PECKIANA **11** · Februar 2016 pp. 21–33

Peter Ax and the System of Metazoa

Andreas Schmidt-Rhaesa

Centrum für Naturkunde, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany
E-mail: andreas.schmidt-rhaesa@uni-hamburg.de

Received 6 Mai 2015 | Accepted 29 January 2016
Published online at www.senckenberg.de/peckiana 12 Februar 2016 | Printed version 19 February 2016

Abstract

Besides his contributions to phylogenetic systematics, to research on flatworms and to the interstitial fauna and environment, the three volume book series 'Multicellular Animals' (German title: Das System der Metazoa) are one of the main outputs of Peter Ax´s scientific career. This article tries to reconstruct how the interest in metazoan systematics grew in Peter Ax. Additionally, some process in animal systematics, which took place around the publication date of Ax´s books is reviewed to estimate its importance. Finally, some selected hypotheses from the 'Multicellular Animals' are compared with current hypotheses.

Between 1995 and 2001, Peter Ax published three volumes of his book 'Das System der Metazoa' (Ax 1995, 1999, 2001) (English translation 'Multicellular Animals': Ax 1996, 2000, 2002). These volumes constitute a unique approach to systematize the multicellular animals according to the principles of phylogenetic systematics. These principles were developed by Willi Hennig (e.g. Hennig 1950, 1966) and elaborated by Ax (1984, 1988). This text is the attempt to outline Peter Ax´s relation to metazoan systematics by asking three questions: 1. Where did Ax´s interest in metazoan systematics come from? 2. How are the three books embedded in a historical context? 3. How did selected phylogenetic hypotheses develop since the publication of the books?

Keywords Peter Ax | Phylogenetic Systematics | Metazoan Relationships | Phylogenetic Hypotheses

1. Where did Ax´s interest in metazoan systematics come from?

After starting to study biology in Hamburg, Peter Ax soon changed to the University of Kiel, where he became associated with the Zoologist Adolf Remane (see Xylander 2013, Bartolomaeus 2014, Reise 2014, Schaefer 2014, Schmidt-Rhaesa 2014, Westheide 2014 for obituaries and biographic data). Remane had a strong interest in animal systematics (see, e.g., Remane 1956, 1957, 1961a; see Weigmann 1973 for the entire reference list of Remane) and had an excellent knowledge in zoology, especially in marine animals. In the 1920s he had discovered that sandy marine sediments harbour a distinctly wider animal diversity than previously expected (e.g. Remane 1933, 1952a, Remane & Schulz 1934, 1964). This marine, benthic community, the interstitial fauna or meiofauna, was a main research focus of him and his students. Peter Ax took care of the flatworms (Plathelminthes or Platyhelminthes), a love that would hold throughout his entire life. Ax´s first publication, which resulted from his PhD thesis, was on flatworms from the Kiel Bight (Kieler Bucht, Germany) (Ax 1951), but he soon extended his range of collection localities to many places, mainly in the Northern hemisphere. Topic of his habilitation thesis was an impressive review of the proseriate taxon Otoplanidae (Ax 1956a). Many publications of flatworms had a taxonomic or morphological background (for a small selection of broader papers see, e.g. Ax 1954a, 1956b, 1957, 1959, 1977a, 2008) and one special focus was on flatworms from brackish waters on the northern hemisphere (Ax & Armonies 1987, 1990, Ax 1959, 1992, 1993a, 2008). With his last publication at the age of 84, a description of new species from the Bay of Biscay (France) (Ax 2011), a circle of 60 years of publishing on Plathelminthes was completed. Ax became, at the latest with his otoplanid

ISSN 1618-1735

monography (Ax 1956a), a member of the community of flatworm researchers (Tor G. Karling, Alex Luther, Erich Reisinger, Otto Steinböck and others), first in Europe and later internationally. Because flatworms were assumed to have a very basal position, they played a major role in evolutionary models and scenaria concerning the origin and early evolution of metazoans. Ax contributed to this discussion starting with his publications in 1961 and 1963 and especially his reconstruction of the flatworm 'archetype' (today we would say ancestor) was widely recognized (Ax 1961, 1963a).

Although being focused on flatworms, Ax must have come during his time in Kiel into contact with diverse other meiofaunal taxa. Adolf Remane published on polychaetes (Remane 1925a, 1926a, 1928a, 1932, 1934a, 1949a), the meiofaunal hydrozoan *Halammohydra* (Remane 1927a), rotifers (Remane 1929–33, 1929, 1949b), kinorhynchs (Remane 1928b, 1928–1933a, 1936a) and extensively on gastrotrichs (Remane 1924, 1925b,c, 1926b–d, 1927b, 1928c, 1928–1933b, 1934b, 1936b, 1950, 1951, 1952b, 1961b). Remane and his working group were at that time one of the most important working groups for meiofauna research.

