On the milliped family Heterochordeumatidae, with comments on the higher classification of the order Chordeumatida (Diplopoda)

William A. Shear

Department of Biology, Hampden-Sydney College, Hampden-Sydney,
Virginia 23942, USA. Email: bills@hsc.edu

Abstract.　A new genus and species, *Infulathrix siam,* gen. et sp. nov. and a new species, *Heterochordeuma petarberoni*, sp. nov. are described from southeast Asia, and the previously known members of the Heterochordeumatidae are reviewed. The genus *Sumatreuma* Hoffman is placed in the synonymy of *Heterochordeuma* Pocock. Heterochordeumatid gonopod structure is not primitive, as previously supposed, but apomorphic within the superfamily Heterochordeumatoidea and the Diplopoda in general. The families of the order Chordeumatida are grouped into four suborders: Chordeumatidea, Heterochordeumatidea, Craspedosomatidea and Striariidea.

Introduction

Pocock (1893, 1894) described two rather unusual milliped species from Burma (now Myanmar) and Sumatera (Indonesia). While obviously chordeumatidans, these two species, which he placed in the new genus *Heterochordeuma,* exhibited a body form that had not been recorded before from the order—broad metazonal paranota (Fig. 16). He recognized their distinctiveness by establishing a new subfamily, Heterochordeuminae. Just a year or so later, Silvestri (1895) raised this name to family level, described a third species (*Heterochordeuma platydesmoide*) from Sumatera, and a second genus, *Pocockia.* (The holotype of *Pocockia sapiens* Silvestri, 1895 was a male. It is not in the collections of the Museo Civito Storia Naturale in Genoa, nor could it be found in the Silvestri collections at Portici. Silvestri did not provide any illustations, but from his brief Latin description, it is clear that this is a species of *Metopidiothrix* Attems, 1907 [Mauriès 1978*b*]. However, it should be verified from specimens if possible, because if this is true, the name *Pocockia* may have to replace the more familiar *Metopidothrix.*) The next year, Cook (1896) corrected the family name to Heterochordeumatidae.

While the subject of speculation for many years following Pocock's original work, it seems that the relevant specimens were not reexamined until 1960, when Richard Hoffman found them in the collections of the British Museum (Natural History). The specimens had been mounted on insect pins and dried. Hoffman carefully rehydrated the material and dissected the gonopods, which he mounted on microscope slides for study. Hoffman's observations, published in 1963, were startling. He observed that the anterior gonopods of both species were distinctly leg-like, consisting of three or four podomeres separated by articulations. From this he argued that *Heterochordeuma* species were the most primitive of chordeumatidans, and that the resemblance of these gonopods, as well as the body form of the animals, to members of the order Platydesmida spoke to a close evolutionary relationship between the orders Chordeumatida and Platydesmida. He also named a new genus, *Sumatreuma,* for *H. monticola.*

Heterochordeumatids primitive?

Upon conducting my own examination of the holotypes of *Heterochordeuma doriae* and *H. monticola,* I found that Hoffman's 1963 descriptions of the gonopods were not accurate. I could find no trace of any segmentation in the anterior gonopods of either species, nor did these appendages appear particularly leg-like, as Hoffman (1963) illustrated them.

The slides have deteriorated substantially over time, but using Nomarski differential interference contrast illumination and oil immersion at 1000×, I was still not able to resolve any patterns of articulation in the anterior gonopods of either species. In particular, the anterior gonopods of *H. doriae* appeared to be similar in general plan to those of some species of *Metopidiothrix,* even to the extent of being partially or entirely fused to their sternum, and were quite similar to those of *H. petarberoni,* sp. nov., a new species described below, which most definitely does not have leglike, articulated gonopods.

As I was able also to see details and features in the posterior gonopod coxites not illustrated or discussed by Hoffman, it seems very likely that his mistaken observations were due to the lack of good optical equipment with which to study the slides he made.

Therefore, my conclusion is that the members of the family Heterochordeumatidae do not represent primitive chordeumatidans, but are clearly the sister group of the Metopidotrichidae (of *Metopidiothrix?*), with whom they share a number of significant characters, including the reduction of the tenth legs of the males, and an obvious gland channel in the posterior gonopod coxites. Indeed it can be argued that the body form of the heterochordeumatids is highly specialized, not primitive. Broad paranota show up erratically in the Chordeumatida among families in which other species do not have them (Diplomaragnidae) or in which their closest relatives lack them (Apterouridae, Urochordeumatidae). The Callipodida and Stemmiulida, both sometimes recognized as the sister group of the Chordeumatida, have cylindrical bodies and no callipodidans or stemmiluidans with paranota are known. Since the presence of paranota is not consistently correlated with primitiveness in any other characters, the most logical interpretation is that they represent adaptive responses to the particular circumstances of their possessors. In the order Polydesmida, where paranota are more typical, many species have lost them entirely—a similar, but opposite, adaptive change.

Where, then, should we search for primitive chordeumatidans? Accepting that the order Callipodida is the sister group of the Chordeumatida, clues are available in the form of the gonopods. Callipodids have only the eighth legpair modified as gonopods, so we could assume that the additional modification of the ninth pair into posterior gonopods is apomorphic for chordeumatidans. Using an argument analogous to that of Hoffman (1963), the most primitive chordeumatidans would be those with the least modified and most leg-like *posterior* gonopods. The obvious answer is the superfamily Cleidogonoidea, in which the 'posterior gonopods' are present in many genera (*Cleidogona, Pseudotremia, Tianella, Pseudoclis*) as only slightly reduced legs in which a remnant of the coxal gland may still be present as a poorly sclerotized knob on the coxa. Within this superfamily, the most leg-like posterior gonopods are found in the genus *Cleidogona* Cook (Cleidogonidae), distributed from northeastern North America to Guatemala. I revised the family in 1972, but many new species await description; cleidogonids are the commonest chordeumatidan millipeds in eastern North America and Mexico.

Infulathrix, *a new genus*

The two new species described below add to our knowledge of the range of form in the family Heterochordeumatidae. Initially reluctant to describe a new genus in so poorly known a family, I was finally convinced to do so by the numerous differences between the four known *Heterochordeuma* species and the one named here as *Infulathrix siam,* gen. et sp. nov. These include the presence, in *I. siam,* gen. et sp. nov., of 30-segmented males, pregonopodal leg modifications, strongly modified male tenth

leg coxae, and two-branched anterior gonopods which do not embrace the posterior gonopod coxites.

Taxonomy

Superfamily **HETEROCHORDEUMATOIDEA** Pocock
Family **HETEROCHORDEUMATIDAE** Pocock

Type genus: *Heterochordeuma* Pocock, 1893, monobasic.

Diagnosis

Differing from other members of the superfamily in the broad metazonal paranota.

Remarks

The bodies of these animals are basically cylindrical, but with long, broad paranota extending from each metazonite behind the collum (Figs 1, 16). The overall appearance of the metazonites is rough, and at the edges of the paranota small microtrichia can be made out. From my observations on fresh material, it seems that this is an adaptation to collect and hold dirt. A secretion may also be involved. The paranota in *Heterochordeuma doriae* and *H. platydesmoide* (Fig. 1) have an evenly curved anterior margin and slightly produced posterior tip, giving them a vague wing-like appearance. The paranota of *H. monticola* have a straight anterior margin and a squared-off appearance. At the anteriomesal corner of each paranotum is a deep notch. In *H. doriae,* this notch is accentuated by the upturned rim of the rebordered paranotum, while in *H. monticola*, the notch is less distinctive and the paranota are not anteriorly rebordered. In most respects the paranota of the two new species are intermediate. Colour pattern is not known for certain, except in the two new species, where one shows a pattern similar to some species of *Metopidiothrix,* with a dark head, white collum, and dusky body.

