

The Importance of a Phylogenetic System for the Study of Deep-Sea Harpacticoid Diversity

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Sybille Seifried (2004) The importance of a phylogenetic system for the study of deep-sea harpacticoid diversity. *Zoological Studies* 43(2): 435-445. The present knowledge about systematics, abundance, diversity, and distribution of deep-sea species of Harpacticoida Sars, 1903 (Crustacea: Copepoda) is summarized. Three new deep-sea species demonstrate the value of the deep-sea fauna for the reconstruction of phylogenetic relationships within Harpacticoida. The importance of a phylogenetic system, i.e., of monophyletic taxa, for the study of deep-sea diversity is stressed. The position of the presently known 460 species of deep-sea Harpacticoida within the phylogenetic system is analyzed, and the question is posed of whether there are true deep-sea taxa within Harpacticoida with representatives only in the deep sea. In contrast to the abundance and biomass of Harpacticoida in general in the deep sea, little is known about the abundance, distribution, and diversity on the species level. To date, more than 95% (often even 100%) of harpacticoids from benthic deep-sea samples are new to science. The question is posed of how many deep-sea species of Harpacticoida can be expected to exist. <http://www.sinica.edu.tw/zool/zoolstud/43.2/435.pdf>

Key words: Deep sea, Harpacticoida, Phylogenetic Systematics, Diversity, Species description.

Knowledge of marine invertebrates is based mainly on macrofauna, especially in deep-sea studies. Gad (2003) pointed out that in estimations of species numbers, marine invertebrates are underestimated, because in such calculations, meiofauna species are underrepresented (e.g., DIVERSITAS 1999). As Gad (2003) emphasized, 1 reason for this is the lack of experts able to identify and describe this fauna. The vast majority of marine invertebrates are meiofauna organisms (e.g., Tietjen 1992). In the deep sea, nematodes are the most abundant metazoans, followed by harpacticoids (e.g., Tietjen 1992, Ahnert and Schriever 2001). Among arthropods, it is the Harpacticoida Sars, 1903 (Crustacea: Copepoda) that are most abundant in the deep-sea benthos, and in terms of biomass, they may even exceed nematodes. "For example, copepods generally comprise 3 to 10% of the individuals in most deep-sea metazoan meiobenthic assemblages, but they may comprise from 15 to 75% of the biomass, because their average individual body weight ... is

larger than that of nematodes..." (Tietjen 1992). Nearly all copepods in the deep-sea benthos are species of Harpacticoida.

In contrast to the abundance and biomass of Harpacticoida in the deep sea, little is known about their systematics, diversity, and species composition. No complete species lists of deep-sea samples are available to date, for either qualitative or quantitative samples. Only a few studies dealing with the diversity of deep-sea Harpacticoida on the species level have been presented (Drzycimski 1969, Coull 1972, Hessler and Jumars 1974, Jumars and Hessler 1976, e.g., Thistle 1978 1998). "Meiobenthic taxonomy is always difficult and time-consuming; in the deep sea this problem is compounded by high species diversity and low species dominance. Most deep-sea meiobenthic investigations have, therefore, dealt with only taxonomic levels higher than the species level (Thiel 1983, and references therein)" (Vincx et al. 1994). Vincx et al. (1994) added: "Also in the case of copepods, no complete diver-

sity analysis has been made of northeast Atlantic deep-sea communities. Nevertheless, some taxonomic studies suggest that these assemblages are highly diverse and comprise many undescribed species.”

In the following, an attempt is made to summarize the present knowledge on deep-sea-inhabiting Harpacticoida. What do we know about their systematics, their species composition, their diversity, and their distribution and, why is it advanta-

geous to have a phylogenetic system for the analysis of these factors? On the other hand, 3 new deep-sea species demonstrate the value of the deep-sea fauna for the reconstruction of phylogenetic relationships within Harpacticoida. It is not my intention here to discuss the ecology of harpacticoids, e.g., the influence of environmental factors. The deep sea in the following is defined as beginning below 200 m in depth (Gage and Tyler 1991).