With the start of a professorship at the University of Göttingen in 1961, Ax had the possibility to build his own working group and to continue and extend the investigation of the interstitial system (see, e.g. Ax 1966a, 1969 for general publications). Some of his publications concerned taxa other than Plathelminthes and Gnathostomulida (see below): *Edwardsia*, Anthozoa (Ax & Schilke 1964), *Hesionides*, Polychaeta (Westheide & Ax 1965), Aeolosomatidae, Oligochaeta (Ax & Bunke 1967), *Diurodrilus*, Polychaeta (Ax 1967), *Trilobodrilus*, Polychaeta (Ax 1968), *Arenadiplosoma*, Tunicata (Menker & Ax 1970) (for completeness, one further publication was before 1961, on *Thalassochaetus*, Polychaeta [Ax 1954b] and one was decades later, on *Turbanella*, Gastrotricha [Ax 1993b]). But, besides his own work, Ax sent out a number of students to study the majority of meiofaunal taxa (see, e.g. Xylander 2013, Reise 2014, Westheide 2014). Usually these students published their research in their own name, the inclusion of the supervisor´s name, which is a standard today, was not in fashion then. The center of this research was the tidal flat research station in List on the island of Sylt (see Xylander 2013, Bartolomaeus 2014, Reise 2014, Westheide 2014). In particular one small beach, conveniently located close to the station, was intensively investigated and became known as the 'Hausstrand'.

The majority of results were published in a journal series edited by Ax, the 'Mikrofauna des Meeresbodens (1970–1983), later renamed Microfauna Marina (1984–1997). Taxa investigated by Ax and his students from Sylt were: Ciliata (Hartwig 1973a, b), Acoela (Faubel 1974a, 1976a,b), Plathelminthes (Ax & Heller 1970, Sopott 1973, Ehlers 1974, Faubel 1974b, 1976, Reise 1984, Xylander & Reise 1984, Dittmann & Reise 1985, Wehrenberg & Reise 1985, Armonies 1987, Armonies & Hellwig 1987, Hellwig 1987, Noldt 1989a, b, Wellner & Reise 1989, Ehlers et al. 1995), Gnathostomulida (Müller & Ax 1971), Rotifera (Tzschaschel 1979, 1980), Gastrotricha (Mock 1979, Potel & Reise 1987), Nemertini (Mock 1978), Oligochaeta (Kosmagk-Stephan 1983), Nematoda (Blome 1974, 1982, 1983), Halacarida (Bartsch & Schmidt 1979) and Copepoda (Mielke 1973, 1975, 1976, Herbst 1974) (not all cited publications were under direct supervision of Peter Ax, some were conducted by his student´s own working groups).

In 1972 and 1973, a large grant allowed to conduct comparative studies on remote beaches on Galapagos (Ax & Schmidt 1973, Ax 1977b, Schmidt 1978; see also Xylander 2013, Schaefer 2014). Publications on these investigations covered even more taxa: Acoela (Ehlers & Dörjes 1979), Plathelminthes (Ax & Ehlers 1973, Ax & Ax 1974a, b, 1977, Ehlers & Ax 1974, Sopott-Ehlers & Schmidt 1974a, b, 1975, Schmidt & Sopott-Ehlers 1976, Ehlers & Ehlers 1981, Noldt & Hoxhold 1984, Ehlers & Sopott-Ehlers 1989), Gnathostomulida (Ehlers & Ehlers 1973), Gastrotricha (Schmidt 1974a), Kinorhyncha (Schmidt 1974b), Polychaeta (Westheide 1974, 1977, 1981, Schmidt & Westheide 1977), Oligochaeta (Westheide & Schmidt 1974, Erséus 1984), Nemertini (Mock & Schmidt 1975), Nematoda (Clasing 1984, Blome 1985), Harpacticoida (Mielke 1979, 1981, 1982, 1984, 1989a,b, 1997a, b), Isopoda (Coineau & Schmidt 1979), Ostracoda (Gottwald 1983), Halacarida (Bartsch 1977, Bartsch & Schmidt 1978) and Tardigrada (McKirdy et al. 1976)

The taxon that probably plays a key role in his broadening interest in metazoan systematics was the Gnathostomulida. The first gnathostomulids were discovered in meiofaunal samples by Remane in 1928 and passed, because they were thought to represent flatworms, to Josef Meixner in Graz (Austria) (see Sterrer & Sørensen 2015). Meixner planned to describe these specimens under the name *Remanella paradoxa* in a manuscript for the series 'Tierwelt der Nord- und Ostsee' (translated: fauna of the North Sea and the Baltic Sea), but the Second World War prevented the publication and Meixner died in 1946. Meixner´s original sketch of a gnathostomulid is now published in Sterrer & Sørensen (2015). From 1951 on, Ax found specimens in the Kiel Bight, on the island of Sylt and in the Western Mediterranean around Banyuls-sur-Mer. In 1956 he described two species, *Gnathostomula paradoxa* and *Gnathostomaria lutheri*, as representatives of a new order within Plathelminthes (Ax 1956c).

Gnathostomulids have a general appearance as flatworms, but differ from these in the possession of monociliary epidermal cells and the possession of a complex jaw apparatus (see, e.g. Ax 1963b, 1964, 1965). These differences led to a kind of 'systematic upgrading' and Ax suggested after a few years that Gnathostomulida should better have the rank of a class within Plathelminthes (Ax 1960, see also Ax 1966). Again a few years later, Riedl (1969) regarded Gnathostomulida as independent of Plathelminthes with the hierarchical rank of a phylum. Decades later, Ax used this 'upgrading' in talks to his students as an example of the arbitrariness of hierarchical ranks. Being first considered the describer of a new order, he could a few years later have been proud to be the describer of a phylum. But Ax had started to think about phylogenetic systematics and became convinced that not a classification with the assignment of a rank should be the main goal of systematics, but the search for sister-taxon relationships.