The anterior gonopods of heterochordeumatids show varying degrees of fusion with each other and with the sternum. In most species, as Hoffman (1963) observed, the sternum of the anterior gonopods is relatively unmodified. The anterior gonopods (in those species in which undissected gonopod complexes have been observed) curve laterally around the coxites of the posterior gonopods in a complex, three-dimensional, sigmoid curve (the pattern is somewhat different in *Infulathrix,* gen. nov. as described below). The posterior gonopods are very similar to those of *Metopidiothrix* species and quite variable from species to species. They include an anterior branch bearing a gland channel that opens at the tip (this could not be verified for *H. doriae* because of the condition of the microscope slide upon which the gonopods were mounted). The gland channels can be easily traced in some species into the swollen femora of the telopodites. Articles distal to the femora have been lost; this has been verified by repeated observations in

heterochordeumatoids of vestigial distal articles appended to the enlarged femora in anomalous individuals. In addition, examination of a developmental series shows that the articles distal to the femur are lost, not incorporated into a swollen syntelopodite.

Pregonopodal leg modifications are found so far only in *Infulathrix siam*, gen. et sp. nov., where the third leg femur is enlarged. The tenth legs have telopodites that are reduced to only two segments, but the coxae are usually of normal size (except in *I. siam,* gen. et sp. nov) and carry eversible glands that are not enlarged or sclerotized. The eleventh legs are unmodified.

The female genitalia are simple and poorly sclerotized, consisting of the usual two valves and a receptacle on each side.

Key to species of Heterochordeumatidae (males required)

1. Males with 30 segments, females with 32; third legs of males with enlarged femora (Fig. 17) ....
     .... *Infulathrix siam,* gen. et sp. nov.
     Males and females with 32 segments; third legs of males with normal femora 2
2. Body length about 16 mm ....
     .... *Heterochordeuma platydesmoides* Silvestri
     Body length 10 mm or less 3
3. Anterior gonopods longer than width of sternum; posterior gonopod colpocoxites simple 4
     Anterior gonopods shorter than width of sternum; posterior gonopod colpocoxites 3-branched ....
     .... *H. monticola* Pocock
4. Posterior gonopods with coxites divided to base, posterior branch strongly curved (Fig. 13) ....
     .... *H. petarberoni,* sp. nov.
     Posterior gonopods not divided, but with a strong, sinuate anterior process .... *H. doriae* Pocock

Genus *Heterochordeuma* Pocock

Heterochordeuma Pocock, 1893: 387; 1894: 342. – Silvestri, 1895: 727. – Hoffman, 1963: 131
Sumatreuma Hoffman, 1963: 133. New synonymy.
Type species: of *Heterochordeuma, H. doriae* Pocock, 1893, by monotypy; of *Sumatreuma, Heterochordeuma monticola* Pocock, 1963, by original designation.

Diagnosis

Differs from *Infulathrix*, gen. nov. in having 32-segmented males, slightly modified tenth leg coxae and normal third leg femora.

Comments

The genus *Sumatreuma* was based by Hoffman on the supposed different segmentation of the anterior gonopods and the tenth leg telopodites in Pocock's two species of *Heterochordeuma*. Both of these observations were mistaken, and as the range of gonopod form in the known

species of *Heterochordeuma* seems no greater than that in related genera (*Metopidiothrix, Australeuma*), there seems to be no reason to maintain *Sumatreuma* as a separate genus.

Heterochordeuma platydesmoide Silvestri

(Fig. 1)

Heterochordeuma platydesmoide Silvestri, 1895: 727.
Sumatreuma platydesmoide. – Hoffman, 1963: 134.

Material examined

Holotype. Specimen, from Si Rambe, Sumatera, Indonesia, (Silvestri Collection, Portici).

Comments

The holotype specimen consists of segment 15, the pleurotergites (Fig. 1) of each side separated, and the two legpairs of that segment, mounted on a microscope slide. Jeekel (1965) pointed out that although the type was originally deposited in the Museo Civico Storia Naturale di Genova, it was later borrowed back by Silvestri and never returned, so it remained in Portici. The fate of the rest of the specimen is unknown. Silvestri's brief Latin description and the type fragments establish the identity of the species as a heterochordeumatid, but do not provide enough information to identify the sex of the specimen.

Silvestri described it as about 50% larger than Pocock's species (16 mm as opposed to about 10 mm), and this is suggested by the size of the pleurotergites. In the absence of gonopods, there was no basis but geography for Hoffman's placement of *platydesmoide* in *Sumatreuma*. Until further material is collected, nothing can be added to our knowledge of this species.

Heterochordeuma doriae Pocock

(Figs 2–5)

Heterochordeuma doriae Pocock, 1893: 387. – Pocock, 1894: 342, pl. 19, figs 14a–d. – Hoffman, 1963: 131, figs 1–3.

Material examined

Male lectotype and female paratype from Thao, Karen Hills, Myanmar, (The Natural History Museum, London).

Comments

Although Hoffman (1963) stated that the gonopods had been returned to the vial containing the type specimen, they are in fact still mounted on a slide. The mounting medium has significantly deteriorated over the past 38 years. Innumerable tiny crystals have formed, air bubbles are being pulled in from the edges of cover glass, and the drying of the medium has crushed the fragile gonopods, themselves partially or nearly entirely covered by particles of dirt. The refractive

indices of the gonopods and the mounting medium are such that the resolution of some details was difficult even with Nomarski illumination.

Hoffman (1963) added details to the descriptions by Pocock (1893) and illustrations (Pocock 1894) provided earlier. However, his description of the anterior gonopods was not correct. Hoffman showed the anterior gonopods as consisting of a broad sternum on which rested small coxae. Attached to each coxa was an even smaller trochanter, followed by two telopodite podomeres, the proximal about twice as long as the distal. My own observations (Fig. 2) were as follows.

The anterior gonopod sternum is a broad, semicircular plate to which the gonopods articulate, perhaps without a clear suture, but the nature of this articulation is obscured by dirt. The base of the sternum is defined by a strongly thickened transverse bar. Just distal to the supposed coxosternal articulation, the gonopods are broken at approximately the

same place on each side; this might have been interpreted by Hoffman (1963) as a joint, but in fact is an irregular fracture due to the crushing of the curved gonopods when the slide was made. The gonopods curve gently posteriorly, then slightly lateral, then posteriorly again, so that in life they probably passed lateral to the posterior gonopod coxites, with the anterior faces of the distal parts of the anterior gonopods in contact with the posterior surfaces of the tips of the posterior gonopod coxites—an arrangement seen in the new species *Heterochordeuma petarberoni*, *Metopidiothrix*, and many genera of the family Conotylidae. The tips of the anterior gonopods are broadly spatulate and narrowly but distinctly rebordered.

