

A CONTRIBUTION TO THE GENERAL MORPHOLOGY OF
PROTOJANIRIDAE (ISOPODA, ASELLOTA) WITH SOME
PHYLOGENETIC CONSIDERATIONS CONCERNING ASELLOTA

BY

B. SKET

Inštitut za biologijo, Univerza E. Kardelja v Ljubljani, p.p.141, YU 61001 Ljubljana,
Yugoslavia

Since most representatives of the superfamily Gnathostenetroidoidea have been described only for "microtaxonomical" purposes, some important features and even peculiarities of the species and probably of the entire group have been overlooked. I took advantage of possessing a good sample of the comparatively very large representative, viz., *Enckella lucei major* Sket, 1982 (as well as some other species of the family Protojaniridae) to demonstrate some such features. Unfortunately, of the family Gnathostenetroididae I could study only specimens of an undescribed species from the Bahamas, while comparison with other representatives was possible only through illustrations. I abstained from comparing *Enckella* with the numerous and diverse Janiroidea, leaving this to a more versed student of that special group. I also abstained from discussing the remarkable idea about possible Asellotan nature of *Microcerberidae* (Wägele, 1980) which is anyway of little importance for the present subject.

Cephalothorax ("head"). — With the exception of having two pairs of antennae, the *Enckella*'s head bears greater resemblance to a prognathous insect head than to an Asellid. The cephalic capsula is closed to a great extent, incorporating completely the first thoracomere. The capsula is closed and slightly sclerotised also behind the insertions of the maxillipeds, uniting them with the set of other mouth appendages. The clypeolabrum protrudes forwards, its inclination downwards is much less expressed than in most other groups of Isopoda. The mandibulae are inserted anteriorly, leaving the genal parts intact. Both pairs of antennae appear to be inserted into the fronto-dorsal plain of the head.

It seems that at least from the dorsal side the head is similar in all known species of *Protojanira* and *Anneckella*, as well as in *Gnathostenetroides* and in the Bahamian species. However, that is not the case with *Caecostenetroides* spp., if the published drawings of both species are compared (but the representation of the head is often inexact in taxonomic papers). In Asellidae as well as in

Stenasellidae the antennae are inserted frontally and the clypeolabrum is positioned steeply downward. At least in *Mexistenasellus* (Magniez, 1972, 1974) and in *Balkanostenasellus* the genal parts are also not affected by mandibular insertions, in contrast to *Asellus* or *Stenetrium*. In Stenasellidae thoracomere I with its maxillipeds is quite deeply incorporated into the cephalothorax, but not as deeply as in Protojaniridae. In *Asellus* and in *Stenetrium* the cephalic capsula appears to be completely open ventro-posteriorly, the gap is covered by the basal parts of the maxillipedes. In Janiroidea, at least *Thambema* and Eurycopidae seem to have to some extent an *Enckella*-like construction of the head (compare Schiecke, 1975, pl. 1; Haugsness & Hessler, 1979, figs.; Wilson & Hessler, 1980, fig. 3). The same seems to be true for *Jaera*, but the expressively peltate shape of its head makes a comparison difficult.

Pereion. — When contracted longitudinally, at least most Asellidae (some *Asellus*, *Proasellus*, *Caecidotea* spp.) and Stenasellidae (*Balkanostenasellus*, some *Stenasellus* spp.) put the anterior margins of all thoracic tergites (except the first) beneath the preceding ones. In *Enckella* and in other Protojaniridae, as well as probably in other Gnathostenetroidoidea and Stenetrioidea, the pereion is strictly bipartite. Pereionite IV is the crucial element, with free anterior and posterior margins. Pereionites I to III are put into each subsequent one. At least in the large *Enckella* this putting together is supported by a fork-like sclerotisation on the intersegmental membrane. Such sclerotisations are not developed posteriorly of pereionite IV.

The pereion seems to be similarly constructed in many Janiroidea, but little attention has been paid to it. At the moment it is impossible to say whether the *Enckella*-like composition of the pereion represents a general improvement, characteristic for entire taxa of a higher category (e.g., superfamilies) or that the pereion composition is a subject of repeated change, with regard to special requirements of the environment and habits.

