

Revision of the endemic Brazilian ‘neotheorid’ hepialids, with morphological evidence for the phylogenetic relationships of the basal lineages of Hepialidae (Lepidoptera: Hepialoidea)

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[#] This study was initiated as a collaborative effort between the authors in 2011. Sadly, Niels P. Kristensen passed away December 06, 2014, before the manuscript could be completed. He had, however, completed an extensive draft of the taxonomic sections of the text. It therefore seems most fitting that he remains first author of the names proposed here.

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Abstract

We revise the little known South American primitive Hepialidae genus *Neotheora* Kristensen, and describe two new species, *N. meyi* **sp.n.** and *N. mielkeorum* **sp.n.** from Brazil based on two female singletons. Furthermore, we describe a new genus, *Paratheora* **gen.n.**, with a single species, *P. speideli* **sp.n.**, of primitive Hepialidae from Brazil based on one male, and a female without the postabdomen. Although the new genus is clearly closely related to *Neotheora* as demonstrated by a unique tentorium modification found in both genera, it is also sufficiently different to warrant its own genus. To explore the phylogenetic relationships of *Paratheora*, we carried out a phylogenetic analysis of 16 terminal taxa in Hepialidae *sensu lato* based on 18 morphological characters scored from adult morphology. The results confirm that *Neotheora* and *Paratheora* are sister taxa, and together these two ‘neotheorid genera’ comprise the sister group of the remaining Hepialidae *s.lat.* Within the latter, the Australian genus *Anomoses* Turner is the sister group of the remaining taxa. The southern African genus *Prototheora* Meyrick is the sister group of a clade comprising the four ‘palaeosetid genera’, the four so-called ‘primitive’ Hepialidae genera, and Hepialidae *s.str.* The ‘palaeosetid genera’ comprise a monophyletic clade, which is the sister group to a clade comprising the ‘primitive’ Hepialidae, and Hepialidae *s.str.* While the exact relationships between the four ‘primitive’ Hepialidae, and Hepialidae *s.str.* cannot be resolved based on our data, the two ‘primitive’ hepialids from sub-Saharan Africa, *Afrothora* Nielsen & Scoble and *Antihepialus* Janse are likely sister taxa, and the Holarctic *Gazoryctra* Hübner is likely the sister of that clade. Similarly, the four genera selected to represent Hepialidae *s.str.* appear monophyletic in the analysis.

Key words

Neotheora, new species, new genus, Hepialoidea phylogeny.

1. Introduction

Hepialoidea (*sensu* REGIER et al. 2015) are the most ecologically diverse and species rich lineage within the basal lepidopterous grade Homoneura, several hundred spe-

cies adapted to a wide variety of lifestyles and habitats (COMMON 1990; KRISTENSEN 1998; REGIER et al. 2015). The superfamily comprises more than 650 species in *ca*

70 genera (SIMONSEN in press; GREHAN & RAWLINS 2016; VAN NIEUKERKEN et al. 2011). Traditionally, most authors have considered Hepialoidea to be one of two superfamilies in the suborder Exoporia, with the other superfamily being the monogeneric New Zealand endemic Mnesarchaeoidea (e.g. KRISTENSEN 1998; NIELSEN et al. 2000; VAN NIEUKERKEN et al. 2011; GREHAN & RAWLINS 2016). Following that classification, Hepialoidea comprise five families: Neotheoridae, Anomosetidae, Prototheoridae, Palaeosetidae, and Hepialidae. However, the monophyly of the non-monogeneric families Palaeosetidae and Hepialidae *s.lat.* remains questionable, and Hepialoidea (sensu NIELSEN et al. 2000) has generally been considered to comprise 12 terminal taxa, viz. *Neotheora* Kristensen, 1978 (Neotheoridae), *Anomoses* Turner, 1916 (Anomosetidae), *Prototheora* Meyrick, 1917 (Prototheoridae), *Genustes* Issiki & Stringer, 1932, *Ogygioses* Issiki & Stringer, 1932, *Oshroes* Druce, 1900, *Palaeoses* Turner, 1922 (all Palaeosetidae), *Afrotheora* Nielsen & Scoble, 1986, *Antihepialus*, Janse, 1942, *Fraus* Walker, 1856, *Gazoryctra* Hüber, 1820 (the so-called "primitive" Hepialidae), and Hepialidae *s.str.* (ca 60 genera) (NIELSEN & SCOBLE 1986; KRISTENSEN 1998; NIELSEN et al. 2000; VAN NIEUKERKEN et al. 2011). Recently, REGIER et al. (2015) formally synonymised all hepialoid families with Hepialidae based on a comprehensive molecular dataset, which nevertheless was missing some key taxa. Mnesarchaeidae was included in Hepialoidea, making the suborder name Exoporia redundant.

As Hepialoidea (together with the small Australian family Lophocoronidae) are the likely sister group to the Heteroneura (e.g. REGIER et al. 2015; BAZINET et al. 2016 – but see KRISTENSEN et al. 2015 for an alternative hypothesis), a group that includes over 99% of all Lepidoptera (> 150,000 species) (KRISTENSEN 1998; KRISTENSEN et al. 2007; VAN NIEUKERKEN et al. 2011), comparative studies of the group are of considerable value for understanding the evolution of Lepidoptera as a whole. However, the phylogenetic and evolutionary relationships of Hepialoidea are poorly understood, although several recent regional faunistic and systematic studies exist (e.g. DUGDALE 1994; BROWN et al. 2000a,b; MIELKE & GREHAN 2012; GREHAN & RAWLINS 2016; SIMONSEN 2015, in press), and recent studies of adult morphology of Hepialidae *s.str.* (GREHAN 2010, 2012) have provided new insight and progress into phylogenetic relationships of Hepialidae *s.str.* A global check list and bibliography of Hepialoidea was presented by NIELSEN et al. (2000).

One problem encountered when attempting to resolve the phylogeny of Hepialidae *s.str.* is that the evolutionary relationships of the 12 terminal Hepialidae *s.lat.* taxa are very poorly understood. Since KRISTENSEN (1978a) described Neotheoridae as the latest family-level taxon in the superfamily, several studies have focused on subsets of Hepialoidea. KRISTENSEN (1978b) revised the morphology of Anomosetidae, and the same author (1978a) suggested that Palaeosetidae might represent the sister group of the remaining superfamily. The latter suggestion was based on the small (primitive) intercalary sclerite found

in the palaeosetid *Ogygioses caliginosa* Issiki & Stringer, 1932 the only palaeosetid for which there were detailed morphological details known at the time. An enlarged intercalary sclerite similar to the structure found elsewhere in Hepialoidea (and believed to be an autapomorphy for the family) has since been found in all other palaeosetid species (including other *Ogygioses*) (KRISTENSEN 1998). NIELSEN & SCOBLE (1986) removed *Afrotheora*, *Antihepialus*, *Fraus* and *Gazoryctra* from Hepialidae *s.str.* as these genera lack the close association (often synsclerotisation) between the trulleum and pseudoteguminal arms found in Hepialidae *s.str.* NIELSEN & KRISTENSEN (1989) revised the Australian genus *Fraus* and carried out very detailed studies of the morphology of the genus, resulting in a total revision of our understanding of the morphology (in particular in the abdomen) of Hepialoidea. KRISTENSEN & NIELSEN (1993) redescribed the enigmatic South American palaeosetid genus *Oshroes* (known only from three specimens) and noted the potential synapomorphies, which it shares with the two southeast Asian genera *Genustes* and *Ogygioses*. DAVIS et al. (1995) revised *Ogygioses* and, while questioning the monophyly of Palaeosetidae, suggested that *Ogygioses* and *Genustes* were potential sister taxa. DAVIS (1996) revised the southern African family Prototheoridae and synonymised the genus *Metatheora* Meyrick, 1919 with *Prototheora* thus reducing the family to a single genus. KRISTENSEN (1998) summarised the systematics of Hepialoidea and repeated the doubt over the monophyly of Palaeosetidae.

While Hepialidae *s.str.* are almost global in their distributions (with the exception of Madagascar), the remaining genera are more restricted to specific regions: southern Brazil (*Neotheora*, *Paratheora* **gen.n.**), Australia (*Anomoses*, *Palaeoses*, *Fraus*), Columbia (*Oshroes*), south-east Asia from Assam to Taiwan (*Genustes*, *Ogygioses*), sub-Saharan Africa (*Prototheora*, *Afrotheora*, *Antihepialus*), and temperate northern hemisphere forests (*Gazoryctra*); *Mnesarchaea* Meyrick, the only genus in Mnesarchaeidae, the other family in Hepialoidea, is endemic to New Zealand (HOLLOWAY & NIELSEN 1998).

Neotheoridae was established more than three decades ago to accommodate the genus *Neotheora* with a single species *N. chiloides* Kristensen, 1978 (Fig. 1A) known from only a single female specimen from Mato Grosso, Brazil (KRISTENSEN 1978a). Evidently, the very incomplete available morphological information about *Neotheora* has remained a major impediment for assessing the affinities of this taxon: alone among the terminal hepialid taxa it has not been the subject of comparative studies since it was originally described. We here describe two additional species of the genus *Neotheora* (Fig. 1B–C), which have recently come to light. Like *N. chiloides* both are from Brazil, and are only represented by female singletons; hence any male-specific genus-level characters, among which the genital segments evidently are of particular interest, still remain unknown. But of course the new species provide information about the breadth of female morphology present in *Neotheora*, and they similarly add to the known distributional range of the genus.

Of even greater interest, however, is the finding of a peculiar new Brazilian hepialoid taxon (Fig. 1D,E), which was discovered in the collections of the Berlin *Museum für Naturkunde* together with one of the new *Neotheora* species. This new taxon does bear some superficial resemblance to members of *Neotheora*, but since its female genitalia are unknown (see below) a number of critical comparisons cannot be made. Some characters do, however, support the two taxa being each other's closest relatives. Plesiomorphic traits observed in the new taxon indicate the existence of a previously unrecognized major clade within the Hepialidae, and hence constitute new challenges for future comparative observations across the superfamily.

Finally, we present a phylogenetic study of the terminal taxa in Hepialidae *s.lat.* based on adult morphology. The aims of the study are: 1) to establish the phylogenetic position of the new genus-level taxon; 2) to test the hypothesis that the neotheorid lineage comprise the sister group of the remaining Hepialidae; 3) to present a phylogenetic framework for the basal lineages of Hepialidae *s.lat.*

2. Material and methods

2.1. Taxonomy and morphological study

The newly discovered *Neotheora* moths are represented by conventionally dried and 'spread' collection specimens. It may be noted that their antennae are all incomplete, as are those of the single *N. chiloides* specimen; hence the full flagellomere number in the genus remains unknown.

The material of the new genus comprises a summarily labelled male specimen and an unlabelled specimen which we confidently consider to be a female, judging from its lack of what is certainly a sex scent apparatus present in the male. Pins and spreading styles are similar in the two, and to the Berlin *Neotheora* as well; the same applies to the labels. The bodies of both are somewhat overgrown with delicate fungus hyphae. The second (unlabelled) specimen is without the posterior part of the abdomen, but was accompanied in the collection by a female moth postabdomen glued on a piece of card and borne on a separate (also unlabelled) pin. After removal from the card and KOH maceration this postabdomen proved, however, to be completely unlike that of any exoporian, and according to our best judgement it belongs to a higher ditrysian moth (possibly a Pyraloidea). We are, therefore, strongly of the opinion that a mistake has been made in associating it with the moth specimen in question sometime during the (likely very long) period that has elapsed since the latter was collected, and we have left it out of consideration in the present context.

The postabdomen/genitalia were examined with standard procedures: KOH-maceration, staining with chlorazol black; examination/photography in glycerol. While the abdomen of the *N. chiloides* type, first studied a quarter-century ago, was preserved as an euparal-embedded slide mount, we decided (albeit reluctantly) to leave the abdomens of the three newly described species as well as the head and metathorax of the new genus unmounted in glycerol, because we consider ease of examining all structures in both lateral and dorsal/ventral view crucially important for future comparisons with additional material of these or neighbouring taxa.

A distribution map for all species combined was constructed in DIVA-GIS 7.5.0.0 using the global country boundaries dataset provided on the program's website (HIJMANS et al. 2012) by locating the collection locality in Google Earth™ with an accuracy of two decimals. As only the types are known from each species, the type localities as given in the Taxonomy section were used, and any precautions are listed therein.

Abbreviations in text: FW = forewing, HW = hindwing; wing veins: A = anal vein, CuA = cubitus anterior, CuP = cubitus posterior, H = humerus, M = median vein, R = radius, Rs = radial sector, Sc = subcosta.

2.2. Phylogenetic study

Taxon sampling. Sixteen Hepialidae *s.lat.* genera representing the 12 "terminal taxa" identified by NIELSEN & SCOBLE (1986) and the new genus *Paratheora* are included as ingroup taxa in the dataset. Four genera of Hepialidae *s.str.* (sensu NIELSEN & SCOBLE 1986) were selected to represent the variation within that group. *Mnesarchaea* was chosen as the single outgroup since the genus is the sole member of Mnesarchaeidae, the well-supported sister group of Hepialidae and the only other member of Hepialoidea. We have treated genera as terminal taxa in the analysis and scored characters as present/absent in the entire genus. For the non-monobasic genera (*Mnesarchaea*, *Neotheora*, *Prototheora*, *Ogygioses*, *Fraus*, *Afrotheora*, *Antihepialus*, *Gazoryctra*, *Bipectilus* Chu & Wang, 1985, *Gorgopis*, Hübner, 1820, *Oxycanus*, Walker, 1856 and *Hepialus*, Fabricius, 1775) we used the species listed in Table 1 as representatives for the genera. A full list of the taxa examined is given in that table.