During the 70s and the early 80s, Ax´s thinking in systematics changed from Remane´s approach to Willi Hennig´s principles of phylogenetic systematics (see Westheide 2014), summarized in two books (Ax 1984, 1988). In 1985 Ax published a book chapter claiming that Plathelminthes and Gnathostomulida were sister taxa within a monophyletic taxon Plathelminthomorpha (Ax 1985). I believe that this search for sister group relationships was one important factor in Ax becoming interested in a wider range of metazoan relationships. When Gnathostomulida and Plathelminthes are sister taxa, where do Plathelminthomorpha belong in the phylogenetic tree? This question was treated in another book chapter (Ax 1989) and therefore phylogenetic relationships of all basal metazoan taxa had to be considered.

One other important factor for Ax´s interest in metazoans may have been the integration of ultrastructural research in his working group. Although he never worked on the electron microscope himself, his students did so and developed a recognized expertise in this technique. For example Ulrich Ehlers followed the research focus on Plathelminthes into the ultrastructural realm and found a number of new arguments for flatworm phylogeny (e.g. Ehlers 1985). Another student, Thomas Bartolomaeus, did focus on a comparison of two organ systems, body cavities and excretory organs, which led to a broadening of taxa investigated by him and students in the working group (e.g. Bartolomaeus & Ax 1992).

The change in systematic thinking towards phylogenetic systematics also took place in teaching. Ax taught a lecture on animal systematics which would later be called 'the phylogenetic system of animals'. It lasted over two semesters and presented an extensive introduction into animal morphology and phylogeny. Ax had the ambition to present animal systematics according to the principles of phylogenetic systematics, but as there were not too many such analyses published, Ax had to develop a number of hypotheses by himself. These lectures were unforgettable to attending students. Ax extensively used chalk to cover the blackboard with trees, characters and well-drawn sketches of animal structures or body plans. He presented autapomorphies with enthusiasm and encouraged listeners to follow the arguments and make up their own mind. In these lectures he developed the main core of hypotheses and arguments for the book series, for which he only found time after his retirement to bring it into printed form.

In summary it can be concluded that Ax´s interest in metazoan phylogeny grew along several lines. His original interest in Plathelminthes made him reconstruct the flatworm archetype and the discovery of Gnathostomulida as a taxon independent from Plathelminthes made him search for relationships of basal metazoan taxa. This was supported and sharpened by his growing interest in phylogenetic systematics and his conviction that this is the perfect tool to reconstruct phylogenetic relationships. Ax´s research on meiofauna broadened his knowledge in taxa other than flatworms and gnathostomulids and all these factors made him adopt his lecture on animal systematics constantly until he was able to present the entire animal kingdom under criteria of phylogenetic systematics.

2. How are the three books embedded in a historical context?

Was the time ripe for the series 'Multicellular Animals'? Were the volumes published too early or too late? Although such a question is difficult to answer and contains a good portion of subjective view, I will try here to integrate the publication of the three books in a context of other publications and trends at that time.

First of all, Ax´s books were and still are outstanding in their attempt to consequently present animal phylogeny as sister group relationships, naming the appropriate autapomorphies. Few books went and still go so far. Nevertheless, their publication fell into a time, where systematics changed heavily from several sides.

Phylogenetic systematics quite slowly entered textbooks on zoology. In Germany, the famous 'Kästner' volumes (Lehrbuch der Speziellen Zoologie) (e.g. Gruner 1982, 1984) and the systematics volume in Siewing´s two-volume 'Lehrbuch der Zoologie' (Siewing 1985) presented animal systematics in the traditional classification. An exception and a kind of forerunner of

Ax´s volumes were two small volumes called 'Wirbellose I' and 'Wirbellose II', written as a manuscript by Willi Hennig and published by his son Wolfgang Hennig (Hennig 1984, 1986). Hennig listed, as Ax did later, autapomorphies supporting the monophyly of taxa. He did not consequently search for sister group relationships and presented very few phylogenetic trees. Additionally, he still kept hierarchical ranks for taxa, which Ax would later abandon completely.

In the late 80s and early 90s, several books that incorporated phylogenetic systematics and were representing broad animal phylogeny at some level became available. These were either conference volumes such as those edited by Conway Morris et al. (1985) or Fernholm et al. (1989) or textbooks such as Willmer (1990), Brusca & Brusca (1990), Ruppert & Barnes (1994), Nielsen (1995) or Westheide & Rieger (1996). All these books showed that phylogenetic systematics had hold entry into textbooks, before Ax published his three volumes. The major difference is that Ax, as has been stated above, did not use hierarchical ranks, the 'Linnean categories'. In his theoretical book (Ax 1984) he convincingly argued that such hierarchical ranks have no equivalent in nature and therefore should not be used. Certainly many people agreed in theory but regarded such a step as impossible in practise. Ax demonstrated that it was possible to present animal taxa and relationships without assigning any rank.

During the 90s, the methodological toolkit of systematics almost exploded, starting to produce an incredible amount of data. Computers entered the field and allowed parsimony analyses of (better or worse) datasets. As far as I know, Schram´s (1991) analysis is one of the first computer aided analyses spanning the entire Metazoa. Analytical software continued to develop and now is an indispensable tool in phylogenetic analyses.