In all pereionites of *Enckella* the sternal side is somehow less strongly sclerotized than the dorsal side, leaving even a narrow longitudinal strip of a pleura-like, largely unsclerotized, cuticula in the midline.

The coxae of the pereiopods in studied Protojaniridae are ring-shaped, they do not form epimera-like plates and are only slightly visible from the dorsal side.

Pleon. — In *Enckella* and in other Protojaniridae (contrary to what is shown in most original figures; see Sket, 1982) pleonite I is free and well developed, but small and almost hidden in the concavity of the last pereionite. The presence and importance of free pleonal somites in other groups have already been discussed by other authors (e.g., Wolff, 1962; Magniez, 1974; Fresi et al., 1980).

In most (all?) Asellidae, Stenasellidae, *Jaera*, *Stenetrium*, and probably in most other Asellota, pleopods I to V, or at least III to V, are very closely in-

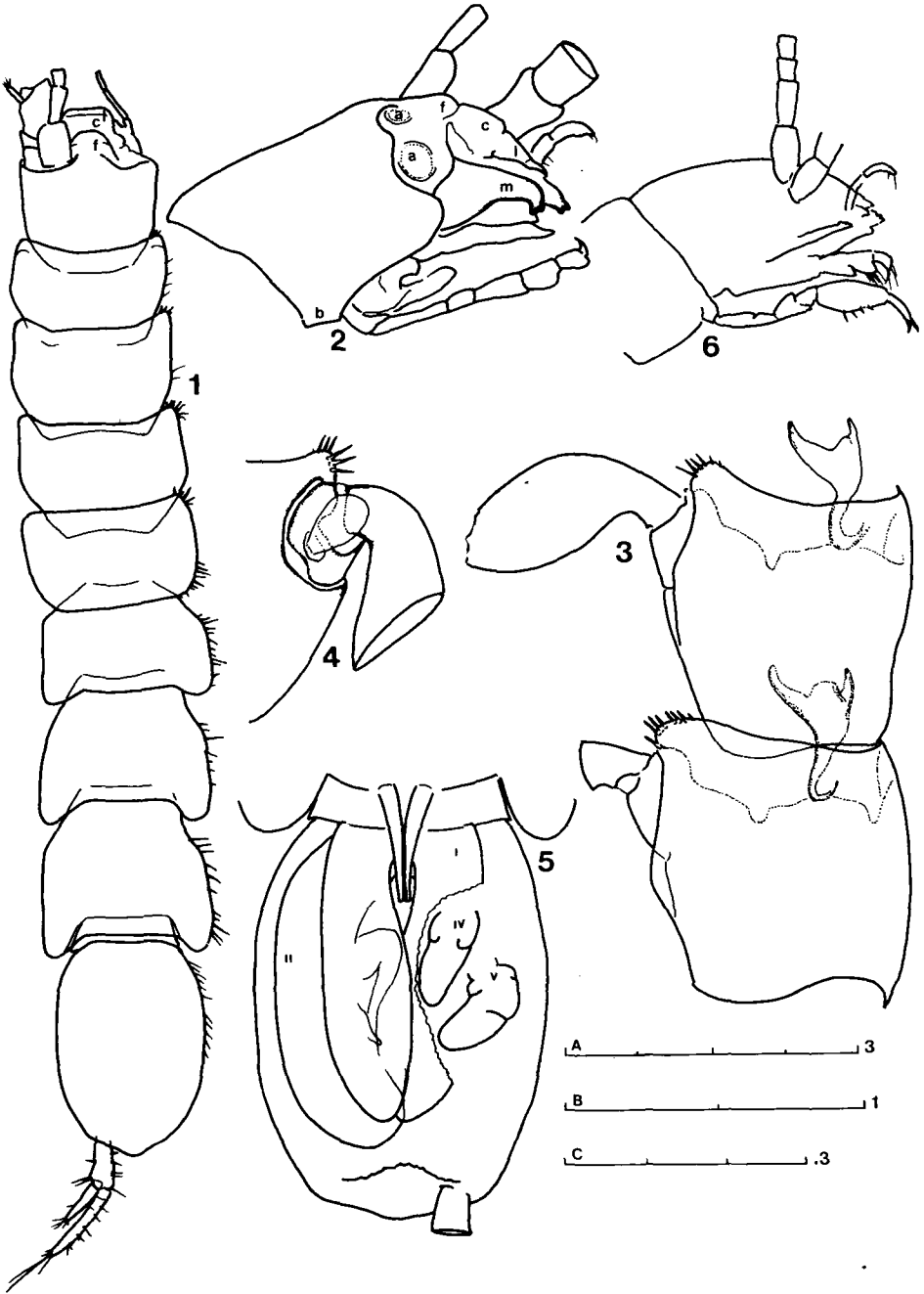


Fig. 1-5. *Encella lucei major* Sket. 1,5, ♂ 7.1 mm; 2-4, ♀ 8.9 mm. 1, body, dorsal side; 2, cephalothorax, laterally; 3, pereionites II-III, dorsolaterally; 4, basal parts of pereopod II, ventrally; 5, pleon, ventrally (schematic), with penes, pleopods I-II (left side), and IV-V (right side of figure). a, insertions of antennae I-II; b, basal symphysis; c, clypeus; f, frons; l, labrum. Scale (in mm): A (= 2 mm, not 3 as indicated), fig. 1; B, fig. 2-5; C, fig. 6.

served, forming a book-like group of leaflets. In *Enckella* and in other Protojaniridae pleopods IV and V are inserted separately, far behind the anterior margin of the pleotelson, along its ventral side. This is not necessarily a primitive situation (corresponding to the former articulation of the pleotelson); since these pleopods are reduced to a great extent (small and uniramous), it is possible that they have been displaced backwards by a coalescence of their basal parts with the ceiling of the pleotelson.