Character scoring and study. Characters were scored based on direct observations and recent literature: the source of characters (as 'direct observations' or 'literature') is given in Table 1. When available, both males and females were examined for potential characters, but males were not available for *Neotheora* and females were not available for *Paratheora*. Existing preparations at BMNH and ZMUC (abbreviations explained below) were examined when available. When new preparations

were required, abdomens, heads, metathorax, or the entire body were macerated in 10% KOH in aqueous solution and stained briefly in chlorazol back, stored in glycerol or 80% ethanol, and examined under a stereo microscope at 6–80 × magnification. Existing microscope slides were examined under both stereo and compound microscopes. Wings were examined in two ways: either being dehydrated and descaled fully or partially in 100% ethanol and embedded in euparal and examined under both stereo and compound microscope; or by placing the specimen upside-down under a stereo microscope and subsequently placing a droplet of absolute ethanol on the wing. Wing fragments and scales were prepared for scanning electron microscopy (SEM) following SIMONSEN (2001), coated with 15 nm platinum-palladium in a JEOL JFC-2300HR High Resolution Fine Coater and examined using a JEOL JSM-6335F Field Emission scanning electron microscope. Terminology follows KRISTENSEN (2003); KRISTENSEN & SIMONSEN (2003); SCHACHAT & GIBBS (2016); and WOOTTON (1979).

Phylogenetic analysis. A maximum parsimony analysis was carried out in TNT (GOLOBOFF et al. 2008) using Traditional Search with equal character weights, TBR branch swapping and 100 random replications with 100 trees saved per step. The character matrix was organised in WinClada 1.00.08 (NIXON 2002) and character transformations were analysed in Mesquite 2.71 (MADDISON & MADDISON 2009).

2.3. Abbreviations for collections

ANIC – Australian National Insect Collection, Canberra, Australia; **BMNH** – Natural History Museum, London, UK; **DZUP** – Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil; **ZMB** – Museum für Naturkunde Berlin, Denmark; **ZMUC** – Natural History Museum of Denmark (Zoology), Copenhagen, Denmark.

3. Results

3.1. Descriptive taxonomy

3.1.1. *Neotheora* Kristensen, 1978 (Figs. 1A–C, 2, 3, 4)

Neotheora Kristensen, 1978: 280.

Neotheora: NIELSEN & ROBINSON 1983: 16; SCOBLE 1992: 208; KRISTENSEN 1998: 60; NIELSEN et al. 2000: 834.

Type species: *Neotheora chiloides*, by original designation.

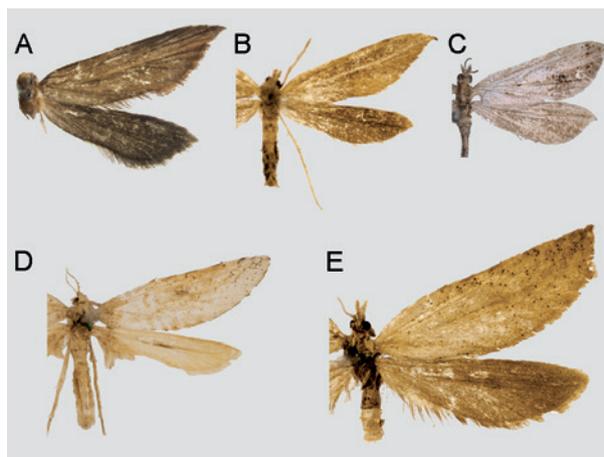


Fig. 1. Species of *Neotheora* and *Paratheora*. **A:** *Neotheora chiloides*, female holotype; **B:** *Neotheora meyi*, female holotype; **C:** *Neotheora mielkeorum*, female holotype; **D:** *Paratheora speideli*, male holotype; **E:** *Paratheora speideli*, female. — All ca 1.25 × natural size.

Diagnosis. Hepialoids pertaining to the grade in which proboscis vestiges are distinct, but short and apparently not coilable. **Probable autapomorphies:** Anterior tentorial arm with pronounced anterior swelling. Elongation of third labial palpomere (> palpomeres 1+2). Fore- and hindwing apices pointed and backwards curved, hence termen appearing concave. Elongation of metathoracic tibiae. Female postabdomen immediately in front of large 'lamella antevaginalis' with a naked, strongly sclerotized plate bearing two prominent, narrow pointed processes on caudal margin; bursa copulatrix long, near-cylindrical or widened and with subapical constriction, with prominent, distinctively shaped signa. The falcate wing shape, to our knowledge unparalleled among lower-grade hepialoid moths (but ± pronouncedly paralleled in some subordinate Hepialidae *s.str.*), seems a useful first-aid for recognition.

Description. Head (Fig. 2A–C): Cranium pale brown; dorsally with smooth scale covering, scales elongate-spatulate and dentate with pale tip; chaetosemata absent; eye smooth, large, ca 0.9 × total height of head; antenna simple [flagellum broken in all available specimens] with smooth scales dorsally and hair-like sensilla ventrally, with rough vestiture; maxillary palp strongly reduced; proboscis small, unscaled; labial palp large and porrect.

Thorax: Colour as head, with very long hair-like scales in addition to spatulate scales similar to those on head. Legs with five tarsal segments; prothoracic leg with numerous spines; metathoracic tibia elongate, with two spurs at mid-length. Pretarsal claws small and simple, arolium and pulvilli distinct, spinose field present between pulvilli. Forewing with posterior margin with concavity basal from vein CuA1. Microtrichiation (examined in *N. chiloides* only) restricted to basal-most part of fore wing dorsum and dorsum of jugum. Marginal scales elongate, but generally somewhat broadened except for very long hair-like scales along the hind wing anal mar-

gin; forewing scale covering appears at dissecting microscope magnification to be ‘type 3 bilayer’ as already documented in *N. chiloides* by SEM and microtome sections (KRISTENSEN 1978a; SIMONSEN 2001). Position of Sc fork relative to R/Rs fork variable in the three specimens examined (proximal from in *N. chiloides*, near-identical in *N. mielkeorum* sp.n., distal from in *N. meyi* sp.n., but it will be unsurprising if this character eventually proves intra-specifically or even intra-individually [i.e., with left/right asymmetry] variable). Rs1+2 stalked, Rs3 and Rs4 ‘sessile’; crossvein M-CuA1 consistently present. Ventral surfaces of both wings uniform, slightly paler than ground colour of dorsal surface.

Female postabdomen (Figs. 2D,E, 3, 4): Structure complex, and as noted by KRISTENSEN (2003: 117) some interpretations in the original description are open to debate, as is also clear from our examination of the new taxa; in any case, however, morphological interpretations must remain tentative until availability of more specimens of at least one species will render more detailed examination (including serial sectioning) possible. The hindmost segment, which has retained a spiracle and a simple tergum, VII somewhat longer than the preceding segments. The dorsal and lateral intersegmental membrane between VII and VIII forms a very deep pocket, the lateral walls of which are highly folded longitudinally, obviously allowing for considerable vertical expansion. In the new species, *N. meyi* and *N. mielkeorum* the two pockets anteriorly fuse above the ductus bursae/antrum, their inner walls being continuous with the sclerotization of the latter. The apparent tergum VIII represented by a ribbon/rod-like sclerotization, paramedially somewhat broadened; eventually it curves strongly forward and downward in each side below tergum VII, extending anteriorly beyond mid-length of the segment; it forms the roof in the afore-mentioned intersegmental pocket, and while its rod-like anterior parts recall the ‘anterior apophyses’ which are commonplace in amphiesmenopteran females, they do not appear to have a free apodemal part. The inner pocket wall may, or may not, be conspicuously melanized.

The interpretation of the ventral region is particularly problematical. In all three known species a rather short, well sclerotized plate is located immediately below the lateral segment VII/VIII intersegmental pockets; the sharply folded, hence double-walled hind margin of the plate, which bears a pair of prominent, pointed and slightly asymmetrical processes, may project backwards beyond the pocket margins. In *N. chiloides* the plate is indistinctly delimited from the unmelanized venter VII, and it has been tentatively ascribed to venter VIII (KRISTENSEN 1978). In *N. mielkeorum* (Fig. 4) the plate is anteriorly more distinctly demarcated from the unmelanized preceding wall (which it even overlaps in the available specimen, whose abdominal end was protracted with forceps to maximally expose details). In contrast, *N. meyi* has on an extensive part of the venter VII a moderately well-developed melanization, which gradually merges into the process-bearing terminal plate. Hence, when this taxon is

considered in isolation, the assignment of the plate to another segmental territory (i.e., VIII) is not obvious, but we shall tentatively continue to uphold it here. The putative venter VIII plate is firmly connected to the anterior margin of the sclerite referred to as the lamella antevaginalis, which forms the ‘lower lip’ of the copulatory orifice, and which has been considered to belong to venter IX.

In all species the lamella antevaginalis is a large and prominent, transversely \pm convex plate with a sparse, but taxonomically informative, setation.

The abdominal apex bears paired dorsal plates (‘anal papillae’), free double-walled lobes, which dorsally are clearly separated. Their vestiture comprises slender pili-form scales on the external surface and strong pointed setae on the inner/medial surface. The paired ‘subanal plates’ are small paramedial, transversely elongate sclerites in the otherwise membranous body wall below the anal papillae, flanking the area above the copulatory orifice where the anus and ovipore are located. Like the preceding process-bearing sclerite it is sharply bent along the topographically posterior margin and hence double-walled, its upper wall forming the sclerotized floor of the ‘antrum’, i.e., the \pm pronouncedly funnel-shaped cavity, which forms the entrance to the bursa copulatrix. The roof of the antrum is variably developed and particularly elaborate in *N. meyi*.

The antrum extends forward for at least half the length of segment VII. The bursa copulatrix is long, extending to near, or beyond, the abdominal base. It is near-cylindrical or with a subdistal swelling; ductus and corpus sections are not distinctly delimited. Large and round signum plates, each with a prominent central, lamellar tooth (with triangular or rounded outline) are present in variable numbers. Sperm obviously deposited in a spermatophore, sizable fragments (partly clearly tubular) of which are retained in the *N. meyi* specimen.

The ductus receptaculi has a thick-walled (but slender) basal part and thin-walled distal part, the latter widening into a utriculus with numerous internal spines. The transition between the thick- and thin-walled sections marked by a small, disk-shaped swelling.

3.1.2. Key to female *Neotheora*

Since only a single specimen is known for each species, reservations must evidently be made about the general validity of the statements about diagnostic traits, particularly those relating to size and wing pattern.

- 1 Robust species, forewing length \approx 18 mm. Forewing dark reddish-brown without lighter markings. Lamella antevaginalis transversely only very modestly convex, with small medial seta group near hind margin and paralateral groups of scattered setae near mid-length (Brazilian Cerrado, Mato Grosso)
..... *chiloides* Kristensen, 1978
- 1' Forewing length less than 16.5 mm. Forewing with whitish markings on dark reddish-brown ground