The second methodological 'explosion' was the development of molecular methods. It was quite clear that phylogenetic relationships should be revealed not only by comparison of morphological characters, but also by comparison of protein or DNA sequences. After a brief period of DNA hybridization (e.g. Sibley et al. 1988), the sequencing of proteins and in particular of DNA became continuously easier and cheaper. PCR and sequencing techniques were the main catalysators for this development. In the competition for grant money the molecular approaches soon were more successful than morphological approaches, but with time it became evident that the comparison of DNA sequences yields similar sources of problems or error than morphological comparisons. Nevertheless, the sequencing of single genes in the 90s developed snowball-like into sequencing of multiple genes, transcriptomes and genomes. One of the first analyses of the entire metazoans (or, better, of selected representatives that span the Metazoa), was by Field et al. (1988) and since then numerous analyses have been published, some of them with heavy impact on established hypotheses.

The snowball of phylogenetic methodology and analyses had started to roll when Ax wrote down his 'Multicellular Animals', but it appears understandable that he was not able to keep track with every new development and decided to concentrate on morphology, which he knew best.

3. How did selected phylogenetic hypotheses develop since the publication of the books?

When comparing phylogenetic hypotheses it is important to keep in mind that there is no common sense in animal phylogeny and therefore any analysis chosen for comparison and any statement that a hypothesis is generally accepted has to be taken with care. Additionally, comparing hypotheses from different time scales must always take the available methodology and available background information into account. We hope, to express it carefully, that the degree of finding correct answers grows constantly. Nevertheless, some hypotheses will turn out to be supported over time, others will change over time and again others will be doubted and turn out to be correct later or vice versa. A careful attempt can be made to see whether Ax´s hypotheses on animal relations have been altered to a great extent or not. Within the frame of this article, only selected hypotheses can be reviewed.

First of all, there seems to be solid backbone in animal phylogeny (see, e.g. Dunn et al. 2015) and major taxa repeatedly come out as monophyletic in the vast majority of analyses. These are Metazoa, Bilateria, Protostomia and Deuterostomia. Along this backbone, some taxa still keep on shifting around, others are still difficult to place and some remain in a more or less stable place.

For the relationships of basal metazoan taxa Ax (1995) assumed a sequential branching of the taxa Porifera, Placozoa (*Trichoplax*), Cnidaria, Ctenophora and Bilateria. While Ax (1989) had presented Cnidaria and Ctenophora as sister taxa (Coelenterata), he later adopted Ehlers´ (1993) hypothesis that Ctenophora and Bilateria are sister taxa, based on the fine structure of the acrosome and also by the presence of 'true' myocytes. This sequential branching of taxa has been challenged in three ways: hypotheses on paraphyletic sponges, on monophyletic 'Diploblasta' and on basally branching Ctenophora. A number of analyses found sponges (Porifera) to be a paraphyletic taxon, with Calcarea or Homoscleromorpha being closer related to the remaining Metazoa than other sponges (see Borchellini et al. 2001 as one example). However, there is also support for the monophyly of Porifera, in particular from more recent analyses (see Wörheide et al. 2012, 2014 for a review and more references). Few analyses have revealed a monophyly of the taxa with diploblastic body organization (Porifera, Placozoa, Cnidaria and Ctenophora) (Schierwater et al. 2009, Eitel et al. 2014), but this is not supported in the majority of other analyses. Recently, several analyses place ctenophores as the earliest branch of Metazoa and therefore as sister group to all remaining Metazoa. This surprising result has severe effects on the interpretation of character evolution, in particular concerning the nervous system (Ryan et al. 2013, Marlowe & Arendt 2014, Moroz et al. 2014, Ryan 2014, Jékely et al. 2015). It has to be assumed under this scenario that either nerve cells evolved twice or that they were present in the metazoan ancestor and were reduced in sponges and *Trichoplax*. This does also account for muscle cells, some types of cell-cell contacts and the presence of an entoderm) (see Ax 1995). I doubt that the last word has been spoken here and, at least from the standpoint of plausibility of character evolution, Ax´s scenario makes more sense than other, more recent scenaria. Interestingly, one recent investigation (Pisani et al. 2015) states that the basal position of ctenophores might be the result of using wrong parameters in the analysis and that under other, probably more realistic parameters, sponges remain the basal branch within Metazoa.

Within Bilateria, Ax favoured a sister group relationship between the taxa Spiralia and Radialia (Ax 1995). On first view, such a relationship is in strong contrast to recent hypotheses, but this can mostly be explained by the three most revolutionary changes in animal phylogeny caused by molecular analyses: the changes in position of Acoelomorpha, of tentaculate taxa and the hypothesis of monophyletic Ecdysozoa.

