based on these results, all *Nipponeurothus* species formed a monophylum, supported by the male gonocoxite 9 with subdistal inflation and additional lobes (char. 18:1) and the female fused gonocoxites 8 much longer than wide with posterior tapering (char. 29:2). The monophyletic group comprising *Rophalis*, *Nevrothus* and *Palaeoneurothus*, which was recovered in the analysis of the primary dataset, was also recovered here and supported by the male gonocoxite 9 ventrally with a long lobe (char. 19:1) and the elongated male gonapophyses 9 with acute projections (char. 23:3). This monophyletic clade of three genera was grouped with *Austroneurothus* and *Electroneurothus*. The synapomorphic characters of the monophyletic group comprising *Austroneurothus*, *Electroneurothus*, *Rophalis*, *Nevrothus* and *Palaeoneurothus* include the elongated and posterodorsally directed male sternite 9 (char. 14:1 and char. 17:1), the ovoid male gonapophyses with several spines (char. 23:2), and the presence of fused gonocoxites 10 (char. 25:1). The phylogenetic positions of *Balticoneurothus*, *Proberotha* and *Sinoneurothus* were not resolved.

Discussion

Phylogenetic position of Nevrothidae

Irrespective of the fact that Nevrothidae was assigned at various positions in different analyses based on morphological and molecular data (U. Aspöck et al. 2001, Haring and U. Aspöck 2004, U. Aspöck and H. Aspöck 2008a, Beutel et al. 2010, Winterton et al. 2010, Zimmermann et al. 2011, Randolph et al. 2013, Randolph et al. 2014, Wang et al. 2016), several hypotheses, which have been catalysed via Nevrothidae, are of general significance regarding Neuropterida:

The hypothesis of aquatic larvae as a synapomorphy of Megaloptera + Neuroptera induces the hypothesis that cryptonephry might be an answer to secondary terrestrial life-style of the crown clade within Neuroptera.

Gaumont (1976) provided comparative studies of the sucking tubes, guts and the Malpighian tubules of Neuropteran larvae. In this connection she studied the phenomenon of cryptonephry of terrestrial larvae. She interpreted the free Malpighian tubules of aquatic larvae of Sisyridae and Nevrothidae as secondary adaptations. We interpret free Malpighian tubules – at least in Nevrothidae – as the plesiomorphic condition and the phenomenon of cryptonephry (= complex connection of the Malpighian tubules with the colon) as an adaptation to secondary terrestrial life style of the remaining families (U. Aspöck et al. 2001).

A compact head capsule with a large gula is interpreted as belonging to a ground pattern in larval Neuropterida. In Neuroptera this feature is retained only in Nevrothidae, thus placing them in a key position within the order. An open or compact head capsule in connection with a loss of the gula (U. Aspöck and H. Aspöck 2010b) represent phylogenetic trends in the remaining Neuroptera (U. Aspöck and H. Aspöck 2007).

A neck-like, somewhat articulating cervix is apomorphic and a larval synapomorphy of Neuroptera. Several families (former Hemerobiformia) have lost this condition (U. Aspöck et al. 2001). The region underwent further elongation in Nevrothidae and is known as the so-called “Rollengelenk” (Zwick 1967).

Pleuritocavae, paired sacks of uncertain, possibly pheromonal, function – a curiosity of male adults – have been found ventrally between segments 6 and 7 in *Nevrothus* (U. Aspöck and H. Aspöck 1983) and *R. relictata* (Wichard et al. 2009), between segments 7 and 8 in *R. relictata*, between segments 8 and 9 in *Ni. fuscinerervis*, *Ni. multilineatus* and *R. relictata*, and dorsally between tergites 8 and 9 in *Ni. fasciatus* and *R. relictata*. These sacks are only visible when they are everted, so they are possibly more common than previously suspected. Similar structures are found in other Neuroptera, especially Nemopteridae. A phylogenetic relevance may be assigned to them, however, the character is unreliable due to the variable pheromonal status of the observed individual specimens.

A most recent study on mitochondrial phylogenomics of the Neuropterida (Wang et al. 2016) corroborates a sister group relationship of Megaloptera + Neuroptera and a sister group relationship of Coniopterygidae + monophyletic remaining Neuroptera. Within the Neuropteran families excluding Coniopterygidae, the clade Sisyridae + Nevrothidae was assigned as sister group to Osmylidae + the monophylum constituted by the remaining twelve families. The sister group relationship of Nevrothidae + Sisyridae has been discussed in detail in Wang et al. (2016) especially with respect to the morphological disparity of the larvae of the two families. This ongoing discussion remains a challenge in our understanding of Nevrothidae.

Intergeneric phylogeny within Nevrothidae

By sharing a number of apomorphic characters, among the four extant genera of Nevrothidae, it is not difficult to

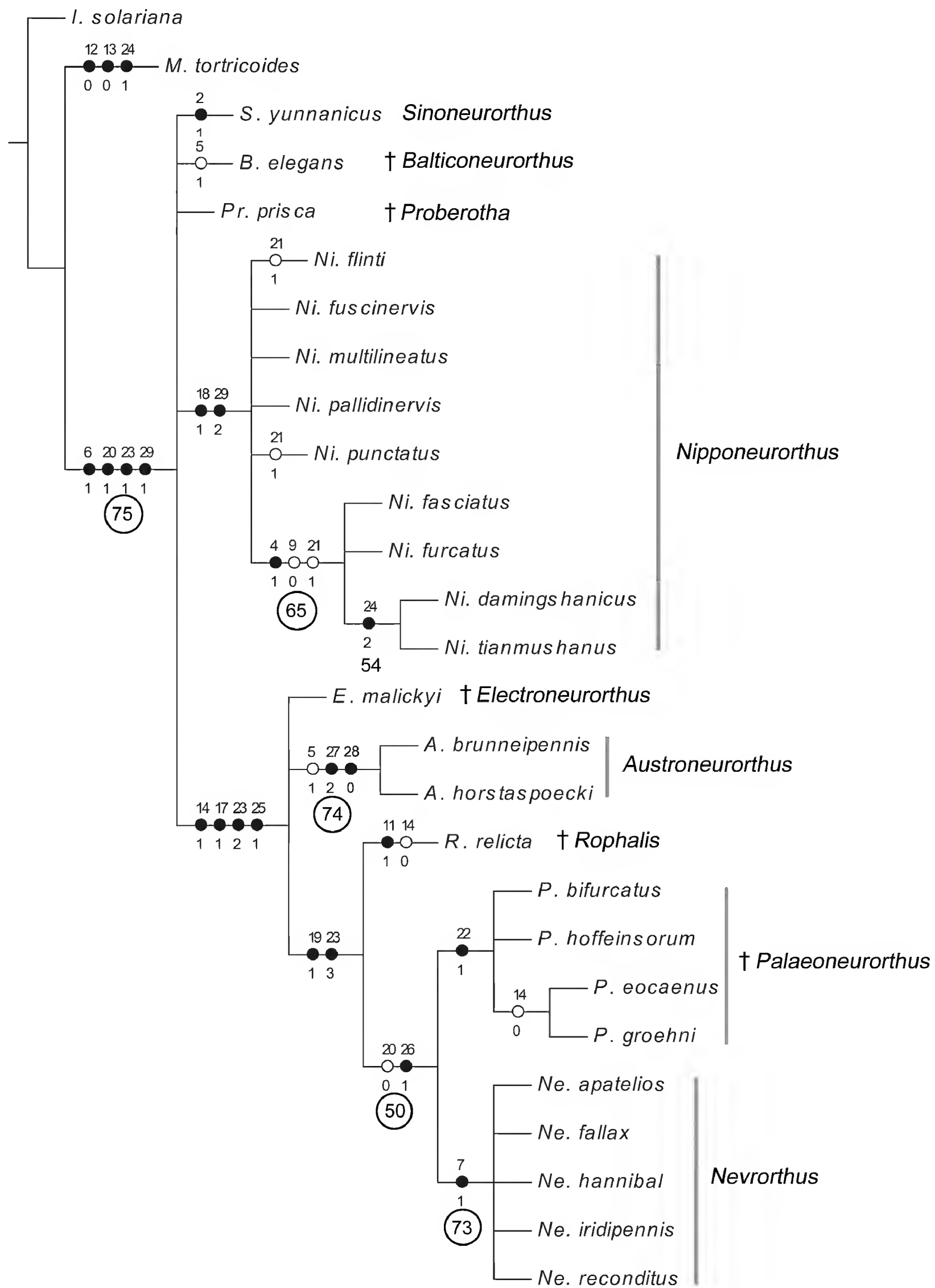


Figure 18. Strict consensus tree of 40 MPTs generated from the refined data matrix. Bootstrap support values are shown at nodes. Only unambiguous character changes are shown. Black circles represent unique changes, white circles represent homoplasious changes. The symbol “†” indicates extinct genus.

infer a close relationship between *Austroneurorthus* and *Nevrorthus*. The phylogenetic position of *Sinoneurorthus* is still unclear due to the lack of male specimens, yet it appears to be similar to *Nipponeurorthus* by having the partially branched forewing costal crossveins and similar

modification of bursa copulatrix. Based on the presently reconstructed phylogeny, the Eocene Baltic amber genera of Nevrorthidae appear to be heterogeneous. *Electroneurorthus*, *Rophalis* and *Palaeoneurorthus* were assigned in the same clade with the extant *Austroneurorthus* and

Nevrorthus. *Balticoneurorthus* and *Proberotha* have unresolved phylogenetic positions, while they seem to be relatively basal groups having few apomorphic characters. Alternatively, they might be closely related to *Nipponeurorthus* by having the partially forked forewing costal crossveins and the similar male gonocoxites 9.

The most interesting discovery in connection with nevrorthid genital sclerites is the complex constituted by the gonocoxites, gonostyli and gonapophyses of segment 10, which is discernible, e.g. in *Ni. pallidinervis* on one hand, but completely camouflaged in all *Nevrorthus* species on the other hand. In these species it appears as an elongated apex (pseudoapex) of sternite 9. This phenomenon in Nevrorthidae plays a key role in the homologisation of the genital sclerites based on the gonocoxite concept developed in U. Aspöck and H. Aspöck (2008a) which draws upon the hypothesis of traceable gonocoxites, gonostyli and gonapophyses in segment 9, as well as in segments 10 and 11, irrespective of the fact that these segments are highly transformed in connection with their functions in copulation. Additionally, the modifications of these sclerites are important for inferring the intergeneric phylogeny of Nevrorthidae. Moreover, a ring of glands between segments 7 and 8 in males of *Nevrorthus*, between segments 8 and 9 in males of *Austroneurorthus* and several species of *Nipponeurorthus* seems to be a more authentic character since it is apparently more stable than the eversible sacks. The feature may have phylogenetic relevance; however, it cannot be traced reliably in fossil specimens.

Biogeography

The world distribution of Nevrorthidae demonstrates the relictual nature of this family. They are “living fossils” in the sense of Thenius (2000) for several reasons – the disjunct distribution, low number of extant species and the archaic shape of the larval head capsule. Although the number of fossils of Nevrorthidae is continuously growing, those known from the Eocene Baltic amber, as well as from the mid-Cretaceous Burmese amber, provide limited evidence to understand the present-day disjunctive pattern. Their characterisation as faunal elements with respect to glacial refugial centres in the sense of de Lattin (1967) has been discussed for Mediterranean species (H. Aspöck et al. 2001, U. Aspöck and H. Aspöck 2010a), all of them constituting the genus *Nevrorthus*. Refugial centres that would be relevant to *Nipponeurorthus* and *Sinoneurorthus* are poorly understood (Liu et al. 2012, 2014). The biogeographic origin of *Austroneurorthus* remains enigmatic (U. Aspöck 2004).

Questions to be asked concern quite different phenomena.

Why are there no Nevrorthidae either in Nearctic and Neotropical regions or the Afrotropics?

The recently discovered *N. reconditus* answers our old perpetuating question as to why Nevrorthidae are absent in the western Mediterranean – because they are already there! Nonetheless, the question why the genus *Nevrorthus* is lacking in the eastern Mediterranean, still remains.

Present climate change: Recent findings of *N. apatelios* in the Alpine regions of Friuli and Slovenia represent the northernmost records of the family in Europe, thus making it a Central European matter, triggering further hypotheses on the distribution of this puzzling family. Have Nevrorthidae been continuously overlooked north of the Alps? Certainly not! Aquatic insects are in general well explored – new discoveries as the above mentioned are therefore more than surprising. Most probably *N. apatelios* reached Friuli from rivers in northern Italy and survived the last glacial period in extramediterranean-European refugial centres south of the Alps (U. Aspöck and H. Aspöck 2010a).

The surprising discovery of the spectacular *Sinoneurorthus yunnanicus* (Liu et al. 2012) in China and the continuous discovery of new nevrorthid species in eastern Asia (Liu et al. 2014) denote this part of the world as a hot-spot of nevrorthid evolution. These recent findings of Nevrorthidae in mainland China weaken our previous hypothesis that *Austroneurorthus*, and partly also *Nipponeurorthus*, show a coastal distribution pattern (the so-called Tethys distribution pattern) (Starmühlner 1982, U. Aspöck 2004). It becomes clear that some taxa occur far from the sea.

Based on male genitalia, *Nevrorthus* is the sister group of *Austroneurorthus* – however, biogeographically this infers a severe conflict.

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Supplementary material 1

Specimens examined and records on which the distribution maps are based

Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu

Data type: (measurement/occurrence/multimedia/etc.)

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Supplementary material 2

Characters used for the phylogenetic analysis

Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu

Data type: (measurement/occurrence/multimedia/etc.)

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Supplementary material 3

Primary data matrix

Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu

Data type: (measurement/occurrence/multimedia/etc.)

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Supplementary material 4

Strict consensus tree of 7712 most parsimonious trees generated from the primary data matrix

Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu

Data type: (measurement/occurrence/multimedia/etc.)

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New findings of *Flagellisargus* J Zhang, 2012 (Diptera, Brachycera, Archisargidae), with discussion of the placements of some controversial taxa

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Mesozoic China

Abstract

A new species of a new subgenus and a similar known species referred to the genus *Flagellisargus* J Zhang, 2012 are described and illustrated based on a male and a female impression fossils of these flies: *Flagellisargus* (*Changbingisargus*) *parvus* **subgen. et sp. n.** and *Flagellisargus* (*Flagellisargus*) cf. *sinicus* J Zhang, 2012. The latter taxon is the first record of a female *Flagellisargus*. Recently taken out of Archisargoidea, this study concludes that *Flagellisargus* should be an archisargid genus based on the known (male) and new (female) impression fossils. The placement of *Daohugosargus* J Zhang, 2012b is reassessed. It demonstrates close similarities in body structure and wing venation to archisargid flies, and can be retained as an archisargid genus. *Archirhagio mostovskii* J Zhang, 2015 is separated from *Archirhagio zhangi* K Zhang et al., 2009. *Helempis* Ren, 1998 could be, as a separate genus, placed in Archisarginae, Archisargidae.

Introduction

Archisargidae is an important, primitive, extinct family of the Lower Brachycera, Diptera. It is undoubtedly the largest early brachycerous group in the Mesozoic. To date, 55 species referred to 14 genera within two subfamilies have been recorded (J Zhang 2015, Wang et al. 2017). Archisargid flies range from the late Middle Jurassic – early Late Jurassic (Callovian – Oxfordian) through to the Early Cretaceous in Laurasia and Gondwana. The vast majority of archisargids are from the Jurassic “Daohugou Formation” (Daohugou Bed), China (29 species, 11 genera) and the Karabastau Formation, Kazakhstan (17 species, eight genera). Both archisargid-bearing sedimentary rocks formations belong to the same geological age: Callovian or Oxfordian (J Zhang 2015), and contain more than 82% of species total. Only a few species occur in the Jurassic Haifanggou Formation, China, Shara-Teg Bed, Mongolia, Talbragar Fish Bed, Australia and the Lower

Cretaceous Yixian Formation, China (Rohdendorf 1938, Mostovski 1996a,b, 1997, J Zhang and H Zhang 2003, K Zhang et al. 2007a,b, 2008, 2009, 2010a,b, J Zhang 2010, 2012a,b, 2015, Oberprieler and Yeates 2012, Wang et al. 2017). An updated list of all the archisargid species is presented herein (see Table 1). Among them, the placement of *Helempis yixianensis* Ren, 1998 has been transformed. A recently erected species *Archirhagio gracilentus* Wang et al., 2017 and a new species *Flagellisargus* (*Changbingisargus*) *parvus* sp. n. described below are also supplemented (see Table 1).

Material and methods

Material. The specimens of shale fossil impression of a male and a female archisargid flies described herein are deposited in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), the Chinese Academy

Table 1. Species of Archisargidae with ages, localities and strata (updated).

Name	Age	Locality	Stratum
<i>Archirhagio gracilentus</i> Wang et al., 2017	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archirhagio mostovskii</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archirhagio obscures</i> Rohdendorf, 1938	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Archirhagio striatus</i> Zhang & Zhang, 2003	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archirhagio varius</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archirhagio zhangi</i> Zhang et al., 2009	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archisargus maximus</i> Mostovski, 1997	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Archisargus pulcher</i> Rohdendorf, 1938	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Archisargus spurivenius</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Archisargus strigatus</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) antiquus</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) bellus</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) daohugouensis</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) hani</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) niger</i> Mostovski, 1997	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Calosargus (Calosargus) tatianae</i> Mostovski, 1997	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Calosargus (Calosargus) talbragarensis</i> Oberprieler & Yeates, 2012	Kimmeridgian	Gulgong, Australia	Talbragar Fish Bed
<i>Calosargus (Calosargus) tenuicellulatus</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Calosargus) validus</i> Zhang et al., 2007	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Pterosargus) sinicus</i> Zhang, 2010	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Calosargus (Pterosargus) thanasymus</i> Mostovski, 1997	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Daohugousargus eximius</i> (Zhang et al., 2008)	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Flagellisargus (Changbingsargus) parvus</i> sp. n.	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Flagellisargus (Flaggelisargus) robustus</i> Zhang, 2012	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Flagellisargus (Flaggelisargus) sinicus</i> Zhang, 2012	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Flagellisargus (Flaggelisargus) venustus</i> Zhang, 2012	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Helempis yixianensis</i> Ren, 1998	Early Cretaceous	Huangbanjigou, China	Yixian Formation
<i>Mesosolva angustocellulata</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva balyshevae</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva daohugouensis</i> Zhang & Zhang, 2003	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Mesosolva dolosa</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva hennigi</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva huabiensis</i> (Hong, 1983)	Callovian–Oxfordian	Yujiagou, China	Haifanggou Formation
<i>Mesosolva imperfecta</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva karataviensis</i> (Mostovski, 1996)	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva longivena</i> Mostovski, 1996	Late Jurassic	Shara-Teg, Mongolia	Shara-Teg Bed
<i>Mesosolva parva</i> Hong, 1983	Callovian–Oxfordian	Yujiagou, China	Haifanggou Formation
<i>Mesosolva rohdendorfi</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Mesosolva sinensis</i> Zhang et al., 2010	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Mesosolva zhangae</i> Zhang, 2012	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Novisargus rarus</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Origoasilus pingquanensis</i> Zhang et al., 2011	Early Cretaceous	Yangshuling, China	Yixian Formation
<i>Ovisargus gracilis</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Ovisargus singulus</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Parvisargus malus</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Parvisargus peior</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Sharasargus fortis</i> Zhang et al., 2008	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Sharasargus maculus</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Sharasargus oresbia</i> (Ren, 1998)	Early Cretaceous	Huangbanjigou, China	Yixian Formation
<i>Sharasargus ruptus</i> Mostovski, 1996	Late Jurassic	Shara-Teg, Mongolia	Shara-Teg Bed
<i>Sharasargus spiniger</i> Mostovski, 1996	Callovian–Oxfordian	Karatau, Kazakhstan	Karabastau Formation
<i>Sinallomyia ruderalis</i> (Ren, 1998)	Early Cretaceous	Huangbanjigou, China	Yixian Formation
<i>Tabanisargus daohugous</i> Zhang, 2015	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Uranorhagio asymmetricus</i> (Zhang et al., 2010)	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Uranorhagio daohugouensis</i> Zhang et al., 2010	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed
<i>Uranorhagio deviatu</i> s Zhang et al., 2010	Callovian–Oxfordian	Daohuguo, China	Daohugou Bed

of Sciences, no. NIGP DHG01701 and no. DHG01702. The fly-bearing sedimentary rocks of the “Daohugou Formation” (Daohugou Bed) are located near the village of Daohugou, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Illustrations. Specimen descriptions, photomicrographs and line drawings were done without immersion with the exception of photographs of details of the antennae and tibial spurs. The line drawings were produced with the aid of a camera lucida and the digital photomicrographs were taken using a stereomicroscope.

Colour described here refers to that of the fossil, where patterning is preserved.

Wing venation terminology follows that of Wootton and Ennos (1989) and Shcherbakov et al. (1995). The cell traditionally named the anal cell is, in fact, considered to be the cubital cell herein.

Taxonomy

Archisargoidea Rohdendorf, 1962

Archisargidae Rohdendorf, 1962

Archisarginae Rohdendorf, 1962

Flagellisargus J Zhang, 2012a

Flagellisargus (Changbingisargus) subgen. n.

<http://zoobank.org/A0D230D5-38BB-4401-8B50-5DB9116C2420>

Type-species. *Flagellisargus (Changbingisargus) parvus* sp. n. (by monotypy)

Included species. The type species only.

Diagnosis. Small-size archisargid flies (body excluding antenna and genitalia less than 5 mm long); antennal scape long; arista (or stylus) absent; fork of R4+5 shallow, distad of level of R2+3 end; R5 ending before wing tip; discal cell short and wide (nearly 2.3 times as long as wide).

Etymology. From Chinese “changbing” (long scape), and sargus referring to the Recent genus *Sargus*.

Distribution. Jurassic, China.

Remarks. The subgenus *Flagellisargus (Flagellisargus)* stat. n. includes three known species: *Flagellisargus (Flagellisargus) robustus* J Zhang, 2012a, *Flagellisargus (Flagellisargus) sinicus* J Zhang, 2012a and *Flagellisargus (Flagellisargus) venustus* J Zhang, 2012a. Among them, the first and the third species are erected based on nearly complete male flies, the second one with head and abdomen missing. This known subgenus differs from *Flagellisargus (Changbingisargus)* subgen. n. in the following aspects: moderate-size archisargid flies (body excluding antenna and genitalia more than 9 mm long); antennal scape short; arista (or stylus) present; fork of R4+5 relatively deep, just at level of R2+3 end; R5 ending just at wing tip; discal cell narrow and long (nearly three times or more as long as wide).

Although the head and abdomen are missing, *Flagellisargus (Flagellisargus) venustus* demonstrates close

similarities in wing venation to that of *Flagellisargus (Flagellisargus) sinicus* and *Flagellisargus (Flagellisargus) robustus*: fork of R4+5 relatively deep, just at level of R2+3 end; R5 ending at wing tip; discal cell narrow and long, nearly 3.5 times as long as wide (Fig. 3A–C). Thus, *Flagellisargus (Flagellisargus) venustus* should be retained in *Flagellisargus (Flagellisargus)* rather than be assigned to *Flagellisargus (Changbingisargus)* subgen. n.

Flagellisargus (Changbingisargus) parvus sp. n.

<http://zoobank.org/6369B635-3716-4AF5-BB41-5375E625DAED>

Figs 1, 2, 3D

Diagnosis. Male archisargid flies 4.9 mm long (excluding antenna); antenna longer than head, scape more than one half of flagellum length; stem of Rs nearly as long as bR4+5; first fork of Rs slightly basad of level of M fork; crossvein r-m linking anterior margin of discal cell near to M fork; crossvein m-m long; section of mM3+4 short; male genitalia large, gonostylus subquadrate with apical denticle medially.

Description. Small male archisargid flies. Body dark brown but antenna, legs and wings yellowish brown (Fig. 1A). Head moderately large, nearly semiglobose; eyes large, holoptic, occupying anterior part of head (Figs 1A, 2A); antenna very long, clavate, nearly 1.7 times as long as head length, scape elongated, nearly 3.7 times as long as wide; pedicel short, subquadrate, wider than long; flagellum elongate-conical, four times as long as wide, ratio of scape, pedicel and flagellum 1.0:0.3:1.7, arista absent (Figs 1B, 2B).

Thorax subovate, longer and wider than head (Figs 1A, 2A). Wing narrow and long, about 3.1 times as long as wide, C not circumambient, terminating just at wing tip; C, Sc, R1 and Rs clearly stouter than M and its branches; Sc long, more than one half of wing length; R1 straight, nearly third-fourths of wing length; origin of Rs slightly basad to wing midlength, Rs stem short, nearly as long as section bR4+5; first fork of Rs basad to d base; R2+3 straight, ending at C far apart from R1 end; section dR4+5 straight, nearly seven times as long as section bR4+5, 3.8 times as long as R5, R4+5 fork distad to level of R2+3 end, R4 slightly shorter than R5, both veins dR4+5 and R5, more or less, not in line, R5 slightly curved downwards, ending at C clearly before wing tip; ratio of costal sections Sc-R1, R1-R2+3, R2+3-R4 and R4-R5 1.0:0.7:0.4:0.3; ratio of Rs, bR4+5, dR4+5 and R5 1.0:1.0:6.5:1.9; r-m shorter than bR4+5, meeting anterior margin of d close to its base; ratio of bM1+2 and dM1+2 1.0:4.3; M1 slightly arched intermediately; M2 and M3+4 straight, bM2 nearly a quarter of m-m length; ratio of bM3+4, mM3+4 and dM3+4 1.0:0.4:1.9; cell br slightly wider but shorter than cell bm; discal cell hexagonal, about 2.3 times as long as wide; m-cu relatively short, its posterior end distad to M fork; cell cu (traditionally anal cell) narrow, widely open (Figs 1A, 2A). Femur of hindleg moderately long and stout, clavate, nearly reach-

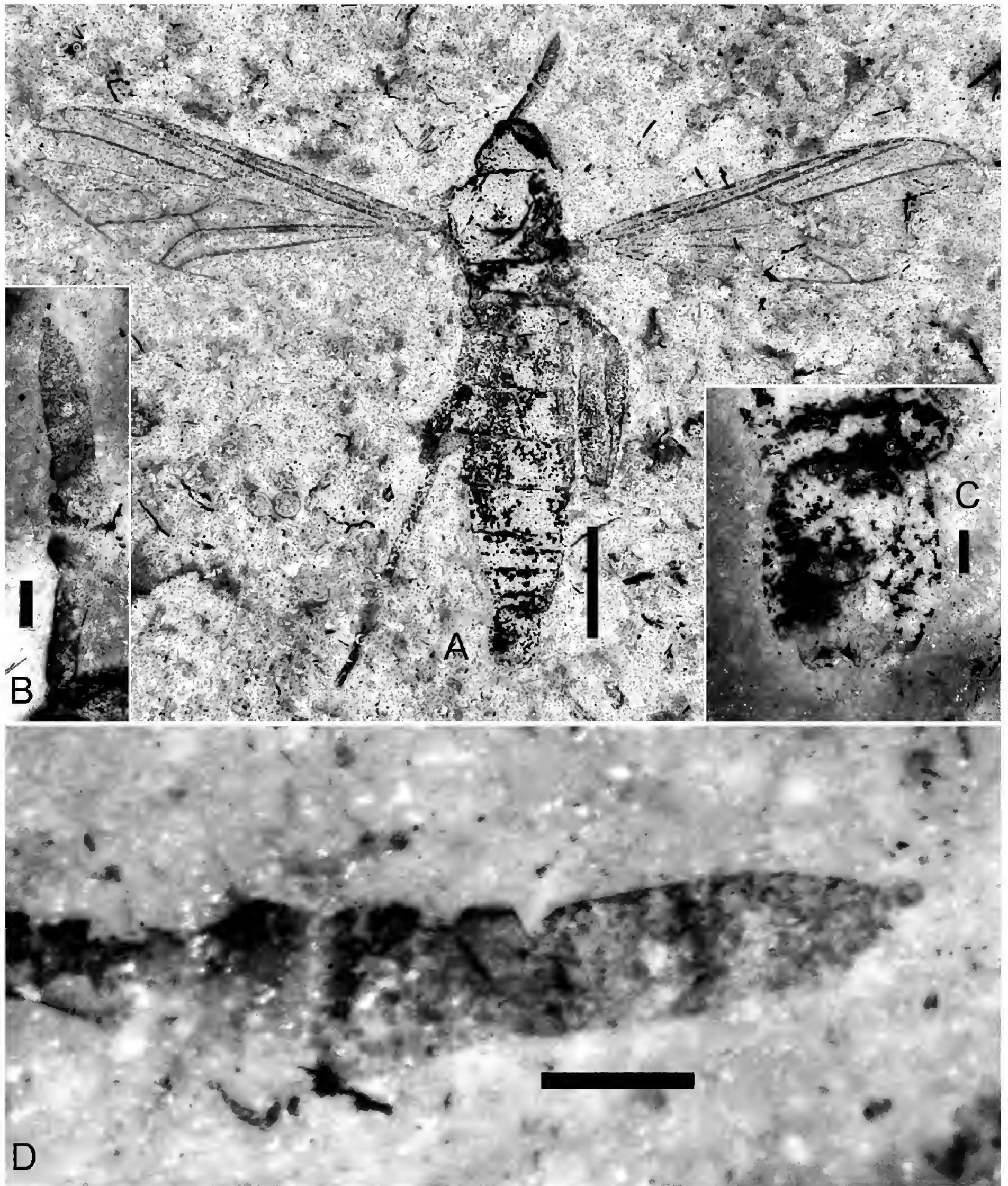


Figure 1. *Flagellisargus* (*Changbingisargus*) *parvus* subgen. et sp. n., photomicrographs, holotype NIGP DHG01701, **A** habitus (dorsal view), **B** antenna, **C** male genitalia, **D** enlarged flagellum. Scale bar 1 mm (**A**), 0.1 mm (**B**, **C**, **D**).

ing posterior margin of fourth abdominal segment, tibia shorter and slightly narrower than femur, tarsus ill-preserved, cylindrical, distinctly thinner than tibia.