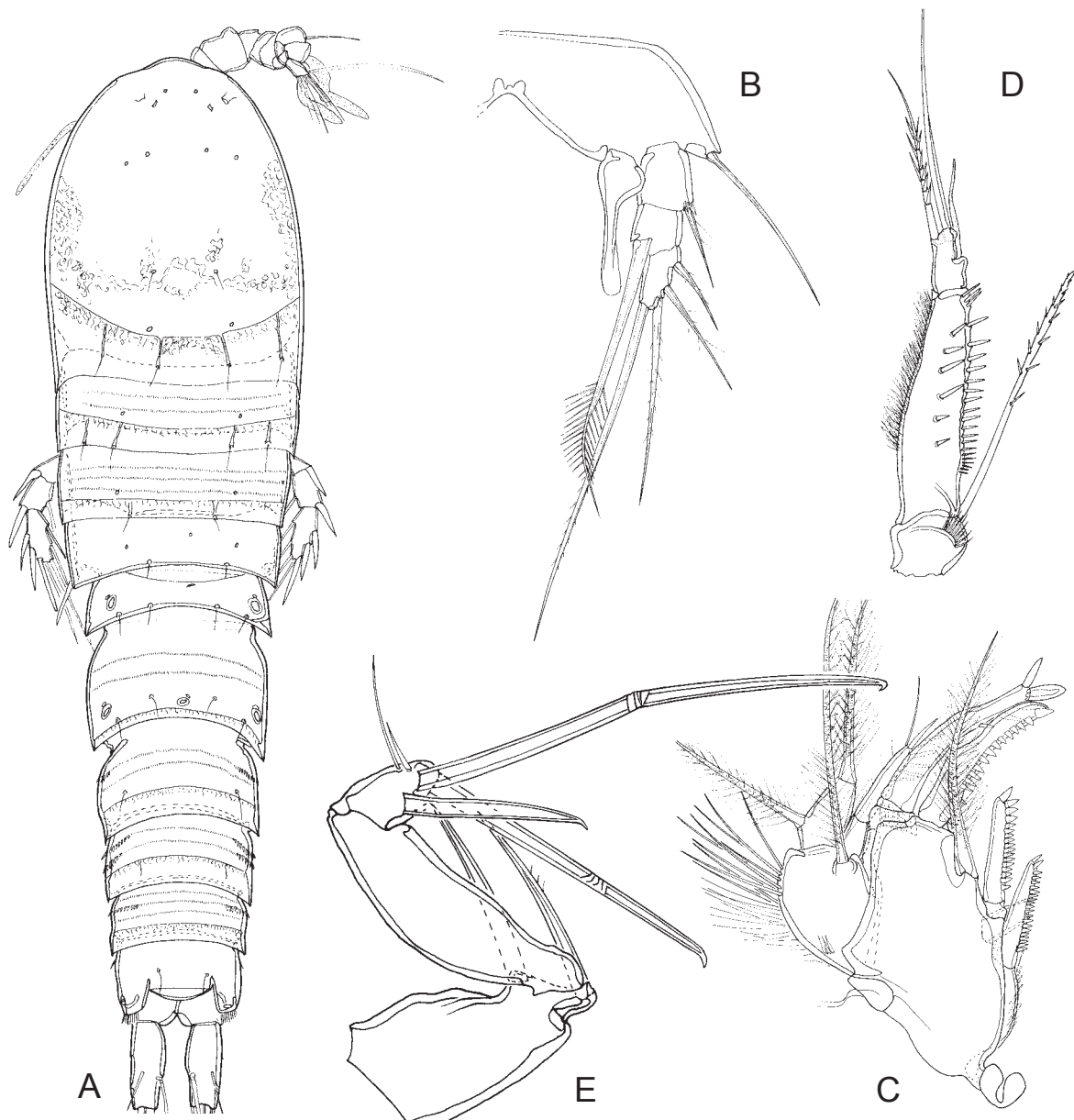


Fig. 1. A. Habitus of *Romete* sp. (Angola Basin, DIVA 1). B. P5 of *Romete bulbiseta* Seifried and Schminke, 2003 (Great Meteor Seamount). C. Maxilliped of Neobradysid sp. (Weddell Sea, Antarctic). D. Maxilliped of *Ectinosoma carnivora* Seifried and Dürbaum, 2000 (Andros, Bahamas). E. Maxilliped of Ectinosomatidae sp. (Weddell Sea, Antarctic).

The value of descriptions of deep-sea species for the reconstruction of phylogenetic relationships

As an example of the value and even indispensability of deep-sea species for the reconstruction of phylogenetic relationships within Harpacticoida and probably other groups of organisms as well, the morphology of 3 new deep-sea species is discussed. Descriptions of two of these species will be published elsewhere. Two single males and a female from the deep sea near the Great Meteor Seamount (455 m) and from the Angola Basin (5400 m) were identified as belonging to 2 different species of a new taxon of Harpacticoida. *Romete bulbiseta* Seifried and Schminke, 2003 and *Romete* sp. (Rometidae Seifried and Schminke, 2003) show the typical habitus of species of Oligoarthra Lang, 1944 (Harpacticoida; Fig. 1A), but at 1st sight, no apomorphy of any known taxon of Oligoarthra (Fig. 2). The characters of these species, as for example the 3-segmented exopod of the male P5, the non-transformed P1, and the maxilliped without a claw are

very plesiomorphic within Harpacticoida. Most other species of Oligoarthra have a 1-segmented male P5 exopod, a prehensile P1, or a maxilliped with a claw (Fig. 1E). The majority of Harpacticoida all have these advanced characters. The 2 rometid species show almost all groundpattern characters of Oligoarthra. The groundpattern represents the hypothetical morphology of members of the last common population of the species group in question. Only the typical fusion of the endopod and basis of the maxillule of Aegisthidae Giesbrecht, 1892 *sensu* Seifried and Schminke (2003) is also present (see figs. 3C and 8A of Seifried and Schminke 2003). However, these species have too many setae and segments on nearly all mouthparts, on the antennule, and the P5 to be regarded as representatives of Aegisthidae. For example, the endopod of P5 is completely reduced in species of Aegisthidae, but is present in males and females of Rometidae (Fig. 1B). The 2 deep-sea species of Rometidae are the most plesiomorphic of all Oligoarthra apart from a few reductions of single seta on P2 to P4 and the few apomorphies shared with the