Acoelomorpha, a taxon comprising the sister taxa Nemertodermatida and Acoela, were traditionally thought to belong to flatworms. In the phylogenetic system of Plathelminths (Ehlers 1985, Ax 1996; see also Ax 1961, 1963a for earlier publications on flatworm systematics), Acoelomorpha represented the second branch and sister taxon of the Euplathelminthes. Some authors (Smith et al. 1986, Haszprunar 1996) already pointed out that the characters supporting the monophyly of Plathelminthes (e.g. multiciliary epidermal and gastrodermal cells, biciliary terminal cells in the protonephridium) were not convincing, because such characters were either also present in other taxa or were inconsistent among plathelminths. Molecular analyses (see Ruiz-Trillo et al. 2004 as one example) found support for a basal position of acoelomorphs among Bilateria. This position has been confirmed in a number of analyses, although an alternative position, together with *Xenoturbella* (as Xenacoelomorpha) among deuterostomes may also be possible (e.g. Philippe et al. 2011). For the reconstruction of the bilaterian ancestor and for hypotheses on character evolution within Bilateria (especially the intestine, excretory organs and the nervous system), the potential basal position of Acoelomorpha is of great importance.

The three tentaculate or lophophorate taxa Brachiopoda, Bryozoa (= Ectoprocta) and Phoronida were usually regarded as closely related, though not forming a monophyletic taxon (e.g. Ax 1999). They were often associated with deuterostomes, mainly based on the presence of tentacles, metanephridia and a bipartite body organization (Ax 1999). It was surprising to see the lophophorate taxa clustering with spiralian taxa in molecular analyses (Halanych et al. 1985). This position has been confirmed in general since then, although the exact position of lophophorate taxa varies greatly, including for example phoronids as derived brachiopods (e.g. Cohen & Weydmann 2005), Byozoa (Ectoprocta) and Kamptozoa (Entoprocta) as sister taxa (e.g. Struck et al. 2014) or monophyletic Lophophorata (= Tentaculata) (e.g. Nesnidal et al. 2013). In general, internal branches within Spiralia are usually very short, which means that fast evolutionary changes might be a severe problem for reconstruction of phylogenetic relationships.

Ax assumed the taxon Spiralia to be the sister group of Radialia. By doing so, he neglected a bunch of taxa that were usually summarized as Nemathelminthes, Aschelminthes or pseudocoelomates (see Schmidt-Rhaesa 2013 for a review of the names in use and the content of such taxa). While Brusca & Brusca still stated in their textbook from 1990: 'Perhaps no other group of phyla is such a phylogenetic mystery as the pseudocoelomates!' (Brusca & Brusca 1990, p. 888), Lorenzen (1985) had already offered a first attempt to recognize phylogenetic relationships. In the late 80s and during the 90s, Ax´s working group, first under his own advice and then continued by Ulrich Ehlers, investigated in a series of diploma and PhD theses almost all taxa of Nemathelminthes in detail to find new characters for phylogenetic analyses: Volker Lammert 1986 on Gnathostomulida, Birger Neuhaus 1991 on Kinorhyncha, Wilko Ahlrichs 1995 on *Seison* and Rotifera, Andreas Schmidt-Rhaesa 1996 on Nematomorpha, Christian Lemburg 1999 on Priapulida and Holger Herlyn 2000 on Acanthocephala (Ahlrichs 1995, Schmidt-Rhaesa 1996, Lemburg 1999 and Herlyn 2000 published their PhD theses with ISBN number). These theses were supplemented by several diploma theses on the same taxa and additionally on nematodes and gastrotrichs.

Indeed the investigations provided a number of ultrastructural data and supported one phylogenetic hypothesis, which is explained in broadest detail in Ahlrichs (1995) (see also Ehlers et al. 1996). Lorenzen´s (1985) assumption that Nemathelminthes/Aschelminthes consisted of two monophyletic clades was supported. One such clade consists of Gastrotricha, Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Wallace et al. (1995, 1996) and Nielsen (1995) had come in parallel to almost similar results. For the other clade, Ahlrichs (1995, see also Ahlrichs 1997) and in parallel Rieger & Tyler (1995) recognized that the jaws of rotifers and gnathostomulids have a similar ultrastructure. The common taxon, also including Acanthocephala as related to rotifers within Syndermata, was named Gnathifera. The later discovery of *Limnognathia maerski* (Micrognathozoa) supported gnathiferan relationships (Kristensen & Funch 2000). There is support for Gnathifera from molecular analyses (Witek et al. 2009, Hankeln et al. 2014, Wey-Fabricius et al. 2014).

Although his own working group had significant share on these developments, Ax did not follow each one of the conclusions. He did accept the monophyly of Nemathelminthes (in the composition: Gastrotricha, Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera) and of Syndermata, but he still regarded the position of Nemathelminthes and also of Syndermata as questionable and did not accept the sister group relationship between Gnathostomulida and Syndermata (see Ax 2001).

Ahlrichs (1995) had hypothesized Nemathelminthes as sister group of Spiralia and soon they, or better the subtaxon Cycloneuralia (Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera), received unexpected neighbors. Aguinaldo et al. (1997) hypothesized a monophyletic taxon of moulting animals which included arthropods and cycloneuralians. This highly disputed hypothesis has been supported since then in numerous analyses, but was, especially in the first years after its publication, a revolution, because the former relationship between annelids and arthropods, also included in Ax´s book (Ax 1999), was regarded as well supported and stable. It has to be added that the taxon Gastrotricha, which seemed to be related to Cycloneuralia due to some similarities in the cuticular structure, the pharynx and the cleavage, occurred in molecular analyses repeatedly close to flatworms (Plathelminthes) and not close to cycloneuralians.