Abdomen with seven segments visible, nearly ovate-oblong, fourth widest, and nearly as wide as thorax, 1.8 times longer than head (excluding antenna) and thorax combined; genitalia rather large, subovate, longer

but narrower than seventh abdominal segment, gonocoxite more or less oblong with its inner and outer margins slightly curved outwards, gonostylus subquadrate, wider than long, with a triangular apical denticle curved upwards, aedeagus invisible (Figs 1C, 2C).

Dimensions. Holotype (NIGP DHG 201701): length of body, 4.9 mm; head (excluding antenna), 0.7 mm;

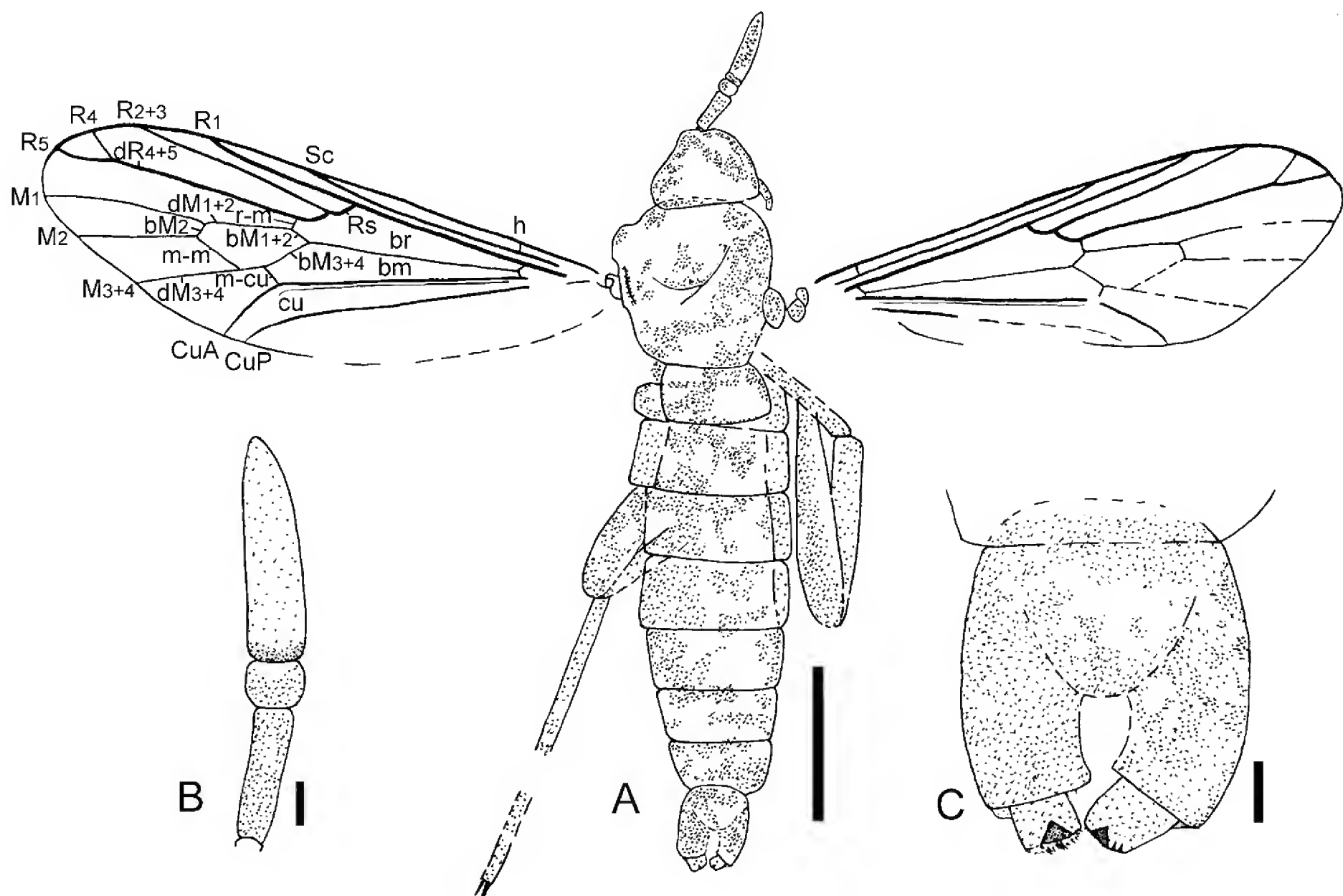


Figure 2. *Flagellisargus (Changbingisargus) parvus* subgen. et sp. n. line drawings of holotype NIGP DHG01701, **A** habitus (dorsal view), **B** antenna, **C** male genitalia. Scale bar 1 mm (**A**) 0.1 mm, (**B**, **C**).

thorax, 1.0 mm; abdomen (including genitalia), 3.2 mm. Length of wing, 3.8 mm, width of wing, 1.2 mm.

Distribution. The “Daohugou Formation” (Daohugou Bed), Callovian-Oxfordian; Daohugou, Wuhua, Ningcheng, Inner Mongolia, China.

Remarks. It should be pointed out that the antennal flagellum (first flagellomere) is ill-preserved near to its base. On first view, it may look like the flagellum has two (or multi) flagellomeres (Figs 1B, 2A), but, the flagellum is, in fact, unsegmented (Figs 1D, 2B).

Flagellisargus (Flagellisargus) J Zhang, 2012a, stat. n.

Type species. *Flagellisargus (Flagellisargus) sinicus* J Zhang, 2012a

Included species. *Flagellisargus (Flagellisargus) robustus* J Zhang, 2012a, *Flagellisargus (Flagellisargus) sinicus* J Zhang, 2012a and *Flagellisargus (Flagellisargus) venustus* J Zhang, 2012a.

Diagnosis. Moderate-size archisargid flies (body excluding antenna and genitalia more than 9 mm long); antennal scape short; arista (or stylus) present; fork of R4+5 relatively deep, just at level of R2+3 end; R5 ending just at wing tip; discal cell narrow and long (nearly three times or more as long as wide).

Distribution. Jurassic, China.

***Flagellisargus (Flagellisargus) cf. sinicus* J. Zhang, 2012a**

Fig. 4

2012a *Flagellisargus sinicus* J Zhang, 879–880, figs 1–3.

Description. Moderate-size female archisargid fly; body yellowish brown (Fig. 4A). Head moderately large, nearly semiglobose; eyes large, dichoptic, occupying most parts of head; antenna long, clavate, nearly 1.5 times as long as head length, scape not elongated, slightly longer than wide, pedicel short, subquadrate, wider than long, flagellum elongate-conical, nearly three times as long as wide, with a darkish brown longitudinal furrow near to its outer margin and connecting base of arista which is darkish brown, stylate, and distinctly curved inwards, ratio of scape, pedicel and flagellum 2.0:1.0:9.0, arista (or stylus) about a quarter of flagellum length (Fig. 4B).

Thorax nearly globose, as long as wide, slightly wider than head (Fig. 4A). Wing narrow and long, about 3.5 times as long as wide, C terminating at wing tip; C, Sc, R1 and Rs clearly stouter than M1 and M2; Sc long, more than one half of wing length; R1 straight, nearly fourth-fifths of wing length; origin of Rs slightly basad to wing midlength, Rs stem short, nearly as long as section bR4+5; R2+3 straight, ending at C far apart from R1 end; section dR4+5 straight, nearly four times as long as section bR4+5, 3.7 times as long as R5, R4+5 fork at level

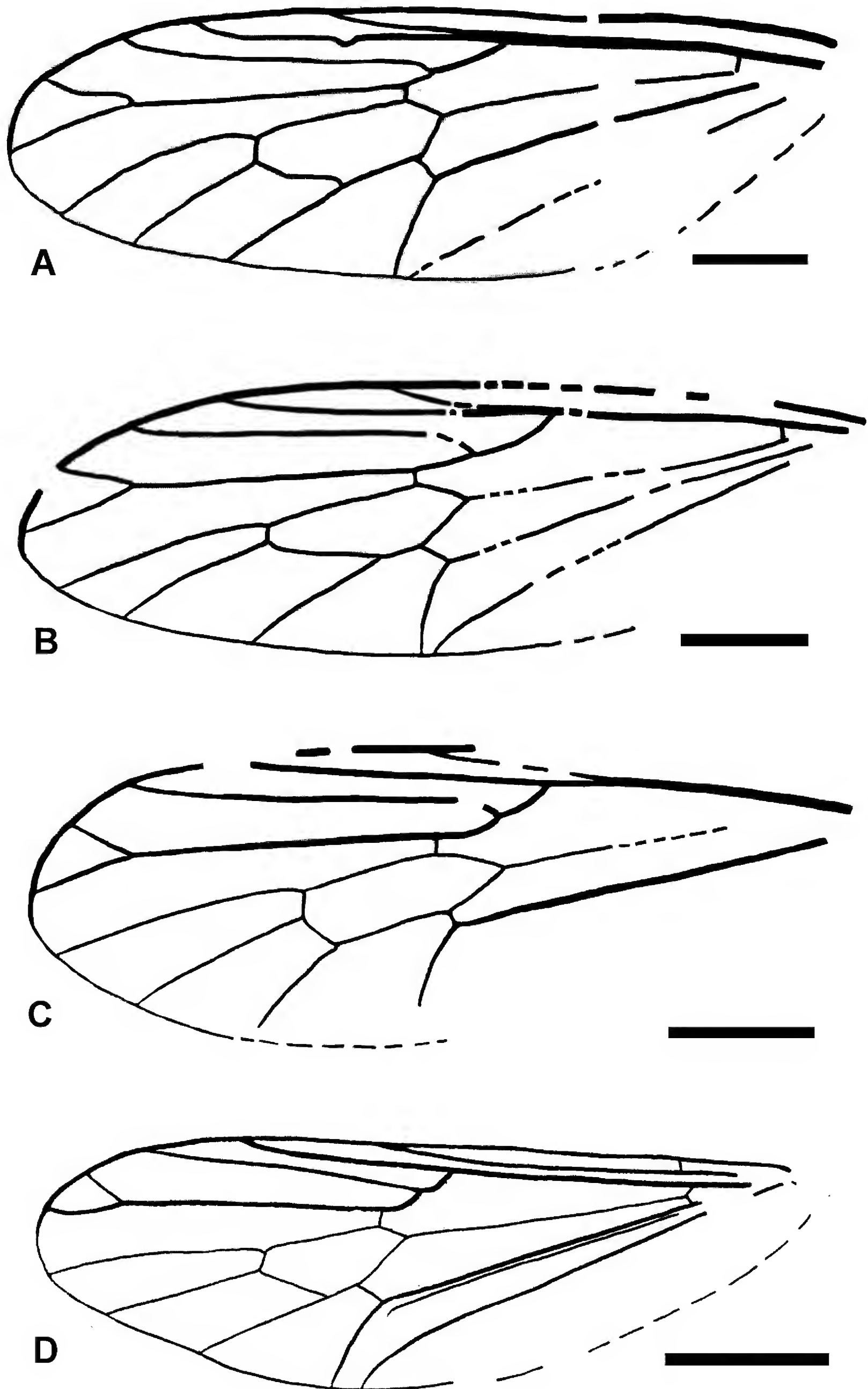


Figure 3. Difference and similarity between four sets of wings, line drawings of holotypes, **A** *Flagellisargus (Flagellisargus) sinicus* J Zhang, 2012a, **B** *Flagellisargus (Flagellisargus) venustus* J Zhang, 2012a, **C** *Flagellisargus (Flagellisargus) robustus* J Zhang, 2012a, **D** *Flagellisargus (Changbingisargus) parvus* subgen. et sp. n. Scale bar 1 mm.

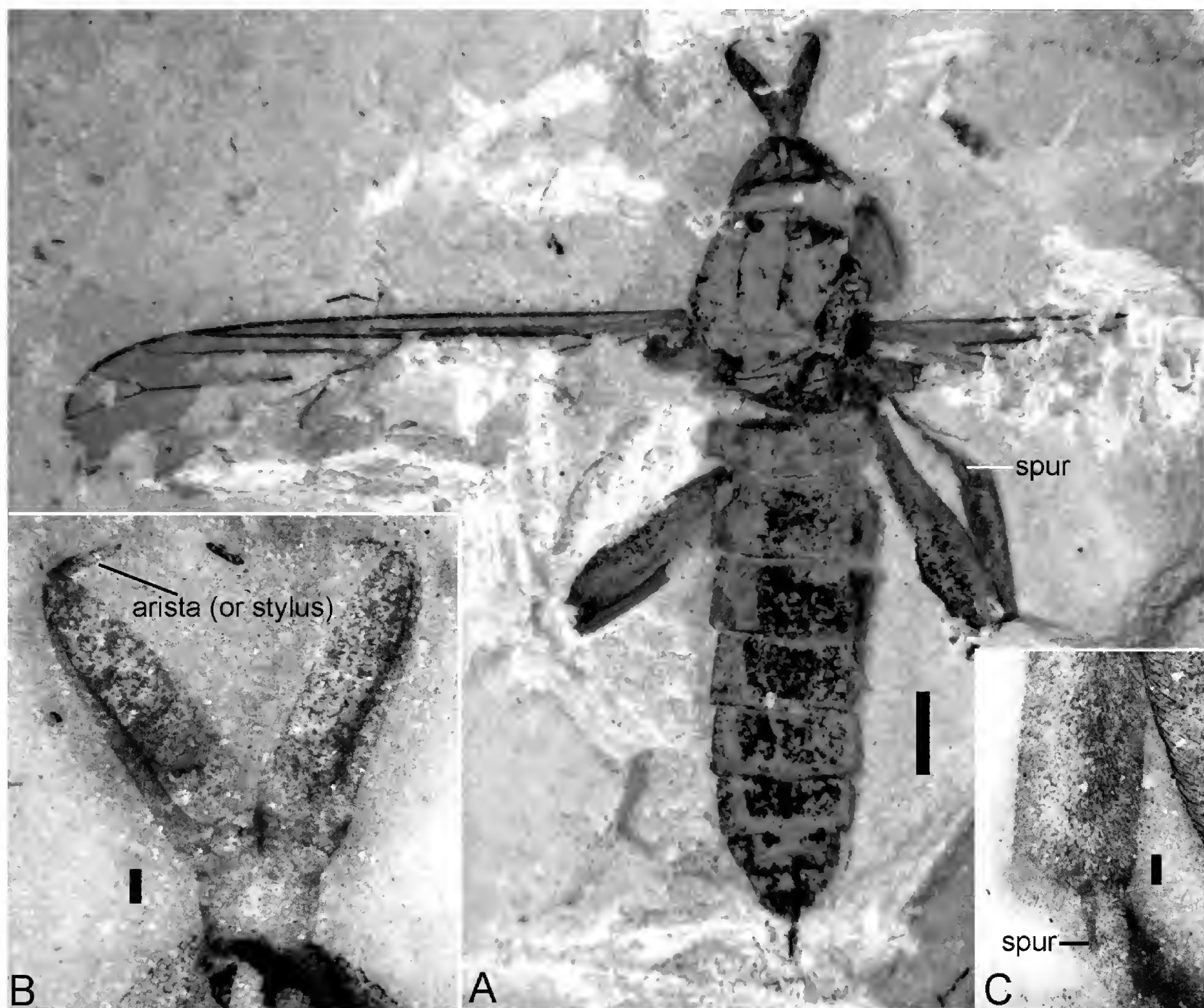


Figure 4. *Flagellisargus* (*Flagellisargus*) cf. *sinicus* J Zhang, 2012a, photomicrographs, NIGP L201702, **A** habitus (dorsal view), **B** antennae, **C** tibial spur of hindleg. Scale bar 1 mm (**A**), 0.1 mm (**B**, **C**).

of R2+3 end, R4 shorter than R5, both veins dR4+5 and R5, more or less, not in line, R5 slightly curved downwards, ending at wing tip; ratio of costal sections Sc-R1, R1-R2+3, R2+3-R4 and R4-R5 1.0:0.3:0.4:0.4; ratio of Rs, bR4+5, dR4+5 and R5 1.0:1.0:4.1:1.8; M1 and M2 almost straight, subparallel (Fig. 4A). Femur of hindleg long and stout, clavate, nearly reaching posterior margin of third abdominal segment, tibia at least with a needle-like spur, and shorter than width of tibia (Fig. 4C).

Abdomen with nine segments visible, nearly cylindrical, just a little narrower than thorax, 1.9 times longer than head (excluding antenna) and thorax combined; each of tergites with a wide, longitudinal, intermediate marking which is darkish brown; apex of abdomen with a sclerotized, needle-like ovipositor, and slightly longer than ninth segment (Fig. 4A).

Dimensions. NIGP DHG 201702: length of body (excluding antenna and ovipositor), 9.6 mm; head, 1.3 mm; thorax, 2.1 mm; abdomen (excluding ovipositor), 6.2 mm; ovipositor ca. 0.5 mm. Length of wing, 7.9 mm, width of wing, ca. 2.3 mm.

Distribution. The “Daohugou Formation” (Daohugou Bed), Callovian-Oxfordian; Daohugou, Wuhua, Ningcheng, Inner Mongolia, China.

Remarks. On the following characters, this fly could be assigned to *Flagellisargus* (*Flagellisargus*): body (excluding antenna and ovipositor) moderate-size (more than 9 mm long); antennal scape short (not elongated); arista (or stylus) well developed (about a quarter of flagellum length); fork of R4+5 just at level of R2+3 end; and R5 ending at wing tip.

Owing to having special characteristics (antennal flagellum with a darkish brown longitudinal furrow near to its outer margin and connecting base of arista and a tibial spur of hindleg well developed) this specimen shows close similarities in antennal and leg’s structures to that of the known species *Flagellisargus* (*Flagellisargus*) *sinicus*. Unfortunately, its wing is incompletely preserved, and the discal cell, posterior branch of M, CuA, CuP and crossvein m-cu are rather ambiguous or invisible. For this reason, this impression fly could only be identified as *Flagellisargus* (*Flagellisargus*) cf. *sinicus*.

Discussion

Recently, Grimaldi and Barden (2016) proposed a single most-parsimonious tree indicating the relationships within the superfamily Archisargoidea. They considered that three genera possessing the plesiomorphic condition of unmodified (non aculeate) female terminalia are not basal to Archisargoidea: *Daohugosargus* J Zhang, 2012b, *Orientosargus* J Zhang, 2012b and *Uranorhagio* K Zhang, 2010. Meanwhile, “*Flagellisargus* has a plesiomorphic, non stylate type of antenna and may also lie outside the Archisargoidea sensu stricto, but this would need to be confirmed with female specimens (only males presently are known)” (Grimaldi and Barden 2016: 17).

However, this study argues that *Flagellisargus* has a well developed arista (or stylus) although it is short. This crucial character had been illustrated in the original generic diagnosis and specific descriptions (J Zhang 2012a: 879, 881, Figs 3, 7). Furthermore, the female *Flagellisargus* has been discovered, and described herein. *Flagellisargus* (*Flagellisargus*) cf. *sinicus* has a sclerotized, needle-like ovipositor (Fig 4A). It is clear that *Flagellisargus* should be an archisargid genus even according to the alternative classification proposed by Grimaldi and Barden (2016).

As for *Daohugosargus*, this genus was proposed for *Sharasargus eximius* K Zhang et al., 2008, which is a monotypic genus based on an incomplete impression fly with terminal abdominal segments missing (K Zhang et al. 2008). Its sex is uncertain. It is difficult to see how this genus could be distinguished as a female fly, let alone with unmodified (non aculeate) female terminalia. *Daohugosargus* demonstrates plesiomorphic similarities in body structures (as preserved) and in wing venation to those uncontested archisargids, and differs only from them by the characteristic vein R2+3 which is short, S-shaped, and arising late from Rs. It would be unreasonable to move this genus out of the superfamily Archisargoidea based only on this difference. This study considers that *Daohugosargus* is related rather to Archisargidae, Archisargoidea than to any other superfamilial groups.

Furthermore, the conclusion is debatable whether genera having non-aculeate female terminalia lie outside of Archisargoidea. For example, there are two species, *Archirhagio striatus* J Zhang et H Zhang, 2003 and *Archirhagio varius* J Zhang, 2015, belonging to the archisargid genus *Archirhagio* Rohdendorf, 1938 that need consideration. The former species has a highly sclerotized, aculeate ovipositor; while, the latter one possesses a blunt, enlarged, fleshy, hook-like ovipositor (Wang et al. 2017: Figs 4D, E, originally the “ovipositor” was labelled as a “hypogynial valve”). However, *Archirhagio varius* cannot be excluded from *Archirhagio* based on its species diagnosis although it has a non-aculeate female terminalia. Another example is the two species of *Ovisargus* Mostovski, 1996: *O. gracilis* Mostovski, 1996 and *O. singulus* J Zhang, 2015. The former species has an aculeate ovipositor but the latter one has a podgy, conical (non aculeate) ovipositor. *O. singulus* should be assigned to *Ovisargus* based on the similarities in body structures and wing venation to that of *O. gracilis*

regardless of the ovipositor. In addition, an aculeate ovipositor has evolved homoplastically in Diptera. It occurs in various groups, including a few Tipulidae, Phoridae, Pipunculidae, some Conopidae, Tephritoidea, Cryptochaetidae and Tachinidae (Pritchard 1983, Feener and Brown 1997, Skevington & Dang 2002, Stireman 2006, Grimaldi et al. 2011, Q Zhang et al. 2016). None of these groups (superfamilies or families) are distinguished based only on the specialized ovipositor. It is evident that the aculeate ovipositor is a convergent development in functional morphology, and does not reveal relationships between these taxa.

Using a geometric morphometric analysis, Wang et al. (2017) reviewed and revised the classification of *Archirhagio*. They redefined the diagnosis of *Archirhagio zhangii* K Zhang et al., 2009, and proposed *Archirhagio mostovskii* J Zhang, 2015 to be a junior synonym for *Archirhagio zhangii* based mainly on some similarities of wing venation and shape of abdominal segments. This study argues that both species were erected based on almost complete impression fossils of the male flies. As the placement is debatable, an overall, further comparative analysis in body structures and wing venation was necessary. Wang et al. (2017) ignored the sharp difference between both holotypes in some key taxonomic characteristics. *Archirhagio mostovskii* differs from *Archirhagio zhangii* in the following aspects: (1) male holoptic vs male dichoptic; (2) markings on abdominal tergites differ sharply; (3) size and shape of wing and wing venation differ distinctly; and (4) male genitalia differ distinctly. Thus, *Archirhagio mostovskii* can be separated from *Archirhagio zhangii*. Some detailed explanations are given as follows. In Diptera, the eyes of most families are holoptic (Cumming and Wood 2009); only a few families have a dichoptic male that is used in the family diagnosis in Lower Brachycera, e.g. Asilidae and Xylophigidae (Fisher 2009, Woodley 2009a). It is clear that the condition (male holoptic or dichoptic) is an important diagnosis for the identification of the Lower Brachycera. Both species, *Archirhagio mostovskii* and *Archirhagio zhangii*, are erected based on males, the former species having holoptic eyes with a very long midline (J Zhang 2015: Figs 2B, 4A); in contrast, the latter one has dichoptic eyes, which are widely separate (K Zhang et al. 2009: Fig. 2). It is impossible that the different compound eye types of the male mentioned above occur in the same species. On the basis of these crucial taxonomic characters, *Archirhagio mostovskii* should be separated from *Archirhagio zhangii*.