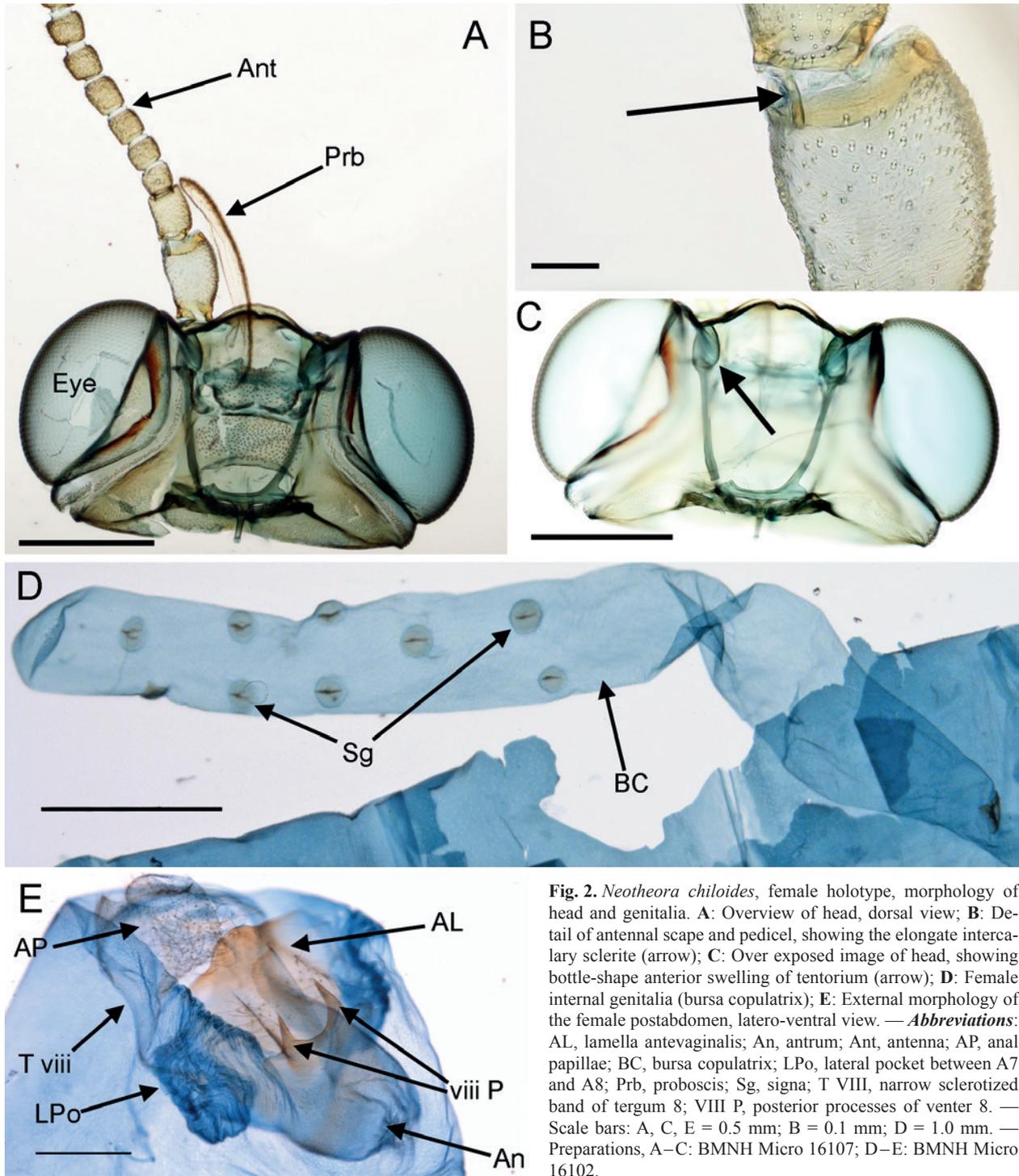


Fig. 2. *Neotheora chiloides*, female holotype, morphology of head and genitalia. **A:** Overview of head, dorsal view; **B:** Detail of antennal scape and pedicel, showing the elongate intercalary sclerite (arrow); **C:** Over exposed image of head, showing bottle-shape anterior swelling of tentorium (arrow); **D:** Female internal genitalia (bursa copulatrix); **E:** External morphology of the female postabdomen, latero-ventral view. — **Abbreviations:** AL, lamella antevaginalis; An, antrum; Ant, antenna; AP, anal papillae; BC, bursa copulatrix; LPO, lateral pocket between A7 and A8; Prb, proboscis; Sg, signa; T VIII, narrow sclerotized band of tergum 8; VIII P, posterior processes of venter 8. — Scale bars: A, C, E = 0.5 mm; B = 0.1 mm; D = 1.0 mm. — Preparations, A–C: BMNH Micro 16107; D–E: BMNH Micro 16102.

- colour. Lamella antevaginalis transversely markedly convex, boat-shaped, with strongly setose median keel **2**
- 2** Forewing length \approx 16.3 mm; relatively more narrow winged: length/width ratio $>$ 3; fore wing with a whitish streak from base to apex. Bursa copulatrix with numerous ($>$ 10) signa (the Brazilian Dense Ombrophilous Forest, Rio de Janeiro) **meyi sp.n.**
- 2'** Forewing length \approx 13.5 mm; relatively more broad winged: length/width ratio $<$ 3; fore wing with more extensive suffusion of dark scales and a distinct whit-

ish dot in outer part. Bursa copulatrix with very few (three) signa (the Brazilian Dense Ombrophilous Forest, Santa Catarina) **mielkeorum sp.n.**

3.1.3. *Neotheora chiloides* Kristensen
(Figs. 1A, 2, 18)

Neotheora chiliodes Kristensen, 1978, Ent. Germ. 4: 272–294
Neotheora chiliodes: NIELSEN & ROBINSON 1983: 16; SCOBLE 1992: 208; KRISTENSEN 1998: 60; NIELSEN et al. 2000: 834.

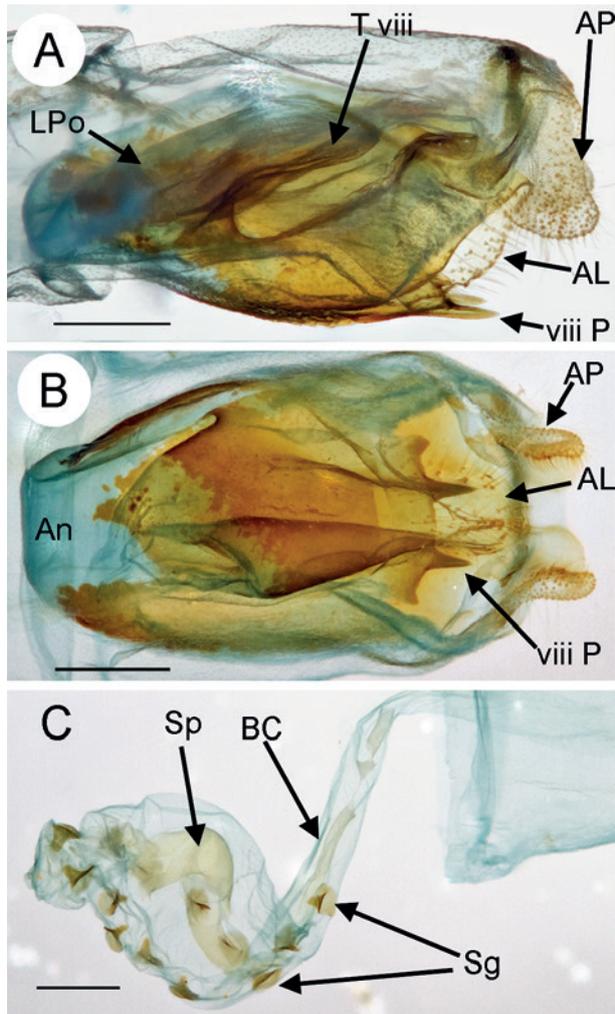


Fig. 3. *Neotheora meyi*, female holotype, genitalia. **A:** External morphology of the female postabdomen, lateral view; **B:** External morphology of the female postabdomen, ventral view; **C:** Female internal genitalia (bursa copulatrix). — **Abbreviations:** AL, lamella antevaginalis; An, antrum; AP, anal papillae; BC, bursa copulatrix; LPO, lateral process of venter 8; T VIII, narrow sclerotized band of tergum 8; VIII P, posterior processes of venter 8. — Scale bars: 0.5 mm. — Preparation, A–C: N.P. Kristensen gen. prep. 1082.

Type data: Holotype, female (BMNH).

Type locality: Burity, Chapanda dos Guimarães, 30 miles NE of Cuiabá, Mato Grosso, Brazil.

Material examined. Holotype ♀: Brazil, labelled “Matto [recte Mato] Grosso, [Chapanda dos Guimarães] Burity [recte Buriti], 30 miles N. E. of Cuyabá, 2250 ft., 20-3-. IX. (19)27. At light. C. L. Collette [leg.]”. Slide series Brit. Mus. (Nat. Hist.) Microlepidoptera 16102–16111. BMNH.

Diagnosis. Adult *N. chiloides* can be distinguished from other members of the genus by the larger forewing length, and uniformly reddish-brown forewing. Female genitalia differing from those of congeners in having the lamella antevaginalis much more smoothly convex transversely, without distinctively developed median setose keel, with setae in open groups paraterally and near posteromedian

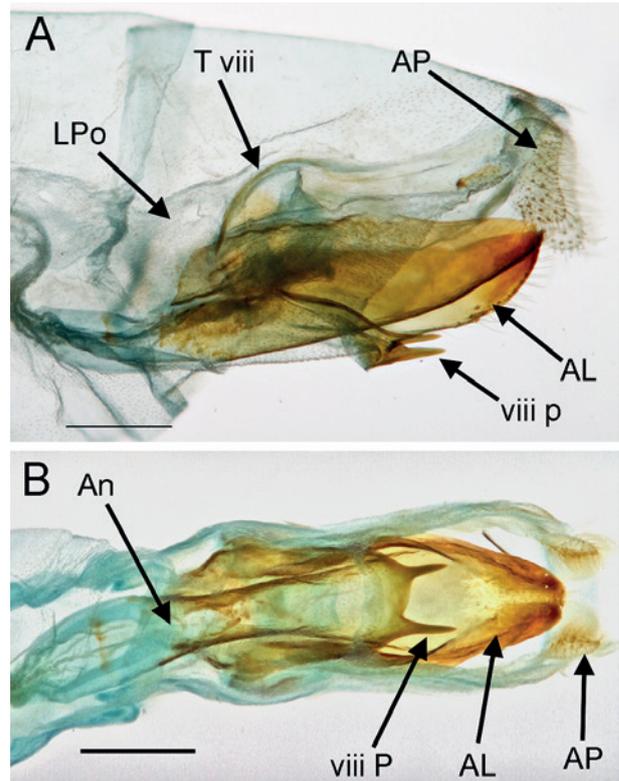


Fig. 4. *Neotheora mielkeorum*, female holotype, genitalia. **A:** External morphology of the female postabdomen, lateral view; **B:** External morphology of the female postabdomen, ventral view. — **Abbreviations:** AL, lamella antevaginalis; An, antrum; AP, anal papillae; BC, bursa copulatrix; T VIII, narrow sclerotized band of tergum 8; VIII P, posterior processes of venter 8. — Scale bars: 0.5 mm. — Preparation, A–C: N.P. Kristensen gen. prep. 1081.

apex. Antrum not nearly extending forwards to anterior margin of tergum VII. Bursa copulatrix near-cylindrical; 10 signa present, nine being located in the anterior part, one single far behind the others.

3.1.4. *Neotheora meyi* Kristensen & Simonsen sp.n.

(Figs. 1B, 3, 18)

Type data: Holotype, female (ZMB).

Type locality: Nova Friburgo [Rio de Janeiro], Brazil.

Etymology. An eponym in honour of the German lepidopterist Wolfram Mey.

Material examined. Holotype ♀: Brazil, labelled “NovFriburgo [recte Nova Friburgo] Sem?[unreadable last letter]! “19314”; body somewhat overgrown with delicate fungus hyphae. Genitalia preparation no 1082 N.P. Kristensen, ZMB, Berlin.

Diagnosis. Recognizable by forewing pattern, with white line running from base to apex. Female genitalia with sclerotizations in VII/VIII intersegmental pouch and antrum roof particularly distinctive.

Description [antennae and legs incomplete, only one prothoracic and one metathoracic leg present]. **Forewing**: length 16.3 mm; length/width ratio ≈ 3.4 ; ground colour dark brown, somewhat lighter and with a warmer reddish tinge in broad marginal zone behind diagnostic longitudinal streak and extending basad below M3 to posterior concavity. **Hindwing**: uniformly dark greyish brown.

Female genitalia (Fig. 3): Tergum VIII with ribbon-like anterior part moderately curved. Intersegmental pockets behind VII particularly large and prominent, their lower internal walls distinctive by having conspicuous and extensive melanizations. Anal papillae with lateroventral part broadly rounded. Subanal plates elongate-convex, their sclerotization not sharply delimited. Venter VIII plate with posterolateral corners markedly produced, right prong slightly larger than left one. Lamella antevaginalis with marked keel-like, heavily setose mediolongitudinal convexity; prominent setae also present on paramedial area. Antrum extending forward to near anterior margin of tergum VII. Antrum roof in anterior 2/3 with distinctive, broad and posteriorly sharply delimited sclerotized plate. Roof plate posteriorly smoothly truncate, medially slightly concave, anteriorly it is continuous with the ventrolateral antrum sclerotization. Bursa copulatrix widened some distance behind anterior end, with 13 signa, some of which arranged as opposing pairs. Genital chamber with opening of ductus receptaculi positioned more anteriorly than in congeners, close to the anterior margin of segment VI; thick-walled section strongly coiled.

3.1.5. *Neotheora mielkeorum* Kristensen & Simonsen sp.n.

(Figs. 1C, 4, 18)

Type data: Holotype, female (DZUP).

Type locality: Joinville, Santa Catarina, Brazil.

Etymology. An eponym in honour of the Brazilian father and son lepidopterists Olaf and Carlos Mielke who collected the single known specimen.

Material examined. Holotype ♀: Brazil, labelled "Joinville – SC 12.xi. 1977 Miers, Mielke. Genitalia preparation no 1081 N.P. Kristensen, Departamento de Zoologia, Universidade Federal do Parana.

Note. The single known specimen was collected in the morning during a day-collecting trip. The individual was likely disturbed and landed on a thin vine on the way to the hilltop of Serrinha Mount to be collected by Olaf Mielke (C. Mielke pers. comm.).

Diagnosis. Recognizable by forewing pattern with silvery white spot in the M1-CuA1 cell. In female genitalia size/shape of lamella antevaginalis and small signum number distinctive.

Description [antennae incomplete, legs missing]. **Forewing**: length ≈ 13.5 mm; length/width ratio ≈ 2.9 ; ground colour greyish brown, with warmer, reddish brown scaling between subcostal and costal margin, also with scattered red-brown or blackish-brown scales in discal cell, area between Rs1 and CuA1, and close to apex; distinct, elongate silvery white spot in M1-CuA1 cell. **Hindwing**: uniformly greyish brown.

