

# Aspects of the evolution and biogeography of stygobiontic Isopoda (Crustacea: Peracarida)

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## Abstract

The evolution of the stygobiontic isopods is discussed correlating the phylogenetic system with biogeography. All stygobiontic isopods probably are derived from remote marine ancestors. The colonization of subterranean aquatic biotopes occurred in two ways: (1) via the coastal groundwater in the case of the Microparasellidae, Gnathostenetroididae, Stenetriidae, and in *Cyathura* (*Stygocyathura*), (2) in most families, however, via epigeic freshwater ancestors. Ancient freshwater isopods that must already have existed before the Cretaceous and whose stygobiontic phylogenetic lines partly must have existed before the opening of the Atlantic are the Aselloidea, Calabozoida, Phreatoicidea, and probably also the Protojaniridae. In the course of Cretaceous and Tertiary regressions other, more apomorphic taxa "stranded" and adapted to stygobiontic biotopes, such as the "Monolistrini" (Sphaeromatidae).

## Zusammenfassung

Die Evolution der stygobiontischen Isopoden wird in einem Vergleich des phylogenetischen Systems mit der geographischen Verbreitung der Taxa diskutiert. Alle stygobiontischen Isopoden haben wahrscheinlich marine Vorfahren gehabt. Die Besiedlung limnischer, unterirdischer Biotope erfolgt auf zwei Wegen: Über das Küstengrundwasser im Fall der Microparaselliden, Gnathostenetroididae, Stenetriidae, und bei *Cyathura* (*Stygocyathura*), bei den meisten Familien jedoch über epigäische Süßwasserformen. Alte Süßwasserisopoden, die schon vor der Kreide gelebt haben müssen und deren hypogäische Linien z.T. schon zum Zeitpunkt der Öffnung des Atlantiks existierten, sind die Aselloidea, Calabozoida, Phreatoicidea und wahrscheinlich auch die Protojaniridae. Im Verlauf von Regressionen während Kreide und Tertiär sind andere, "modernere" Taxa "gestrandet" und ins Süßwasser und Grundwasser gelangt, wie die "Monolistrini" (Sphaeromatidae).

## Introduction

The increasing knowledge on the taxonomy and distribution of stygobiontic isopods allows some general observations on their phylogeny and biogeography. The "Amsterdam Expeditions to the West Indian Islands" and other expeditions of the group of Prof. Dr. Jan H. Stock proved that many hypogean genera have a wide distribution, not only in the peri-Caribbean area, but also on both sides of the Atlantic, some even reaching into the Indo-Pacific (e.g. Botosaneanu et al., 1986; Botosaneanu, 1987; Notenboom, 1984; Stock, 1977; 1985). These stygobionts are of high scientific interest, as some of them obviously are relicts, without close relatives in marine biotas (e.g. *Calabozoa*, *Curassanthura*), stimulating research and speculation because of their distribution and phylogenetic age. Evolution and biogeography cannot be separated in any effort to understand the origin of the aquatic hypogean species.

## Monophyly and biogeography

A summary of hitherto accumulated knowledge on the evolution of the Isopoda has recently been prepared (Wägele, 1989). A simplified scheme of the results containing all those taxa and groups of genera that are stygobiontic is represented in Fig. 1. Aquatic hypogean biotopes were conquered several

