

- ENGELMANN, G. F.; WILEY, E. O., 1977: The Place of Ancestor-Descendant Relationships in Phylogeny Reconstruction. Syst. Zool. 26, 1-11.
- ELDRIDGE, N.; CRACRAFT, J., 1980: Phylogenetic Patterns and the Evolutionary Process. New York.
- HENNIG, W., 1949: Zur Klärung einiger Begriffe der phylogenetischen Systematik. Forschungen u. Fortschritte 25, (11/12) 136-138.
- 1950: Grundzüge einer Theorie der phylogenetischen Systematik. Berlin: Deutscher Zentralverlag. Univ. Illinois Press.
- 1966: Phylogenetic Systematics. Urbana: Univ. Illinois Press.
- 1969: Die Stammesgeschichte der Insekten.
- 1974: Kritische Bemerkungen zur Frage „Cladistic analysis or cladistic classification?“ Z. zool. Syst. Evolut.-forsch. 12, 279-294.
- 1982: Phylogenetische Systematik. (Deutsche Fassung von HENNIG, W., 1966: Phylogenetic Systematics). Berlin und Hamburg: Paul Parey.
- HENNIG, W.; SCHLEE, D., 1978: Abriß der phylogenetischen Systematik. Stuttgarter Beitr. Naturk. A 319, 1-11.
- LORENZEN, S., 1976: Zur Theorie der phylogenetischen Systematik. Verh. Dtsch. Zool. Ges., 229.
- 1981: Entwurf eines phylogenetischen Systems der freilebenden Nematoden. Veröff. Inst. Meeresforsch. Bremerhaven Suppl. 7, 1-472.
- MAYR, E., 1969: Principles of systematic zoology. New York: McGraw-Hill.
- SCHLEE, D., 1971: Die Rekonstruktion der Phylogenese mit HENNIGS Prinzip. Aufsätze u. Reden d. Senckenberg. Naturforsch. Ges. 20.
- TUOMIKOSKI, R., 1967: Notes on some principles of phylogenetic systematics. Ann. Ent. Fenn. 33, 137-147.
- VAN VALEN, L., 1978: Why not to be a cladist? Evolutionary Theory 3, 285-299.
- WILEY, E. O., 1981: Phylogenetics - The Theory and Practice of Phylogenetic Systematics. New York, Chichester, Brisbane: J. Wiley & Sons.
- WILLMANN, R., 1976: Zur Kenntnis der italienischen Mecoptera (Insecta). Boll. Mus. Civ. St. Nat. Verona III, 157-177.
- 1981: Evolution, Systematik und stratigraphische Bedeutung der neogenen Süßwassergastropoden von Rhodos und Kos/Ägäis. Palaeontographica A 174, 10-235. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

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On the origin of the Microcerberidae (Crustacea: Isopoda)

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Received on 3. January 1983

Introduction

When investigating the subterranean fauna of Macedonia, KARAMAN (1933) discovered several new Crustacea, among them a new isopod, *Microcerberus stygius*, of enigmatic origin and relationship. The tiny, slender animals were regarded as possible relatives of the marine Anthuridea, a group of elongated Isopoda, some of which use to burrow in the sediments of brackish lagoons and estuaries (genus *Cyathura*) and therefore seemed to be pre-adapted to the colonization of subterranean freshwater habitats. Later on species of the genus *Microcerberus* were found in many parts of the world, mainly in the brackish groundwater of sandy beaches, and for a long time they were included in the suborder Anthuridea (KARAMAN 1933; REMANE and SIEWING 1953; CHAPPUIS and DELAMARE 1954; PENNAK 1958) or at least they were considered as relicts, whose ancestors had been primitive Anthuridea (LANG 1960; COINEAU 1969; SCHULTZ 1969, 1974; KUSSAKIN 1973). LANG (1960)

perceived some differences in the morphology of Anthuridea and *Microcerberus* and proposed to keep the microisopods in a separate suborder, which despite of all differences was thought to have had a common origin with the Anthuridea. MAGNIEZ (1974) remarked that there were similarities between the Microcerberidea and the Stenasellidae, and WÄGELE (1982 b) finally rejected any possible connections of the Microcerberidea with the Anthuridea.

Two recent discoveries brought new light into the dark around the origin of the Microcerberidea. In a cave of the Bermudas SKET and ILIFFE discovered a tiny isopod (*Atlantasellus cavernicolus* Sket, 1979) with a sphaeromid-like habitus but obvious aselloid features (SKET 1979). As these animals could neither be placed within the family Asellidae nor in the Stenasellidae, the new family Atlantasellidae Sket, 1979 was erected. The published drawings of these animals revealed some astonishing similarities with typical features of the Microcerberidea. The second discovery pertains to some new types of Microcerberidea collected in Malawi and in the Krueger National Park (WÄGELE 1982 c). These animals have several primitive features, which are remarkable for their occurrence in freshwater far from the sea. So the possibility must be considered, that these species are primary freshwater animals. Their morphology is that of asellote isopods, the pereopods still have a coxa in contrast not only to the marine Microcerberidea but also to most other Isopoda. These discoveries have several consequences. The systematic position of the Microcerberidea within the Asellota has to be reconsidered, new questions about the evolution and the zoogeography of the Asellota arise, many of which cannot be answered at present.

Fundamental for all zoogeographic, phylogenetic and taxonomic studies are good descriptions of the species in question. Such descriptions are essential for comparative work and for the study of the phylogenetic relationships. Unfortunately, in many cases this basis does not exist, many taxonomists restrict their descriptions to only a few specific characters. This problem is not new. RACOVITZA (1907) complains in a study of some Oniscoidea: "Les spécialistes qui se sont occupé d'Isopodes terrestres n'ont presque jamais publié de figures et toutes leurs diagnoses sont différentielles. On comprend donc quelles difficultés soulève cette manière de procéder . . . Et que dire encore de ces diagnoses qui sont basées, pour les espèces d'un même genre, tantôt sur un caractère, tantôt sur un autre, sans qu'on puisse savoir si le caractère non mentionné manque réellement ou si on a négligé de le citer! . . . il est plus honorable d'être le père heureux d'un petit nombre d'espèces bien établies, que le prolifique progéniteur de rejetons mal conformés et parus avant terme, destinés le plus souvent à finir leur malfaisante existence dans un vengeur tableau synonymique . . .". This complaint can be expressed today in the same way. The present study would not have been possible without the reexamination of several species put at my disposal by various colleagues.

Material and methods

An adult female of *Atlantasellus cavernicolus* Sket, 1979, several adult specimens of *Stenasellus buili* Remy, 1949 and a collection of African Microcerberidea (*Protocerberus* and *Afrocerberus*, new genera: WÄGELE 1982 c) were studied.

Drawings have been prepared with the help of a camera lucida, the SEM pictures were taken with a Cambridge Stereoscan 180. The phylogenetic views are based on the works of REMANE (1961) and HENNIG (1965).