The posterior gonopods are in very poor condition and I was only able to satisfactorily resolve the distal parts of the coxite on the right side. The single coxite bears a long, curved subapical branch that probably arises from the anterior side (Figs 3, 4). I could trace an internal gland channel
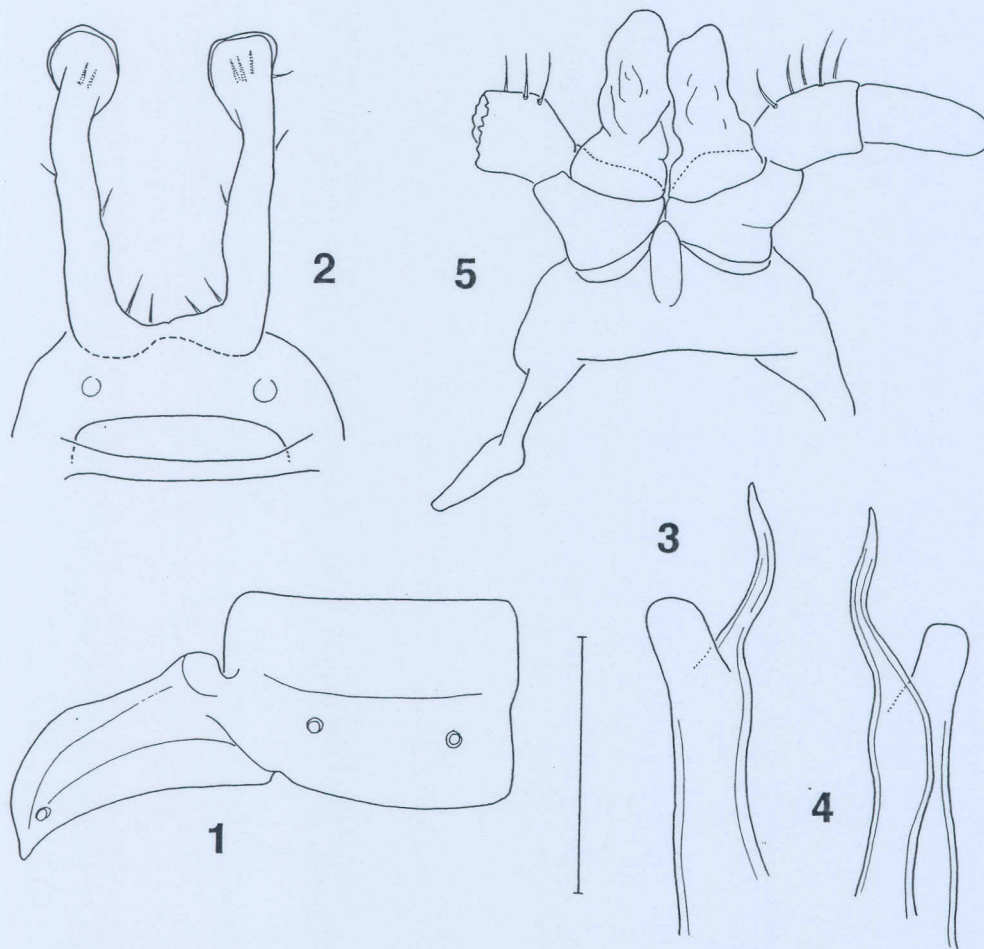
Figs 1–5. *1, Heterochordeuma platydesmoide* Silvestri, left heminotum of segment 15 of ?male, dorsal view. *Heterochordeuma doriae* Pocock: *2,* anterior gonopods, anterior view; *3,* tip of posterior gonopod coxite, anterior view; *4,* same, posterior view; *5,* legpair 10 of male, anterior view. Scale line = 0.3 mm for Figs 1, 2, 5; 0.15 mm for Figs 3, 4.

through part of the coxite, but not into this branch; typically these channels open on an anterior branch of the coxite. The coxite terminates in a rounded lobe that is difficult to see, even with Nomarski illumination. Hoffman (1963) depicted it as covered with fine microtrichia.

The tenth legs are essentially as illustrated by Hoffman (1963), with a slightly enlarged coxa bearing an eversible gland pouch. The telopodite consists of two short segments (Fig. 5).

Heterochordeuma monticola Pocock

Figs (6–10)

Heterochordeum monticola Pocock, 1894: 342.
*Sumatreuma monticola.* – Hoffman, 1963: 133, figs 4–6.

Material examined

Holotype.   Male from Mt Singalang, Sumatera, Indonesia, (The Natural History Museum, London).

Comments

As with the preceding species, the holotype was mounted dry on a pin. Hoffman (1963) noted the absence of the head and a few anterior segments. The slide on which the gonopods and tenth legs are mounted is likewise in bad condition.

The anterior gonopods (Figs 6, 7) are relatively short and subtriangular apically. They give the impression of being poorly sclerotized. No trace of an articulation with the sternum could be seen and I assume that the coxae are fused with the sternum, a common condition in other, related, chordeumatidans. Again, I could find no evidence supporting Hoffman's (1963) description of the gonopod as consisting of a free coxa and four telopodite elements; I suspect that folds in the gonopod cuticle induced by drying and then flattening on the slide were misinterpreted as articulations. On the anterior sides of the gonopods, about midway in their length, is a distinctive patch of setae. This setal patch is not found in *H. doriae,* but does occur in both *H. petarberoni,* sp. nov. and *Infulathrix siam,* gen. et sp. nov. Because the ante-
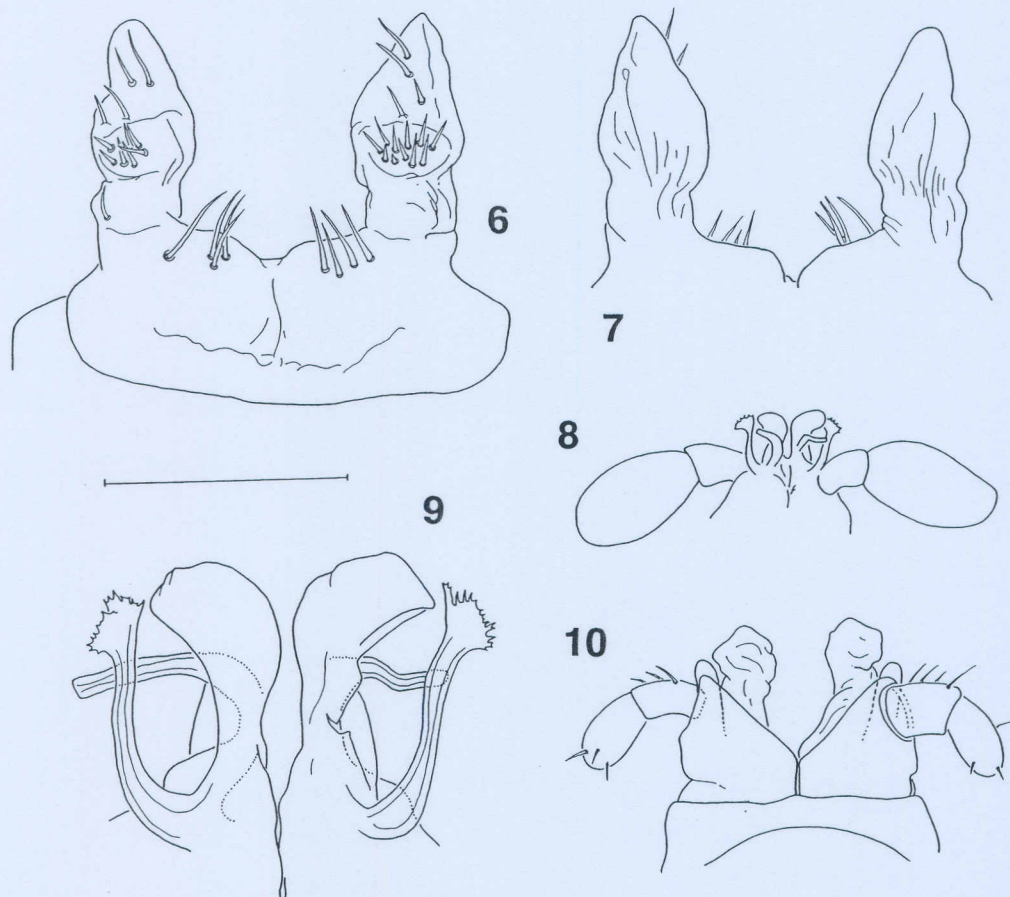
Figs 6–10.   *Heterochordeuma monticola* Pocock: *6,* anterior gonopods, posterior view; *7,* anterior gonopods, anterior view; *8,* posterior gonopods, anterior view; *9,* posterior gonopod coxites, anterior view; *10,* legpair 10 of male, posterior view. Scale line = 0.6 mm for Fig. 8; 0.3 mm for Fig. 10; 0.15 mm for Figs 6, 7, 9.

rior gonopods of *H. monticola* are so short, they could not have passed lateral to the posterior gonopod coxites in life. The first impression is of the gonopod *analagen* of a penultimate instar male, but as the posterior gonopods are fully developed, this must be their mature form.

