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## A New Familia of Hepialoidea from South America, With Remarks on the Phylogeny of the Subordo Exoporia (Lepidoptera)

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The new familia *Neotheoridae* is erected for *Neotheora chiloides* n. gen., n. sp., described from a single female specimen from Matto Grosso, Brazil. The monophyly of the subordo Exoporia is demonstrated on the basis of five synapomorphies of its constituent superfamiliae. The monophyly of the superfamilia Hepialoidea is demonstrated on the basis of two or three synapomorphies of its constituent familiae. The status of the previously known hepialoid familiae is discussed and the Anomosetidae removed from synonymy with Prototheoridae. The primary dichotomy in the superfamilia probably lies between the Palaeosetidae and the remaining familiae together. The Neotheoridae is assigned to the Hepialoidea. Its sister-group is probably either the Prototheoridae or the Anomosetidae.

### 1. Introduction

The known diversity among the homoneurous Lepidoptera (the lowest grade within the order) in South America is strikingly small. Apart from the recently described Chilean species of Neopseustidae, *Apoplania chilensis* DAVIS, 1975, only representatives of the cosmopolitan familia Hepialidae have so far been known from this region. On the other hand, the Old World tropics and/or south temperate regions are inhabited by no less than nine homoneurous familiae (Micropterigidae, Agathiphagidae, Lophocoronidae, Neopseustidae, Mnesarchaeidae, Prototheoridae, Anomosetidae, Hepialidae and Palaeosetidae) and on the basis of present knowledge of lepidopteran age and Gondwanaland palaeogeography it may be safely assumed that a more diverse South American fauna of homoneurous moths will eventually be discovered.

Reported here is the discovery in southwestern Brazil of a new and systematically isolated hepialoid genus and species, which for the present is placed in a familia of its own. The description of the new taxon is based on a single specimen from the collections of the British Museum (Natural History). A critical review of available evidence on the monophyly of the subordo Exoporia and on the status and interrelationships of its constituent familiae is presented as a prerequisite for a meaningful discussion of the affinities of the new taxon, *Neotheoridae* n. fam.

### 2. Material and methods

The unique specimen representing the new taxon was somewhat defective. The distal parts of the antennae and most parts of the legs were missing, the left wing pair and the abdomen

(damaged in terga IV-VI and right ovipositor lobe) were broken off and stored (as were a few leg fragments) in gelatine capsules with the specimen.

For the comparative survey, informations from the literature were supplemented by original observations on *Mnesarchaea loxoscia* MEYRICK, 1888, *M. fusca* PHILPOTT, 1922, *M. paracosma* MEYRICK, 1885 and *M. acuta* PHILPOTT, 1929 (Mnesarchaeidae), *Prototheora petrosema* MEYRICK, 1917 (Prototheoridae), *Anomosos hylecoetes* TURNER, 1916 (Anomosetidae), *Ogygioses caliginosa* ISSIKI & STRINGER, 1932 (Palaeosetidae) and representatives of several genera of Hepialidae including the primitive *Fraus*<sup>1</sup> WALKER, 1856 (*Hectomanes* MEYRICK, 1890).

KOH-treated preparations were lightly stained in chlorazol black. For scanning electron microscopy of antennae and mouthparts preparations were freeze-dried after dehydrating through an ethanol-benzene series. Sections of scales for light and transmission electronmicroscopy were made after embedding wing fragments in epon. The light micrographs (except Figs. 5 and 13) were taken in interference contrast.

### 3. Description of the new taxon

*Neotheoridae*, nova familia for *Neotheora chiloides*, n. gen., n. sp. Female

**Caput:** Head-capsule as well as labium densely covered with long narrow scales (Figs. 2-4); most of these apically widened but some almost parallelsided, hairlike. Apical margin of widened scales usually with medial notch. Apex and base of scales whitish, middle zone brown. Scales inserted in a frontoclypeal group below the antennal bases and in a large dorsal group continuing posterolaterally as a narrow area along the margins of the compound eyes to the level of the mouth.

Dorsal surface of epicranium with a smoothly curved V-shaped suture, anteriorly extending to margin of compound eye just above the level of the antennal bases (Fig. 4). Sutura occipitalis absent. Sutura postoccipitalis particularly distinct along the upper lateral margins of the foramen occipitale, but obsolete along its upper middle margin; ventrally the suture continues to the level of the mouth.

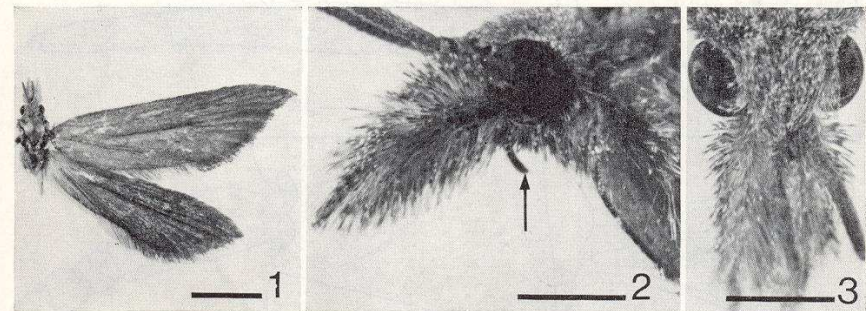


Fig. 1-3: *Neotheora chiloides* n. gen. n. sp. [Lepidoptera: Hepialoidea], holotype. 1 Dorsal. 2 Caput, lateral, arrow indicates proboscis. 3 Caput, dorsal. Scales: 1: 5 mm; 2-3: 1 mm.

<sup>1</sup> The species studied is the Australian pasture feeder generally known as *Fraus simulans* WALKER, 1856 (see HARDY 1973). This species does not have prominent proboscis remnants, present in some other *Fraus* species including what was called *simulans* by PHILPOTT (1927). A taxonomic revision of this primitive and apparently diverse genus is obviously needed.

Galeal proboscis relatively stout, its length only slightly less than long axis of head-capsule. In the intact dried specimen (Fig. 2) it was held in a slightly curved position; it is almost certainly not capable of spiral coiling in the living animal. Lateral galeal surface apparently entirely soft-walled, with scattered delicate microtrichia. Dorsal galeal surface densely covered with long and spinelike, somewhat pigmented microtrichia. Similar formations present along ventral margin of food-groove, constituting together with the most medial dorsal spines the linking apparatus of the two proboscis halves. Food-groove proper, i.e., concave medial galeal surface, not divided into discrete plates; microtrichial spines present in food-groove, mostly arranged in pairs with common base (Fig. 8), shortened and simple near apex.

Postlabium an arched plate, praelabium bilobed; ligula/hypopharynx territory bearing salivary orifice entirely reduced. Palpi labiales very prominent, three-segmented, about twice the length of the head-capsule; apical segment longer than two basal segments together (Fig. 4). No patch of sensillae («Basalfleck») on proximal segment and no invaginated group of sensillae («von Rath's organ») on distal segment.

Thorax and Pedes: Pro- and mesonotum as well as tegulae with dense scale-covering similar to that of caput. Anterior portion of metascutum (to level of anterior scutellar apex) taken up by microtrichia-field of wing-locking device (COMMON 1969, KUYTEN 1974), otherwise naked; posterior part of metanotum with long hairs. Ventrolateral surfaces of thorax with covering (poorly preserved) of scales and hairs.

The legs are very incomplete in the unique specimen, all being broken beyond the trochanter except one hind leg which is broken in the tibia. Three of the leg fragments were preserved: a profemur-tibia, a fragment carrying two pairs of spurs and therefore probably (by analogy with conditions in other primitive hepialoids) the distal part of a metatibia, and finally a tarsus-praetarsus not with certainty referable to segment.

Profemur-tibia with a smooth scale-covering and a series of moderately strong «spines» on one side of the tibia; at tibial apex such spines have apparently been arranged in a short transverse row (judging from the presence of conspicuous sockets). Tibia apically widened. Epiphysis well developed.

Least-damaged P-III with smooth scale-covering and series of long and slender spines dorsally and ventrally on the proximal tibial remnant (there are no spurs on the latter). Spines darker, but less prominent (or less well preserved) on supposed distal metatibial fragment. If the latter is correctly identified, then tibia is more than 2.1 times longer than the femur.

Praetarsus (Figs. 10–11) with prominent pseudempodial<sup>2</sup> seta on elevated base. Ungues, arolium and fringed pulvilli unspecialized. Unguitractor plate with dense patch of short, stout microtrichia distal to pulvillar base.

Alae: Both wing pairs with apex distinctly produced and termen concave (Fig. 12). Praeala with Sc forked.  $S_3^3$  reaching termen just below apex. Cross-vein S-M connecting basal part of  $S_4$  with first primary medial branch immediately proximal to  $M_1/M_2$  furcation at level of inter-M cross-vein. Neither  $S_2/S_3$  nor  $M_1/M_2$  therefore «stalked». First principal median branch weak although distinctly discernible, tracheated at least basally (but  $M_1$  and  $M_2$  supplied from S-trachea via S-M cross-vein). M-Cu cross-vein originating on  $M_3$  far proximad to inter-M cross-vein. P very weak, connected by crossveins to both the M/Cu stem and the well-developed E, but vanishing a short distance beyond this cross-vein. Vein A single, extremely weakly demarcated but continued to margin, basally vanishing completely near the level of the P-E cross-vein; trachea of A (double, slender) branching off from stout E-trachea at this level. A basal trachea, unaccompanied by modifications in the surrounding cuticle, bends backwards before reaching A.