Comparison of the morphology of Stenasellidae, Atlantasellidae and Microcerberidae

Some features of the Microcerberidae are typical for asellote isopods. The species of *Afrocerberus* and *Protocerberus* (WÄGELE 1982 c) have normal, unaltered coxae, which are otherwise known only in Asellota and Phreatoicoidea. In most Microcerberidae the coxae of

the pereopods 2-4 are transformed into acute, forwardly directed dorsolateral plates, which, in literature, usually have been regarded as part of the tergites. Because of this misunderstanding it was possible to assume a relationship between *Microcerberidae* and *Anthuridea* (KARAMAN 1940; LANG 1960), which also have no coxae. But the new African *Microcerberidae* have short dorsolateral coxae at the same places, where they can be seen in *Stenasellus* (Figs. 3 B, C, D). The pereopods have no resemblance with those of the *Anthuridea*, but are similar to those of the *Asellota*: The pereopods 2-7 have long, cylindrical segments, the dactylus is much shorter than the propodus and bears two claws of approximately equal size. The mouthparts are very reduced in size, but they have "normal" appearance and are not specialized as in some carnivorous or parasitic *Isopoda* (*Cymothoidea*, *Anthuridea*, *Epicaridea*, *Gnathiidea*). The mandibles are not transformed into cutting or piercing tools, the first maxilla is not a stiletto, the second maxilla is not reduced, in other words, the mouthparts have a general plesiomorphic appearance as in most *Asellota* (and in other *Isopoda*). As in all *Asellota* the pleon consists of 2 free pleonites and a short pleotelson, the uropods are styliform. The pleopods even help us to determine the position of these microisopods within the known groups of *Asellota*: In both sexes the third pair of pleopods is operculiform and covers the biramous fourth pleopods, which (generally) lie in a gill chamber. This arrangement is characteristic for the "aselloid-line", while in *Janiroidea* the first and second pleopods form the operculum.

It is noteworthy that some very special features of the *Microcerberidae* are also present in *Atlantasellidae* and in *Stenasellidae*:

Mandibles

The right mandible of *Microcerberus* consists of a stout pars incisiva, a small lacinia mobilis, two serrated spines and an acute, slender pars molaris. The palp has only one segment and a single seta. The left mandible differs in having a broad, immovable lacinia and three serrated spines. In most *Asellota* a row of many spines or setae can be found between lacinia and pars molaris, the pars molaris normally having a broad grinding surface. There are astonishing similarities with the mandibles of *Atlantasellus*: Though the corpus of the mandibles is broad as in other *Aselloidea* (Fig. 2 B), the endite is constructed as in the *Microcerberidae* with the only difference, that the left mandible has only 2 (instead of 3) serrated spines and the acute pars molaris bears apically 3 long setae (Fig. 1). Many other dwarfish *Asellota* also have a spine row with a reduced number of spines (*Angeliara*, *Iais*, *Microcharon*, *Microparasellus* etc.), but the form and the arrangement of the structures described in the present study have a more than casual similarity. Despite the lack of a grinding surface on the pars molaris (Fig. 1) *Stenasellus* has the most plesiomorphic mandible.

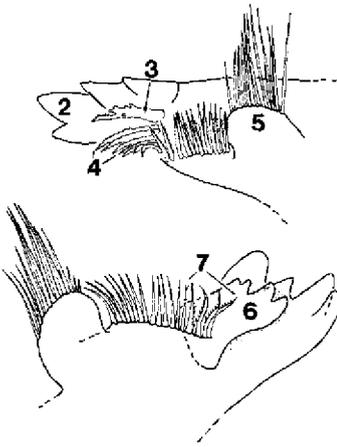
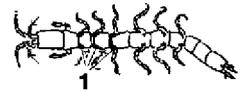
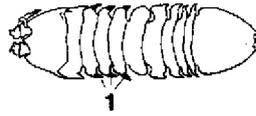
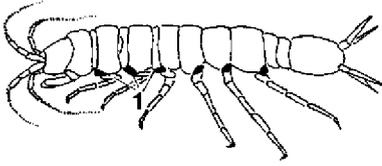
Pereopod 1

A convincing argument for the close relationship of the 3 groups discussed here can be found in the chaetotaxy of propodus and dactylus of pereopod 1. Just because of the many variations of P1-structures in *Asellota*, from the slender legs of *Ilyarachna* or *Acanthocope* to the huge subchelae of some males of *Stenetrium*, the similar form and arrangement of spines is so remarkable. In Fig. 1, 7 to 8 spines of *Microcerberus tabai* and of *Atlantasellus cavernicolus* can be found, which because of their similar shape and position can be identified as homologous spines. In *Stenasellus* the total number of spines and setae is much higher, but, and this is important for the further discussion, the manca-stages (which unfortunately are poorly known) have on propodus and dactylus nearly the same arrangement of spines and setae as *Atlantasellus* and *Microcerberus*; the homologies are obvious. Apart from the two remarkable basal spines (or teeth) of the propodus (Fig. 1: 11) it will be difficult to find the homologous spines in the adult *Stenasellus* without a detailed study of the postmarsupial development.

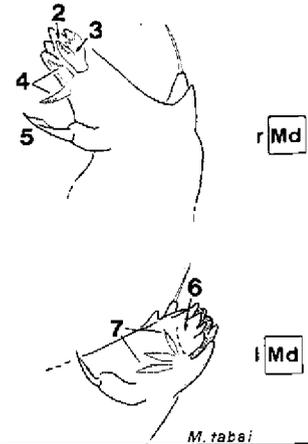
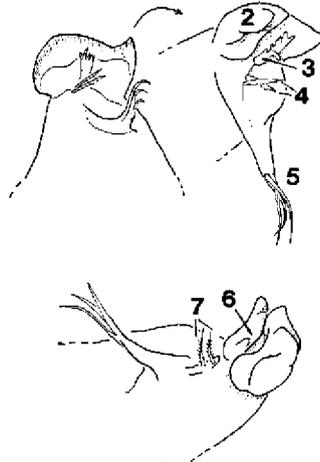
Stenasellus

Atlantasellus

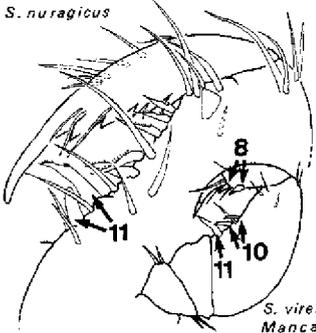
Microcerberus



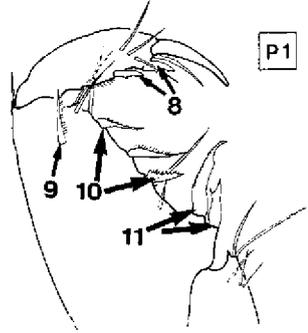
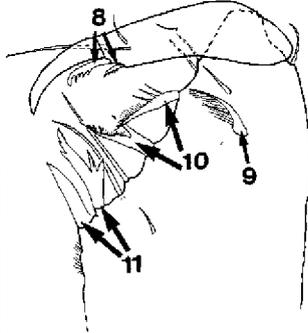
S. buffi