Female genitalia (Fig. 4): Tergum VIII with curved anterior part extending beyond antrum sclerotization. Intersegmental pockets behind VII less conspicuously folded than in congeners, without noticeable melanizations on lower inner surface. Anal papillae in lateral view with ventral margin shorter than in congeners. Subanal plates narrow, elongate and well defined. Venter VIII with left prong longer than right one. Lamella antevaginalis large, transversely particularly strongly convex, hence particularly narrow in ventral view, setation restricted to median keel, which is less melanized than immediate surroundings. Antrum extending forward to near anterior margin of tergum VII. Bursa copulatrix extending to base of abdomen, strongly S-curved in basal (posterior) part. Corpus bursae slightly widened, with subapical constriction; with three signa, one relatively basal, and two close together near apex. [The corpus bursa is missing from the preparations TJS received after NPK's death, and no photography of the corpus bursa could be located. The authors have, however, previously discussed the corpus bursa and the relevant characters. They are therefore left in the description, but not illustrated.]

3.1.6. *Paratheora* Kristensen & Simonsen gen.n. (Figs. 1D,E, 5, 6, 7, 8A, 9, 10, 16)

Type species: *Paratheora speideli* sp.n.

Etymology. A name indicating the relationship of the genus with other basal hepialids (several names being based on the suffix *-theora*). The prefix *Para-* (Greek meaning 'besides', 'next to' but also 'opposite to') indicates it is clearly distinct from these genera.

Diagnosis. Hepialoids pertaining to the grade in which proboscis vestiges are distinct, but short and apparently not coilable. **Probable autapomorphy**: Forewing shape markedly differing from that of *Neotheora*, with termen smoothly convex but costal margin just before apex concave.

Description. **Head** (Fig. 5): Cranium with somewhat arched, scaly anteromedial surface laterally framed by strengthening ridges ('laterofacial sulci') extending from mandibles to antennal frame; anteromedial area markedly bent just below facial scale bed. Posterior cranial surface flat, naked. Dorsal surface with weakly developed V/(U)-shaped strengthening ridge extending between margins of compound eyes behind antennal bases. Anterior tentorial arms strongly swollen near base, dorsal arms well

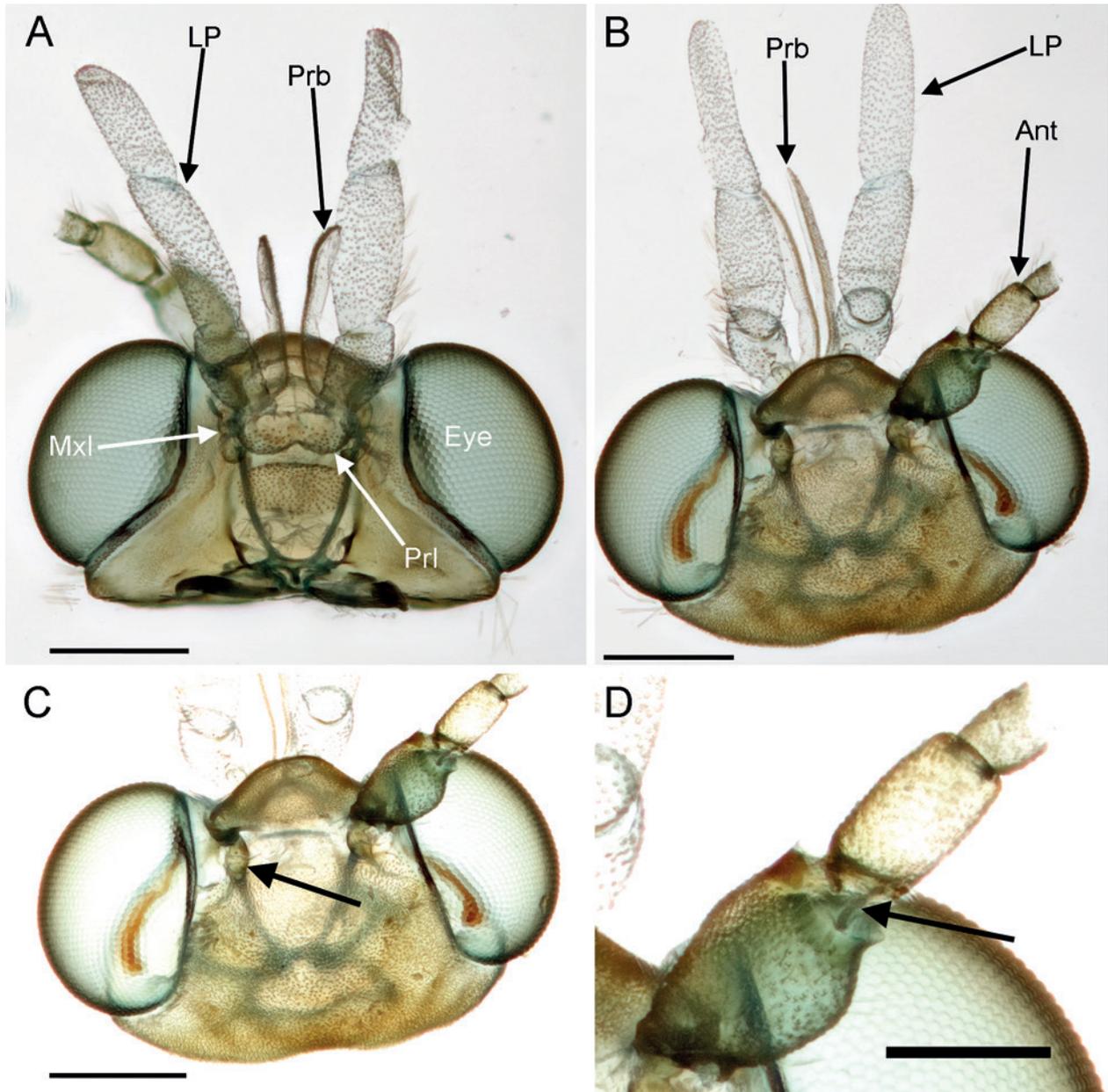


Fig. 5. *Paratheora speideli*, male holotype, head morphology. **A:** Overview of head, ventral view; **B:** Overview of head, dorsal view; **C:** Over exposed image of head (dorsal view), showing bottle-shaped anterior swelling of tentorium (arrow); **D:** Detail of antenna scape and pedicle, showing the elongate intercalary sclerite (arrow). — Scale bars: A–C = 0.5 mm; D = 0.25 mm. — Preparation: H15088.

developed, pointed, laterally directed. Antennae with scapo-pedicellar intercalary sclerite of ‘normal hepialoid type’, i.e., elongate and lowered into membranous pocket. Proboscis remnant large by hepialoid standards, \approx head capsule length; maxillary palps 2-segmented, extending to just beyond apex of basal labial palp segment. Labial palp with segment 1 : 2 : 3 length ratio \approx 1 : 2 : 2 in male, 1 : 2.7 : 3.1 in female.

Vestiture on frons separated from dorsal scale bed by naked zone around and between antennal bases. Dorsal scale bed extending across the head capsule and along posterior and ventral margin of compound eye; cranial area along anteroventral margin of compound eye naked from level of proboscis vestige to short distance above antenna. Vestiture comprising piliform scales and (pre-

dominantly) elongate, largely near-parallel-sided lamellar scales, which are bicoloured and with serrate apical margin; scales on facial area below antennae and on labial palps more pronouncedly triangular.

Forewings (Figs. 6, 16): length \approx 18.2 mm in male, 22.3 mm in female. Forewing shape unusual because of costa being smoothly convex just before apex. Microtrichia absent. The wing scales are overall similar to those found in *Neotheora* (SIMONSEN 2001: fig. 9A–D), with elongate and parallel sided cover scales with a dentate apical margin, and rounded ground scales. As in *Neotheora*, the windows on the abwing scale surface are large, but ridge dimorphism is not prominent. At least not in the common pale scale type – the uncommon dark-brown scales have more elaborate secondary ridges. The ground

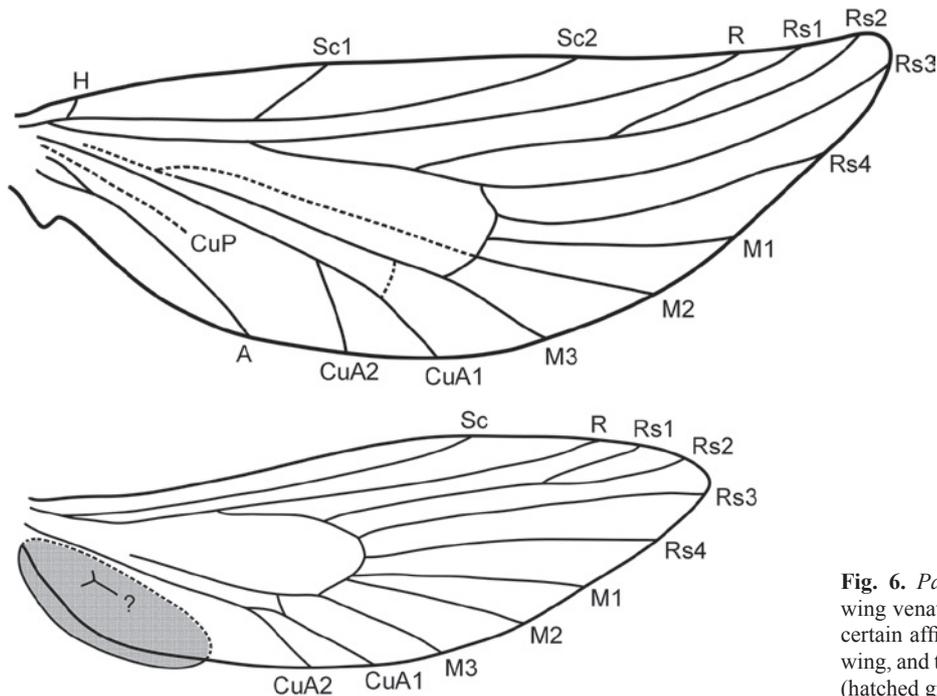


Fig. 6. *Paratheaora speideli*, male holotype, wing venation. Note the Y-shaped vein of uncertain affinity in the anal region of the hindwing, and the large hindwing anal scale pocket (hatched grey area).



Fig. 7. *Paratheaora speideli*, male holotype, foreleg. Note the large, thickened tibia. — Scale bar: 2.0 mm.

scales have no perforations and are presumably solid, but as in *Neotheora* ridge dimorphism is outspoken. The venation is overall very similar to that of *Neotheora*, forewing R/Rs fork located a short distance proximal from Sc fork. In male a pocket immediately behind the base of

the forewing vein 1A forms a distally tapering bulge on the wing ventral surface; the pocket opening is a narrow slit and its lumen is densely set with narrow, obliquely backwards-directed scales. **Hindwings** (Figs. 6, 16): venation largely as in forewing, Sc unforked. Male anal hair-pencil pocket very voluminous reaching from the wing base 2/3 to CuA2. In cross section, the hair-pencil appears as a two-chambered pocket. The main (ventral) chamber is filled with elongate, thin and hair-like scales, which are hollow in cross-section. The smaller (dorsal) pocket is filled with thicker, but still elongate and hair-like scales, which appear sponge-like or semi-hollow in cross-section. Microtrichia absent except for the anal region. **Legs** (Fig. 7): Fore tibia without epiphysis, but fore tibia thickened and tarsomeres very short. Mid and hind legs unmodified. Spurs 0:0:4.

Metendosternum (Fig. 8A): The metafurca is highly distinctive with a long, downwards curved anterior process, which even connects anteriorly to the basisternal discrimen.

Sternum I (Fig. 9): A sizable, scaled and arched, near-rectangular plate; its anterior part is raised while its posterior margin slightly overlaps the anterior border of the sternum II plate.

Male genitalia (Fig. 10): The male genital apparatus is highly complex, and we remain in doubt about the morphological interpretations of some details, particularly since we have been unable with certainty to locate the anal opening in the preparation made from the single dried specimen available. The genitalia segments IX(-XI) are largely concealed within segment VIII. The largely apodemal vinculum (ventral IX sclerotization) is a well sclerotized plate with a deeply concave anterior margin. Its posterior margin is very shallowly concave, in the mid-region almost straight; it is markedly thickened,

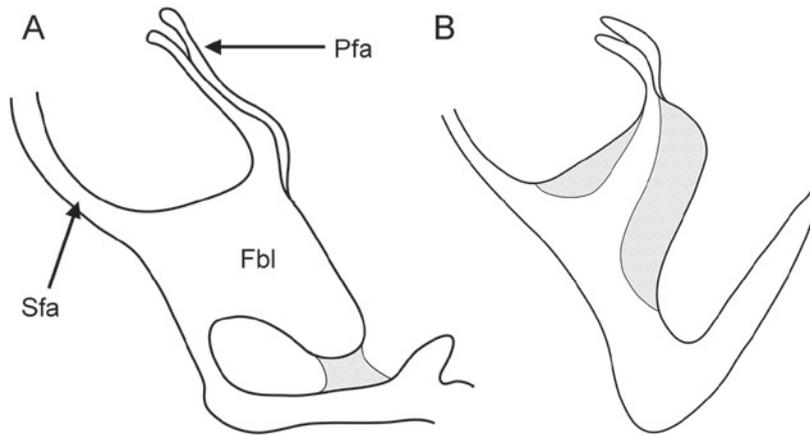


Fig. 8. Metafurca morphology, lateral view. **A:** Metafurca of *Paratheora speideli*, note the anteriorly elongate furca-basisternal lamella, which connects to the basisternal discrimen through a lamellar bridge; **B:** Metafurca of *Genustes minutus*, note the upright, narrower furca-basisternal lamella. Grey hatching indicates thinner, more lamellar structures. — **Abbreviations:** Bst, basisternum; Fbl, furca-basisternal lamella; Pfa, primary furcal arms; Sfa, secondary furcal arms. — Preparation, A: H15088; B: BMNH Micro 33276.