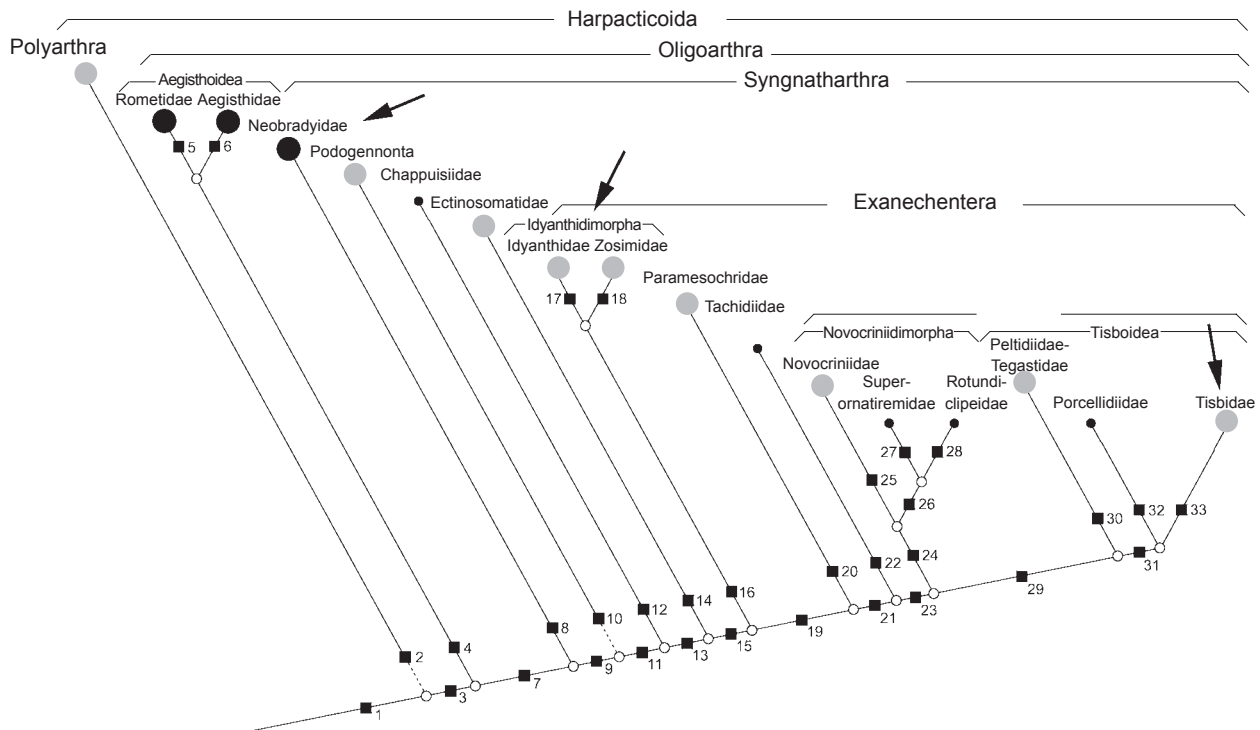


Fig. 2. Diagram of phylogenetic relationships within Harpacticoida after Seifried (2003). The autapomorphies 1 - 33 are listed in Seifried (2003). Arrows indicate the membership and position of the taxa of Tisbidae *sensu* Lang (1944). The big black spots represent taxa enclosing only benthic, planktic, or parasitic deep-sea species (some also found between 20-200 m in depth) and species found between 20 and 200m in depth; the grey spots represent taxa with a mix of species from the deep sea and from the continental shelf, littoral, phytal, or even from freshwater and the small black spots taxa without described deep-sea species.

Aegisthidae (Fig. 2). The morphology of the species of Rometidae therefore helped to reconstruct the morphology of the last common ancestor of all Oligoarthra, to ascertain the position of the taxon Aegisthidae within Oligoarthra (Seifried and Schminke 2003) and to reconstruct the phylogenetic relationships at the base of Harpacticoida and Oligoarthra (Seifried 2003).

The 2nd species mentioned here is widely distributed in the Antarctic Weddell Sea (300 - 540 m). Neobradidae sp. has all the autapomorphies of the taxon Neobradidae Olofsson, 1917 such as the sexual dimorphism in P2 and P3 and the characteristic setation of the syncoxa of the maxilliped (Fig. 1C). Otherwise Neobradidae sp. is also a very plesiomorphic species within Oligoarthra (Seifried 2003). It was very fortunate that this species shows the more-plesiomorphic states in all characters in which the taxa Rometidae and Aegisthidae are apomorphic. Therefore it was also helpful, in reconstructing the morphology of the last common ancestor of all Oligoarthra, to unravel the phylogenetic relationships at the base of Harpacticoida (Seifried 2003) and additionally, to determine the position of the taxon Neobradidae within Oligoarthra.

