

The Penis as a Phylogenetic Character in the Millipede Family Julidae

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ABSTRACT

The double penis provides useful characters for analysing phylogenetic relationships within the family Julidae. In his treatment of the Diplopoda in Bronn's *Klassen und Ordnungen des Tierreichs*, VERHOEFF (1926-32) noted the difference between *Pachyiulus* and the other Julids examined. Study of numerous julid genera has confirmed this distinction: All Pachyiulini have one type of penis - other julids (with a few, obviously secondary, exceptions) have another type. The pachyiuline type is taken to be primitive, being more similar to penis types found in related families. The other type thus constitutes a potential synapomorphy for all Julidae except Pachyiulini. The non-pachyiuline penis type shows several further modifications which probably qualify as synapomorphies at lower hierarchical levels. Thus, all Paectophyllini and Calyptophyllini have an unusually stout and sclerotized penis, and all species of *Anaulaciulus* have the terminal lobes of the penis particularly long.

RÉSUMÉ

Le pénis comme caractère phylogénétique dans la famille Julidae (Diplopoda).

Dans la famille Julidae, le double pénis fournit des caractères très utiles pour l'analyse des relations phylogénétiques. Dans son traité des diplopodes dans le Bronn's *Klassen und Ordnungen des Tierreichs*, VERHOEFF (1926-32) notait déjà la différence entre *Pachyiulus* et les autres julides qu'il avait observés. L'étude de nombreux genres de julides a confirmé cette distinction : tous les Pachyiulini possèdent un même type de pénis alors que les autres julides (sauf quelques exceptions traduisant à l'évidence des modifications secondaires) présentent un autre type. Le type de pénis des Pachyiulini est considéré comme primitif (plésiomorphe) à cause de sa similitude avec le type de pénis des familles phylogénétiquement voisines. L'autre type constitue une synapomorphie potentielle pour tous les Julidae sauf les Pachyiulini. Plusieurs modifications du type de pénis non-Pachyiulini constituent probablement des synapomorphies établies à des niveaux inférieurs. Par exemple, tous les Paectophyllini et les Calyptophyllini possèdent un pénis exceptionnellement robuste et sclérifié, et toutes les espèces du genre *Anaulaciulus* présentent des lobes péniers terminaux particulièrement longs.

INTRODUCTION

As in most other millipede groups, the taxonomy of the large Palearctic family Julidae relies heavily on the gonopods. This is true both on species level and on higher levels. Recent studies have demonstrated, however, that certain species in some julid genera cannot be distinguished on gonopodal characters (see, e.g., ENGHOFF, 1987, 1992), and also that the phylogenetic relationships of julidan families cannot be satisfactorily analysed by means of gonopodal characters alone (ENGHOFF, 1981, 1991). At the intermediate level, the only recent

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attempt at a phylogenetic analysis of the tribes within the Julidae is that of READ (1990) which relies very much on gonopods.

The present study focuses on another part of the male sexual system, namely the penis, and on the phylogenetic significance of the morphological variants found within this family.

In those millipedes which do have a penis, it is a single or double tube situated behind the second pair of legs. The penis is used to load the proper copulatory organs, the gonopods, with sperm (HAACKER & FUCHS, 1970).

Although the penis has received relatively little attention from diplopodologists, it is noteworthy that the higher classification of the Diplopoda by COOK (1895) to some extent was based on the nature of the penis (or rather: of the male gonopore, since some groups have no penis proper). Many of the names that COOK gave to higher groups, and which refer to the penis (see HOFFMAN, 1980: 44) survive in the current classification of millipedes (HOFFMAN, 1980): *Merocheta*, *Diplocheta*, etc.

The julid penis is double in nature: there are two gonopores and the *vasa deferentia* remain separate throughout the length of the penis. The latter is therefore sometimes referred to as a double penis, or in the plural Latin form: penes. However, it is actually only its apical lobes which are paired, the penial basis being externally undivided. This is also true of several other julid families having a "double" penis, although in some the two "hemipenes" seem to be fully separated. The julid penis is devoid of setae, whereas penial setae occur in several other julidan families (Fig. 1). In most julids each apical lobe terminates in a hyaline "membranous tube" which probably may be retracted into the more basal, more sclerotized part of the apical lobe. The apical lobes are sometimes separated by a median lobe.

VERHOEFF (1926-32, p.687-689) described several important details of julid penis structure. His most important conclusions were:

1) The penis of *Pachyiulus* is fundamentally different from that of the other genera he examined: *Julus*, *Megaphyllum* (sub *Brachyiulus*), *Unciger* (sub *Oncoiulus*), *Ommatoiulus* (sub *Schizophyllum*), and *Leptoiulus*.

2) There may be considerable intraspecific variability, as demonstrated by *Unciger foetidus*.

3) Some genera seem to be characterized by particular penial features (*Ommatoiulus*: hood-like median lobe; *Leptoiulus*: penis slender, parallel-sided).

Several other authors have described the penis of various julid species but it was not until 1962 that another comprehensive treatment appeared, viz., in STRASSER's monograph of the erstwhile tribe Typhloiulini in which he presented outline drawings of the penis of 16 "typhloiuline" species (Fig. 32).

On this background, the aim of the present study is to explore the diversity of penis structure within the Julidae, and to assess the utility of the penis as a phylogenetic character by interpreting the differences found in a cladistic framework.

MATERIAL AND METHODS

More than a hundred species, representing forty-four julid genera were examined, as well as representatives of all other julidan families (see appendix). Euparal mounts were made of isolated penes of many species, but some species were examined with the stereo microscope only. Some penes were prepared for scanning electron microscopy (SEM) through dehydration in absolute alcohol, transfer to acetone, and air-drying. After being mounted and coated with gold, the penes were examined with a Jeol SP840 scanning electron microscope. Drawing conventions: Although the paired gonoducts can often be seen by transparency, they have only been drawn in a few species.

INTRASPECIFIC VARIABILITY

VERHOEFF (1913) described intraspecific variability in penis shape, and named four varieties of *Unciger foetidus*, partly based on penial characters. The varieties appeared, at least in part, to be allopatrically distributed. Also STRASSER (1962), studying the Typhloiulini,

emphasized the individual variability. ENGHOFF (1995) found that in spite of modest individual variability, penis shape may be species-characteristic in the Paectophyllini and Calyptophyllini.

The present, more sweeping study suggests that at most moderate intraspecific variability is in fact the rule, and that penis characters therefore may be of taxonomic-phylogenetic value in the Julidae.

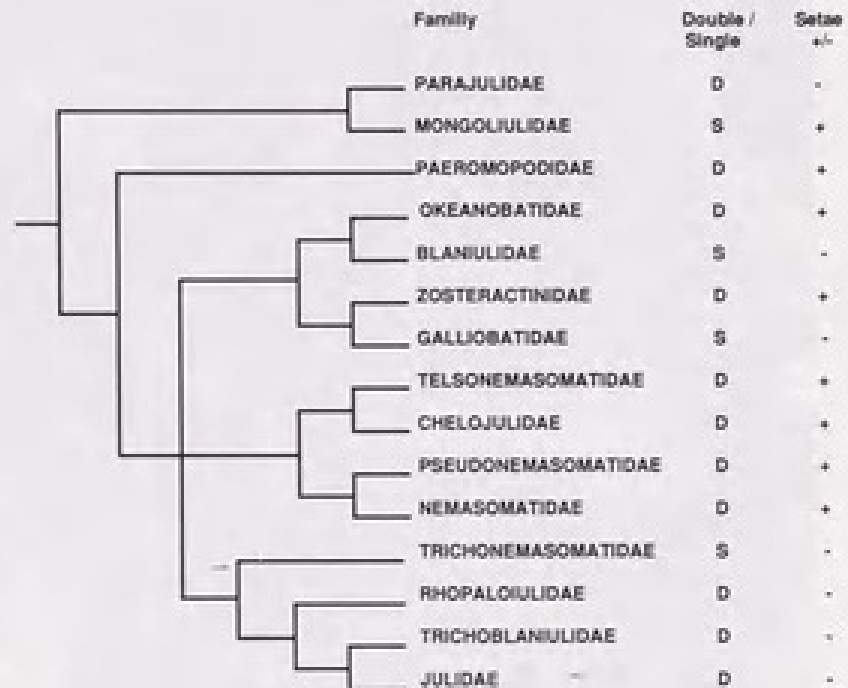


FIG. 1. — Penis types in julidan families. The cladogram is that of ENGHOFF (1991). The columns to the right show whether the penis is double (D) or single (S), and whether penial setae are present (+) or absent (-).

