

ASPECTS OF THE EVOLUTION AND ORIGIN OF THE DEEP-SEA ISOPOD CRUSTACEANS

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A study of the morphology of some isopod taxa suggests that Protallocoxoidea (Asellota) and Plakarthriidae (Flabellifera) represent the most ancient groups of extant isopods. The main reason is the presence of free coxae of the first pair of pereopods. The Stenetrioidea (Asellota) probably evolved from ancestors like *Protallicoxa*. The present distribution of the three taxa does not reveal the center of their evolution.

Studies of cave-living oniscoids in the New World and Europe combined with our knowledge of the development of the Atlantic suggest a time-scale of 150 million years for the evolution of taxa to the subfamily level. Whether or not this time-scale is applicable also for marine isopods is unknown. The evolution of the isopods as well as the origin of deep-sea species is still poorly understood.

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INTRODUCTION

There are three recent hypotheses on the origin of the deep-sea isopods. According to MENZIES & al. (1973) present-day deep-sea isopods originated in the shallow waters of the polar regions, especially the Antarctic, after the warm periods of the Mesozoic were followed by polar cooling. KUSSAKIN (1973) assumed that the most primitive isopods developed on the continental shelves in the tropics. They then evolved into groups which were well represented in the shallow waters of the polar regions. From there they immigrated into the deep-sea. HESSLER & THISTLE (1975) argued, however, that some janiroidean isopod groups evolved in the deep-sea and from there they emerged to the cold waters of the polar regions. They did not give any clues as to where in the deep-sea they might have evolved and they limited their discussion to the Ilyarachnidae and only by implication included other groups. Thus the present-day distribution of the asellotes in the deep-sea or along the continental shelf does not provide direct evidence of their evolutionary origin.

Each hypothesis is based on the analyses of many taxa of isopods, especially from the suborder Asellota. All the other suborders of isopods are mainly restricted either to shallow marine, terrestrial, or limnic habitats. Some abyssal species are, however, found among the Valvifera, Gnathiidea, and Anthuridea, and a de-

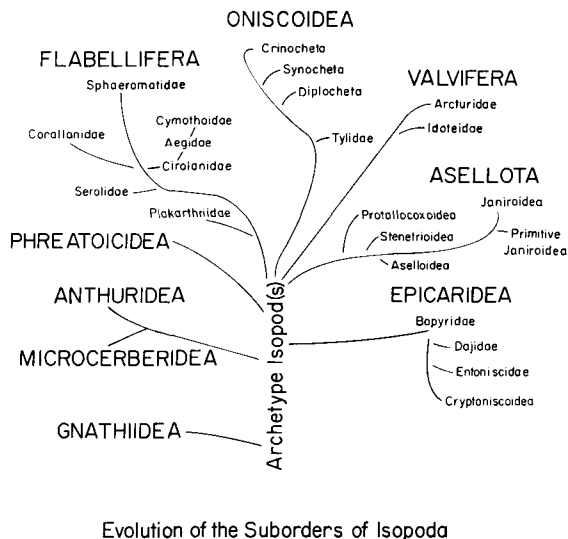
tailed study of them might reveal more about the evolution of the isopods in general.

The distribution and morphology of some particular taxa of isopods (e.g. Stenetrioidea, Plakarthriidae, and *Glyptonotus*) are discussed. The morphology and distribution are examined to discover if obvious indications of the evolution and geographic origin of the deep-sea isopods is in any way indicated. It is also suggested that the terrestrial isopods (Oniscoidea), especially species adapted to live in caves, be examined using the time scale provided by continental drift to determine the rate of speciation and of new taxa formation. This knowledge along with that of distribution and morphology can then be applied to the study of the evolution of the other suborders and to the evolution of the order Isopoda in general. A phylogenetic picture of the suborders of isopods is shown in Fig. 1, and a classification of the Asellota in Table 1.

DISCUSSION

Superfamily Protallocoxoidea (Asellota)

The evolutionary pattern of the Asellota shown in Fig. 2 is similar to that suggested by MENZIES & IMBRIE (1958) with the exception of the recently described superfamily Protallocoxoidea (SCHULTZ 1978.) This group represents one of the most ancient or primitive of the marine asellotes and it is closer related to the marine Stenetrioidea than to the freshwater asellids.