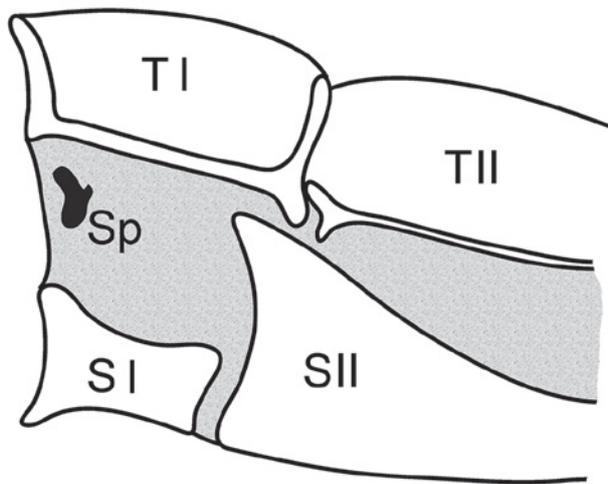


Fig. 9. *Paratheora speideli*, male holotype, base of abdomen, lateral view. Note the large sternum I. — **Abbreviations:** S, sternum; Sp, spiracle; T, tergum. — Preparation: P15088.

with the thickenings on each side being extended forwards for some distance. The upper part of the vinculum is produced into a prominent posterodorsal process. The valve is deeply divided into a ventromedian and a much longer dorsolateral lobe. The former bears two dorsal processes, short, stout and pointed apical sensilla a very numerous long setae, particularly on the inner surface. The latter are naked, narrow at base, apically markedly widened; the dorso-apical corner is rounded, the ventro-apical corner sharply angled. A 'juxta' sclerotization has its widened anterior (topographically posterior) part located between the posterior vinculum margin and the valve bases; it extends upwards between the latter and eventually bends sharply forwards. Its topographically anterior corners are in close contact with the produced morphologically and topographically anterior corners of the prominent, sclerotized trulleum, which posteriorly is a freely projecting tubular formation, the lower subapical surface of which bears a series of transverse ridges.

On each side the thickened anterior rim of a dorsal sclerotization, surely belonging to segment IX, is produced into a tapering ventral process, which extends downwards medially from the vinculum and apically ar-

ticulates with the upper valve base. The posteroventral corners of the left and right sclerotizations are confluent in the mid-line, forming a prominent 'medioventral process' which constitutes the ventral surface of a near-conical protuberance in the membrane between/above the valve bases. The posterodorsal corners of these sclerotizations are produced into long, curved processes which apically articulate with a pair of 'posteromedial sclerites' which similarly may belong to IX. Each comprises a posteriorly tapering 'lateral plate' which obviously accommodates the insertion of a sizable muscle on the apex (as evidenced by a strong tendon-bundle remaining in the KOH-treated specimen), and an extremely prominent 'median horn' which is hollow, smooth and syringe-like pointed; the latter is, from its base, directed backwards and then turns, forming a full circle so that the apex again points backwards, extending far beyond the medioventral part of the valve. Between the two 'posterolateral sclerites' is a 'posteromedial sclerite', which presumably belongs to segment X. It bears a pair of anteriorly directed, stout and pointed apodemes, and a prominent median process with a medio-longitudinal groove (indicating it is a pair of fused processes), curving in a way recalling that of the afore-mentioned 'median horns' and lying in the dorsal mid-line of the membranous protuberance of which the lower surface is formed by the medioventral process. We are confident that the gonopore is located on the apex of this protuberance, but are uncertain whether the anus is also located, in a topographically more posterior position here, or (what may seem more likely) in the membranous area above.

Female genitalia: Unknown (see 'Material and methods' section).

3.1.7. *Paratheora speideli* Kristensen & Simonsen sp.n.

(Figs. 1D,E, 5, 6, 7, 8A, 9, 10, 16, 18)

Type data: Holotype, male (ZMB).

Type locality: [Unknown, but possibly Rio de Janeiro, Brazil — see below].

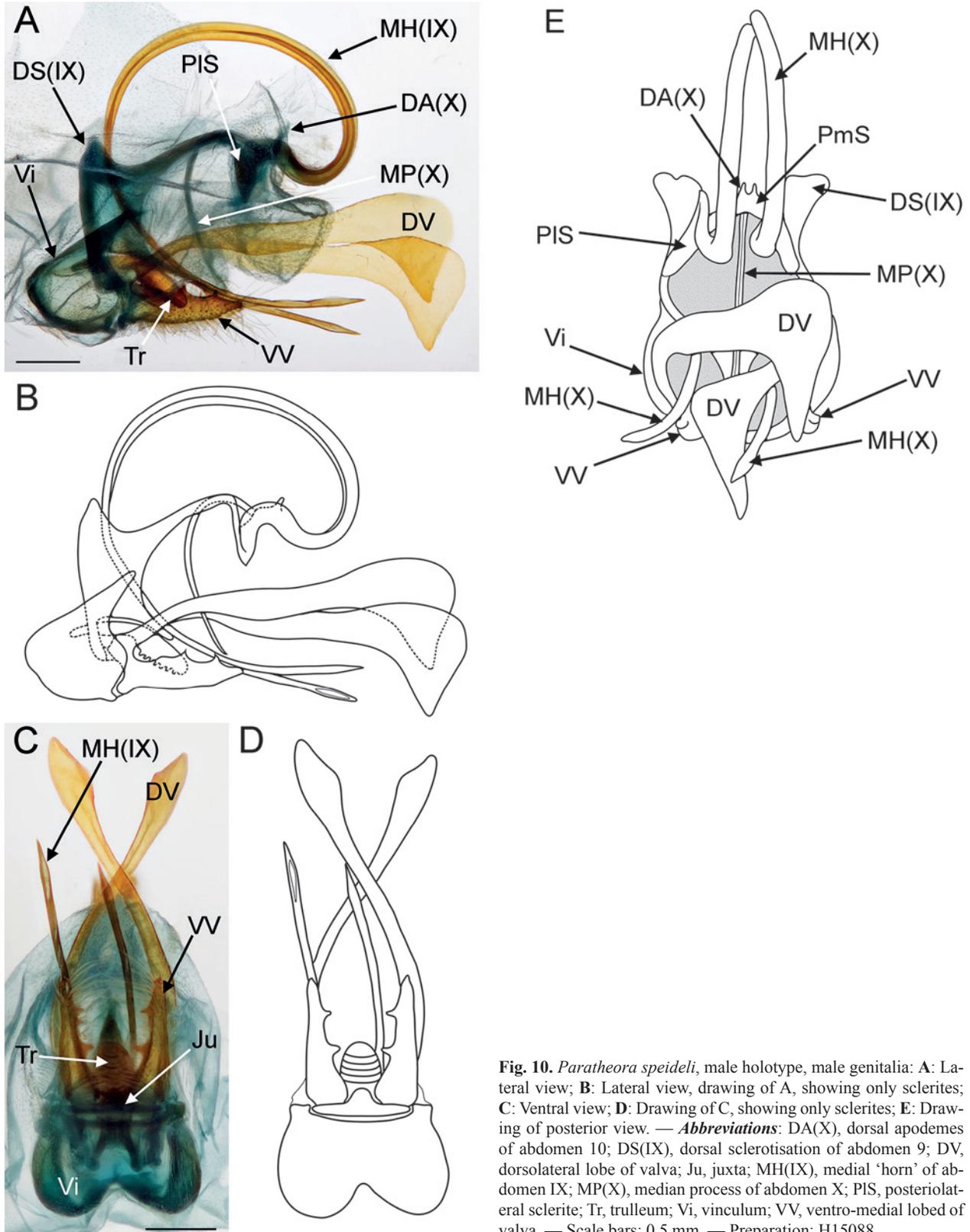


Fig. 10. *Paratheora speideli*, male holotype, male genitalia: **A:** Lateral view; **B:** Lateral view, drawing of A, showing only sclerites; **C:** Ventral view; **D:** Drawing of C, showing only sclerites; **E:** Drawing of posterior view. — **Abbreviations:** DA(X), dorsal apodemes of abdomen 10; DS(IX), dorsal sclerotisation of abdomen 9; DV, dorsolateral lobe of valva; Ju, juxta; MH(IX), medial ‘horn’ of abdomen IX; MP(X), median process of abdomen X; PIS, posteriolateral sclerite; Tr, trulleum; Vi, vinculum; VV, ventro-medial lobed of valva. — Scale bars: 0.5 mm. — Preparation: H15088.

Etymology. An eponym in honour of the German lepidopterist Wolfgang Speidel.

Material examined. Holotype ♂ labelled “Brasil Virmond”/ “15088”: ZMB. Additional material, not included in type series: one (likely conspecific ♀) specimen without data and postabdomen (see ‘Material and methods’ section): ZMB.

Diagnosis & description. See generic account. **Head:** Cephalic scales uniformly pale yellowish-whitish or with broad brownish subapical band.

Note. HORN & KAHLE (1936: p. 290) listed a “Virmond” without initials and with unknown birth/death dates as

Table 1. Species examined for the morphological dataset, with methods of character observation, major references, preparation IDs, and collections where specimens and preparations are deposited. Notes regarding *Mnesarchaea* and *Fraus*: NPK had a number of whole-body preparations of several species from both genera, which were all examined during the study.

Species	Char. sources	Relevant references	Dissection ID	Collection
<i>Mnesarchaea</i> [sp.] Meyrick, 1886	Direct, literature	KRISTENSEN (1998), SIMONSEN (2001)	See note	ZMUC
<i>Neotheora chiloides</i> Kristensen, 1978	Direct, literature	KRISTENSEN (1978a, 1998), SIMONSEN (2001)	BMNH Micro 16102-16111	BMNH
<i>Paratheora speideli</i> sp.n.	Direct		H15088, TJS SEM H48	ZMB
<i>Anomoses hylacoetes</i> Turner, 1916	Direct, literature	KRISTENSEN (1978b, 1998), SIMONSEN (2001)	NPK ANO 1	ANIC, ZMUC
<i>Prototheora</i> [sp.] Meyrick, 1917	Literature	DAVIS (1996), KRISTENSEN (1998), SIMONSEN (2001)		
<i>Ogygioses</i> [sp.] Issiki & Stringer, 1932	Literature	DAVIS et al. (1995), KRISTENSEN (1998), SIMONSEN (2001)		
<i>Genustes minutus</i> (Hampson, 1896)	Direct, literature	ISSIKI & STRINGER (1932a,b)	BMNH Micro 32212, 33166, 33276, 33277, TJS SEM H52	BMNH
<i>Palaeoses scholastic</i> Turner, 1922	Direct, literature		BMNH Gen. slide 1367, NPK H81, NPK Gen. 1084, TJS SEM H53	BMNH, ANIC
<i>Osrhoes coronta</i> Druce, 1900	Literature	KRISTENSEN & NIELSEN (1993), KRISTENSEN (1998)		
<i>Fraus</i> [sp.] Walker, 1856	Direct, literature	NIELSEN & KRISTENSEN (1989), KRISTENSEN (1998)	See note	ZMUC
<i>Afrotheora jordani</i> (Niette, 1956)	Direct, literature	NIELSEN & SCOBLE (1986), KRISTENSEN (1998)	BMNH Micro 20476, 32214, 33161, 33280, 33281	BMNH
<i>Antihepialus antarcticus</i> (Wallengren, 1860)	Direct, literature	NIELSEN & SCOBLE (1986), KRISTENSEN (1998)	BMNH Micro 33215, 32225, 33278, 33279	BMNH
<i>Gazoryctra roseicaput</i> (Barnes & Benjamin, 1926)	Direct	KRISTENSEN (1998), SIMONSEN (2001)	BMNH Micro 32226, 32227	BMNH
<i>Gazoryctra hyperboreus</i> (Möschler, 1862)	Direct	KRISTENSEN (1998), SIMONSEN (2001)	BMNH Micro 32213	BMNH
<i>Gazoryctra novigannus</i> (Barnes & Benjamin, 1926)	Direct	KRISTENSEN (1998), SIMONSEN (2001)	BMNH Micro 33269, 33270	BMNH
<i>Bipectilus tindalei</i> (Nielsen, 1988)	Direct, literature	NIELSEN (1988)	BMNH Micro 32216, 33160	BMNH
<i>Gorgopis caffra</i> Walker, 1856	Direct		BMNH Micro 33163, 33165	BMNH
<i>Hepialus humuli</i> (Linnaeus, 1758)	Direct, literature	KAABER et al. (2009)	BMNH Micro 32217, 33162, 33164	BMNH
<i>Oxycanus antipoda</i> (Herrich-Schäffer, 1853)	Direct		BMNH Micro 32218, 32228	BMNH

source of “Auswahl brasilian Ins. (spec. Coleoptera) ca 1830 [in the publication’s 1937 *Nachtrag*: 387 corrected to 1833] an Zool. Mus. Berlin”. Virmond collected in Brazil in the early 1800s, most likely in the Rio de Janeiro region as this was one of two main entrances to Brazil at that time, and others of his types in the ZMB are said to be from Rio (C. Mielke pers. comm.). We therefore find it likely that the specimen came from the vicinity of Rio de Janeiro, Brazil, and use this locality for the distribution map (Fig. 18).

