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

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Abstract

This monographic review of the Nevrorthidae 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: *Nevrorthus* Costa, 1863 (with five species occurring in the Mediterranean region), *Austroneurorthus* Nakahara, 1958 (with two species restricted to eastern Australia), *Nipponeurorthus* Nakahara, 1958 (with 11 species from eastern Asia: Japanese islands, mainland China, Taiwan), and *Sinoneurorthus* 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. *Austroneurorthus*, together with *Nevrorthus* and some Eocene Baltic amber genera, form a monophylum. The disjunct distribution of modern nevrorthid 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 Nevrorthidae 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 nevrorthid 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 ("Rollengelenk") 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 Nevrorthidae 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 Neurorthini, yet placed it in the Hemerobiidae: Hemerobiinae. Forty years later he raised Neurorthini to the subfamily level (Nakahara 1958), yet retained them within Sisyridae.

Zwick (1967) finally awarded family status to Neurorthinae Nakahara: Neurorthidae Nakahara, 1915, and discussed a sister group relationship of Neurorthidae 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 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).

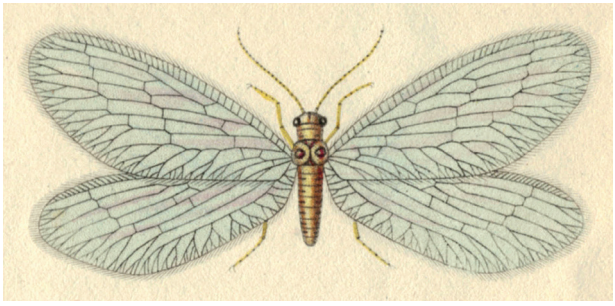

Figure 1. *Nevrorthus iridipennis* Costa. Italy: Calabria. From Costa (1863), who published the first illustration of a nevrorthid.

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 reinstalled) 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 Randolf 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 Randolf et al. (2014). In addition a submental gland with multiporous opening – apparently unique among insects – was described for Nevrorthidae and Osmylidae (Randolf 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 Dilaridae. 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

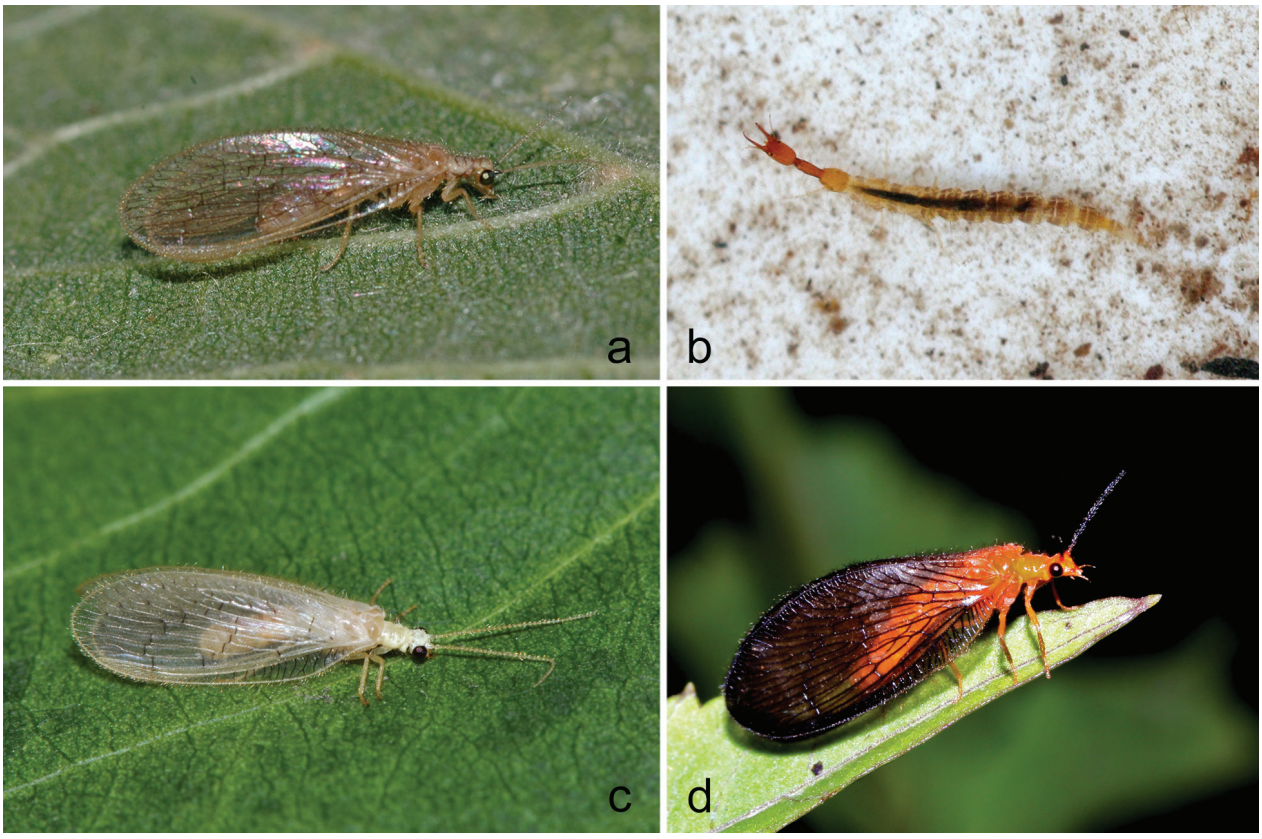

Figure 2. Photographs of living nevrorthids. **a** *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, female, Italy: Friuli (Photo P. Sehnal) **b** *Nevrorthus apatelios*, larva, Italy: Friuli (Photo F. Denner (former Anderle) **c** *Nipponeurorthus fuscinervis* (Nakahara), female, Japan, Hokkaido (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 redescriptions 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.

Redescriptions

In the redescriptions 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

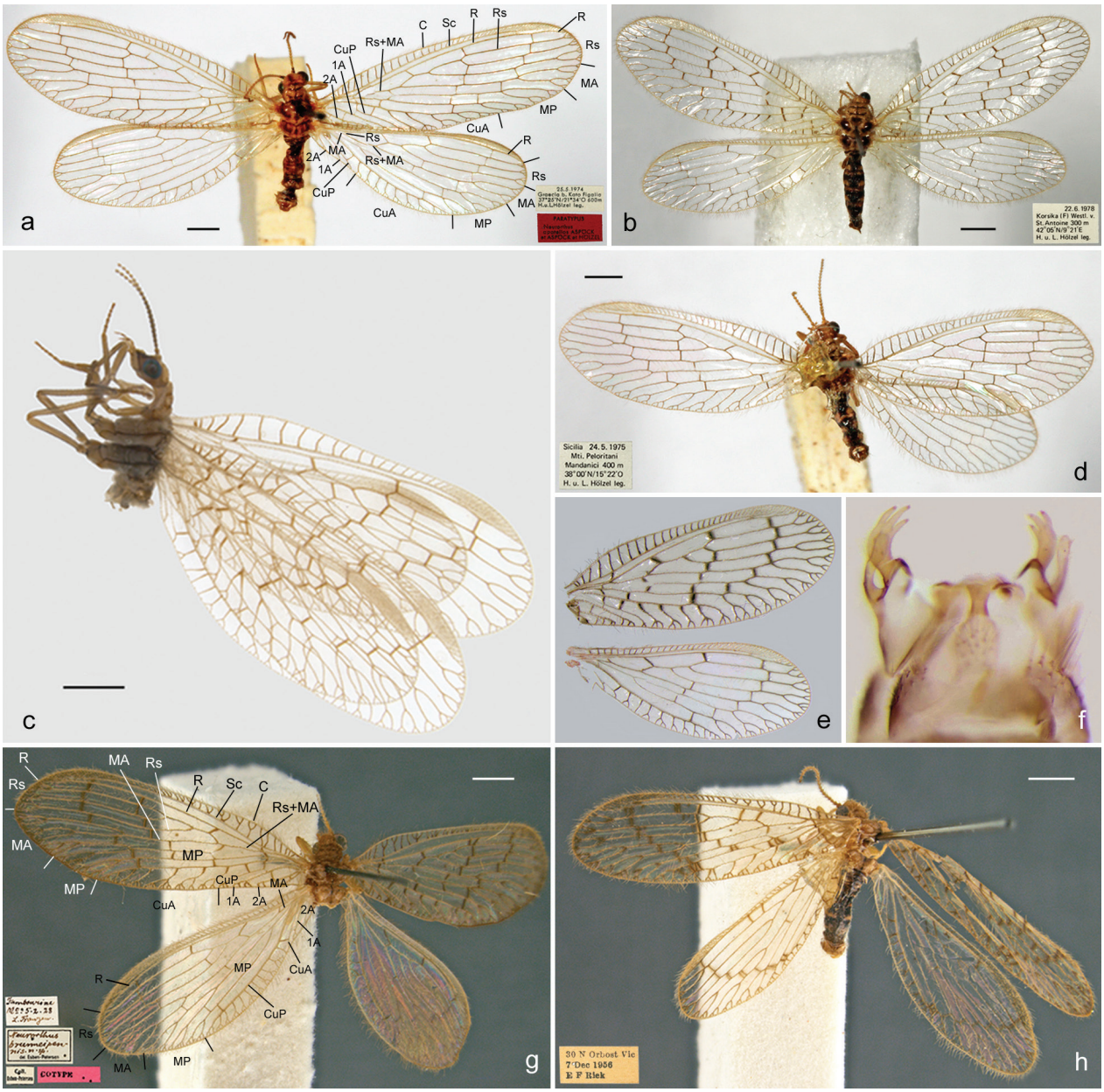

Figure 3. Wings and genital segments of representatives of the genera *Nevrorthus* Costa and *Austroneurorthus* Nakahara. **a** *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, male paratype, Greece: Peloponnesus/Peloponnese (Photo H. Bruckner) **b** *Nevrorthus fallax* (Rambur), female, Italy: 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'Universitá 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).