THE PENIS IN EACH JULID TRIBE

The tribes recognized by READ (1990) have been used as the taxonomic framework of this study, with a few modifications. The differences from READ (1990) are:

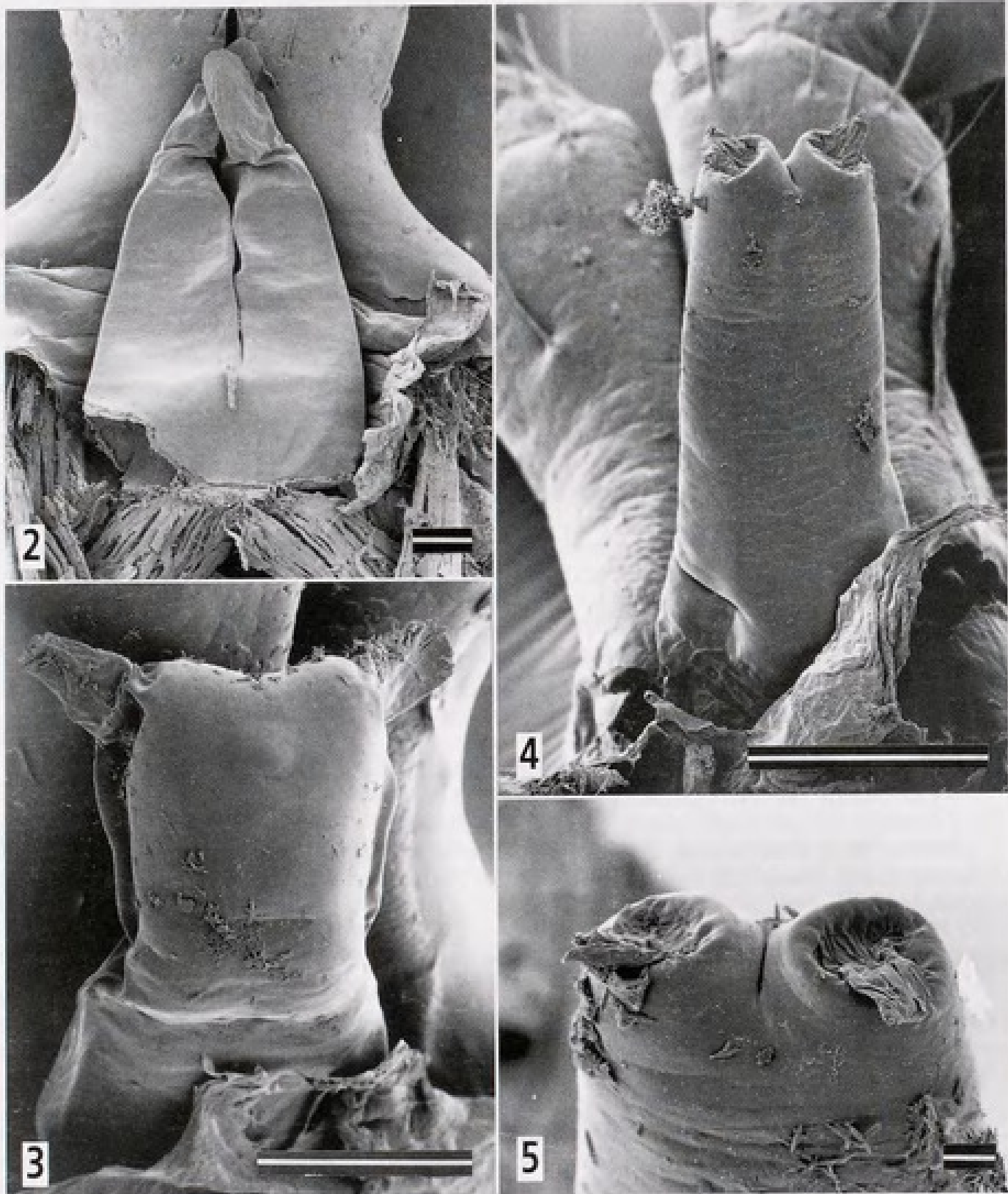
- Pteridoiulini are treated separately
- Catamicrophyllini and Symphyoiulini are included in Paectophyllini
- Calyptophyllini are considered
- Typhloiulini and Leptoiulini are included in Julini.

Neither this arrangement, nor the sequence of the tribes in the treatment reflects any definitive ideas about julid interrelationships. See, however, the section "Phylogenetic interpretation".

Pachyiulini

According to VERHOEFF (1926-32), the penis of *Pachyiulus* differs from that of the other julids in having the apical, separate lobes relatively much longer and lying parallel to each other (see Fig. 2). In the other julids, the separate apical lobes were much shorter and directed obliquely lateral.

Whereas the penis structure of "other julids" is much more diverse than envisaged by VERHOEFF, there is a remarkable constancy within the tribe Pachyiulini. ENGHOFF (1992) found that the penis in *Dolichoulus* spp. is similar to that of *Pachyiulus*, and subsequent studies have shown this to be true of numerous genera of the tribe. All Pachyiulini have a hyaline penis, without any visible cuticular reinforcements. The two "hemipenes" are fused basally as in all julids, and the apical lobes are long and are lying parallel to each other (Figs 2, 6, 7). Only in *Mesoiulus ciliciensis* do the apical lobes diverge (STRASSER, 1975, confirmed by present study). There are no differentiated membranous tubes at the orifices, and there is no median lobe.

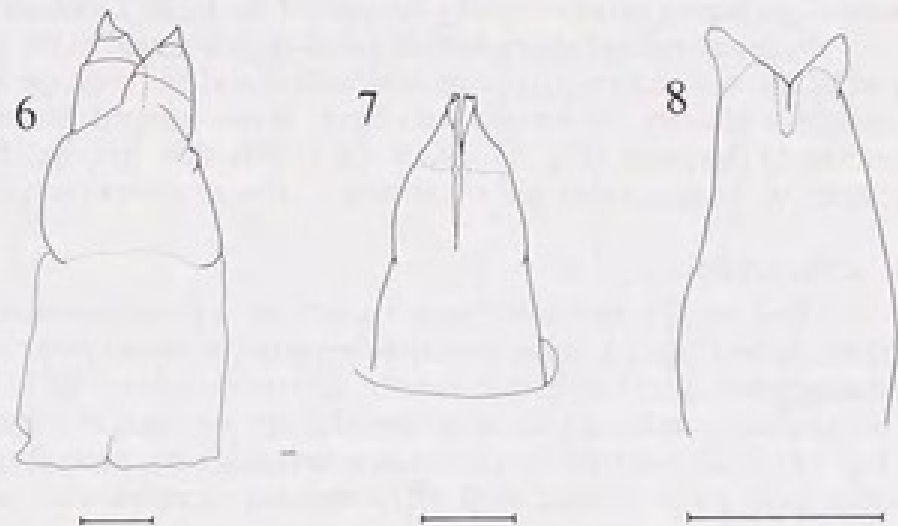


FIGS 2-5. — Scanning electron micrographs of penis in situ of 2: *Pachyiulus flavipes*, posterior view, 3: *Cylindroiulus caeruleocinctus*, posterior view, 4: *Ophiulus pilosus*, posterior view, 5: *Ophiulus pilosus*, close-up of tip, antero-distal view. Part of the second coxae is also shown in 2-4. — Scales: 0.1 mm (2-4), 0.01 mm (5).