Secondly, the shape and arrangement of the abdominal markings frequently provide useful taxonomic characters for dividing various groups of the Lower Brachycera, at least at species level, and many such studies have been published (Jones and Anthony 1964, Smith 1989, Woodley 2009a,b, etc.). *Archirhagio zhangii* shows each of abdominal tergites I-VI with a patch at the posterolateral corner (a left patch in segments II-IV is also present but badly preserved to judge from the original photomicrograph – see K Zhang et al. 2009: Fig. 1A, Fig. 5B herein). In contrast, *Archirhagio mostovskii* has a wide, medially longitudinal stripe and a wide transverse band along the

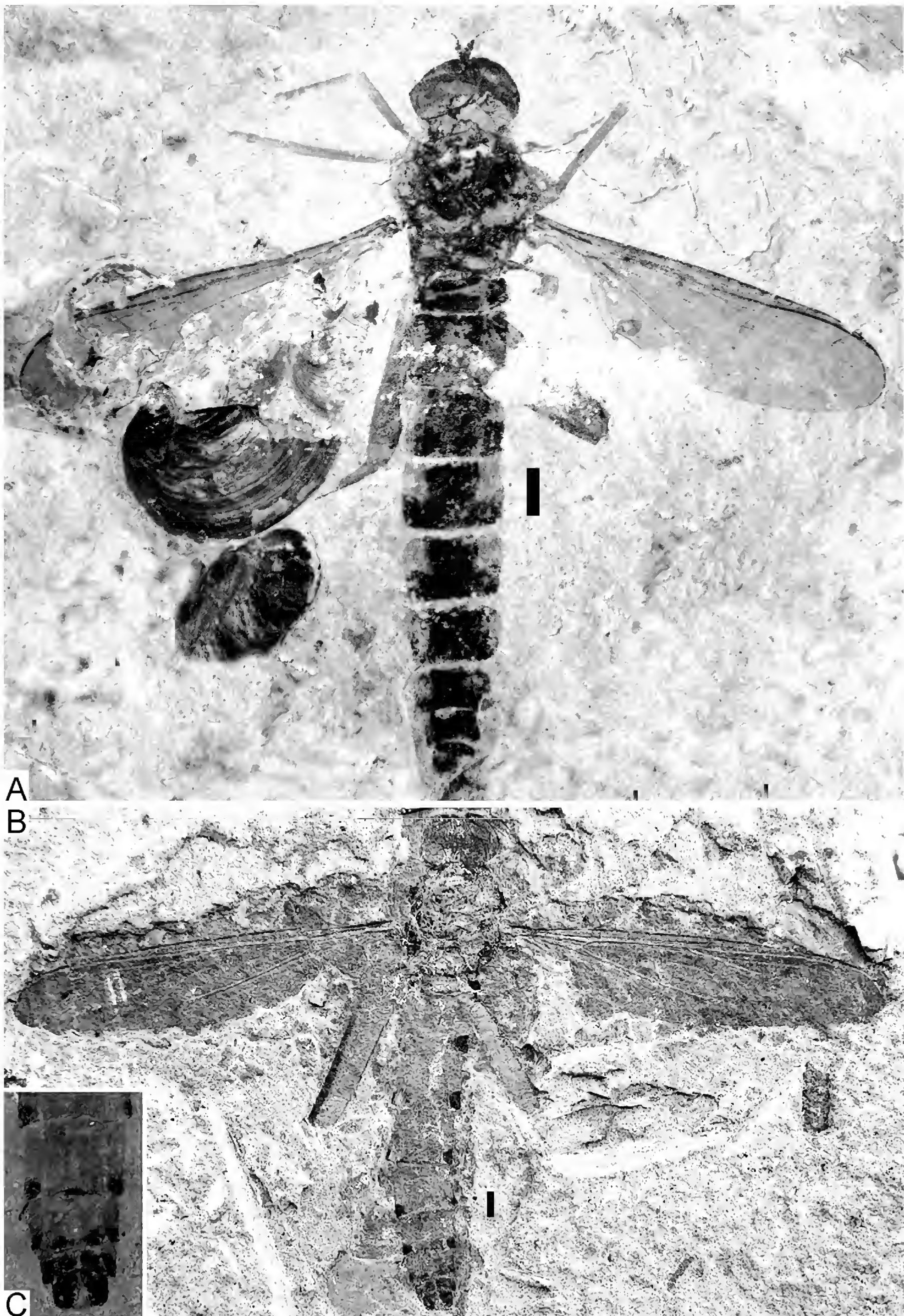


Figure 5. *Archirhagio mostovskii* J Zhang, 2015 and *Archirhagio zhangii* K Zhang et al., 2009, photomicrographs of holotypes (males) **A** *Archirhagio mostovskii* J Zhang, 2015, **B** *Archirhagio zhangii* K Zhang et al., 2009 (after K Zhang et al., 2009, modified), **C** male terminalia (after K Zhang et al., 2009, modified). Scale bars 1mm.

hind margin on each of the abdominal tergites IV-VII, and the markings occupy almost the whole of tergites I-III (Fig. 5A herein). The sharply different markings on the abdominal tergites indicate that both male holotypes cannot be assigned to one and the same species.

Thirdly, *Archirhagio mostovskii* shows the wings are clearly shorter and wider than that of *Archirhagio zhangii*, (wing 12.1–13 mm long, 3.0–3.4 mm wide, about three times as long as wide vs wing 17.5 mm long, 3.8 mm wide, 4.6 times as long as wide); the wing is about one half of body length in the former species vs about fourth-fifths in the latter one. It should be pointed out that the revised diagnosis of *Archirhagio zhangii* defining body length between 29 and 32 mm, wing length between 20 and 23 mm, is questionable because the holotype of *Archirhagio zhangii* (body 21 mm long, wing 17.5 mm long) and the holotype of *Archirhagio mostovskii* (body 22.2 mm long, wing 12.1–13 mm long) falls distinctly short of that size. This revised diagnosis is related neither to *Archirhagio zhangii* nor to *Archirhagio mostovskii*. Furthermore, in wing venation the character of cell r1 closed or nearly so is an important diagnosis for *Archirhagio mostovskii*, differing from *Archirhagio zhangii*, in which cell r1 is clearly open. This crucial character demonstrates close similarity to that of *Calosargus* Mostovski, 1997, another archisargid genus. Nevertheless, in *Calosargus* the cell r1 is closed before the anterior margin of the wing, which has a very short or relatively long petiole apically [e.g. *Calosargus (Pterosargus) sinicus* J Zhang, 2010 and *Calosargus (Pterosargus) thanasy-mus* Mostovski, 1997]. This key character mainly differentiates *Calosargus* from *Archirhagio*. It is interesting that *Archirhagio mostovskii* is considered as a connecting link between *Archirhagio* and *Calosargus*. On balance, one should keep *Archirhagio mostovskii* as a separate species referred to *Archirhagio* but closely related to *Calosargus*.

Finally, the structural characteristics of male terminalia provide an unparalleled array of taxonomic characters in Diptera (McAlpine et al. 1981). “Male terminalia are a key morphological source of characters used to distinguish species in the vast majority of Diptera families and there are few modern taxonomic studies that do not include illustrations of male terminalia to aid in species diagnoses” (Sinclair et al. 2013). However, Wang et al. (2017) did not describe and illustrate the characteristics of male terminalia in the revised species diagnosis of *Archirhagio zhangii*, although they also commented that the original description of the male terminalia was incorrect. They only supplied two photomicrographs of an unnumbered specimen instead of the holotype male terminalia of *Archirhagio zhangii* (Wang et al. 2017: Figs 4B, C). Furthermore, they claimed that there are no significant modifications in male terminalia across the genus *Archirhagio*, consisting of the reduced ninth tergite, unsegmented gonocoxites, and pair of large parameres (Wang et al. 2017). Meanwhile, without providing any reference and citation, they declared that the terminology “aedeagus” used by J Zhang (2015) is incorrect, and should be instead of paired “parameres” (Wang et al. 2017). These deductions proposed by them clearly run counter to what many dipterists have concluded (McAlpine

et al. 1981, Woodley 1989, Cumming and Wood 2009, Sinclair et al. 2013). This study argues that the kidney-shaped gonocoxite, bipectinate gonostylus and short and stout aedeagus demonstrate *Archirhagio mostovskii* as having distinctly different structures in the male terminalia from the specimens provided by Wang et al. (2017: Figs 4A,B,C). Unfortunately, there is neither description nor line drawing of the male terminalia of *Archirhagio* provided in their article; and thus a further comparison of male terminalia between *Archirhagio mostovskii* and *Archirhagio zhangii* is difficult herein. On the other hand, if those male terminalia investigated by them possess the same structures, then those specimens most likely belong to one and the same species that differs from *Archirhagio mostovskii*. It should be also noted that in Stratiomyomorpha + Muscomorpha sensu Woodley (1989), the aedeagus is indistinguishably fused to the parameral sheath to form the phallus (Cumming and Wood 2009). Currently, Archisargidae is assigned either within or near to the Stratiomyomorpha (Oberprielar and Yeates 2012) or Archisargoidea is probably an extinct sister group to the Muscomorpha (Grimaldi and Barden 2016). In any case, the paired parameres should be indistinguishable in the male terminalia of archisargids [e.g. *Flagellisargus (Flagellisargus) sinicus* – see J Zhang 2012a: Fig. 3] The so-called parameres of *Archirhagio*, an undouble archisargid genus, identified by Wang et al. (2017) should be phallus “(aedeagus sensu authors concerning Stratiomyomorpha and Muscomorpha sensu Woodley, 1989)” (Cumming and Wood 2009).

Originally, the genus *Helempis* Ren, 1998 including two species: *H. yixianensis* and *H. eucalla* Ren, 1998 was placed in Protempididae (Ren 1998). The present author (J Zhang 2012b) thought that the two species could be united into one species, namely *H. yixianensis*, and *Helempis*, as a subgenus, could be transferred into *Ovisargus* referred to Archisardinae, Archisargidae. Through further contrastive studying, it could be reasonable to retain *Helempis* as a separate genus within the Archisarginae, Archisargidae. It differs from *Ovisargus* by the elongated discal cell and the deeper fork of R4+5, which is distinctly basad to R2+3 end.

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Anthropogenic dispersal of a snakefly (Insecta, Neuropterida) – a singular phenomenon or a model case in Raphidioptera?

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Abstract

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Key Words

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The Mediterranean snakefly *Raphidia mediterranea* H. Aspöck, U. Aspöck & Rausch, 1977 – known from many parts of the Balkan Peninsula, several Aegean islands, southern parts of Italy, northwest of Anatolia and a few localities in Eastern Europe, yet not recorded in Central Europe – was surprisingly found with an astoundingly high population density on bushes in the yard of an old farmhouse at a comparatively high altitude (800 m) in Upper Austria, north of the Danube River, in 2013. This spectacular phenomenon was again observed in the following years (2014, 2015, 2016, 2017), and in 2016 the suspicion that the larvae develop in the straw of the thatched roof of the farmhouse could be confirmed by findings of larvae, pupae, and exuviae. It is most likely, that the occurrence of this *Raphidia* species in Austria is to be traced back to a human-caused introduction at some point in time. It remains, however, unknown when and specifically how this event might have occurred.

Morphologically no substantial differences were found between specimens from Greece, Italy and Upper Austria. In addition, the genetic uniformity (using 3 genes: *cox1*, *cox3*, and *28S*) of the populations was verified. This supports an earlier hypothesis that the occurrence of the species, as well as that of *R. mediterranea* in Italy, Anatolia and perhaps elsewhere, may be related to importation of goods involving wood or soil.

A molecular genetic analysis of several *Raphidia* species confirmed the present morphology-based concept of their systematic position.

The means of dispersal of Raphidioptera are largely unknown. We do not know of any other similar cases of anthropogenic dispersal of a snakefly, but it cannot be excluded that human activities may have played a greater role in the dispersal of Raphidioptera than previously assumed. Phylogenomic studies would therefore be promising to solve some of these questions.

Introduction

By the 1960s, it was revealed that the Balkan Peninsula was a distribution (and evolution) centre of the order Raphidioptera with an incredibly high number of spe-

cies (H. Aspöck and U. Aspöck 1965). In the course of the following years, extensive field studies were carried out in various parts of the Balkan Peninsula (H. Aspöck 1987, H. Aspöck et al. 1989, H. Rausch and R. Rausch 2004). These investigations led to the discovery of nu-

merous new species and among them a snakefly species, which – despite slight differences – was morphologically so similar to *Raphidia ophiopsis* Linnaeus, 1758, that we hesitated to separate it from *R. ophiopsis*. However, after discovery of unusually large populations of this taxon in various parts of Greece and in biotopes (e.g. in coastal areas with maquis vegetation) ecologically entirely different from those of *R. ophiopsis*, which is associated with coniferous trees, we decided to describe it as a subspecies of *Raphidia ophiopsis*: *R. ophiopsis mediterranea* (H. Aspöck et al. 1977). In the meantime, the taxon was surprisingly found in Italy (Apulia) and later in northwest Anatolia. In our monograph (H. Aspöck et al. 1991) we argued that the disjunct distribution could hardly be explained by natural dispersal and we therefore considered that human activities might have been a significant cause of the amplification of the distribution of *R. o. mediterranea*. One of our arguments was that *R. o. mediterranea* occurs on the eastern coast of the Apennine Peninsula around Brindisi, a region known for its intensive ship traffic with Greece, which dates back to antiquity. Subsequently, entomologists from Italy found *R. o. mediterranea* in western parts of the Apennine Peninsula, and from this they concluded that *R. o. mediterranea* had not been introduced from Greece to Italy by human activities, but that its occurrence in Italy was due to natural dispersal (Letardi 2002, Letardi and Pantaleoni 1996, Pantaleoni 2005). Meanwhile, the taxon was unexpectedly found in Romania (Kis 1984) and Hungary (Sziráki 1993a, b, 2010). Both latter authors studied the taxon carefully and arrived at the conclusion that *R. mediterranea* is a good

species and not a subspecies of *R. ophiopsis*. Aside from the known and corroborated morphological differences, an important argument for the status of a separate species was the sympatry of both taxa in Romania and Hungary. The arguments of Kis (1984) and Sziráki (1993a) were convincing and accepted by us (H. Aspöck and U. Aspöck 2007, 2013, 2014). Finally, in 2013 *R. mediterranea* was found in the yard and on the outer walls of an old farmhouse, now representing an open-air museum, at a considerably high altitude (800 m) in Upper Austria (Rausch et al. 2016). It was an absolute surprise to find this Mediterranean snakefly in a comparatively cold region of Austria (Figs 1, 2). Moreover, *R. mediterranea* occurs there in an extremely high population density. It was suspected that the larvae develop within the straw covering the roof (Rausch et al. 2016), and this could recently be confirmed (Gruppe et al. 2017) (Figs 3, 4). Thus, the question arose: How has *R. mediterranea* achieved the establishment of a stable population in a locality in Central Europe, which offers unfavourable climatic conditions compared to many other parts of Austria (Fig. 5)? To better evaluate the phylogeographic scenarios of this species, i.e. natural expansion of the distribution range vs. human mediated dispersal, we performed molecular genetic analyses of specimens from Austria, Greece and Italy. The specimens analysed genetically were compared morphologically with specimens from many localities covering the currently known distribution. Moreover, specimens of *R. ophiopsis* from Upper Austria and other parts of Central Europe were included to corroborate the morphological differences between the two taxa.

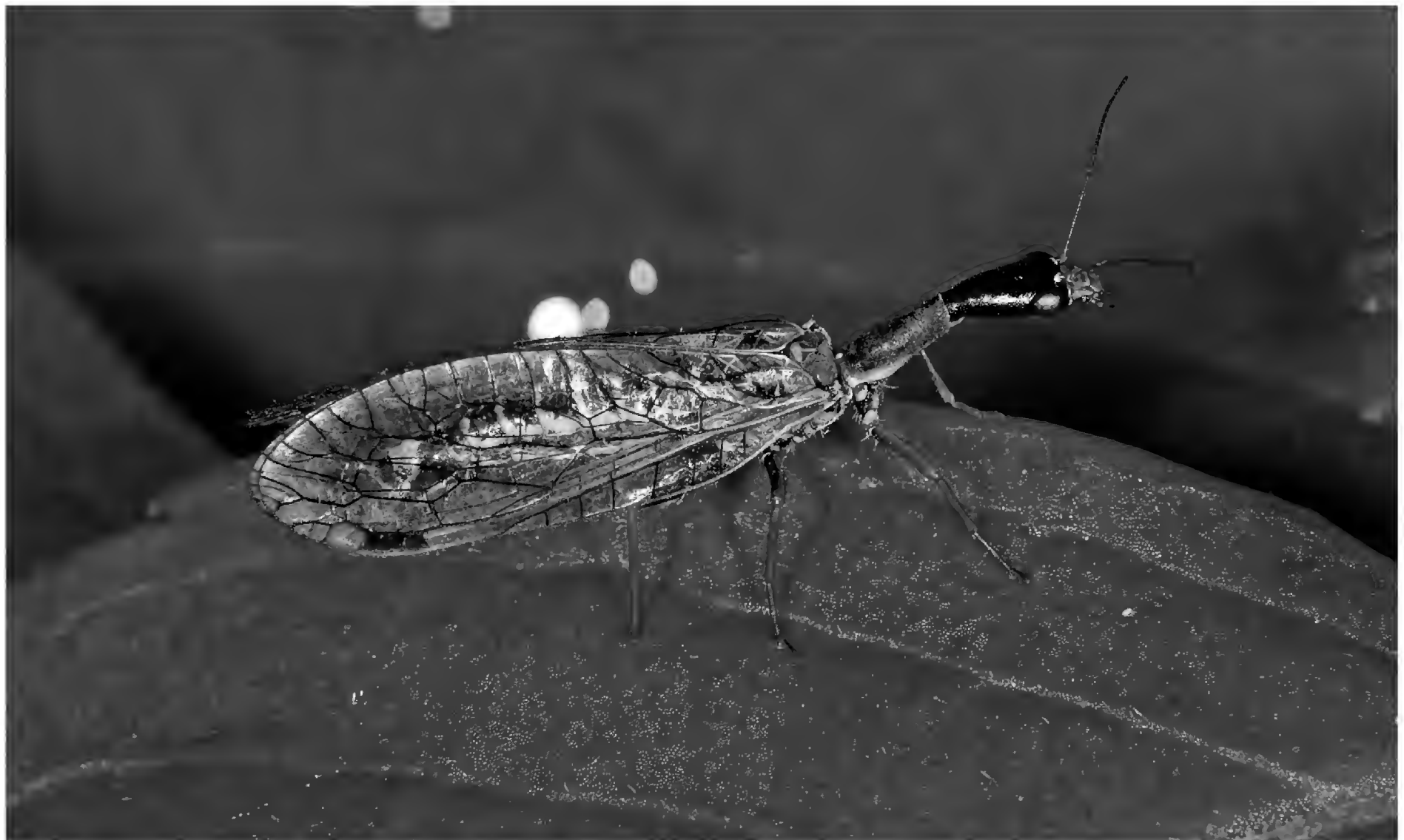


Figure 1. *Raphidia mediterranea*, male, from Pelmburg (Upper Austria). Photo H. Bruckner.



Figure 2. *Raphidia mediterranea*, female, from Pelmberg (Upper Austria). Photo H. Bruckner.



Figure 3. *Raphidia mediterranea*, full-grown larva, from Pelmberg (Upper Austria). Photo H. Bruckner.



Figure 4. *Raphidia mediterranea*, pupa, from Pelmborg (Upper Austria). Photo H. Bruckner.

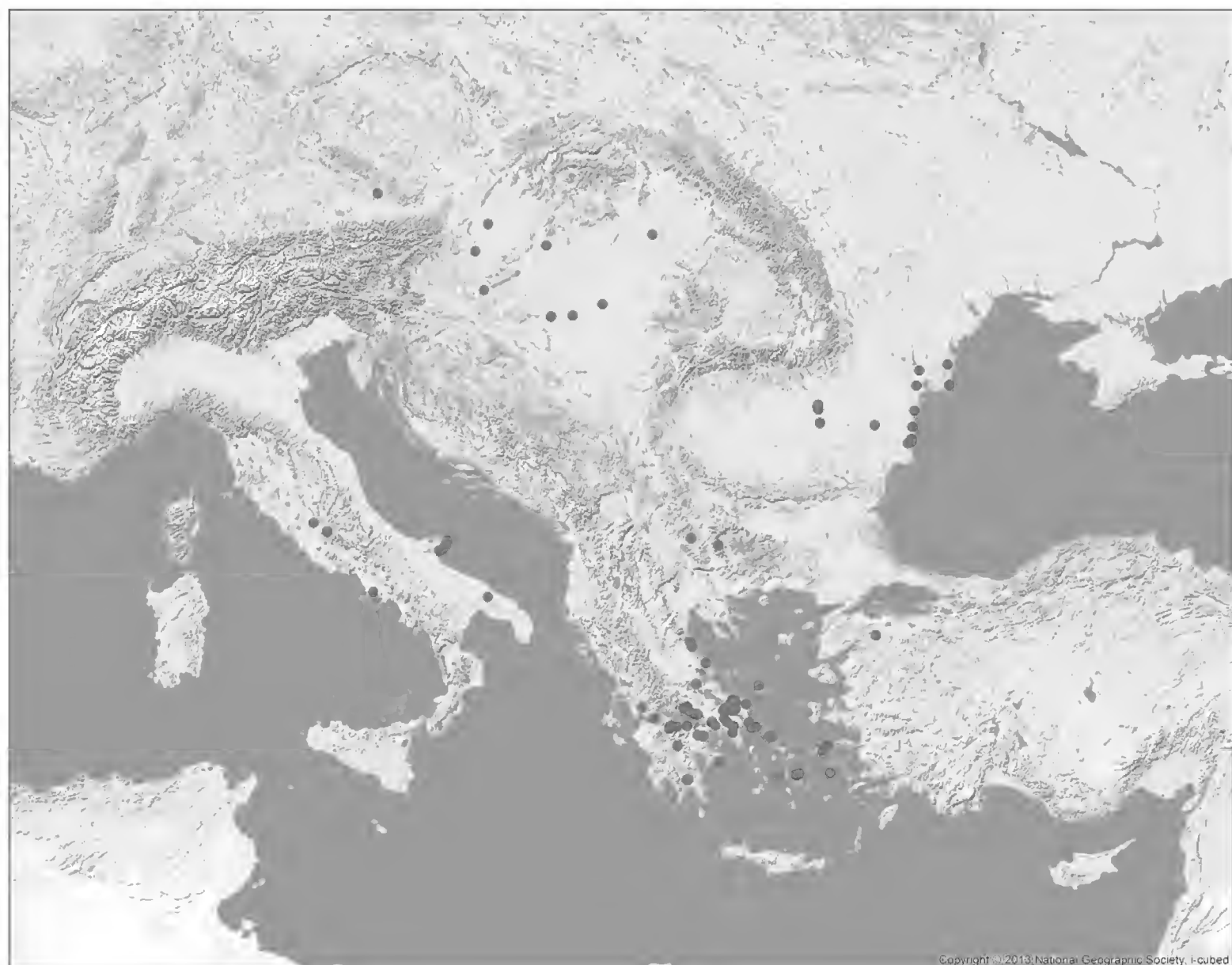


Figure 5. Known distribution of *Raphidia mediterranea* H.A. & U.A. & Rausch. Source of the map see under Material and methods.

Material and methods

Morphological studies

Numerous adults of both sexes of *Raphidia mediterranea* from many localities in Greece, Italy, Anatolia, as well as specimens of *R. ophiopsis* from Upper Austria and other parts of Central Europe were compared with imagines from Pelmberg (Upper Austria) based on the well-known morphological characters of male and female genitalia (H. Aspöck et al. 1991). Genital segments were cleared in KOH and processed in the usual manner described elsewhere.

The distribution map was provided with ArcGis/ArcMap ver. 10.3.1.4959 based on the distribution records provided in the Suppl. material 2. Source of the map: National Geographic-Weltkarte - Content may not reflect National Geographic's current map policy. Sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.

Molecular genetic analysis

For DNA analysis samples of four individuals of *Raphidia mediterranea* were selected, which had been collected in Pelmberg (Upper Austria), Gargano (Italy) and Zachlorou (Peloponnesus, Greece). Moreover, five representatives of the genus were included: *Raphidia ophiopsis* Linnaeus, 1758, *Raphidia alcoholica* H. Aspöck & U. Aspöck, 1969, *Raphidia ulrikae* H. Aspöck, 1964, *Raphidia ariadne* H. Aspöck & U. Aspöck, 1964, and *Raphidia ligurica* Albar-da, 1891. A list of specimens analysed with exact localities is given in Table 1. Tissue samples were taken from one leg of alcohol-preserved specimens with sterile forceps. Vouchers are stored at the Entomological Department of the Museum of Natural History Vienna (NHMW). Remaining DNA is stored in the DNA and Tissue Collection of the Central Research Laboratories at the NHMW.

Marker sequences and laboratory procedures

Two mitochondrial marker sequences were amplified using primers listed in Table 2: (1) A partial sequence of the *cytochrome c oxidase subunit 3* gene (*cox3*) which

has been also used in a previous study on Neuropteri-da, as well as Raphidioptera (Haring and Aspöck 2004; Haring et al. 2011) and (2) the complete sequence of the *cytochrome c oxidase subunit 1* gene (*cox1*) plus partial sequences of the adjacent tRNA genes. In addition, a partial sequence of the *28S rRNA* gene (*28S*) was used as a nuclear marker sequence. The fragment lengths of *cox1* sequences ranged from 1604–1610 bp (due to indels in the flanking tRNA genes). The amplicon length of the *cox3* sequence was 712 bp. The amplicon length of the *28S* sequence was 1155–1161 bp.

DNA extraction was performed using the DNeasy-Blood and Tissue Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions. The final volume of elution buffer was 40 µl. DNA solutions were stored in aliquots to avoid too frequent thawing. Control extractions with pure extraction buffer (without tissue) were prepared. PCR was carried out in an Eppendorf Thermocycler in a volume of 25 µl, containing Taq Polymerase (1.25 units/reaction; QIAGEN, Hilden, Germany) 1 µM of each primer, and 0.2 mM of each dNTP, 1.5 mM MgCl₂, 5 µl Q-Solution, 2.5 µl 10x PCR buffer and 1 µl of template DNA. The PCR protocols were as follows: *cox3*: initial denaturation 94° C (3 min); 35 cycles: 94° C (60 s) / 50° C (30 s) / 72° C (60 sec); final extension at 72° C (10 min). *cox1*: initial denaturation 94° C (3 min); 35 cycles: 94° C (60 s) / 50° C (30 s) / 72° C (60 sec); final extension at 72° C (10 min). *28S*: initial denaturation 94° C (3 min); 35 cycles: 94° C (60 s) / 55° C (30 s) / 72° C (60 sec); final extension at 72° C (10 min). Negative PCR controls were carried out to screen for contaminated reagents: (1) control extractions without tissue and subsequent PCR reactions (i.e. instead of template DNA); (2) PCR reactions with distilled water instead of template. PCR products were purified with the QIAquick PCR Purification Kit (QIAGEN, Hilden, Germany) prior to sequencing. Sequencing (both directions) was performed at Microsynth (Vienna, Austria) using the PCR primes as well as various internal primers (Table 2). Sequences obtained in the present study are deposited in GenBank under the accession numbers listed in Table 1.

Table 1. Specimens analysed genetically in the present study and GenBank accession numbers for *Cox1*, *Cox3* and *28S* sequences.

Species	Sampling locality	Labcode	GenBank		
			Cox1	Cox3	28S
<i>Raphidia mediterranea</i>	Austria, Upper Austria, Pelmberg near Hellmonsödt	Ramed-1	MF975675	MF975666	MF975657
<i>Raphidia mediterranea</i>	Austria, Upper Austria, Pelmberg near Hellmonsödt	Ramed-2	MF975676	MF97567	MF975658
<i>Raphidia mediterranea</i>	Greece, Peloponnesus, Kato Zachlorou	Ramed-3	MF975677	MF975668	MF975659
<i>Raphidia mediterranea</i>	Italy, Puglia, Gargano, Punta Lunga	Ramed-4	MF975678	MF975669	MF975660
<i>Raphidia ariadne</i>	Greece, Crete, W Omalos	Raari-1	MF975679	MF975672	MF975661
<i>Raphidia alcoholica</i>	Greece, Phokis, S Pendayi	Raalc-1	MF975680	MF975671	MF975662
<i>Raphidia ophiopsis</i>	Germany, Bayerischer Wald, Ruckwiesberg	Raoph-1	MF975681	MF975670	MF975663
<i>Raphidia ulrikae</i>	Austria, Styria, Gulsen near Kraubath	Raulr-1	MF975682	MF975673	MF975664
<i>Raphidia ligurica</i>	Italy, Sila Grande, near Viváio	Ralig-1	MF975683	MF975674	MF975665

Table 2. Primers used.