The morphology and systematic position of the taxon Ectinosomatidae Sars, 1903 have always been a problem. An outgroup is needed to polarize the characters or to root the cladograms. However, no synapomorphy indicates with which other taxon Ectinosomatidae might be related. The species of Ectinosomatidae have a unique morphology of the mouthparts, as for example the maxilla with the increased basis and the pen-shaped maxilliped (Fig. 1D; Seifried and Durbaum 2000), but otherwise they show completely plesiomorphic morphology. Lang (1944) placed the taxon Ectinosomatidae in the "Maxillipedasphalea" Lang, 1944 because species of Ectinosomatidae have no maxillipedal claw. The "Maxillipedasphalea" was based by Lang (1944) on the primary lack of a maxillipedal claw. The situation changed when 1 female was discovered in material from the Antarctic Weddell Sea (300 m), which showed most autapomorphies of the taxon Ectinosomatidae but also a maxilliped with an endopodal claw (Fig. 1E). This claw and the geniculated terminal setae of the maxilliped clearly showed that the taxon Ectinosomatidae belong to a group of Harpacticoida characterized by such a maxilliped (Seifried 2003). The lack of the claw thus has to be interpreted as a reduction within the taxon Ectinosomatidae. As these 3 examples show, the

deep sea seems to harbor many phylogenetically important taxa.

Monophyly of taxa

As almost all deep-sea species of Copepoda have not yet been described and the systematics of described species is in a state of flux (see below), species level analyses are very difficult and time-consuming. Therefore nearly all studies of deep-sea Copepoda are restricted to an analysis of higher taxonomic level. But analysis on higher taxonomic level makes sense only when the taxa dealt with are monophyletic or when an exact specification of the species belonging to the taxon is given.

The taxon Tisbidae Stebbing, 1910 *sensu* Lang (1944) (Harpacticoida) is a good example of what can result from analyses made with taxa that are not monophyletic. Species of Tisbidae have been recorded as being abundant in benthic deep-sea samples (e.g., Vincx et al. 1994, Martínez Arbizu et al. 1998, Ahnert and Schriever 2001). The Tisbidae *sensu* Lang (1944) contains 3 subfamilies: Idyanthinae Lang, 1944, Tisbinae Stebbing, 1919, and Cholidiinae Boxshall, 1979. After a revision of the system of Harpacticoida (Fig. 2), it became clear that the species of Tisbidae *sensu* Lang (1944) belong to 3 different not very closely related taxa (Fig. 2; Seifried 2003). The subfamily Idyanthinae *sensu* Lang (1944) had to be divided into 3 taxa (Seifried 2003). *Marsteinia* Drzycimski, 1968, *Tachidiopsis* Sars, 1911, former genera of Tisbidae *sensu* Lang (1944), were moved to taxon Neobradidae (Seifried 2003). The taxon Idyanthinae was excluded from Tisbidae and raised to family rank (Idyanthidae Lang, 1944), and a new taxon Zosimidae Seifried, 2003, was established, as *Idyanthe* Sars, 1909 and *Zosime* Boeck, 1872 and related genera belong to 2 different monophyletic taxa which have their own autapomorphies (Seifried 2003; Fig. 2). The monophyletic taxon Tisbidae *sensu* Seifried (2003) contains only species of Tisbinae and Cholidiinae. Tisbinae are mainly littoral and phytal and extremely rare in the deep-sea benthos. Species of Cholidiinae reach the deep sea only occasionally with their hosts. One consequence of the new phylogenetic system of Harpacticoida therefore is that the free benthic Tisbidae are very rare in the deep-sea benthos. Rare deep-sea tisbids are either parasitic or planktic (see below). On the other hand, species of *Marsteinia* (Neobradidae) and *Zosime* (Zosimi-

dae) are very abundant, while species of Idyanthidae are regularly found in the deep sea. Those former references to deep-sea tsebids which were not more specific, are worthless today, because it is unclear whether Neobradidae *sensu* Seifried (2003), Idyanthidae, Zosimidae, or Tsebidae *sensu* Seifried (2003) was intended (Fig. 2).

Coull (1972) pointed out that Cletodidae Scott, 1905 together with Aegisthidae dominate the harpacticoid fauna in samples from the deep West Atlantic. It is very fortunate that Coull (1972) mentioned some of the “cletodid” genera, because all of them belong to different families today (Argestidae Por, 1968; Canthocamptidae Sars, 1906; Huntmanniidae Por, 1986; and Pseudotachidiidae Lang, 1936). In samples from the Iceland-Faeroer Ridge, Schriever (1986) found 31% Cletodidae (266 individuals of 858). The fact that they have been determined to genus and species level by Schriever (1986) makes it possible to check their current taxon membership. Only three of the 44 species formerly belonging to the Cletodidae belong there today. The remaining species now belong to the taxa Argestidae, Canthocamptidae, Huntmanniidae, and Pseudotachidiidae. According to current knowledge, 6% (53 out of 858) and not 31% of individuals collected in samples from the Iceland-Faeroer Ridge belong to the Cletodidae *sensu strictu*.

Before taxa are used in ecological or biodiversity studies, it should always be determined whether they are monophyletic, and a phylogenetic system is a prerequisite for this. When a phylogenetic system is not available, an exact specification of the genera or species belonging to the used taxa is essential. On the other hand, rearrangements of systematics always cause problems for ecological and biodiversity analyses. One of the major advantages of a strongly supported phylogenetic system is that it is mostly more stable than traditional taxonomic concepts based on a typological taxon concept. As new phylogenetic analyses within Harpacticoida have been done (e.g., Huys 1990, Willen 2000, Seifried 2003) and more are in progress, amplification of the knowledge of these crustaceans may be based on a better foundation.