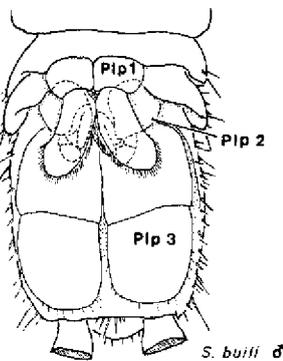
M. tabai



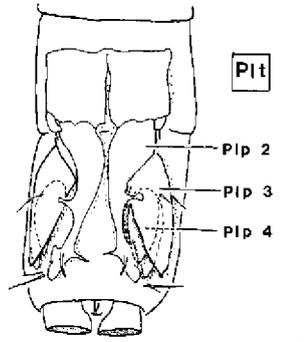
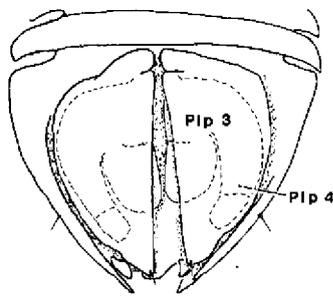
S. nuragicus



S. virei
Manca



S. buffi ♂



M. mirabilis ♂

Fig. 1. Comparison of Stenasellidae, Atlantasellidae and Microcerberidae. The numbers and arrows indicate homologies (1: coxae; 2: pars incisiva; 3: right lacinia mobilis; 4: right serrated spines; 5: pars molaris; 6: left lacinia mobilis; 7: left serrated spines; 8-11: spines on P 1). *S. nuragicus* after ARGANO 1968; *S. virei* after MAGNIEZ 1976; *M. mirabilis* after WÄGELE 1982 a; *M. tabai* (Md of *Microcerberus*) after WÄGELE 1982 b. rMd, lMd: right or left mandible; P 1: pereopod 1; Plt: pleotelson; Pip 1-4: pleopods

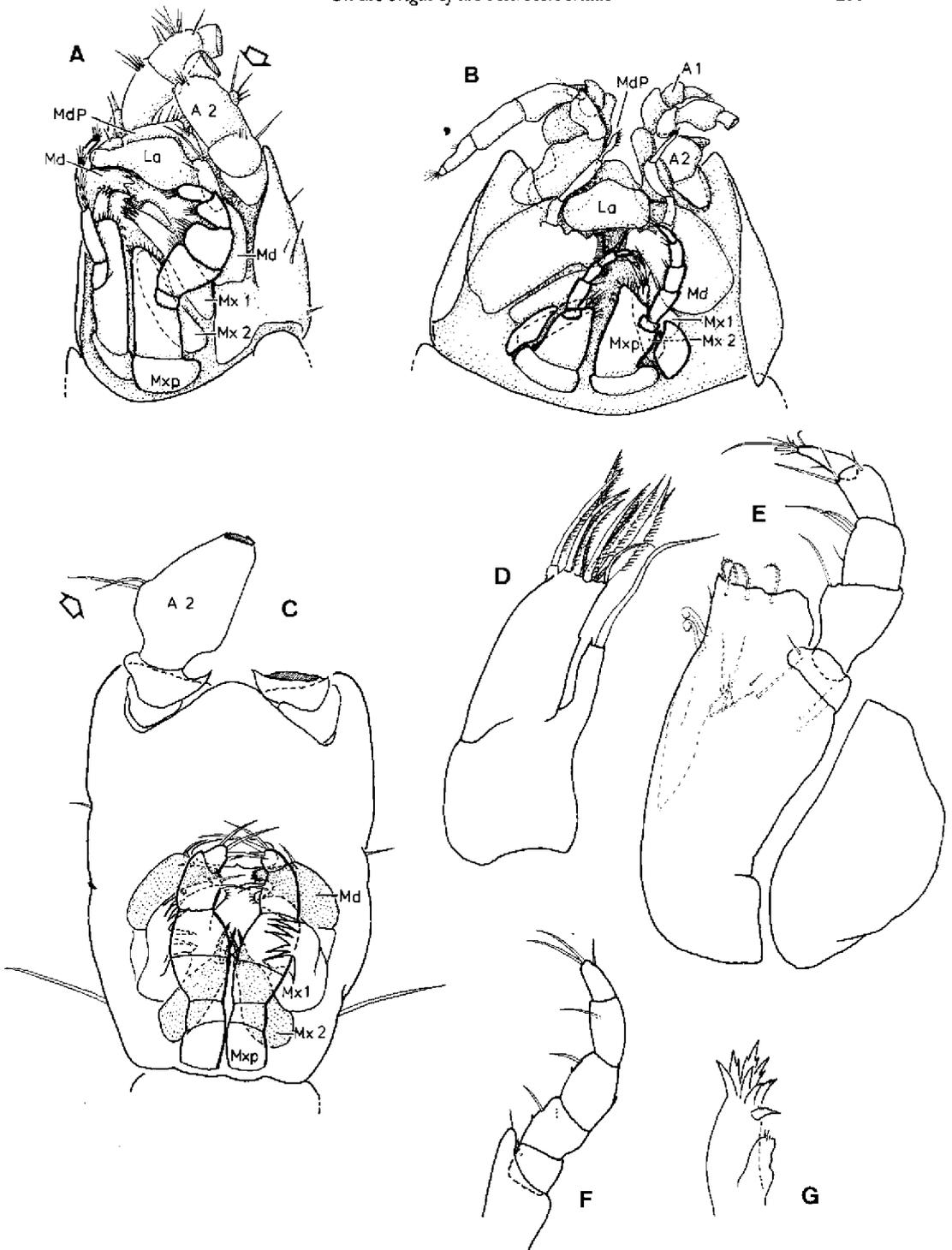


Fig. 2. A–C: Ventral view of the cephalothorax of Stenasellidae, Atlantasellidae and Microcerberidae. A: *Stenasellus buili* Remy, 1949; B: *Atlantasellus cavernicolus* Sket, 1979; C: *Protocerberus schminkei* Wägele, 1982 c; D: maxilla 1 of *A. cavernicolus* Sket; E: maxilliped of *A. cavernicolus* Sket; F: maxilliped of *Microcerberus tabai* Wägele, 1982; G: maxilla 1 of *M. tabai* Wägele. Arrows pointing to setae of exopod of antenna 2. (A 1, 2 = antenna 1, 2; La = labrum; Md = mandible; MdP = mandibular palp; Mx 1, 2 = maxilla 1, 2; Mxp = maxilliped)

Pleopods

The pleopods of Asellota show conspicuous variations, the importance of which had been recognized by HANSEN (1905) and RACOVITZA (1920, 1924). The pleopods of *Atlantasellus* principally have the same arrangement as in *Stenasellus* (Fig. 1; SKET 1979). In *Microcerberus* the males of most species have no first pleopods (exception: *M. phreaticus* Cvetkov, 1963) and the fifth pair of pleopods is reduced. The pleopods of the Microcerberidae are very small, the gill chamber is divided into two separate shallow cavities, covered by the operculate third pleopod. This pleopod, like the operculum of *Atlantasellus*, has no endopod and the sympod is fused with the exopod. The fourth pleopod is a biramous gill hidden under the operculum.