Nevrorthidae 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

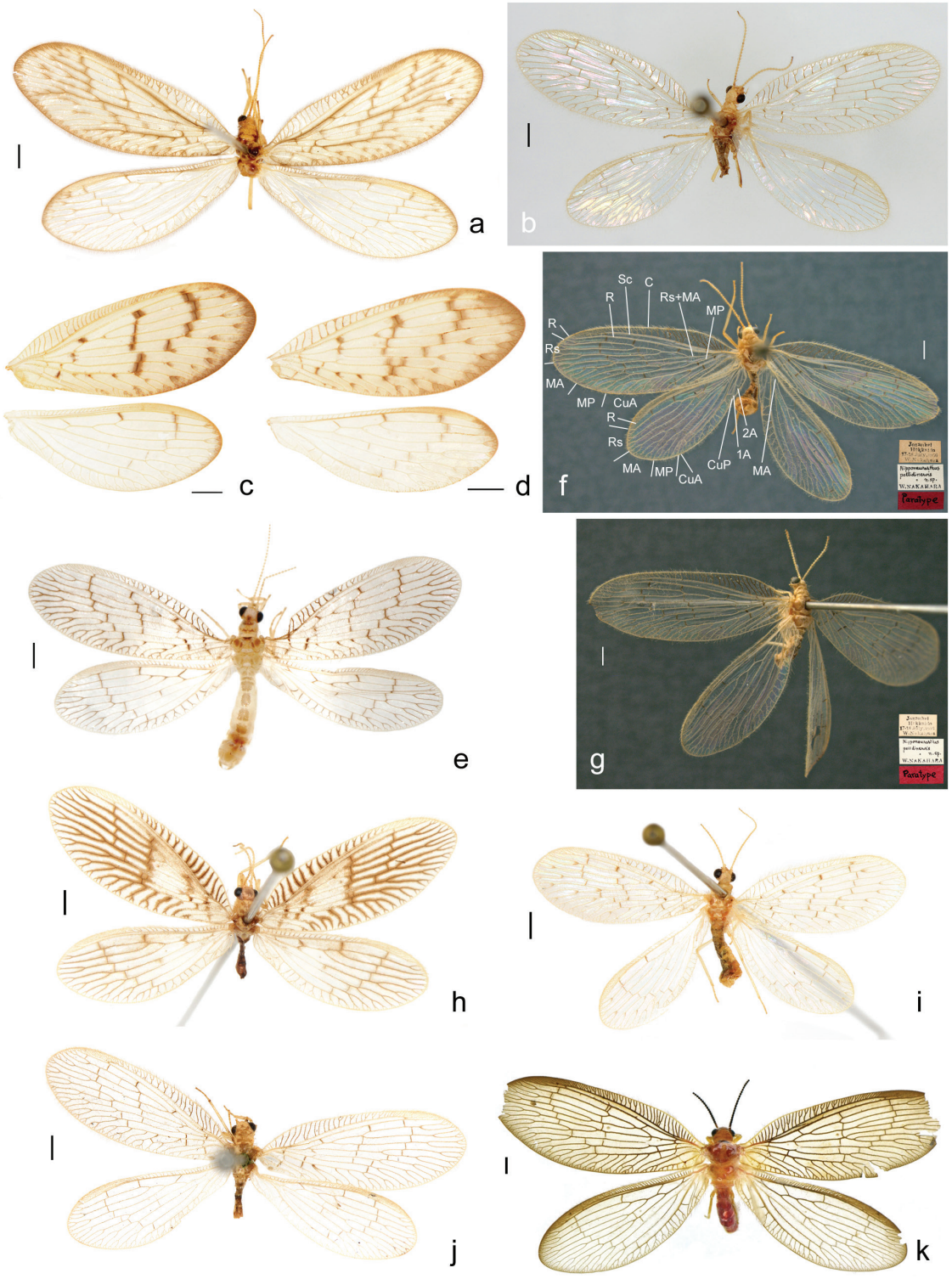

Figure 4. Wings of representatives of the genera *Nipponeurorthus* Nakahara and *Sinoneurorthus* Liu, H. Aspöck & U. Aspöck. **a**. *Nipponeurorthus fasciatus* Nakahara, male, Taiwan: Nantou (Photo H. Bruckner); **b**. *Nipponeurorthus fuscinervis* (Nakahara), Japan: Aomori (Photo X. Liu); **c**. *Nipponeurorthus 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 Nevrorthidae are a species-poor relic family with an extremely vicariant distribution pattern (Fig. 17) of its four extant and five extinct genera: *Nevrorthus* Costa, 1863, comprising five disjunctively scattered Mediterranean species: *N. iridipennis* Costa, 1863 (Italy: Calabria, Sicily), *N. apatelios* 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. horstaspoecki* (U. Aspöck, 2004) (Victoria, New South Wales); *Nipponeurorthus* 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, Amamioshima), *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. relicta* (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. hoffeinsorum* Wichard, 2009, *P. groehni* Wichard, Buder & Caruso, 2010, *P. eocaenus* Wichard, 2016, *Balticoneurorthus* Wichard, 2016, with *B. elegans* Wichard, 2016, and *Proberotha* Krüger, 1923, comprising *Pr. prisca* Krüger, 1923, and *Pr. dichotoma* Wichard, 2016.

Nevrorthidae 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 Nevrorthidae 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 *Nevrorthus* Costa, 1863

Nevrorthus 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

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

Neurorthus 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 Klokočovnik 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).

Neurorthus fallax (Rambur): McLachlan 1881 (nom); 1898 (com); Klapálek 1917 (descr, distr, figs: wings, gs male); Esben-Petersen 1913 (distr); Lestage 1924 (syst); Kimmins 1930 (distr); Nakahara 1958 (charact, 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