<sup>2</sup> Since empodium in general entomological usage refers to a bristle-like process of the unguitractor plate (SNODGRASS 1935, VON KÉLER 1955) the term pseudempodium (DEBAIZIEUX 1935) is preferable for the dorsal formation characteristic of the Lepidoptera-Trichoptera complex.

<sup>3</sup> In acceptance of HAMILTON's (1971–72) interpretations of the basic pterygote venation, the veins usually termed «radius sectors» ( $R_s$  or  $R_2-R_3$ ) are here considered an independent, primarily four-branched, vein system, «sector» (S). HAMILTON's terminology of the post-cubital veins viz., «plica» (P), «empusa» (E), and «anals» (A) is likewise adopted.

A short reinforcement line («sutura laterofacialis») present along frontoclypeal margin, lateral of pretentorial pit to antennal level.

Phragma ocularis with distinctly pigmented zone along margins of central aperture.

Tentorium with well-developed dorsal arms (appearing foreshortened in the ventral view shown in Fig. 4). The portion of each anterior arm lying in front of dorsal arm origin markedly swollen, pretentorial pits correspondingly large. Anterior arm just behind swollen portion with small ventral process (most probably the tendon of a stipital muscle). Posterior arms and corporotentorium short, posteromedian process well developed.

Compound eyes anteriorly separated by a distance subequal to their greatest diameter. Ocelli absent.

Antennal base articulating with an upper and a lower cranial condyle, the last-mentioned most distinctly developed.

Antennae simple, filiform. Scapus and pedicellus entirely covered with scales. Intercalary sclerite between scapus and pedicellus tongue-shaped, lowered into lumen of scapus (Fig. 5). Flagellum with dense covering of long and slender microtrichia (non-articulate nature of these confirmed in scanning electron micrographs, Fig. 7). Microtrichia on dorsal flagellar surface overlaid by slender scales not forming a complete covering (Fig. 6). Total length of flagellum unknown, both antennae being broken (14 segments present in longest fragment).

Labrum not externally delimited. Mandibulae exceedingly small, almost indiscernible as differentiations in body wall, but adductor apodeme from inner margin distinct.

Cardo maxillaris a small, arched, moderately sclerotized plate, visible laterad of praelabial base. Stipes soft-walled and, in situ, largely concealed above the praelabium. Palpus maxillaris short, most probably two-segmented, but segmental limit difficult to trace. A suboval sclerotization present proximally on area interpreted as basal palp segment. Lateral surface of distal palp segment very slightly sclerotized (Figs. 4, 9).

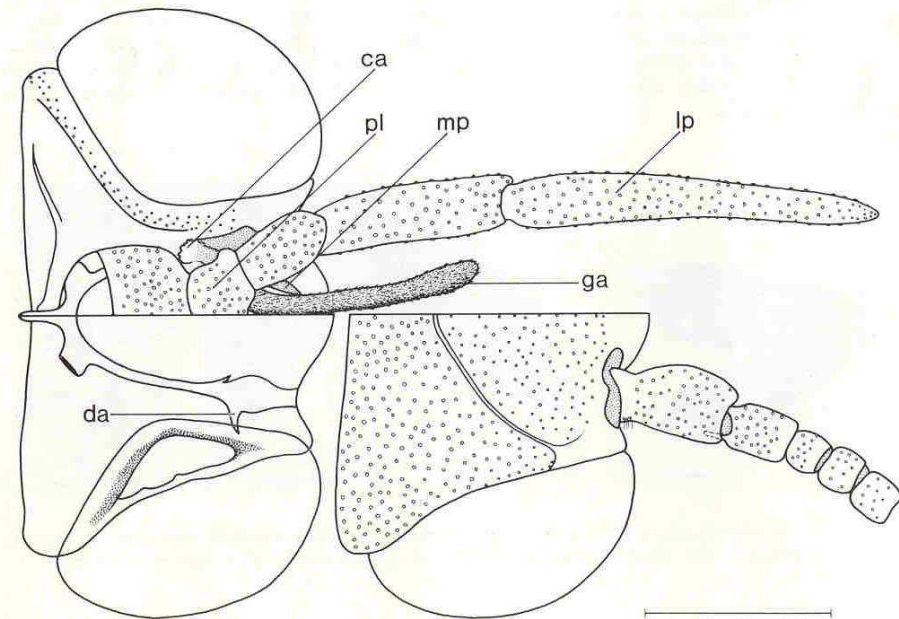


Fig. 4: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea], head. Upper left: ventral, lower left: endoskeleton, right: dorsal; ca cardo, da dorsal tentorial arm, ga galea, mp palpus maxillaris, lp palpus labialis, pl lobus praelabialis. Scale 0,5 mm.

Postala venation essentially similar to that of praeala. No trace of Sc furcation. First principal branch of M practically indiscernible, untracheated.

Both wing-pairs devoid of microtrichia («aculeae») on wing surface proper (Fig. 14). Dorsally on fore wing scattered, slender microtrichia present basad to the humeral veinlet; on the ventral surface a larger and denser patch of stouter microtrichia present in same area. Wing-locking microtrichial field rather small. Hind wing with small patch of microtrichia dorsally on jugum.

Forewing jugal lobe prominent, without ventral spines. Hind wing with close-set and long, but weak frenular hairs, not differentiated from the more distal costal hairs.

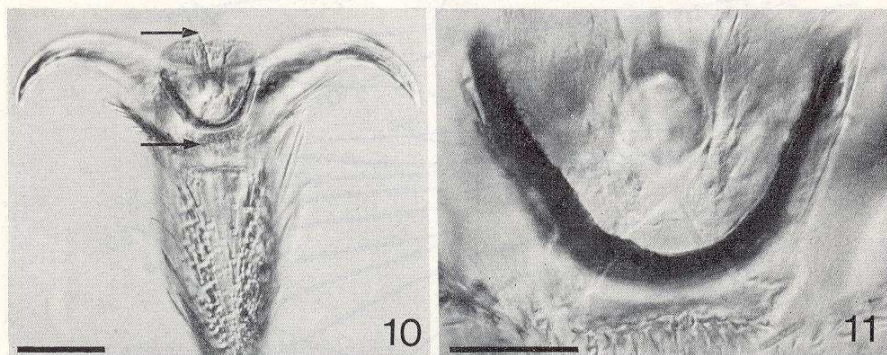


Fig. 10–11: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea], praetarsus. 10 Ventral, arrows indicate pseudempodial setae and spiny area between pulvilli. 11 Magnification of pseudempodial base, arolium base and spiny area. Scales: 10: 100  $\mu$ m; 11: 40  $\mu$ m.

Scale covering (Figs. 13–19) of both wing pairs two-layered, upper layer almost completely concealing lower layer. Scales of upper layer (Fig. 15) almost parallel-sided in distal part, with scalloped apical borders. The scales are pigmented and of «normal type» (see section 4.3). A weak differentiation into primary and secondary ridges (terminology of Kristensen, in pressa) is evident in the distal parts of the scales. These parts moreover show a more or less regular longitudinal alteration of areas in which the bottoms of the inter-ridge channels (terminology of DOWNEY & ALLYN 1975) are close to the lower wall and areas where they are widely separated from the latter (Figs. 13, 16). The secondary ridges are located on the lastmentioned areas which appear as weak «second order» ridges (KRISTENSEN, in pressa). Basally the secondary and second order ridge pattern disappears. Obverse surface with distinct scutes and lateral fluting on the longitudinal ridges. Inter-ridge areas with close-set windows, septa between adjacent windows traversed by one or two medially thickened transverse flutes. Occasionally no window is formed between transverse flutes (Fig. 16). Reverse surface with ridges and fluting in peripheral areas only; perforations by a few irregularly scattered small pores.

Scales of lower layer (Fig. 17) smaller, rounded, with less distinct apical scalloping. They are unpigmented and of the «primitive type». No lumen present even under the ridges (Fig. 18). Longitudinal ridges of obverse surface low, with distinct scutes. Interridge areas (Fig. 19) with close-set transverse fluting and no perforations.

**Praeabdomen:** Basal articulation of abdomen damaged. Tergum largely soft-walled with marginal sclerotized rim, interrupted posteromedially. Tergum II with distinct antecosta and lateral ridges which anterolaterally are complexly united with apodeme-bearing process from the hind corners of tergum I. Tergum III and following without lateral ridges. Pleural membranes II–VI with single subdorsal rounded «tuberculate plate» behind spiracles (Fig. 22); similar but less distinct formation present below spiracle III.