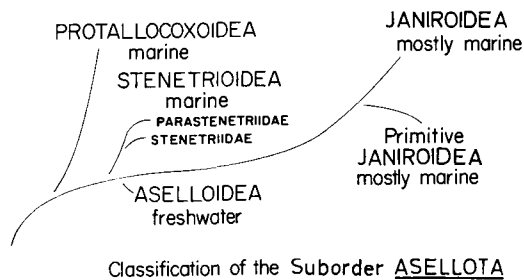
Evolution of the Suborders of Isopoda

Fig. 1. Evolution of the suborders of Isopoda.

Primitive features for these two taxa include squama or antennal scale (vestigial exopod), six peduncular articles on antenna 2, two pleonal segments, operculate pleopod 3 of female and

Table 1. Classification of Asellota

Superfamilies
Protallocoxoidea SCHULTZ 1978
Protallocoxidae SCHULTZ 1978
<i>Protallocoxa weddellensis</i> SCHULTZ 1978
<i>Protallocoxa</i> sp. nov. SCHULTZ 1979
Stenelrioidea (c. 44 spp.)
Stenetriidae HANSEN 1905
<i>Stenetrium</i> HASWELL 1881 (c. 42 spp.)
Gen. nov. SCHULTZ 1979
(1 sp., <i>S. siamense</i> HANSEN 1905)
Gen. nov. SCHULTZ 1979
(1 sp. nov. SCHULTZ 1979)
Parastenetriidae AMAR 1957
(all tiny, can only be told from janiroidaeans by male pleopods)
<i>Gnathostenetriodes</i> AMAR 1957
(1 sp. <i>G. laodicense</i> AMAR 1957)
<i>Maresia</i> FRESI 1973
(1 sp., <i>M. barringtoniana</i> FRESI 1973)
<i>Caecostenetriodes</i> FRESI & SCHIECKE 1968
(1 sp., <i>C. ischitanum</i> FRESI & SCHIECKE 1968)
<i>Caecostenetriodes nipponicum</i> NUMOMURA 1975
Aselloidea
Asellidae
<i>Asellus</i> (many species)
Many other genera
Janiroidae
Many families (c. 19)
Most genera of asellotes
Primitive with 2 free pleonal segments
Advanced with 1 or no free pleonal segment



Classification of the Suborder ASELLOTA

Fig. 2. Evolution of the superfamilies of Asellota.

small pleopod 1 of male (with unique pleopod 2 of male) (HANSEN 1905; MENZIES & IMBRIE 1958). Other primitive features are: anus outside of branchial cavity, large number of flagellar articles on antenna 1, and well developed molar process on mandible.

In addition there is a notable feature in *Protallocoxa* (Fig. 3) in that the lateral extensions

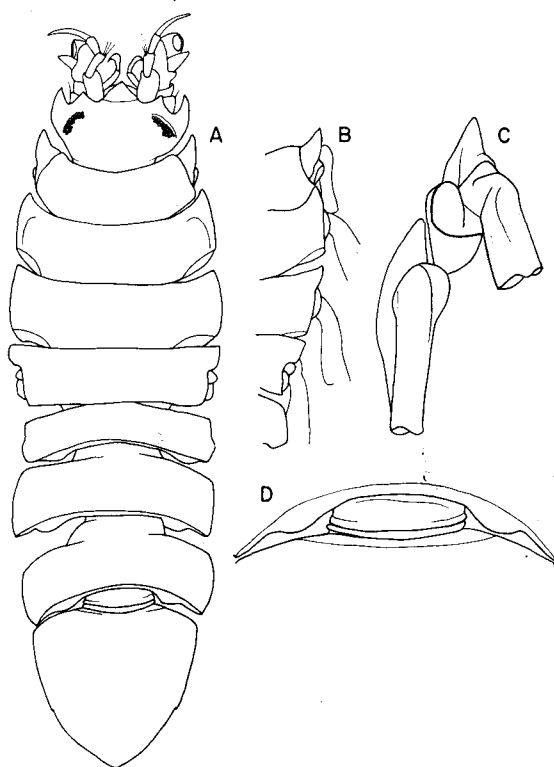


Fig. 3. *Protallocoxa* sp. A. In dorsal view. B. Lateral parts of pereonites 1-5 in dorsal view. C. Proximal parts of pereopods 1-2 with free coxal segment on pereopod 1. D. Anterior segments of abdomen in dorsal view.