The reduction of one branch of the hind pleopods is not very rare even for specialised Asellidae (e.g. *Proasellus deminutus* Sket, 1965; *P. rouchi* Henry, 1980; *Calasellus longus* Bowman, 1981). Very characteristic is the papillose appearance of the soft parts of hind pleopods in Protojaniridae (see Sket, 1982, figs. 18, 22).

Operculum (σ). — In *Enckella* the male pleopods I are smaller than in other Protojaniridae (and Gnathostenetroididae) and therefore, do not completely cover the succeeding ones. An operculum is formed by combining pleopods I with the lateral and apical parts of the protopodite of pleopods II. Also in some other Protojaniridae the lateral parts of pleopods II share the opercular function; however, this does not seem to be the case in Gnathostenetroididae. (For other groups see phylogenetic discussion and table I).

TABLE I

Major steps in the development of pleopods I to III in Asellota (schematized). The sequence of figures does not represent the phylogenetic sequence in all details

	σ I	σ II	♀ II	III
Stenasellidae	A (-B)	A-D	A (C)	B
Asellidae	A-C	C	A (C)	B
Atlantasellidae	A	C	B	C
Stenetriidae	B-C	B	D	B
Gnathostenetroididae	D (-E)	D	E	A
Protojaniridae	E	E	E	A
Janiroidea	F	F	E	A-B

The male copulatory complex (penes + pleopods I-II). — Data are available neither for *Enckella*, nor for other Asellota—with the exception of *Asellus* (Maercks, 1930)—concerning the filling of the gonopods with sperma. But the composition of the complex makes it probable, that in Protojaniridae this act is carried out by protrusion of the penial papillae through the hole in the plate formed by pleopods I. The papillae are inserted closely together in the middle of pereionite VII. At the base of both branches of the just mentioned plate there is a well elaborated hole through which the penes, even in preserved specimens, always partly protrude. Thus, the statement by Chappuis &