Similar structures have been found in some other homoneurous Lepidoptera (KRISTENSEN unpublished). In *Micropterix* plates corresponding topographically to the distinct series in

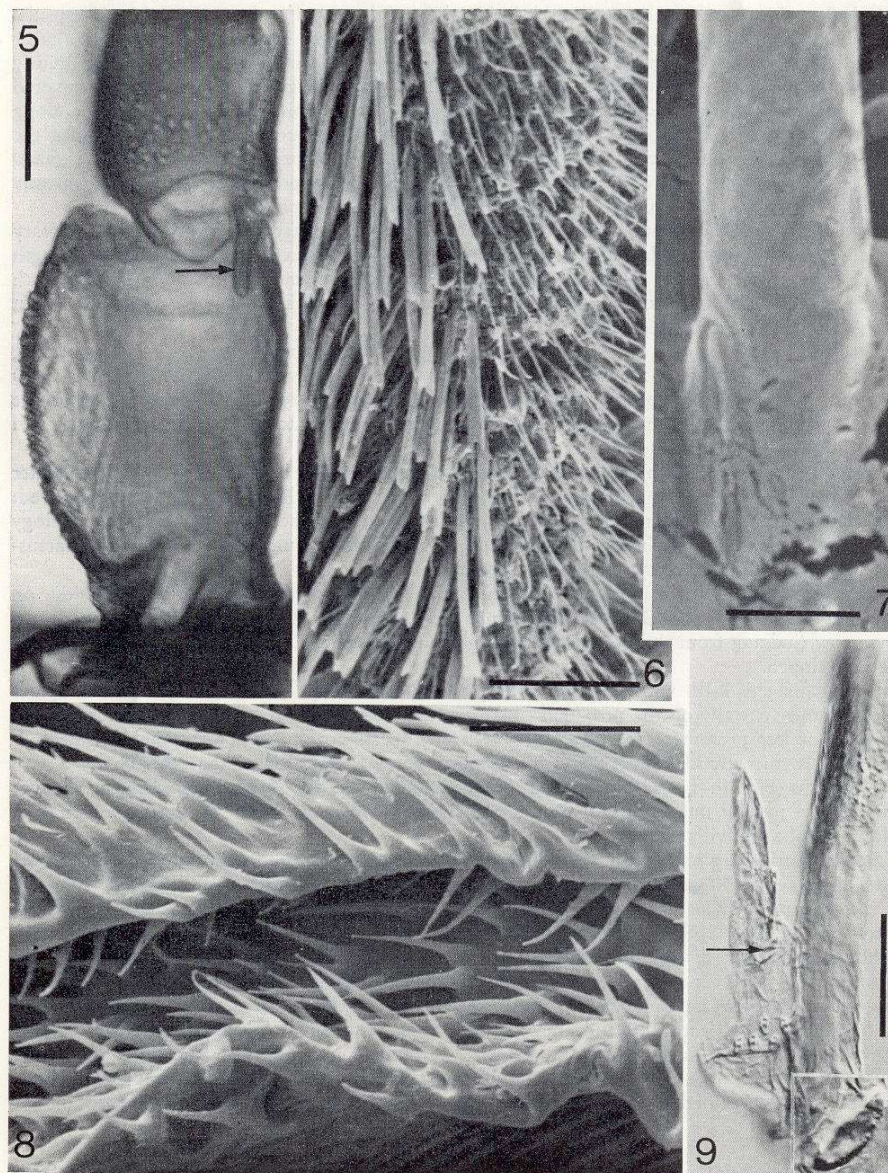


Fig. 5–9: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea]. 5 Antennal scapus/pedicellus showing elongate intercalary sclerite (arrow). 6 Antennal flagellum, dorsal side left. 7 Base of flagellar microtrichium. 8 Galea, medial. 9 Maxilla. Arrow indicates oval sclerite on basal palpus segment, shown at greater magnification at lower right (inset). Scales: 5–6, 9: 100  $\mu$ m; 7: 2  $\mu$ m; 8: 20  $\mu$ m.

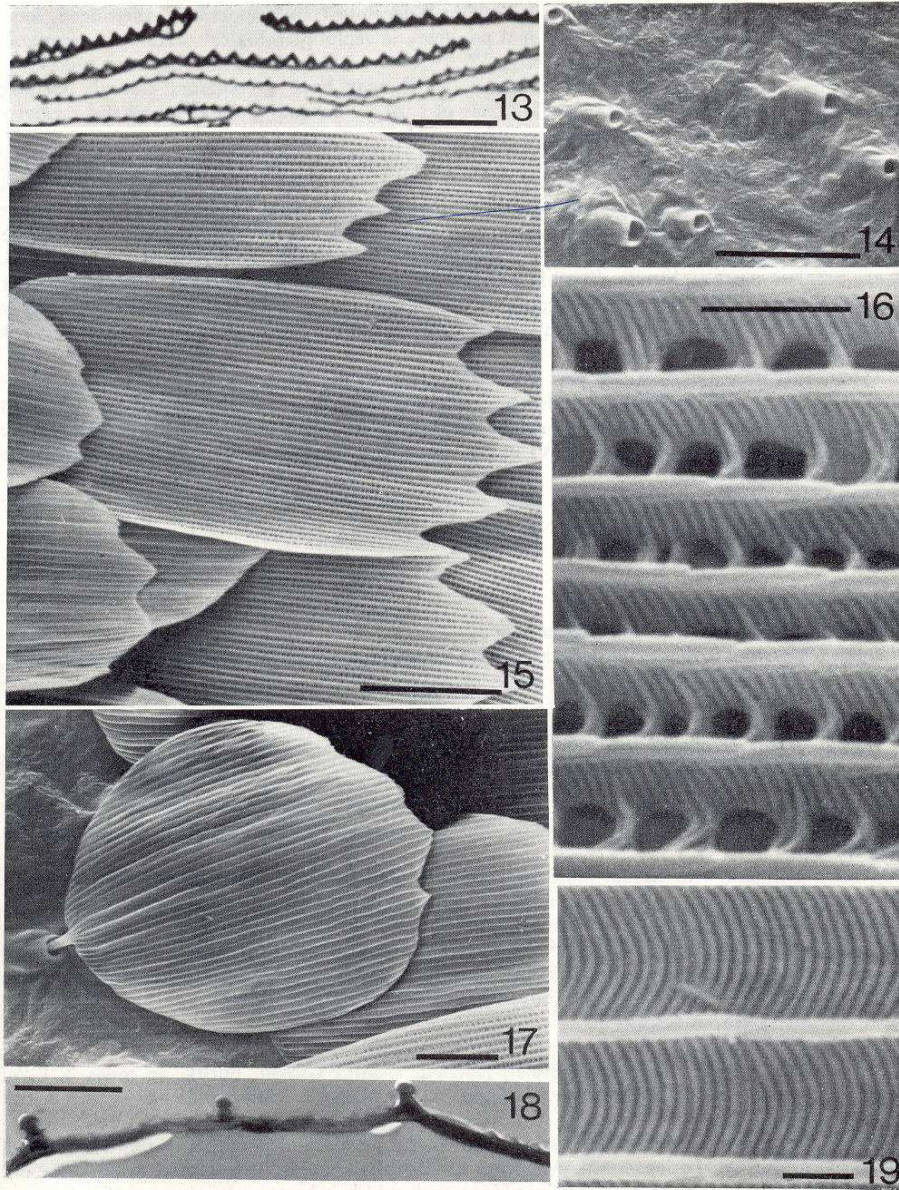


Fig. 13-19: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea], wing and scale structure. 13 Cross section of forewing scales outside M-Cu crossvein. 14 Descaled forewing surface. 15 «Normal type» forewing scales (apices of some «primitive type» scales visible to left). 16 Hindwing «normal type» scale, detail. 17 «Primitive type» forewing scale. 18 «Primitive type» scale, cross section (transmission electron micrograph). 19 «Primitive type» scale, detail. Scales: 13: 10  $\mu\text{m}$ ; 14-15: 40  $\mu\text{m}$ ; 16: 2  $\mu\text{m}$ ; 17: 20  $\mu\text{m}$ ; 18-19: 1  $\mu\text{m}$ .

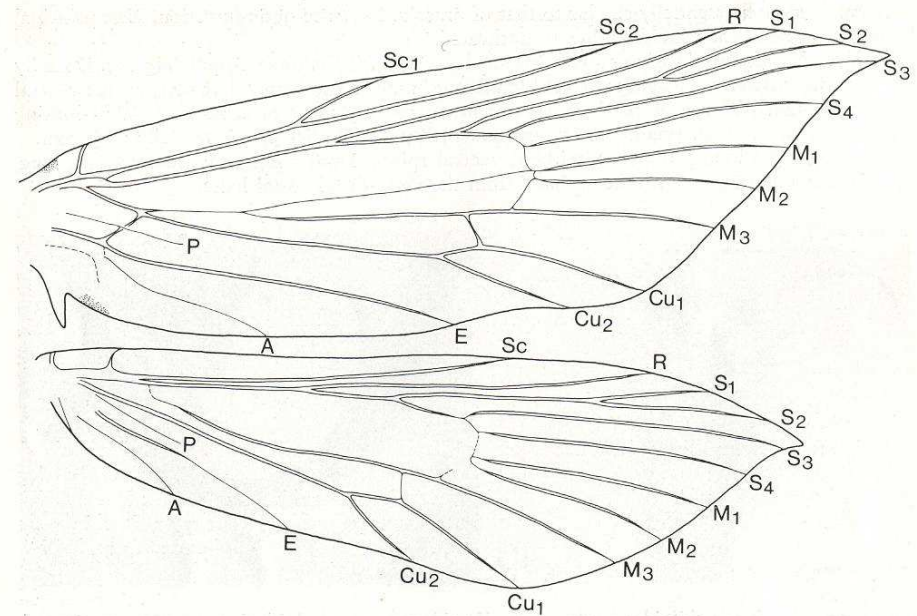


Fig. 12: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea] wing venation. A analis, Cu cubitus, E empusa, M media, P plica, R radius, S sector, Sc subcosta.