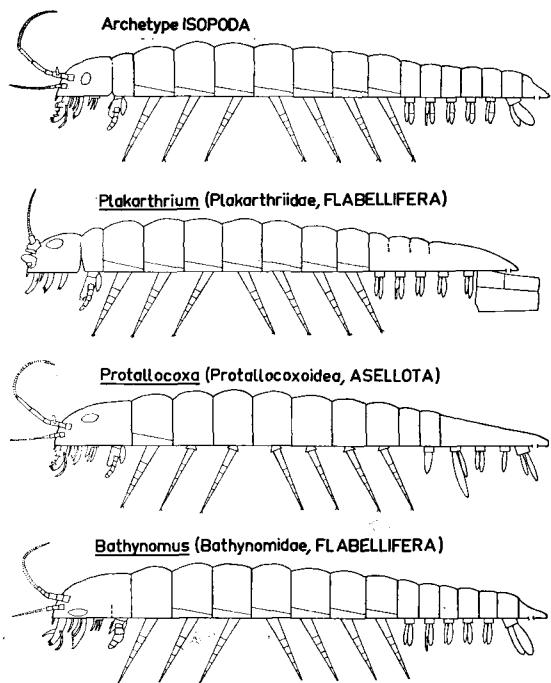


Fig. 4. Schematics of archetype isopod and three primitive representatives of Flabellifera and Asellota.

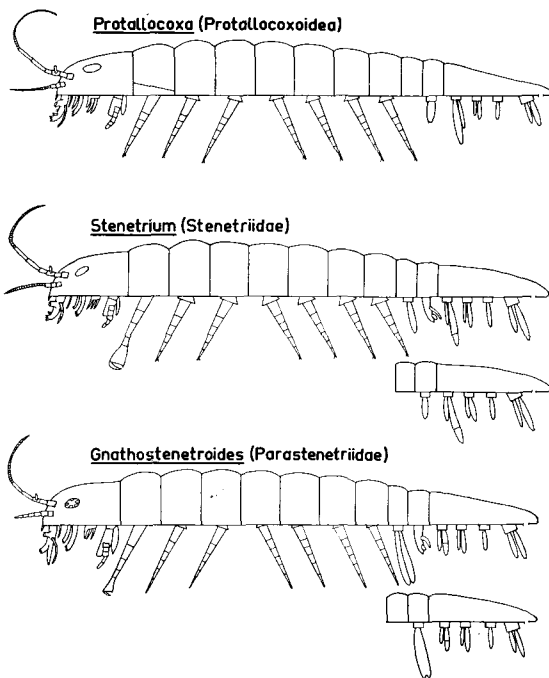


Fig. 5. Schematics of three superfamilies of Asellota.

of the first pereopod segment comprise the free coxal segments of the first pereopods. Thus the coxae are not fused with the pereopod as they are on the first pereopod segment of most other isopods. Such a feature is found only in *Protallocoxa* and the Plakarthriidae (Flabellifera) among the isopods and I therefore regard these two groups as among the most ancient of the extant isopods (Fig. 4). Free coxal segments on pereopods II to VII are present on many isopods and are especially easy to see on common cirrolanids.

In attempting to understand the evolution of the species of Stenetrioidea and Protallocoxoidea the present day distribution and data from depth records is analyzed here.

Superfamily Stenetrioidea (Asellota)

The genus *Stenetrium* (based on *S. armatum* HASWELL from Port Jackson, Sydney, Australia) is the most generalized and ancient of the Stenetrioidea (Fig. 5). It is from ancestors like *Protallocoxa* that the species of Stenetrioidea evolved. The species of the group are discussed in detail in a paper now in press (SCHULTZ 1979). The approximately 46 species of Stenetrioidea (both

Stenetriidae and Parastenetriidae) are distributed in ecologically diverse habitats from the Antarctic seas north to the Mediterranean and to Hawaii in the Pacific. They are especially well represented in the West Indies and two species are from Bermuda. The superfamily is well represented among the islands of the tropical Pacific and in Australia and New Zealand. South Africa has nine representatives. The collections made by the R/V *Eltanin* from off Argentina and in Antarctic waters contained seven species. Species of the group are absent only in the northern temperate and Arctic regions. Thus the distribution of its species is similar to that of Serolidae although that family is not well represented in the shallow tropics.