Gene	Primer	Sequence (5'-3')	Reference
Cox3 external primers			
	Arth-cox3-fwd	5'-TAGTTGATTATAGACCATGACC-3'	a
	Arth-cox3-rev	5'-ACATCAACAAAATGTCAATATCA-3'	a
Cox3 internal primers			
	Raph-cox3-1+	5'-ACAAATTCCTTTATTAAATAC-3'	present study
	Raph-cox3-2-	5'-CAWGTAATTGTTAATCCTGA-3'	present study
Cox1 external primers			
	Tyr-myr-1+	5'-CCCATAAATAAATTTACAGTTTA-3'	present study
	Leu-Myr-1-	5'-GCACTATTCTGCCATATTAG-3'	present study
Cox1 internal primers			
	Raph-cox1-int1+	5'-TAGCAGGAGCTATCACTATACT-3'	present study
	Raph-cox1-int2-	5'-ATATAAACTTCTGGATGTCC-3'	present study
	Raph-cox1-int5+	5'-CGAATACCTTTATTTGTATGATC-3'	present study
	Raph-cox1-int4-	5'-AGAATAGGGTCTCCTCCTCC-3'	present study
28S internal primers			
	Raph-28S1+	5'-CAGGGGTAAACCTGAGAAA-3'	b
	Raph-28S-4-	5'-AGCGCCAGTTCTGCTTACC-3'	b
28S external primers			
	Raph28S-3+	5'-AGCTTTGGGTACTTTTCAGGA-3'	b
	Raph28S-2-	5'-ACATGCTAGACTCCTTGGT-3'	b

a: Haring and Aspöck (2004); b: Haring et al. (2011)

Phylogenetic analyses

Raw sequences were manually aligned in BioEdit v.7.1.3 (Hall 1999) and checked for errors. The alignment was straightforward for the three marker sequences and was done in BioEdit v.7.1.3. In *cox1* and *cox3* sequences there were no insertions or deletions, and in the *28S* gene there were only a few indels allowing clear assessment of positional homology. The final alignment of the complete *cox1* gene had a length of 1534 positions. The *cox3* gene had 667 positions and the *28S* gene 1144 positions. As outgroup, *Agulla*, another genus of Raphidiidae was used. The *cox3* and *28S* sequences have been published in our previous paper (Haring et al. 2011; HM543275; HM543340; *Agulla adnixa*). The complete *cox1* sequence was derived from GenBank (FJ207460.1; *Agulla* sp.). By comparing this sequence with published partial *cox1* sequences of *Agulla adnixa* (e.g., KR141904.1), we deduced that the sequence FJ207460.1 is derived from *Agulla adnixa* (which has an identical sequence). As a result, in the concatenated data set, the outgroup sequence was derived from different individuals of the same species, which however appears to be unproblematic in this case.

Bayesian Inference (BI) was used for calculating phylogenetic trees. For BI the best fitting substitution model was determined for each of the three genes as well as codon positions of the protein coding genes by jModelTest v.2.1.5 (Darriba et al. 2012) with the corrected Akaike information criterion (AICc). The BI analyses were calculated using MrBayes v.3.2.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Phylogenetic trees were also calculated from a combined alignment in which all three marker sequences were concatenated (length of alignment: 3345 positions). BI analyses were

run for 7×10^6 generations (2 runs each with 4 chains, one of which was heated), sampling every hundredth tree. The first 25% of trees were discarded as burnin and from the remaining trees a 50% majority rule consensus tree was calculated. In addition, Neighbour Joining (NJ) trees (Saitou and Nei 1987) were calculated. Nodal support of NJ trees was evaluated with nonparametric bootstrapping based on 1000 replicates. These trees are shown to illustrate p distances among taxa in comparison of the three marker sequences.

Results

In former studies (H. Aspöck et al. 1991 and unpublished), based on male and female genitalia, populations of *Raphidia mediterranea* from various localities in Greece, Anatolia, and Italy could not be differentiated from each other. This was confirmed again on the basis of more material, particularly specimens from Pelmburg (Upper Austria) whose morphological characters coincide perfectly with those figured in H. Aspöck et al. (1991). Specimens of the genus *Raphidia* from other parts of Central Europe (except *Raphidia ulrikae*) proved to be conspecific with *Raphidia ophiopsis*.

The DNA sequence analysis revealed that the four specimens of *R. mediterranea* are identical in *cox1* and *28S*, while in *cox3* a single substitution differentiating Ramed-4 from the other (identical) sequences was found. In general, the variation within *28S* was extremely low. Except *R. ligurica*, which shows distances to the other ingroup taxa of 1.08 and 1.35%, respectively, sequences of all other ingroup species differ with p distances below

1% or are even identical. Between *Raphidia* and *Agulla* 28S distances ranged from 6.0 to 6.5%. Concerning the mitochondrial marker sequences, p distances between *R. mediterranea* and *R. ophiopsis* (the closest relative) were 5.08% in *cox1* and 5.62% in *cox3*, while the other species of *Raphidia* differed between 8.63–14.83% (*cox1*) and 7.46–16.94% (*cox3*) from *R. mediterranea*. Distances between species in the various gene sequences are illustrated by the NJ trees in Suppl. material 1.

To assess the systematic position of *R. mediterranea* not only on the basis of morphological characters, we performed a phylogenetic analysis based on three genes (*cox1*, *cox3*, 28S). The two mt sequences resulted in trees in which the sister group of *R. mediterranea* is *R. ophiopsis*. In most analyses, *R. alcoholica* is the sister group of those two lineages, followed by *R. ariadne*; only in the BI tree of *cox1* the relationships were unresolved (Suppl. material 1). With respect to the relationships of the other species there is a difference concerning *R. ligurica* and *R. ulrikae* depending on the marker sequence and the method applied. In some trees *R. ulrikae* splits from the most basal node, in others it is *R. ligurica*. Yet, in all trees this node is poorly supported. The tree based on 28S sequences (Suppl. material 1) is congruent with the mt based trees, yet, due to the low variation within this gene, the amount of phylogenetic information is limited. In a BI tree based on the combined marker genes (Fig. 6) all nodes are highly supported.

Discussion

The discovery of an isolated and unusually large population of *Raphidia mediterranea* – a Mediterranean species which has never been found elsewhere in Central Europe – in a farmhouse in a comparatively climatically unfavourable part of Upper Austria had raised the question concerning the origin of this population. It was assumed that morphological and/or genetic differences would be found, if the species had reached Upper Austria long ago by natural means of expansion of the distribution range. Therefore, specimens of the population from Upper Austria were compared with specimens from Greece and Italy. In the present study, the morphology-based results were clearly confirmed by molecular genetic analyses: The four specimens of *R. mediterranea* (two from Pelmburg (Austria), one from Greece, one from Italy) had almost identical sequences. It is legitimate to conclude that these populations were not separated long ago. The other species of *Raphidia* are clearly separated (see Fig. 6).

Substantial differences could not be found in morphological characters, particularly in male and female genitalia, or in the sequences of three genes (*cox1*, *cox3*, 28S). This implies that all presently known and examined populations of *R. mediterranea* originated from a single glacial refugium. This refugium can reasonably be assumed to be in the south of the Balkan Peninsula as a part of the large balkanopontomediterranean refugium (H. Aspöck

et al. 1991). From there the species reached other parts of Europe (and Anatolia) not long ago. Natural dispersal from the south of the Balkan Peninsula to isolated areas of the north of the Balkan Peninsula, to southern parts of Italy, to parts of Eastern Europe and particularly parts of Central Europe is highly unlikely. Consequently, an anthropogenic introduction into various regions is highly probable. *Raphidia mediterranea* is a euryoecious species, whose larvae live mainly in the detritus of roots of bushes, but sometimes also under bark.

In Greece, the species occurs in many regions, in various habitats at altitudes of 10 – 1200 m and often in high population densities. Thus, it might have been occasionally transported to new habitats by ships carrying wood or soil. This could have occurred already in antiquity and throughout the past centuries.

The discovery of the isolated population of *R. mediterranea* in Upper Austria and the failure to detect any morphological or genetic differences between these vastly distant populations supports our previous hypothesis (Aspöck et al. 1977, 1980, 1991, 2001) of unintentional introduction by human activities. A natural dispersal – per continuitatem or by wind – can convincingly be excluded. How did *R. mediterranea* come to Upper Austria? We now know definitely that the larvae develop within the straw of the roof (Gruppe et al. 2017). Thus, it is a reasonable assumption that this snakefly was introduced with straw from somewhere on the Balkan Peninsula. The straw presently on the roof is from Austria, but in the past it may have been imported. It is also possible that live adults (theoretically one female would be sufficient) were introduced (e.g. via car, truck or bus) from the Mediterranean region to Pelmburg and subsequently the female laid eggs in the straw. Until now, no studies have been published indicating that larvae develop in straw on roofs. In Central Europe thatched roofs have become rare, but in eastern and southeastern parts of Europe such roofs are still frequent in certain regions. It would be easy and exciting to examine these habitats for snakeflies. It would particularly be interesting to know whether other species of Raphidioptera can also develop in straw of thatched roofs where they would feed on mites, spring-tails, Psocoptera, larvae of beetles and other small arthropods living in the straw.

Concerning the systematic position of *R. mediterranea*, the phylogenetic analysis based on three genes confirmed our view of the systematics of *R. ophiopsis*, *R. mediterranea*, *R. alcoholica*, *R. ariadne*, *R. ulrikae* and *R. ligurica* (H. Aspöck et al. 1991, 2001). It is of particular interest that *R. alcoholica* is the sister species of *R. ophiopsis* + *R. mediterranea*, thus confirming the close relationship of the three taxa once regarded as subspecies of *R. ophiopsis*.

We know little about the formation of distribution patterns of Raphidioptera. Snakeflies are generally characterised by low, in many cases extremely low, expansivity, and many species have hardly enlarged their distribution beyond their glacial refugial areas. In Central Europe, 16

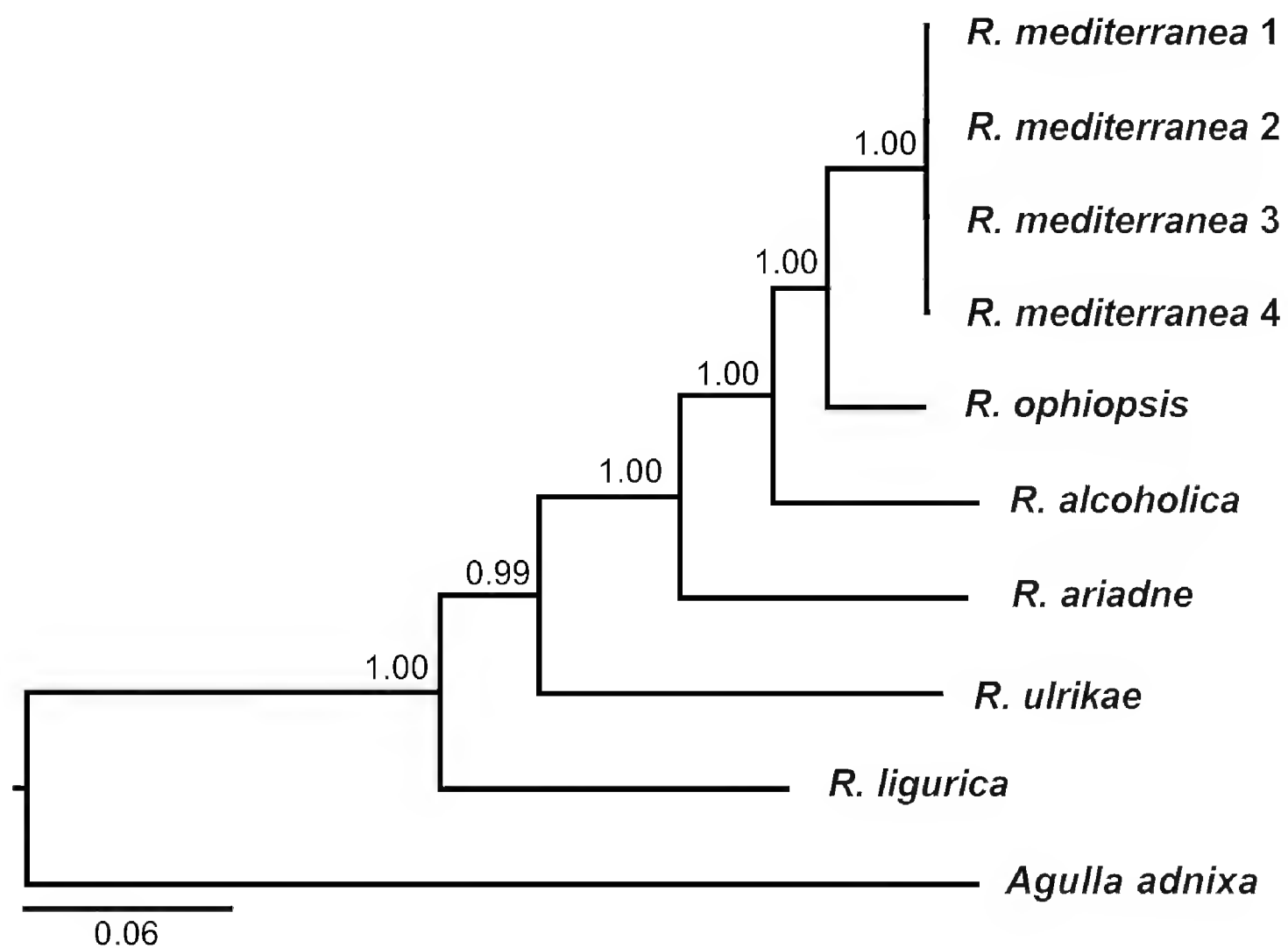


Figure 6. Phylogenetic tree based on BI analysis of six species of *Raphidia* (with *Agulla adnixa* as outgroup). Posterior probability values are indicated at the nodes.

species of Raphidioptera (13 Raphidiidae and 3 Inocelliidae) occur, 10 of these are of Mediterranean origin and presumably have reached Central Europe after the last glacial period, i.e. within the past 10,000 years (H. Aspöck 2008, 2010, H. Aspöck et al. 1991, 2001, H. Aspöck and U. Aspöck 2015). At least in Austria, *R. mediterranea* must be regarded as a human introduced neozoon.

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Supplementary material 1

BI and NJ trees

Authors: Horst Aspöck, Ulrike Aspöck, Axel Gruppe, Marcia Sittenthaler, Elisabeth Haring

Data type: molecular data

Explanation note: BI and NJ trees calculated with *cox1*, *cox3* and 28S sequences, respectively. Posterior probability values (BI trees) and bootstrap values (in %, NJ trees) are indicated at the nodes.

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Link: <https://doi.org/10.3897/dez.64.19859.suppl1>

Supplementary material 2

Records of *Raphidia mediterranea*

Authors: Horst Aspöck, Ulrike Aspöck, Axel Gruppe, Marcia Sittenthaler, Elisabeth Haring

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Records of *Raphidia mediterranea* documented in the distribution map (Fig. 5).

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Link: <https://doi.org/10.3897/dez.64.19859.suppl2>

Revised taxonomic check list of the Eurasiatic species of the subtribe Poliina (Noctuidae, Noctuinae, Hadenini)

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<http://zoobank.org/48A44E23-7C73-45A5-A86E-F391F0C9383F>

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Abstract

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Key Words

Classification

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Poliina genera

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new subgenera

new combinations

lectotype designations

illustrations

The revised checklist of the subtribe Poliina Hampson, 1902 is presented; one new genus, *Multisigna* **gen. n.**, three new subgenera (*Atropolia*, *Leuconephropolia* and *Protopolia* **subgen. n.**) and a new species (*Polia* (*Atropolia*) *posterodiluta* **sp. n.**) are described. The taxonomic position of the recently described subgenus *Metallopolia* is discussed. The subtribe Pachetrina Beck, 1996 is synonymised with Poliina; two genera (*Kollariana* Hacker, 1996 and *Spiramater* McCabe, 1980) are transferred to the subtribe Mamestrina Hampson, 1902. A number of lectotype designations and new combinations are given; the newly designated lectotypes and the genitalia of the disputed taxa are illustrated.

Introduction

The subtribe Poliina Hampson, 1902 was originally defined as “*Polia* complex” by McCabe (1980) based on external and genital characters of both sexes. However, in this review, some genera of Mamestrina Hampson, 1902 (in original form: Mamestrinae) were also included to this “complex”. Later, Poliina was shortly characterised and separated from the closely related subtribe Mamestrina by Beck (1996). Subsequently, in the volume 4 of the Noctuidae Europaeae series (Hadeninae I.) Hacker et al. (2002)

re-defined the subtribe Poliina Beck, 1996 and also provided a short differential diagnosis of the subtribes Poliina and Mamestrina Beck, 1996. According to the re-description and interpretation, the subtribe consists of the following genera: *Polia* Ochsenheimer, 1816 (its synonyms: *Chera* Hübner, [1821]; *Polia* Boisduval, 1829; *Aplecta* Guenée, 1838; *Anartodes* Culot, 1915; *Bompolia* Beck, 1999; *Ripolia* Beck, 1999; *Antipolia* Beck, 1999), *Pachetra* Guenée, 1841, *Kollariana* Hacker, 1996, *Haderonia* Staudinger, 1896 (= *Lasiridia* Draudt, 1950), *Ctenoceratoda* Varga, 1992 and *Tricheurois* Hampson, 1905.

In the next step, Fibiger and Lafontaine (2004, 2005) reviewed the higher classification of the Noctuoidea, and proposed a new tribal (and partly subtribal) system for the Holarctic fauna. In these seminal papers the authors accepted the act of Hampson (1902) who distinguished the *Polia* generic complex under the name “Polianae” with the type genus *Polia*. Thus, the subtribe Poliina Beck, 1996 was synonymised by them with Poliina Hampson, 1902. However, the taxonomic position of the closely related, formerly monotypic genus *Pachetra* Guenée, 1841 and the subtribe Pachetrina Beck, 1996 has remained unchanged. The latter subtribe is synonymised here with Poliina in the taxonomic part of this paper (syn. n.).

The genera of Poliina are Holarctic (*Polia*) or only Eurasiatic with centre of diversity in the monsoonic mountainous areas of South-Eastern Asia (Himalayan – Sino-Tibetan faunal type). Twenty-six species of *Polia* are present in Eurasia and thirteen species in North America; from them only one is a Holarctic, circum-polar species (*P. richardsoni* (Curtis, 1835)). Further genera of the subtribe are exclusively Palaearctic. The most diverse genus is *Ctenoceratoda* with more than thirty, mostly Central Asiatic species. The members of this subtribe have a characteristic “ground plan” of genital structures (including some lock-and-key mechanisms, see Varga 1992; Varga and Ronkay 2013) with several shared apomorphies as the identical structure of ampulla-harpe complex, the regularly (*Polia*, *Haderonia*) asymmetrical saccular processes covered by specialised brushes, the long, tubular endophallus (vesica) without subbasal diverticulum and cornutus but with long medio-subterminal field of fasciculate cornuti (males), the globular corpus bursae and the tubular appendix bursae (females). Abdominal brush-organs of males are mostly present and the last abdominal segment of females often shows specific strongly sclerotised, often shield-shaped structures.

In this review, based on the presence of the T-shaped vesica and the subbasal diverticulum with cornutus, typifying numerous Mamestrina genera (Varga and Ronkay 1991), but also on several characters of the genital capsula (see below), which are categorically absent in Poliina, certain genera and species formerly associated with Poliina have been excluded from this subtribe. The genus *Kollariana* includes three large, externally confusingly *Polia*-like species, the genitalia of which demonstrate, however, their close relationship with the *Sideridis* clade of the subtribe Mamestrina Hampson, 1902. They do not have e.g. saccular processes and ampullae on the valvae, but an ear-shaped costal process near to the cucullus. They also have claw- or spine-like sclerotisation of carina; the vesica is T-shaped, with long subbasal diverticulum and acute cornutus. *Kollariana* species do not have in the female genitalia elongate tubular appendix bursae, as most genera of Poliina, but they have two complete and one shorter row of small, elliptical stigmata on the corpus bursae. This genus is transferred, therefore, into Mamestrina. It is worth to mention that there are some

additional large-sized, *Polia*-like species occurring in the mountains of the SE frontier of the Tibetan plateau (e.g. the taxa of the genus *Irene*, the two members of the newly described genus *Multisigna* (“*Polia*”) *costirufa* Draudt, 1950 and “*P.*” *hofer* (Saldaitis, Benedek & Behounek, 2016), and the still less investigated “*Hyssia*” *hadulina* Draudt, 1950, etc.) which all belong to Mamestrina based on the shared characters mentioned above (see: taxonomic part in details).

Materials and methods

Abbreviations

BMHN	The Natural History Museum London (formerly British Museum, Natural History)
EIHU	Entomological Institute, Hokkaido University, Sapporo
HNHM	Hungarian Natural History Museum, Budapest
MNHG	Museum of Natural History, Geneva
MNHNP	Museum National d’Histoire Naturelle, Paris
MNB	Museum für Naturkunde, Berlin
NHMW	Naturhistorisches Museum, Vienna
NRS	Naturhistoriska Riksmuseet, Stockholm
SMND	Senckenberg Museum für Naturkunde, Dresden
SMNK	Staatliches Museum für Naturkunde, Karlsruhe
USNMW	Natural History Museum, Washington, United States
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn (AKM)
ZISP	Zoological Institute, Russian Academy of Sciences, St. Petersburg
ZMUH	Finnish Museum of Natural History, Helsinki
ZSM	Zoologische Staatssammlung, München

Taxonomic review of Eurasiatic Poliina genera and species

Poliina Hampson, 1902

Polianae Hampson, 1902, *Annals of the South African Museum* 2: 255. Type genus: *Polia* Ochsenheimer, 1816.

Remarks. The taxa are enumerated here in alphabetic sequence in the sake of simplicity. The taxonomic relationships and phylogenetic implications will be discussed in this and the forthcoming papers.

Genus *Ctenoceratoda* Varga, 1992

Ctenoceratoda Varga, 1992, *Acta Zoologica Academiae Scientiarum Hungaricae* 38(1-2): 95.

Type-species. *Haderonia sukharevae* Varga, 1974, by original designation.

***Ctenoceratoda aksakal* Varga & Gyulai, 1999**

Ctenoceratoda aksakal Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 179, figs 11, 41, 57, 85. Type-locality: Tadjikistan, E Pamir Mts, Sarykolskiy Mts, Dunkeldyk lake, 4100 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda anthracina* Varga & Gyulai, 1999**

Ctenoceratoda anthracina Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 180, fig. 63, 86; gen. figs 12, 13, 31, 46, 63. Type-locality: Kirghisia, Naryn region, Maly Naryn, Orukhtau, 2700 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda argyrea* Varga, 1992**

Ctenoceratoda argyrea Varga, 1992, Acta Zoologica Academiae Scientiarum Hungaricae 38 (1-2): 98, pl. 2, figs 9-10, gen. figs 5-10, 16-17. Type-locality: Mongolia, Govi Altai aimak, Govi Altai Mts, 6 km S of Tögrög. Holotype: male, in coll. Z. Varga (Debrecen).

***Ctenoceratoda brassicina* (Draudt, 1934)**

Figs 1, 2, 49

Scotogramma brassicina Draudt, 1934, in A. Seitz, Die Groß-Schmetterlinge der Erde 3: 98, pl. 14, row c. Type-locality: [Russia or Kazakhstan] “*Altai occ.*”. Holotype: female, in coll. MNB.

***Ctenoceratoda contempta* (Püngeler, 1914)**

Figs 3, 4, 50

Hadula (Mamestra) contempta Püngeler, 1914, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 28: 39, pl. 2, fig. 14. Type-locality: [China, Xinjiang] “Ost-Turkestan, Aksu”, “910 R[ue]ckb[eil]”. The specimen was dissected by Boursin (slide No. MB 810). Lectotype: male, in coll. MNB.

***Ctenoceratoda gandhara* (Hacker & Varga, 1990)**

Haderonia gandhara Hacker & Varga, 1990, Esperiana 1: 340, pl. E, fig. 16. Type-locality: Pakistan, Karakoram Mts, Kunjerab pass, 3600 m. Holotype: male, in coll. L. Weigert (Griesbach im Rottal).

***Ctenoceratoda graeseri* (Püngeler, 1898)**

Figs 5, 6, 51

Haderonia tancrei var. *graeseri* Püngeler, 1898, Societas Entomologica 13: 58. Type-locality: [Kazakhstan or

China] Ili region (“Ili 1897 M Juli”). Lectotype: male, in coll. MNB.

Remarks. This taxon was repeatedly described by the same author one year later and first illustrated the species (Iris 12: 102; Plate 9, fig. 3).

***Ctenoceratoda gyulaii* Volynkin, Varga & Matov, 2012**

Ctenoceratoda gyulaii Volynkin, Varga & Matov, 2012, Proceedings of the Tigirek State Natural Reserve 5: 205, pl. 3, figs 5-6; pl. 15, figs 18-23; pl. 28, figs 3-4; pl. 33, fig. 3. Type-locality: Russia, Altai Republic, Kosh-Agach district, 10 km WSW of Tashanta village, Bolshoy Shibety valley, 2200 m, 49°40'N, 89°04'E. Holotype: male, in coll. ZISP.

***Ctenoceratoda juliannae* Varga, 1992**

Ctenoceratoda juliannae Varga, 1992, Acta Zoologica Academiae Scientiarum Hungaricae 38 (1-2): 99, pl. 3, fig. 19, gen. figs 33-36. Type-locality: Mongolia, Khovd aimak, Dzhungar Govi, Bulgan sum (in the village). Holotype: male, in coll. Z. Varga (Debrecen).

***Ctenoceratoda khorgossi* (Alphéraky, 1882)**

Mamestra khorgossi Alphéraky, 1882, Horae Societatis Entomologicae Rossicae 17: 65, pl. 2, fig. 49. Type-locality: [China, Xinjiang] Kuldja district; Khorgoss. Syntypes: 2 males and 2 females, in coll. ZISP.

Synonymy. *Hadula corgossi* Hampson, 1905, Catalogue of the Lepidoptera Phalaenae in the British Museum 5: 244. An unjustified emendation of *Mamestra khorgossi* Alphéraky, 1882.

***Ctenoceratoda leucostigma* Gyulai & Varga, 2010**

Figs 17, 18

Ctenoceratoda leucostigma Gyulai & Varga, 2010, Folia Entomologica Hungarica 70: 182, figs 1-3, gen. figs 9-13. Type-locality: China, Qinghai [Kuku-Noor region], 20 km N of Da Qaidam city, 4,000 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda longicornis* (Graeser, 1892)**

Figs 7–10, 52, 53

Mamestra longicornis Graeser, 1892, Berliner Entomologische Zeitschrift 37: 306. Type-locality: [Kirghisia] Kisyl-Yart. Lectotype: male, here designated, in coll. MNB.