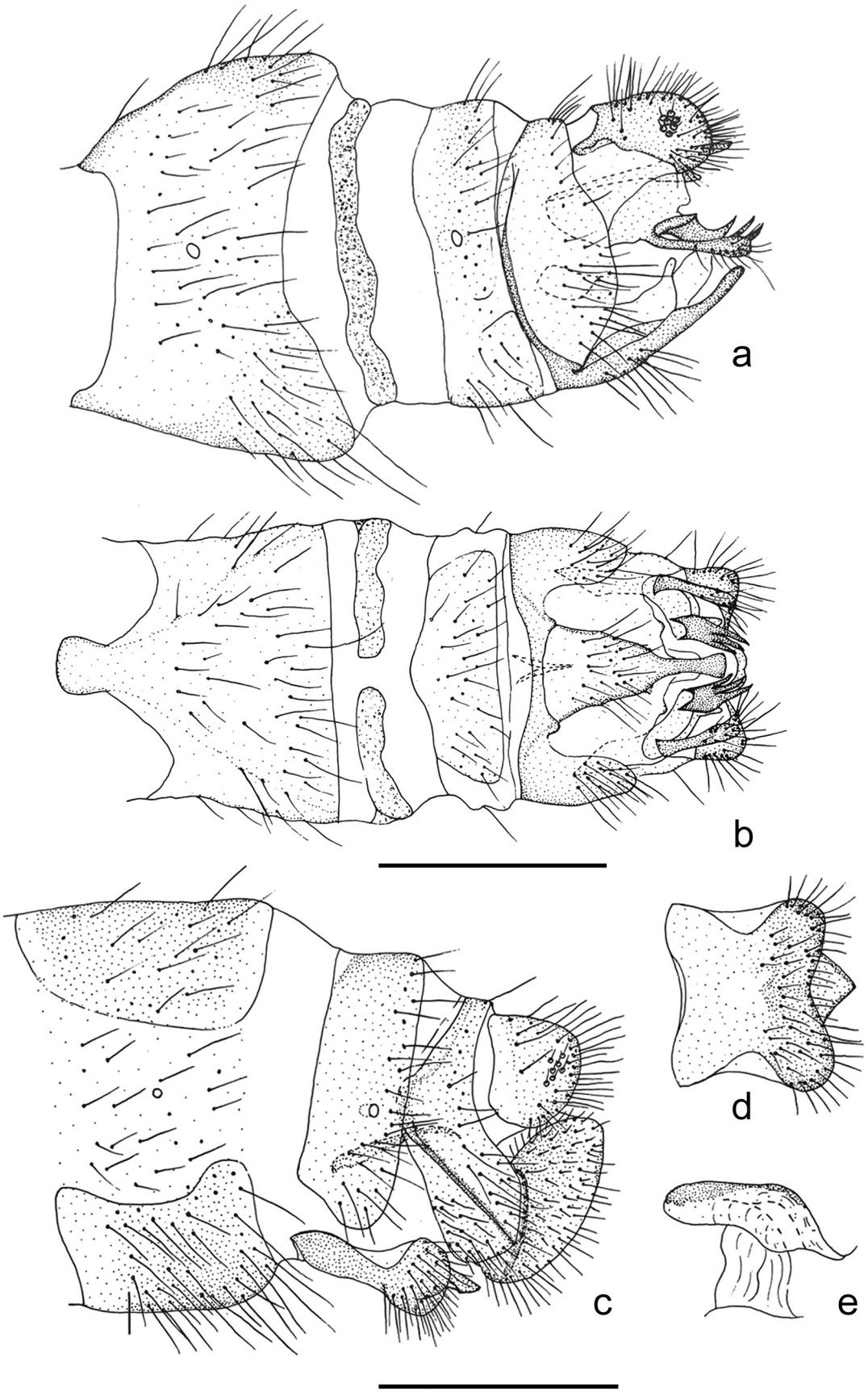

Figure 5. *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel. **a**. Male, genital segments, lateral; **b**. Same, ventral; **c**. Female, genital segments, lateral; **d**. Gonocoxites 8 and gonapophyses 8, ventral; **e**. Bursa copulatrix, lateral. Scale bars: 0.5 mm.

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).

Nevrorthus hannibal U. Aspöck & H. Aspöck, 1983

Figs 3c; 6d–e; 6h–i; 14

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

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

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

Nevrorthus 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 Draham).

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 Draham, 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.

Nevrorthus iridipennis Costa, 1863

Figs 1; 3d; 6b; 14

Nevrorthus 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).

Neurorthus 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).

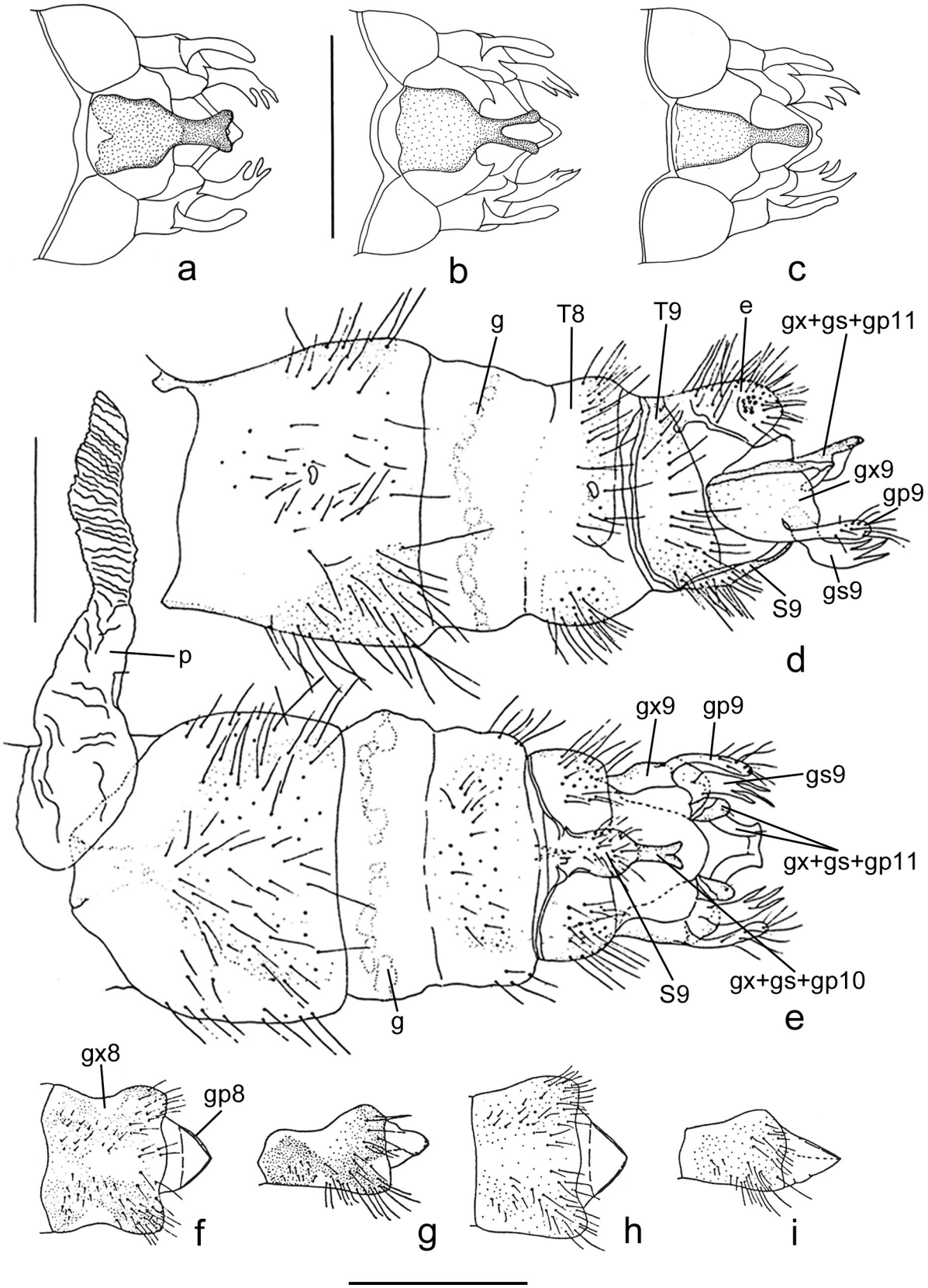

Figure 6. Male genital segments of *Nevrorthus* spp. **a** *Nevrorthus fallax* (Rambur), ventral **b** *Nevrorthus iridipennis* Costa, ventral **c** *Nevrorthus apatelios* H. Aspöck, U. Aspöck & Hölzel, ventral **d–e** *Nevrorthus hannibal* U. Aspöck & H. Aspöck, male holotype: **d** lateral **e** ventral **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** – pleuritocava; **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).