The posterior gonopod coxites (Figs 8, 9) consist of three branches (Hoffman saw only two of these). The anteriormost branch is strongly curved and bears a fimbriate, apical calyx. A distinct gland channel traverses this branch but cannot be traced back into the coxa. The mesal branch is cupped and hoodlike, embracing a posterior, curved, rodlike process (this was broken off on one side but the fragment was restored to life position in the drawing).

The tenth legs (Fig.10) have only two telopodite articles, not three, as Hoffman (1963) showed. The coxa is somewhat produced laterally, then slightly folded, giving the false impression of a third small article.

Heterochordeuma petarberoni, sp.nov.

(Figs 11–15)

Material examined

Holotype. Male. Indonesia: Mentawai Islands, Siberut Is., Muarasiberut, 15–20 August 1995, P. Beron, T. Ivanova; (Bulgarian National Museum, Sofia).
Paratypes. Two males, one female, same depository, same locality.

Diagnosis

Close to *H. doriae,* but distinct from that species in the deeply divided coxites of the posterior gonopods.

Description

Male

Thirty two trunk segments. Length *c.* 8.0 mm, width *c.* 1.8 mm. Structure of head and trunk typical of heterochordeumatids. Head and antennae unmodified. Nine ocelli well pigmented, clearly separated from one another in oval patch. Paranota wing-like, slightly recurved, anterior paranotal notch deep, strongly rebordered. Paranota reduced on last few segments. Segmental setae short, blunt, inconspicuous; surfaces of metatergites minutely roughened, small soil particles adhering. Head dark grey, collum creamy tan, trunk segments darker brown, mottled purplish grey.

Pregonopodal legs not modified. Anterior gonopods (Fig. 11) fused to sternum, meeting basally in midline, erect, curving posterior at about half their length, curvature marked by patch of stout setae, distal third of gonopod curves sharply back anteriorly, inclines to midline slightly, distal part rebordered on mesal margin, apex bluntly swollen. Dense patch of fine setae on posterior surface. *In situ,* anterior gonopod curves round, and embraces laterally, posterior gonopod coxites. Posterior gonopods (Figs 12, 13) with enormously swollen telopodite femora. Coxae articulate with sternum; coxites with anterior and posterior branches, posterior branch curves posteriorly, long acute process at apex; anterior branch not so strongly curved, ending in two blunt fingers, with distinct gland channel traceable into telopodite prefemur. Legs 10 (Fig. 14) typical, enlarged coxae with glands, telopodite reduced to two articles. Legs 11 not modified, lacking glands.

Female

Similar to male in size, colour and form. Cyphopods as in Fig. 15, with two spherical receptacles on each side.

Distribution

Known only from the type locality; collected in rain forest litter at 0–150 m elevation.

Etymology

Named for Dr Petar Beron, Sofia, collector of the type series.

Infulathrix, gen. nov.

Type species: *Infulathrix siam,* sp. nov.

Diagnosis

Distinct from *Heterochordeuma* in having the leg 10 coxae much swollen, with large internal glands and a distal process, legs 3 with swollen femora, 30 trunk segments in males (32 in females), and in that the anterior gonopods do not laterally embrace the posterior gonopod coxites.

Infulathrix siam, sp. nov.

(Figs 16–22)

Material examined

Holotype. Male. Thailand: Phuket Is., E of Ton Sui Waterfall, 17 February 1988, M. Anderson; (Zoological Museum, Copenhagen).
Paratypes. Male, three juvenile females, same data as holotype.

Description

Male

Thirty trunk segments. About 10 mm long, 1.25 mm wide. Ocelli 8, well-developed and pigmented, separated from each other in oval patch. Trunk segments as in Fig. 16, paranota squared laterally, not winglike or produced at posteriordistal corners, paranotal notches deep, rebordered. Segmental setae short, blunt, inconspicuous. Head and body light brown, mottled darker purplish brown, collum unmarked and slightly lighter than following trunk segments.

Legpair 3 (Fig. 17) with femora enlarged, other pregonopodal legs normal. Anterior gonopods (Figs 18, 19) complex, fused to sternum, coxosterna fused in midline; gonopod with swollen, anteriorly-projecting base with two groups of strong setae distally, distal third deeply notched laterally about one-half its length, divided into two closely appressed branches with complex tips. Anterior gonopods *in situ* do not imbrace posterior gonopod coxites laterally but are strongly deflexed and cover them, with anterior gonopod apices in contact with tenth legs. Posterior gonopods (Figs 20, 21) with greatly swollen femora filled with glandular tissue; coxites each with two branches, which are in turn divided, anteriormost branch with gland channel that can be traced into telopodite femur, mesal branches bladelike, posteriormost branch longest, acuminate, curved posteriorly.

Legpair 10 (Fig. 22) with coxae fused to each other and to sternum, with oblique posteriordistal process bearing nubbly microsculpture; large glands within coxa, opening through valvelike flaps; telopodites much reduced, two-articled. Legpair 11 not modified, lacking glands.

Comments

Cyphopods remain unknown, as the three females in the collection all lack a single molt of maturity. However, they already have 32 trunk segments. The type specimens were collected in monsoon forest, in cavities in a rotten log.