The further comparison reveals that the cephalic appendages of *Atlantasellus* and *Stenasellus* have more primitive features than those of the Microcerberidae (Fig. 2). The latter have very reduced mouthparts, which only cover the caudal half of the cephalothorax. The cephalothorax is not so much reduced in size as the mouthparts, probably due to the necessary volume of the brain. The microcerberid maxillipeds are very slender, the basipodite is short or reduced, while most other isopods have a broad basipodite with a large

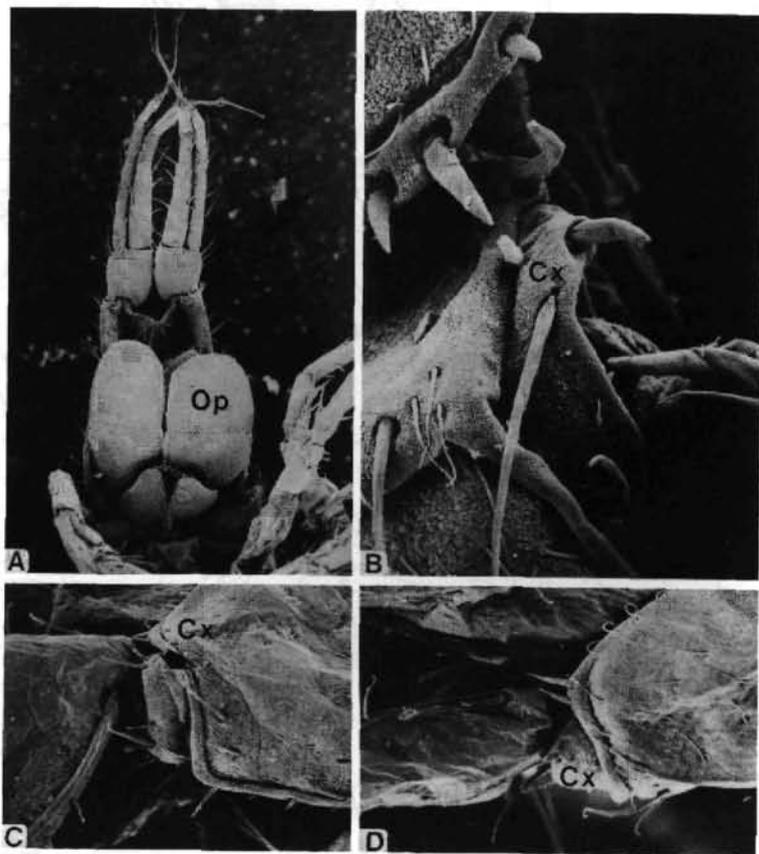


Fig. 3. SEM pictures of female *Stenasellus buili* Remy. A: pleon and pleotelson in ventral view; B: coxa of pereopod 3 in dorsal view; C, D: coxa of pereopod 6 in lateral (C) and dorsal (D) view. (Cx = coxa; Op = operculiform pleopod 3)

endite, as also in *Atlantasellus* and *Stenasellus*. The epipodite is missing in Stenasellidae and Microcerberidae. The reason for this reduction is not known. Both pairs of antennae of *Atlantasellus* and *Microcerberus* are considerably shorter than the multisegmented antennae of the Stenasellidae. Stenasellids still bear an exopodite on the second antenna, the Microcerberidae have at the same place a knob with few setae (arrows in Fig. 2).

The body of Atlantasellidae is dwarfish (length: 1.1 mm) as is that of the Microcerberidae, but proportionally it is broader than that of the Stenasellidae. SKET (1979) compares them with the Sphaeromatidae, which usually roll up when disturbed, a behaviour not common among Aselloidea. The Stenasellidae are as slender as many Asellidae, the Microcerberidae are more elongated, as nearly all mesopsammal animals.

In summarizing it can be said that the morphological comparison reveals a close relationship of Stenasellidae, Atlantasellidae and Microcerberidae, the Stenasellidae having more primitive features and the Atlantasellidae being a link between the mesopsammal Microcerberidae and the Stenasellidae.

The systematic position of the Microcerberidae

Having demonstrated the asellote nature of the Microcerberidae, their position in the system of the Asellota has to be discussed in order to assess the correct position and taxonomic status of these microisopods. For this purpose only those features can be considered, which are usually acknowledged as significant for taxonomy (HANSEN 1905; AMAR 1957; WOLFF 1962; KUSSAKIN 1967, 1979 etc.), since the data for a more precise analysis are lacking.

In the morphology of pleon and tail-fan the "Flabellifera", in particular the *Cirolanidae*, are most reminiscent of the mysid-like ancestor of the Peracarida (VANDEL 1943; MENZIES et al. 1961; SCHULTZ 1969; KUSSAKIN 1973; WILSON et al. 1976; WÄGELE 1981 etc.). All of the pleopods have the same outline and insert on free pleonites, the uropods are leaf-like. In the Asellota the pleopods are modified, some are larger than others, and variations can be observed from superfamily to superfamily. By compiling the plesiomorphies of all groups the features of the hypothetical common ancestor appear (below in Fig. 4). The first pair of pleopods of the female is reduced (NEEDHAM 1938), all pleopods have principally the same form, pleopods 1 and 2 have no endopod. The appendix masculina on pleopod 2 of other Isopoda is lacking in Asellota, the whole endopod forms a two-segmented, geniculate copulatory organ, details of the structure of the apex cannot be reconstructed at present; in *Stenasellus* the endopod seems to be rolled up to form a receptacle for the sperms (RACOVITZA 1919). Only 2 free pleonites are present, the uropods are styliiform.

Subsequent evolution resulted in two different lines. In the "janiroid-line" the second pair of pleopods becomes operculiform for the protection of the gills, in the male the operculum is formed by the first pleopod as the second pleopod functions as copulatory organ. In the other, the "aselloid-line", pleopods 1 and 2 remain short and an operculum is formed by the third pleopods, thus "avoiding" the sexual dimorphism of the "janiroid-line". The copulatory organ is not covered by the operculum. With these two very different arrangements a deep gap appears between the Gnathostenetrioidea and the Stenetrioidea (Fig. 4). Links between these two diverging evolutionary lines are impossible, it is completely out of question that these two groups should "connect" the Janiroida and the Aselloidea, as has been proposed so many times (HANSEN 1905; AMAR 1957; FRESI and SCHIECKE 1968; KUSSAKIN 1979; FRESI et al. 1980).