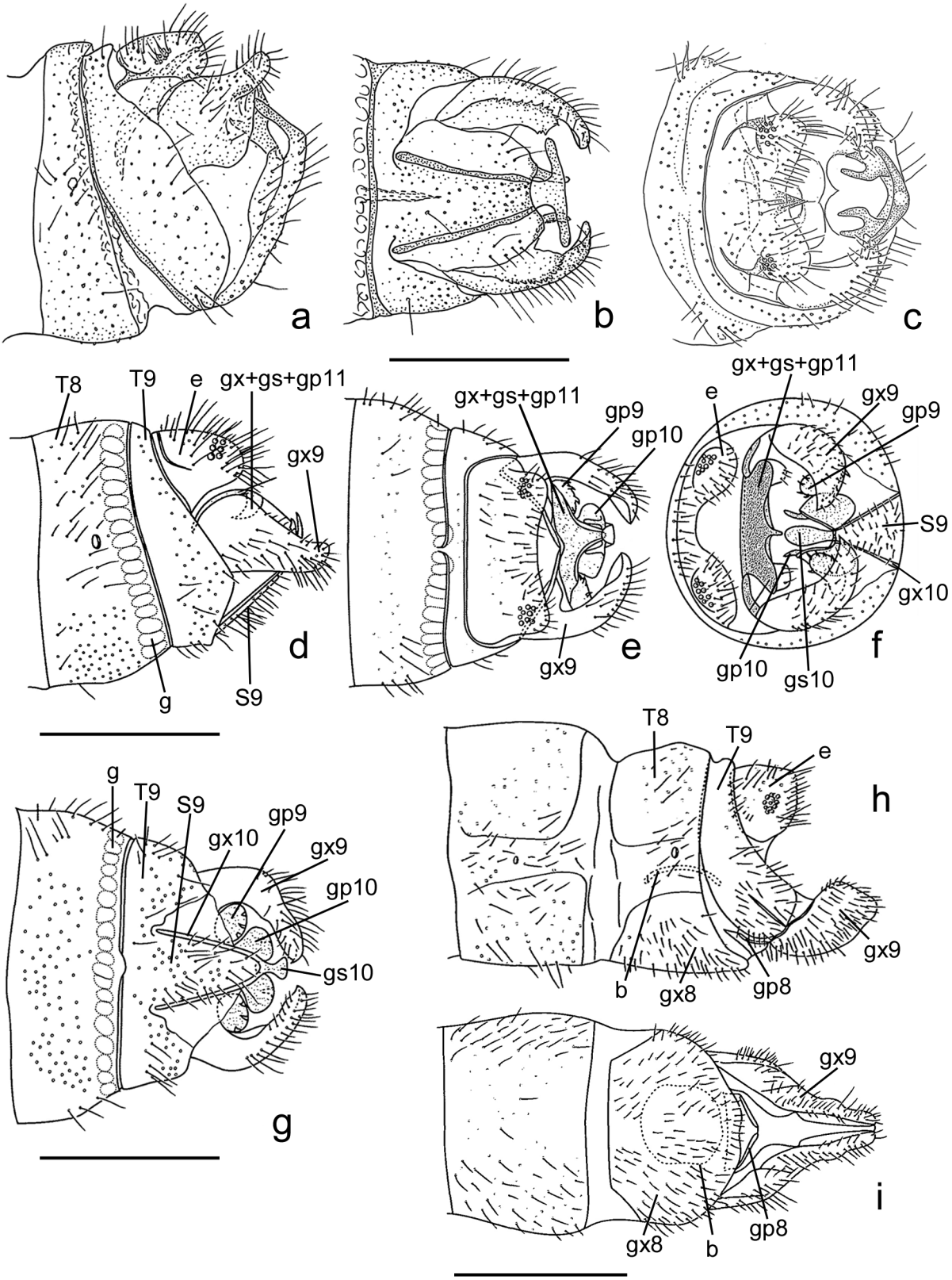

Figure 7. Genital segments of *Austroneurorthus* spp. **a–c** *Austroneurorthus brunneipennis* (Esben-Petersen), male paratype: **a** lateral **b** ventral **c** caudal **d–g** *Austroneurorthus horstaspoecki* U. Aspöck, male holotype, genital segments: **d** lateral **e** dorsal **f** caudal **g** ventral **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. bruneipennis* (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. Forewings 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 posteriad; 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

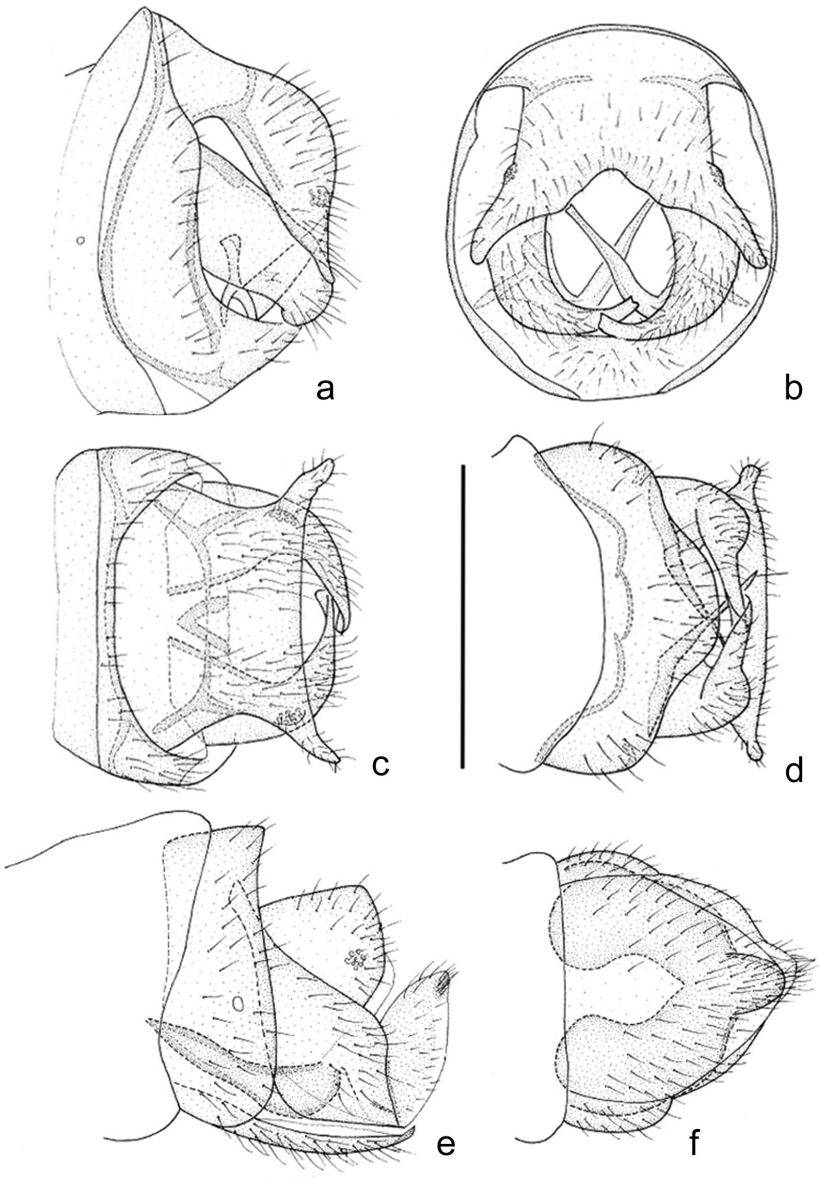

Figure 8. Genital segments of *Nipponeurorthus damingshanicus* Liu, H. Aspöck & U. Aspöck. **a–d** Male holotype: **a** lateral **b** caudal **c** dorsal **d** ventral **e–f** Female paratype: **e** genital segments, lateral **f** ventral. Scale bar: 0.5 mm.

+ 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).

Nipponeurorthus fasciatus Nakahara, 1958

Figs 4a; 9a–f; 16

Nipponeurorthus 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, Amamioshima).