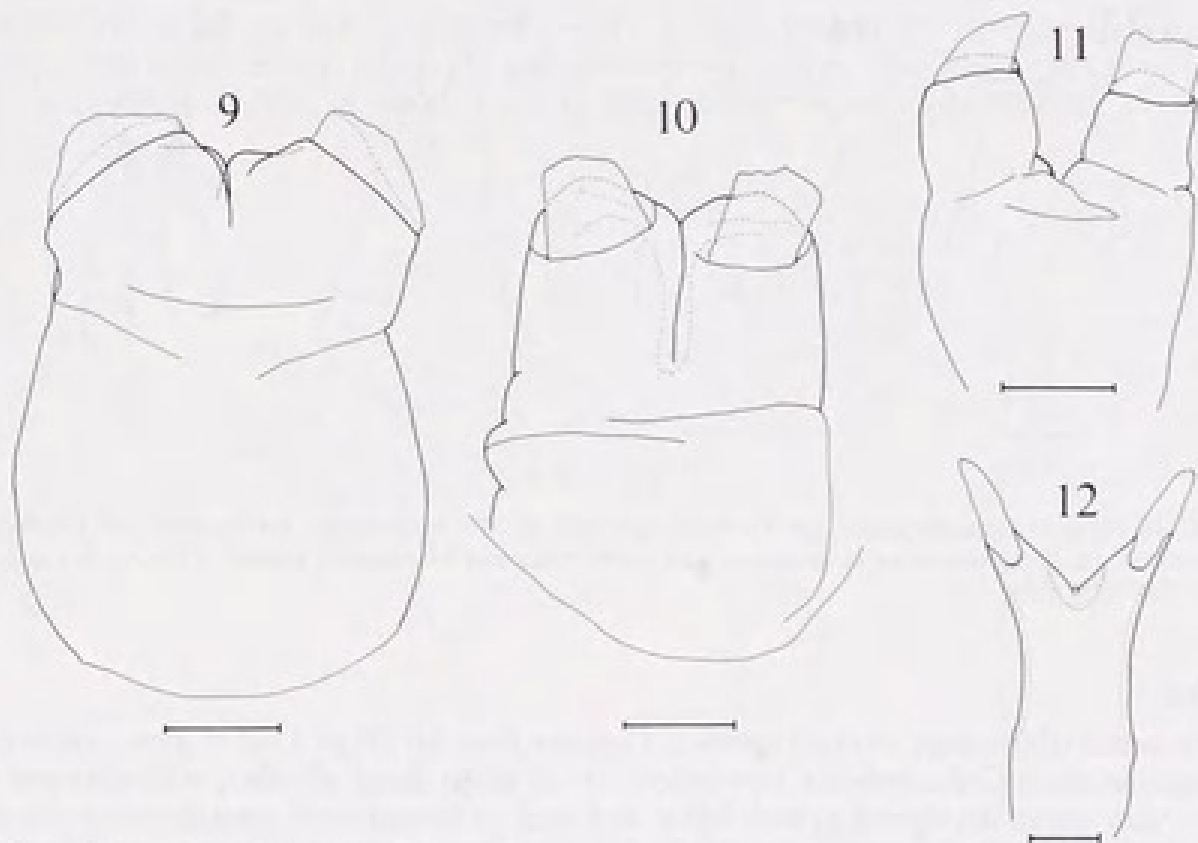
Pteridoiulini

In *Pteridoiulus aspidiorum* (Fig. 8), the only species of this tribe, the body of the penis is somewhat less hyaline than in the pachyiulines. The apical lobes are short and each ends in a hyaline "membranous tube". The sclerotization of the penis is most evident in the narrow sinus between the apical lobes. There is no median lobe.

FIGS 6-8. — Penis of Pachyiulini (6, 7) and Pteridoiulini (8).
6: *Dolichoiulus vosseleri*,
7: *Amblyiulus barroisi*, 8:
Pteridoiulus aspidiorum. -
Scales: 0.1 mm.

*Brachyiulini*

In the genus *Brachyiulus* and in the genus *Megaphyllum*, the penis is very short and stout.



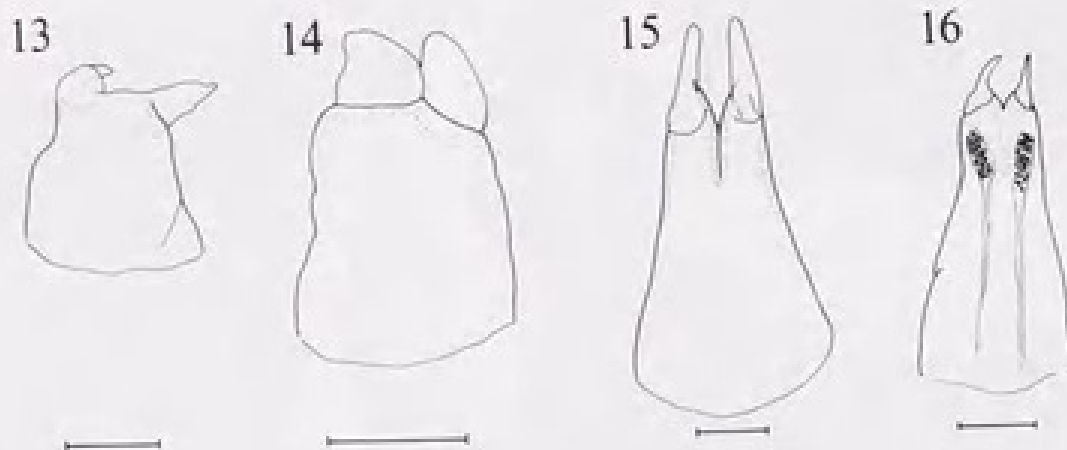
FIGS 9-12. — Penis of Brachyiulini. 9: *Megaphyllum hercules*, 10: *M. adanense*, 11: *Brachyiulus apfelbecki*, 12: *Anaulaciulus inaequipes*. - Scales: 0.1 mm (9, 12), 0.05 mm (10, 11).

It is moderately sclerotized, and the lateral margins of the basal part only occasionally have a constriction (*M. hercules*, Fig. 9). The apical lobes are parallel and short (relatively long in *M. adanense*, Fig. 10); they lie close to each other in *Megaphyllum* (Figs 9 & 10) but are separated in *Brachyiulus apfelbecki* (Fig. 11). The membranous tubes are broad and $\pm$ parallel-sided. There is no median lobe. In *M. adanense* (Fig. 10), *M. geniculatum*, and *M. brachyurum* the membranous tubes do not arise apically but subapically on the caudal surface of the apical tubes - perhaps a synapomorphy for part of the large, catch-all genus *Megaphyllum*?