Within the "aselloid-line" the Stenetrioidea have some typical structures which remind us of features of the Gnathostenetrioidea, but in the light of the above considerations these features must be regarded as plesiomorphic or as due to convergent evolution. Such features are: pleonites 1 and 2 short, female pleopod 2 fused medially, pleopod 5 without endopod. The Aselloidea contain two diverging groups. The Asellidae always have a male copulatory

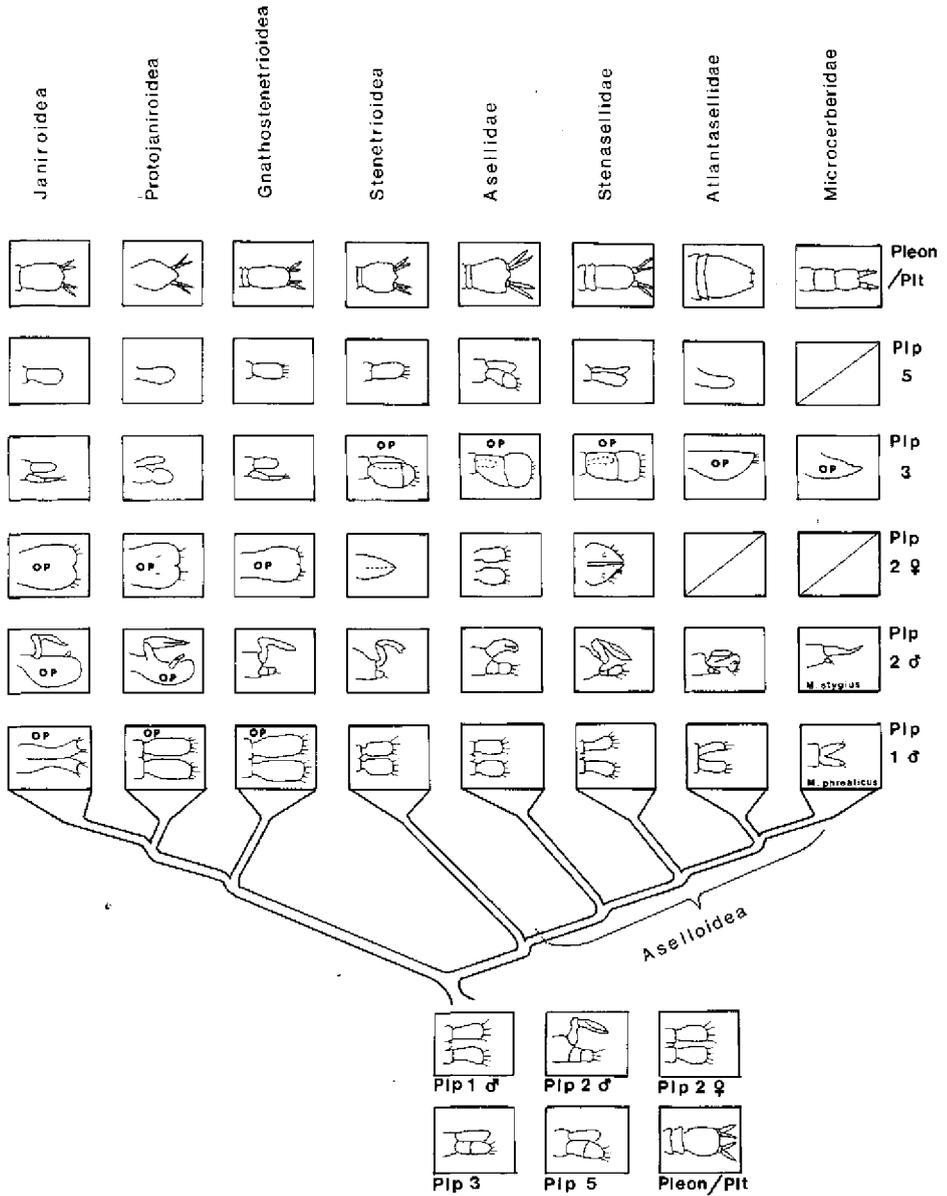


Fig. 4. Pleopod features of Asellota and features of the hypothetical ancestor (below). OP: operculiform pleopod; Plp: pleopod; Plt: pleotelson

organ with a one-segmented, not geniculate endopod, pleonites 1 and 2 are short, the exopod of antenna 2 is reduced. The second group has a similar chaetotaxy of pereopod 1, the eyes are always absent, as in most subterranean crustacea. Within this group the larger Stenasellidae have a plesiomorphic morphology, a specialization is the reduction of the maxillipedal epipodite, a feature met again in the Microcerberidae (convergence). The common apomorphies of Atlantasellidae and Microcerberidae could partly be understood as convergences, but the high number of such coinciding features makes it very probable, that a

close relationship exists. Synapomorphies are the dwarfish habitus, the nearly identical chaetotaxy of pereopod 1 in the adult specimens, same structures of the endite of the mandible, pleopod 2 reduced in the female, pleopod 3 without endopod, male pleopod 2 with one-segmented, not geniculate endopod (partly convergence to Asellidae, details of the copulatory organs still have to be compared). Further specializations are characteristic for only one of both groups: the Atlantasellidae have a sphaeromid-like habitus (body broad and bendable, antennae short), the uropods are reduced to tiny, not segmented structures. The very slender Microcerberidae have no fifth pleopods; these pleopods are already small and monoramous in Atlantasellidae. The oostegites are reduced (WÄGELE 1982 a), of the exopod of antenna 2 only the setae remain, the maxilliped has no endite and a short sympod.

Remarks

The comparison of the pleopod features leads to an idea of the possible phylogenetic system of the suborder Asellota, but the number of known synapomorphies is far too low to attempt a reconstruction of the evolution of this group. Nothing is known about the systematic importance of the evolution of mouthparts, pereopods, internal structures. These need a revision using HENNIG's method (HENNIG 1965), to avoid misinterpretations. Similarities are often the common inheritance consisting of plesiomorphies or, more difficult to prove, convergencies with no significance for the demonstration of monophyly, as in the case of the Gnathostenetrioidea and Stenetrioidea (e. g. FRESI and SCHIECKE 1968). For the 3 families discussed in the present study, features of the mouthparts and of the pereopods are correlated with the evolution of the pleopods and the size of the body, thus making it very probable that the correct systematic position of the Microcerberidea has been found.

Ecological and zoogeographical implications

DAVIES (1982: 392) writes in a study on the zoogeography of the freshwater molluscs: "Understanding the origin of a modern distribution of any group is dependent on a phylogenetic analysis". In our case the still superficial analysis at family-level is in no severe contradiction with the ecological and zoogeographical data; it seems possible to integrate all available information to a picture of the evolution of the Aselloidea. An analysis at the level of species and genera is not possible at present.