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

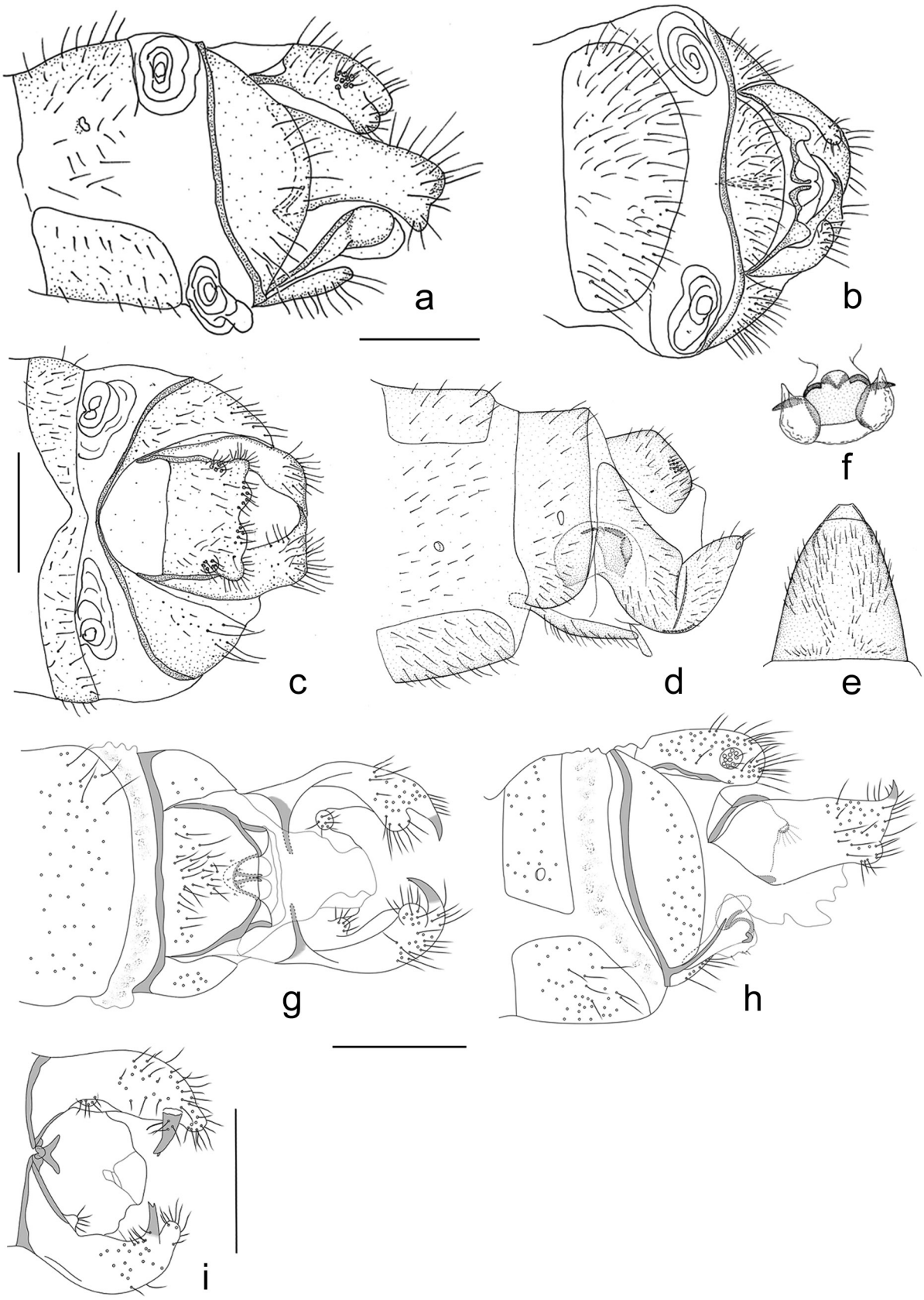

Figure 9. Genital segments of *Nipponeurorthus* spp. **a–f** *Nipponeurorthus fasciatus* Nakahara, **a–c** male: **a** lateral **b** ventral **c** dorsal **d–f** female: **d** lateral **e** gonocoxites 8 and gonapophyses 8, ventral **f** bursa copulatrix **g–i** *Nipponeurorthus flinti* U. Aspöck & H. 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 fuscinervis (Nakahara, 1915)

Figs 2c; 10d–h; 16

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

Nipponeurorthus fuscinervis: 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 concaved. 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.

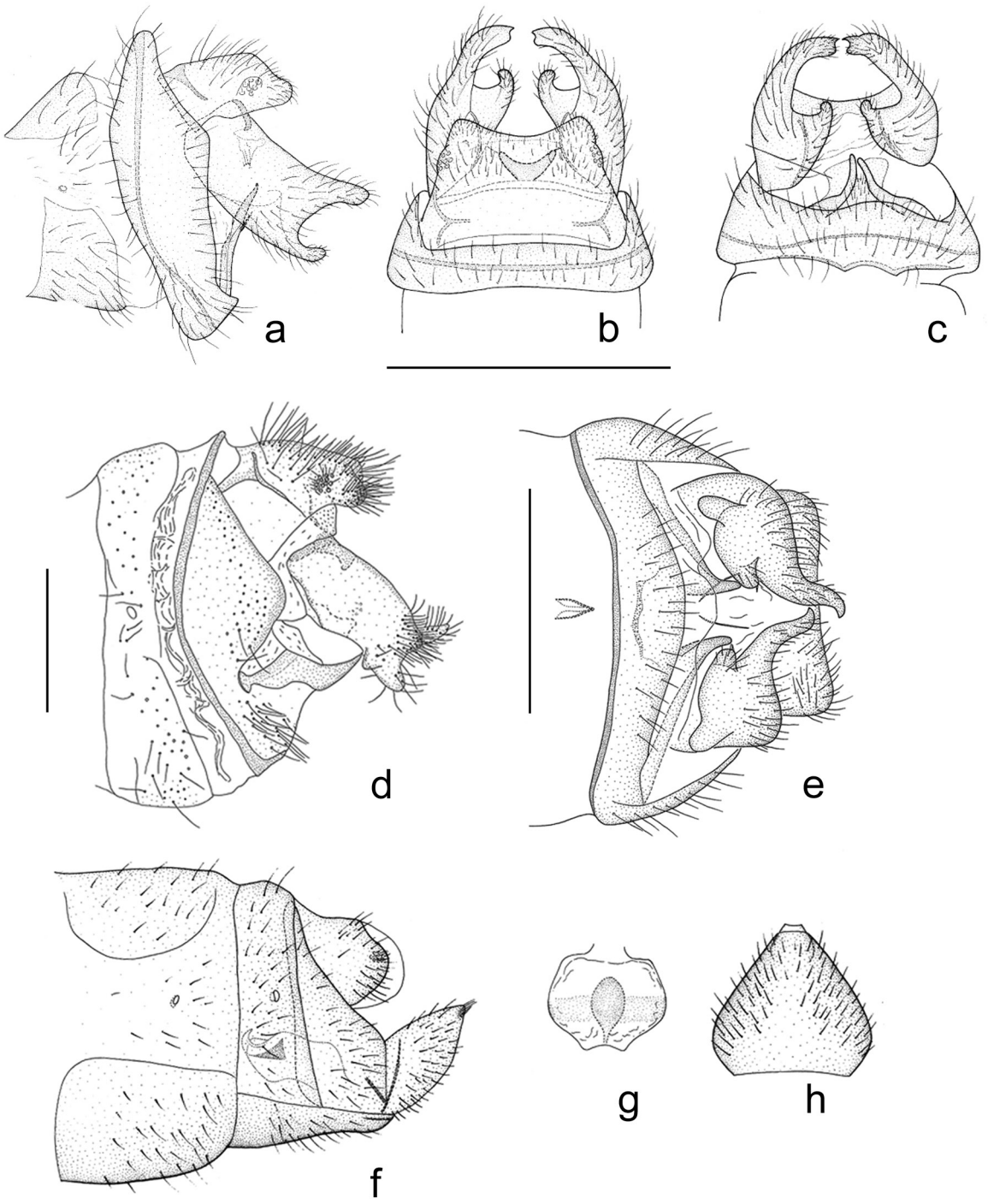

Figure 10. Genital segments of *Nipponeurorthus* spp. **a–c**. *Nipponeurorthus furcatus* Liu, H. Aspöck & U. Aspöck, male holotype, **a**: lateral; **b**: dorsal; **c**: ventral; **d–h**. *Nipponeurorthus fuscinervis* (Nakahara), **d-e**: male, **d**: lateral, **e**: ventral, **f–h**: female, **f**: 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).

Nipponeurorthus pallidinervis Nakahara, 1958

Figs 4f–g; 11g–k; 16

Nipponeurorthus 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 + gonapophyses10 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).

Nipponeurorthus punctatus (Nakahara, 1915)

(Figs 4i; 12a–e; 16)

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

Nipponeurorthus 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).