Etymology

The species name is a noun in apposition, the traditional western name for Thailand.
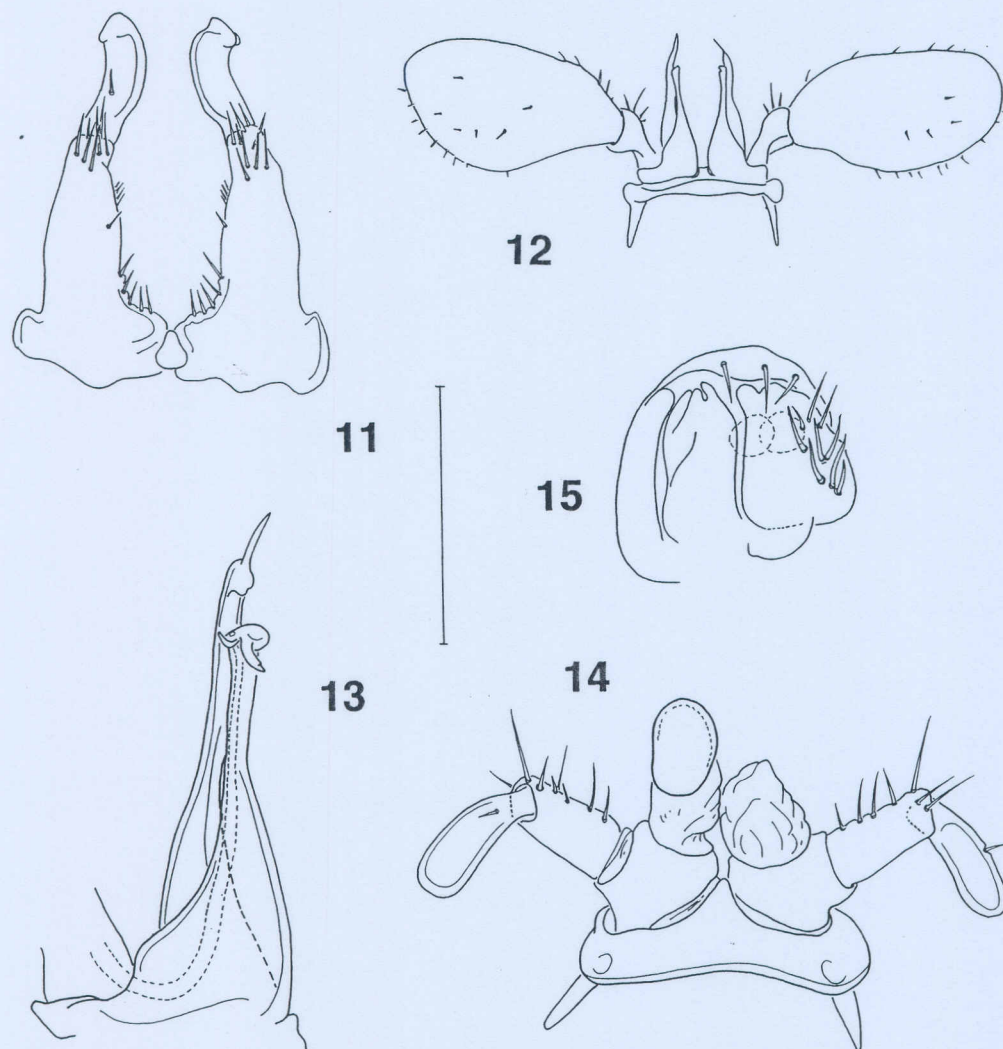
Figs 11–15. *Heterochordeuma petarberoni,* sp. nov.: *11,* anterior gonopods, posterior view; *12,* posterior gonopods, anterior view; *13,* left posterior gonopod coxites, anterior view; *14,* legpair 10 of male, posterior view; *15,* cyphopod, ventral view. Scale line = 0.6 mm for Fig. 12; 0.3 mm for Figs 11, 14; 0.15 mm for Figs 13, 15.
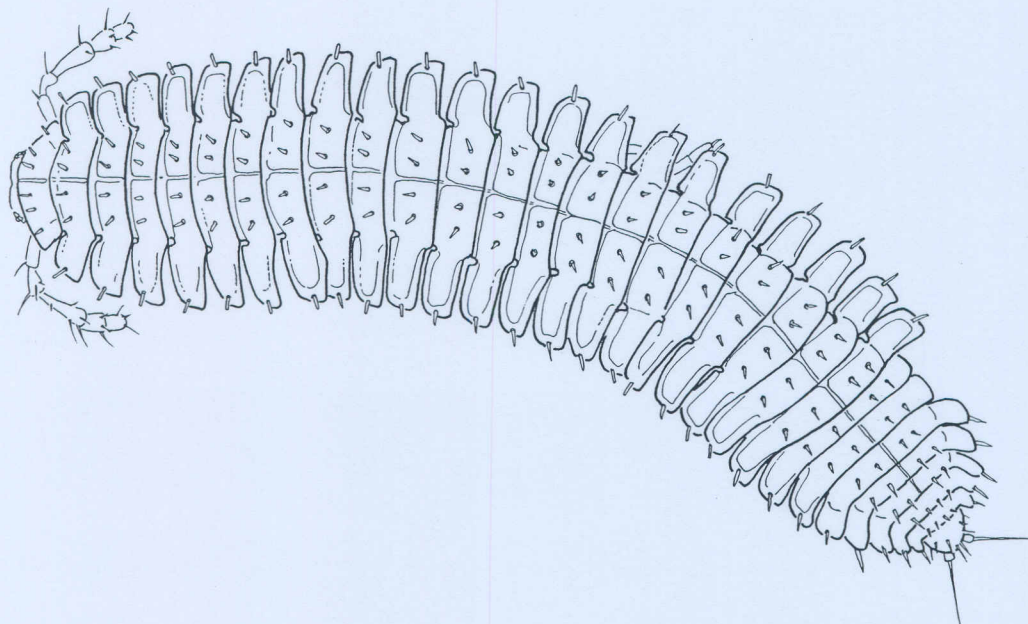
Fig. 16.   *Infulathrix siam,* gen. et sp. nov.: dorsal view of male. Animal is 10 mm long.

Some thoughts on higher classification

In the class Diplopoda, the composition of suprafamilial taxa is often very difficult to arrange, and nowhere more so than in the order Chordeumatida. (I suggest that we use the term *chordeumatidans* to refer to the members of the entire order Chordeumatida, *chordeumatideans* to refer to members of the suborder Chordeumatidea, and *chordeumatids* to refer to members of the family Chordeumatidae. While this may seem clumsy at first, it will eliminate the potential for a good deal of confusion.) Systematic work on this group is fraught with difficulties, not the least of which is a scattered and often contradictory literature in which early systematists proceeded to describe new genera and families without regard for one another's previous work (or in Verhoeff's case, even his own) and the rules of priority. Nevertheless, Verhoeff and Attems were often in some agreement on the higher classification of the order, both favouring an arrangement proposed by Verhoeff in 1929.

In addition, the almost bewildering complexity of the gonopods in this order, coupled with a wide range of modifications to other secondary sexual characters in males, have induced a fragmented system marked by numerous monotypic genera and monobasic families. So we face a situation in which an inherently difficult group bears with it an initial literature that is, to put it mildly, less than helpful. Of the nineteenth century work, only the North American synopsis of Cook and Collins (1896) has stood the test of time, probably because they published before the European specialists had become very active and therefore could look at their animals without preconceived notions.

Further problems are posed by incomplete knowledge of the world fauna. Only recently have chordeumatidan millipeds been discovered or their presence verified for Australia, South America, India and Madagascar. Asia in particular continues to be productive of new families and genera. Even such a supposedly well-collected region as the Japanese Archipelago has been found to support a host of new forms, and China is virtually *terra incognita* for chordeumatidan millipeds. So any proposed system must be considered as tenative, even more so than usual.

Contributions to resolving this Augean mess have been made by a number of twentieth-century taxonomists. Excellent beginnings were made by Henry W. Brolemann (1935) in his *Faune de France* volume on chordeumatidans, and by Otto Schubart (1934) in *Tierwelt Deutschlands*. The latter volume dealt with the entire northcentral European fauna, and so was necessarily less analytical than Brolemann's work. Karl Strasser, in a series of papers published from the 1940's to the 1970's, did much to clarify our understanding of the complex fauna of the Balkans.

More recently, J.-P. Mauriès has worked on material from Europe, Asia and Australia, greatly expanding the geographical limits of the chordeumatidans; thanks to his taxonomic acumen and extraordinary skill at illustration, much confusion has been resolved. My own work has focused on North America and the Pacific rim, including east Asia, Australia and southern South America.

With regard to the higher classification, a major step forward was made by R. L. Hoffman (1979) in his *Classification of the Diplopoda*. Hoffman listed all thenknown genera and families of chordeumatidans and provided

at least a rudimentary arrangement of them into superfamilies. In this task he had immeasurable aid from Casimir Jeekel's *Nomenclator Generum et Familiarum Diplopodorum,* a 1971 compilation of generic and family-level names proposed in the class. Hoffman also gave a careful *precis* of past attempts at a classification, ultimately favoring a Verhoeffian approach, which emphasized the plan of the anterior gonopods.