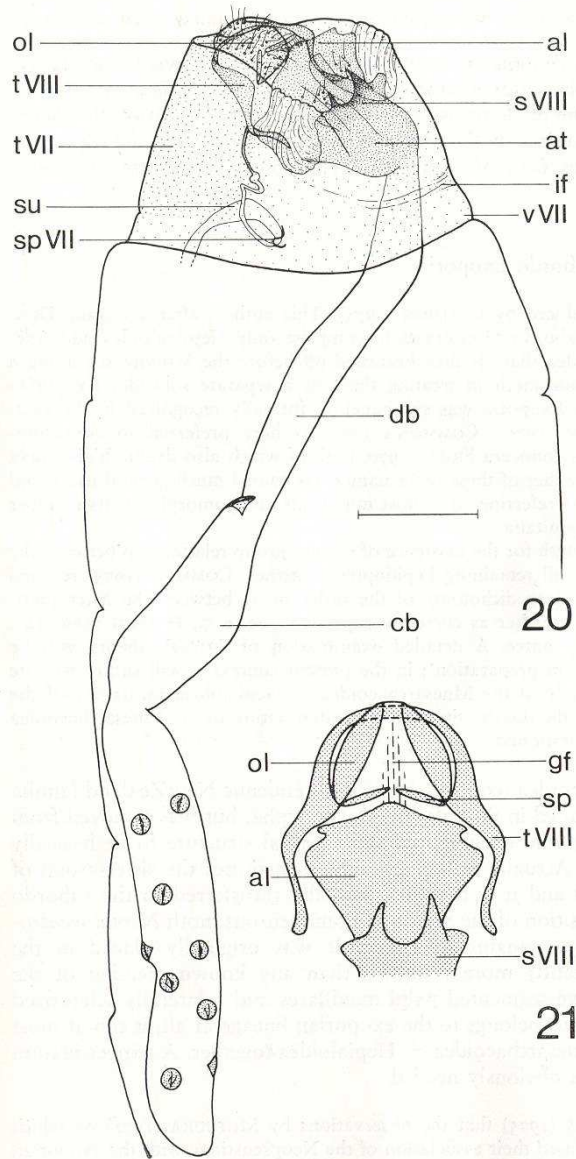
*Neotheora* (i. e., postspiracular subdorsals) serve the attachment of chordotonal organs whereas in *Eriocrania* the homologous plates serve the attachment of the spiracular opening ligaments. The functional significance in other cases remains unknown.

Female Postabdomen and Genitalia: (Figs. 20-24). The hindmost unmodified segment is VI. Segment VII with normal tergum and well-developed spiracle. Tergum VIII represented by a medially narrowed sclerotized band, its anterior corners produced into a pair of curved, ventrally directed apophyses; it is completely retractible below tergum VII. Intersegmental membrane VII/VIII in pleural region forming deep pockets with strongly folded walls around the aforementioned apophyses of tergum VIII.

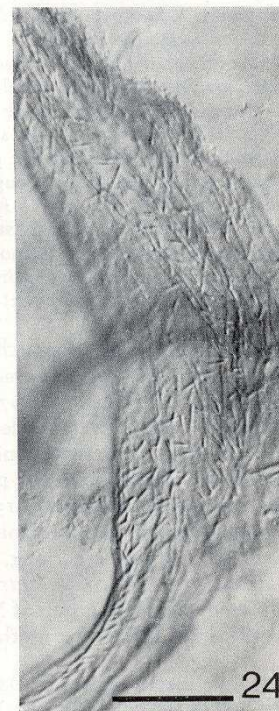
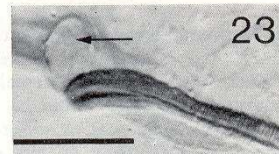
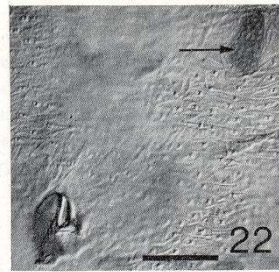
Behind sternum VI is a short (less than half the length of tergum VII) unsclerotized area delimited posteriorly by close-set integumental folds (if) vanishing in the pleural membrane. Some distance behind these folds is a sclerotized plate, SVIII, with a prominent bifurcated postero-medial process; lateralmost portions of SVIII concealed in shallow folds formed by the lowermost margins of the intersegmental pleural pockets. SVIII is followed by the antevaginal lamella, SIX, a sclerite forming the lower lip of the copulatory orifice.

No trace of spiracle VIII identifiable.

A morphological interpretation of the ventral region behind sternum VII is difficult. Sclerite SVIII might be considered sternum VII because its posterior margin is approximately on line with that of tergum VII. However, an alternative interpretation is preferred here, viz., that SVIII represents the eighth sternum; accordingly, the folds (if) should demarcate the ventral intersegmental limit VII/VIII and the antevaginal lamella should be formed by (at least the anterior part of) sternum IX. This is well in accordance with the above-mentioned location of the lateral parts of SVIII in relation to the lower ends of the dorsal intersegmental furrow VII/VIII and is also in accordance with the interpretation chosen below (section 4.2) for the hepialoid female genitalia in general.



of genital segments, posteroventral, diagram. 22 Pleural membrane V showing tuberculate plate (arrow) behind spiracle. 23 Thickwalled ductus spermathecae and swelling (arrow). 24 Utriculus. al lamella antevaginalis, at antrum, cb corpus bursae, db ductus bursae, gf folded genito-anal field, if integumental folds, ol ovipositor lobe, s VIII sternum VIII, sp subanal plate, sp VII spiracle VII, su utriculus spermathecae, TVII, VIII tergum VII and VIII, vVII venter VII. Scales 21: 1 mm, 22: 200  $\mu$ m, 23-24: 100  $\mu$ m.



Abdomen dorsally terminating in a pair of well-developed and moderately sclerotized, seta-bearing lobes («ovipositor lobes» or «anal papillae» in lepidopterological taxonomic terminology), probably containing elements of terga IX + X. The membranous area between and below these lobes contains the anus and oviporus (which may have a common, cloacal, opening although this could not be ascertained). A pair of narrow «subanal plates» (sp) extend medially from the lower corners of the ovipositor lobes.

Under lip of copulatory orifice formed by a membranous, longitudinally folded area belonging to venter IX-X (gf, Fig. 21). It is conceivable that folds in this area form a gutter through which the sperm are conveyed to the ovipore, but details cannot be made out from the whole-mount preparation. Copulatory sinus incompletely partitioned by a pair of longitudinal ridges on the lamella antevaginalis. Antrum wide, funnel-shaped, its walls densely granulate. Bursa copulatrix long, tubular, topographically divisible into a proximal ductus and a distal, somewhat wider corpus. Bursal intima with ornamentation of small, serrate, scale-like formations, particularly close-set in ductal part. Corpus with conspicuous sclerotized signa: circular plates bearing a pointed crest.

Ductus receptaculi in proximal part with a thin-walled and a thick-walled compartment, opening into a small swelling (Fig. 23) and then continuing as a simple tube which eventually widens to an elongate saccular utriculus the apical termination of which was not distinctly observable (probably damaged as are terga IV-VI in the specimen). Utriculus with numerous needle-like spines in intima (Fig. 24).

Details of rectum and oviduct not observable in the preparation. Also no trace of accessory glands identified; most probably they are absent.

Male unknown.

#### *Neotheora*, nov. gen.

Characters as described for the familia above.

(The generic name is chosen for similarity with the generic names in the familia Prototheoridae, the prefix indicating the New World origin of the taxon).

Generis species typica: *Neotheora chiloides* n. spec. (Fig. 1).

Forewing length 18 mm. Palpi labiales slightly drooping, including scalevestiture projecting beyond compound eyes by almost three times (2.8) the diameter of the latter; length ratio of palp segments proper about 1:1.4:4. Forewing upperside light brown, gradually darkening towards the termen; hindwing upperside and undersides of both wing pairs darker, greyish brown.

Female genitalia with sternal plate SVII smooth, indistinctly delimited anteriorly; prongs of posteromedian process about the length of plate proper, pointed and slightly asymmetrical. Lamella antevaginalis strongly sclerotized, posterior part with rounded incision in lateral margin. Two paramedial patches of scattered long setae on anterior part of lamella. The slightly produced median part of the hind margin with patch of shorter, but stouter setae. Bursa copulatrix with nine signa (see generic description) in distal (anterior) parts of corpus and a tenth located near the ductus/corpus transition.