Depth records of 46 species of Stenetrioidea show that over half (28) were collected in shallow water, 12 from depths between 82 and 680, and 6 from over 1097 m with 3 of them from depths over 3000 m. Two of the species from the Antarctic region have wide bathymetric ranges (150–3397 m, *S. acutum* VANHÖFFEN; 150–1480 m, a new species from north of South Georgia, lacking eyes, and apparently belonging to a

monotypic new genus, SCHULTZ 1979). The deepest record for any species is 4696 m.

The ecology of species of the superfamily is poorly known. Many species are found on algae and encrusting organisms in the littoral zone. One blind species (there are only two) lives interstitially in the sands of the Bay of Naples while other species have been recorded from the deep-sea soft bottoms. Most likely the habitat diversity within the Stenetrioidea is greater than the few ecological observations indicate.

There is, however, no immediately apparent pattern of evolution among the species as judged from the geographical or bathymetric distribution. Their ancient origin is indicated by their morphology and most likely they evolved from the morphologically more primitive *Protallicoidea*. The species of *Protallicoxa* are perhaps relict species, evolutionary left overs from a time when they were more widely distributed. No indication remains of their center of evolution. There are only many related species from many different habitats and locations so at this time we can only state that they evolved in place from more primitive types which are now extinct.

Other groups of interest are the Haplonicidae, a family of highly specialized deep-sea Asellota, the Plakarthriidae and Serolidae, two families of primitive Flabellifera, and *Mesidotea* and *Glyptonotus*, two primitive genera of Valvifera. The groups will be discussed in terms of my understanding of the archetype isopod.

Family Haplonicidae (Asellota)

The approximately 73 species of this family are especially well represented in the deep-sea. They are referred to five genera with inconspicuous but consistent morphological differences. The general morphology is highly modified when compared both to that of the generalized, advanced, and primitive Asellota (Fig. 6). The pereopodal segments are sometimes fused with the pleon. The abdominal segments are always fused but laterally they can most often be discerned. The mouth parts and the pleopods are primitive. The maxillipedal palp and molar process are present, and the other mouth parts are only slightly altered in their general pattern from that of the primitive asellote. The pleopods are of the general janirioidean type. Although advanced in many characters the Haplonicidae have retained a number of primitive or more

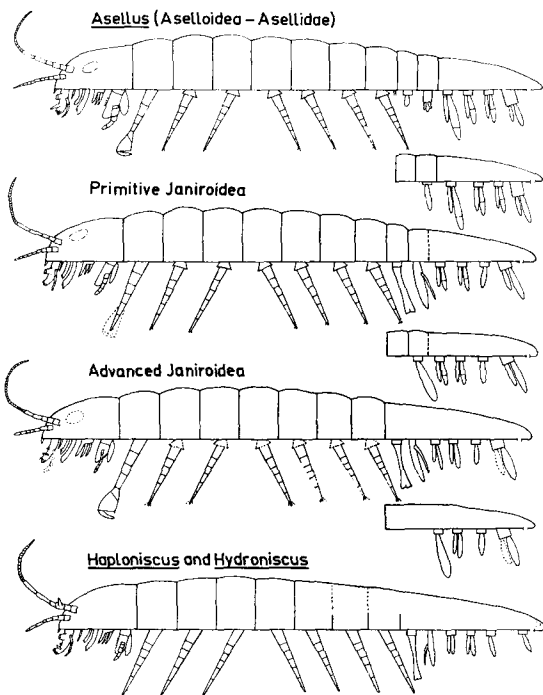


Fig. 6. Schematics of the superfamily Aselloidea and three groups of janirioideans.

conservative characters showing that the family evolved early during the evolution of the aselotes.

Family Plakarthriidae (Flabellifera)

The family comprises only one genus, *Plakarthrium*, with two species, which were recently redescribed by WILSON & al. (1976). *P. punctatissimum* (PFEFFER) has been recorded from the region of the Antarctic Peninsula, southern South America, and some of the subantarctic islands, e.g. the islands of Bouvet, Crozet, the type-locality at South Georgia, and perhaps Kerguelen. It is known from both the shallow water off South America and the shallow water off the Antarctic Peninsula, and is the only species to be so distributed. *P. typicum* CHILTON is known from New Zealand. Both species occur from the intertidal zone down to 110 m, thus being part of both the littoral and shelf faunas. Probably it was more widely distributed in the past.