3.2. Phylogeny

Eighteen characters were scored: three were from the head, ten were from the thorax including wings, and five were from the abdomen including male genitalia. 16 characters were binary and two were ordered multistate (characters 3 and 12). All characters had equal weight. The full list of characters is given below, and the character matrix is given in Electronic Supplement 1.

The TNT analysis yielded nine equally parsimonious trees, each 24 steps long (Electronic Supplement 2). The consensus tree is shown in Fig. 11. For the discussion we selected the tree shown in Figs. 12 and 13 based on character evolution as discussed below. The tree is based on an apparently fully resolved tree from the nine equally

parsimonious trees, but the two polytomies in Figs. 12 and 13 represent zero-length branches, which were not collapsed in the TNT analysis. The original trees from the TNT analysis are given in Electronic Supplement 2.

3.2.1. Character list

Head

1. Intercalary sclerite: **(0)** small, restricted to the membrane between scape and pedicellus (KRISTENSEN et al. 2015: fig. 2c); **(1)** elongate, basal end sunken into a pocket below terminal edge of scape (Figs. 2B, 5D).
2. Anterior base of tentorium: **(0)** narrow (e.g. KRISTENSEN & NIELSEN 1993: fig. 7; DAVIS et al. 1995: fig. 12; DAVIS 1996: fig. 11; SIMONSEN in press: figs. 17–22); **(1)** with bottle-shape swelling (Figs. 2C, 5C).
3. Proboscis: **(0)** fully developed and coilable (e.g. KRISTENSEN 1998: fig. 5.4B); **(1)** clearly visible, but reduced (non-coilable and markedly shorter than labial palp) (Figs. 2A, 5A,B); **(2)** fully reduced (e.g. KRISTENSEN & NIELSEN 1993: fig. 6; DAVIS et al. 1995: fig. 11; DAVIS 1996: fig. 10; SIMONSEN 2015: fig. 16) (ordered).

Thorax

4. FW Rs3: **(0)** reaching wing margin anterior to apex (e.g. KRISTENSEN 1998: fig. 5.4A); **(1)** reaching wing margin posterior to apex (Figs. 6, 14).

5. FW Rs2: **(0)** reaching wing margin clearly anterior to apex (Fig. 6); **(1)** reaching wing margin at or posterior to apex (Fig. 14).
6. FW Radial Sector veins: **(0)** Rs1–4 do not share common stem beyond the cell (Fig. 6); **(1)** Rs1+2 stalked with Rs3+4 fork (Fig. 14).
7. FW M2–M3 inter cross vein: **(0)** present (Fig. 6); **(1)** reduced (Fig. 14).
8. FW microtrichia: **(0)** absent (Fig. 16A); **(1)** present (Figs. 17A,D).
9. FW scale covering: **(0)** Solid wing scales present (Fig. 16A–C); **(1)** Solid wing scales absent (Fig. 17).
10. HW Radial Sector veins: **(0)** Rs1–4 do not share common stem beyond the cell (Fig. 6); **(1)** Rs1+2 stalked with Rs3+4 fork (Fig. 14).
11. Metatibia: **(0)** at most $1.5 \times$ the length of femur; **(1)** $2 \times$ the length of femur.
12. Male metatibia: **(0)** not swollen; **(1)** markedly swollen (KRISTENSEN & NIELSEN 1993: fig. 12); **(2)** markedly swollen with hair-pencil in concealed groove (DAVIS et al. 1995: fig. 14) (ordered).
13. Metafurca: **(0)** with long, well-developed anterior process (Fig. 8A); **(1)** of "hepialoid type" without (or at most with weakly developed) anterior process (Fig. 8B).

Abdomen

14. S1: **(0)** well developed (Fig. 9); **(1)** poorly developed.
15. T3 with thick lateral list: **(0)** absent; **(1)** present (NIELSEN & SCOBLE 1986: fig. 40).
16. Distal tip of trulleum in male genitalia: **(0)** not closely associated with pseudotergumal arms (Fig. 15); **(1)** closely associated with pseudotergumal arms (e.g. SIMONSEN in press: fig. 200).
17. Intermediate plate in male genitalia: **(0)** absent; **(1)** present (Fig. 15; NIELSEN & KRISTENSEN 1989: fig. 102; SIMONSEN in press: fig. 200).
18. Ventral tip of Intermediate plate in male genitalia: **(0)** separate from dorsal base of valve (e.g. SIMONSEN 2015: figs. 26, 45, 50); **(1)** closely associated with dorsal base of valve (Fig. 15).

3.2.2. Phylogenetic relationships

The phylogenetic analysis resulted in nine most parsimonious trees 24 steps long, the strict consensus tree is shown in Fig. 11, the preferred tree is shown in Figs. 12 and 13. The following discussion is based on the tree in those two figures. Clade numbers refer to Fig. 12, whereas apomorphic character changes and taxon distributions are shown in Fig. 13.

Clade 1 – Hepialidae. Hepialidae *s.lat.* is monophyletic and supported by three autapomorphies: char. 1:1, intercalary sclerite elongate with basal end sunken into a pocket; char. 3:1, proboscis clearly reduced and probably non-functional, but still recognisable; and char. 4:1, FW Rs3 reaching wing margin posterior to apex.

Clade 2. The two Brazilian genera *Neotheora* and *Paratheora* are supported as a monophyletic group based on two synapomorphies: char. 2:1, tentorium with bottle-shape anterior swelling; and char. 11:1, meta tibia at least twice the length of meta femur. Although the latter is paralleled in *Prototheora*.

Clade 3. The remaining genera appear as a monophyletic group, and the clade is well supported by two autapomorphies: char. 13:1, metathoracic furca reduced and of the "hepialid type"; and char. 14:1, abdominal S1 poorly developed.

Clade 4. The clade comprising *Prototheora*, the "palaeosetid genera", the four 'primitive hepialid' genera, and Hepialidae *s.str.* is monophyletic, supported by char. 9:1, the absence of solid wing scales on the forewing (SIMONSEN 2001).

Clade 5. A sister group relationship between the "palaeosetid genera" and Hepialidae *s.lat.* (*sensu* NIELSEN & SCOBLE 1986) is fairly well supported by two synapomorphies: char. 3:2, proboscis fully reduced; and char. 5:1, FW Rs2 reaching the margin at or posterior to apex. The former is, however, reversed in some members of *Fraus*.

Clade 6. The 'palaeosetid genera' appear as a fairly well supported monophyletic group. The clade is supported by two autapomorphies: char. 7:1, FW M2–M3 inter cross vein absent; char. 10:1, HW Rs1+2 stalked with Rs3+4 fork beyond cell. The latter is further modified in *Ogygioses*. Furthermore, the forewing cover scales appear to be specialised within the group, as they have windows with elaborate frames with internal sculpturing, and the frames are separated by a single continuous cross-rib (Fig. 17B,E). While this kind of sculpturing is unique among the genera examined here, a similar sculpturing has recently been found in the Australian Hepialidae *s.str.* genus *Oncopera*, Walker, 1856 (SIMONSEN in press). As the type of sculpturing varies between the 'palaeosetid' genera as well, it has been omitted from the analysis.

Clade 7. Although a sister group relationship between *Oshroes* and the two south-east Asian genera *Ogygioses* and *Genustes* does not appear in the strict consensus tree, such a relationship is supported by a single synapomorphy: char. 12:1, male hind tibia markedly swollen.

Clade 8. A sister group relationship between *Ogygioses* and *Genustes* is supported by a single unique and remarkable synapomorphy: char. 12:2, male hind tibia markedly swollen with a hair pencil concealed in a groove. It is a further modification of the state found in *Oshroes*.

Clade 9. The representatives of the classic Hepialidae *s.lat.* form a monophyletic group supported by one unique autapomorphy: char. 17:1, male genitalia with an Intermediate Plate.

Clade 10. Although a sister group relationship between *Gazoryctra* and the two African genera *Afrotheora* and *Antihepialus* does not appear in the strict consensus tree, such a relationship is supported by a single synapomorphy: char. 18:1, ventral tip of Intermediate Plate closely associated with dorsal base of valve.

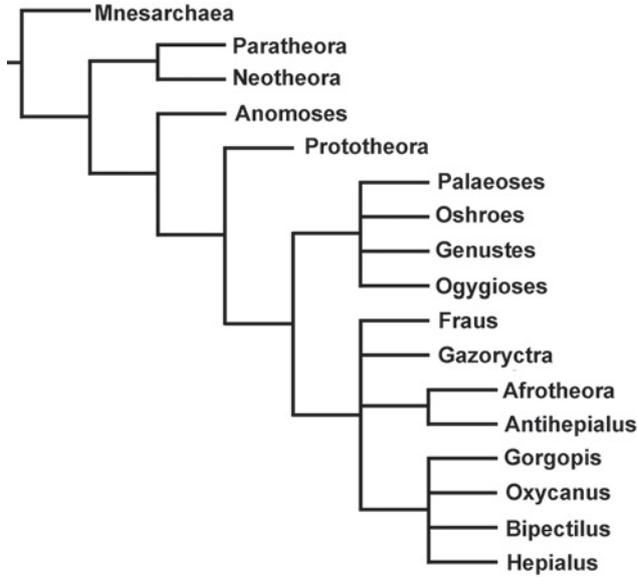


Fig. 11. Strict consensus tree of Hepialoidea genera of nine equally parsimonious trees each 24 steps long.

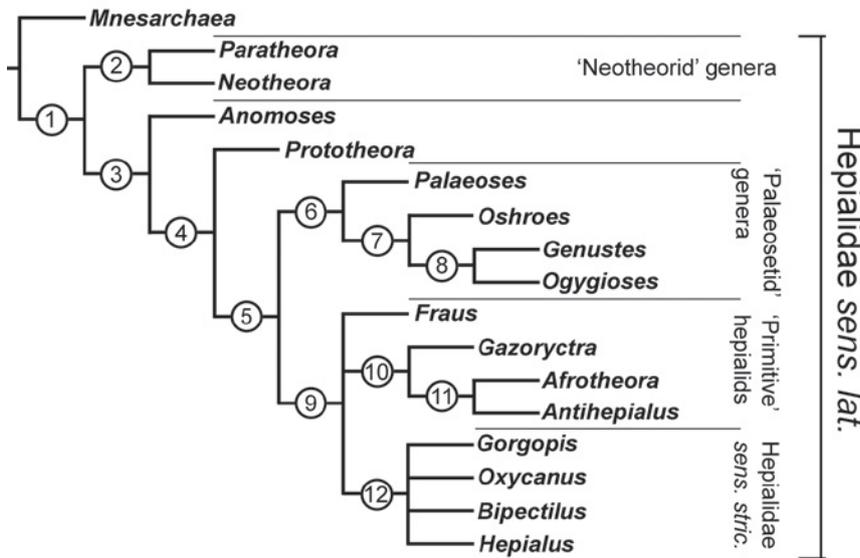


Fig. 12. The preferred tree of Hepialoidea genera out of the nine equally parsimonious trees. The numbers in circles refer to the clade numbers as discussed in the text.

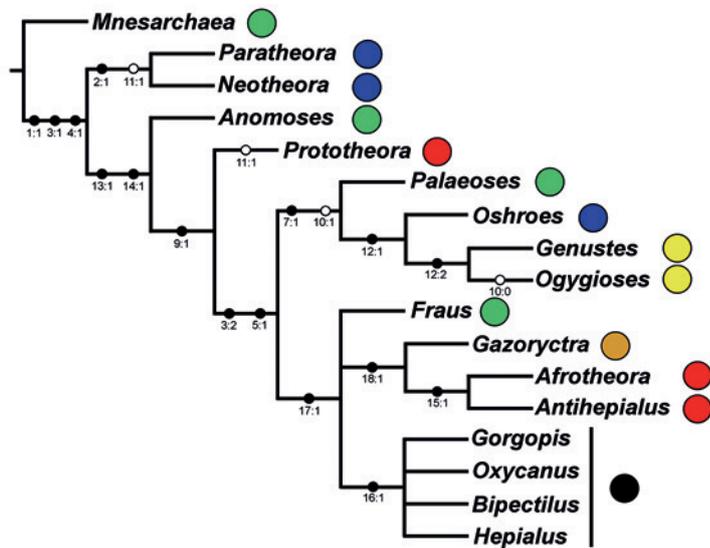


Fig. 13. The preferred tree of Hepialoidea genera showing apomorphies of the clades, and overall geographical distributions of the terminal taxa. Unique apomorphies are shown by closed circles on the branches, whereas non-unique (homoplasious or later reduced) apomorphies are indicated by open circles on the branches. Numbers indicate character and state for each apomorphy. Distributions are shown by coloured circles. Green: Australia and New Zealand; blue: South America; red: sub-Saharan Africa; yellow: Oriental; orange: Holarctic; black: global except Madagascar (indicates the overall distribution for Hepialidae *s.str.*, not just the four genera in the tree).