Life history unknown.

Specimen data: Holotypus. Brazil, labelled. «Matto Grosso, Burity, 30 miles N.E. of Cuyabá, 2250 ft., 20-30. IX. (19) 27. At light. C. L. Collenette». Slideseries no. 12311. British Museum (Nat, Hist.).

Additional material of this new taxon is obviously needed and particularly the discovery of male specimens will be important. Attention should be drawn to its potential presence in unsorted materials of larger Pyralidae-Crambinae with which it bears a definite superficial resemblance (cf. the specific name; *Chilo* ZINCKEN 1817, a familiar genus of Crambinae).

Fig. 20-24: *Neotheora chiloides* n. gen., n. sp. [Lepidoptera: Hepialoidea], female abdominal and genital structures. 20 Holotype preparation, left lateral view; genital segments in oblique posterior view, contours of sclerites sp (visible behind ovipositor lobe) reinforced. 21 Sclerites

#### 4. Discussion

In general facies *Neotheora chiloides* is unlike any previously known homoneurous moth and the sum of its morphological characteristics confirms its status as an isolated taxon. Before an attempt can be made to assess the phylogenetic position of *Neotheora* it will be necessary to evaluate critically the available evidence concerning the status and interrelationships of the higher taxa of exoporian Lepidoptera which are at present largely typologically defined.

##### 4.1. The monophyly of the subordo Exoporia

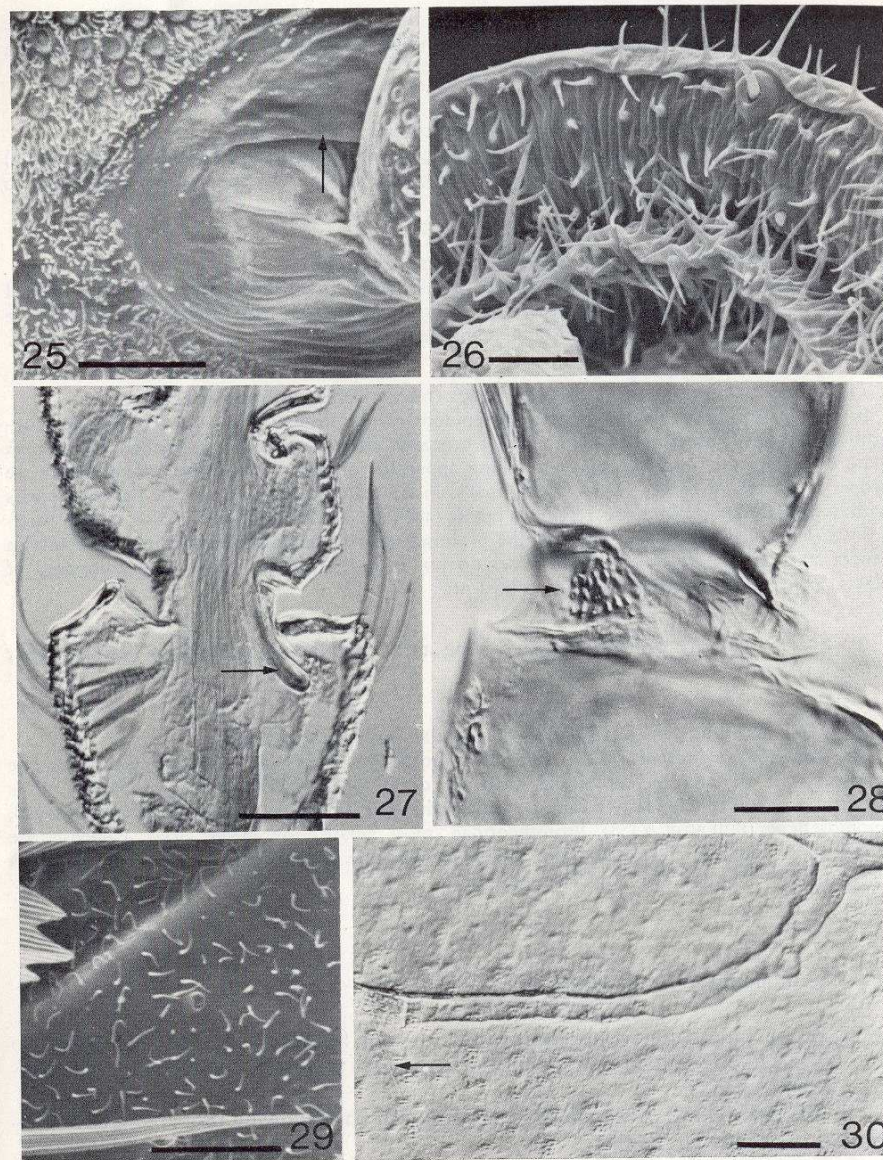
The name Exoporia was introduced by COMMON (1975). This author, after accepting DUGDALE'S (1974) restriction of the subordo Monotrysia to comprise only Nepticuloidea and Adeuloidea, stated about the Hepialoidea that «If they branched off before the Monotrysia, along a separate line, there would be some merit in treating them as a separate suborder Exoporia» (COMMON 1975: 196). A subordo Exoporia was subsequently formally recognized in the catalogue by KARSHOLT & NIELSEN (1976). COMMON'S name is here preferred to Aplostomatoptera KIRIAKOFF 1948, and Gymnocera FRIESE 1970, both of which also denote higher taxa centered round the Hepialidae. Neither of these older names has gained much general usage and Exoporia has the didactic value of referring to a most important autapomorphy of its member taxa, viz., the exoporian female genitalia.

FRIESE (1970) argues at some length for the existence of a sister-group relationship between the Hepialoidea (his Gymnocera) and all remaining Lepidoptera together. COMMON (1975) rejected FRIESE'S theory, assuming the primary dichotomy of the order to be between the Micropterigoidea and all remaining groups together as currently supposed (see, e.g., HENNIG 1966: 227, 1969), and with this view I fully agree. A detailed examination of FRIESE'S theory will be presented elsewhere (KRISTENSEN, in preparation); in the present context it will suffice to note that the evidence for the monophyly of the Mnesarchaeoidea + Hepialoidea forms one of the main bodies of arguments against the theory, since the glossatan nature of the Mnesarchaeoidea has never been (and cannot be) questioned.

The superfamilia Mnesarchaeoidea (comprising only the endemic New Zealand familia Mnesarchaeidae) has been included in the subordo Dacnonypha, but was removed from this group by DUGDALE (1974) who showed its female genital structure to be basically similar to that of Hepialoidea. Actually it very probably constitutes the sister-group of the last-mentioned superfamily and it is herewith formally transferred to the subordo Exoporia. The phylogenetic position of the Szechuan homoneurous moth *Nematocentropus omeiensis* CHI-LING, 1965, remains uncertain. It was originally placed in the Mnesarchaeidae but is significantly more primitive than any known member of the Exoporia, having, e.g., long, five-segmented palpi maxillares and a laterally sclerotized «aedeagus». If *Nematocentropus* belongs to the exoporian lineage at all, it can at most represent the sister-group of Mnesarchaeoidea + Hepialoidea together. A reinvestigation of this most interesting moth is obviously needed.

It was recently shown by DAVIS (1975) that the observations by MUTUURA (1972) on which this author and DUGDALE (1974) based their association of the Neopseustidae with the exoporian groups are erroneous. The Neopseustidae have monotrysonian ♀♀ with ventral oviduct.

Fig. 25–30: Structural details of homoneurous Lepidoptera. 25–26 *Mnesarchaea acuta* PHILPOTT, 1929 [Exoporia: Mnesarchaeidae]. 25 Left antennal base showing dorsal cranial condyle (arrow). 26 Galea, medial. 27 *Alphus sylvinus* (LINNAEUS, 1761) (Hepialidae). Longitudinal sec-



tion of scapus/pedicellus showing intercalary sclerite (arrow). 28 *Ogygioses caliginosa* ISSIKI & STRINGER, 1932 (Palaeosetidae). Scapus/pedicellus transition showing intercalary sclerite (arrow). 29 *Prototheora petrosema* MEYRICK, 1917 (Prototheoridae). Descaled forewing surface. 30 *Agathiphaga vitienses* DUMBLETON, 1952 (Agathiphagidae). Forewing anal loop with trace of free  $A_1$  (arrow). Scales: 25, 29: 40  $\mu\text{m}$ ; 26: 10  $\mu\text{m}$ ; 27, 30: 100  $\mu\text{m}$ ; 28: 20  $\mu\text{m}$ .

The monophyly of the subordo Exoporia is indicated by the following probable synapomorphies of its constituent superfamiliae Mnesarchaeoidea and Hepialoidea (see table 1 and Fig. 31):

(1) Exoporian female genitalia (DUGDALE 1974).

The copulatory orifice and oviporus are separate, no internal communication (in ground plan) between bursa copulatrix and other parts of the genital system. Oviductus communis dorsal to bursa. Accessory glands absent.

(2) Dicondyloous articulation of antennal base (Fig. 25).