Deep-sea taxa of Harpacticoida

Are there any harpacticoid taxa with species occurring only below 200 m in depth? These taxa are called deep-sea taxa here. The identification of such taxa can be very valuable for, among other

things, the study of the origin of the deep-sea fauna. With the aid of a phylogenetic system and knowledge of the monophyly of the taxa, the question can be asked, if the ancestors of all Harpacticoida or all Oligoarthra could be of deep-sea origin.

The 1st difficulty in identifying deep-sea taxa of Harpacticoida is that many species simultaneously occur both above and below 200 m. The 2nd difficulty is the scant knowledge of the distribution of marine harpacticoid species living far from the coast. Most described species have only been found once to date. It is possible that species currently reported only from the deep sea, also live on the higher continental shelf and vice versa. Therefore, it is nearly impossible at this moment to precisely delimit the depth distribution of harpacticoid species. Despite these difficulties, the present knowledge of Harpacticoida allows a preliminary insight into the depth distribution and, in combination with the phylogenetic system, into the probable origin of harpacticoid taxa. In the following, taxa of Podogenonta Lang, 1944 (Fig. 2) are discussed separately from the rest of Harpacticoida.

Within Harpacticoida, no real deep-sea family has been described. Taking the new phylogenetic system of Harpacticoida as the base (Fig. 2), approximately 870 described species of Harpacticoida are known from outside Podogenonta. For the depth distribution of species in fig. 3, all species descriptions listed in Bodin (1997), all descriptions of species new to science described after Bodin (1997), and the summary of ecology of the species in Lang (1948) were evaluated. Species for which no depth distribution is known were not considered. To date only 1 species of the taxon Rometidae is described (Seifried and Schminke 2003) and another description is in preparation. Both species are from the deep sea. However, it is too early yet to be sure that Rometidae is a deep-sea taxon. So far 10 species of 4 genera are described for the taxon Neobradidae *sensu* Seifried (2003). Eight species were found between 300 and 5171 m depth. However, *Neobradia pectinifera* Scott, 1892 and *Tachidiopsis cyclopoidea* Sars, 1911 were found between 25 and 90 m in depth. Neobradidae is therefore not a deep-sea taxon. For the taxon Aegisthidae, the former Cerviniidae Sars, 1903 (Seifried and Schminke 2003), 77 species are known. Four species were only found between 20 and 200 m in depth, and 6 species were found in the deep sea and between 20 and

200 m in depth. Eight (benthic-) pelagic and 59 (hyper-) benthic species have exclusively been reported from the deep sea, far more than for the other taxa outside Podogennonta. This could lead to the impression that species of Aegisthidae are common in the deep-sea benthos. Por (1969), Coull (1972), Dinet (1977), and Montagna and Carey (1978) found a high percentage of species of Aegisthidae (as Cerviniidae) in their samples, whereas they were very rare or even absent in other studies (Ahnert and Schriever 2001; unpubl. data from South and East Atlantic, the Arctic Ocean, the Antarctic Weddell Sea, and the West Pacific). As most species of the taxon Aegisthidae belong to the epi- or hyperbenthic fauna, differences may have been due to the sampling methods. Data of Ahnert and Schriever (2001) and own data were from Multicorer samples, which might entail an underestimation of the hyperbenthic fauna. Por (1969) used a trawl, and Coull (1972) took his samples with an epibenthic sled, which, on the other hand, may entail an underestimation of the inbenthic fauna. Montagna and Carey (1978) used different mesh sizes, so that the high number of species of Aegisthidae might have been due to differences in sample processing. The fact, however, that 77 species of the taxon Aegisthidae are known has nothing to do with their being rare

or not in the deep-sea benthos, but predominantly with the preference of authors who like to describe big and beautiful copepods (> 1- 3 mm). For example, species of Zosimidae, Neobradyidae *sensu* Seifried (2003), and Ectinosomatidae are far more abundant than that of Aegisthidae in most deep-sea Multicorer samples (e.g., Martínez Arbizu et al. 1998, Ahnert and Schriever 2001; unpubl. data from the South and East Atlantic, the Arctic Ocean, the Antarctic Weddell Sea, and the Angola Basin (DIVA 1 expedition; 491 km transect; 5300 to 5500 m in depth)). However, species of these taxa are hardly ever described. The taxon Zosimidae currently contains 17 species. Thirteen of them were found in the deep sea, among which 6 species were also found above 200 m, 2 species were found only on the continental shelf until now, and for 1, no observed depth was given. As *Zosime mediterranea* Lang, 1948 was found between algae, Zosimidae is not a deep-sea taxon. Looking at known species of the taxon Ectinosomatidae (Fig. 3), one may gain the impression that they are rare in the deep sea. However, species of plesiomorphic *Bradya* Boeck, 1872 and other ectinosomatid taxa are very abundant there, but they are not described (e.g., Martínez Arbizu et al. 1998, Ahnert and Schriever 2001; unpubl. data from the South Atlantic, the