Specimens of *Plakarthurium* are rarely over 5 mm long. They are ovoid, dorsoventrally flattened, and apparently well adapted to cling to hard substrates. They are often found in sponges and on algae and can best be compared ecologically to *Cassidinidea ovalis* (SAY), another small flabelliferan. They also resemble Oniscoidea of the genus *Armadilloniscus*. The *Plakarthurium* species apparently cling to hard substrates and press their bodies against the surface to form scale-like protrusions on it.

The ancient origin of the family is demonstrated by the presence of a free coxal extension on pereopod I (like in species of *Protallocaloxa*) (Fig. 4). There is also a maxillipedal or occipital groove on the posterior margin of the cephalon. A highly specialized feature is found in the shape of the uropods which form what are most probably valves which open and close the branchial cavity and regulate the flow of water through it while the animal clings to the substrate. This apparatus is unique among the isopods.

The two species have been placed in a separate family because of the uncommon combination of primitive and specialized characters.

Family Bathynomidae (Flabellifera)

In my opinion the species of *Bathynomus* are of a primitive cirolanid type and probably as much related to the terrestrial Oniscoidea as to any other isopod. *B. giganteus* MILNE EDWARDS, from the shelf off Georgia and the Gulf coast, ranges up to 46 cm long and is thus the largest of all isopods. The six free coxal segments and five free pleonal segments are the only primitive characters, although six definitive peduncular articles are present on antenna 2 (Fig. 4). The species, at least *B. giganteus*, have a well marked maxillipedal segment on the posterior margin of the cephalon. Except for the six peduncular articles and the maxillipedal segment on the cephalon, the bathynomids share most of the characters with members of the cirolanids, and are really just more or less overgrown primitive cirolanid types.

Family Serolidae (Flabellifera)

Species of Serolidae have a primitive morphology. With one exception all belong to the genus *Serolis*. They are circumantarctic and also found northward to just above the northern subtropical region, thus further north than

species of Stenetrioidea, which, however, are limited to shallow tropical and subtropical waters. *Serolis* contains many species with a quite diversified morphology. All are broad and flat which apparently is a modification for exploiting the upper few millimeters of the mud and sand. Which species of the genus are most primitive and which are more advanced will not be discussed here, but the general morphology of the group is definitely primitive although it is also highly specialized to meet the requirements of its particular habitat. It has at least a partially separated coxal segment on pereopod I, but this is visible only in ventral view of the segment (Fig. 7). Coxal segments are obvious on segments II, III, and IV, but visible only ventrally on segments V to VII. This suggests that the species of Serolidae are related to those of Plakarthuridae.

Valvifera

Glyptonotus is a genus of Valvifera with one species, *G. antarcticus* EIGHTS. It is exclusively from the Antarctic where it has a wide depth range, intertidal to about 1000 m. It is large (up to 14 cm long), primitive, and apparently fairly abundant. It is found in the McMurdo region and abundant at the Antarctic Peninsula and off South Georgia as well as other subantarctic islands. It definitely is circumantarctic in distribution.

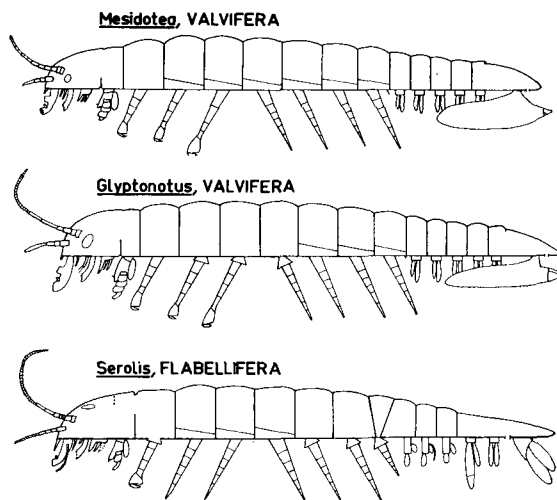


Fig. 7. Schematics of two valviferan and one flabelliferan isopods.