A deviating and characteristic penis type is found in the genus *Anaulaciulus*. Here the basal part of the well-sclerotized penis is slenderer and has concave lateral margins; the apical lobes are divergent and are drawn out into long, finger-shaped projections, giving a donkey-headlike outline to the penis (Fig. 12). KORSÓS (1996, this volume) found this penis type in numerous species of *Anaulaciulus* and suggested it to be an autapomorphy for the genus.

Leucogeorgiini

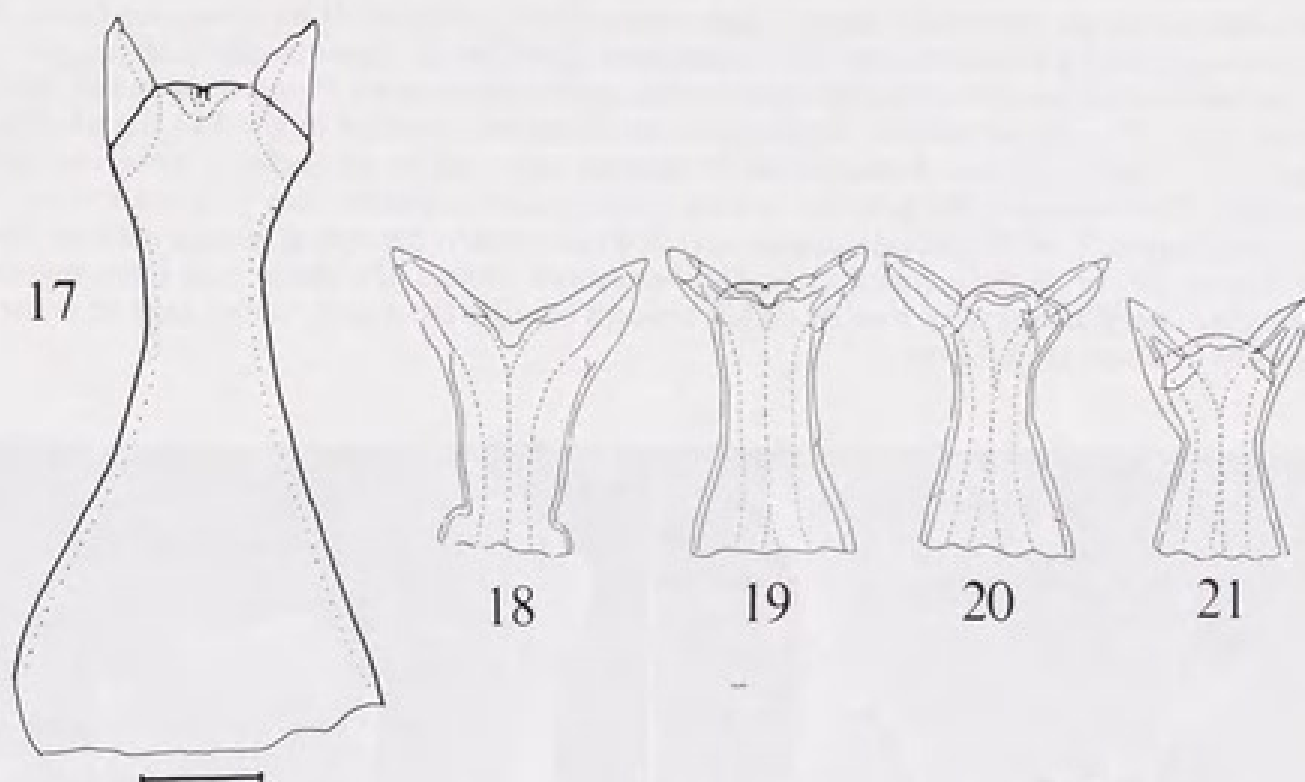
This small tribe shows great variability in penis structure. *Archileucogeorgia* (Fig. 13) and *Heteroiulus* (Fig. 14) have poorly sclerotized penes approaching the type found in Pachyiulini, although the apical lobes are shorter. *Chromatoiulus* (Fig. 15) looks quite like the brachyiuline *Anaulaciulus*, although the long apical lobes are parallel rather than diverging. *Nepalmatoiulus* (Fig. 16) is well-sclerotized like *Chromatoiulus* but instead of being drawn-out the short apical lobes have long, slender well-differentiated membranous tubes. Neither genus has a median lobe.



FIGS 13-16. — Penis of Leucogeorgiini. 13: *Archileucogeorgia* sp., 14: *Heteroiulus intermedius*, 15: *Chromatoiulus podabrus*, 16: *Nepalmatoiulus birmanicus* (with sperm ducts and spermatozoa shown). - Scales: 0.1 mm (13, 15, 16), 0.05 mm (14).

Oncoiulini

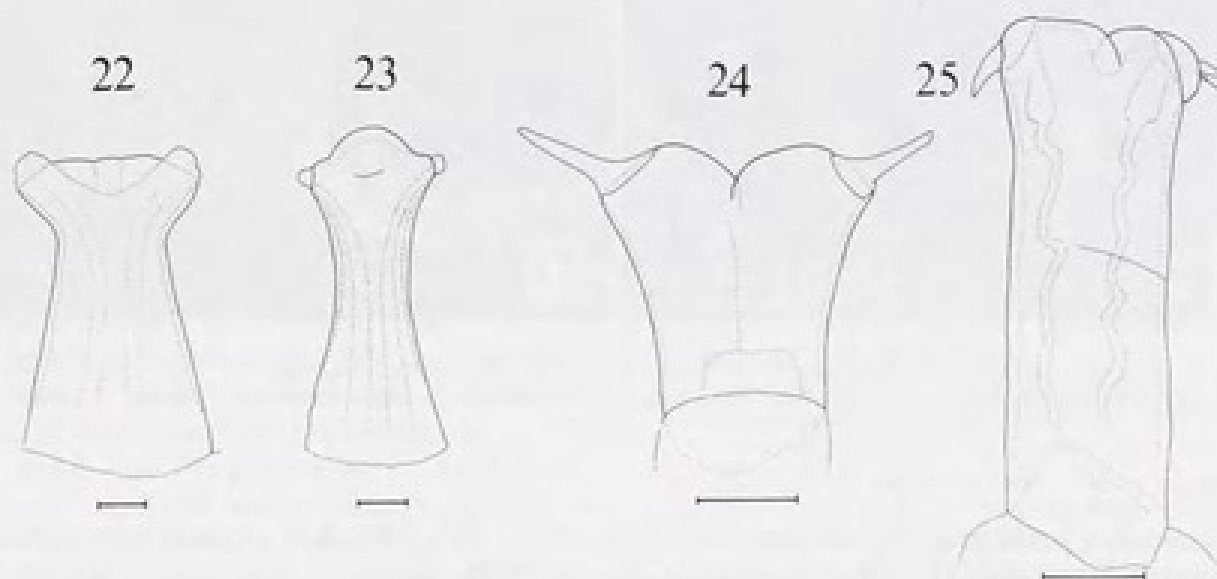
The penis of the only studied species, *Unciger foetidus* (Figs 17-21) looks quite like the penis found in most Cylindroiulini (see below): well-sclerotized, slender, with concave lateral margins, very short diverging apical lobes and well-differentiated membranous tubes. The species is notable for intraspecific variability, especially as regards the presence/absence and shape of a median lobe (VERHOEFF, 1913).



FIGS 17-21. — Penis of *Unciger foetidus* (Oncoiulini). 17: specimen from Italy, 18-21 (from VERHOEFF, 1913): specimens from Austria (18,19), Tatra Mts. (20), and Romania (21). - Scale (17): 0.1 mm.