A more or less distinct dorsal cranial condyle is present in addition to the primitive ventral one. This unusual feature was first described (KRISTENSEN 1968 a) from *Mnesarchaea*, and I have now found it also in members of all familiae of Hepialoidea.

(3) Galeal proboscis with cuticular spines (microtrichia) on medial surface.

In the most primitive proboscis-bearing Lepidoptera, the Eriocraniidae, the wall of the food-groove is divided into discrete plates. Spiny processes from the lower anterior margin of each plate constitute the ventral proboscis linking apparatus of the proboscis but the food-groove proper is devoid of spines (KRISTENSEN 1968). In the Mnesarchaeidae the food-groove plates with ventral linking-spines are retained, but in addition spines are present also in the food-groove (Fig. 26). Most hepialoids have the proboscis greatly reduced. The distinct remnants in genera such as *Prototheora* and *Anomoses* do not have the median galeal wall composed of plates, but a dense covering of spines is present.

(4) Scales on more or less extensive wing areas with secondary ridges (KRISTENSEN, in pressa).

(5) Male genitalia without sclerotized tubular intromittent organ.

The gonopore is located on the apex of a protuberance with a ventral sclerotization, the «trulleum» or (if laterally continuous with the dorsal parts of IX/X) «suspensorium». It is apparent from available descriptions of Mnesarchaeidae (most detailed by PHILPOTT 1927 a), Anomosetidae (PHILPOTT 1928), Prototheoridae (most detailed by JANSE 1942), Palaeosetidae (EYER 1925, ISSIKI & STRINGER 1932) and Hepialidae (e.g., PHILPOTT 1927 b, BIRKET-SMITH 1974) that all share this aberrant basic pattern.

#### 4.2. The monophyly of the Hepialoidea

Within the superfamiliae Hepialoidea three or four familiae have been recognized so far, viz., the Anomosetidae (often included in the next familia), Prototheoridae, Hepialidae and Palaeosetidae.

The monophyly of the Hepialoidea is indicated by the following probable synapomorphies of its constituent familiae:

(6) Backwards displacement of posterior fork of sector;  $S_3$  ( $R_4$  auct.) reaching termen, not costa.

In other homoneurous Lepidoptera all branches of sector reach the costa or  $S_4$  only reaches the termen (or apex) (see e.g. ISSIKI 1931, COMMON 1973, DAVIS 1975). The specialized condition in Hepialoidea is evident from figures given by e.g. TURNER (1922), PHILPOTT (1926, 1928) and ISSIKI & STRINGER (1932) but has apparently passed unnoticed.

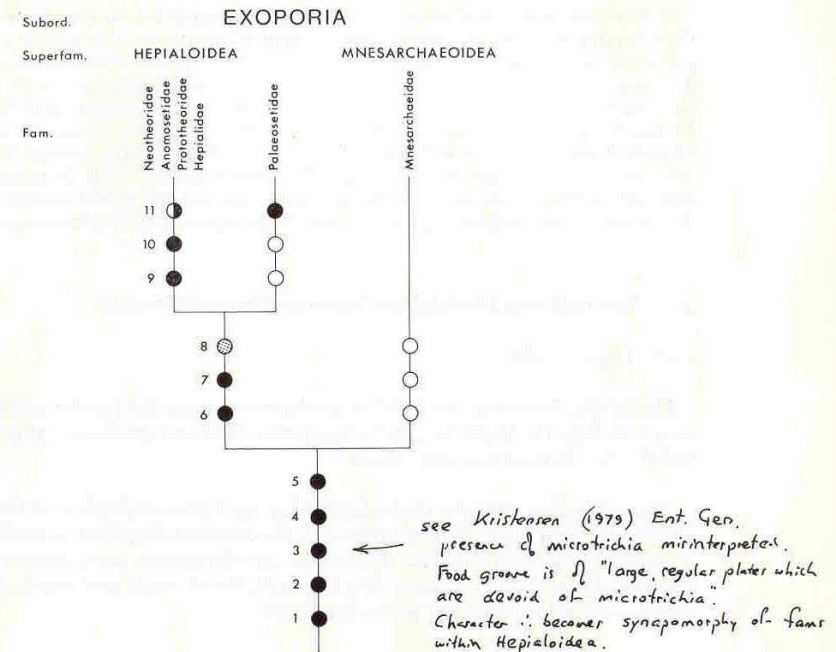


Fig. 31: Cladogram demonstrating the monophyly and primary divisions of the subordo Exoporia [Lepidoptera]. Autapomorphies of individual familiae not indicated. Character numbers refer to main treatment in text and table 1, where further information is given. Symbols: filled circles: apomorphies; open circles: plesiomorphies; shaded circle: apomorphy doubtfully present in ground plan; half-filled circle: apomorphy present in some members, but not in ground plan.

(7) Reduction of maxillary appendages.

Palpus always very short (absent in all Palaeosetidae), its segmentation more or less indistinct. Proboscis probably never coillable, its length less than length of head capsule (in Palaeosetidae and many Hepialidae the proboscis is completely reduced).

ROBINSON (1977: 108) stated that the palpus in the hepialid genus *Zenophassus* TINDALE 1941 has as many as five segments (cf. TINDALE 1941) but he later informed me (in litt.) that he believes apparent segmentation in the palpi maxillares of Hepialidae to be largely due to preparation artefacts.

The following character is of doubtful significance:

(8) Female with specialized sperm transport tract on genital segments.

According to DUGDALE (1974), female Hepialoidea are characterized by having a seminal gutter (or closed tubular canal) between the copulatory and ovipository orifices of their exoporian genital system, whereas in the Mnesarchaeoidea there is a simpler type of communication between the orifices, in that they can be directly opposed against each other. However, DUGDALE did not examine members of Prototheoridae s. str., and from my own observations on female *Prototheora* I find it unlikely that a conclusive demonstration of a connective tract between the orifices can be made at all on the available dried museum material.

In this context it should be noted that there is disagreement on the segmental assignment of the ventral sclerites in the female genital region of hepialoids. The sclerite forming the lower lip of the copulatory orifice, the so-called lamella antevaginalis (BOURGOGNE 1949a, b), was by TINDALE (1941), MUTUURA (1972), DUGDALE (1974) and MATSUDA (1976) considered to be sternum VIII. Alternatively the lamella antevaginalis has been interpreted as belonging to venter IX and I find the evidence for this view (BOURGOGNE 1949b) strong: In some members of *Hepialus* there is a distinct plate (probably a sternum VIII) between sternum VII and the lamella antevaginalis. Moreover, in those hepialoids where spiracle VIII is retained, it is located distinctly in front of the lamella. The paired sclerites (subanal plates) usually present laterad to the oviporus most probably belong to venter X as supposed by BÖRNER (1939).

#### 4.3. The familiae of Hepialoidea: Status and interrelationships

##### 4.3.1. Hepialidae

Hepialidae STEPHENS, 1828, is by far the most successful familia within the homoneurous Lepidoptera. About 80 genera<sup>4</sup> and more than 500 species are at present recognized and the distribution is cosmopolitan.

The only autapomorphy of the hepialid ground plan established so far is the complete absence of tibial spurs. In most hepialids the antennal flagellum is modified in one way or another (segments angulate, dentate, bi- or tripectinate, see COMMON 1970) but some genera do have simple antennae (VIETTE 1948, PACLT 1953) and this probably represents the plesiomorphic condition within the familia.

##### 4.3.2. Prototheoridae

Prototheoridae MEYRICK, 1917 comprises two very closely related South African genera *Prototheora* MEYRICK, 1917 (5 species) and *Metatheora* MEYRICK, 1919 (2 species). Being phenetically (JANSE 1942) as well as zoogeographically a «compact» group its monophyly has not been questioned although the diagnostic features by which it is currently separated from the Hepialidae are admittedly plesiomorphies. However its derived features 14–15 (section 4.4.3.) do indicate, that it is not paraphyletic in terms of the hepialids.

##### 4.3.3. Anomosetidae

Anomosetidae TURNER, 1922 contains only the monobasic Australian genus *Anomoses* TURNER, 1916. This taxon differs from other previously known Hepialoidea in the characters 17–20 (section 4.4.4.) and its autapomorphies are enumerated by KRISTENSEN (in press b).

The Anomosetidae and the Prototheoridae have been considered the most overall primitive hepialoids. The two familiae were synonymized by PHILPOTT (1928) and although TURNER retained the separation in his 1947 review, PHILPOTT'S view has been adopted in the more influential modern treatises (BOURGOGNE 1951, REMINGTON 1954,

<sup>4</sup> PACLT (1953) questioned the justification of several of the more recent generic divisions.

COMMON 1970). However, no certain synapomorphies of the two groups have hitherto been demonstrated. PHILPOTT referred exclusively to the retention in both of some plesiomorphies, viz., the forked Sc (now known to be a more widespread condition in hepialoids), the simple antennae (also now known to occur in the other hepialoid familiae as well) and the tibial spur complement 0–2–4.