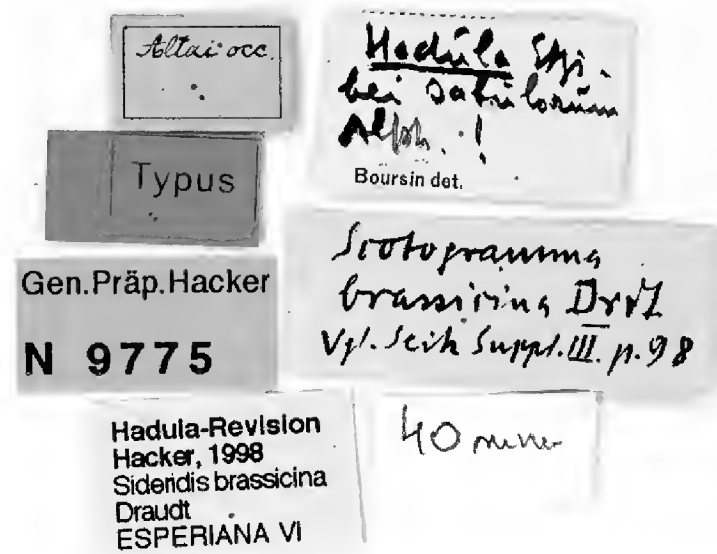
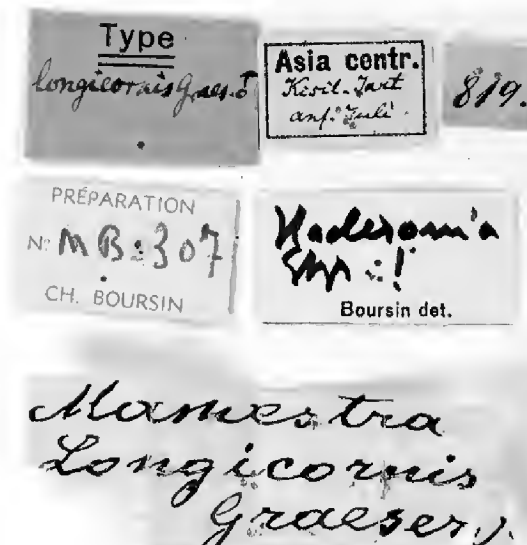
Fig. 1. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype maleFig. 2. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype male, labelsFig. 3. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype maleFig. 4. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype male, labelsFig. 5. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype maleFig. 6. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype male, labelsFig. 7. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype, maleFig. 8. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype, male, labels

Figure 1–8. 1. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype male. 2. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype male, labels. 3. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype male. 4. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype male, labels. 5. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype male. 6. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype male, labels. 7. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype, male. 8. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype male, labels.



Fig. 9. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype male

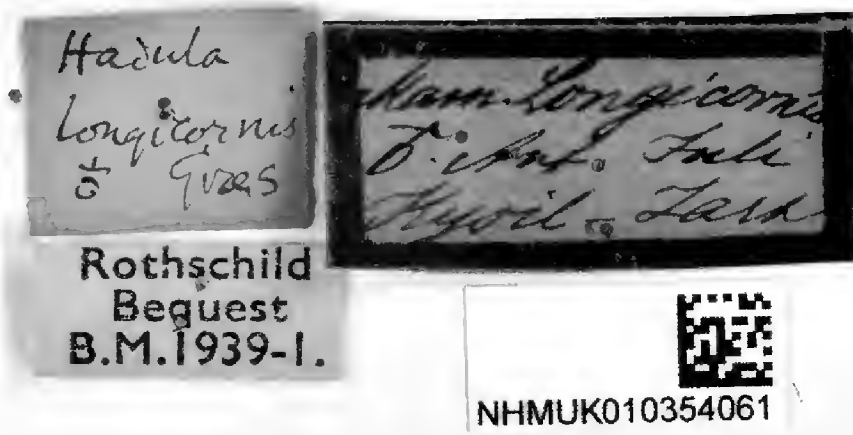


Fig. 10. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype male, labels



Fig. 11. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype male



Fig. 12. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype male, labels



Fig. 13. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype male



Fig. 14. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype male, labels



Fig. 15. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype male (Photo A. Matov)

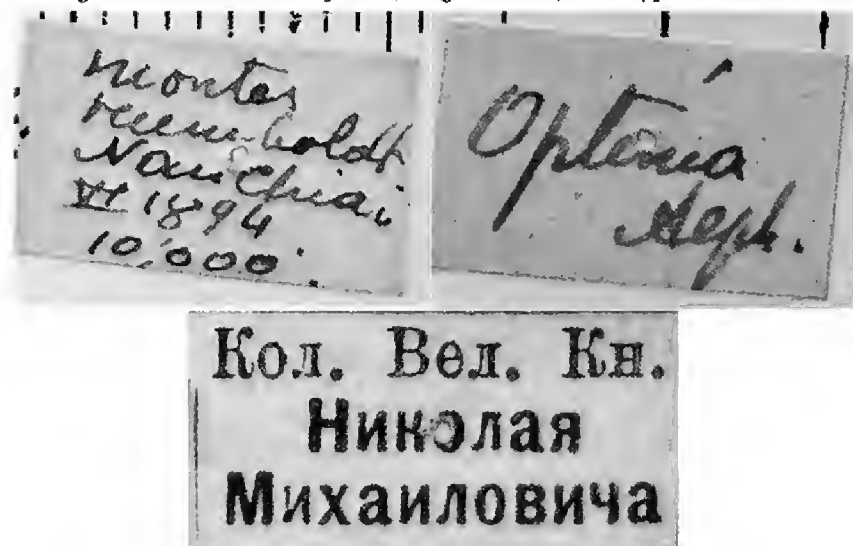


Fig. 16. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype male, labels (Photo A. Matov)

Figure 9–16. 9. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype male. 10. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype male, labels. 11. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype male. 12. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype male, labels. 13. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype male. 14. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype male, labels. 15. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype male. 16. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype male, labels.

Lectotype designation. Lectotype: male: “*Mamestra longicornis* Graeser”, “Asia centr.[alis] Kisyl-Yart Anf. [ang] Juli”. The lectotype specimen was dissected by Boursin (Slide No. MB 307); in coll. MNB.

***Ctenoceratoda lukhtanovi* Varga & Gyulai, 1999**

Ctenoceratoda lukhtanovi Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 172, figs 1-2, 23, 41, 50-52, 82. Type-locality: Tadjikistan, Pamir Mts, Muzkol Mts, Ak-Baital Pass, 4200 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda lupa* (Christoph, 1893)**

Figs 11, 12, 54

Mamestra lupa Christoph, 1893, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 6: 91. Type-locality: [Iran] Hyrcania, Shahkuh (“Schahkuh”, “Coll. Christoph [580]”, “Ex Coll. H.J. Elwes, 1920” “Joicey Bequest, Brit. Mus. 1934-120.”). Lectotype: male, in coll. BMNH.

Remarks. The type material has long been considered to be harboured in the collection of the ZISP. The male specimen from “Schahrud”, dissected by Rjabov (ZISP 7565) cannot be considered as an original type however, since the locality does not agree with the original description. The original specimens (two males, “Schahkuh, Hyrcaniae”) were most probably sold by Christoph and one of them was found in the collection of the NHM London, with the labels illustrated in the Fig. 12. This specimen has been designated as lectotype of *Mamestra lupa* (slide No. RL11753m) (Varga et al. 2017).

***Ctenoceratoda naryna* Varga & Gyulai, 1999**

Ctenoceratoda naryna Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 189, figs 15-16, gen. figs 33, 47, 66-67, 87. Type-locality: Kirghisia, Naryn region, Maly Naryn, Uzungyr, 2700 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda nefasta* (Püngeler, 1907)**

Figs 13, 14, 55

Hadula nefasta Püngeler, 1907, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 19: 221, pl. 8, fig. 2. Type-locality: [China, Xinjiang] Lob-Noor. Lectotype: male, here designated; coll. MNB.

Lectotype designation. Lectotype: male, “nefasta Püngeler”, “Lob-Noor”, “Juni, R[ue]ckb[eil]”. The specimen was dissected by Boursin (slide No. MB 309); coll. MNB.

***Ctenoceratoda optima* (Alphéraky, 1897)**

Figs 15, 16, 56

Haderonia optima Alphéraky, 1897, in Romanoff: Mémoires sur les Lépidoptères 9: 236, pl. 12, fig. 7. Type-locality: [China] Oulan-boulak, Nan-chan. Lectotype: male, here designated, in coll. ZISP.

Lectotype designation. Lectotype: male, “Montes Humboldt Nan-Chiai”, “VI 1894, 10.000”, “optima Alph.” “Kol.[lekciya] Vel.[ikogo] Kn.[yaza] Nikolaia Michailoviča” (with Cyrillic letters). The specimen was dissected by Matov (slide No. Matov 0148 ZISP; in coll. ZISP).

***Ctenoceratoda oxyptera* Varga, 1992**

Ctenoceratoda oxyptera Varga, 1992, Acta Zoologica Academiae Scientiarum Hungaricae 38 (1-2): 99, pl. 3, figs 17-18, gen. figs 37-43. Type-locality: Mongolia, Govi Altai aimak, Govi Altai Mts, 6 km S of Tögrög. Holotype: male, in coll. Z. Varga (Debrecen).

***Ctenoceratoda peregovitsi* Varga & Gyulai, 1999**

Ctenoceratoda peregovitsi Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 174, figs 4-5, gen. figs 25-26, 55, 83. Type-locality: Mongolia, Ömnögovi aimak, Tost Mts, 42 km WSW Gurt, 2450 m, 43°11'11"N, 100°36'60"E. Holotype: male, in coll. HNHM.

***Ctenoceratoda psychrogena* Varga & Gyulai, 1999**

Ctenoceratoda psychrogena Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45(2): 175, figs 6-8, gen. figs 27-29, 42-44, 58-62, 84. Type-locality: Tadjikistan, Pamir Mts, Vakhanskiy Mts, 4200 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda septemlacustris* Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012**

Ctenoceratoda septemlacustris Gaal-Haszler, Lödl, Ronkay, Ronkay & Varga, 2012, Fibigeriana 1: 125, pl. 112, figs 19-20, gen. figs 12-13. Type-locality: Afghanistan, Koh-i-Baba Mts, Band-i-Amir, 3000 m. Holotype: male, in coll. NHMW.

***Ctenoceratoda stenocera* Varga & Gyulai, 2002**

Ctenoceratoda stenocera Varga & Gyulai, 2002, Esperiana 9: 230, pl. 20, fig. 16. Type-locality: China, Kunlun Mts, 60 km NW of Xaidullah village, 4000–4500 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda sukharevae sukharevae* (Varga, 1974)**

Haderonia sukharevae Varga, 1974, Annales Historico-Naturales Musei Nationalis Hungarici 66: 301, pl. 7, fig. 7. Type-locality: Mongolia, Bayankhongor aimak, Zhinst Mts, 50 km E of Shinezhinst somon, 2000 m. Holotype: male, in coll. HNHM.

***Ctenoceratoda sukharevae excellens* (Varga, 1974)**

Haderonia sukharevae excellens Varga, 1974, Annales Historico-Naturales Musei Nationalis Hungarici 66: 302, pl. 1, figs 7-8. Type-locality: Mongolia, Khövsgöl aimak, Delger mörön river, 8 km N of Burenchaan somon, 1450 m. Holotype: male, in coll. HNHM.

***Ctenoceratoda tancrei* (Graeser, 1892)**

Figs 19, 20, 57

Mamestra tancrei Graeser, 1892, Berliner Entomologische Zeitschrift 37: 305. Type-locality: [Kirghisia] Alexander Mts. Lectotype: male, here designated; coll. MNB.

Lectotype designation. Lectotype: male, “tancrei Graeser Type”, “Alexander Gb. R[ue]ckb[eil] E. Juli”.

Remarks. The lectotype was not dissected by Boursin, since the end of the abdomen seems to be slightly damaged. The completely similar paralectotype specimen from the same locality was dissected by Varga (gen. slide VZ 9526).

***Ctenoceratoda thermolimna* (Boursin, 1964)**

Haderonia thermolimna Boursin, 1964, Zeitschrift der Wiener Entomologischen Gesellschaft 49: 174, pl. 22, figs 1, 4. Type-locality: Kirghisia, Issyk-Kul. Holotype: male, in coll. ZSM.

***Ctenoceratoda transalaica* Varga and Gyulai, 1999**

Ctenoceratoda transalaica Varga & Gyulai, 1999, Acta Zoologica Academiae Scientiarum Hungaricae 45(2): 189, figs 17, gen. figs 34, 48, 68-69, 88. Type-locality: Kirghisia, Transalai, Aram Kungei, 2800 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda turpis* (Staudinger, 1899)**

Figs 21, 22, 58

Phoebophilus turpis Staudinger, 1899, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 12: 341, pl. 7, fig. 8. Type-locality: [China,

Xinjiang] Korla. Lectotype: male, here designated, in coll. MNB.

Lectotype designation. Lectotype: male, „Korla”, „Origin” (pink label); the specimen was dissected by Boursin (slide No. MB 298).

Remarks. The types are incorrectly cited by Poole as „2 females”, in the original description were mentioned 1 worn male and 2 fresh females.

***Ctenoceratoda weigerti* (Hacker & Varga, 1990)**

Haderonia weigerti Hacker & Varga, 1990, Esperiana 1: 340, pl. E, fig. 16. Type-locality: Pakistan, Karakoram Mts, Kunjerab pass, 3600 m. Holotype: male, in coll. L. Weigert (Griesbach im Rottal).

***Ctenoceratoda zetina zetina* (Staudinger, 1899)**

Hadena zeta var. *zetina* Staudinger, 1899, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 12: 342. Type-locality: [China, Tien Shan region] „Thian or”. Holotype: female, in coll. MNB.

Synonymy. *Mamestra (Hadula) impia* Püngeler, 1905, Societas Entomologica 19: 153. Type-locality: [China, Xinjiang] Aksu. Syntypes: 1 male and 1 female, in coll. MNB;

Mamestra desquamata Filipjev, 1931, Abhandlungen der Pamir-Expedition 1928, 8: 152, text fig. 2, pl. 3, fig. 3. Type-locality: [Tadjikistan] Pamir, Khorog; [China, Xinjiang] Aksu; Kashgar; Dashi-Kulj. Syntypes: in coll. ZISP.

***Ctenoceratoda zetina rhodoptera* Varga, 1992**

Ctenoceratoda zetina rhodoptera Varga, 1992, Acta Zoologica Academiae Scientiarum Hungaricae 38(1-2): 100, pl. 1, fig. 7. Type-locality: Afghanistan central, Band-i-Amir, 3600 m. Holotype: male, in coll. NHMW.

The descriptions of the following four new species and a new subspecies have been recently published in a separate paper on the taxonomy of the genus *Ctenoceratoda* (Varga et al. 2017).

***Ctenoceratoda persephone* Varga, Ronkay & Ronkay, 2017**

Ctenoceratoda persephone Varga, Ronkay & Ronkay, 2017, Acta Zoologica Academiae Scientiarum Hungaricae 64 (1) .Type-locality: Mongolia, Khovd aimak, 60 km E of Altay somon centre, 1600 m, 45°48'N, 92°50'E. Holotype: male, in coll. HNHM.

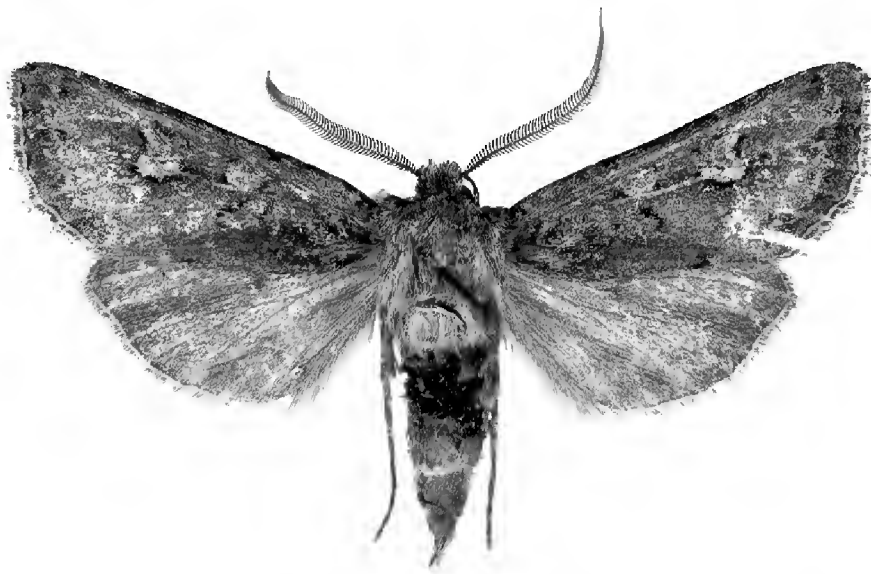


Fig. 17. *Ctenoceratoda leucostigma* Gyulai & Varga, 2010 Holotype male

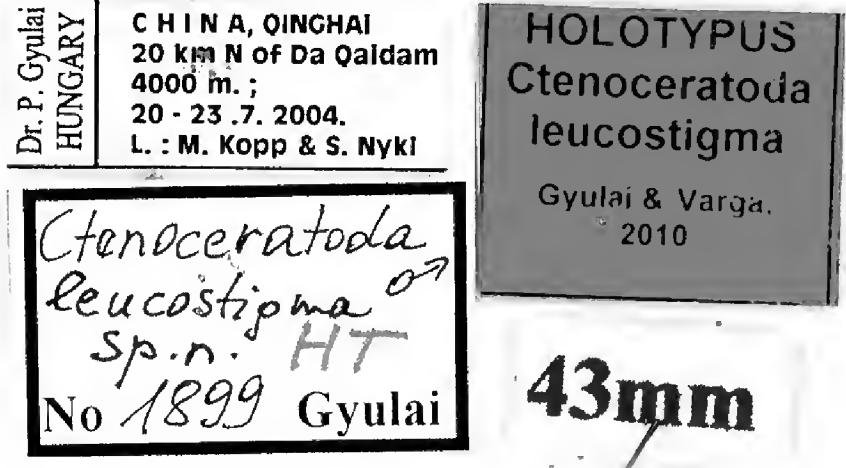


Fig. 18. *Ctenoceratoda leucostigma* Gyulai & Varga, 2010 Holotype male



Fig. 19. *Ctenoceratoda tancrei* (Graeser, 1892) Lectotype male

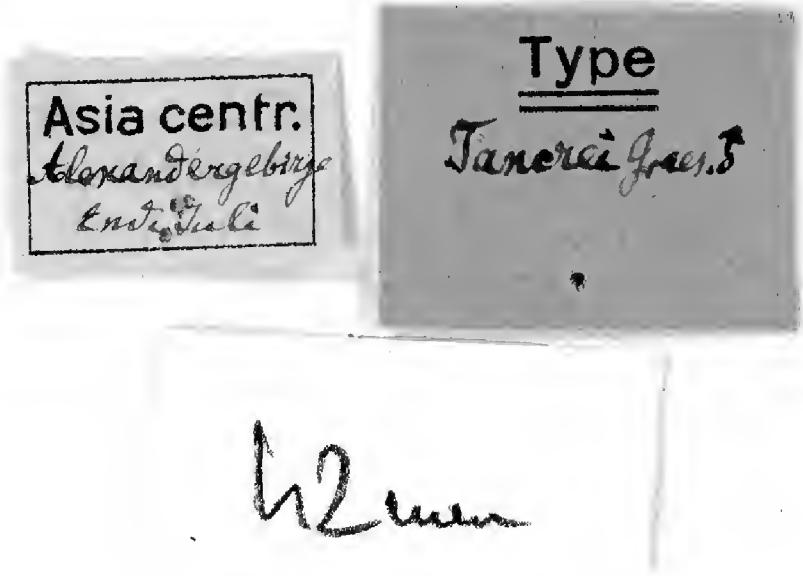


Fig. 20. *Ctenoceratoda tancrei* (Graeser, 1892) Lectotype male, labels



Fig. 21. *Ctenoceratoda turpis* (Staudinger, 1900) Paralectotype female

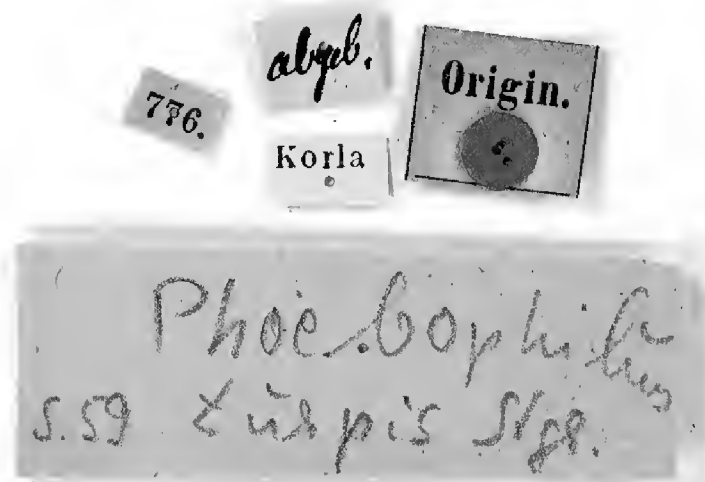


Fig. 22. *Ctenoceratoda turpis* (Staudinger, 1900) Paralectotype female, labels



Fig. 23. *Haderonia aplectoides* (Draudt, 1950) Lectotype male

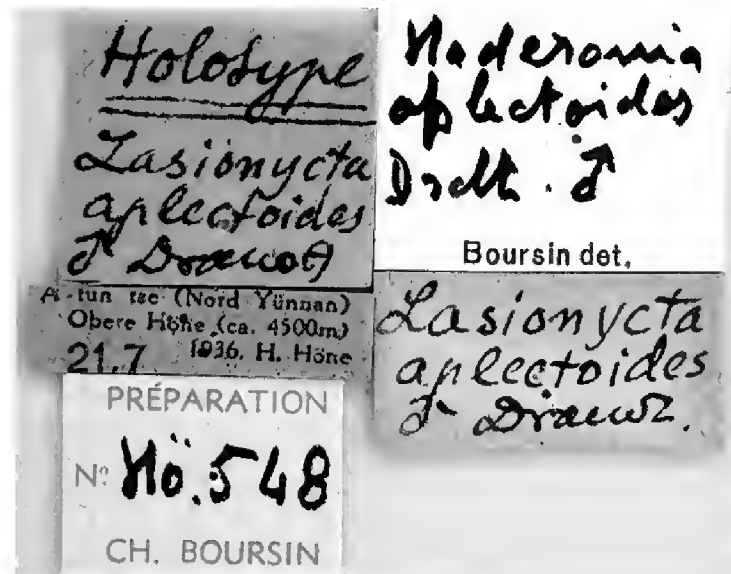


Fig. 24. *Haderonia aplectoides* (Draudt, 1950) Lectotype male, labels

Figure 17–24. 17. *Ctenoceratoda leucostigma* Gyulai & Varga, 2010 Holotype male. 18. *Ctenoceratoda leucostigma* Gyulai and Varga, 2010 Holotype male, labels. 19. *Ctenoceratoda tancrei* (Graeser, 1892) Lectotype male. 20. *Ctenoceratoda tancrei* (Graeser, 1892) Lectotype male, labels. 21. *Ctenoceratoda turpis* (Staudinger, 1900) Paralectotype female. 22. *Ctenoceratoda turpis* (Staudinger, 1900) Paralectotype female, labels. 23. *Haderonia aplectoides* (Draudt, 1950) Lectotype male. 24. *Haderonia aplectoides* (Draudt, 1950) Lectotype male, labels.

***Ctenoceratoda scotosparsa* Varga, Ronkay & Ronkay, 2017**

Ctenoceratoda scotosparsa Varga, Ronkay & Ronkay, 2017, Acta Zoologica Academiae Scientiarum Hungaricae 64 (1). Type-locality: Mongolia, Govi Altai aimak, Mongolian Altay Mts, Sutay uul, 16 km SE of Dzuyl, 46°11'N, 94°01'E; 2070 m. Holotype: male, in coll. P. Gyulai (Miskolc).

***Ctenoceratoda cyanochrea* Varga, Ronkay & Ronkay, 2017**

Ctenoceratoda cyanochrea Varga, Ronkay & Ronkay, 2017, Acta Zoologica Academiae Scientiarum Hungaricae 64 (1). Type-locality: Mongolia, Khovd aimak, Mongolian Altay Mts, 1430 m, Mönkh Khayrkhan uul, 41 km N of Bulgan, 46°28'N, 91°24'E. Holotype: male, in coll. G. Ronkay (Budapest).

***Ctenoceratoda mallopyga* Varga, Ronkay & Ronkay, 2017**

Ctenoceratoda mallopyga Varga, Ronkay & Ronkay, 2017, Acta Zoologica Academiae Scientiarum Hungaricae 64 (1). Type-locality: Pakistan, Karakoram Mts, Naltar valley, 2800 m, N36°09', E74°12'. Holotype: male, in coll. Z. Varga (Debrecen).

***Ctenoceratoda mallopyga dyschroa* Varga, Ronkay & Ronkay, 2017**

Ctenoceratoda mallopyga dyschroa Varga, Ronkay & Ronkay, 2017, Acta Zoologica Academiae Scientiarum Hungaricae 64 (1). Type-locality: India, Himachal Pradesh, Spiti, Spiti valley, 6 km SE Kaza, 4100 m. Holotype: male, in coll. G. Ronkay.

Genus *Haderonia* Staudinger, 1896

Haderonia Staudinger, 1896, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 8: 320. Type-species: *Haderonia subarschanica* Staudinger, 1896, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 8: 320, pl. 6, fig. 12, by monotypy; a junior synonym of *Mamestra (Dianthoecia) miserabilis* Alphéraky, 1892.

Synonymy. *Lasiridia* Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 39, plate II., fig. 9. Type-species: *Lasiridia iomelas* Draudt, 1950, by monotypy.

***Haderonia alpina* (Draudt, 1950)**

Lasiestra alpina Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 23, pl. 1, fig. 20. Type-locality: China, [Sichuan] “Batang, alpine Zone”. Syntypes: both sexes, in coll. ZFMK Bonn.

Taxonomic notes. The figure of the genital slide (Plate XIII, Fig. 13) was changed in the original publication (showing the genitalia of a *Xestia* sp.). Boursin (1964b) dissected and figured the specimen labelled by Draudt as holotype (Plate XIII, Fig. 53) and stated correctly its generic placement in *Haderonia*.

***Haderonia aplectoides* (Draudt, 1950)**

Figs 23, 24, 59

Lasionycta aplectoides Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 25, pl. 1, fig. 24. Type-locality: China, Prov. Yunnan, Li-kiang. Lectotype: male, here designated, in coll. ZFMK.

Lectotype designation. Lectotype: male, [China] “Prov. Nord-Yuennan, Li-kiang”. The lectotype specimen was dissected by Boursin (slide No. Hö 613); it is deposited in the ZFMK.

Remarks. A specimen of this species from the same locality was labelled by Draudt as *Lasionycta bombycioides*. This taxon has never been published, however. The specimen was dissected by Boursin (Hö 612).

***Haderonia arshanica* (Alphéraky, 1882)**

Hadena arshanica Alphéraky, 1882, Horae Societatis Entomologicae Rossicae 17: 78, pl. 2, f. 45. Type-locality: [Xinjiang] Kuldja district, Archane. Lectotype: male, here designated, in coll. ZISP.

Lectotype designation. Lectotype: male, „Tien Chan, 13.VI.1879.”, „arschanica Alph. Original”, „Kol.[lekcija] vel.[ikogo] kn.[jaza] Nikolaya Michailovicha (in Cyrillic letters); coll. ZISP.

***Haderonia chinensis* (Draudt, 1950)**

Trichestra chinensis Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 19, pl. 1, f. 3-4. Type-locality: [Yunnan], Li-kiang; Atuntse; Mien-shan. Syntypes: numerous specimens of both sexes, in coll. ZFMK.

***Haderonia iomelas* (Draudt, 1950)**

Lasiridia iomelas Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 39, pl. 2, f. 19. Type-locality: [Sichuan] Batang. Syntypes: males, in coll. ZFMK.

***Haderonia lasiestrina* (Draudt, 1950)**

Figs 25, 26, 60

Polia lasiestrina Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 27, pl. 2, f. 1. Type-locality: [Sichuan] Batang. Holotype: male, in coll. ZFMK. Lectotype: male, here designated.