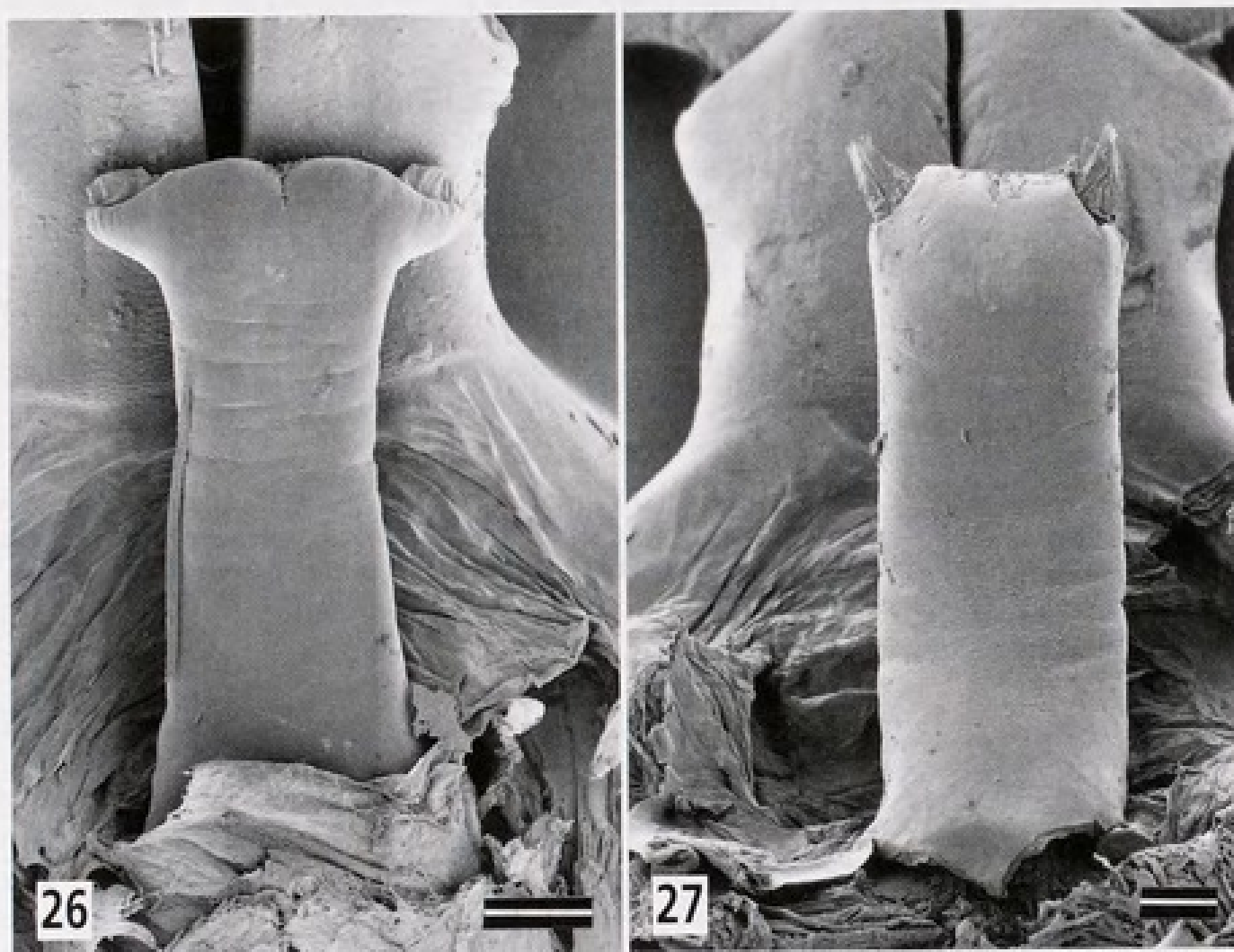
Paectophyllini and Calyptophyllini

These two tribes, which are probably sister-groups (ENGHOFF, 1995) share a distinctive penis type characterized by relatively extreme sclerotization. The basal part may be either parallel-sided (Figs 25, 27), or with diverging (Fig. 24) or concave (Figs 22 - 23, 26) margins.



FIGS 22-25. — Penis of Paectophyllini (22, 23) and Calyptophyllini (24, 25). 22: *Macheiroiulus libicus*, 23: *Catamicrophyllum mesorientale*, 24: *Calyptophyllum trapezolepis*, 25: *C. digitatum*. Sperm ducts shown in 22, 23, and 25. - Scales: 0.1 mm.

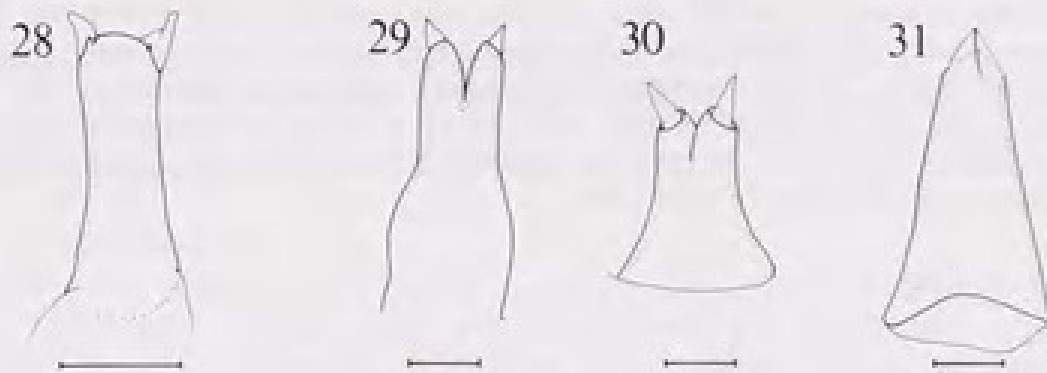
The apical lobes are extremely short to apparently absent, with small membranous tubes. The apical margin may be straight (Fig. 27), emarginate (Figs 24-26, the emargination interpretable as representing the sinus between the apical lobes, or as representing a bipartite median lobe) or convex (Fig. 23, interpretable as representing an undivided median lobe). The detailed penis shape seems to be species-characteristic in several cases, although there is some individual variability. For instance, the penis of *Catamicrophyllum caifanum* may be parallel-sided as shown in Figure 27, or the lateral margins may diverge slightly; the apical margin may be simple as in Figure 27, or slightly concave. In *Macheiroidulus libicus*, the penis may have regularly converging lateral margins, or may be parallel except basally; the apical margin may be entire, or shallowly trilobate as in Figure 22.



FIGS 26-27. — Scanning electron micrographs of penis in situ of Paectophyllini, posterior view. Part of the second coxae is also shown. 26: *Paectophyllum escherichii*, 27: *Catamicrophyllum caifanum*. — Scales: 0.1 mm.

Metaiulini

Metaiulus pratensis (Fig. 28), the only species of this tribe, has a penis which resembles that found in Paectophyllini and Calyptophyllini in being strongly sclerotized. Its shape also resembles that found in certain paectophyllines; in particular, the regularly convex apical margin, without any indication of a separation of two apical lobes, is a trait which is otherwise seen only in some *Catamicrophyllum* species (cf. Fig. 23).



FIGS 28-31. — Penis of Metaiulini (28) and Julini (29-31). 28: *Metaiulus pratensis*, 29: *Ophiulus major*, 30: *Leptoiulus disparatus*, 31: *Julus scandinavicus*. - Scales: 0.1 mm.