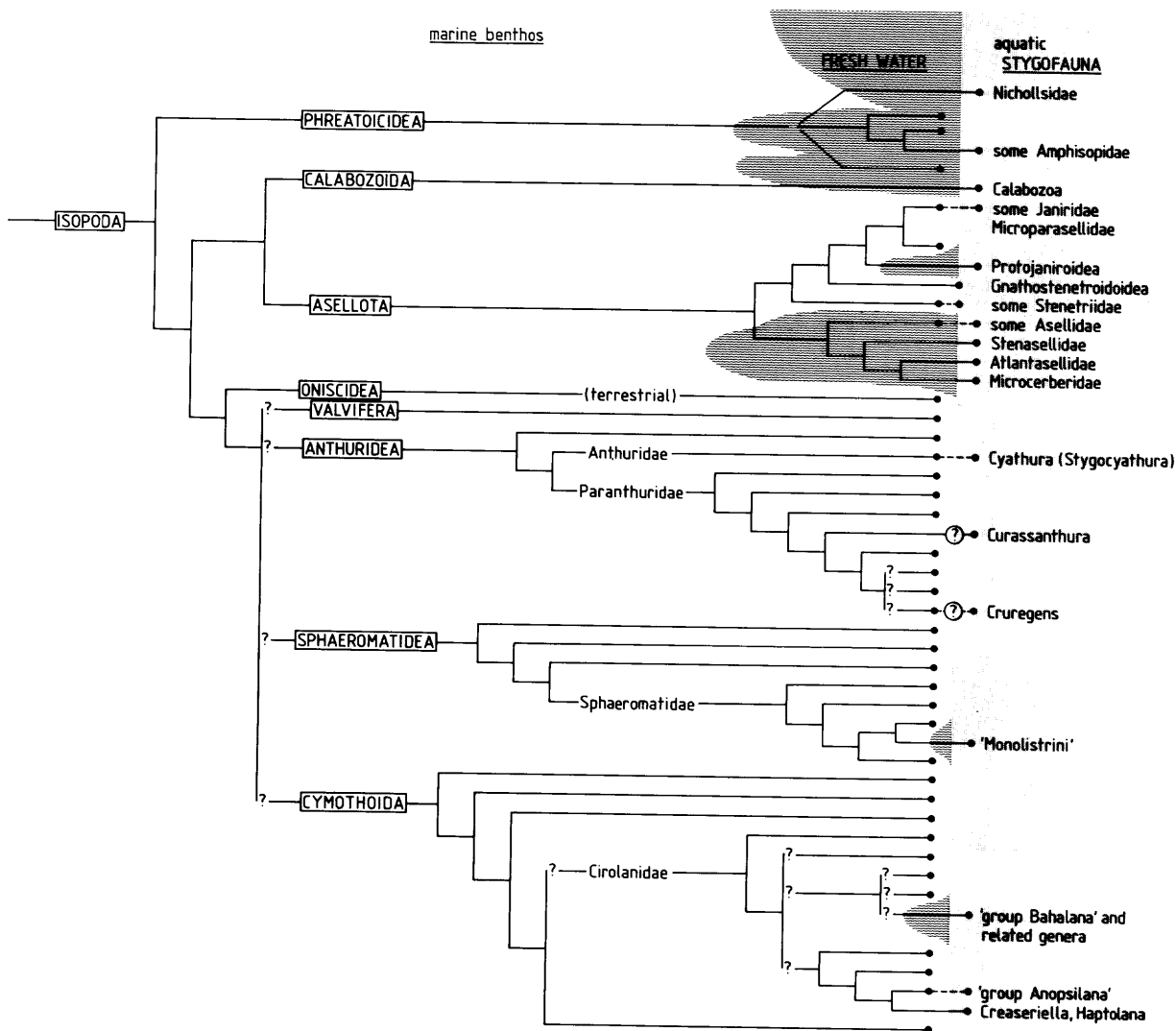


Fig. 1. Dendrogram for the phylogenetic system of the Isopoda (after Wägele, 1989), representing the taxa that belong to the stygofauna. Note that most groups evolved via epigeal freshwater ancestors. Question marks indicate that it is not known if such epigeal ancestors could have existed. Black circles without names represent single taxa or groups of taxa.

times by members of nearly all isopod suborders, with the exception of the Oniscidea (which have some cave-dwelling species) and the Valvifera. Nearly always some marine sister-group is known and there is no doubt about the marine origin of most families. To understand the mechanisms leading to present-day distribution it is necessary to find out whether within a phylogenetic line crossing the border marine benthos/aquatic stygofauna only a single event (adaptation to hypogean biotas) is to be

expected or if several parallel invasions took place within a genus or a family. In the first case a genus occurring for example at both sides of the Atlantic must have a common stygobiont ancestor and be at least as old as the central Atlantic Ocean. In the second case populations of a marine ancestor species of wide distribution could adapt independently in remote areas to the coastal or estuarine interstitial or other hypogean biotas. Monophyly of the adapted group of species can be an indication of vicari-

ance by continental drift, other mechanisms being less probable.

### *Phreatoicidea*

The Phreatoicidea is the oldest known isopod suborder (300 million years: Schram, 1970). Present-day species live exclusively in fresh water of Gondwana fragments (New Zealand, Australia, Tasmania, India, South Africa). The Nichollsidae, a subterranean family known only from India, most probably evolved on this subcontinent independently of other subterranean groups. Other not closely related hypogean species are known for the Amphisopidae (Hypsimetopinae), obviously representing several separate invasions of the underground (Knott, 1986); the species in question occur in Australia and Tasmania. In the third family (Phreatoicidae) hypogean species are known from New Zealand and Tasmania. The Nichollsidae are the only monophyletic hypogean family; the phylogeny of the other hypogean groups of species is not known.

### *Calabozoida*

According to Wägele (1989) the Calabozoida are the sister-group of the Asellota, the close relationship having been noted already by Van Lieshout (1983). Only one species is known (from Venezuela): *Calabozoa pellucida* (Van Lieshout, 1983). It seems to be a relict; no close marine relatives are known.