Lectotype designation. Lectotype: male, [China], "Li-kiang, Batang, alpine Zone, 5000 m". The lectotype specimen was dissected by Boursin (slide No. Hö 610), coll. ZFMK.

***Haderonia miserabilis* (Alphéraky, 1892)**

Mamestra (Dianthoecia) miserabilis Alphéraky, 1892, in Romanoff: Mémoires sur les Lépidoptères 6: 33. Type-locality: [China] „entre Tchatchakou et Tchangla, dans la province Sétchouén". Holotype: female, in coll. ZISP (slide No. ZIN 4367).

Synonymy. *Hadena subarschanica* Staudinger, 1895, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 8: 320, pl. 6, f. 12. Type-locality: [China] between Lob Noor and Kuku Noor. Holotype: male, in coll. MNB.

Haderonia subarschanica nepalensis Boursin, 1964, Veröffentlichungen der Zoologischen Staatssammlung München 8: 26, pl. 2, f. 41-42. Type-locality: Nepal, Mustangbhot, Gargompa. Holotype: male, in ZSM.

***Haderonia persimilis* (Draudt, 1950)**

Trichestra persimilis Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 20, pl. 1, f. 7-8. Type-locality: [Sichuan] Batang. Syntypes: both sexes, in coll. ZFMK.

Genus *Polia* Ochsenheimer, 1816

Polia Ochsenheimer, 1816, Die Schmetterlinge von Europa 4: 73. Type-species: *Phalaena nebulosa* Hufnagel, 1766, by subsequent designation by Curtis, 1829.

Synonymy. *Chera* Hübner, 1821, Verzeichniss bekannter Schmetterlinge: 211. Type-species: *Polia serratilinea* Ochsenheimer, 1816, by subsequent designation by Hampson, 1902;

Polia Boisduval, 1828, Europaeorum Lepidopterorum Index Methodicus: 73. Type-species: *Phalaena nebulosa* Hufnagel, 1766, by subsequent designation by Curtis, 1829;

Aplecta Guenée, 1838, Annales de la Société Entomologique de France 7: 217. Type-species: *Phalaena nebulosa* Hufnagel, 1766, by subsequent designation by Guenée, 1852;

Anartodes Culot, 1915, Noctuelles et Géométrés d'Europe. Première Partie Noctuelles 2: 125. Type-species: *Mamestra rangnowi* Püngeler, 1909, by monotypy;

Bompolia Beck, 1996, Neue entomologische Nachrichten 36: 73. Type-species: *Phalaena bombycina* Hufnagel, 1766, by original designation;

Ripolia Beck, 1996, Neue entomologische Nachrichten 36: 73. Type-species: *Hadena richardsoni* Curtis, 1834, by original designation;

Antipolia Beck, 1996, Neue entomologische Nachrichten 36: 73. Type-species: *Mamestra conspicua* Bang-Haas, 1912, by original designation.

Subgenus *Atropolia* subgen. n.

<http://zoobank.org/262A8F7C-9CC5-4A1B-903E-0B6490C1E15C>

Type-species. *Mamestra mortua* Staudinger, 1888, here designated.

Diagnosis. The two species of this subgenus are characterised by the most often unicolorous black or deep blackish-brown forewing ground colour and some unique structures of the male genitalia. The most conspicuous character of the male genitalia is the long, slightly falcate extension of the basal plate of the harpe-ampulla complex, superficially resembling the digitus of some not closely related groups. The sacular processes are relatively short and simple, slightly asymmetric with a brush of specialised setae on the right (on figures left) side. The vesica is helicoidal with a full coil; the distal section of the vesica is armed by a long stripe of fasciculate cornuti. In the female genitalia, the ductus bursae is strongly sclerotised and dorso-ventrally compressed, somewhat similar as in *Ctenoceratoda* species, however the appendix bursae is very different, relatively short, tubular.

Etymology. The name is the amalgamation of the names *Atropos* and *Polia*.

***Polia (Atropolia) mortua mortua* (Staudinger, 1888)**

Mamestra mortua Staudinger, 1888, Entomologische Zeitung. Entomologischen Vereine zu Stettin 49: 249. Type-locality: [Russia] Askold (Island). Holotype: female, in coll. MNB.

Synonymy. *Mamestra afra* Graeser, 1889, Berliner Entomologische Zeitschrift 32 (2): 326. Type-locality: [Russia] Amur region, Vladivostok. Holotype: female, in coll. MNB;

Polia persicariae minorita Bryk, 1949, Arkiv för Zoologi 41A (1): 73. Type-locality: North Korea, near Kyeongseong, Hamgyeong bugdo (Shuotsu). Holotype: male, in coll. NRS.

***Polia (Atropolia) mortua kala* (Swinhoe, 1900)**

Hadena kala Swinhoe, 1900, Catalogue of Eastern and Australian Lepidoptera Heterocera in the Oxford University Museum 2: 17. An objective replacement name of *Mamestra nigerrima* Warren, 1888 (primary homonymy with *Mamestra nigerrima* Guenée, 1854).



Fig. 25. *Haderonia lasiestrina* (Draudt, 1950) Lectotype male

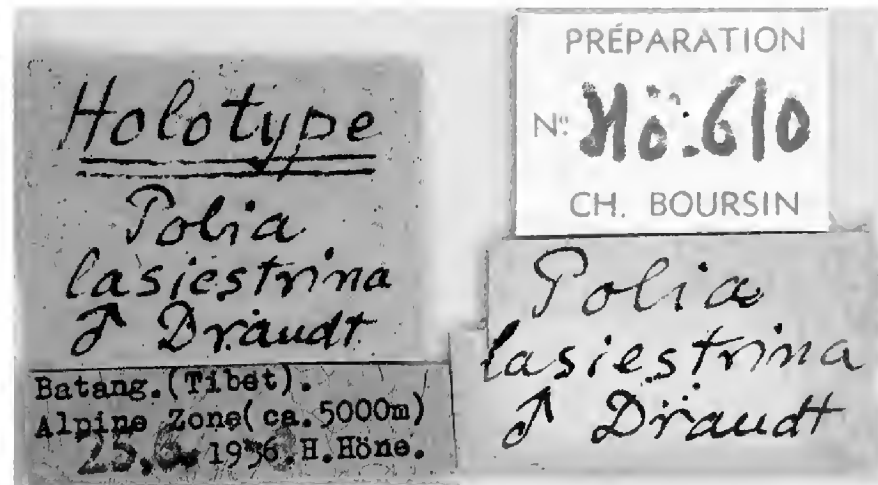


Fig. 26. *Haderonia lasiestrina* (Draudt, 1950) Lectotype male, labels



Fig. 27. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Lectotype male



Fig. 28. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Lectotype male, labels



Fig. 29. *Polia (Atropolia) posterodiluta* sp. n. Holotype male

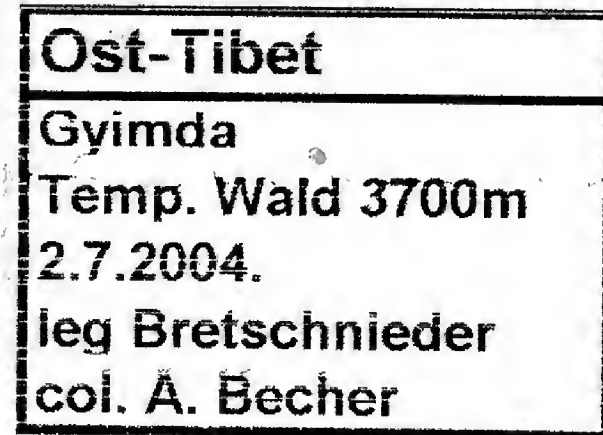


Fig. 30. *Polia (Atropolia) posterodiluta* sp. n. Holotype male, labels



Fig. 31. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype male

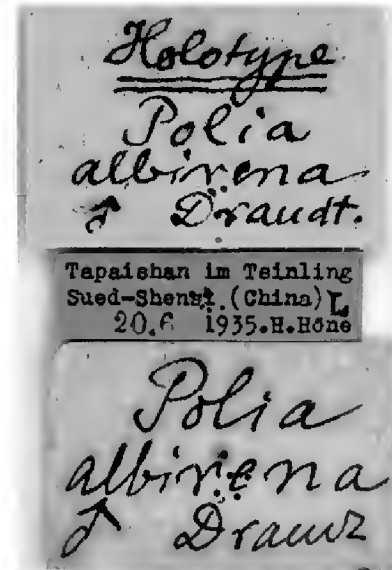


Fig. 32. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype male, labels

Figure 25–32. 25. *Haderonia lasiestrina* (Draudt, 1950) Lectotype male. 26. *Haderonia lasiestrina* (Draudt, 1950) Lectotype male, labels. 27. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Lectotype male. 28. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Lectotype male, labels. 29. *Polia (Atropolia) posterodiluta* sp. n. Holotype male. 30. *Polia (Atropolia) posterodiluta* sp. n. Holotype male, labels. 31. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype male. 32. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype male, labels.

Synonymy. *Mamestra nigerrima* Warren, 1888, Proceedings of the Zoological Society of London 1888: 302. Type-locality: India, Himachal Pradesh, Thundiani. Syn-types: 2 males and 4 females. Preoccupied, a junior primary homonym of *Mamestra nigerrima* Guenée, 1852.

***Polia (Atropolia) mortua szetschwana* Draeseke, 1928, stat. rev., comb. n.**

Figs 27, 28, 61

Polia szetschwana Draeseke, 1928, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 42: 301. Type-locality: [China] Sichuan, Sunpanting. Lectotype: male, here designated, in coll. SMND.

Lectotype designation. Lectotype: male, “*Polia szetschwana*” (sic!) “Szetschwan, Sunpanting” “Exp. Stötzner 1927 9” “*Polia mortua* Stgr. det. Boursin”. Two male and three female paralectotypes from the same locality (male gen. slide VZ Dresden 09).

Synonymy. *Polia adustaeoides* Draeseke, 1928, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 42: 302. Type-locality: [China], “Setchwan, Tatsien-lou Exp. Stötzner” “1927 9”, syn. n.

Taxonomic notes. The revision of the type series confirms the recognition of the subspecific rank of this south-western population, as well as the taxonomic identity of *szetschwana* and *adustaeoides*. This taxon inhabits the high mountains on the SE edge of the Tibet (Xizang) plateau.

***Polia (Atropolia) mortua caeca* Hreblay & Ronkay, 1997**

Polia mortua caeca Hreblay & Ronkay, 1997, Acta Zoologica Academiae Scientiarum Hungaricae 43 (1): 28, figs 12-13, 132-133. Type-locality: Taiwan, Nantou County, Tayuling, 3000 m, 24°08'N, 121°16'E. Holotype: male, in coll. M. Hreblay (deposited in HNHM).

***Polia (Atropolia) posterodiluta* sp. n.**

<http://zoobank.org/BA96EDBF-AC47-49FE-81D1-CE9B3555625C>

Figs 29, 30, 62

Holotype. Male, China, “Ost-Tibet, Gyimda, 3700 m, „temp. Wald”, 2.VII.2004, leg. Bretschneider; slide No. RL8670m (coll. A. Becher).

Diagnosis. The new species is a sympatric sister taxon of the widespread and polytypical *Polia (Atropolia) mortua*, occurring together with the ssp. *szetschwana* at the SE frontier of the Tibetan plateau. The new species differs externally from all subspecies of *P. (A.) mortua* by its smaller size (wingspan 38 mm), intense pale ochreous-to ochreous-brownish suffusion in the inner parts of the forewing running from the basal area to the inner half of the marginal field (with some reddish hue only at the lower part of the basal area and along the subterminal line), the

narrower reniform stigma with fine whitish line at middle (while the regular white line along the outer edge of the stigma and the characteristic two white dots at lower edge are missing), and the diluted (ochreous-whitish) inner area of the hindwing with well-developed discal spot on the underside. The marginal area of the hindwing has rather pale greyish-brown suffusion, with small darker grey patches at tornal area, covering also the fringes. The sympatrically occurring populations of *P. (A.) mortua* are usually dimorphic, having either dark brown to blackish-brown forewings with only weak reddish-brownish hue or with intensely red-brownish suffusion (the form described as *adustaeoides*), but this reddish suffusion is less extensive than in *P. (A.) posterodiluta*, the reniform stigma is larger, with the typical whitish markings at outer edge, and the male hindwing is more evenly greyish-brown suffused, with much smaller discal spot. Female unknown.

The male genitalia are essentially similar to those of *P. (A.) mortua* but the sclerotised medial extension of valvae is less falcate, evenly broad, except the finely tapering and terminally pointed distal quarter. This process is medially narrower and distally dilated, apically rounded in all four subspecies of *P. (A.) mortua*. In addition, the clavi are broader and more evenly rounded, and the juxta is smaller and thinner than in different subspecies of *P. (A.) mortua*.

Distribution. SE Tibetan. The species is known from the type-locality only; the holotype specimen was collected in a high altitude forest region in the midsummer period.

Subgenus *Metallopolia* Varga, Ronkay & Ronkay, 2017

Metallopolia Varga, Ronkay & Ronkay, 2017, Journal of Asia-Pacific Entomology 21. Type-species: *Mamestra culta* Moore, 1881, Proceedings of the Zoological Society of London 1881: 347.

Taxonomic notes. The revision of the subgenus *Metallopolia* is published in a separate paper (Varga et al. 2017b). It contains five easily distinguishable species representing three main lineages, the *culta*-, the *subviolacea*- and the *kalikotei*-lineages. The shortened diagnosis of the subgenus is presented below; the detailed analysis of the clade is given in the above-mentioned publication.

Diagnosis. *Metallopolia* species are large, robust moths, resembling the larger south Siberian *Polia* species but have shorter abdomen bearing 3-4 prominent blackish tufts on the first abdominal segments dorsally. The most conspicuous external character of the members of this subgenus is the presence of optically structured “metallic” scales with „neon-greenish” colouration (see: Etymology) within or near to the maculation and the anal edge of the postmedial transversal line. The forewing ground colour is rather dark brown to blackish-brown with some purplish-violaceous hue and diffuse, smaller or larger reddish-brownish patches; the hindwings are also dark brown or grey-brown. The members of the subgenus

are externally often confusingly similar, the proper identification often requires the study of genitalia.

In the male genitalia, the saccular processes are slightly asymmetrical, extended, acute or obtuse, with strong setae terminally, in most species with characteristic brush of specialised setae on the right (in figures left) side. Vesica long, tubular, partly or entirely coiling, medial and distal sections armed by numerous small, spiniform cornuti arranged into a long and variably dense stripe. In the female genitalia, the ductus bursae is sclerotised, compressed dorso-ventrally; the appendix bursae is tubular, sausage-shaped, slightly retroflexed, bursa globular with longitudinal, extremely faint signa.

Etymology. The name refers to the scales with light greenish optical colouration and metallic shine on the fore wings as unique character within the genus *Polia*.

Polia (Metallopolia) culta (Moore, 1881)

Mamestra culta Moore, 1881, Proceedings of the Zoological Society of London 1881: 347. Type-locality: [India, Himachal Pradesh] Dalhousie N.W. Himalaya. Holotype: female, in coll. NHML. Gen. slide 4442.

Polia (Metallopolia) dysgnorima Varga, Ronkay & Ronkay, 2017, in press

Polia (Metallopolia) dysgnorima Varga, Ronkay & Ronkay, 2017, Journal of Asia-Pacific Entomology 21. Type-locality: China, Sichuan, Daxue Shan, Gongga Shan, NW Moxi, 3200 m, 101°58'E, 29°41'N. Holotype: male, in coll. Z. Varga.

Polia (Metallopolia) metagnorima Varga, Ronkay & Ronkay, 2017, in press

Polia (Metallopolia) metagnorima Varga, Ronkay & Ronkay, 2017, Journal of Asia-Pacific Entomology 21. Type-locality: China, Sichuan, Daxue Shan, Gongga Shan, NW Moxi, 2850 m, 101°58'E, 29°41'N. Holotype: male, in coll. Z. Varga.

Polia (Metallopolia) ignorata (Hreblay, 1996)

Haderonia ignorata Hreblay, 1996, Acta Zoologica Academiae Scientiarum Hungaricae 42 (1): 70, figs 5-7, gen. fig. 12. Type-locality: China, Sichuan, Putsu-fong. Holotype: male, in coll. BMNH.

Polia (Metallopolia) kalikotei (Varga, 1992)

Haderonia kalikotei Varga, 1992, Acta Zoologica Academiae Scientiarum Hungaricae 38: 97, pl. 1, fig. 1. Type-locality: “Nepal, Prov. 3 East, Junbesi, 2750 m”. Holotype: male, in coll. ZSM.

Polia (Metallopolia) subviolacea subviolacea (Leech, 1900)

Hadena culta var. *subviolacea* Leech, 1900, Transactions of the Entomological Society of London 1900: 55. Type-locality: [China, Sichuan] Omei Shan (Emei Shan). Holotype: male, in coll. BMNH.

Remarks. A *Metallopolia* specimen from China, North Yunnan, Likiang was selected by Draudt as a distinct taxon and labelled as *Lasiadena purpureonitens*. This taxon has never been published; the selected holotype specimen is conspecific with *P. (M.) subviolacea*.

Polia (Metallopolia) subviolacea kanchenjunga Varga, Ronkay & Ronkay, 2017

Polia (Metallopolia) subviolacea kanchenjunga Varga, Ronkay & Ronkay, 2017, Journal of Asia-Pacific Entomology 21. Type-locality: Nepal, Kanchenjunga Himal, Deorali Danda, Torontan, 3200 m. Holotype: male, in coll. G. Ronkay.

Subgenus *Leuconephropolia* subgen. n.

<http://zoobank.org/CD44616F-690F-491F-A96F-A33062B3F0CA>

Type-species. *Polia albirena* Draudt, 1950, by monotypy.

Diagnosis. This isolated species is strikingly different from all other *Polia* species by its slenderer body, more elongate triangular and somewhat acute forewings, longer pectinated and relatively long antennae of males, by dark greyish-brown colouration of thorax and fore wings with some violaceous shine.

The male genitalia also differ conspicuously from those of all other known *Polia* species, the diagnostic features are as follows: the saccular processes are symmetrical, relatively short and densely covered by a “bush” of strong setae terminally, and the vesica is completely helicoid and recurved, bearing a large number of thin, spiniform cornuti and a small terminal diverticulum.

The female genitalia are also very specific: the sclerotisation of the antrum is weak, connected to ductus bursae with a slightly constricted membranous section (“neck”), the ductus bursae is flattened and more sclerotised, the corpus bursae is saccate, lacking signa, while the appendix bursae is broad and retroflexed.

Etymology. The name refers to the light reniform stigma of the type-species.

Polia (Leuconephropolia) albirena Draudt, 1950

Figs 31, 32, 63

Polia albirena Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 84, pl. 6, fig. 5. Type-locality: China, Prov. Shaanxi, Tsinling Mts,

Tapaishan. Lectotype: male, here designated, in coll. ZFMK.

Lectotype designation. Lectotype: male, [China], “Shaanxi, Tapaishan in Tsinling Shan”, dissected by Z. Varga (Slide No. ZV 8946); coll. ZFMK.

Subgenus *Polia* Ochseneimer, 1816

Polia Ochseneimer, 1816, Die Schmetterlinge von Europe 4: 73. Type-species: *Phalaena nebulosa* Hufnagel, 1766, by subsequent designation by Curtis, 1829.

Polia (Polia) atrax atrax Draudt, 1950

Figs 33, 34, 64

Polia atrax Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 31, pl. 2, fig. 17. Type-locality: China, Prov. Yunnan, Atuntse. Lectotype: male, here designated, in coll. ZFMK.

Lectotype designation. Lectotype: male, [China], “Prov. Nord-Yuennan, A-tun-tse”, dissected by Varga (Slide ZV 8945); coll. ZFMK.

Polia (Polia) atrax vargai Gyulai & Saldaitis, 2017

Polia atrax vargai Gyulai & Saldaitis, 2017, Zootaxa 4311 (2): 296, figs 9, 10, 17. Type-locality: China, Prov. Gansu, Atuntse. Holotype: male, in coll. P. Gyulai (Miskolc).

Polia (Polia) bombycina (Hufnagel, 1766)

Phalaena bombycina Hufnagel, 1766, Berlinisches Magazin 3(4): 410. Type-locality: [Germany] vic. of Berlin. Types destroyed.

Synonymy. *Noctua advena* [Denis and Schiffermüller], 1775, Ankündigung eines systematischen Werkes von den Schmetterlingen der Wiener Gegend 1775: 77. Type-locality: [Austria]: Vienna region. Types destroyed;

Noctua nitens Haworth, 1809, Lepidoptera Britannica; sistens Digestionem novam Insectorum Lepidopterorum quae in Magna Britannia Reperiuntur, Larvarum Pabulo, Temporeque Pascendi; Expansione Alarum; Mensibusque Volandi; Synonymis atque Locis Observationibusque Variis 2: 267. Type-locality: [England] Norfolk.

Polia (Polia) bombycina grisea (Butler, 1878)

Alysia grisea Butler, 1878, The Annals and Magazine of Natural History 5(1): 82. Type-locality: Japan, Yokohama. Holotype: female, in coll. BMNH.

Synonymy. *Mamestra advena* var. *adjuncta* Staudinger, 1888, Entomologische Zeitung, Entomologischen Vereine Stettin 49: 249. Type-locality: [Russia] Vladivostok; Sidemi (Bezverkhovo); Askold Island; Ussuri; Suifun (Razdolnaya river). Syntypes: in coll. MNB. Preoccupied, a junior primary homonym of *Mamestra adjuncta* Boisduval, 1852;

Mamestra tetrica Graeser, 1889, Berliner Entomologische Zeitschrift 32 (2): 325. Type-locality: [Russia] Amur region, Chabarofka (Khabarovsk). Holotype: female, in coll. MNB;

Mamestra advena var. *mongolica* Staudinger, 1896, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 9: 241. Type-locality: [Mongolia] Urga (Ulanbaatar). Syntypes: 3 specimens, in coll. MNB.

Parastichtis sordida var. *sachalinensis* Matsumura, 1931, 6000 Illustrated Insects of Japan-Empire. Sapporo 1931: 829. Type-locality: [Russia] Sakhalin. Type(s): in coll. EIHU;

Aplecta mongolica advenina Bryk, 1949, Arkiv för Zoologi 41A (1): 75. An unnecessary replacement name for *Mamestra advena* var. *adjuncta* Staudinger, 1888;

Aplecta mongolica chidisana Bryk, 1949, Arkiv för Zoologi 41(1): 829. Type-locality: North Korea, Chidisan. Holotype: female, in coll. NRS;

Aplecta mongolica koreagena Bryk, 1949, Arkiv för Zoologi 41A(1): 75. Type-locality: North Korea, Hamgyeongbugdo (Shuotsu). Holotype: female, in coll. NRS.

Polia (Polia) bombycina psammochrea Varga, 1974

Polia bombycina psammochrea Varga, 1974, Annales Historico-Naturales Musei Nationalis Hungarici 66: 302, fig. 8. Type-locality: Mongolia, Govi Altai aimak, Khasaght Khajhran Mts, 20 km S of somon Zhargalan, 2400 m. Holotype: male, in coll. HNHM.

Polia (Polia) bombycina puengeleri Lehmann, 1998

Polia bombycina puengeleri Lehmann, 1998, Esperiana 6: 475. Type-locality: [Kirghisia] Asia Centralis, Alexander Mts. Holotype: male, in coll. MNB.

Polia (Polia) goliath (Oberthür, 1880)

Dichonia goliath Oberthür, 1880, Études d'Entomologie 5: 68, pl. 6, fig. 7. Type-locality: [Russia] Askold [Island]. Holotype: male, in coll. BMNH.

Polia (Polia) griseifusa Draudt, 1950

Figs 35, 36, 65

Polia griseifusa Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 30, pl. 2, fig. 14. Type-locality: China, Prov. Yunnan, Li-kiang;

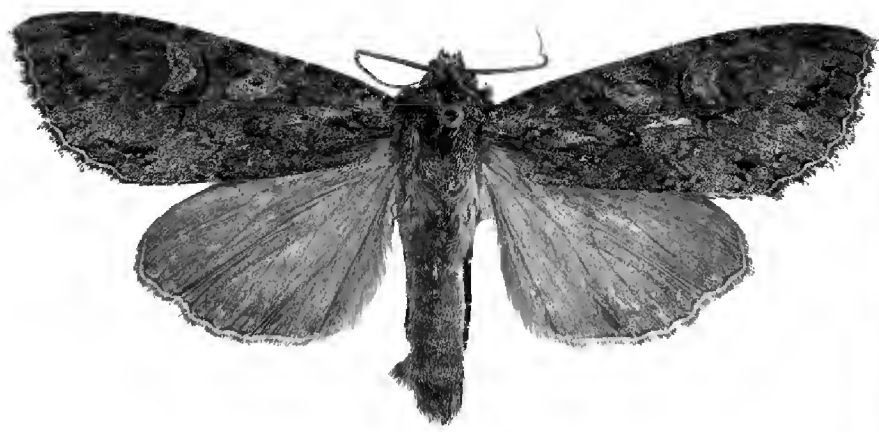


Fig. 33. *Polia (Polia) atrax* Draudt, 1950 Lectotype male

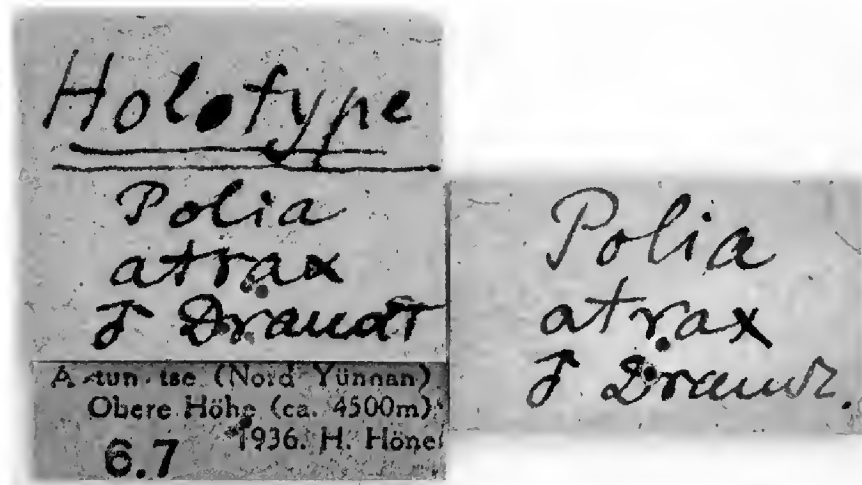


Fig. 33. *Polia (Polia) atrax* Draudt, 1950 Lectotype male, labels



Fig. 35. *Polia (Polia) griseifusa* Draudt, 1950 Lectotype female

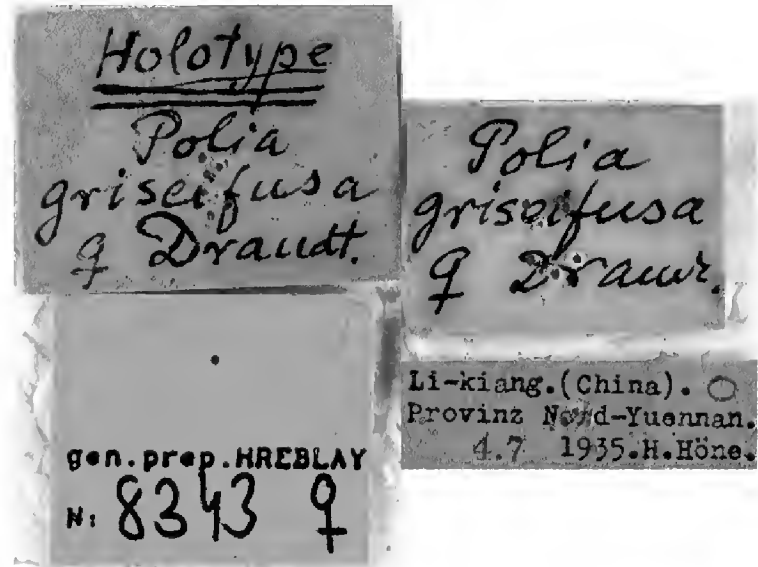


Fig. 36. *Polia (Polia) griseifusa* Draudt, 1950 Lectotype female, labels



Fig. 37. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype male



Fig. 38. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype male, labels



Fig. 39. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype male



Fig. 40. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype male, labels

Figure 33–40. 33. *Polia (Polia) atrax* Draudt, 1950 Lectotype male. 34. *Polia (Polia) atrax* Draudt, 1950 Lectotype male, labels. 35. *Polia (Polia) griseifusa* Draudt, 1950 Lectotype female. 36. *Polia (Polia) griseifusa* Draudt, 1950 Lectotype female, labels. 37. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype male. 38. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype male, labels. 39. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype male. 40. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype male, labels.