Comparing the systematic position with the distribution of the groups, it appears that the less specialized Asellota live in shallow parts of the sea or on the continents in freshwater. With the exception of *Atlantasellus* and the Microcerberidae, all Aselloidea live in freshwater; the Protojaniroidea live on the continent, the Gnathostenetrioidea colonize, as far as known, the upper littoral or the coastal mesopsammal. Only the Janiroidea, especially the aberrant forms, and the Stenetrioidea conquered all marine benthic environments, including the deep sea. The Janiroidea have also some representatives in the coastal groundwater and in freshwater. Till now for the radiation of the Asellota only one possibility has been taken into account: the origin of this group from ancestors that lived in shallow seas and from there conquered the deep sea and the continents. For the Janiroidea it seems very probable, that their evolution started in shallow seas, as all aberrant and obviously derived species predominate in the deep sea (discussion in HESSLER and THISTLE 1975; HESSLER et al. 1979). HENRY (1976) discusses a polyphyletic colonization of freshwater by Asellidae, MAGNIEZ (1981) admits the possibility of a polyphyletic origin of the subterranean Stenasellidae, which surely evolved for the most part on the continent but could have ancestors in the sea (Tethys?). Stenasellidae and Asellidae are thought to have entered separately the limnic system (MAGNIEZ 1976). SKET (1979) assumes that the Atlantasellidae might have relatives in the deep sea. All these views are in accordance with

similar phenomena observed in other crustaceans. STOCK (1977 a, b) supposes that the Microparasellidae, Thermosbaenacea and Hadziidae (Amphipoda) of the Caribbean are Tethys-relicts, which by stranding during regression came to live in freshwater, while most of the Ingolfiellidae were already living on the continent before the opening of the Atlantic Ocean; some of them colonized islands at a later time.

A very different but equally probable hypothesis can be formulated, beginning with a common mesozoic ancestor of all Asellota, living somewhere in the freshwater of Pangaea. Before the opening of the Atlantic all known superfamilies had evolved. The first asellote isopod must necessarily have had a marine ancestor. Only a few groups went back to the sea and spread into the different habitats, the most successful of them being the Janiroidea.

Which of these opposed views is closer to the truth cannot be decided at present. It seems to me that at least for the Aselloidea it is much more probable to assume a continuous evolution in freshwater, than to consider several polyphyletic invasions into the freshwater systems of different continental areas. The following evidences support this view:

1. No truly marine Aselloidea are known. The Microcerberidae are bound to the coastal groundwater, the Atlantasellidae are relicts living in a cave, which (secondarily?) are adapted to the local subterranean conditions (salty groundwater of the Bermudas).
2. The present geographic distribution of the Aselloidea shows that Asellidae and Stenasellidae must be relatively old faunal elements of the continents, which before the opening of the Atlantic already colonized the limnic systems. Both families live on both sides of the Atlantic Ocean. Also the Microcerberidae are known from continental localities on both sides of the Atlantic. That at least some of the latter isopods (*Protocerberus* and *Afrocerberus*) probably do not originate from marine interstitial populations, as is suspected in the analogue case of the Microparasellidae (STOCK 1977 c), has already been mentioned.

The Microcerberidae of the coastal groundwater seem to be world-wide distributed organisms, which obviously can overcome geographic obstacles much more easily than the limnic species (colonization of islands, of both southern Atlantic coasts). An analogue case is known from the Bathynellacea (Synacarida), which evolved in fresh water but have one widely distributed genus with euryhaline species (SCHMINKE 1972). As in Microcerberidae, this euryhaline genus (*Hexabathynella*) has more apomorphic features than the limnic relatives, which have a more restricted distribution. Studies on the phylogenetic relationship between the microcerberid species do not exist, wherefore nothing can be said about their radiation. Of the limnic species at least *Microcerberus ruffoi* Chappuis, 1953 must be regarded as a "stranded relict" of Oligocene Tethys coasts, as this species has a typical "marine" morphology (form of the coxae of P 2-4). Whether the same is true for some other limnic species remains uncertain, as many details of their morphology are unknown. The features of *Afrocerberus* and *Protocerberus* (primitive morphology, colonization of areas that were not below sea-level during the Oligocene) seem to indicate, that the Microcerberidae probably evolved from their aselloid ancestors in *freshwater*. There are also some biological arguments which help us to understand how the process could have taken place.

Biological arguments

The Stenasellidae live among gravel, burrow in hypogean sand and mud and appear in some cave waters. In contrast to some hypogean Asellidae, the populations living in caves cannot be derived from epigeal species, but from neighbouring interstitial populations (MAGNIEZ 1970, 1971, 1973). Thus all Stenasellidae, including those living in caves, are adapted in their biology to the subterranean habitats. The observations of MAGNIEZ (1971, 1973, 1976) on the biology of *Stenasellus virei* give us an idea of the possible evolution of the dwarfish Atlantasellidae and Microcerberidae.

The populations of *Stenasellus virei* in French caves consist often surprisingly of only adult animals. MAGNIEZ found out that *Stenasellus* is omnivorous and does not stop at feeding on its own brood. Therefore the smaller and young animals can be found in the deposits of sand and gravel adjoining the pools, where they search for food and protection. So among populations of *S. virei* there exists a selective advantage for young, small animals that are able to find a living in the small interstitial spaces of sandy deposits, and in the past a similar situation among ancient stenasellids could have led to the evolution of dwarfish individuals which were capable to reproduce without leaving the sand. This behaviour could be the reason for evolution of Atlantasellidae and Microcerberidae. At least, we can find here a model that explains how dwarfish mesopsammal species evolved. And, is not natural selection by means of predation one of the most effective evolutionary mechanisms?

Stenasellus is predisposed for an adaptation to such mesopsammal habitats from the morphological as well as from the biological point of view. This process of evolution is a fetalization, the sexually mature animals of the dwarfish species have a morphology of young, immature "normal" individuals. We have already compared the P 1-structures of *Atlantasellus* and *Microcerberus* with those of the manca stage of *Stenasellus* and we noted the resemblance. But it is to be remembered that neither of the dwarfish isopods is a sexually mature manca; the animals have fully developed seventh pereopods. The partly reduction of pleopods reminds of the postmarsupial development of *Stenasellus* (MAGNIEZ 1976), the male second pleopod passes through a stage with a single-jointed endopod with outlines similar to the copulatory organ of *Atlantasellus* and *Microcerberus*.

A very similar way of evolution has been proposed for another group of typical mesopsammal crustacea. In the light of the "zoëa theory" (SCHMINKE 1981) the Bathynellacea (Syncarida) had a limnic epigean ancestor with larval stages comparable to those of the marine Penaeidae, and these larvae could have been living in the hyporheic interstices to avoid predators and water currents. The Bathynellacea most likely evolved from such larval stages by neoteny, the adult Bathynellacea retain (in contrast to the Microcerberidae) a larval morphology.

Diagnosis of the Microcerberidae, new family of Aselloidea (Isopoda: Asellota)

This diagnosis has preliminary character, as a revision of the family is necessary to find the typical features of all species and the features of their common ancestor.

Aselloidea with slender body, eyes lacking. Antennae short, peduncle of A 1 with 3 segments, peduncle of A 2 with 6 segments. Mandible with stout pars incisiva, large (left) or small (right) lacinia mobilis; 2-3 serrated spines between acute pars molaris and lacinia. Mandibular palp of one small article. Lateral endite of maxilla 1 distally with several acute spines, medial endite short. Maxilla 2 monoramous, with 2 distal serrated lobes. Hypopharynx U-shaped. Maxilliped with short basipodite and slender, 5-jointed palp; epipodite not present.