(Brolemann's view focused on the *relationship* between the anterior and posterior gonopods.) In any case, Hoffman's classification, which has the virtue of conservatism, is the only recent attempt to place every taxon in the system, and must be the starting point for any subsequent arrangement. His work on establishing priorities for the names of genera and families and his discussion of his own and past classifications places
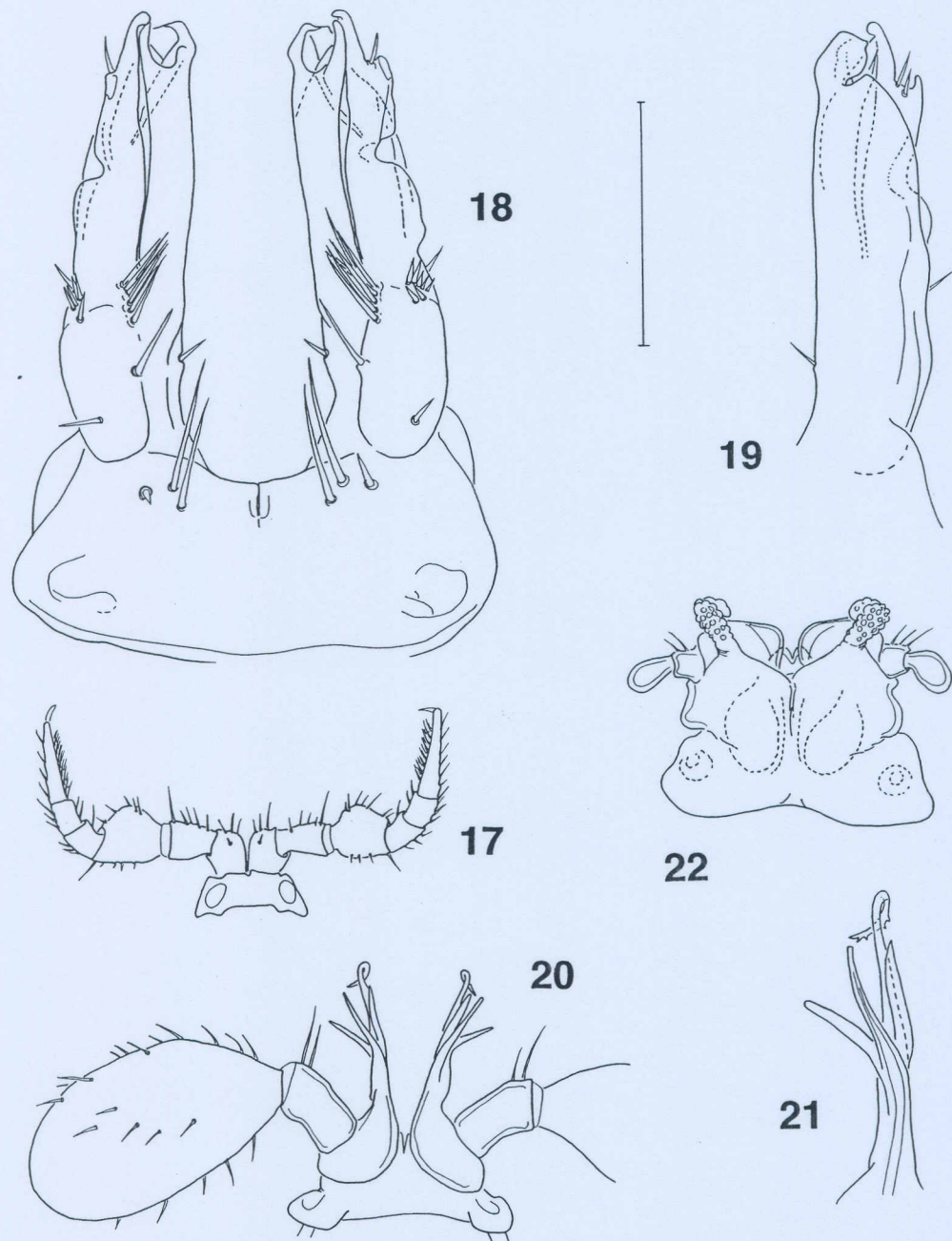
Figs 17–22. *Infulathrix siam*, gen. et sp. nov.: *17,* legpair 3 of male, anterior view; *18,* anterior gonopods, posterior view; *19,* right anterior gonopod, anterior view; *20,* posterior gonopods, anterior view; *21,* left posterior gonopod coxites, anterior view; *22,* legpair 10 of male, posterior view. Scale line = 0.6 mm for Fig. 17; 0.3 mm for Figs 20, 22; 0.15 mm for Figs 18, 19, 21.

this chapter among the most valuable documents ever produced on chordeumatidan systematics.

I think Brolemann's genius was to see the fundamental dichotomy in the order Chordeumatida as between two groups he recognized as suborders: Craspedosomidea and Chordeumatidea. The grouping was based on the degree of participation of the ninth legpair in the gonopod complex. Brolemann distinguished, usually on purely anatomical grounds, between what he called *peltogonopods* (which actually functioned in sperm transfer) and *paragonopods* (which played at best a supporting role). He also recognized that much of the complexity of the gonopods arose from modifications of coxal structure, and not from the telopodite of the gonopodal appendage. But in some craspedosomatideans, he described a structure he called a *cheirite,* which he postulated to consist of the telopodite of the appendage fused to lateral sternal remnants and the tracheal apodeme. Between the left and right cheirites, and articulated with them, is a more or less elborate coxosternum. Cheirites appear to be limited to the anterior gonopods, and seem to define a monophyletic group, but need reanalysis to establish their actual derivation: how does the telopodite in fusing with the tracheal apodeme bypass its own coxa? At this point I would suggest an entirely coxal origin for the functional elements of all chordeumatidan anterior gonopods. This is different from my 1972 view, in which I argued for the presence of telopodite derivatives in chordeumatidan anterior gonopods. Undoubted telopodites occur on the anterior gonopods of species of only a few families, such as Hoffmaneumatidae and Golovatchiidae. Here they are single segments with clear articulations; we have no knowledge of any species in which the telopodites functionally integrate as such with the rest of the gonopod. Similarly, in posterior gonopods, we can easily compose an evolutionary series in which the telopodite is reduced to a smaller and smaller remnant and finally disappears entirely. These observations support the idea that the functional parts of both gonopods are entirely coxal.

In Brolemann's Craspedosomidea, the ninth legs were paragonopods, reduced in size and function, and having little or nothing to do with sperm transfer, only supporting or protecting the eighth legpair, the peltogonopods. In the Chordeumidea, however, it was the ninth pair that Broelmann saw as peltogonopods, while the paragonopodal part was taken by the eighth pair.

Brolemann, however, worked from limited data. While the fauna of western Europe is complex in itself, it is not entirely representative of the world fauna. For example, little was known of the North American chordeumatidans, the only synopsis being that of Cook and Collins (1896), which, while excellent for its time, gives a far from complete picture. While chordeumatidans had already been described from South America and tropical southeast Asia, the accounts were sketchy. Brolemann knew little of the complex Balkan and Italian faunas, still difficult to work with today.

Now it would appear that Brolemann's dichotomy was somewhat overdrawn. The distinction between paragonopods and peltogonopods is no longer as clear as it once seemed. We know from observation that in many chordeumatidans, both the eighth and ninth legpair (better termed anterior and posterior gonopods) are involved in actual sperm or spermatophore transport. But Brolemann was indeed correct in suspecting that the form of the posterior gonopods (ninth legpair) carried the clues to a more realistic classification. Thus, while Hoffman (1979) seemed to reject Brolemann's proposal, his broad experience actually led him to the core of it, and the clue to successfully grouping chordeumatidan families.