One final hypothesis shall be reviewed here. Ax had quite innovative ideas concerning basal deuterostome relationships, with paraphyletic hemichordates being a central topic (Ax 2001). He hypothesized Enteropneusta as being the sister group of Chordata (as Cyrtotreta) and Pterobranchia also as being paraphyletic, with Cephalodiscida being the sister group of Cytrotreta (as Pharyngotremata) and *Rhabdopleura* being the sister group of Pharyngotremata. Such relationships were not confirmed by subsequent analyses. Some analyses supported paraphyletic enteropneusts (e.g. Cameron et al. 2000, Peterson & Eernisse 2001), but later genomic analyses supported monophyletic Hemichordata with a sister group relationship to Echinodermata in a taxon Ambulacraria (e.g. Dunn et al. 2008; see also Nielsen 2012). Especially enteropneusts are central in the discussion of dorsoventral inversion (see, e,g. Brown et al. 2008) and in the evolution of the neural tube (e.g. Kaul-Strehlow et al. 2015).

Regardless of differences and correspondence between Ax´s phylogenetic suggestions and recent outcomes of animal phylogeny the three volumes of ‘multicellular animals’ prove what had always been claimed to be one advantage of phylogenetic systematics over classical classification: to provide arguments for hypotheses of relationship by naming potential autapomorphies (= synapomorphies of sister taxa) and by this make it possible to discuss relationships on the basis of the character evolution. Even in the era of molecular tools character evolution should not get out of focus.

Acknowledgements

I thank all colleagues who participated in the 56. Phylogenetic Symposium in Hamburg on November 22, 2014 for discussion and helpful comments. Many thanks go to a reviewer for his helpful and extensive comments, several of which I have incorporated.

References

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff, & J. A. Lake (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. – Nature **387**: 489–493.

Ahlrichs, W. (1995): Ultrastruktur und Phylogenie von *Seison nebaliae* (Grube 1859) und *Seison annulatus* (Claus 1876). Hypothesen zu phylogenetischen Verwandtschaftsverhältnissen innerhalb der Bilateria. – Cuvillier Verlag, Göttingen: 310 pp.

Ahlrichs, W. (1997): Epidermal ultrastructure of *Seison nebaliae* and *Seison annulatus*, and a comparison of epidermal structures within the Gnathifera. – Zoomorphology **117**: 41–48.

Armonies, W. (1987): Freilebende Plathelminthen in supralitoralen Salzwiesen der Nordsee: Ökologie einer borealen Brackwasser-Lebensgemeinschaft. – Microfauna Marina **3**: 81–156.

Armonies, W. & M. Hellwig (1987): Neue Plathelminthes aus dem Brackwasser der Insel Sylt (Nordsee). – Microfauna Marina **3**: 249–260.

Ax, P. (1951): Die Turbellarien des Eulitorals der Kieler Bucht. Zoologisches Jahrbuch für Systematik **80**: 277–378.

Ax, P. (1954a): Die Turbellarienfauna des Küstengrundwassers am Finnischen Meerbusen. – Acta Zoologica Fennica **81**: 1–54.

Ax, P. (1954b): *Thalassochaetus palpifoliaceus* nov. gen. nov. spec. (Archiannelida, Nerillidae), ein mariner Verwandter von *Troglochaetus beranecki* Delachaux. – Zoologischer Anzeiger **153**: 64–75.

Ax, P. (1956a): Monographie der Otoplanidae (Turbellaria). Morphologie und Systematik. – Abhandlungen der Akademie für Wissenschaft und Literatur, Mathematisch-Naturwissenschaftliche Klasse 1955: 501–796.

Ax, P. (1956b): Les Turbellariés des Étangs Cotiers du Littoral Méditerranéen de la France Méridionale. – Vie et Milieu Supplement **5**: 1–215.

Ax, P. (1956c): Die Gnathostomulida, eine rätselhafte Wurmgruppe aus dem Meeressand. – Abhandlungen der Akademie für Wissenschaft und Literatur, Mathematisch-Naturwissenschaftliche Klasse **1956**: 535–562.

Ax, P. (1957): Vervielfachungen des männlichen Kopulationsapparates bei Turbellarien. – Verhandlungen der Deutschen Zoologischen Gesellschaft: 227–249.

Ax, P. (1959): Zur Systematik, Ökologie und Tiergeographie der Turbellarienfauna in den ponto-kaspischen Brackwassermeeren. – Zoologisches Jahrbuch für Systematik **87**: 43–184.

Ax, P. (1960): Die Entdeckung neuer Organisationstypen im Tierreich. – Die neue Brehm-Bücherei, vol. 258, A.- Ziemsen Verlag, Wittenberg.

Ax, P. (1961): Verwandtschaftsbeziehungen und Phylogenie der Turbellarien. – Ergebnisse der Biologie **24**: 1–68.

Ax, P. (1963a): Relationships and phylogeny of the Turbellaria. – In: Dougherty, E. C. (ed.): The lower Metazoa. – University of California Press, Berkeley: 191–224.

Ax, P. (1963b): Das Hautgeißelepithel der Gnathostomulida. – Verhandlungen der Deutschen Zoologischen Gesellschaft 1963: 452–461.

Ax, P. (1964): Die Kieferapparatur von *Gnathostomaria lutheri* Ax (Gnathostomulida). – Zoologischer Anzeiger **173**: 174–181.