Julini

In the Julini the penis has well-differentiated apical lobes and membranous tubes. The apical lobes are usually very short (as in Fig. 4); those of *Ophiulus major* (Fig. 29), are quite unusual for the tribe. In most species the penis is slender, although in a few, e.g., *Leptoiulus disparatus* (Fig. 30), it is stout. The lateral margins are often straight and parallel but may also be converging or concave. STRASSER (1962) studied the penis in several species of Typhloiulini (part of Julini in the present sense) and found that the penis shape was often characteristic of genera/subgenera in this group (see Fig. 32).

The genus *Julus* itself seems to be characterized by a very constant penis shape (Fig. 31). The lateral margins of the slender penis are straight and converging, and the short apical lobes and membranous tubes are closely applied to each other, so that the apical outline of the penis is distinctively angled. This shape was seen in all *Julus* species examined by me and was also recorded in *Julus terrestris* L., 1758, and *Julus scanicus* Lohmander, 1925 by LOHMANDER (1925). Of the other genera referred to Julini s.s. by HOFFMAN (1980) I have examined *Haplopodoiulus* where the penis is, however, similar to that found in *Ophiulus* etc. On the other hand, the "typhloiulines" *Serboiulus lucifugus* and *Typhloiulus lobifer* appear to have penes like those in *Julus* (Fig 32, o, p).

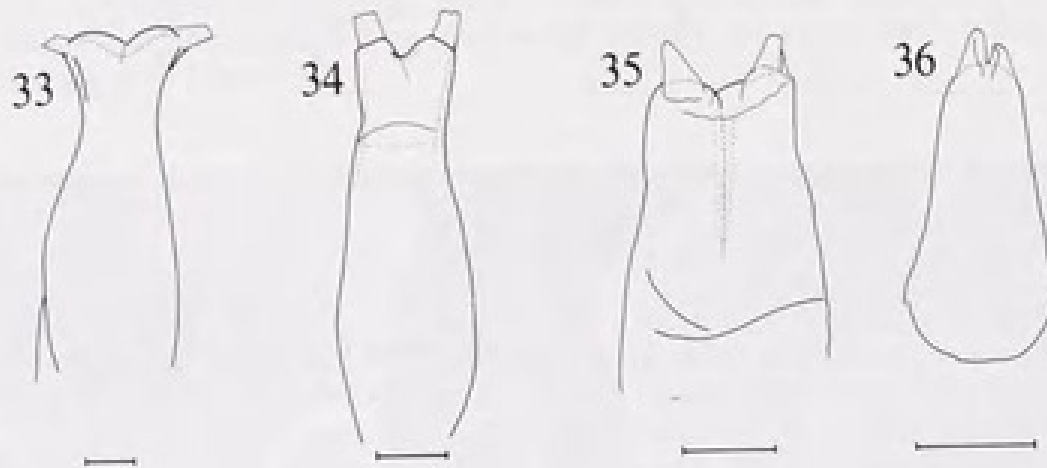
Cylindroiulini

Most Cylindroiulini have a slender penis with very short apical lobes and well-



FIG. 32. — Penis of various "typhloiulines" (Julini) (from STRASSER, 1962). a: *Buchneria sicula* Strasser, 1959, b: *B. cornuta* Verhoeff, 1941, c: *Trogloiulus mirus* Manfredi, 1931, d: *T. boldorii* Manfredi, 1940, e: *Typhloiulus serbani* (Ceuca, 1956), f: *T. iobias* Berlese, 1886, g: *T. maximus* (Verhoeff, 1929), h: *T. ausugi* Manfredi, 1953, i: *T. illyricus* Verhoeff, 1929, j: *T. montellensis* Verhoeff, 1930, k: *T. albanicus* Attems, 1929, l: *T. bureschi* Verhoeff, 1926, m: *T. psilonotus* (Latzel, 1884), n: *T. strictus* (Latzel, 1882), o: *Serboiulus lucifugus* Strasser, 1962, p: *Typhloiulus lobifer* Attems, 1951.

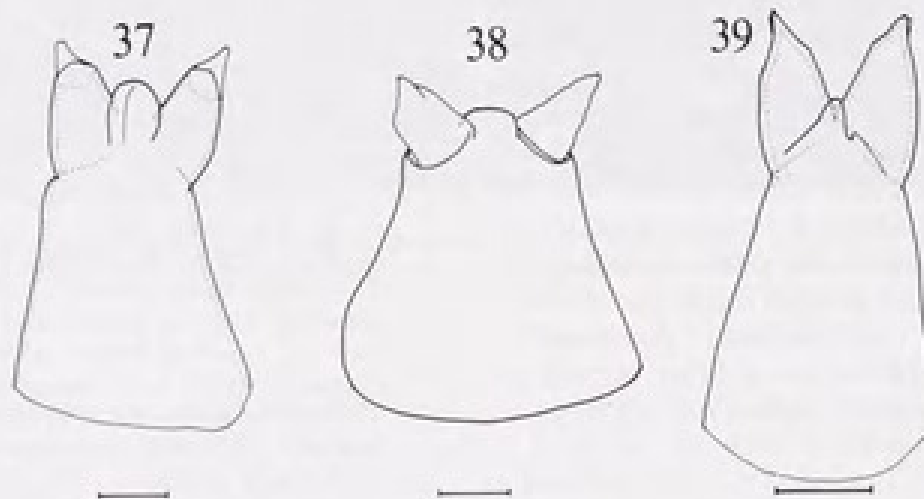
differentiated membranous tubes. The main difference from the Julini lies in the fact that the openings are separated by a distinct apical margin which is usually emarginate (Figs 3, 33, 34). *Cylindroiulus ruber* (Fig. 35) is somewhat deviating in being stouter. However, the penis of the closely related *C. bicolor* (cf. READ, 1992) looks like that found in most other cylindroiulines. *Styrioiulus pelidnus* (Fig. 36) deviates in having the lateral margins converging and the membranous tubes parallel close to each other.



FIGS 33-36. — Penis of Cylindroiulini. 33: *Cylindroiulus broti*, 34: *C. laurisilvae*, 35: *C. ruber*, 36: *Styrioiulus pelidnus*. - Scales: 0.1 mm.

Schizophyllini

Whereas the penis of *Tachypodoiulus* looks quite like that found in most Cylindroiulini, the examined species of *Ommatoiulus* differ in having a poorly sclerotized penis with a well-developed, undivided median lobe. In *O. rutilans* (Fig. 37) and *O. moreleti* the median lobe is remarkably well-developed: almost the same size as each of the well-differentiated apical lobes. In other species (Figs 38, 39) the median lobe is more modest. The apical lobes may be large and well-differentiated (Figs 37, 39) or virtually undifferentiated (Fig. 38).



FIGS 37-39. — Penis of Schizophyllini. 37: *Ommatoiulus rutilans*, 38: *O. kessleri*, 39: *O. navasi*. - Scales: 0.1 mm.

PHYLOGENETIC INTERPRETATION

In the light of the considerable variation in penis structure found both within the Julidae, and among julidan families, it appears worthwhile to examine whether penial characters may be useful for elucidating phylogenetic relationships. For the sake of clearness, the analysis is arranged in three hierarchical levels: family, tribe, and genus.

Family-level considerations

According to ENGHOFF (1981, 1991) the Julidae occupy a very subordinate phylogenetic position in the order Julida. The closest relatives of the family are, in descending order, three small families: Trichoblaniulidae, Rhopaloiulidae, and Trichonemasomatidae. Together with the Julidae, these families constitute the superfamily Juloidea, one of five superfamilies in the order.