Pereopod 1 with broad, subchelate propodus; cutting edge bearing 2 basal teeth and several serrated spines. Pereopods 2-7 with short coxae; or P 2-4 with acute, frontally directed coxal plates and P 5-7 with reduced coxae. Dactylus of P 2-7 much shorter than propodus, 2 claws of equal size present. Only 2 free pleonites, which have nearly the same size as the remaining pleotelson. Telson reduced. Male pleopod 1 nearly always reduced, male pleopod 2 with copulatory endopod of specifically varying form, exopod very small. Pleopod 3 operculiform, monoramous, sympod fused with exopod. Pleopod 4 biramous, pleopod 5 reduced. Uropods styliform, exopod shorter than endopod.

Acknowledgements

I am very grateful to Prof. MAGNIEZ for the specimens of *Stenasellus*, to Prof. H. K. SCHMINKE for the South African Microcerberidae and to Prof. B. SKET for the specimen of *Atlantasellus* kindly placed at my disposal. Without this material the theory presented in this study would have remained a weak hypothesis. I have also benefited from the discussion with Prof. H. K. SCHMINKE and his useful comments on the manuscript.

Summary

An attempt is made to demonstrate the close relationship of the families Stenasellidae, Atlantasellidae and Microcerberidae. It is shown that a high number of homologous features exists on mouthparts, pereopods and pleopods. In conclusion the Microcerberidae are regarded not as a separate suborder but as a new family within the Aselloidea (Isopoda: Asellota). The zoogeographical and biological implications of this theory are discussed. Repeated colonization of freshwater by marine species does not seem very probable, the aselloid microisopods most likely evolved in freshwater. Within modern Stenasellidae there appears to exist an intraspecific selection pressure favouring dwarfish forms, and it seems probable that such conditions led to the evolution of Atlantasellidae and Microcerberidae.

Zusammenfassung

Über den Ursprung der Microcerberidae (Crustacea: Isopoda)

Es wird versucht, die enge Verwandtschaft der Familien Stenasellidae, Atlantasellidae und Microcerberidae zu demonstrieren. An Mundwerkzeugen, Pereopoden und Pleopoden wird eine hohe Zahl von homologen Merkmalen aufgezeigt. Infolgedessen werden die Microcerberidae nicht mehr als eigene Unterordnung, sondern als neue Familie der Aselloidea (Isopoda: Asellota) geführt. Die hiermit verknüpften zoogeographischen und biologischen Fragen werden angesprochen. Eine wiederholte Besiedlung des Süßwassers durch marine Arten erscheint wenig wahrscheinlich, die aselloiden Mikroasseln haben sich eher im Süßwasser entwickelt. Innerhalb der modernen Stenasellidae gibt es offenbar einen intraspezifischen Selektionsdruck zugunsten verzweigter Formen, und es erscheint wahrscheinlich, daß ähnliche Bedingungen zur Evolution der Atlantasellidae und Microcerberidae führten.

References

- AMAR, R., 1957: *Gnathostenetroides laodicense* n. g. n. s., type nouveau d'Asellota et classification des isopodes asellotes. Bull. Inst. Océanogr. Monaco 1100, 1-10.
- ARGANO, R., 1968: Due nuovi *Stenasellus* di Sardegna (Crustacea, Isopoda, Asellota). Fragm. entom. 6, 1-22.
- BARNARD, K. H., 1927: A study of freshwater isopodan and amphipodan Crustacea of South Africa. Trans. R. Soc. S. Afr. 14, 139-215.
- CHAPPUIS, P. A.; DELAMARE-DEBOUTTEVILLE, CL., 1954: Les isopodes psammiques de la Méditerranée. Arch. Zool. exp. gén. 91, 103-138.
- CVETROV, L., 1963: Nouveaux représentants du genre *Microcerberus* trouvés en Bulgarie. Izv. zool. Inst. Sofia 14, 153-163.
- DAHL, E., 1954: Some aspects of the ontogeny of *Mesamphisopus capensis* (Barnard) and the affinities of the Isopoda Phreatoicoidea. K. fysiogr. Sällsk. Lund Forh. 24, 1-6.
- DAVIS, G. M., 1982: Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater molluscs. Amer. Zool. 22, 375-395.
- FRESI, E.; SCHIECKE, U., 1968: *Caecostenetroides ischitanum* (Isopoda, Parastenetriidae), a new genus and species from the Bay of Naples. Pubbl. Staz. Zool. Napoli 36, 427-436.
- FRESI, E.; IDATO, E.; SCIPIONE, M. B., 1980: The Gnathostenetroides and the evolution of primitive asellote isopods. Monitore Zool. Ital. 4, 119-136.
- HANSEN, H. J., 1905: On the morphology and classification of the Asellota-group of crustaceans, with descriptions of the genus *Stenetrium* Haswell and its species. Proc. zool. Soc. Lond. 2, 302-331.
- HENNIG, W., 1965: Phylogenetic systematics. Ann. Rev. Entomol. 10, 97-116.
- HENRY, J. P., 1976: Recherches sur les Asellidae hypogés de la lignée *cavaticus* (Crustacea, Isopoda, Asellota). Thèse, Univ. Dijon (Sci. Nat.).
- HESSLER, R. R.; THISTLE, D., 1975: On the place of origin of deep-sea isopods. Mar. Biol. 32, 155-165.
- HESSLER, R. R.; WILSON, G. D.; THISTLE, D., 1979: The deep-sea isopods: a biogeographic and phylogenetic overview. Sarsia 64, 67-75.