### *Asellota*

Most species of asellotes are marine. The more primitive families live in shallow coastal areas, while a large number of specialized genera and families radiated in the deep-sea. A separate phylogenetic line evolved in fresh water, namely the Aselloidea. Within this line the less specialized family Asellidae has epigeal as well as hypogean species. It is very obvious that hypogean species of this family evolved very often in independent, not closely related groups. In *Asellus aquaticus* (Linné, 1758) epigeal as well as hypogean populations exist. It is

not known how the genera of this family are related to each other; some may belong to monophyletic subterranean groups. Neither is known, if hypogean species of North America and Eurasia have a common stygobiontic ancestor.

The remaining families of the aselloid line evolved in a different way: arising from an unknown common aselloid ancestor this line evolved completely in subterranean fresh water. The Stenasellidae still have the size of epigeal asellids and have a wide distribution in southern Europe, Africa, Central America, and Asia (summary in Henry et al., 1986). The last common ancestor must have lived in Laurasia and descendants will have spread over this continent before the formation of the Atlantic. Gondwana was probably also populated. The less derived species of the sister-group, the dwarfish Atlantasellidae and Microcerberidae, occur partly in southern Africa (*Protocerberus*, *Afrocerberus*), partly on Bermuda (*Atlantasellus*). Likewise, this line of dwarfish forms was already in existence before the Atlantic was formed. *Atlantasellus* has an intermediate morphology between stenasellids and microcerberids, sharing some synapomorphies with the microcerberids (Wägele, 1983), suggesting that some connection between the present-day Bermuda Island and older continental fragments must have existed. While the most primitive Microcerberidae live in fresh water, the more apomorphic species occur for the most part in the brackish or marine coastal mesopsammal. They must have means for dispersal over ocean basins, as they have been found e.g. on the Maldives and Laccadives, and on many Caribbean islands (summary in Coineau, 1986a). Some freshwater species with the more apomorphic "coastal" morphology may be a product of marine regressions (e.g. *Mexicerberus troglodytes* Schultz, 1979, *Microcerberus plesai* Chappuis & Delamare, 1958, and *M. remyi* Chappuis, 1954).

Further stygobiontic species are known in those of the remaining asellote families, which probably evolved in shallow marine habitats. Interestingly, the more primitive genera in the janiroid line (Wilson, 1987) have an affinity to interstitial conditions (*Caecostenetroides*, *Neostenetroides*, *Anneckella*, *Enckella*, *Protojanira*). Species of these genera are

rare and must be survivors derived from ancient stocks which were displaced by the more advanced Janiroidea. Africa (Gondwana) and the areas adjacent to the Tethys Sea seem to be the regions, where these genera radiated. The Gnathostenetroidoidea have oculated and blind species; they evolved in the marine interstitial. The Protojaniroidea are exclusively freshwater stygobionts (Sket, 1982; Henry et al., 1986). This superfamily is morphologically intermediate between the Gnathostenetroidoidea and the higher evolved Janiroidea/Pseudojaniroidea (Wilson, 1987; Wägele, 1989). The distribution (South Africa, Sri Lanka) suggests that the Protojaniroidea are rather old (more than 130 My?) and of Gondwana origin.

Within the Janiroidea the less derived, non-monophyletic “family” Janiridae contains several lines of marine origin which most probably radiated independent of each other in fresh water. The genera *Heterias*, *Protocharon*, and *Mackinia* are closely related; only *Mackinia* is subterranean, known from East Asia and Japan (summary in Coineau, 1986b). A second group, for which the phylogenetic system is not known in detail, contains the genera *Microjanira*, *Caecianiropsis*, and *Microjaera*. These are coastal mesopsammic, without major speciation and dispersion.

“Monophyly or polyphyly?” is the question not definitely solved in the case of the Microparasellidae (Wägele, 1989). All genera are represented by interstitial species, mostly coastal mesopsammic in *Angeliara*, *Paracharon*, partly in *Microcharon*, while *Microparasellus* has been found in caves and wells (eastern Europe and Lebanon). The phylogenetic relationships of the species are not known. The coastal mesopsammic groups could have evolved and spread similarly to *Microcerberus*, as many populations occur in marine or brackish water (Coineau, 1986b). In the case of *Microcharon*, a genus known from marine coastal waters and from fresh water in Europe, Mediterranean islands, North Africa, Iran, Russia, Polynesia, New Caledonia, and Bonaire, it is not known whether its origin is in fresh water or in the marine interstitial. Stock (1977) has shown that most localities lie near the Oligocene shore-lines of the Tethys Sea. Inland species therefore might be offsprings of popula-

tions that “stranded” during Miocene regression. The Australian freshwater species of *Angeliara* is of enigmatic origin (Stock, 1985); Stock suggests that populations could have stranded during late Tertiary uplift in Australia. The Microparasellidae then could have been a coastal interstitial family widely distributed in the Cretaceous Tethys, of which single populations stranded during regressions and evolved to inland species.