A-tun-tse; Batang. Lectotype, female, designated here, in coll. ZFMK.

Lectotype designation. Lectotype: female, “Li-kiang China, Nord-Yuennan 4.9.1935 H. Höne” (printed label), “Holotype *Polia griseifusa* Drdt.” (handwritten label on pink paper). Slide No. HM8343. The specimen is figured by Hacker (1990:Plate D, fig. 9.); coll. ZFMK.

Polia (Polia) hepatica (Clerck, 1759)

Phalaena hepatica Clerck, 1759, *Icones Insectorum Rariorum cum Nominibus eorum Trivialibus, Locisque e C. Linnaei* 1: pl. 8, fig. 3. Type-locality: no locality given.

Synonymy. *Phalaena trimaculosa* Esper, 1788, *Die Schmetterlinge in Abbildungen nach der Natur mit Beschreibungen* 4: pl. 131, fig. 5. Type-locality: no locality given;

Phalaena tinctoria Brahm, 1791, *Handbuch der Ökonomischen Insektengeschichte in Form eines Kalenders bearbeitet* 2: 393. Type-locality: no locality given;

Noctua argentina Haworth, 1809, *Lepidoptera Britannica; sistens Digestionem novam Insectorum Lepidopterorum quae in Magna Britannia Reperiuntur, Larvarum Pabulo, Temporeque Pascendi; Expansione Alarum; Mensibusque Volandi; Synonymis atque Locis Observationibusque Variis* 2: 186. Type-locality: Great Britain;

Mamestra tinctoria var. *obscurata* Staudinger, 1897, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 10: 335. Type-locality: [Russia] Apfelgebirge (Yablonoviy range). Syntypes: 2 females, in coll. MNB.

Polia (Polia) lama lama (Staudinger, 1896)

Figs 37, 38, 66

Mamestra nebulosa var. *lama* Staudinger, 1896, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 9: 241. Type-locality: [Mongolia, Khangay Mts] Uliassutay. Holotype: male, in coll. MNB.

Synonymy. *Polia enodata expallidata* Varga, 1974, *Annales Historico-Naturales Musei Nationalis Hungarici* 66: 306, fig. 10. Type-locality: Mongolia, Bayan Ölgii aimak, Khovd river. Holotype: male, in coll. HNHM.

Polia (Polia) lama enodata (Bang-Haas, 1912)

Figs 39, 40, 67

Mamestra enodata Bang-Haas, 1912, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 26: 145, pl. 6, fig. 10. Type-locality: [Kazakhstan] Karagai-Tau. Lectotype: male, here designated, in coll. MNB.

Lectotype designation. Lectotype: male, „Karagai-Tau”, „Original” (pink label); the specimen was dissected by Boursin (slide No. MB 356); coll. MNB.

Polia (Polia) lamuta (Herz, 1903)

Anarta lamuta Herz, 1903, *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Pétersbourg* 8: 82. Type-locality: [Russia] Uruata Camp place; W of Verkhoyansk. Syntypes: 1 male, 1 female, in coll. ZISP.

Synonymy. *Anarta richardsoni* var. *asiatica* Staudinger, 1901, in Staudinger and Rebel, *Catalog der Lepidopteren des Palaearctischen Faunengebietes* 1901: 218. Type-locality: [Norway] Dovre. Syntypes: in coll. MNB. Preoccupied, a junior secondary homonym of *Polia asiatica* Alphéraky, 1887; syn. of *Bryoxena centralasiae* (Staudinger, 1882);

Mamestra rangnowi Püngeler, 1909, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 21(4): 288. Type-locality: [Sweden] Lulea Lappmark. Syntypes: in coll. MNB;

Anarta lamuta tunkinski O. Bang-Haas, 1927, *Horae Macrolepidopterologiae regionis palaearticae* 1: 86, pl. 10, figs 27-28. Type-locality: [Russia] Irkutsk Pref., Tunkinskiy Mts, SW of Irkutsk, 2000 m. Holotype: male, in coll. MNB.

Polia (Polia) malchani (Draudt, 1934)

Aplecta malchani Draudt, 1934, in A. Seitz, *Die Gross-Schmetterlinge der Erde* 3: 108, pl. 14, row i. Type-locality: [Russia] Transbaikalia, Malchan Mt, “Borochojew”, 800 m. Holotype: female, in coll. MNB.

Polia (Polia) nebulosa nebulosa (Hufnagel, 1766)

Phalaena nebulosa Hufnagel, 1766, *Berlinisches Magazin* 3(3): 298. Type-locality: Germany, Berlin district.

Synonymy. *Phalaena Noctua thapsi* Brahm, 1791, *Handbuch der Ökonomischen Insektengeschichte in Form eines Kalenders bearbeitet* 2: 135. Type-locality: no locality given;

Phalaena grandis Donovan, 1801, *The Natural History of the British Insects* 10: 51, pl. 345, fig. 1. Type-locality: England;

Noctua plebeja Hübner, 1803, *Sammlung europäischer Schmetterlinge* 4: pl. 16, fig. 78. Type-locality: Europe; nec *Phalaena plebeja* Linnaeus, 1761; *Fauna Suecica* 320; TL: Sweden, Uplandia

Polia (Polia) nebulosa askolda (Oberthür, 1880)

Aplecta nebulosa var. *askolda* Oberthür, 1880, *Études d'Entomologie* 5: 79. Type-locality: [Russia] Askold [Island]. Syntypes: 4 males and 1 female, in coll. BMNH.

***Polia (Polia) richardsoni* (Curtis, 1835)**

Hadena richardsoni Curtis, 1835, Appendix to John Ross Narrative of a Second Voyage 1835: 72, pl. A, fig. 11. Type-locality: [Canada] 15 miles from River Tatchick (Eskimo name), 200 miles S of Port Bowen, very near Comptroller's Island. Types: in coll. USNMW.

Synonymy. *Anarta algida* Lefebvre, 1836, Annales de la Société Entomologique de France 5: 396, pl. 10 fig. 5. Type-locality: "Laponie". Syntypes, in coll. MNHNP;

Anarta septentrionis Walker, 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum 11: 700. Type-locality: [Canada] Repulse Bay. Holotype: in coll. BMNH;

Mamestra feildeni McLachlan, 1878, Journal of the Linnean Society (Zoology) 14: 112. Type-locality: Canada Arctic Territories, Dobbin Bay. Holotype: female;

Anarta fumida Graeser, 1889, Berliner Entomologische Zeitschrift 32(2): 323. Type-locality: [Russia], Amur region, Amur region, Nicolajefsk (Nikolajevsk). Holotype: male, in coll. ZISP;

Anarta lanuginosa Smith, 1900, in: Dyar, Proceedings of the Washington Academy of Sciences 2: 493. Type-locality: USA, Alaska, Popof Island. Holotype: male, in coll. USNMW;

Anarta richardsoni var. *dovreensis* Staudinger, 1901, in Staudinger and Rebel, Catalog der Lepidopteren des Palaearctischen Faunengebietes 1901: 218. Type-locality: [Norway] Dovre. Syntypes: in coll. MNB;

Anarta squara Smith, 1908, Annals of the New York Academy of Sciences 18: 112. Type-locality: Greenland. Lectotype: male, in coll. AMNHN;

Anarta magna Barnes and Benjamin, 1924, Entomological News 35: 117. Type-locality: USA, Colorado, Hall valley, Bullion peak. Holotype, female, in coll. USNMW;

Anarta richardsoni tamsi Benjamin, 1933, Pan-Pacific Entomologist 9: 58. Type-locality: [Canada] Labrador, Hopedale. Holotype: male, in coll. USNMW;

Aplecta richardsoni groenlandica Heydemann, 1944, Entomologische Zeitung, Entomologischen Vereine zu Stettin 105: 22, pl. 7, figs 5-6. Type-locality: East Greenland. Syntypes: in coll. MNB.

Taxonomic notes. This circumpolar Holarctic species shows intense subspeciation in both continents; the taxonomic status of the described taxa are to be clarified.

***Polia (Polia) serratilinea serratilinea* (Treitschke, 1825)**

Figs 41, 42

Mamestra serratilinea Treitschke, 1825, Die Schmetterlinge von Europa 5(2): 38. Type-locality: Vienna district. Lectotype designated here, male in coll. HNHM.

Lectotype designation. Lectotype: male, with the following labels: "Ochs. 961" (printed label with black margin),

"Hung. Nat. Hist. Mus. Coll. Lepidoptera, Collectio Ochsenheimer No. 975"; coll. HNHM.

Synonymy. *Mamestra serratilinea* Ochsenheimer, 1816, Die Schmetterlinge von Europa IV, p. 74. (nomen nudum);

Mamestra serratilinea var. *helvetica* Schawerda, 1925, Mitteilungen der Münchner Entomologischen Gesellschaft 15: 70, fig. 2. Type-locality: Switzerland, Zermatt. Type(s): in coll. LSNK;

Mamestra serratilinea var. *heinrichi* Schawerda, 1925, Mitteilungen der Münchner Entomologischen Gesellschaft 15: 70, fig. 2. Type-locality: France, Digne. Holotype: male, in coll. LSNK.

***Polia (Polia) serratilinea eremorealis* Varga, 1974**

Polia serratilinea eremorealis Varga, 1974, Annales historico-naturales Musei nationalis hungarici 66: 306, fig. 11. Type-locality: Mongolia, Khovd aimak, 5 km SW of Khovd (Kobdo), 1500 m. Holotype: male, in coll. HNHM.

***Polia (Polia) serratilinea kowatschevi* Drenovsky, 1931**

Polia serratilinea kowatschevi Drenovsky, 1931, Mitteilungen der Bulgarischen Entomologischen Gesellschaft in Sofia 6: 56. Type-locality: Makedonia, Ali Botush Mts. Holotype: male, in coll. NHM Sofia.

***Polia (Polia) serratilinea pinkeri* Varga, 1974**

Polia serratilinea pinkeri Varga, 1974, Annales historico-naturales Musei nationalis hungarici 66: 307, fig. 11. Type-locality: Turkey, Prov. Kayseri, ErciyasDagh, Develi, 1700 m. Holotype: male, in coll. ZSM.

***Polia (Polia) serratilinea spalax* (Alphéraky, 1887)**

Mamestra spalax Alphéraky, 1887, Entomologische Zeitung, Entomologischen Vereine zu Stettin 48: 168. Type-locality: [Kirghisia] Aram-Kungei. Lectotype: male, here designated, in coll. ZISP.

Lectotype designation. Lectotype: male, "Aram-Kungaj" "Gr[oum].Gr[shimailo]." "Spalax Alph. Orig." (Coll. ZISP).

***Polia (Polia) serratilinea tenebricosa* Hacker & Weigert, 1990**

Polia serratilinea tenebricosa Hacker & Weigert, 1990, Esperiana 1: 339, pl. E, fig. 18, text fig. 57a. Type-locality: Pakistan, Himalaya Mts, Babusar Pass, 3200 m. Holotype: male, in coll. Weigert (Griesbach im Rottal).



Fig. 41. *Polia (Polia) serratilinea serratilinea* (Treitschke, 1825)
Lectotype male

Hung. Nat. Hist. Mus.
Coll Lepidoptera
Collectio
Ochsenheimer No. 975



Fig. 42. *Polia (Polia) serratilinea serratilinea* (Treitschke, 1825)
Lectotype male, labels

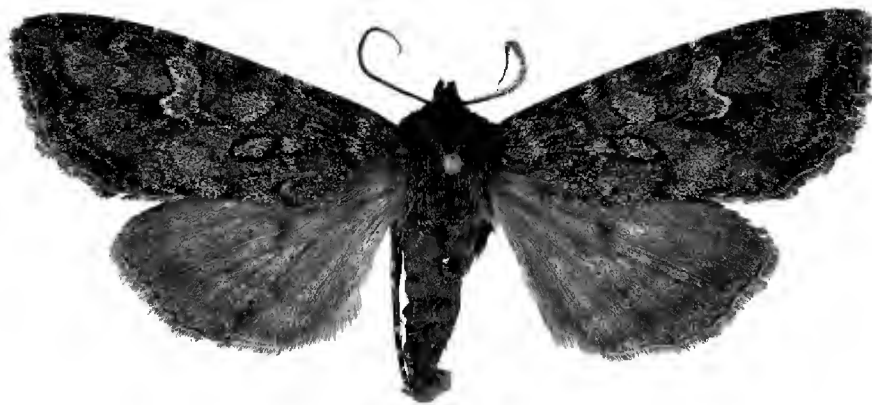


Fig. 43. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype male



Fig. 44. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype male, labels



Fig. 45. *Pachetra cherrug* (Rákosy & Wieser, 1997) Paratype male

21-22.05.-1996
Greci, 250m
Mții Măcin
Romania
leg. L.Rákosy



Fig. 46. *Pachetra cherrug* (Rákosy & Wieser, 1997) Paratype male, labels



Fig. 47. *Multisigna costirufa* (Draudt, 1950) Holotype female

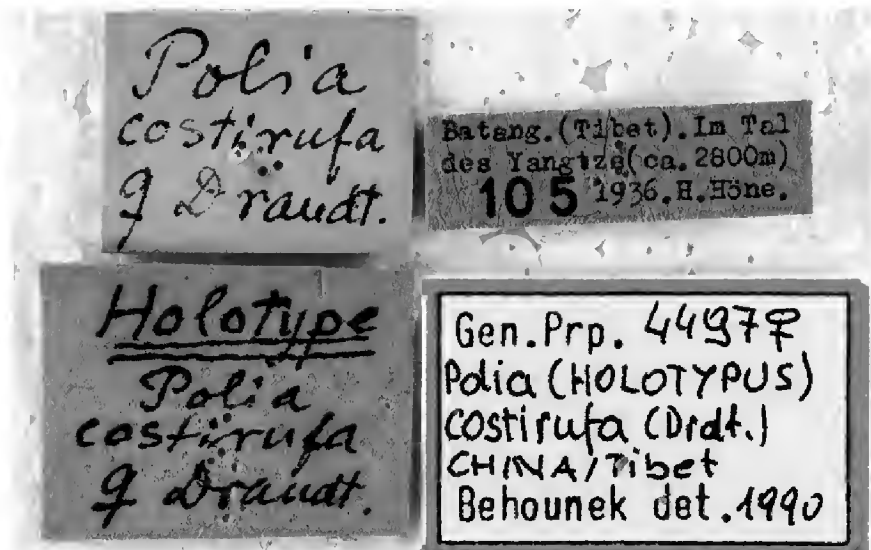


Fig. 48. *Multisigna costirufa* (Draudt, 1950) Holotype female, labels

Figure 41–48. 41. *Polia (Polia) serratilinea serratilinea* (Treitschke, 1825) Lectotype male. 42. *Polia (Polia) serratilinea serratilinea* (Treitschke, 1825) Lectotype male, labels. 43. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype male. 44. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype male, labels. 45. *Pachetra cherrug* (Rákosy & Wieser, 1997) Paratype male. 46. *Pachetra cherrug* (Rákosy & Wieser, 1997) Paratype male, labels. 47. *Multisigna costirufa* (Draudt, 1950) Holotype female. 48. *Multisigna costirufa* (Draudt, 1950) Holotype female, labels.

***Polia (Polia) subcontigua* (Eversmann, 1852), stat. rev., comb. n.**

Hadena subcontigua Eversmann, 1852, Bulletin de la Société Impériale des Naturalistes de Moscou 25 (1): 155. Type-locality: [Russia, Orenburgskaya obl.] “Spask.” “Jul[y]” (handwritten labels). Holotype: female, in coll. ZISP.

Synonymy. *Hadena altaica* Lederer, 1853, Verhandlungen des Zoologisch-Botanischen Vereins in Wien 3: 370, pl. 2, fig. 6. Type-locality: [Russia or Kazakhstan] Altai Mts. Holotype: male, in coll. MNB; syn. n.

Mamestra monotona Bang-Haas, 1912, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 26: 145. Type-locality: [Russia] Sayan region. Syntypes: in coll. MNB.

Polia (Mamestra) praecontigua Turati, 1933, Bollettino della Società Entomologica Italiana 65: 18. Type-locality: [India/Pakistan] Baltistan, Biaho valley near Baltoro. Syntypes, in coll. Turati (if exist).

Taxonomic notes. Based on the type catalogue of the Lepidoptera collection of ZISP it became evident that *Hadena subcontigua* Eversmann represent the same species as *Hadena altaica* Lederer and at the same time also its westernmost occurrence. This species exist in most localities from the Tien-Shan Mts. to Central Mongolia and also Nepal in polymorphic, contrasting vs. concolorous forms. Therefore, *Mamestra monotona* Bang-Haas cannot be considered as own taxon. According to the description and photos, the taxon *Polia (Mamestra) praecontigua* Turati, 1933 also represents this species. The occurrence of *P. subcontigua* in the Karakoram and the Western Himalayan mountains was confirmed by the recent surveys, too.

***Polia (Polia) tiefi* Püngeler, 1914**

Figs 43, 44, 68, 69

Polia (Mamestra) tiefi Püngeler, 1914, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 28: 38, pl. 2, fig. 22. Type-locality: [Russia] Sayan Mts, Munko Sardyk. Lectotype: male, here designated, coll. MNB.

Lectotype designation. Lectotype male, Sayan Mts, Munko Sardyk; slide No. MB 417, coll. MNB.

Synonymy. *Aplecta schawerdae* Sheljuzhko, 1933, Zeitschrift des Österreichischen Entomologen Vereines 18: 70, pl. 13. Type-locality: Russia, Siberia, Yakutsk Province, Dzhugzhur Mts. Syntypes: in coll. ZIN.

***Polia (Polia) vespertilio* (Draudt, 1934)**

Aplecta vespertilio Draudt, 1934, in A. Seitz, Die Gross-Schmetterlinge der Erde 3: 109, pl. 14, row i. Type-locality: [Russia], Irkutsk, Tunkinski Mt. Lectotype: male, in coll. MNB.

Lectotype designation. Lectotype: male, Irkutsk, Tunkinski Mt., slide No. Varga MB 2-75V, coll. MNB.

***Polia (Polia) vesperugo* Eversmann, 1856**

Polia vesperugo Eversmann, 1856, Bulletin de la Société Impériale des Naturalistes de Moscou 29 (3): 48, pl. 2, fig. 6. Type-locality: [Russia] Transbaikalia, Irkutsk. Lectotype: female, here designated, in coll. ZISP.

Lectotype designation. Lectotype: female, “Irkutsk”, “vesperugo”, Gen. sl. 00908 Kuznetzov; coll. ZISP.

Synonymy. *Mamestra conspicua* Bang-Haas, 1912, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 26: 144, pl. 6, fig. 8. Type-locality: [Russia] Sayan region. Holotype: male, in coll. MNB; syn. n.

Remarks. The lectotype female specimen is illustrated by A. Matov on the homepage of the ZISP.

***Polia (Polia) vesperugo vasjurini* Sukhareva, 1976, stat. rev.**

Polia vasjurini Sukhareva, 1976, Proceedings of the Zoological Institute Academy of Sciences of USSR 64: 58, fig. 1. Type-locality: Russian Far East, Primorye territory, Partizansky district, Lysaya Benevskaya Mt. Holotype: male, in coll. ZISP.

***Polia (Polia) vesperugo sabmeana* Mikkola, 1980, stat. rev.**

Polia sabmeana Mikkola, 1980, Notulae Entomologicae 60: 217, figs 1, 3-4. Type-locality: Finland, Inari. Holotype: male, in coll. ZMUH.

Subgenus *Protopolia* subgen. n.

<http://zoobank.org/5387F65E-A106-4DFC-B524-1C09169C21FA>

Type-species. *Mamestra praecipua* Staudinger, 1895, Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden 8: 316.

Diagnosis. The three species belonging to this subgenus are large, robust moths with simple ochreous-brownish or purplish-blackish-brown (generally unicolorous but sometimes, individually, contrasting) colouration and regular pattern, somewhat resembling certain forms of *Apamea monoglypha* (Hufnagel, 1766).

In the male genitalia, the saccular processes are simple, short or acute, symmetrical, with prominent tuft of specialised setae on the right side. Vesica is tubular, relatively short and retroflexed, with only a short fascia of cornuti subterminally.

In the female genitalia, the appendix bursae is slightly prominent only, the corpus bursae has two short longitudinal signa.

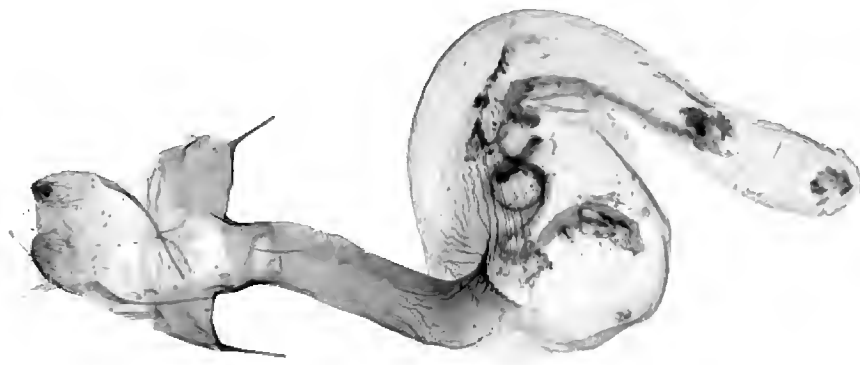


Fig. 49. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype, Hacker9775



Fig. 50. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype, Boursin MB310



Fig. 51. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype, GP8191

Figure 49–51. 49. *Ctenoceratoda brassicina* (Draudt, 1934) Holotype female. 50. *Ctenoceratoda contempta* (Püngeler, 1914) Lectotype male. 51. *Ctenoceratoda graeseri* (Püngeler, 1898) Lectotype male.

Etymology. The name refers to the relative simplicity of colouration and configuration of male genitalia as opposed to the huge majority of *Polia* and *Poliina*, respectively.

***Polia (Protopolia) minae* Saldaitis, Benedek & Behounek, 2013**

Polia minae Saldaitis, Benedek & Behounek, 2013, *Zootaxa* 3693(4): 594, figs 5-8, 13-16, 19-20. Type-locality: China, N. Sichuan, near Jiuzhaigou, 2100 m, 33°18,85'N, 103°55,5'E. Holotype: male, in coll. ZSM.

***Polia (Protopolia) praecipua praecipua* (Staudinger, 1895)**

Mamestra praecipua Staudinger, 1895, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 8: 316. Type-locality: [China, Xinjiang-Qinghai] between Lob-Noor and Kuku-Noor. Lectotype: male, designated here in MNB.

Lectotype designation. Lectotype: male, “Kuku-Noor 94 Rückb[ei].”, “Origin” (pink label), “Praecipua Stgr.” “Ex coll. 1/3 Staudinger”, slide No. GB 12024 (figured in Saldaitis et al. 2013), coll. MNB.

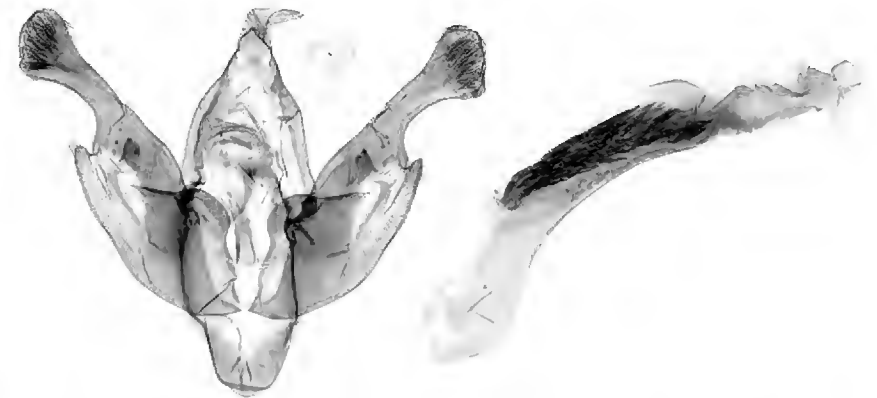


Fig. 52. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype, Boursin MB307



Fig. 53. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype, RL11751



Fig. 54. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype, RL11753

Figure 52–54. 52. *Ctenoceratoda longicornis* (Graeser, 1892) Lectotype male. 53. *Ctenoceratoda longicornis* (Graeser, 1892) Paralectotype male. 54. *Ctenoceratoda lupa* (Christoph, 1893) Lectotype male.

***Polia (Protopolia) praecipua angusta* (Hreblay & Ronkay, 1998)**

Haderonia praecipua angusta Hreblay & Ronkay, 1998, in Haruta, T. (ed.) *Tinea* 15 (Supplement 1): 150, pl. 146, fig. 5. Type-locality: Nepal, Annapurna Himal, 11 km S of Jomsom, Noma pasture, 4000 m, 28°44,5'N, 83°48'E. Holotype: male, in coll. G. Ronkay (Budapest).

***Polia (Protopolia) sublimis* (Draudt, 1950)**

Hadula sublimis Draudt, 1950, *Mitteilungen der Münchener Entomologischen Gesellschaft* 40: 37. Type-locality: China, Prov. Yunnan, A-tun-tse; Batang. Lectotype: male, in coll. ZFMK.

Genus *Pachetra* Guenée, 1841

Pachetra Guenée, 1841, *Annales de la Société Entomologique de France* 10: 241. Type-species: *Noctua leucophaea* [Denis and Schiffermüller], 1775, by monotypy.