After examining either specimens or illustrated literature accounts of 52 of the approximately 135 chordeumatidan genera recognized by Hoffman (1979) as valid, I detected a pattern of gonopod organization not entirely different from that seen by Brolemann in the French fauna. Using this pattern (which will emerge from the diagnoses given below) I was able to group the chordeumatidan families into four taxa, which I propose here to recognize as suborders. One of the suborders is newly named, two use the names Brolemann set up in 1935, and the remaining one was recognized by Hoffman (1979, 1999) *ex* Cook. The contents of each of the proposed suborders, differing from what has been placed in them in previous classifications, is given below.

This classification represents a very preliminary hypothesis and obviously is not fully argued here. I have not proceeded properly by demonstrating the monophyly of each of the families and superfamilies, but that Herculean chore must lie in the future and will require the analysis of hundreds of species, as well as an intensive search for new characters of the female genitalia, mouthparts, male sperm ducts, and segmental setae. Instead I began with what seemed to be a coherent group of families, the Heterochordeumatoidea, and moved out from there, in each case seeking the closest related taxon to those already established. The absence of a phylogenetic scheme is not a matter of philosophical choice, but more a recognition that our knowledge of this group of animals is not adequate to the task and that to accumulate the requisite data will take many years. In the meantime, I feel obliged to go on record with my hypotheses, to expose them to discussion and criticism by others.

Order **CHORDEUMATIDA** Koch

Suborder **CHORDEUMATIDEA** Koch

Diagnosis

Thirty (or 26?) trunk segments. (*Segment* in this context refers to divisions of the trunk behind the head, and includes

the collum, possibly a haplosegment, the first three [probable] monosegments, and all the remaining diplosegments, including the anal segment, the nature of which is not known.) Posterior gonopods with coxites functioning in sperm transfer in conjunction with anterior gonopods; telopodite reduced to single swollen article. Legpair 7 variously and strongly reduced. Legpair 10 reduced or vestigial. Legpair 11 with coxal glands. Gnathochilarium lacking promentum.

Contents

Suborder Chordeumatidea Pocock 1894
Superfamily Chordeumatoidea Koch 1847
Family Chordeumatidae Koch 1847
? Family Speophilosomatidae Takakuwa 1949

Comments

The placement here of the Japanese family Speophilosomatidae (Shear *et al.* 1994) is extremely tentative. The posterior gonopods differ from those of the chordeumatids in having strongly reduced but multisegmented telopodites. The tenth legs are not at all reduced. I based my decision primarily on the form of the seventh legs, oddly reduced and probably paragonopodal in both families. But I have to add that Mauriès has described *Osellasoma caoduroi*, otherwise a typical neotractosomatid (suborder Craspedosomatidea), which also has reduced Legpair 7 evidently paragonopodal, and lesser modifications to the seventh legs are scattered throughout the order. Speophilosomatids may eventually have to be placed in their own superfamily in the Craspedosomatidea.

Suborder **HETEROCHORDEUMATIDEA**, nom. nov.

Diagnosis

Thirty-two, 30, 28 or 26 trunk segments. Posterior gonopods with coxites functioning in sperm transfer in conjunction with anterior gonopods, or rarely as the only gonopods; telopodites two-segmented, apical segment swollen and glandular. Legpair 10 with coxal glands, coxae and glands often much enlarged, telopodite often reduced or vestigial. Legpair 11 with or without coxal glands. Gnathochilarium lacking promentum.

Contents

Suborder Heterochordeumatidea, new name
Superfamily Heterochordeumatoidea Pocock 1894
Family Heterochordeumatidae Pocock 1894
Family Metopidiotrichidae Attems 1907
Family Eudigonidae Verhoeff 1914
Family Megalotylidae Golovatch 1978
? Family Peterjohnsiidae Mauriès 1987

Superfamily Conotyloidea Cook 1896
Family Conotylidae Cook 1896
Family Adritylidae Shear 1971
Superfamily Diplomaragnoidea Attems 1907
Family Diplomaragnidae Attems 1907
Superfamily Pygmaeosomatoidea Carl 1941, new status
Family Pygmaeosomatidae Carl 1941
Family Lankasomatidae Mauriès 1978a

Comments

This suborder is the most coherent and best understood of the four, and is also most clearly a monophyletic unit, based on form of the posterior gonopods. The posterior gonopod coxa always bears coxites, and these play a role in sperm transfer. The telopodite is reduced to two articles, the prefemur and femur, and the femur is swollen with gland tissue. In several families that have been closely examined, a duct leads from this femoral gland to the tip of a coxite (see Shear and Mesibov 1997). In addition, nearly all species have lost the coxal glands of the eleventh legs (the glands are still present in diplomaragnids and in some species of megalotylids). The relationship between the anterior and posterior gonopods would have baffled Brolemann. In some families (Conotylidae), the posterior gonopod coxites range from very complex (*Crassotyla* Golovatch, *Yasudatyla* Shear & Tsurusaki) through various degrees of reduction (*Taiyutyla* Chamberlin, *Austrotyla* Causey) to small, presumably functionless remnants which have lost the telopodites (*Idagona* Buckett & Gardner). Meanwhile, in genera like *Megalotyla* Golovatch and *Nepalella* Shear, the anterior gonopods have been reduced to mere rudiments and the posterior gonopod colpocoxites have taken over their function entirely.

The superfamily Heterochordeumatoidea was established by me in 1972, but the present arrangement differs from the original one—conotyloids have been removed and placed in their own superfamily. Diplomaragnoids have also been recognized as distinct at the superfamily level, as perceived by Mauriès (1978a).

The heterochordeumatoids, as discussed in the first section of this paper, are united by the peculiar modifications to the tenth coxae of males. Megalotylidae is placed here, rather than in Conotyloidea, because of similar modifications to the tenth coxae of *Megalotyla brevichaeta* Golovatch & Mikhaljova 1978. I have some misgivings about the placement of *Nepalella* in Megalotylidae; it may belong in Conotylidae after all. The anterior gonopods resemble those of *Brunsonia* Loomis & Schmitt from western North America, but this could be homoplasy. Then again, so could the enlarged tenth coxal glands of some of the included species. Eleventh coxal glands are also present in *Megalotyla* and some *Nepalella,* but are somewhat reduced. Peterjohnsiidae is quite enigmatic; the posterior gonopod

telopodites are a single reduced article, but there is a gland channel in one of the colopocoxite branches, just as in meto-pidiotrichids; the tenth coxae are enlarged. Mauriès (1987a) originally placed the family in Cleidogonoidea, but the gonopods were misinterpreted (see Shear and Mesibov 1994).

The superfamily Diplomaragnoidea was first recognized by Mauriès in 1972; I reviewed the group in 1990, syn-onymizing all families with Diplomaragnidae and all genera with *Diplomaragna* Attems. This is a very large genus, spread out from the Urals to Japan and Taiwan. Undoubtedly there are many species in China. The anterior gonopods of species of *Diplomaragna* actually pass dorsal to the posterior gonopod sternum and are appressed to the posterior surface of the posterior gonpod colpocoxites. Coxal glands appear on legs 11; perhaps the megalotylids are intermediate between diplomaragnids and conotylids.