The penis types found in the Julida can roughly be divided into four categories according to whether they are double (with separate gonopores) or single, and to whether they have setae or not (Fig. 1). Using the Spirostreptida as an outgroup (the penis in the third juliformian order, Spirobolida, is highly deviant and hardly comparable), one may conclude that a double, setose penis is primitive within the Julida. All examined Spirostreptida have double penes, and although both setose and naked penes occur in this order, it is regarded more likely that the penial setae have been lost several times independently than that they have arisen several times independently. (Furthermore, the preliminary observations on Spirostreptida suggest that there may have been only one loss of penial setae). In the Julida at least four losses appear to have occurred (Fig. 1).

As shown in Figure 1 the Julidae agree with other Juloidea in lacking penial setae, and they agree with Trichoblaniulidae and Rhopaloiulidae in having a double penis. Lack of penial setae can be considered apomorphic for Juloidea but is a weak character since several non-Juloidea share the character. The double nature of the julid penis is obviously plesiomorphic.

The two closest relatives of Julidae, Trichoblaniulidae and Rhopaloiulidae agree in having the penis extremely short and without differentiation into membranous tube and basal part (Fig. 40). The longer penis of Julidae could therefore be interpreted as an autapomorphy of the family, but this interpretation is counterindicated by the generally longer penes found in Trichonemasomatidae and non-juloid Julida.

The penis therefore does not provide any very useful phylogenetic information at family-level.

Tribe-level considerations

In his classification of Diplopoda, HOFFMAN (1980) recognized three subfamilies of Julidae but admitted that "this family may merit the distinction of being the most difficult family of all diplopod groups to resolve". At the present state of knowledge of julid intra-family

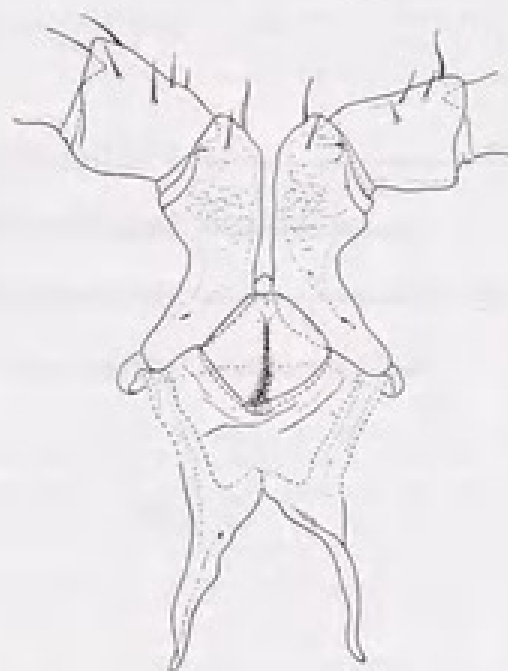


FIG. 40. — Penis in situ of *Trichoblaniulus hirsutus* (from BROLEMAN, 1923). The basal parts of the second legs are also shown, as are their tracheal apodemes.

phylogeny it therefore appears advisable to follow READ (1990) in only operating with one suprageneric categorial level: the tribe.

In the preliminary cladogram of julid tribes given by READ (1990) there is a basal trichotomy between Brachyiulini, Pachyiulini (incl. Pteridoiulini) and other julids. The "other julids" have a strong potential synapomorphy in the pro-mesomerital forceps of the gonopods, whereas neither of the two basal subfamilies have any convincing apomorphies.

The present study has confirmed the idea of VERHOEFF (1926-32): that the penis of Pachyiulini differs from that of other julids. Although the contrast is less striking than it appeared to VERHOEFF, the Pachyiulini are still distinguished by having a hyaline penis with relatively long, parallel apical lobes and no differentiated membranous tubes. Most other julids have the penis more or less sclerotized, the apical lobes are mostly shorter and are mostly directed obliquely lateral, and there are well-differentiated membranous tubes. Those non-pachyiulines which resemble the Pachyiulini in one or more penis characters are comfortably nested within groups with typical non-pachyiuline penis types. For instance, species of the genus *Ommatoiulus* have hyaline penes, and some species even have very long apical lobes. However, *Ommatoiulus* has convincing synapomorphies with *Tachypodoiulus*, the latter genus having a typical non-pachyiuline penis. *Ommatoiulus* + *Tachypodoiulus* (= Schizophyllini) in turn have synapomorphies with other non-pachyiulines (See READ, 1990: Fig. 16).

On the whole, the pachyiuline penis type more resembles that found in other julidan families, although the long apical lobes in Pachyiulini do not at all resemble the very short ones in Trichoblaniulidae and Rhopaloiulidae. In particular, the lack of differentiated membranous tubes is a trait shared with the non-julids.

The Pachyiulini might therefore tentatively be placed as sister-group to all other julids,

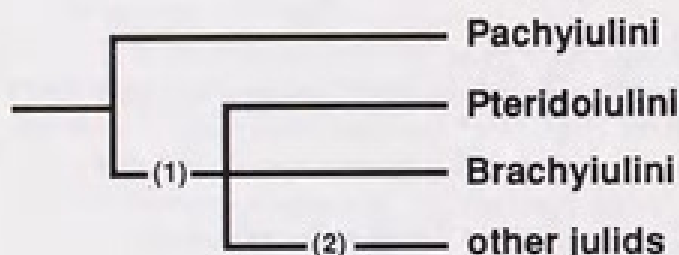


FIG. 41. — Tentative basal julid phylogeny. The non-pachyiulini penis type is a potential synapomorphy for non-pachyiuline julids (1). The gonopodal pro-mesomerital forceps is a potential synapomorphy for the "other julids" (2).

which are united by the potential synapomorphy: "non-pachyiuline" penis, with differentiated membranous tubes. Pteridoiulini would have to be included with the latter group, the penis of *Pteridoiulus* being obviously non-pachyiuline (see Fig. 41).

A second tribe-level relationship supported by penial characters is the sister-group relationship between Paectophyllini (= Catamicrophyllini + Paectophyllini + Symphyoiulini in HOFFMAN, 1980 and READ, 1990) and Calyptophyllini. (ENGHOFF, 1995). Whether the resemblance between the penis type found in these tribes and in Metaiulini has any phylogenetic significance, remains to be shown.

Genus-level considerations

Several julid genera have a consistent penis shape which in some cases may be regarded as a generic autapomorphy. This is probably true of

-*Anaulaciulus*, in which the apical lobes are diverging and are drawn out into long, finger-shaped projections (Fig. 12, see also KORSÓS, this volume).

-*Julus*, in which the lateral margins of the slender penis are straight and converging, and the short apical lobes and membranous tubes are closely applied to each other, so that the apical outline of the penis is distinctively angled (Fig. 31).

- perhaps some "Typhloiulini" (STRASSER, 1962).

-*Ommatoiulus*, in which the penis is poorly sclerotized and has a well-developed, undivided median lobe (Figs 37-39).

In some other cases, the potential significance of the penis lies at the subgeneric-species group level, as in some Typhloiulini (STRASSER, 1962) and in *Megaphyllum* (see above).

The penial similarity between *Tachypodoiulus* and *Cylindroiulus* deserves special mention, because this similarity would seem to support HOFFMAN's (1980) reallocation of *Tachypodoiulus* in the *Cylindroiulini*. It is, however, not clear whether the similarity is due to synapomorphy, symplesiomorphy or convergence, so the penial similarity cannot be regarded as a serious challenge to the similarities (in part clear synapomorphies) between *Tachypodoiulus* and *Ommatoiulus* mentioned by READ (1990).