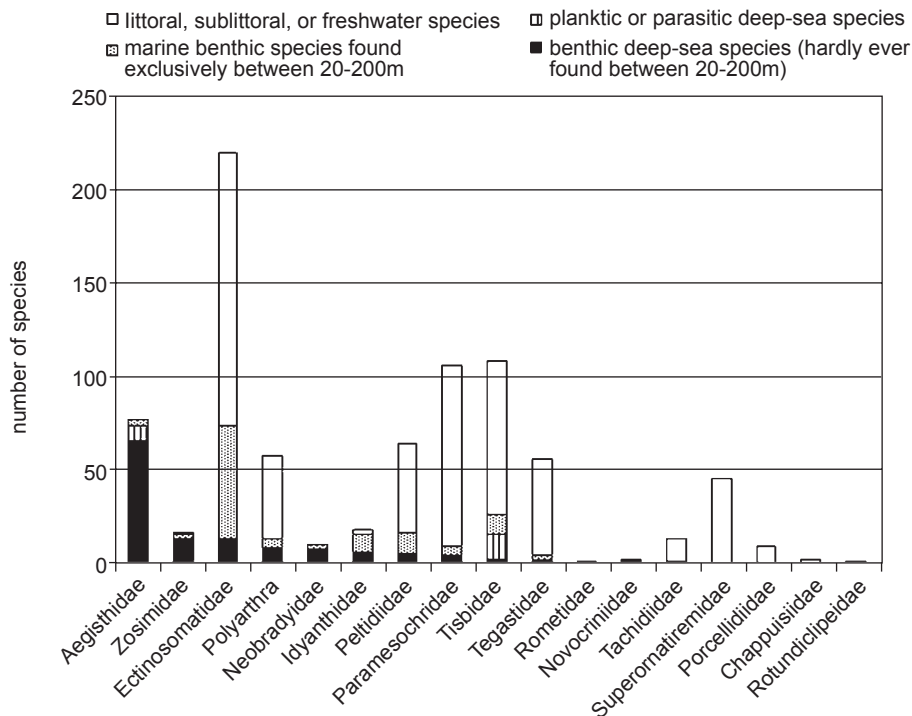


Fig. 3. Distribution of species of Harpacticoida outside Podogennonta. The taxa with the greatest number of described benthic deep-sea species (some also found between 20 - 200 m in depth) appear more on the left. The figure is explained in the text.

Antarctic Weddell Sea, the West Pacific, and DIVA 1 samples). Tisbidae *sensu* Seifried (2003) contains only 2 benthic, 2 planktic, and 9 parasitic species reaching the deep sea to date (Fig. 3). Indeed, they are really very rare in benthic deep-sea samples. Out of over 16 000 specimens of Harpacticoida in the DIVA 1 samples only 2 are tisbids, both undescribed females of *Volkmannia* Boxshall, 1979. The 2 described *Volkmannia* species are both planktic. For the taxa Ildyanthidae, Peltidiidae Sars, 1904, Paramesochridae Lang, 1944, Tegastidae Sars, 1904, Novocriniidae Huys and Iliffe, 1998, and Polyarthra Lang, 1944 (Fig. 2; Canuellidae Lang, 1944, Longipediidae Sars, 1903), 1 to 8 benthic deep-sea species are known (some also found from between 20 and 200 m; Fig. 3). *Euterpina acutifrons* Dana, 1848 is the only species of Tachidiidae Sars, 1909 reaching the deep sea (Seifried 2003); however, it is a planktic species. For 4 taxa, the Porcellidiidae Sars, 1904, Superornatiremidae Huys, 1996, Chappuisiidae Chappuis, 1940, and Rotundiclipeidae Huys, 1988, no deep-sea species have been described so far.

Within Podogennonta there are many species-rich families, yet none is a real deep-sea taxon even though species of the taxa Argestidae, Pseudotachidiidae *sensu* Willen (2000), and Ameiridae Monard, 1927 are very abundant in the deep sea (e.g., Martínez Arbizu et al. 1998, Ahnert and Schriever 2001; unpubl. data from the South Atlantic, the Antarctic Weddell Sea, the West Pacific, and DIVA 1 samples). More than 80 species of the taxon Argestidae are described, most of them from the deep sea. The rest are from the higher continental shelf or even from the littoral. More than 70 species of the taxon Pseudotachidiidae *sensu* Willen (2000) have been described, most but not all from the deep sea. Species of Ameiridae are abundant in all marine and freshwater habitats, so that the species from the deep sea are only a small fraction. Some benthic or planktic deep-sea species are also known within the taxa Adenopleurellidae Huys 1990, Ancorabolidae Sars, 1909, Canthocamptidae, Cletodidae, Dactylopusiidae Lang, 1936, Harpacticidae Sars, 1904, Hunttemanniidae, Laophontidae Sars, 1904, Miraciidae Dana, 1846, Normanellidae Lang, 1944, Orthopsyllidae Huys, 1990, Parastenheliidae Lang, 1944, Rhizothricidae Por, 1986, Tetragonicipitidae Lang, 1944, and Thalestridae Sars, 1905. However, the majority of their species are from the continental shelf, littoral, phytal, or even freshwater areas. It is remarkable

that Ancorabolidae and Hunttemanniidae, which traditionally have been regarded as typical deep-sea taxa, contain only a few deep-sea species. Most records of these 2 taxa are from the sublittoral or littoral and they are found in the deep sea only in low abundances (Ahnert and Schriever 2001; unpubl. data from the South Atlantic, the Antarctic Weddell Sea, the West Pacific, and DIVA 1 samples). Species of Cletodidae were reported to be abundant in the deep sea (Coull 1972, Schriever 1986). However, Cletodidae as understood today are relatively rare in the deep-sea benthos (see above). No deep-sea species have been recorded for the remaining families of Podogennonta so far.