Clade 11. A sister group relationship between *Afrotheora* and *Antihepialus* is moderately well supported by one synapomorphy: char. 15:1, abdominal T3 with thick lateral list.

Clade 12. The representatives of Hepialidae *s.str.* form a moderately well supported monophyletic group supported by one unique apomorphy: char. 16:1, trulleum distally closely associated with pseudoterguminal arms.

4. Discussion

While the morphological differences between the three *Neotheora* taxa now known leave no doubt about the specific distinctness of them all, they evidently constitute a phenetically tightly knit assemblage. It is perhaps noteworthy that a forewing pattern with a long whitish streak extending towards the apex, here reported from *N. meyi*, is also recurrent in some species groups in the 'primitive hepialid' genus *Fraus* as well as in prototheorids and a species group in *Mnesarchaea*, hence it has been suggested that the potential for the formation of this pattern was present in the exoporian ground plan (NIELSEN & KRISTENSEN 1989).

The discovery of *Paratheora* is exciting and highlights how incomplete our knowledge of homoneuran Lepidoptera still is, especially in the Southern Hemisphere. The unfortunate absence of female material of *Paratheora* and male material of *Neotheora*, means that the sex-specific diagnostic characters listed here may not 'stand the test of time', and new material of the unknown sex from each of the genera may in the future result in the two genera being synonymised. But at present, we think that the unique alar scale organ and genitalia in *Paratheora* warrant the description of a new genus.

The apparent scarcity of the species treated here is striking, and paralleled in other lower Hepialidae such as *Genustes* (ISSIKI & STRINGER 1932a), *Anomoses* and *Palaeoses* (COMMON 1990), and *Oshroes* (KRISTENSEN & NIELSEN 1993). However, even though the species may be relatively rare in 'real life', the extreme scarcity is probably a collecting artefact caused by a combination of short adult life span and cryptic habits. As all Hepialidae are non-feeding as adults, their lifespan is necessarily limited by fat reserves inherited from the pupal stage (e.g. KRISTENSEN 1998). Small and fragile species such as the ones treated here (and the ones listed above) likely have small fat reserves and thus short lifespans. Furthermore, at least *Anomoses* and *Palaeoses* appear to be active at night, but not readily attracted to light (COMMON 1990), meaning that successful collecting of specimens depends on a considerable element of chance. In contrast, the equally small (and presumably short-lived) *Ogygioses* is active by day, albeit at relatively low light levels, and thus more commonly encountered (DAVIS et al. 1995 and references therein). If *Neotheora* and *Paratheora* have cryptic hab-

its similar to *Anomoses* and *Palaeoses* this could explain their apparent scarcity, and both genera may well occur much more widely in southern South America. Indeed, as shown in Fig. 18 the collecting localities are widely separate in southern Brazil, indicating the possibility of a wider distribution.

We find that Hepialidae (*sensu* REGIER et al. 2015) are monophyletic and well supported by three classic apomorphies listed by KRISTENSEN (2003). The first split within the family is between a clade comprising the two Neotropic genera *Neotheora* and *Paratheora*, and a clade comprising the remaining taxa. The sister group relationship between *Neotheora* and *Paratheora* is strongly supported by the synapomorphies discussed above, and our results confirm the suggestion therein that the two genera are sister taxa.

The remaining taxa form a reasonably well supported monophyletic group supported by the strong reduction of the abdominal S1 and the remarkable modification of the metathoracic furca associated with a shift in the insertion of the sterno-trochanter muscle (KRISTENSEN 2003). The discovery that the metathoracic furca in *Paratheora* is overall similar to the condition found in non-Hepialoidea homoneuran Glossata is indeed surprising, and our study has confirmed the presence of a "hepialid type" metafurca in *Anomoses*, *Genustes*, *Gazoryctra*, *Afrotheora* and *Antihepialus*. The "hepialid type" metafurca has previously been documented in *Prototheora* (DAVIS 1996), *Ogygioses* (DAVIS et al. 1995), and *Fraus* (NIELSEN & KRISTENSEN 1989). SIMONSEN (in press: figs. 48, 49) does illustrate some Hepialidae *s.str.* with an elongate anterior process. But in these cases the process is lamellar, and never as well-developed as seen in *Paratheora*. The scarcity of available material did not allow us to examine *Neotheora*, *Palaeoses* or *Oshroes* for this character, and these taxa were therefore scored "?" in the phylogenetic analysis. Our results do, however, predict that a "hepialid type" metafurca is absent in *Neotheora*, but present in *Palaeoses* and *Oshroes*.

Anomoses is found to be the sister group of a clade comprising all the remaining taxa. The latter is supported by two apomorphies related to the wing vestiture: the presence of microtrichia and the absence of solid wing scales. The presence of microtrichia is not a straight forward character, as microtrichia is present in Mnesarchaeoidea as well as all other non-Hepialoidea homoneuran Glossata families with the exception of Acanthopteroctetidae (SIMONSEN 2001). Indeed, the absence of microtrichia on most of the wing surfaces in *Neotheora* and *Anomoses* has earlier been suggested as a potential synapomorphy for the two taxa (KRISTENSEN 1978a,b). Our analysis suggests that the general absence of microtrichia is better explained as an apomorphy of Hepialidae *s.lat.* and the presence of microtrichia in this clade then becomes an apomorphic character reversal. The absence of solid wing scales appears to be a unique and universal apomorphy within Hepialoidea (although the three families Acanthopteroctetidae, Lophocoronidae and Neopseustidae all lack solid scales too indicating a

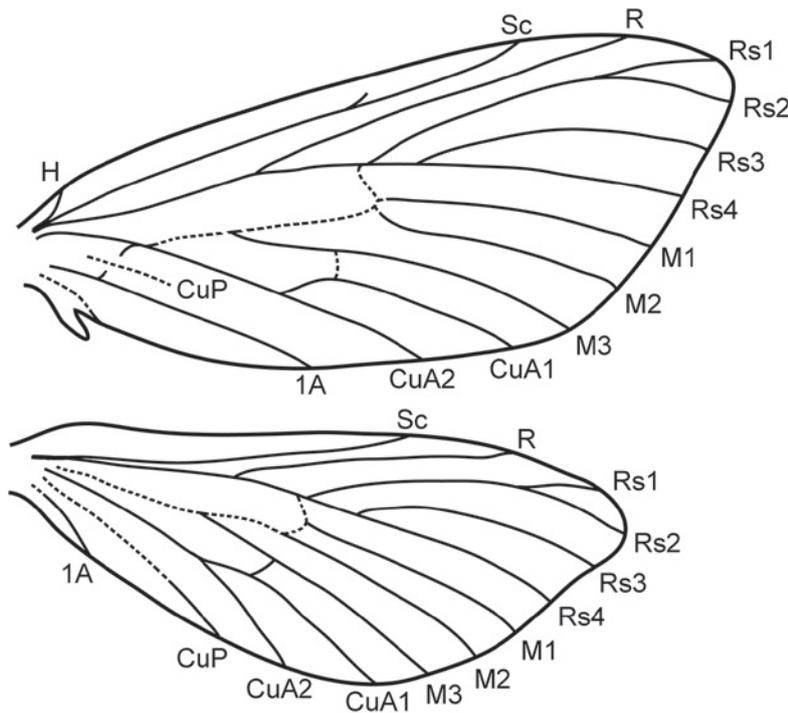


Fig. 14. Character illustration. 'Palaeosetid' wing venation exemplified by *Osrhoes corona* Druce, 1900 (redrawn from KRISTENSEN & NIELSEN 1993). Note the absence of an M2-M3 cross vein, and that all Rs veins share a short, common stalk beyond the cell in both wing pairs.

complex evolutionary history of this character within the homoneuran Lepidoptera). This is in agreement with SIMONSEN (2001) who suggested that the absence of solid scales within Hepialidae could be due to a single evolutionary event.

Prototheora is the sister group of a clade comprising the four palaeosetid genera *Palaeoses*, *Oshroes*, *Geneustes*, and *Ogygioses*, as well as the genera representing Hepialidae *s. lat.* (sensu NIELSEN & SCOBLE 1986). The latter appears fairly well supported although the characters support for the clade is not entirely unproblematic. The full reduction of the proboscis is reversed in some members of *Fraus* (NIELSEN & KRISTENSEN 1989). The second character supporting the clade appears more convincing. In all members of the clade the FW Rs2 vein reaches the wing margin either at the apex or just posterior to it, whereas the vein reaches the wing margin clearly anterior to the apex in all other homoneuran Lepidoptera.

The four genera previously joined in Palaeosetidae comprise a monophyletic clade, and our results thus support the monophyly of this group. This is interesting since this has been questioned by previous authors (e.g. SCOBLE 1992; KRISTENSEN & NIELSEN 1993; DAVIS et al. 1995; KRISTENSEN 1998). Nevertheless, not only is the classical palaeosetid character (the reduction of the FW M2-M3 cross vein) found to be an apomorphy, one additional potential apomorphy has been identified. The character, HW Rs1 + 2 stalked with Rs3 + 4 fork beyond cell, is not found in *Ogygioses*, but the branching of the Radial Sector in both wing pairs is highly apomorphic in that genus with Rs1 – 3 sharing a common stem and Rs4 originating by itself from the cell (e.g. DAVIS et al. 1995: fig. 13), a condition that to our knowledge is not found elsewhere in Hepialoidea. This difference between *Ogygioses* and the remaining palaeosetid genera is therefore likely best

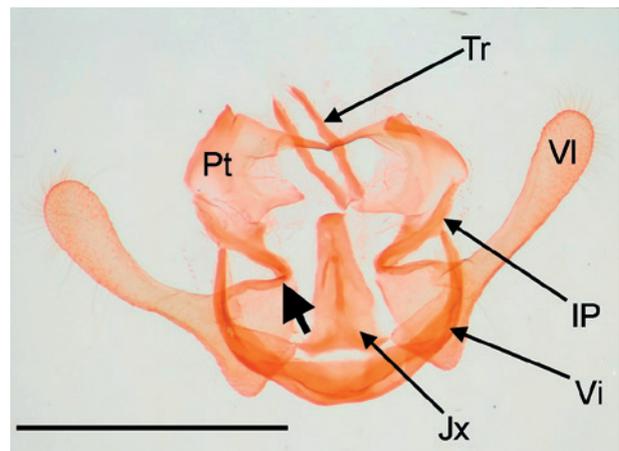


Fig. 15. Character illustration. Male genitalia of *Afrotheora jordani* (Viette, 1956). Note the close association between the intermediate plate and the base of the valva. — **Abbreviations:** IP, intermediate plate; Jx, juxta; Pt, pseudotegumen; Tr, trulleum; Vi, vinculum; VI, valva. — Scale bar: 1.0 mm. — Preparation: BMNH Micro 20476.

viewed as a genus-level autapomorphy in the former. A further potential synapomorphy (FW cover scales with windows with elaborate frames with internal sculpturing, frames separated by a single continuous cross-rib) is consistent within the four genera (although the scale ultrastructure otherwise varies between them). This condition is to our knowledge only paralleled in the Australian genus *Oncopera* (SIMONSEN 2001, 2002, 2015, in press). Within the palaeosetid clade, we favour a sister group relationship between *Oshroes* and *Geneustes* + *Ogygioses*. This relationship is supported here by the markedly swollen metatibia in the three genera; KRISTENSEN & NIELSEN (1993) also stated that the three genera are the only Hepialoidea genera where the mesonotum width /