### *Anthuridea*

The Anthuridea are worm-like marine isopods, mostly living on the shelf of warmer seas. Only three genera have stygobiontic species. The subgenus *Cyathura* (*Stygocyathura*) evolved from marine ancestors, adapting to the coastal mesopsammal and to brackish and fresh water (Wägele et al., 1987). The wide Tethys distribution, ranging from the Caribbean to Borneo, New Caledonia, and Melanesia, suggests a radiation and speciation on the shores of the former Tethys Sea. Their absence in the peri-Mediterranean area and occurrence on Easter Island and Pitcairn (Botosaneanu, 1987) are enigmatic. Parallel evolution in the development of the “interstitial habitus” in different populations is not very probable because of the nearly identical morphology of the species, which indicates monophyly. Species of *Curassanthura*, the most primitive of the stinging-sucking paranthurids, obviously are relicts (Wägele, 1985; Wägele & Brandt, 1985). They are only known from the Caribbean and from the Canary Islands; the amphi-Atlantic distribution suggests for the genus an age of at least 50 My. *Cruregens* is an endemic monotypic genus of New Zealand, occurring on the Southern and on the Northern Island; it evolved from specialized tropical shallow-water ancestors (sister-group: *Colanthura*, *Califanthura*) (Wägele, 1982, 1989).

### *Sphaeromatidea*

The suborder Sphaeromatidea is composed for the most part of exclusively marine families (Wägele, 1989). Only within the Sphaeromatidae some genera are adapted to tolerate brackish and even fresh water. Hypogean species are only present in

specialized genera occurring in those areas of southern Europe, which had been covered by the sea during Tertiary periods (Yugoslavia, northern Italy, southern France; summary in Sket, 1986). All these genera (*Monolistra*, *Caecosphaeroma*, *Microlistra*) are closely related (Wägele, 1989) and possibly evolved from an ancestor species that tolerated brackish or fresh water and “stranded” during regressions.

### *Cymothoida*

In the suborder Cymothoida only the family Cirolanidae has stygobiontic species. A first survey of the phylogeny on generic level (Wägele, 1989) has shown that at least two monophyletic lines and further single species invaded the hypogean world.

In some epigean genera (*Annina*, *Anopsilana*) with an affinity to fresh water, hypogean species are found (summary in Botosaneanu et al., 1986). A large group of genera (including *Bahalana*, *Arubolana*, *Antrolana*, *Typhlocirolana*, *Skotobaena*, etc.) is a monophyletic group of stygobionts, distributed over several localities in the Caribbean, Mexico, Texas, and Virginia in the West, and in North Africa, Somalia, Ethiopia, and peri-Mediterranean areas in the East. This points to a Tethyan origin of these genera. It even seems that subgroups of hypogean genera already existed before the opening of the Atlantic: the western genera *Antrolana*, *Mexilana*, and *Cirolanides* are probably related with the eastern genera *Typhlocirolana* and *Turcolana*; the western genus *Sphaerolana* may be a close relative of the eastern *Faucheria* and *Skotobaena*. All these genera belong to the same monophylum (group E of the Cirolanidae in Wägele, 1989). A second line, related to *Hansenolana* and *Anopsilana*, is known from the Caribbean (*Creaseriella*, *Haptolana*). It is very improbable that within these monophyletic groups stygobiontic species evolved independently of each other in localities of the Old and the New World.

### Conclusions

The colonization of the subterranean environment is very complex, as every single case has a different

history. A single model, as the “active colonization model” of Rouch & Danielopol (1987) can not explain all known phenomena, such as the presence of primitive relict taxa, of local “stranding”, of a large radiation within a stygobiontic monophylum. In isopods two main processes can be discerned: (1) preadaptation in epigean fresh water, followed by penetration into karst systems (caves etc.), or into phreatic or hyporheic habitats, and (2) colonization via the coastal mesopsammal. The latter case can be observed in *Cyathura* (*Stygocyathura*) and in the families Gnathostenetroididae, Stenetriidae, Microparasellidae, and possibly in some Cirolanidae. But most genera seem to have direct freshwater ancestors. Here two different groups can be found: (a) Old freshwater groups, whose transition from marine to inland waters probably happened before the Cretaceous; to this group belong the Phreatoicoidea, the Aselloidea, possibly also the Calabozoida and Protojaniroidea. These isopods are more primitive than representatives in the remaining suborders. It is interesting that the coastal mesopsammal was also conquered by an inland group (Microcerberidae) (see Wägele, 1983).

(b) Groups of freshwater genera, originating from Cretaceous/Tertiary ancestors that “stranded” during regressions, viz. “Monolistrini” and cirolanids, especially of the amphi-Atlantic “*Bahalana*” group and related genera.

Local (regional) speciation of the stygobiontic taxa took place at all times and is not considered in this paper.

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