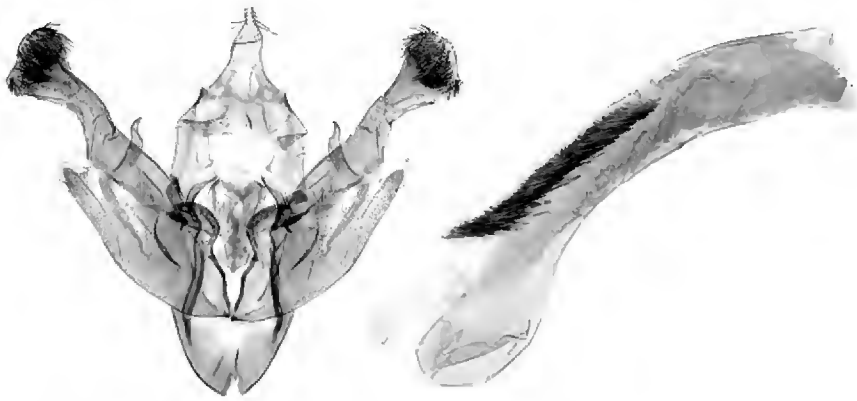
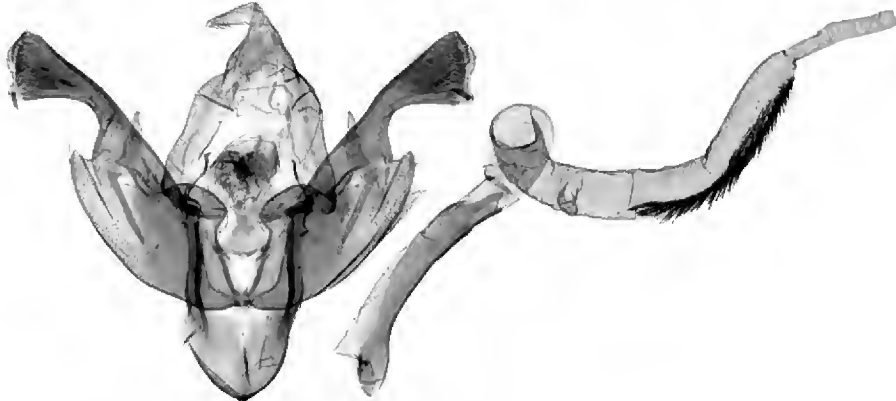
Fig. 55. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype, Boursin MB309Fig. 56. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype, Matov0148 (Photo A. Matov)Fig. 57. *Ctenoceratoda tancrei* (Graeser, 1892) Paralectotype, VZ9526

Figure 55–57. 55. *Ctenoceratoda nefasta* (Püngeler, 1907) Lectotype male. 56. *Ctenoceratoda optima* (Alphéraky, 1897) Lectotype male. 57. *Ctenoceratoda tancrei* (Graeser, 1892) Paralectotype male.

Pachetra sagittigera (Hufnagel, 1766)

Phalaena sagittigera Hufnagel, 1766, Berlinisches Magazin 3(3): 410. Type-locality: Germany, Berlin district. Type(s) destroyed.

Synonymy. *Noctua leucophaea* [Denis & Schiffermüller], 1775, Ankündigung eines systematischen Werkes von den Schmetterlingen der Wiener Gegend 1775: 82. Type-locality: [Austria] Vienna district. Types destroyed;

Bombyx fulminea Fabricius, 1781, Species Insectorum Exhibentes Eorum Differentias Specificas, Synonyma Auctorum, Loca Natalia, Metamorphosis in Adiectis, Observationibus, Descriptionibus 2: 205. Type-locality: [Germany] Hamburg;

Bombyx vestigialis Esper, 1785, Die Schmetterlinge in Abbildungen nach der Natur mit Beschreibungen 3: 270, pl. 53, fig. 5. Type-locality: [Germany] Leipzig;

Hadena bombycina Eversmann, 1847, Bulletin de la Société Impériale des Naturalistes de Moscou 20(3): 78, pl. 6, figs 1-2. Type-locality: [Russia] Urals. Syntypes: in coll. ZIN;

Mamestra leucophaea var. *incana* Millière, 1885, Il Naturalista Siciliano 4: 198. Type-locality: [Italy, Sicily] St. Martin, Berthemot;

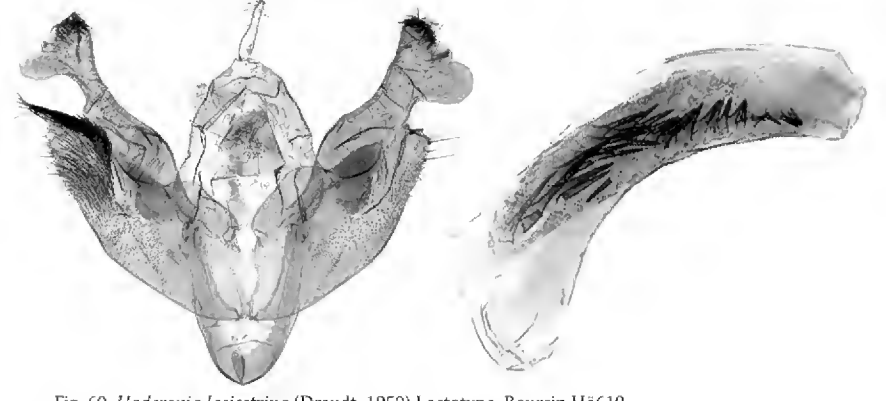
Fig. 58. *Ctenoceratoda turpis* (Staudinger, 1900) Lectotype, Boursin MB298Fig. 59. *Haderonia aplectoides* (Draudt, 1950) Paralectotype, Boursin H6612Fig. 60. *Haderonia lasiestrina* (Draudt, 1950) Lectotype, Boursin H6610

Figure 58–60. 58. *Ctenoceratoda turpis* (Staudinger, 1900) Lectotype male. 59. *Haderonia aplectoides* (Draudt, 1950) Paralectotype male. 60. *Haderonia lasiestrina* (Draudt, 1950) Lectotype male.

Pachetra leucophaea britannica Turner, 1933, Entomologist's Record and Journal of Variation 45: 282. Type-locality: "British examples". Syntypes: in coll. BMNH.

Pachetra sagittigera pyrenaica Oberthür, 1884, stat. rev.

Pachetra leucophaea var. *pyrenaica* Oberthür, 1884, Études d'Entomologie 8: 50. Type-locality: France, Pyrenees, Cauterets. Type(s): in coll. BMNH.

Pachetra sagittigera bombycina Eversmann, 1847

Hadena bombycina Eversmann, 1847, Bulletin de la Société Impériale des Naturalistes de Moscou 20(3): 78, pl. 6, figs 1-2. Type-locality: [Russia] Urals. Syntypes: in coll. ZIN.

Taxonomic note. The small, short-winged and contrasting *P. sagittigera* specimens from Mongolia were considered as belonging to this subspecies until yet (Sheljuzhko 1967). The question needs further survey.

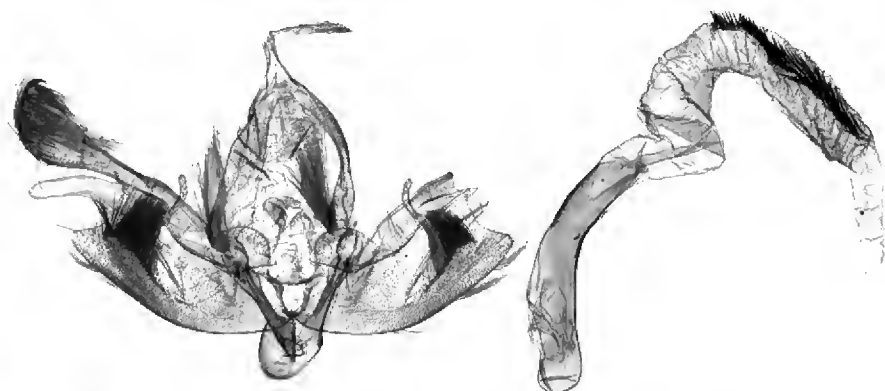
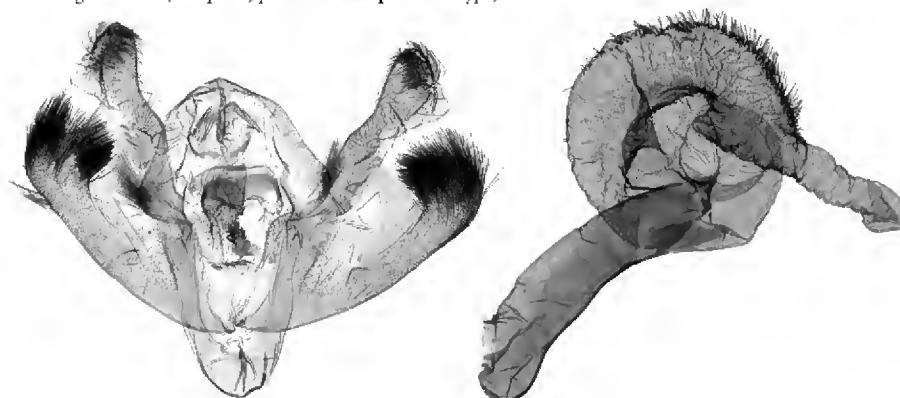
Fig. 61. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Holotype, VZ Dresden09Fig. 62. *Polia (Atropolia) posterodiluta* sp. n. Holotype, RL8670Fig. 63. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype, VZ8946

Figure 61–63. 61. *Polia (Atropolia) mortua szetschwana* Draeseke, 1928 Lectotype male. 62. *Polia (Atropolia) posterodiluta* sp. n. Holotype male. 63. *Polia (Leuconephropolia) albirena* Draudt, 1950 Lectotype male.

***Pachetra cherrug* (Rákósy & Wieser, 1997), comb. n.**

Figs 45, 46, 70, 71

Polia cherrug Rákósy & Wieser, 1997, Linzer Biologische Beiträge 29: 1153. Type-locality: Romania, N Dobrogea, Macin Mts, Greci. Holotype: male, in coll. L. Rákósy (Cluj-Napoca).

Taxonomic notes. *P. cherrug* shows in the genitalia of both sexes a very close relationship with *P. sagittigera*. The shared characters are as follows: in male genitalia the similar and unusual shape of the cucullus, the very long tubular and completely helicoid vesica nearly completely covered by a long and broad stripe of dense spinulose structures; in female genitalia the long and broad, dorso-ventrally flattened ductus bursae, the similar shape of the appendix bursae and one long and one shorter stripe of sigma. Both species are also bionomically closely related, they have grass-feeding larvae in contrast to the dicot herbaceous and woody food plants of *Polia* spp. The distribution and certain taxonomic questions are discussed in detail by Dinca (2010).

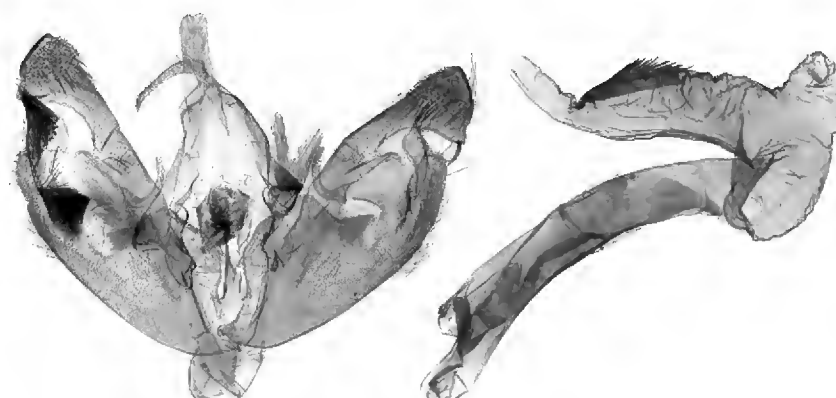
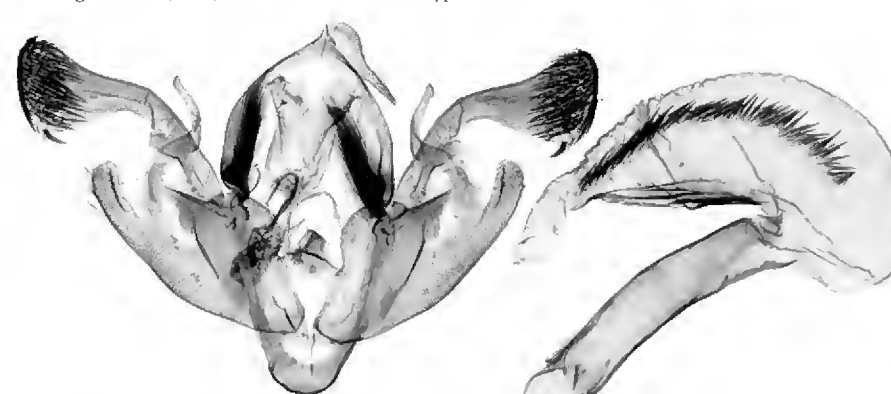
Fig. 64. *Polia (Polia) atrax* Draudt, 1950 Lectotype, VZ8945Fig. 65. *Polia (Polia) griseifusa* Draudt, 1950, VZ9523Fig. 66. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype, VZ2-71

Figure 64–66. 64. *Polia (Polia) atrax* Draudt, 1950 Lectotype male. 65. *Polia (Polia) griseifusa* Draudt, 1950. 66. *Polia (Polia) lama lama* (Staudinger, 1896) Holotype male.

Genus *Tricheurois* Hampson, 1905

Tricheurois Hampson, 1905, Annals and Magazine of Natural History 7(15): 451. Type-species: *Mamestra nigrocuprea* Moore, 1867, by original designation.

Synonymy. *Acanthopolia* Boursin, 1943, Zeitschrift der Wiener Entomologischen Gesellschaft 50: 339. Type-species: *Apamea cuprina* Moore, 1881, by original designation.

***Tricheurois cuprina* (Moore, 1881)**

Apamea cuprina Moore, 1881, Proceedings of the Zoological Society of London 1881: 345, pl. 38, fig. 2. Type-locality: India, Sikkim. Holotype: male, in coll. MNB.

***Tricheurois nigrocuprea* (Moore, 1867)**

Mamestra nigrocuprea Moore, 1867, Proceedings of the Zoological Society of London 1867: 52. Type-locality: [India or Bangladesh] Bengal. Lectotype: male, dissected by M. Hreblay (slide No. HM8376); in coll. BMNH.

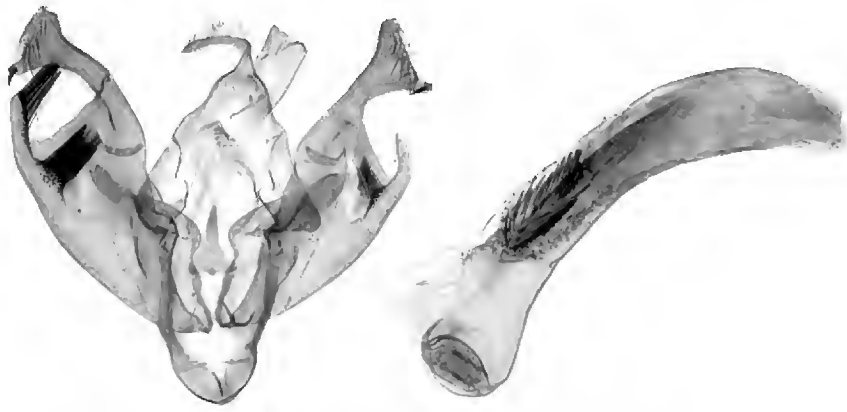
Fig. 67. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype, Boursin MB356Fig. 68. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype, Boursin MB417Fig. 69. *Polia (Polia) tiefi* Püngeler, 1914 Paralectotype, VZ2-73

Figure 67–71. 67. *Polia (Polia) lama enodata* (Bang-Haas, 1912) Lectotype male. 68. *Polia (Polia) tiefi* Püngeler, 1914 Lectotype male. 69. *Polia (Polia) tiefi* Püngeler, 1914 Paralectotype male.

Tricheurois retrusa (Püngeler, 1906)

Polia (Mamestra) retrusa Püngeler, 1906, Deutsche Entomologische Zeitschrift. Gesellschaft Iris zu Dresden 19: 91, pl. 7, fig. 13. Type-locality: [China, Qinghai] Tibet, Kuku-Noor. Holotype: male, in coll. MNB.

Tricheurois tamangi Hreblay & Plante, 1996

Tricheurois tamangi Hreblay & Plante, 1996, Lambillionea 96: 665, figs 11-12, 35-36. Type-locality: Nepal, Ganesh Himal, Khurpudanda Pass, 3600 m, 28°12'N, 85°13'E. Holotype: male, in coll. MNHG.

Tricheurois tibetica Boursin, 1965

Tricheurois tibetica Boursin, 1965, Zeitschrift der Wiener Entomologischen Gesellschaft 50: 119, pl. 14, fig. 1. Type-locality: India, Sikkim, Yatung (“Tibet, Yatung”), 4500 m. Holotype: male, in coll. SMNK.

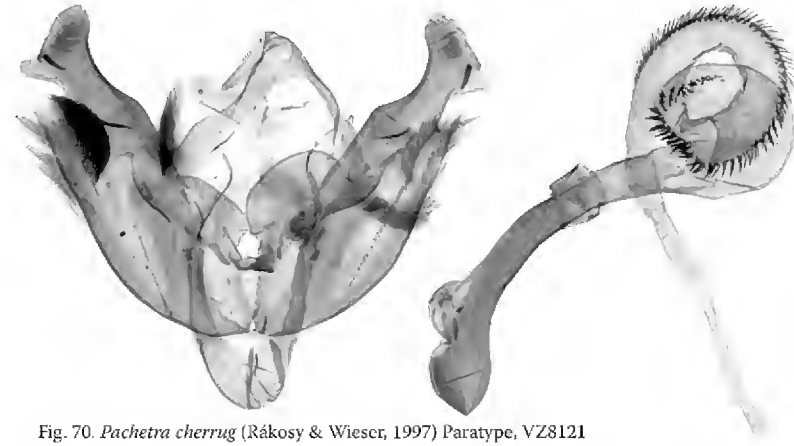
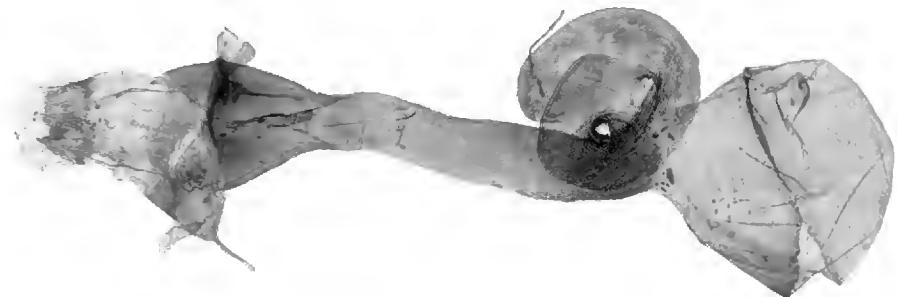
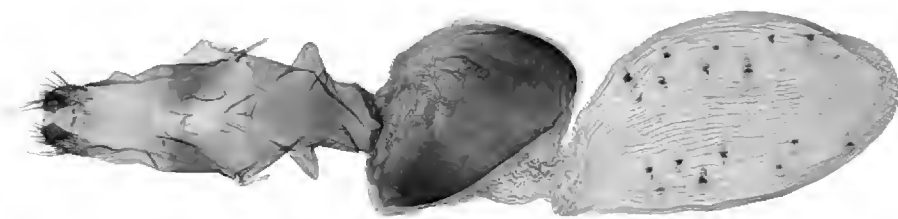
Fig. 70. *Pachetra cherrug* (Rákósy & Wieser, 1997) Paratype, VZ8121Fig. 71. *Pachetra cherrug* (Rákósy & Wieser, 1997) Paratype, VZ9596Fig. 72. *Multisigna costirufa* (Draudt, 1950) RL9711

Figure 70–72. 70. *Pachetra cherrug* (Rákósy & Wieser, 1997) Paratype male. 71. *Pachetra cherrug* (Rákósy & Wieser, 1997) Paratype female. 72. *Multisigna costirufa* (Draudt, 1950).

Poliina incertae sedis

Polia (Mamestra) confusa Turati, 1933, Bollettino della Società Entomologica Italiana 65(1): 19. Type-locality: [China/India/Pakistan] valley of the Tarim; [Pakistan] Deosai Plains. Syntypes: 4 females, 2 males, in coll. Turati (if exist).

Genera and species excluded from *Poliina*

Genus *Kollariana* Hacker, 1996, stat. rev.

Kollariana Hacker, 1996, Esperiana 4: 386. Type-species: *Polia scotochlora* Kollar, 1849, by original designation.

Taxonomic notes. Despite of the “*Polia*-like” habitus the genital structures of both sexes clearly show that *Kollariana* belong to the “*Sideridis*” line of the subtribe Mamestrina (See also: Introduction). In the male genitalia, the genital capsule is very similar to that of certain large *Sideridis* species as e.g. *S. turbida* (Esper, 1790) or *S. egena* (Lederer, 1853). The diagnostic features are as follows: valva without saccular process and ampulla, but with ear-

shaped costal process near to cucullus; aedeagus with claw- or spine-shaped sclerotisation of carina; vesica T-shaped, with long subbasal diverticulum and acute cornutus. In the female genitalia there are two complete and one shorter row of small, elliptical stigmata on the corpus bursae; the ductus bursae is rather strongly sclerotised with lateral pouch corresponding to the sclerotised extension of carina.

***Kollariana albomixta* (Draudt, 1950), comb. n.**

Polia albomixta Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 31, pl. 2, fig. 13. Type-locality: China, Prov. Yunnan, Li-kiang. Holotype: female, in coll. ZFMK.

***Kollariana scotochlora* (Kollar, 1844)**

Polia scotochlora Kollar, 1844, in Hügel, Kaschmir das Reich der Siek 4: 480. Type-locality: (India) Kashmir, (Mussorree) Massuri. Holotype: male, in coll. BMNH.

Synonymy. *Polia stevensii* Guenée, 1852, in Boisduval and Guenée, Histoire Naturelle des Insectes, Species général de Lépidoptères 6: 38. Type-locality: Central India. Holotype: male, in coll. BMNH.

***Kollariana similissima* Plante, 1982**

Polia similissima Plante, 1982, Bulletin de la Société Entomologique de France 87: 286, figs 1-2, 9-10. Type-locality: Nepal, Langtang Himal, Kyangin Gompa, 3900 m. Holotype: male, in coll. MNHG.

***Multisigna* gen. n.**

<http://zoobank.org/FAB6052C-C62C-42AF-80D1-9D4390212563>

Type-species. *Polia costirufa* Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 28, pl. 2, fig. 9, here designated.

Diagnosis. The two species of this new genus show some external similarity with the larger *Polia* species (as e.g. *P. vesperugo*) but they also resemble the larger *Sideridis* species (as e.g. *S. egena*, *S. turbida*) but also *Apamea* species according the robust body, dark brownish-greyish colouration and pattern of fore wing with regular maculation and crenulate or zigzag-shaped crosslines. The most important differential characters are in the genitalia of both sexes. In male genitalia the saccular part of valvae is not extended, no any trend of asymmetrisation and/or presence of specialised saccular brushes can be observed. Free „clasper” of the harpe-ampulla complex – which is usually present in *Polia* – is reduced. Vesica is not elongate-tubular as in *Polia*, but it shows the modified form of the T-shaped vesica of the *Sideridis*-clade of the Mamestrina while it is more saccate with subbasal diverticulum

and the subterminal field of cornuti is transformed to a single huge cornutus, unusual for other related genera. The female genitalia are also strikingly different from *Polia* but also from the genera of the subtribe Mamestrina (e.g. *Sideridis*, *Conisania* which seem to be most closely related) by the presence of very numerous pearl-shaped signa and by the conical appendages of ductus bursae. Based on these characters we place this genus near to the also habitually similar genera *Kollariana* and *Irene*.

Etymology. The generic name refers to the most peculiar character of the female genitalia.

***Multisigna hofer* (Saldaitis, Benedek & Behounek, 2016), comb. n.**

Polia hofer Saldaitis, Benedek & Behounek, 2016, Zootaxa 4093(4): 577. Type-locality: China, Sichuan, 20 km N of Maoxian. Holotype: male, in coll. G. Behounek (later in ZSM).

***Multisigna costirufa* (Draudt, 1950), comb. n.**

Figs 47, 48, 72

Polia costirufa Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 28, pl. 2, fig. 9. Type-locality: [China] Yunnan, Batang, Yangtze valley, 2800 m. Lectotype: female, here designated, in coll. ZFMK.

Lectotype designation. Lectotype: female, “Batang (Tibet), im Tal des Yangtze (ca 2800 m), 10.5.1936, H. Höne”, “Holotype *Polia costirufa* ♀ Draudt” (pinkish label), “*Polia costirufa* ♀ Draudt”, “*Polia costirufa* 4497”, “Gen. Prp. 4497 ♀ Holotypus, *Polia costirufa* (Drdt.), CHINA/Tibet, Behounek det. 1990” (red bordered label); in coll. ZFMK.

Genus *Irene* Saldaitis & Benedek, 2017

Irene Saldaitis & Benedek, 2017, Zootaxa 4238(2): 275. Type-species: *Irene litanga* Saldaitis & Benedek, 2017, by original designation.

***Irene litanga* Saldaitis & Benedek, 2017**

Irene litanga Saldaitis & Benedek, 2017, Zootaxa 4238(2): 276. Type-locality: China, Sichuan, near Litang. Holotype: male, in coll. G. Behounek (later ZSM).

Taxonomic notes. As it was stated correctly in the original description, this genus shows close relationship with *Hada* Billberg, 1820, especially to *Hada tenebra*, etc. The lateral “pouches” of ductus also show some similarity to *Kollariana* but the short, globular corpus bursae without

signa clearly shows that this genus is differentiated from the former genus.

Genus *Spiramater* McCabe, 1980, stat. n.

Spiramater McCabe, 1980, Bulletin of the New York State Museum 432: 10 (key), 31. Type-species: *Haderonia lutra* Guenée, 1852, by original designation.

Taxonomic notes. This genus is not closely related with *Polia*. Recently (Lafontaine and Schmidt 2010, Zookeys 40: 90) *S. lutra* (Guenée, 1852) was associated with *Lacanobia* and *S. grandis* (Guenée, 1852) was introduced to this genus (*Lacanobia grandis*).

Tycomarptes proximoides (Wiltshire, 1982)

Haderonia proximoides Wiltshire, 1982, Fauna of Saudi Arabia 4: 311, pl. 3 fig. 37. Type-locality: Saudi Arabia, Risayah. Holotype: male, in coll. BMNH.

Taxonomic notes. This curiously looking Arabian species was illustrated by Hacker (2006; Esperiana 12: 352; Pl. 9, fig. 8) as belonging to the genus *Tycomarptes* Fletcher, 1961, however, without argumentation.

Conisania roseipicta (Draudt, 1950)

Polia roseipicta Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 29, pl. 2, fig. 10. Type-locality: [China] Yunnan, Atuntse. Holotype: male, in coll. ZFMK.

Taxonomic notes. The species was first proposed to transfer from *Polia* to the *Sideridis-Conisania* generic complex by Boursin (1966). Subsequently, Varga and Ronkay (1991) listed the species in the genus *Conisania* Hampson, 1905 in the general survey of the genus-group (p. 152; figs 98-99). The vesica of the holotype specimen has not been everted by Boursin; the recent investigations indicated the T-shaped vesica structure which is typical of certain species-groups of *Conisania*.

Mythimna (Morphopoliana) yuennana (Draudt, 1950)

Polia yuennana Draudt, 1950, Mitteilungen der Münchner Entomologischen Gesellschaft 40: 27, pl. 2, fig. 6. Type-locality: [China] Yunnan, Atuntse. Syntypes: in coll. ZFMK.

Taxonomic notes. The species has long been misplaced although the male genitalia illustrated already by Draudt in the original description (Draudt 1950: Plate 13, fig. 15), versus its closest relative, *M. (M.) consanguis* (Guenée, 1852) (Plate 13, fig. 16). The subgenus *Morphopoliana* was erect-

ed by Hreblay and Legrain in 1996; *Polia yuennana* was transferred to *Mythimna (Morphopoliana)* in the 4th volume of the Noctuidae Europaeae series (Hacker et al. 2002), using the World Checklist of M. Hreblay and A. Legrain.

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