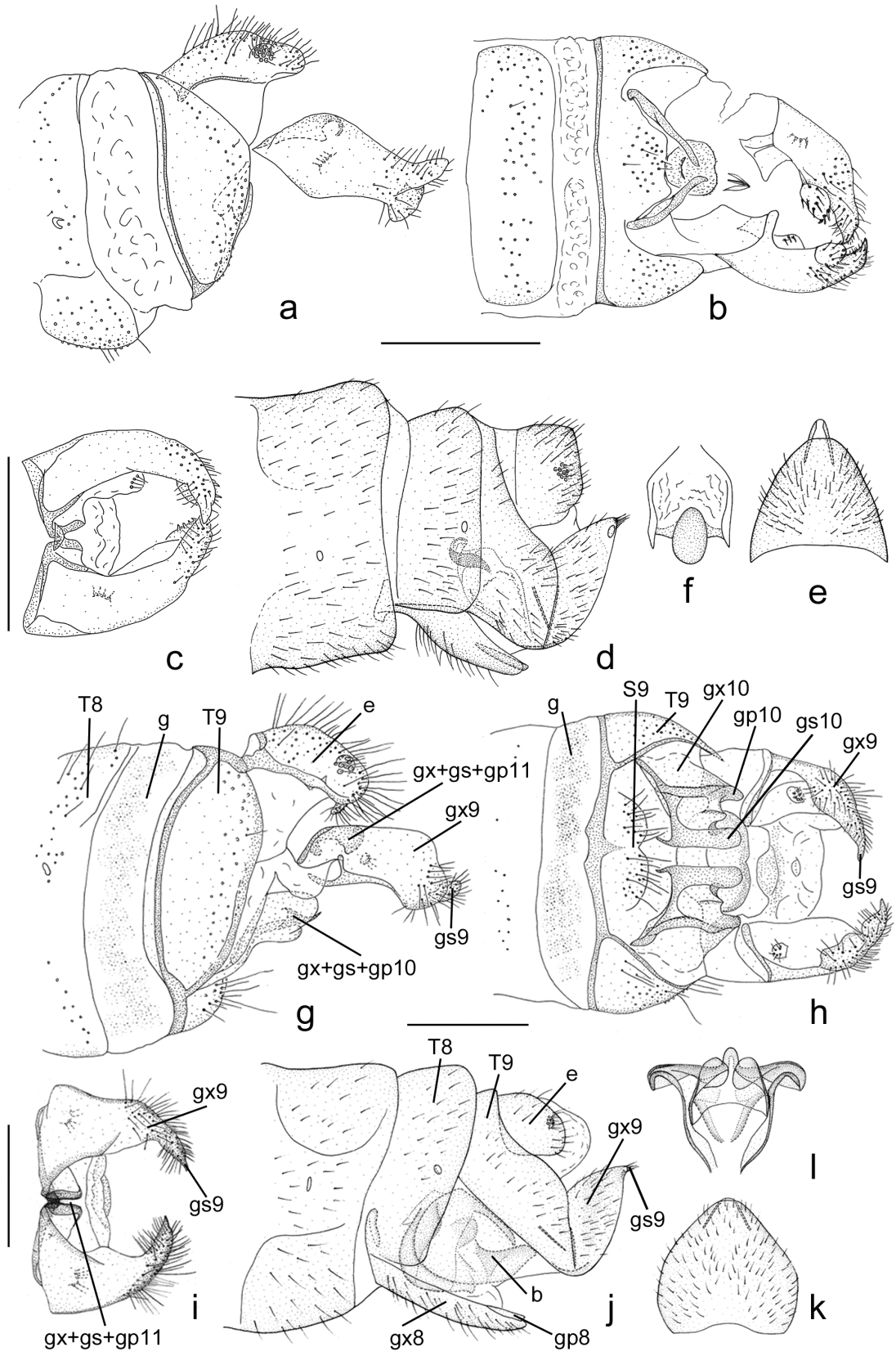

Figure 11. Genital segments of *Nipponeurorthus* spp. **a–f** *Nipponeurorthus multilineatus* Nakahara **a–c** male: **a** lateral **b** ventral **c** dorsal **d–f** female: **d** lateral **e** gonocoxites 8 and gonapophyses 8, ventral **f** bursa copulatrix, ventral **g–j** *Nipponeurorthus pallidinervis* 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 processus. 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).

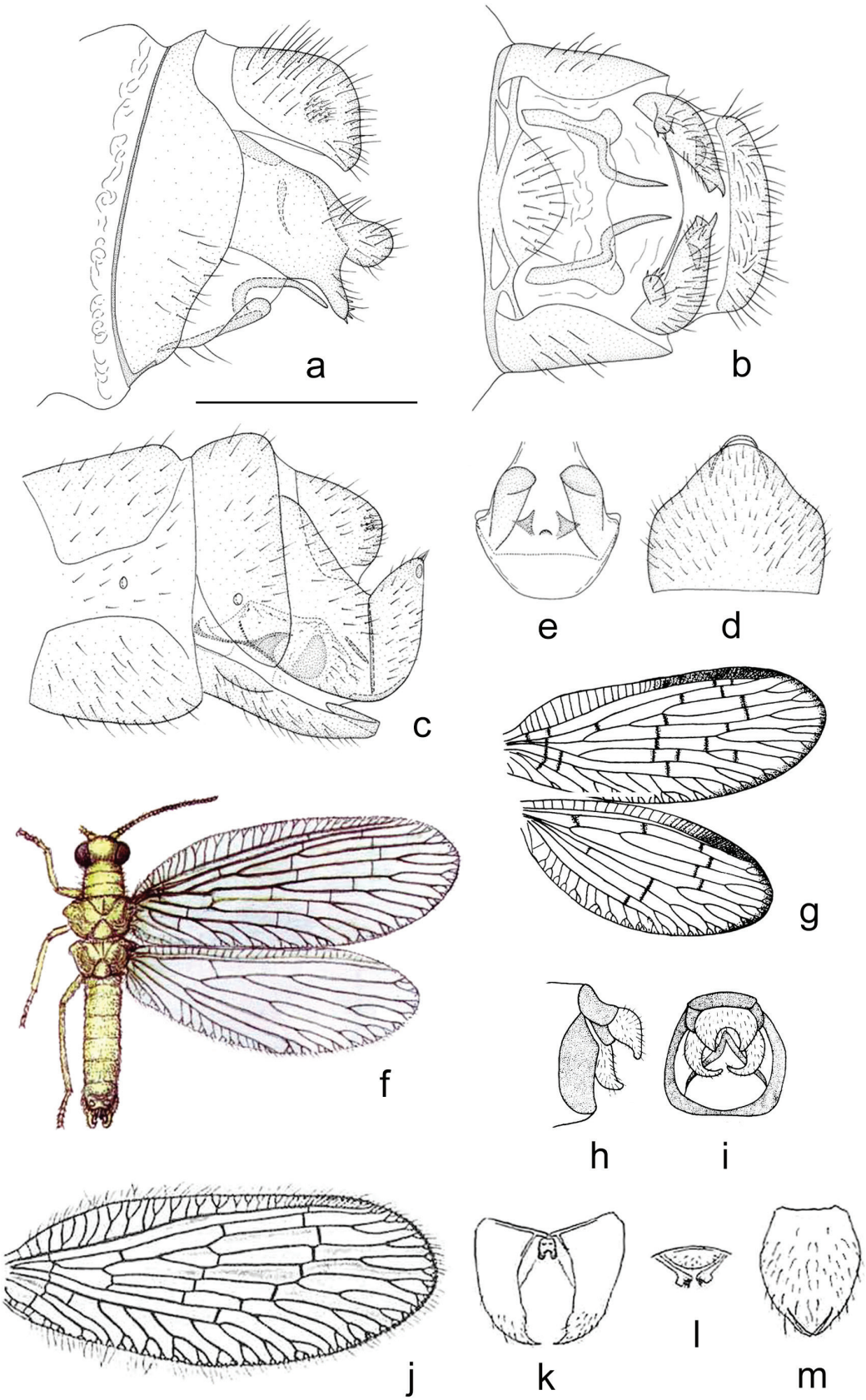

Figure 12. *Nipponeurorthus* spp. **a–e** *Nipponeurorthus punctatus* (Nakahara) **a–b** male genital segments: **a** lateral **b** ventral **c–e** female genital segments: **c** lateral **d** gonocoxites 8 and gonapophyses 8, ventral **e** bursa copulatrix **f** *Nipponeurorthus qinicus* Yang in Chen,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