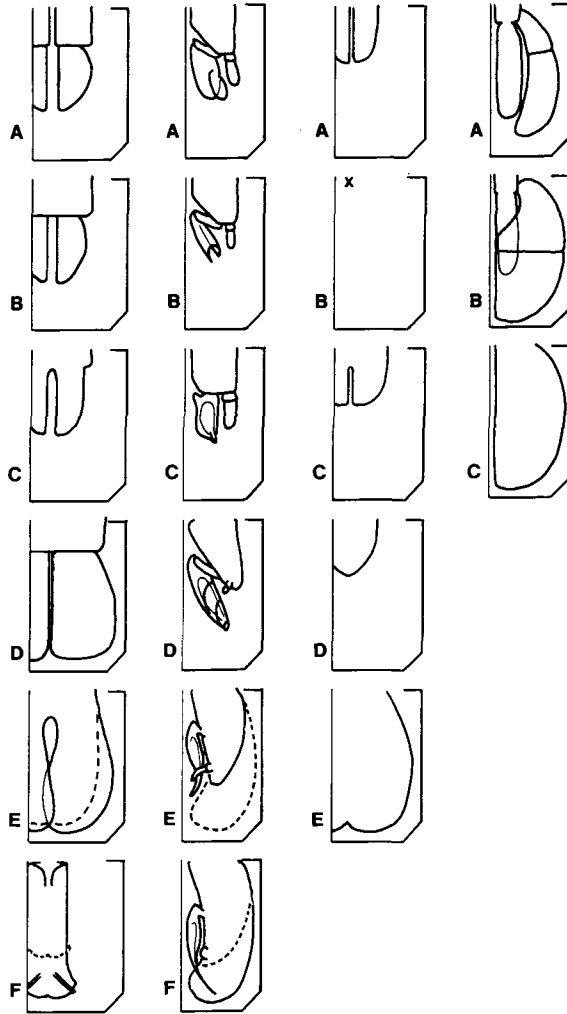


Fig. 6. *Anneckella srilankae rectecopulans* Sket, ♂ 1,3 mm, anterior part of body. Scale, see previous figure.

Delamare (1957) that in their new *Anneckella ficki* the penes are inserted near the bases of pereopods VII, is very confusing. If that statement is correct, the penes could touch pleopods II only laterally, since they are almost rectilinear.

In the new Bahamian Gnathostenetroid the situation is similar to that in *Enckella*. At least in drawings of other Gnathostenetroids an appropriate hole in the pleopods I is not visible and at least in *Caecostenetroides nipponicum* Nunomura the penes are inserted apart (laterally) (Nunomura, in litt.). In *Asellus aquaticus* (L.) the penes are moderately short and inserted apart, but nevertheless they protrude, during filling of the gonopods, between both

pleopods I (Maercks, 1930). In *Stenetrium longicorne* (Lucas) and *S. occidentale* Hansen the penes are inserted near the bases of pereopods VII. Even though they are very long and slightly curved backwards, it is easier to imagine that they reach the gonopods laterally and not between pleopods I.

The filling of gonopods has not yet been observed in any Janiroidea, where the fused pleopods I form a funnel, supporting subdistally the tips of the endopodites of the second pleopods. The penial papillae exhibit very diverse development and position. They can be inserted at the bases of pereopods VII (*Angeliera*; Coineau & Rao, 1972; Renaud-Mornant & Coineau, 1978) or close together (*Iais*; Coineau, 1977) or even fused (*Pseudasellus*; Chappuis, 1951). However, in most cases they are covered by the basal parts of pleopods I (Wilson, 1981), which in other species may obscure the total disappearance of penial papillae (as seems to be a case in *Jaera*). The ("macro"-)taxonomical importance of these features will be clarified only after a thorough study of the problem. However, one has to take into account that in the genus *Cirolana* Leach (Flabellifera) the penes can be very variable, from moderately long to absent (Barnard, 1940), but the function of the appendix masculina of the pleopod II in Flabellifera need not be the same as that of the gonopod in Asellota.

Digestive tract. — The stomach (proventriculus) of *Enckella* resembles that of *Jaera* (cf. Flasarova, 1969) in its elongated shape as well as in the armament of lateralialia and plicae laterales; but it is similar to that in some Stenasellidae (cf. Ličar & Sket, 1971) in lacking the primary filter ("scrapping plates"). For other Aselloidea (except Asellidae) the stomach structure is unknown. There is only 1 pair of hepatopancreatic caeca in *Enckella*.

Phylogenetic relationships within the Asellota. — The most recent review concerning the different views on the phylogeny of Asellota was published by Fresi, Idato & Scipione (1980). It is obvious that most authors consider Janiroidea to be the most modern group of Asellota. In my opinion this is strongly supported by the fact, that only Janiroidea succeeded in sustaining the competition of all possible competitors in comparatively favourable marine habitats, where they even developed into a great variety of different taxa. All other groups are either small or had almost escaped into less favourable fresh waters and partly even underground.