- KARAMAN, S., 1933: *Microcerberus stygius*, der dritte Isopod aus dem Grundwasser von Skoplje, Jugoslavien. Zool. Anz. 102, 165–169.
- 1940: Die unterirdischen Isopoden Südserviens. Glasn. Skops. nauč. Društ. 22, 19–53.
- KUSSAKIN, O. G., 1967: Isopoda and Tanaidacea from the coastal zones of the Antarctic and Subantarctic. In: Biological results of the Soviet Antarctic Expedition (1955–58). (In Russ.) 3. Issl. Fauny Morei 4, 220–380.
- 1973: Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. Mar. Biol. 23, 19–34.
- 1979: Marine and saltwater Isopoda of the cold and temperate waters of the Northern Hemisphere. I. Suborder Flabellifera. (In Russ.) Leningrad: Akad. Nauk.
- LANG, K., 1960: Contributions to the knowledge of the genus *Microcerberus* Karaman (Crustacea, Isopoda) with a description of a new species from the central Californian coast. Ark. Zool. (2) 13, 493–510.
- MAGNIEZ, G., 1970: Sur un aselle cavernicole de France, *Proasellus ibericus* (Braga, 1946). Sous le plancher 9 (2), 21–27.
- 1971: Données récents sur les *Stenasellus* (Crustacea, Asellota) des eaux souterraines continentales. C. R. 96èmes Congr. Nat. Soc. Sav. Toulouse, Sci. 3, 179–191.
- 1973: Les populations naturelles de *Stenasellus virei* Dollfus (Crustacé asellote troglobie). Int. J. Speleol. 5, 31–48.
- 1974: Données faunistiques et écologiques sur les Stenasellidae (Crustacea, Isopoda, Asellota). Int. J. Speleol. 6, 1–80.
- 1976: Contribution à la connaissance de la biologie des Stenasellidae (Crustacea Isopoda Asellota des eaux souterraines). Thèse, Univ. Dijon.
- 1981: Biogeographical and palaeobiogeographical problems in stenasellids (Crustacea Isopoda Asellota of underground waters). Int. J. Speleol. 11, 71–81.
- MENZIES, R. J.; IMBRIE, J.; HEEZEN, B. C., 1961: Further considerations regarding the antiquity of the abyssal fauna with evidence for a changing abyssal environment. Deep-sea Research 8, 79–94.
- NEEDHAM, A. E., 1938: Abdominal appendages in the female and copulatory appendages in the male *Asellus*. Quart. J. Micr. Sci. 81, 127–150.
- PENNAK, R., 1958: A new micro-isopod from Mexican marine beach. Trans. Am. microsc. Soc. 77, 298–303.
- RACOVITZA, E. G., 1907: Isopodes terrestres (première série). Arch. Zool. expér. (4) 7, 145–225, plates 10–20.
- 1919: Notes sur les isopodes. 6. *Asellus communis* Say. 7. Les pléopodes I et II des asellides; morphologie et développement. Arch. Zool. exp. gén. 58, 79–115.
- 1924: Morphologie et morphogenie des pléopodes I et II des femelles des asellides. Arch. Zool. exp. gén. 62, Not. Rev. 2, 35–48.
- REMANE, A.; SIEWING, R., 1953: *Microcerberus delamarei*, eine marine Isopodenart von der Küste Brasiliens. Kieler Meeresforsch. 9, 278–284.
- 1961: Gedanken zum Problem: Homologie und Analogie, Praeadaptation und Parallelität. Zool. Anz. 166, 447–465.
- REMY, P., 1949: *Stenasellus buili* n. sp. de la grotte de la Giraudasso à Soulatgé, Aude (Crust. Isopodes). Bull. Soc. Linn. Lyon 18, 153–157.
- SCHMINKE, H. K., 1972: *Hexabathynella halophila* gen. n. sp. n. und die Frage nach der marinen Abkunft der Bathynellacea (Crustacea: Malacostraca). Mar. Biol. 15, 282–287.
- 1981: Adaptation of Bathynellacea (Crustacea, Syncarida) to life in the interstitial (“Zoea Theory”). Int. Rev. ges. Hydrobiol. 66, 575–637.
- SCHULTZ, G. A., 1969: How to know the marine isopod crustacean. Dubuque: W. C. Brown Co.
- 1974: *Mexicerberus troglodytes* n. gen. n. sp. from a cave in Mexico, with notes on isopod crustaceans of the Microcerberidea from the New World. Crustaceana 26, 308–312.
- STOCK, J. H., 1977 a: The taxonomy and zoogeography of the hadziid Amphipoda with emphasis on the West Indian taxa. Stud. Fauna Curaçao 55, 1–130.
- 1977 b: The zoogeography of the crustacean suborder Ingolfiellidea with descriptions of new West Indian taxa. Stud. Fauna Curaçao 55, 131–146.
- 1977 c: Microparasellidae (Isopoda, Asellota) from Bonaire – with notes on the origin of the family. Stud. Fauna Curaçao 51, 69–91.
- 1981: L’origine géologique des îles des Indes Occidentales en relation avec la dispersion de quelques Malacostracés stygobiontes. Géobios 14, 219–227.
- VANDEL, A., 1943: Essai sur l’origine, l’évolution et la classification des Oniscoides (Isopodes terrestres). Bull. biol. France-Belg., suppl. 30, 1–143.
- WÄGELE, J. W., 1981: Zur Phylogenie der Anthuridea (Crustacea, Isopoda). Mit Beiträgen zur Lebensweise, Morphologie, Anatomie und Taxonomie. Zoologica, Stuttgart, 132, 1–127.

- 1982 a: Isopoda (Crustacea: Peracarida) ohne Oostegite: Über einen *Microcerberus* aus Florida. Mitt. Zool. Mus. Univ. Kiel 1, 19-23.
 - 1982 b: On a new *Microcerberus* from the Red Sea and the relationship of the Microcerberidea to the Anthuridea (Crustacea, Isopoda). Zool. Scripta 11, 281-286.
 - 1982 c: *Protocerberus* gen. n. und *Afrocerberus* gen. n., neue limnische Microcerberidea aus Afrika. Bull. Zoöl. Mus. 9, 65-74.
- WOLFF, T., 1962: The systematics and biology of bathyal and abyssal Isopoda Asellota. Galathea Rep. 6, 1-320.

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Nuclear DNA content of *Asellus aquaticus* and *Proasellus coxalis*

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Received on 21. March 1983

Introduction

In recent years, *Asellus (Asellus) aquaticus* (L.) Racovitza and *Proasellus coxalis* (Dollfus), two species of isopod crustaceans previously considered allopatric have been found together in the epigeal fresh waters of central and southern Italy; the latter species appears to be slowly occupying biotopes which were formerly exclusive to *Asellus aquaticus*. Until 1970, the two species were considered to belong to the same genus *Asellus* and attributed to two sub-genera, *Asellus* and *Proasellus* (DUDICH 1925).

In 1970, HENRY and MAGNIEZ proposed to make the two sub-genera to full separate genera, because their origin and age appeared very different to them. The genus *Asellus*, in the opinion of these authors, consists of Euro-Asian forms, of which only one has reached Western Europe recently. *Asellus (Asellus) aquaticus* is the most common species of this genus found in north European epigeal fresh waters. The genus *Proasellus* has colonized Europe south of a line running from the Black Sea to Britain, as also, the Mediterranean Middle East and North Africa. In these regions, as in all those surrounding the Mediterranean Sea, *Proasellus* is represented by the widely distributed polytypical species *Proasellus coxalis*. CHAPPUIS (1949) maintains that the Asellides owe their origin to a single freshwater line, which diverged and spread through the continent in a series of migrations, whereas HENRY and MAGNIEZ (1970) are of the opinion that the group was formed by multiple migrations, which started independently from marine Asellide lines, from widely separate places at different times.

Caryological research has frequently been used to clarify phylogenetic problems. The karyotype of *Asellus aquaticus* (MONTALENTI and ROCCHI 1964 a) consists of $2n = 16$ chromosomes, all metacentric or submetacentric, with the exception of one pair which is subtelocentric. The karyotype of *Proasellus coxalis* consists of $2n = 12$ chromosomes, all metacentric or submetacentric (MONTALENTI and ROCCHI 1964 b) and considerably smaller than those of *Asellus aquaticus*.