Ax, P. (1965): Zur Morphologie und Systematik der Gnathostomulida. – Zeitschrift für Zoologische Systematik und Evolutionsforschung **3**: 259–276.

Ax, P. (1966a): Die Bedeutung der interstitiellen Sandfauna für allgemeine Probleme der Systematik, Ökologie und Biologie. – Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Special Volume **2**: 15–66.

Ax, P. (1966b): Eine neue Tierklasse aus dem Litoral des Meeres - Gnathostomulida. – Umschau in Wissenschaft und Technik **1**/1966: 17–23.

Ax, P. (1967): *Diurodrilus ankeli* nov. spec. (Archiannelida) von der nordamerikanischen Pazifikküste. – Zeitschrift für Morphologie und Ökologie der Tiere **60**: 5–16.

Ax, P. (1968): Das Fortpflanzungsverhalten von *Trilobodrilus* (Archiannelida, Dinophilidae). – Marine Biology **1**: 330–335.

Ax, P. (1969): Populationsdynamik, Lebenszyklen und Fortpflanzungsbiologie der Mikrofauna des Meeressandes. – Verhandlungen der Deutschen Zoologischen Gesellschaft 1968: 66–113.

Ax, P. (1977a): Life cycles of interstitial Turbellaria from the eulittoral of the North Sea. – Acta Zoologica Fennica **154**: 11–20.

Ax, P. (1977b): Problems of speciation in the interstitial fauna of the Galapagos. – Mikrofauna des Meeresbodens **61**: 29–43.

Ax, P. (1984): Das Phylogenetische System. – Gustav Fischer Verlag, Stuttgart: 349 pp.

Ax, P. (1985): The position of the Gnathostomulida and Platyhelminthes in the phylogenetic system of the Bilateria. – In: Conway Morris, S., J. D. George, R. Gibson & H. M. Platt (eds): The origins and relationships of lower invertebrates. – Oxford University Press, Oxford: 168–180.

Ax, P. (1988): Systematik in der Biologie. – Gustav Fischer Verlag, Stuttgart: 181 pp.

Ax, P. (1989): Basic phylogenetic systematization of the Metazoa. – In: Fernholm, B., K. Bremer & H. Jörnwall (eds): The hierarchy of life. – Elsevier, Amsterdam: 229–245.

Ax, P. (1992): Plathelminthes from brackish water of Northern Japan: no identical species with the corresponding boreal community. – Microfauna Marina **7**: 341–342.

Ax, P. (1993a): Die Brackwasserart *Coelogynopora hangoensis* (Proseriata, Plathelminthes) von Grönland und den Faröer. – Microfauna Marina **8**: 145–152.

Ax, P. (1993b): *Turbanella lutheri* (Gastrotricha, Macrodasyoida) im Brackwasser der Färöer. – Microfauna Marina **8**: 139–144.

Ax, P. (1995): Das System der Metazoa I. Ein Lehrbuch der phylogenetischen Systematik. – Gustav Fischer Verlag, Stuttgart: 226 pp.

Ax, P. (1996): Multicellular animals I. A new approach to the phylogenetic order in nature. – Springer, Berlin: 213 pp.

Ax, P. (1999): Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik. – Gustav Fischer Verlag, Stuttgart: 383 pp.

Ax, P. (2000): Multicellular animals II. The phylogenetic system of the Metazoa. – Springer, Berlin: 396 pp.

Ax, P. (2001): Das System der Metazoa III. Ein Lehrbuch der phylogenetischen Systematik. – Spektrum Akademischer Verlag, Heidelberg: 283 pp.

Ax, P. (2003): Multicellular animals III. Order in nature – system made by man. – Springer, Berlin: 317 pp.

Ax, P. (2008): Plathelminthes aus Brackgewässen der Nordhalbkugel. Abhandlungen der Akademie für Wissenschaft und Literatur, Mathematisch-Naturwissenschaftliche Klasse 2008, Nr. 1: 1–696.

Ax, P. (2011): New marine interstitial Plathelminthes from the Bay of Biscay, France. – Meiofauna Marina **19**: 33–39.

Ax, P. & W. Armonies (1987): Amphiatlantic identities in the composition of the boreal brackish water community of Plathelminthes. – Microfauna Marina **3**: 7–80.

Ax, P. & W. Armonies (1990): Brackish water Plathelminthes from Alaska as evidence for the existence of a boreal brackish water community with circumpolar distribution. – Microfauna Marina **6**: 7–109.

Ax, P. & R. Ax (1974a): Interstitielle Fauna von Galapagos. V. Otoplanidae (Turbellaria, Proseriata). – Mikrofauna des Meeresbodens **27**: 1–28.

Ax, P. & R. Ax (1974b): Interstitielle Fauna von Galapagos. VII. Nematoplanidae, Polystyliphoridae, Coelogynoporidae (Turbellaria, Proseriata). – Mikrofauna des Meeresbodens **29**: 1–28.

Ax, P. & R. Ax (1977): Interstitielle Fauna von Galapagos. XIX. Monocelididae (Turbellaria, Proseriata). – Mikrofauna des Meeresbodens **64**: 1–44.

Ax, P. & D. Bunke (1967): Das Genitalsystem der Aeolosomatidae mit phylogenetisch ursprünglichen Organisationszügen für die Oligochaeten. – Naturwissenschaften **54**: 222–225.