Unfortunately the ancestors of Asellota are unknown. In constructing phylogenetic trees we much too often unconsciously tend to derive modern taxa from other modern taxa of a presumably primitive character. We do not take into account that these animals have been developing parallelly, that many convergences occurred, and that some characters (e.g., copulatory complex, pleon concentration) improved separately, not always in combination with others.

At the moment it would be difficult to say whether the complex of pleopods I + II (sometimes I + II + III) took over the opercular function of pleopods III (or reverse), or had the operculum developed differently in two separate phyletic lines. The copulatory pleopods II probably exhibit the most primitive construction in *Magniezia* and *Stenetrium*. In one phyletic line (in higher Aselloidea) its endopodite became shorter, uniarticulate, and more complicate. In another the exopodite joined the endopodite (Protojaniridae) holding its outlet kennel (Sket, 1982, fig. 11), up to the grade, when the kennel became longer and pleopod I took over the function of exopodite II (Janiroidea). Already Barnard (1927) stated that the protojanirid type of pleopods I is the connecting link between the aselloid (resp. gnathostenetroid) and the janirid (described in details by Cvetkov, 1968) type of appendage. At the same time (simultaneously) sympodites of pleopods II could have been enlarged and joined pleopods I in forming the operculum. When the operculum is formed entirely by pleopods I + II, pleopods III can retain their primitive shape.

Parallel with the development of the opercular and copulatory complexes, some other features improved. First of all the pleon sometimes concentrated by diminishment of the free pleonites I-II (Aselloidea, Gnathostenetroididae, Stenetriidae), sometimes even by fusing pleonite II into the complex pleotelson (Protojaniridae, Janiroidea). Species or groups living predominantly in interstitial or similarly narrow-spaced habitats, often retained (or again obtained) long segmented parts of their pleons, thus retaining a greater flexibility. It is difficult to assess whether the groups with 2 and 1 free pleonites respectively represent two phyletic lines or whether they developed successively.

SUMMARY AND CONCLUSIONS

Some features of the general morphology of Protojaniridae are described and compared with those of some other Asellota. Characteristic is the very concentrated cephalothorax with a highly closed cephalic capsula, dorsally inserted antennae and prognathous appearance. The pereion is divided into two groups of somites, which are joined in a different manner. Penial papillae protrude through a specially arranged hole in the plate of pleopods I. Pleopods IV and V are inserted separately along the ventral side of the pleotelson. The diversity of the penes' position in Asellota is discussed.

Some new ideas concerning the phylogeny of Asellota are presented. The main phyletic line of development of the copulatory-opercular complex (not taking into account other characteristics of the mentioned genera!) most probably led through stages corresponding to *Magniezia* - *Caecostenetroides* - *Anneckella* - *Enckella* - *Jaera* (see table 1). Thus the *Asellus*-line should be an important side branch, where the development of the above mentioned complex separated in an early stage.

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RÉSUMÉ

Quelques traits de la morphologie générale des Protojaniridae sont décrits et comparés à ceux d'autres Asellotes. Caractéristique est le céphalothorax très concentré avec la capsule céphalique fortement fermée, l'insertion dorsale des antennes et l'aspect prognathe. Le péreion est divisé en deux groupes de somites, dont la liaison est différente. Les papilles péniennes émergent par un orifice spécialement disposé dans la plaque des pléopodes I. Les pléopodes IV-V sont insérés séparément le long du bord ventral du pléotelson. La diversité de la position des pénis chez les Asellotes est discutée.

Quelques idées nouvelles sont présentées, relatives à la phylogénie des Asellotes. La principale ligne phylétique de développement du complexe operculo-copulateur (sans tenir compte des autres caractéristiques des genres cités plus loin) passe probablement par des stades correspondant à *Magniezia* - *Caecostenetroides* - *Anneckella* - *Enckella* - *Jaera* (voir tabl. I). Ainsi la ligne *Asellus* représenterait une importante branche latérale, où le développement du complexe mentionné ci-dessus se serait séparé à un stade précoce.

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