CONCLUDING REMARKS

Although the phylogenetic conclusions of the present study may seem to be of modest extent, it is nonetheless obvious that future students of Julidae (and Juliformia in general) should pay more attention to penial characters than has been commonplace so far. A better understanding of the relationships between the numerous species of Julidae, many of which abound in a wide range of habitats in Europe, temperate Asia and (introduced) other temperate parts of the World, can only be achieved through consideration of all kinds of characters. Gonopods are good, but they are not everything.

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APPENDIX: EXAMINED SPECIES

With the exception of *Rhopaloiulus cameratanus*, all examined material belongs to the Zoological Museum, University of Copenhagen.

NB : The Paeromopodidae sensu ENGHOFF (1981, 1991) have recently been divided into two families: Paeromopodidae and the monospecific Aprosphylosomatidae (SHELLEY, 1994) which together constitute the superfamily Paeromopodoidea. The penis of *Aprosphylosoma darceneae* Hoffman, 1961, is double and setose (HOFFMAN, 1961: Fig. 5), like that found in Paeromopodidae *sensu stricto*.

Class DIPLOPODA

FAMILY JULIDAE:

Pachyiulini

- Amblyiulus barroisi* (Porat, 1893)
"A." creticus (Verhoeff, 1901)
Baskoiulus nammeri Verhoeff, 1938
Chertoiulus sphinx Strasser, 1962
Dolichoaiulus vossleri (Verhoeff, 1900)
 (+ 37 further spp. (see ENGHOFF 1992))
Japanoiulus lobatus Verhoeff, 1937
Mesoiulus ciliciensis Strasser, 1975
Pachyiulus flavipes (C. L. Koch, 1847)
Parapachyiulus recessus Golovatch, 1979
Rhoposiella heroni (Strasser, 1966)
Syrioniulus cf. andreevi Maurits, 1984
S. continentalis (Attems, 1903)

Pteridoiulini

- Pteridoaiulus aspidiorum* Verhoeff, 1913

Brachyiulini

- Megaphyllum adanense* (Verhoeff, 1943)
M. boanense (Verhoeff, 1897)
M. brachyurum (Attems, 1899)
M. geniculatum (Lohmander, 1928)
M. hercules (Verhoeff, 1901)
M. rossicum (Timotheev, 1897)
M. taylori (Strasser, 1976)
M. tenenbaumii (Jawlowski, 1931)
Brachyiulus apfelbecki Verhoeff, 1898
Anaalaciulus inaequipes Enghoff, 1986
A. tonginus (Karsch, 1881)

Leucogeorgiini

- Heteroiulus intermedius* (Brölemann, 1892)
Archileucogeorgia sp.
Chromatoiulus podabrus (Latzel, 1884)
Nepalmatoiulus himanicus (Pocock, 1893)

Oncoidulini

- Unciger foetidus* (C. L. Koch, 1838)

Paectophyllini

- Paectophyllum escherichii* Verhoeff, 1898
Macheiroaiulus compressicauda Verhoeff, 1901
M. libicus Manfredi, 1939
Symphysiulus impartitus (Karsch, 1888)
Mesomeritius indivisus Enghoff, 1990
Catamicrophyllum californum Verh., 1901
C. mesorientale Enghoff, 1995

Calypsohyllini

- Calypsohyllum digitatum* Enghoff, 1995
C. trapezolepis Enghoff, 1995

Metaiulini

- Metaiulus pratensis* Blower & Rolfe, 1956

Julini s.l.

- Julus scandinavicus* Latzel, 1884
J. colchicus Lohmander, 1936
J. subalpinus Lohmander, 1936
J. ghilarovi Gulicka, 1963
J. jedryczkowski Golovatch, 1981
Haploporoiulus spathifer (Brölemann, 1897)
Pachypodoiulus eurytus (Attems, 1895)
Hypoiulus alpinus (Verhoeff, 1897)
Ophiulus pilosus (Newport, 1843)
O. major Bigler, 1929
O. chilopogon (Berlese, 1886)
O. otellii Strasser, 1970
O. germanicus Verhoeff, 1896
O. targionii Silvestri, 1898
Leptoiulus brölemanni (Verhoeff, 1895)
L. cibelius (Chamberlin, 1921)
L. macedonicus (Attems, 1927)
L. proximus (Nemec, 1896)
L. disparatus Lohmander, 1936
L. belgicus (Latzel, 1884)
L. alemannicus (Verhoeff, 1894)
L. tanyomorphus (Attems, 1900)
Xestoiulus laeticoilis (Porat, 1889)
Pellipodoiulus schestoperoi Lohmander, 1932
Chaetoleptophyllum sp.
Sibiraiulus dentiger Gulicka, 1963
Pacificiulus imbricatus Mikhajlova, 1982

Cylindroiulini

- Allaiulus spinosus* (Ribaut, 1904)
Cylindroiulus brosi (Humbert, 1893)
C. laurilivae Enghoff, 1982
C. caeruleocinctus (Wood, 1864)
C. ruber (Lignau, 1903)
C. bicolor Lohmander, 1932
C. perforatus Verhoeff, 1905
C. lateli (Berlese, 1884)
C. propinquus (Porat, 1870)
C. punctatus (Leach, 1815)
Stryioidulus pelidnus (Latzel, 1884)
Enantoiulus dentigerus (Verhoeff, 1901)
Kryphioidulus occultus (C. L. Koch, 1847)

Schizophyllini

- Tachypodoiulus niger* (Leach, 1815)
Ommatoiulus cingulatus (Attems, 1927)
O. kessleri (Lohmander, 1927)
O. lapidarius (Lucas, 1846)
O. moreleti (Lucas, 1860)
O. navasi (Brölemann, 1919)
O. nivialis (Schubart, 1959)

- O. oxygyus* (Brandt, 1840)
O. rufians (C. L. Koch, 1847)
O. sabulosus (L., 1758)

FAMILY TRICHOBLANIULIDAE

- Trichoblanaiulus hirsutus* (Brölemann, 1889)

FAMILY RHOPALOIULIDAE

- Rhopaloiulus cameratanus* Attems, 1927

FAMILY TRICHONEMASOMATIDAE

- Trichonemasoma peloponnesius* (Maurits, 1966)

FAMILY NEMASOMATIDAE

- Nemasoma varicorne* (C. L. Koch, 1847)
Orinisobates spp.
Basanopus filiformis Enghoff, 1985

FAMILY PSEUDONEMASOMATIDAE

- Pseudonemasoma femorotuberculata* Enghoff, 1991

FAMILY CHELOIULIDAE

- Cheloiulus sculpturatus* Enghoff, 1982

FAMILY TELSONEMASOMATIDAE

- Telsonemasoma microps* Enghoff, 1979

FAMILY GALLIOBATIDAE

- Gallioabates gracilis* (Ribaut, 1909),
 see BRÖLEMANN 1923: Fig. 18)

FAMILY ZOSTERACTINIDAE

- Ameractis chirogona* Enghoff, 1982

FAMILY BLANIULIDAE

- (see Brölemann 1923: Figs 39, 57)

FAMILY OKEANOBATIDAE

- Okeanobates serratus* Verhoeff, 1939
Yosidaiulus tuberculatus Takakuwa, 1940

FAMILY PAEROMOPODIDAE

- Californiulus yosemitensis* Chamberlin, 1941

FAMILY MONGOLJULIDAE

- Skleroprotopus coreanus* (Pocock, 1895)

FAMILY PARAJULIDAE

- Aniulus* sp.
Karteroiulus alaskanus (Cook, 1905)
Urobaniulus sp.



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