Further plesiomorphies attributed to Prototheoridae s. lat. are the retention of (minute) ocelli and of frenulum bristles (COMMON 1970). I have failed to find ocelli in *Anomoses* and *Prototheora petrosema*, though they were reported present by MEYRICK in his original description of the genus *Prototheora* (of which *P. petrosema* is the type). I have found no noteworthy difference in the development of the frenulum in *Anomoses*, *Prototheora* and *Fraus*; in all cases are the hairs soft and not differentiated from those of the costa.

It has been stated that the Prototheoridae s. lat. have only basal aculeae on the wings (COMMON 1970). This is certainly an apomorphic condition within the homoneurous Lepidoptera, but I find that it applies only to *Anomoses*; *Prototheora* has a normal covering of aculeae on the main surface of the wings (fig. 29).

There is thus no evidence at all that the Prototheoridae + Anomosetidae is a monophyletic group; consequently the latter is herewith removed from synonymy of the former.

##### 4.3.4. Palaeosetidae

Palaeosetidae TURNER, 1922, includes three genera, the Australian *Palaeoses* TURNER, 1922 (monobasic), and the oriental *Genustes*, ISSIKI & STRINGER 1932 (monobasic), and *Ogygioses*, ISSIKI & STRINGER 1932 (two described species). The monophyly of this familia is quite problematical. Unlike the other hepialoids its members have no inter-M cross-vein, but as discussed in section 4.3.5. this is probably a plesiomorphy. According to the available descriptions, an autapomorphy of the palaeosetid ground plan is the extreme reduction of the maxillae. Maxillae with distinct proboscis and palpus remnants are retained in primitive members of the other hepialoid familiae (PHILPOTT 1927, 1928) although they are also extremely reduced in most Hepialidae. The tibial spur formula in the familia is 0–1–1 (*Genustes*) or 0–0–0 (*Palaeoses*, *Ogygioses*).

##### 4.3.5. The primary dichotomy of the Hepialoidea

The interrelationships between the four hitherto known hepialoid familiae are difficult to unravel due to the reticulate character-distribution in the superfamily. It is probably most likely that the primary dichotomy of the group lies between the Palaeosetidae and Anomosetidae + Prototheoridae + Hepialidae. Two probable synapomorphies of the three last-mentioned familiae are:

(9) Presence of an inter-M cross-vein (i.e., a cross-vein between  $M_3$  and either  $M_2$  or  $M_{1+2}$ ).

The vein configuration hereby produced may be alternatively described as «Discal cell subdivided into three cells...» (REMINGTON 1954) or «M forked in discal cell» (COMMON 1970). The presence of the cross-vein may be considered an apomorphy at the hepialoid level, since it occurs neither in Mnesarchaeidae nor in any other homoneurous moths. On the other hand it



appears to be of general occurrence in Trichoptera-Annulipalpia (but not in Integripalpia sensu ROSS 1967; see, e. g. figures in RIEK 1970) and Mecoptera and therefore probably was present in ancestral mecopteroid insects. If this is correct, its presence in subgroups of Hepialoidea (and in some Heteroneura as well) represents a case of evolutionary reversibility, which is also not altogether unlikely in the case of such simple structures (see, e. g., HENNIG 1966: 116).

(10) Intercalary sclerite between antennal scapus and pedicellus specialized.

The presence of a sclerite in the scapus-pedicellus membrane is apparently a ground-plan characteristic of the Lepidoptera (KRISTENSEN unpublished). In the lower homoneurous groups it is a rounded or triangular, spiny (smooth in Mnesarchaeidae) plate located superficially; this condition is retained in Palaeosetidae (Fig. 27). In the remaining Hepialoidea the plate is markedly elongate, smooth and largely sunk into the scapus lumen inside a narrow pocket (Fig. 28). It is noteworthy that the elongate sclerite does not have any connection with the scapo-pedicellar musculature, as far as could be ascertained from examinations of serially sectioned antennae of fixed *Alphus sylvinus* (LINNAEUS, 1761) (Hepialidae).

An alternative theory of the primary division of the Hepialoidea is that the Anomosetidae is the sister-group of Palaeosetidae + Prototheoridae + Hepialidae. A derived character shared by the last-mentioned families is:

(11) Lack of «primitive type» wing scales.

In the lowest Lepidoptera all scales on the wing surface proper are of the «primitive type», i. e., their upper and lower walls are appressed against each other without leaving an internal lumen, and the upper wall is concomitantly unperforated. In Mnesarchaeidae and Anomosetidae there is a lower layer of «primitive type» scales more or less covered by an upper layer of «normal type» scales, i. e., scales with a more or less ample, in places trabeculated internal lumen and perforated upper wall (COMMON 1973, KRISTENSEN 1971, in press a & b). In *Prototheora*, *Ogygiodes* and in the several hepialid genera examined (including *Fraus*) I have found only «normal type» scales. The loss of the «primitive type» scales must have taken place independently in these hepialoids and in the Heteroneura; the structurally «primitive type» scales found in some Aegerioidea have not been considered a true plesiomorphy (KRISTENSEN 1975), but this question should still be considered open. It is unknown whether «primitive type» scales occur in Neoseustidae and in the genus *Acanthopteroctetes* BRAUN, 1921, hitherto placed in the Eriocraniidae; from these taxa only «normal type» scales have so far been reported (DAVIS 1975 and unpublished).

In spite of the evidence from character 11 the assumption of a sistergroup relationship between Palaeosetidae and the other hepialoids together seems the best substantiated working hypothesis of the primary division of the superfamilia. It should be noted that contrary to apomorphies 9 and 10, no. 11 is a regressive character and as such particularly liable of independent occurrence (see e. g. MAYR 1969: 222).

#### 4.4. The question of the sister-group of *Neotheora*

As evident from table 1 the new genus *Neotheora* can with great certainty be assigned to the Exoporia-Hepialoidea because of its possession of apomorphies no. 1–4 (the very weak development of no. 4 is probably a secondary simplification) and 6–7. Moreover, its possession of apomorphies 9–10 shows its relationships to be with the Anomosetidae-Prototheoridae-Hepialidae group rather than with the Palaeosetidae. However, the exact position of the new taxon is difficult to establish, since the distribution patterns of the derived features relevant in this context are discordant and suggest (with various degrees of probability) a variety of possible phylogenies.

Table 1: Distribution of characters within the subordo Exoporia [Lepidoptera]. Character numbers refer to main treatment in text. Symbols: – plesiomorphic state, + apomorphic state, ? interpretation uncertain, () state not fully developed, [] state doubtfully present, NC no comparison (information not available or structure absent in taxon).

Taxa	Character numbers									
	1	2	3	4	5	6	7	8	9	10
Mnesarchaeoidea	+	+	+	+	+	—	—	—	—	—
Hepialoidea										
Neotheoridae	+	+	+	[+]	NC	+	+	[+]	+	+
Anomosetidae	+	+	+	+	+	+	+	+	+	+
Prototheoridae	+	+	+	+	+	+	+	[+]	+	+
Hepialidae	+	+	NC	+	+	+	+	+	+	+
Palaeosetidae	+	+	NC	+	+	+	+	+	—	—
	11	12	13	14	15	16	17	18	19	20
Mnesarchaeoidea	—	—	—?	—	—	—?	—	—	—	—
Hepialoidea										
Neotheoridae	—	—	+?	+	+	+?	+	+	+	+
Anomosetidae	—	+	—?	—	—	—?	+	+	+	+
Prototheoridae	+	+	+?	+	+	+?	—	—	—	—
Hepialidae	+	+	+?	—	—	—?	—	—	—	—
Palaeosetidae	+	+	—?	—	—	—?	—	—	—	—

#### 4.4.1. Evidence of the sister-group relationship «*Neotheora* / Anomosetidae + Prototheoridae + Hepialidae».

An indication of a sister-group relationship between *Neotheora* and all remaining members of the group together might be seen in the fact that the latter all have the

(12) proboscis more reduced.

In Prototheoridae and Anomosetidae the proboscis is considerably shorter relative to the total head size than in *Neotheora* and its medial surface is not distinctly concave (KRISTENSEN unpublished); the proboscis remnants described from a few hepialids (genus *Fraus*) also appear much reduced (PHILPOTT 1927 b).

There does not seem to be any other evidence in favour of the abovementioned relationship and much weight cannot be attributed to this single regressive character.

The slender anterolateral processes of tergum VIII in *Neotheora* might be considered a unique plesiomorphy, representing the anterior pair of apophyses generally present in Lepidoptera-Glossata but reduced (like the posterior pair) in all previously known Exoporia (DUGDALE 1974). This homology is probably not tenable, however, since the processes in *Neotheora* are not apodemal. The retention of dorsal tentorial arms in *Neotheora* is certainly a plesiomorphy, but I have now found (unpublished) the same condition in representatives of all hepialoid familiae. Similarly, mandibular remnants are present in representatives of all hepialoid familiae despite statements to the contrary in standard texts; already Tillyard (in MEYRICK 1920) identified small mandibulae in *Prototheora* and I have confirmed their presence in this genus and in *Anomosetidae*, though PHILPOTT (1928) claimed them to be absent in both. TINDALE (1941) even reported heavily sclerotized mandibular remnants from the hepialid genus *Zenophassus*, but the structures in question are the cardines maxillares; the true mandibulae are represented by TINDALE'S «postantennal organs» (ROBINSON 1977).