That the species is a primitive valviferan is shown by the presence of four free pleonal segments and six free coxal plates (Fig. 7). Three of the free coxae are apparent dorsally and three only ventrally. Otherwise *G. antarcticus* is much like most other species of Valvifera. It is related to *Mesidotea*, a circumarctic genus of several species, which live in habitats comparable to the littoral and deep-water habitats of *Glyptonotus*. They might be considered more primitive than *Glyptonotus* because all six free coxae are visible in dorsal view. The two genera are otherwise morphologically similar (Fig. 7).

Some fossils from eastern Europe have been named *Proidotea*. The specimens have a general body configuration similar to that of *Glyptonotus* and *Mesidotea*.

Oniscoidea (terrestrial isopods)

Both the Trichoniscidae and Philosciidae have members which cannot be overlooked when considering isopod evolution. Both families contain many species which are adapted to live in forest leaf litter, but each also contains many members which live exclusively in caves. Like many deep-sea asellotes, the species which live in caves are blind and lack pigment showing a parallel in morphology to deep-sea species. One such species of trichoniscid inhabits caves in Mexico where it lives in pools. It is thus truly aquatic although it is an oniscoid. It is not related to the asellids, the common freshwater isopods of streams, lakes, and underground water. Another closely related species also lives in the cave pools in Spain. It has been postulated that the two related species were separated from a single population when the continents split. The caves of both the New World and Europe contain a rich and diversified series of other species of trichoniscids and to a lesser extent philosciids which might be studied in terms of their evolution as related to continental drift. For these species from caves there is thus a generally accepted time scale involved in their evolution.

The continents separated 150 to 185 million years ago so genetic isolation of the various populations of cave-living species started then. After this long time the isolated species are separated only at the generic and subfamily levels. Perhaps evolution is faster in marine environments than on land or in caves, but since the oniscoids, in spite of as much as 150 million

years of evolution, have not evolved into taxa higher than subfamilies it is suggested that a time much greater than that is necessary for the evolution of families and higher taxa.

The cave and also non-cave oniscoids have been the subject of many studies on distribution related to continental drift. These studies should be used to determine what they can contribute to our knowledge of the evolution of both terrestrial and marine isopods in general and perhaps to the knowledge of the speed of speciation in particular.

Fossil records and general conclusions

Although I have looked at many primitive species and groups of marine and terrestrial isopods, I have only a vague idea of how they are related through evolution. It would seem that most of the suborders of isopods were well defined before the Trias (185 million years ago); that is, before the Atlantic was formed. Most superfamilies and well-defined families were also present at this time. All families which are defined today probably could be distinguished well before or at least by the end of the Mesozoic (60 million years ago).

The only suborder which has a well defined fossil record is the Phreatoicoidea. The record extends back beyond the Mesozoic to more than 225 million years ago. Fossils are best defined in Australia, but a specimen (the oldest known fossil isopod) has been found in the Middle Pennsylvanian of Illinois in North America. Species presently live in rivers and ground water in Australia, South Africa, and India, but the fossil record suggests that they were even more widely distributed. The group has a primitive morphology which suggests that it is at least as old and perhaps older than the oldest Flabellifera. According to MENZIES & al. (1961) fossils recognized as Sphaeromatidae were present at the beginning of the Mesozoic. This is in my opinion one of the most advanced and successful groups of Flabellifera. Serolidae by comparison is much older and Plakarhriidae even older than Serolidae. Unfortunately neither have a fossil record. This suggests that the Flabellifera is a very old group. *Bathynomus*, or a closely related form, is represented in the Eocene of England (about 40 million years ago), but, in my opinion, it is a relatively recent flabelliferan. The Flabellifera then, although the fossil record does not show it, is probably as old or older than the Phreatoicoidea.

The Oniscoidea and Valvifera are unfortunately only known as fossils back to the beginning of the Cenozoic (50 or 60 million years ago). Thus the fossil record includes no really old forms, but their morphology suggests that they evolved at least as early as the Phreatoicoidea and Flabellifera, so that they are much older than indicated by the geological record.

Unfortunately no fossil Asellota are known so the age of the Protallocoxoidea and other asellotes can only be extrapolated by comparing this group to other isopods with similar morphology. The group is at least as old as the Plakarthriidae of the Flabellifera, and it is in my opinion like them pre-Mesozoic in origin. The evolution of the isopods and the origin of the various taxa as well as ecological groups such as the deep-sea species remain enigmatic and must be subjected to more study.

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