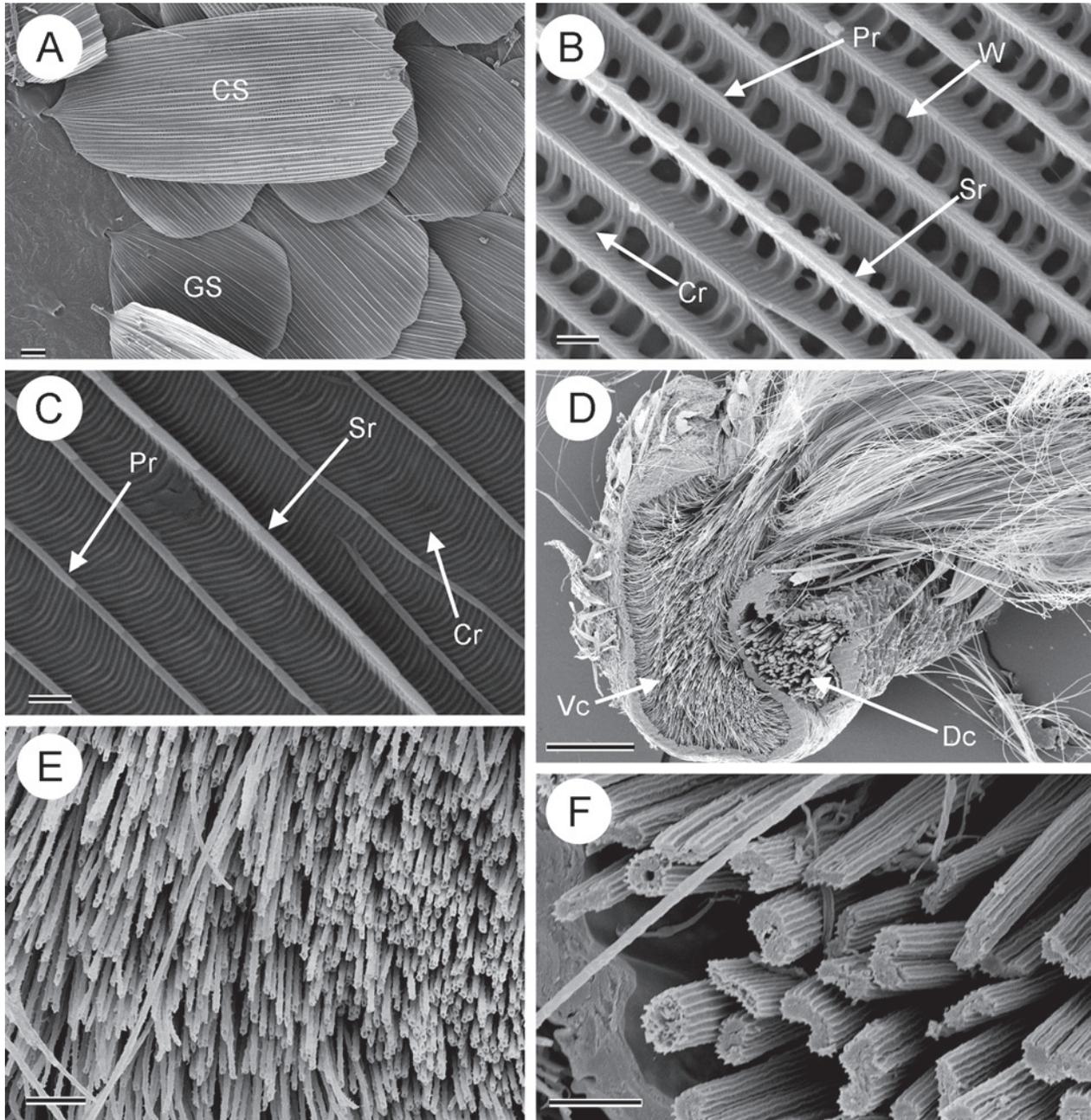


Fig. 16. SEM micrographs of *Paratheaora speideli* wing vestiture: **A:** Overview of dorsal forewing scales, note absence of microtrichia; **B:** Details of cover scale, abwing surface; **C:** Detail of ground scale, abwing surface; **D:** cross section of hindwing anal scale pocket; **E:** Details of scales in ventral chamber; **F:** Details of scales in dorsal chamber. — **Abbreviations:** Cr, cross ribs; CS, cover scale; Dc, dorsal chamber; GS, ground scale; Pr, primary ridge; Sr, secondary ridge; Vc, ventral chamber; W, window. — Scale bars: A, E, F = 10 µm; B, C = 1 µm; D = 100 µm.

forewing width ratio is below 0.35, yielding further support to this relationship. In support of the opposing possibility that *Palaeoses* and *Oshroes* are sister taxa is the character: FW Rs1+2 stalked with Rs3+4 fork beyond cell. Further, albeit tentative, support of this arrangement comes from the fact that both *Oshroes* (KRISTENSEN & NIELSEN 1993: fig. 30) and *Palaeoses* (unpublished obs.) have a very large lamella antevaginalis in the female genitalia. However, the structure and shape of the lamella antevaginalis differs considerable between the two taxa, and a large lamella antevaginalis is found in various other hepialoid taxa as well (unpublished obs.). We therefore

find that *Oshroes* as sister group to *Geneustes* + *Ogygioses* is a more likely working hypothesis. Although the sister group relationship between *Geneustes* and *Ogygioses* does not appear in the strict consensus tree, it appears to be well supported by two unique characters as listed in the results chapter. The close relationship between these two genera has been realised since ISSIKI & STRINGER (1932a,b) first described them and explored their systematic relationships. This original assessment was followed by DAVIS et al. (1995) who, based on the similarities in the male metatibia, suggested that *Ogygioses* was closest related to *Geneustes*. They also remarked that although

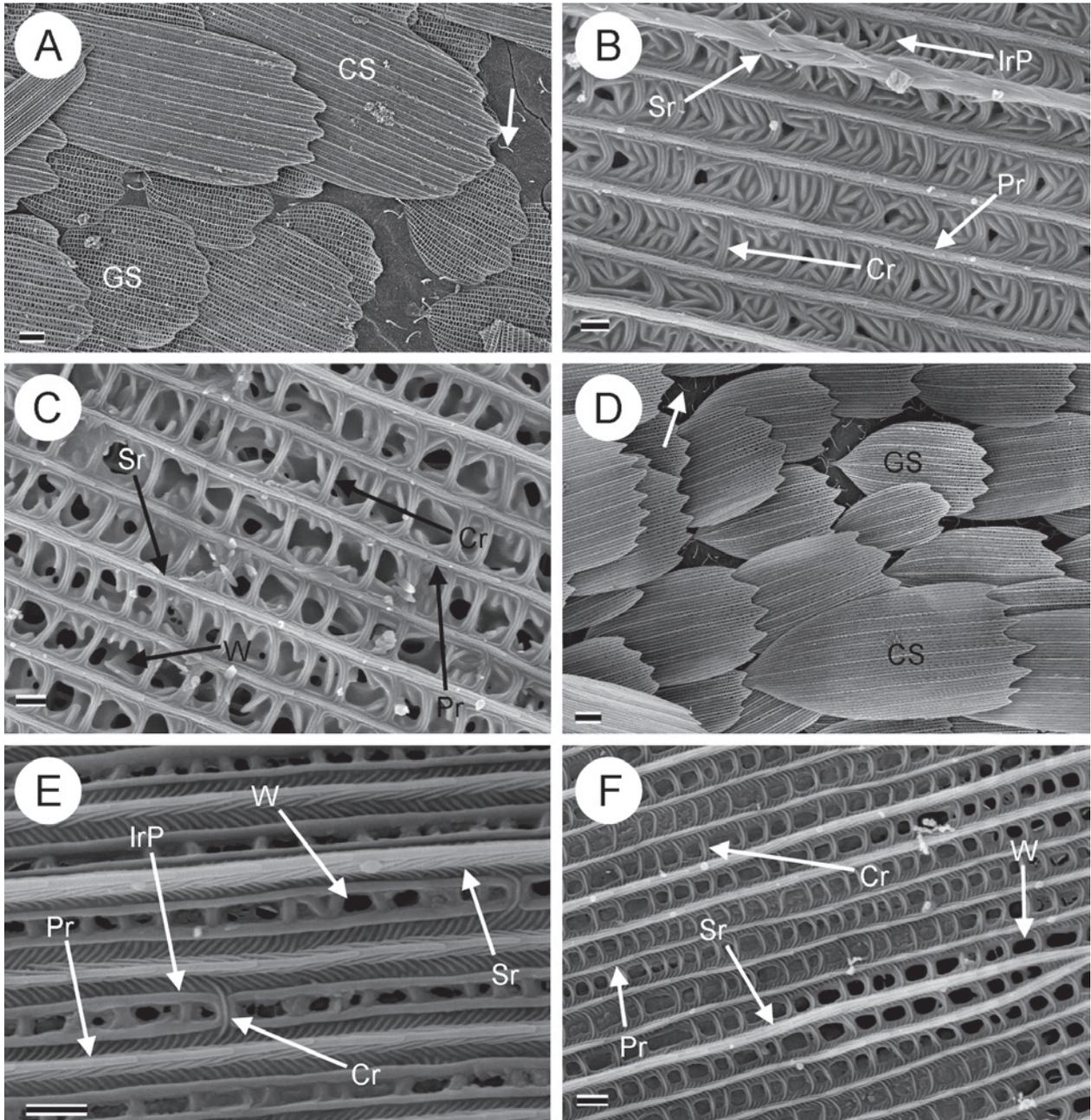


Fig. 17. SEM micrographs of ‘palaeoesetid’ dorsal forewing vestiture. **A–C:** *Genustes minutus* (Hampson, 1896): **A:** Overview of wing scales, note the well-developed microtrichia (arrow); **B:** Details of cover scale, abwing surface; **C:** Details of ground scale, abwing surface; **D–F:** *Palaeoses scholastica* Turner, 1922: **D:** Overview of wing scales, note the well-developed microtrichia (arrow); **E:** Details of cover scale, abwing surface; **F:** Details of ground scale, abwing surface. — **Abbreviation** not previously used: IrP, inter-ridge plate. — Scale bars: A, D = 10 µm; B, C, E, F = 1 µm.

the male genitalia in the palaeoesetid genera differ considerably, *Ogygioses* and *Genustes* show similarities in the pseudotegumen.

The genera representing the classic Hepialidae *s.lat.* appear monophyletic in our analysis. This is somewhat surprising since the monophyly of this group has been questioned since NIELSEN & SCOBLE (1986) removed the four genera *Fraus*, *Gazoryctra*, *Afrotheora* and *Antihepialus* from Hepialidae *s.str.* Indeed these authors found it unlikely that Hepialidae *s.lat.* comprised a monophyletic clade. However, the presence of an intermediate plate in the male genitalia (NIELSEN & SCOBLE 1986; KRISTENSEN

& NIELSEN 1989) appears to be a unique apomorphy. The basal relationships within Hepialidae *s.lat.* remains unresolved. While we favour a sister group relationship between *Gazoryctra* and *Afrotheora* + *Antihepialus*, supported by the close association between the intermediate plate and the dorsal base of the valve in the male genitalia, it is not possible to resolve the relationship between this clade, *Fraus* and Hepialidae *s.str.* The alternative scenario would be that the close association between the intermediate plate and the dorsal base of the valve is plesiomorphic, and the separation between the two is a synapomorphy of *Fraus* + Hepialidae *s.str.* This inter-



Fig. 18. Map showing the collecting localities of the species. Closed circle: *Neotheora chiliodes*; open circle: *Neotheora mielkeorum*; crossed circle: *Neotheora mayi* and *Paratheora speideli* combined.

pretation would leave the relationship between *Gazoryctra*, *Afrotheora* + *Antihepialus*, and *Fraus* + Hepialidae *s.str.* unresolved. However, if NIELSEN & SCOBLE (1986) are correct and the intermediate plate is derived from the pseudotegumen, it seems unlikely that a close association between the intermediate plate and the dorsal base of the valve would be the plesiomorphic condition, as the dorsal base of the valve normally is associated with the vinculum in other Hepialoidea. SIMONSEN (2001) suggested that a singlelayer scale covering could be a synapomorphy for *Fraus* + Hepialidae *s.str.*, and SIMONSEN (2002) further suggested that a type-2 bilayer scale covering could be a synapomorphy for a smaller group within Hepialidae *s.str.* However, recent studies demonstrate that type-2 bilayer scale covering is more widespread with Hepialidae *s.str.* and may even differ between the sexes of the same species (SIMONSEN 2015, in press). In fact, a number of the species not examined by SIMONSEN (2001, 2002) appear to have type-2 bilayer wing scale covering (unpublished obs.). It is therefore clear that this character is less informative for higher-level phylogenetic relationships than hitherto suggested, and clearly in need of more detailed study. The two sub-Saharan African genera *Afrotheora* and *Antihepialus* are sister taxa supported by the presence of thick lateral lists along the ventral margin of the third abdominal tergite. This relationship was suggested by NIELSEN & SCOBLE (1986) based on the same character. It should be noted that similar lists occur in a few supposedly subordinate Hepialidae *s.str.*: not included in this study, such as the Indo-Australian genus *Aenetus* Herrich-Schäffer, 1855 (NIELSEN & SCOBLE 1986; SIMONSEN in press). Finally, Hepialidae *s.str.* are monophyletic as suggested by NIELSEN & SCOBLE (1986); SCOBLE (1992); KRISTENSEN (1998) supported by the hinged or synsclerotized connection between truelum and the ventral pseu-

doteguminal arms as identified by NIELSEN & SCOBLE (1986), although the truelum is membranous or absent in the Australian genus *Aenetus* (e.g. SIMONSEN in press).

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Electronic Supplement Files

at <http://www.senckenberg.de/arthropod-systematics>

File 1: simonsen&kristensen-neotheoridhepialoids-asp2017-electronicsupplement1.ss – Character matrix in NONA format.

File 2: simonsen&kristensen-neotheoridhepialoids-asp2017-electronicsupplement2.tre – TNT tree file containing the nine trees from the phylogenetic analysis

Zoobank registrations

at <http://zoobank.org>

Present article: <http://zoobank.org/urn:lsid:zoobank.org:pub:EC8672B4-9071-4B5B-89BD-2434424C957A>

Paratheaora Kristensen & Simonsen, 2017: <http://zoobank.org/urn:lsid:zoobank.org:act:E0EBB43A-CB44-4BB0-9AE5-0FE0719B1BAF>

Paratheaora speideli Kristensen & Simonsen, 2017: <http://zoobank.org/urn:lsid:zoobank.org:act:7F67C0DB-71A8-467C-93E7-CFDD826701C9>

Neotheora meyi Kristensen & Simonsen, 2017: <http://zoobank.org/urn:lsid:zoobank.org:act:1D031528-6F22-4588-9F01-ECB8D103D687>

Neotheora mielkeorum Kristensen & Simonsen, 2017: <http://zoobank.org/urn:lsid:zoobank.org:act:3282BBC4-2B1F-4E00-B4CB-876B1A593E60>