Within Harpacticoida, no deep-sea family is described; however, many genera of the presently known 51 families are deep-sea taxa. Significantly, most genera of the basal oligoarthran taxa, Aegisthidae and Neobryidae, are deep-sea taxa (e.g., *Cerviniopsis* Sars, 1909, *Expansicervinia* Montagna, 1981, *Pontostratiotes* Brady, 1883 (Aegisthidae); *Antarcticobryda* Huys, 1987, and *Marsteinia* (Neobryidae)). Species of some of them are omnipresent in the deep sea.

Projecting the data about the depth distribution of the taxa onto the phylogenetic system (Fig. 2), it is highly probable that the ancestor of Oligoarthra lived in the deep sea or on the lower continental shelf. If we assume that the lower continental shelf and the deep sea are not a refuge, it is highly probable that the ancestor of Oligoarthra lived in this zone (Seifried and Schminke 2003). All species of the more-basal taxa of Oligoarthra, namely the Rometidae, Aegisthidae, and Neobryidae, are reported from the deep sea or sometimes from 20 to 200 m in depth (big black spots in Fig. 2). Polyarthra as the sister group of Oligoarthra contains some deep-sea species, but most are from the littoral. Taxa with only some deep-sea species and otherwise littoral, sublittoral, or freshwater ones are scattered all over the phylogenetic system. The origin of Oligoarthra and maybe of Harpacticoida was probably in the deep sea or on the lower continental shelf. Within the more-derived Syngnatharthra Seifried and Schminke, 2003 (Fig. 3) the littoral was colonized several times with some lines returning to the sublittoral and even to the deep sea.

Abundance, diversity and distribution of Harpacticoida in the deep sea: State of knowledge

Half of the earth's surface is deep sea below

1000 m depth; to be exact, 3×10^{14} m² (Grassle and Maciolek 1992). Additionally, there is the zone between 200 and 1000 m which is also regarded as deep sea. However, the deep-sea area sampled for meiofauna is rather minute, namely 5 m² (Lambhead 1993). At the same time the knowledge of deep-sea Harpacticoida in relation to their occurrence is alarmingly small. More than 95%, often even 100% of Harpacticoida from benthic deep-sea samples are new to science (Thistle 1998; unpublished data from the South Atlantic, the Arctic Ocean, the Antarctic Weddell Sea, the West Pacific, and DIVA 1). To determine these species and to make an analysis of species abundance, diversity, and distribution therefore is a great challenge. No identification keys can really help in the identification of these undescribed species. The only possibility to establish order in this undescribed diversity is to use a phylogenetic system with the autapomorphies for the respective taxa. Ectinosomatidae, for example, have a unique morphology of the mouthparts, e.g. the maxilla with an increased basis. No other taxon is characterized with these autapomorphies which are evolutionary novelties developed within the ancestral line of the taxon in question. The autapomorphies of Ectinosomatidae and all other taxa outside Podogennonta are described in Seifried (2003). A species with a maxilla with such an increased basis can only be an ectinosomatid. As details of the maxilla are also characteristic for different genera of Ectinosomatidae, an undescribed species can preliminarily be allocated to a genus and therefore some assumptions, e.g. about the life-style of the species, are possible. Not all species show all autapomorphies of their supraspecific taxon, however, in most species at least some of these autapomorphies are visible. The autapomorphies allow the taxon membership to be determined and the species to be given a working name and a short characterization so that comparative studies e.g. of the distribution of different species are possible. However, this can only be a makeshift procedure. In the long run, only detailed species descriptions and excellent identification keys on species-level can shed light onto species diversity and the role of Harpacticoida in the deep sea.

It was reported that Harpacticoida could constitute between 0 and 36% of the total metazoan meiofauna in the deep sea (e.g. Dinét 1976: maximum 36% Harpacticoida). In the majority of cases they constitute between 5 and 15% (e.g. Tietjen 1971: 2-15%; Ahnert and Schriever 2001:

9-12%; unpublished data from South Atlantic, the Arctic Ocean and DIVA 1 samples). Their abundance can range between 0 and 319 individuals per 10 cm² deep-sea bottom (Shirayama and Kojima 1994: 319 harpacticoid copepods per 10 cm² in 245 m depth; Chen et al. 1999: 303,7 Copepoda including nauplii per 10 cm² in 352 m depth). There are harpacticoids in nearly all benthic deep-sea meiofauna samples so far analysed. They are also recorded from depths down to 10 000 m (Wolff 1960).

Where enough material was available some species were represented by a large number of individuals. Dinét (1977), for example, found up to 160 adult individuals of nine species of *Pontostratiotes* in one area. Dinét (1985) also reported that the species composition of *Pontostratiotes* changes markedly between 2000 and 3000 m depth. Coull (1972) had "examined 696 deep-sea copepods from 18 stations and very few are duplicated from sample to sample". Por (1965) suggests a pan-bathyal fauna, as several genera from different families are reported from most oceans. As Coull (1972) stated, this has to be checked on the species level, because only few species seem to be widely distributed.