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Anomosetidae	+	+	+	+	+	+	+	+	+	+
Prototheoridae	+	+	+	+	+	+	+	[+]	+	+
Hepialidae	+	+	NC	+	+	+	+	+	+	+
Palaeosetidae	+	+	NC	+	+	+	+	+	-	-
	11	12	13	14	15	16	17	18	19	20
Mnesarchaeoidea	-	-	-?	-	-	-?	-	-	-	-
Hepialoidea										
Neotheoridae	-	-	+?	+	+	+?	+	+	+	+
Anomosetidae	-	+	-?	-	-	-?	+	+	+	+
Prototheoridae	+	+	+?	+	+	+?	-	-	-	-
Hepialidae	+	+	+?	-	-	-?	-	-	-	-
Palaeosetidae	+	+	-?	-	-	-?	-	-	-	-

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#### 4.4.2. Evidence of the «*Neotheora* + Prototheoridae + Hepialidae» monophyly.

A character shared by *Neotheora*, Prototheoridae and Hepialidae but with very doubtful significance is:

(13) The restriction of the scale covering of the antennal flagellum to the dorsal surface only.

In *Mnesarchaea* and *Ogygioses* scales are present on the entire surface of the flagellum and in *Anomoses*, where the scales are replaced by setae, these are arranged in complete circles around each segment. Complete coverings are found also in *Lophocorona* and some species groups among Eriocraniidae, whereas in other eriocraniid species groups and in *Agathiphaga* there is a scale-free area ventrally on the flagellum (KRISTENSEN unpublished). On the basis of this reticulate distribution of the character states it seems impossible to decide which character state is plesiomorphic at the hepialoid level.

It may be noted in this context that Hepialidae may have the entire flagellum devoid of scales, but FRIESE'S (1970) assumption that this is a general condition in the familia is incorrect. The diversity of antennal scaling within the Hepialidae was actually noted already by JORDAN (1898).

#### 4.4.3. Evidence of the sister-group relationship «*Neotheora* / Prototheoridae»

Most serious attention should be paid to two (discordant) bodies of evidence indicating that the sister-group of *Neotheora* is either the Prototheoridae or the Anomosetidae (see 4.4.4.). It shares with both the plesiomorphic retention of two pairs of metatibial spurs and will key out together with them in available familia keys (REMINGTON 1954, COMMON 1970). Derived characters shared by *Neotheora* and Prototheoridae are:

(14) Specialized scale-covering of caput/thorax.

In *Prototheora petrosema* the dense covering, like that of *Neotheora*, largely consists of long, narrowly triangular and apically notched scales with lightly pigmented distal areas contrasting with dark areas below (but basalmost parts not again light as in *Neotheora*). Conditions in other Exoporia examined are different.

In *Mnesarchaea* the scales are unicoloured, narrow, almost parallel-sided and have finely scalloped apices. In *Anomoses* the palpi labiales have scattered long hairs and narrow scales whereas the epicranium in addition to hairlike scales has broadly triangular scales with finely scalloped apical borders. The scales form a pair of brown spots surrounded by white, but as in mnesarchacids the individual scales are unicoloured *Ogygioses* and representatives of several hepialid genera examined (including *Fraus*) have a head/thorax vestiture of unicoloured hairlike scales.

(15) Tibia of P-III unusually long.

In both sexes of *Prototheora petrosema* the tibia/femur ratio is above 2, 1, as in *Neotheora*, whereas in all other homoneurous moths examined the tibia is less than twice the femoral length.

In *Anomoses* the ratio is about 1.5, in *Mnesarchaea* about 1.7–1.8 whereas in *Ogygioses* it is only about 1.2 and in *Fraus* as low as about 1. Outside the exoporian lineage the greatest value (1.8 to just under 2) was found in *Agathiphaga*, whereas in *Eriocrania* it is about 1.5–1.6 and in *Lophocorona* about 1.8.

A *Neotheora*-*Prototheora* similarity which is very difficult to evaluate is:

(16) Porrect and almost parallel posture of palpi labiales.

Because of their length and dense vestiture the palpi hereby acquire a peculiar «snout»-like

appearance not encountered elsewhere among the primitive Exoporia examined. Long and porrect palpi occur in some genera of Hepialidae, but whether this represents the ground plan condition in the familia is uncertain. However, a porrect posture seems also characteristic of the long (but much more short-scaled) palpi of *Agathiphaga* (KRISTENSEN unpublished, see also ROBINSON & TUCK 1976, Fig. 1) and this casts some doubt on whether the condition in *Neotheora*-*Prototheora* is truly apomorphic.

#### 4.4.4. Evidence of the sister-group relationship «*Neotheora*/Anomosetidae»

The evidence presented in the preceding sections must be weighed against the evidence provided by the following derived characters shared by *Neotheora* and *Anomoses*:

(17) The absence of microtrichiation of the wing surface.

Alar trichiation is retained in all other homoneurous Lepidoptera, but it has been reduced independently on more occasions within the lower Heteroneura (BÖRNER 1939).

(18) Extreme faintness or absence of anterior branch of hind wing primary median fork (stem of  $M_1/M_2$ ).

In the ground plan of the other familiae of Hepialoidea this branch is retained in a stronger condition.

(19) Veins  $S_3/S_4$  ( $R_4/R_5$  auct.) not usually «stalked».

There can be no doubt that the stalked condition of these veins is plesiomorphic judging from its prevalence in non-exoporian homoneurous moths and mnesarchacids. The non-stalked condition is also present in most hepialids, but the primitive condition is retained in some members of the subfamilia Hepialinae (DUMBLETON 1966). However, reservations must be made with respect to this similarity between *Neotheora* and *Anomoses*, since the latter shows a noticeable individual variation and occasional specimens have been found which had veins  $S_3/S_4$  distinctly stalked (TURNER 1927, PHILPOTT 1928).

(20) Absence of an «anal loop» in the forewing.

The anal loop is formed by the basal part of  $A_1$  ( $A_2$  auct.) and a crossvein joining this part to E ( $A_1$  auct.). It is a characteristic feature of the ground plan of the entire superordo Amphimenoptera (HENNIG 1969), and within the Hepialoidea it is retained in Prototheoridae as well as in some primitive Hepialidae (PHILPOTT 1926, 1928); it is lost also in many Hepialidae and (most probably by parallel evolution) in the Palaeosetidae (TURNER 1922, ISSIKI & STRINGER 1932).

An alternative explanation of the origin of the anal loop is that it is formed by anastomosis of the distal parts of the longitudinal veins themselves. However, in Agathiphagidae, which exhibit the most plesiomorphous venation within the Lepidoptera, a trachea branches off from the apparent vein  $A_1$ , before the fusion of the latter with E, and extends toward the wing margin. This trachea (Fig. 30) is accompanied by an extremely slight sclerotization of the surrounding cuticle, similar to that of vein A in *Neotheora*, and the whole formation most probably represents the remnants of the true apical part of vein  $A_1$ .

It should be noted also that *Neotheora* like *Anomoses*, has retained a two-layered wing covering with a lower layer of «primitive type» scales; as previously discussed this condition has been found nowhere else in Hepialoidea. Being a symplesiomorphy this similarity does not directly support a *Neotheora*-*Anomoses* sister-group relationship, but it contributes to the evidence against the principal alternative model, viz., the *Neotheora*-Prototheoridae sister-group relationship, since this latter would demand

one further instance of parallel loss of the «primitive type» scales (i. e., in Prototheoridae independent of Palaeosetidae and Hepialidae).

#### 4.4.5. Conclusion

Although more of the known derived characters of *Neotheora* are shared by *Anomoses* than by any other hepialoid group, a definitive choice in favour of *Neotheora-Anomoses* sister-group relationship seems premature because of the admittedly discordant nature of the total evidence. Also it should be noted that the *Neotheora-Anomoses* (derived) similarities are mainly regressive characters with modest systematic weight. For the time being *Neotheora* is therefore preferably placed in a familia of its own.

In conclusion, it should be stressed that future increased knowledge may well provide definitive answers to now unsettled questions in phylogeny of Hepialoidea: investigations have just begun. *Neotheora* ♂♂ are unknown and so are the internal organs and immature stages of all Hepialoidea except some Hepialidae. Finally, a more adequate sampling of the southern hemisphere faunas of primitive Lepidoptera is not only likely to provide us with some now missing links, but will permit distributional patterns to be applied with confidence in the phylogenetic analyses of the group (Fig. 31).

#### 4.5. Appendix: Neotheorid autapomorphies

The following specializations found in *Neotheora* do not occur in either *Anomoses* or *Prototheora* (and have so far not been recorded from any other Hepialoidea); these characters therefore do not contribute to the understanding of the affinities of the new taxon, but they are of much diagnostic value:

Marked swelling on anterior tentorial arm, elongated third segment of palpus labialis, sinuate wing termens, strong development of spinose field between pretarsal pulvilli, furcate process on sternum VIII, elaborate signum complement in bursa copulatrix, spinose utriculus spermathecae.

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