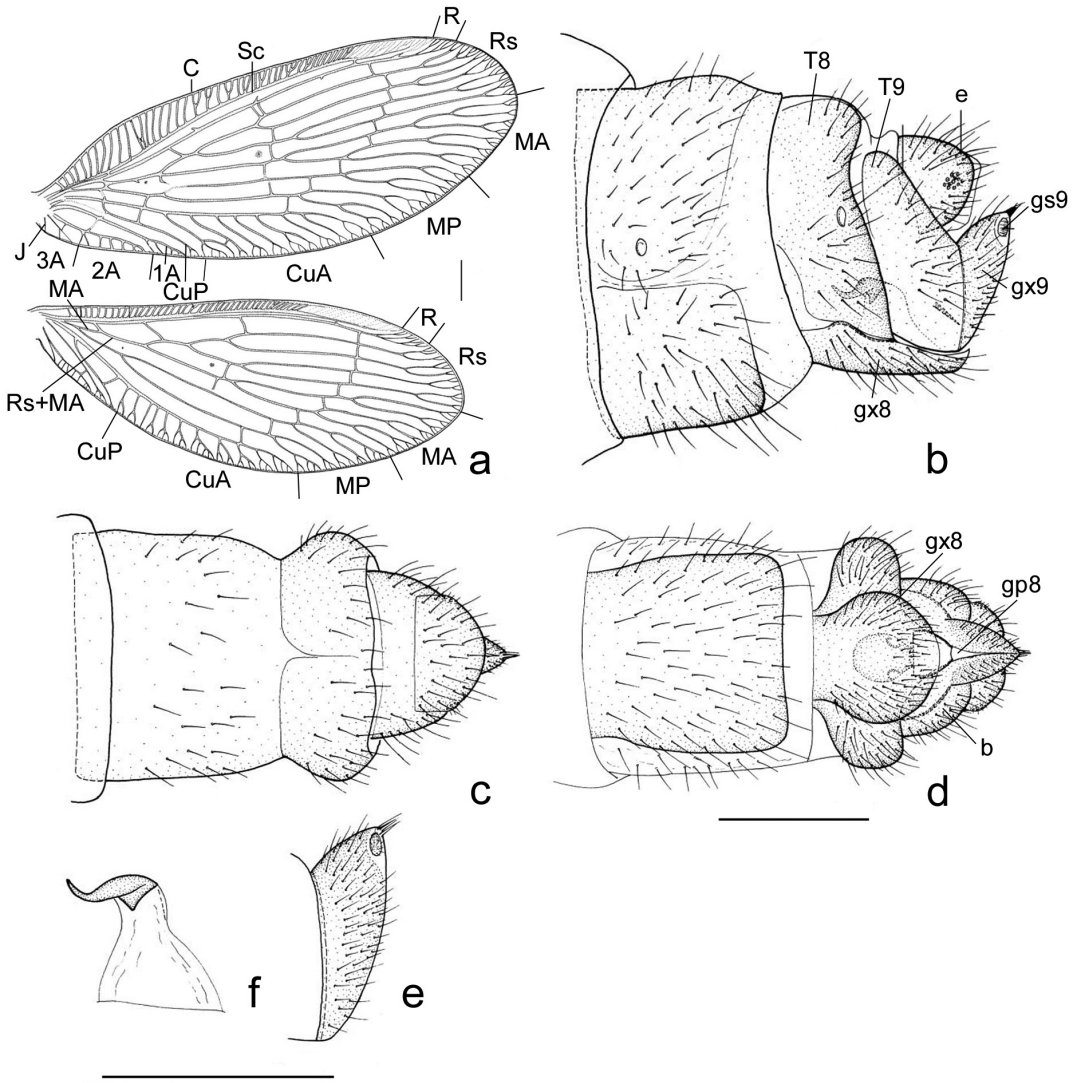

Figure 13. *Sinoneurorthus yunnanicus* Liu, H. Aspöck & U. Aspöck, female holotype **a** wings **b** genital segments, lateral **c** same, dorsal **d** same, ventral **e** gonocoxites 9, lateral **f** bursa copulatrix, lateral. **Abbreviations. A** – Analis; –: Costa; **CuA** – Cubitus anterior; **CuP** – 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 *Nipponeurorthus*

See Liu et al. (2014)

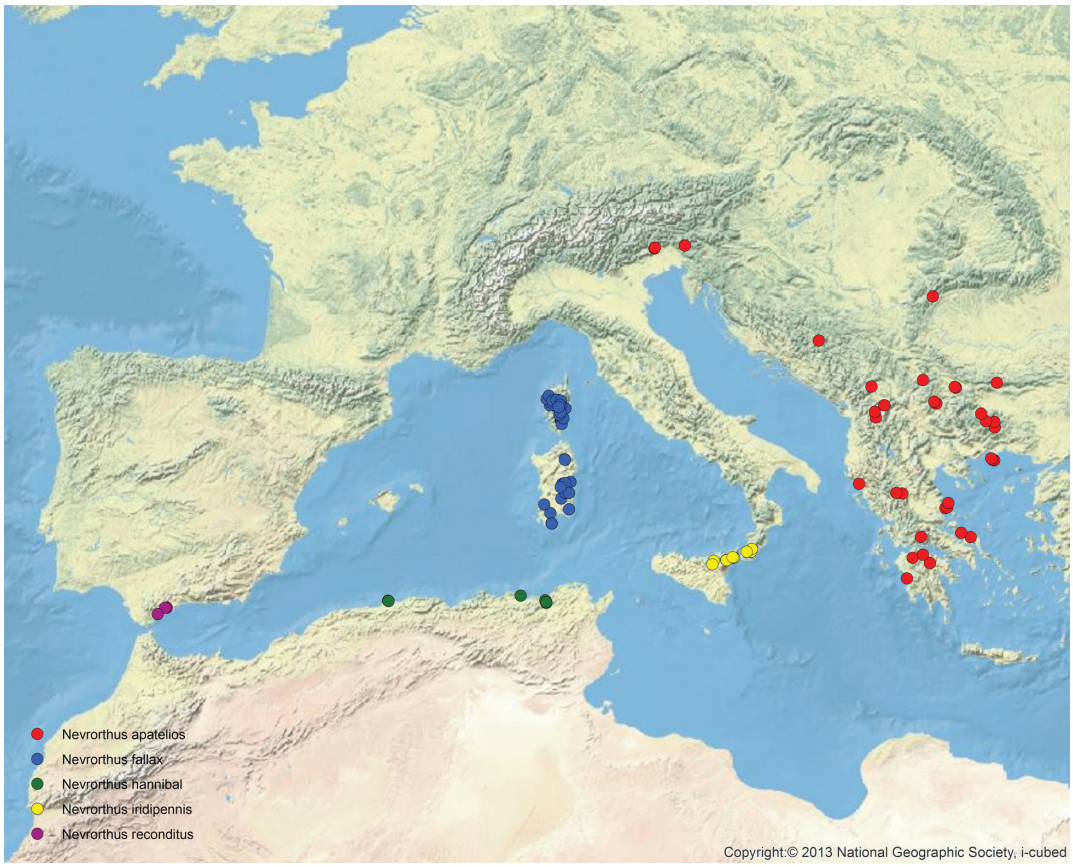

Figure 14. Distribution map of the species of *Nevrorthus*.

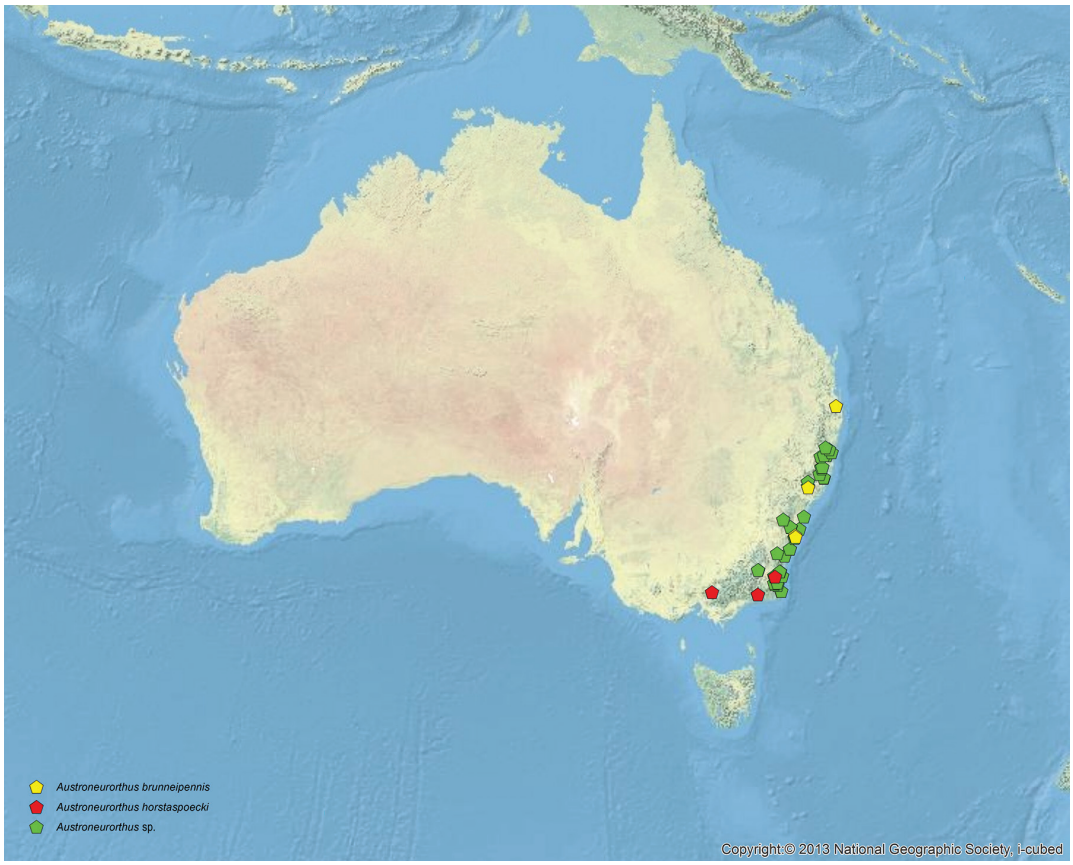

Figure 15. Distribution map of the species of *Austroneurorthus*.