The Conotyloidea has been intensively studied by me for nearly 30 years. It is predominantly North American, with two genera in Japan (*Japanosoma* and *Yasudatyla*) and another in northeast Asia (*Crassotyla* Golovatch). There is a definite trend in this·family to the reduction of the posterior gonopods; in some *Austrotyla* Chamberlin their coxites are so reduced that they could not play a role in sperm transfer, and in *Idagona* the posterior gonopods have lost their telopodites and the coxites are very small. An internal arrangement of the family with which I entirely agree was presented by Hoffman (1979). The eudigonine genus *Apodigona* Silvestri is quite conotylid-like, but also clearly closer to *Eudigona* Silvestri and *Ancudia* Shear, undoubted heterochordeumatoids. Thus the relations between the super-families and families of this suborder still require attention.

The superfamily Pygmaeosomatiodea is newly estab-lished here, and *sin verguenza* I explain it on the basis of my inability to put Pygmaeosomatidae and Lankasomatidae, doubtless heterochordeumatoids, anywhere else. At the very least it makes geographical sense; Pygmaeosomatidae is from India (*Pygmaeosoma* Carl) and Madagascar (18 known species of *Betscheuma* Mauriès) and Lankasomatidae endemic to Sri Lanka.

Suborder **CRASPEDOSOMATIDEA** Brolemann

Diagnosis

Thirty, 31, 29, 28 or 26 trunk segments. Posterior gonopods leglike or variously reduced; telopodites not inflated or glan-dular, often without coxites. Legpairs 10 and 11 with coxal glands. Legpair 10 usually not reduced. Gnathochilarium with promentum.

Contents

Suborder Craspedosomatidea Brolemann 1935
    Superfamily Craspedosomatoidea Gray 1843

        Family Craspedosomatidae Gray 1843
        Family Attemsiidae Verhoeff 1898
        Family Haplobainosomatidae Verhoeff 1909
    Superfamily Verhoeffioidea Verhoeff 1899
        Family Verhoeffiidae Verhoeff 1899
    Superfamily Haaseoidea Attems 1899
        Family Haaseidae Attems 1899
    Superfamily Cleidogonoidea Cook 1896
        Family Cleidogonidae Cook 1896
        Family Entomobielziidae Verhoeff 1899
        Family Opisthocheiridae Ribaut 1913
        Family Trichopetalidae Verhoeff 1914
        Family Lusitaniosomatidae Schubart 1953
    Superfamily Brannerioidea Cook 1896
        Family Branneriidae Cook 1896
        Family Trachygonidae Cook 1896
        Family Heterolatzeliidae Verhoeff 1897
        Family Brachychaeteumatidae Verhoeff 1911
        Family Chaemosomatidae Verhoeff 1913
        Family Macrochaeteumatidae Verhoeff 1914
        Family Niponiosomatidae Verhoeff 1941
        Family Tingupidae Loomis 1966
        Family Kashmireumatidae Mauriès 1982
        Family Golovatchiidae Shear 1992
    Superfamily Neotractosomatoidea Verhoeff 1901
        Family Mastigophorophyllidae Verhoeff 1899
        Family Neotractosomatidae Verhoeff 1901
        Family Faginiidae Attems 1926
        Family Hoffmaneumatidae Golovatch 1974
    Superfamily Antroleucosomatoidea Verhoeff 1899, new status
        Family Antroleucosomatidae Verhoeff 1899
        Family Haplobainosomatidae Verhoeff 1909
        Family Origmatogonidae Verhoeff 1914
        Family Vandeleumatidae Mauriès 1970
        Family Haasiidae Hoffman 1979

Comments

This is the largest and most heterogenous of the suborders, and certainly qualifies as a 'wastebasket,' the contents of which await careful study and redistribution. It is conceiv-able that at least one additional suborder could be carved out of it, and that some families could be moved elsewhere in the present system. There are no clear synapomorphies holding this suborder together. The form of the posterior gonopods varies from the quite leg-like ones of the Cleidogonoidea (but even in Cleidogonidae we see *Cabraca unigon* Shear, a species in which the posterior gonopods are reduced to a single, very unleg-like article) through the more reduced (2–4 articles) ones of the brannerioids, which may bear small coxites, to entirely vestigial remnants in a not a few Old World families. I have adopted Hoffman's 1979 arrangement with a few changes, primarily in what is placed in the Superfamilies Cleidogonoidea and Brannerioidea, and I have

restored to family status some of the taxa placed by him as subfamilies of Antroleucosomatidae.

Hoffmaneumatidae has been added to Hoffman's Neotractosomatoidea on the basis of a suspected relationship with Mastigophorophyllidae (Shear *et al.* 1997).

Lusitaniosomatidae, Entomobielziidae and Opisthocheiridae all have an anterior gonopod plan like Cleidogonidae, and in nearly all species the posterior gonopods are leg-like.

Among the brannerioids, considerable divergence occurs and the contents of the superfamily may have to be regrouped. Tingupidae and Niponiosomatidae are very closely related; it may not be feasible to maintain both families (Niponiosomatidae is the older, but less used, name; see Shear 1988). Macrochaeteumatidae and Brachychaeteumatidae are likely synonyms, based on newly collected material of *Macrochaeteuma* Miyosi, currently under study. Kashmireumatidae is placed here, rather than in Cleidogonoidea, because of the vestigial telopodites on the anterior gonopods, though this must be a plesiomorphy.

Antroleucosomatoidea, as a superfamily here, includes everything (with a few exceptions) that Hoffman (1979) placed in a much-expanded family Antroleucosomatidae. This is the most poorly known superfamily of the order. Species belonging to it occur from central Europe through the Balkans and Caucasus to central Asia; several important new higher taxa have recently been described and many more likely await discovery.

Suborder **STRIARIIDEA** Cook

Diagnosis

Thirty or 28 trunk segments. Posterior gonopods with telopodites a single article, usually inflated, serving as a shield for the anterior gonopods (which act alone in spermatophore tranfer), sometimes glandular (?); posterior gonopod coxites present, supporting anterior gonopods at rest. Legpairs 10 and 11 with coxal glands. Legpair 10 not reduced. Gnathochilarium with promentum.

Contents

Suborder Striariidea Cook 1898
Superfamily Striarioidea Cook 1898
Family Striariidae Bollman 1893
Family Rhiscosomididae Silvestri 1909
Family Apterouridae Loomis 1966
Superfamily Caseyoidea Verhoeff 1909, new status
Family Caseyidae Verhoeff 1909
Family Urochordeumatidae Silvestri 1909

Comments

Cook (1898), Chamberlin and Hoffman (1958) and Hoffman (1979, 1999) recognized a suborder containing only the

family Striariidae, largely because of a single character: the sperm ducts of the males open as long, membranous tubes from the posterior faces of the second coxae, while in (supposedly) all other families, they open flush on the coxal surface. However, the state of this character is not known for many chordeumatidan families. In 1972, I used the name Striarioidea to designate a superfamily containing the families Striariidae, Caseyidae, Rhiscosomididae, Apterouridae and Urochordeumatidae. The last three are all monobasic. The suborder as a whole is almost exclusively North American, with but a single species of Caseyidae in Siberia.

Hoffman (1979) presented an alternative arrangement, but I still maintain that there must be a taxon at some level including these families, due to their very similar anterior and posterior gonopod plan. Here I propose to distribute the families of the suborder between two superfamilies, Striarioidea and Caseyoidea. The former rests on what admittedly might be a convergent development, the lack of a posterior gonopod coxite.

The members of the suborder not only share a common gonopod plan, but are biogeographically coherent, as mentioned above. Many of the animals in this group from western North America are winter active and hence poorly collected. I expect many new taxa in years to come.

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