No complete species lists of deep-sea samples are available to date, neither for qualitative nor for quantitative samples. Drzycimski (1969) lists 49 species that he found below 200 m at the west coast of Norway. As yet, there are only a few studies on species diversity of Harpacticoida in the deep sea: Drzycimski (1969), Coull (1972), Hessler and Jumars (1974), Jumars and Hessler (1976), and several by Thistle (e.g. 1978, 1998). Drzycimski (1969) and Coull (1972) were the first to recognise that harpacticoids have a higher diversity in the deep sea than in shallow marine habitats. Drzycimski (1969) studied the diversity of Harpacticoida at three depths. At 680 m he found the highest species diversity, which was lower in two subtidal samples. Harpacticoids in the deep sea are characterized by high species diversity and low species dominance. Thistle (1978) summarized harpacticoid diversity using the Shannon-Weaver diversity index H' (Pielou 1969) and compared the values of subtidal habitats with two deep-sea ones (Quagmire site, Eastern Pacific, approximately 1220 m; bathyal muds, Norway, 680 m, in Drzycimski 1969). The Shannon-Weaver diversity index of deep-sea sites often seems to be higher than that of shallow water habitats.

Thistle and Levin (1998) compare the abundance and diversity of metazoan meiofauna, espe-

cially of adult Harpacticoida in unmanipulated and manipulated locations with rarefaction curves *sensu* Hurlbert (1971). The aim of the study was to investigate the effects of strong near-bottom flow on deep-sea meiofauna. Despite the ongoing discussion on the validity of different diversity indices and rarefaction curves and their value for comparing the diversity of different habitats, the state of knowledge is that compared to shallow marine habitats Harpacticoida have a lower abundance but a higher diversity in the deep sea. As Thistle explained at the 7th International Conference on Copepoda in 1999: "Harpacticoida are unusually successful in the deep sea" (see also Thistle 2001). This statement contrasts with our knowledge of the structure of harpacticoid diversity, e.g. taxa composition and phylogenetic relationships of species. In such a situation, a phylogenetic system with its characterization of groundpatterns and autapomorphies of taxa is a great help.

How many deep-sea Harpacticoida?

How many deep-sea species of Harpacticoida do exist? As there is a lack of studies at the species level, the total number can only be guessed at. One possibility to do so is to infer the total species number of a taxon from the percentage of undescribed species in new samples (Hodkinson and Casson 1991). Almost 98% of the Harpacticoida in samples from the Angola Basin (DIVA 1) are unknown. From this one could assume that 2% of the deep-sea Harpacticoida are described. Taking the 460 described deep-sea harpacticoids as reference value (2%), a number of 23 000 species of Harpacticoida in the deep sea would result (100%). To extend this to the Harpacticoida as a whole one could take the number of 3000 described harpacticoids according to Huys et al. (1996) as 2% and thus arrive at a total number of 150 000 species of Harpacticoida. At the 7th International Conference on Copepoda in Curitiba, Brazil Bodin mentioned the number of 5000 described species of Harpacticoida (Bodin 1999, pers. com.). Calculation with this number would lead to even 250 000 species of Harpacticoida. All these estimates, however, may be too low. Most known species have been recorded from the Atlantic, and since the DIVA 1 samples used as the base for these estimates are also from the Atlantic the percentage of 2% described species could be too high. What about the number of undescribed species in the Indian

and Pacific Oceans or the Polar Seas? Sometimes the percentage of undescribed species is higher than 98% (Thistle 1998; unpublished data from the Antarctic Weddell Sea, the West Pacific) so that on the base of this percentage the number of Harpacticoida would exceed 250 000 species.

Grassle and Maciolek (1992) estimated that there are 1 to 10 millions macrofaunal species in the deep sea. Humes (1994) therefore stated: "From such studies, we may expect the number of species of copepods in deep-sea benthic communities to be likewise very large". As mentioned previously, by far the most of them are Harpacticoida. Gray (1996) corrected the numbers of Grassle and Maciolek (1992) to 500 000 macrofaunal species in the deep sea. Poore and Wilson (1993) estimated that there are 5 million macrofaunal species. However, there are much more individuals of Harpacticoida per area deep-sea benthos than macrofaunal species (e.g. Tietjen 1992, Thistle 2001). As Thistle (2001) summarized "harpacticoids are not only successful in the deep sea, they are unusually so when compared to the macrofauna taken as a whole". It would be no surprise if there were more species of Harpacticoida in the deep sea than macrofaunal species altogether.

To date, approximately 460 species of Harpacticoida have been described from the deep sea. Thistle (1998), who has been working on the ecology of Harpacticoida for 25 years, wrote: "Adult harpacticoids were identified to working species because the species found have not been formally described." This is a typical situation. Lamshead (1993) estimated that at the present rate of description, it would take 500 to 5000 years to describe all nematode species of the deep sea. The same is probably true for Harpacticoida. There are probably more species of Nematoda than of Harpacticoida, but there are also more scientists describing nematodes than scientists describing harpacticoids.

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