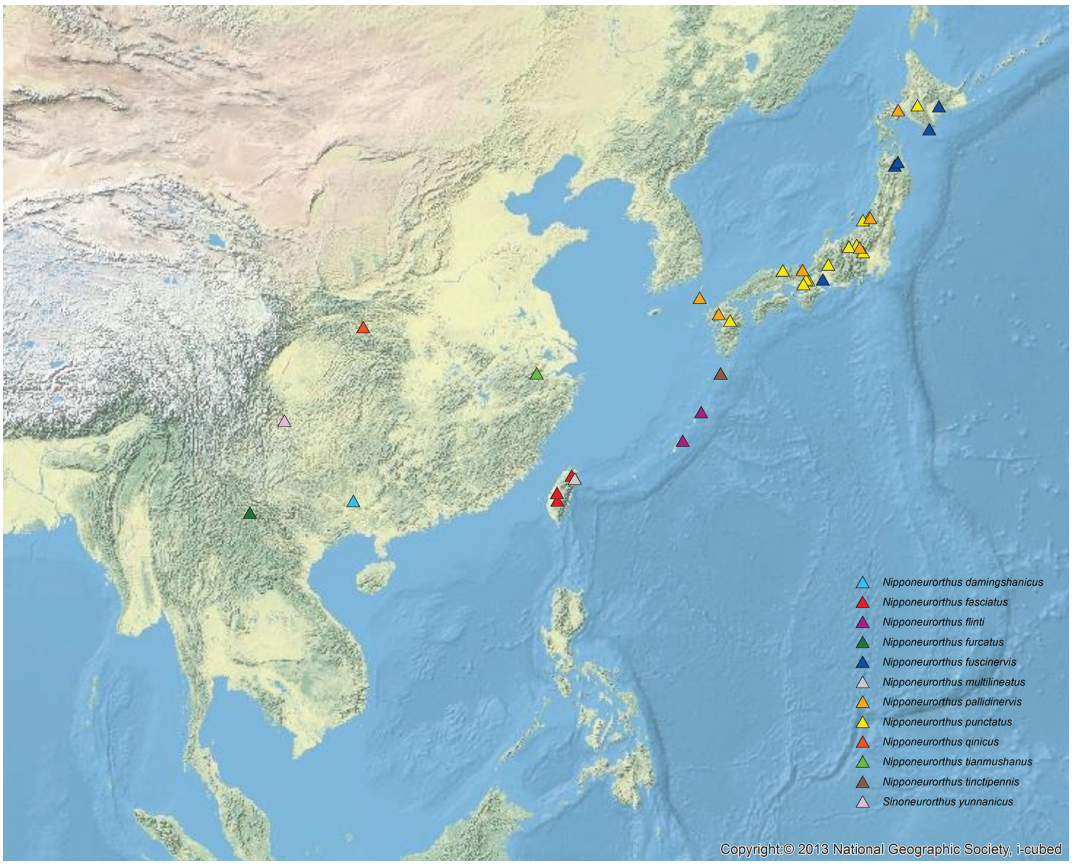

Figure 16. Distribution map of the species of *Nipponeurorthus* and *Sinoneurorthus.*

Figure 17. Distribution map of the family Nevrorthidae.

Phylogenetic analysis

The parsimony analysis of the primary matrix including all species of Nevrorthidae 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 *Austroneurorthus*, *Nevrorthus* and *Palaeoneurorthus*. 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 *Nipponeurorthus* (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 *Nipponeurorthus* 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*, *Nevrorthus* and *Palaeoneurorthus*, 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 *Austroneurorthus* and *Electroneurorthus*. The synapomorphic characters of the monophyletic group comprising *Austroneurorthus*, *Electroneurorthus*, *Rophalis*, *Nevrorthus* and *Palaeoneurorthus* 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 *Balticoneurorthus*, *Proberotha* and *Sinoneurorthus* were not resolved.

Discussion

Phylogenetic position of Nevrorthidae

Irrespective of the fact that Nevrorthidae 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, Randolf et al. 2013, Randolf et al. 2014, Wang et al. 2016), several hypotheses, which have been catalysed via Nevrorthidae, 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 Nevrorthidae as secondary adaptations. We interpret free Malpighian tubules – at least in Nevrorthidae – 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 Nevrorthidae, 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 Nevrorthidae 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 *Nevrorthus* (U. Aspöck and H. Aspöck 1983) and *R. relicta* (Wichard et al. 2009), between segments 7 and 8 in *R. relicta*, between segments 8 and 9 in *Ni. fuscinervis*, *Ni. multilineatus* and *R. relicta,* and dorsally between tergites 8 and 9 in *Ni. fasciatus* and *R. relicta.* 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 + Nevrorthidae was assigned as sister group to Osmylidae + the monophylum constituted by the remaining twelve families. The sister group relationship of Nevrorthidae + 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 Nevrorthidae.

Intergeneric phylogeny within Nevrorthidae

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

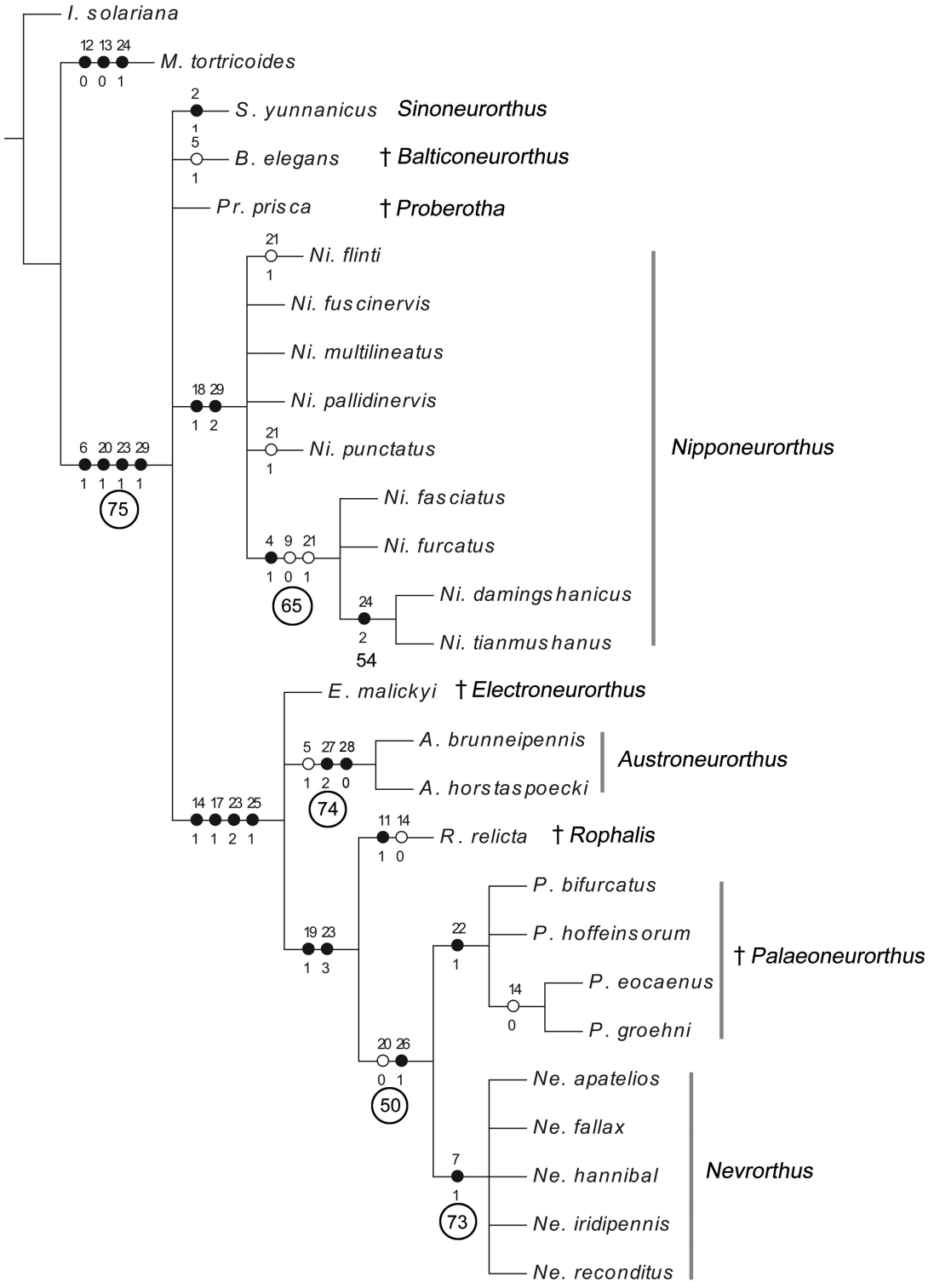

Figure 18. Strict consensus tree of 40 MPTs generated from the refined data matrix. Bootstrap support values are shown at nodes. Only unambiguous character changes are shown. Black circles represent unique changes, white circles represent homoplasious changes. The symbol "†" indicates extinct genus.

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? Ceratinly 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/occurence/multimedia/etc.)

Link: https://doi.org/10.3897/dez.64.13028.suppl1

Supplementary material 2
Characters used for the phylogenetic analysis
Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu
Data type: (measurement/occurence/multimedia/etc.)

Link: https://doi.org/10.3897/dez.64.13028.suppl2

Supplementary material 3
Primary data matrix
Authors: Ulrike Aspöck, Horst Aspöck, Xingyue Liu
Data type: (measurement/occurence/multimedia/etc.)

Link: https://doi.org/10.3897/dez.64.13028.suppl3

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/occurence/multimedia/etc.)

Link: https://doi.org/10.3897/dez.64.13028.suppl4