Ax, P. & U. Ehlers (1973): Interstitielle Fauna von Galapagos. III. Promesostominae (Turbellaria, Typhloplanoida). – Mikrofauna des Meeresbodens **23**: 1–16.

Ax P. & R. Heller (1970): Neue Neorhabdocoela (Turbellaria) vom Sandstrand der Nordsee-Insel Sylt. – Mikrofauna des Meeresbodens **2**: 1–46.

Ax, P. & K. Schilke (1964): Zur Kenntnis von *Edwardsia danica* Calgren (Anthozoa, Actiniaria) aus der Kieler Bucht. – Kieler Meeresforschungen **20**: 192–197.

Ax, P. & P. Schmidt (1973): Interstitielle Fauna von Galapagos. I. Einführung. – Mikrofauna des Meeresbodens **20**: 1–38.

Bartolomaeus, T. (2014): In love of meiofauna, morphology, and phylogenetic systematics: an obituary for Peter Ax 29.03.1927-02.05.2013. – Zoomorphology **133**: 3–6.

Bartolomaeus, T. & P. Ax (1992): Protonephridia and metanephridia - their relation within the Bilateria. – Zeitschrift für Zoologische Systematik und Evolutionsforschung **30**: 21–45.

Bartsch, I. (1977): Interstitielle Fauna von Galapagos. XX. Halacaridae (Acari). – Mikrofauna des Meeresbodens **65**: 1–108.

Bartsch, I. & P. Schmidt (1978): Interstitielle Fauna von Galapagos. XXII. Zur Ökologie der Halacaridae (Acari). – Mikrofauna des Meeresbodens **69**: 1–38.

Bartsch, I. & P. Schmidt (1979): Zur Verbreitung und Ökologie einiger Halacaridae (Acari) in Sandstränden der Ostsee (Kieler Bucht), der Nordsee (Sylt) und des Europäischen Nordmeeres (Tromsö). – Mikrofauna des Meeresbodens **74**: 1–37.

Blome D. (1974): Zur Systematik von Nematoden aus dem Sandstrand der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **33**: 1–25.

Blome D. (1982): Systematik der Nematoda eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **86**: 1–194.

Blome D. (1983): Ökologie der Nematoda eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **88**: 1–76.

Blome, D. (1985): Interstitielle Fauna von Galapagos. XXXV. Chromadoridae (Nematoda). – Microfauna Marina **2**: 271–329.

Borchiellini, C., M. Manuel, E. Alivon, N. Boury-Esnault, J. Vacelet & Y. Le Parco (2001): Sponge paraphyly and the origin of Metazoa**. –** Journal of Evolutionary Biology **14**: 171–179.

Brown, F.D., A. Prendergast & B.J. Swalla (2008): Man Is but a Worm: Chordate Origins. – Genesis **46**: 605–613.

Brusca, R. C. & G. J. Brusca (1990): Invertebrates. – Sinauer, Sunderland: 922 pp.

Cameron, C. B., J. R. Garey & B. J. Swalla (2000): Evolution of the chordate body plan: new insights from phylogenetic analyses of deuterostome phyla. – Proceedings of the National Academy of Sciences of the USA **97**: 4469–4474.

Clasing, E. (1984): Interstitielle Fauna von Galapagos. XXXII. Epsilonematidae (Nematodes). – Microfauna Marina **1**: 149–189.

Cohen, B.L. & A. Weydmann (2005): Molecular evidence that phoronids are a subtaxon of brachiopods (Brachiopoda: Phoronata) and that genetic divergence of metazoan phyla began long before the early Cambrian. – Organisms Diversity & Evolution **5**: 253–273.

Coineau, N. & P. Schmidt (1979): Interstitielle Fauna von Galapagos. XXIV. Microparasellidae (Isopoda, Asellota). – Mikrofauna des Meeresbodens **73**: 1–19.

Conway Morris, S., J.D. George, R. Gibson & H.M. Platt (1985): The origins and relationships of lower invertebrates. – The Systematics Association Special Volume 28. – Clarendon Press, Oxford: 394 pp.

Dittmann, S. & K. Reise (1985): Assemblage of free-living Plathelminthes on an intertidal mud flat in the North Sea. – Microfauna Marina **2**: 95–115.

Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, W. E. Browne, S. A. Smith, E. Seaver, G. W. Rouse, M. Obst, G. D. Edgecombe, M. V. Sørensen, S. H. D. Haddock, A. Schmidt-Rhaesa, A. Okusu, R. M. Kristensen, W. C. Wheeler, M. Q. Martindale & G. Giribet (2008): Broad phylogenomic sampling improves resolution of the animal tree of life. – Nature **452**: 754–749.

Dunn, C. W., G. Giribet, G. D. Edgecombe & A. Hejnol (2015): Animal phylogeny and its evolutionary implications. – Annual Review of Ecology, Evolution and Systematics **45**: 371–395.

Ehlers, B. & U. Ehlers (1973): Interstitielle Fauna von Galapagos. II. Gnathostomulida. – Mikrofauna des Meeresbodens **22**: 1–27.

Ehlers, U. (1974): Interstitielle Typhloplanoida (Turbellaria) aus dem Litoral der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **49**: 1–102.

Ehlers, U. (1985): Das phylogenetische System der Plathelminthes. – Gustav Fischer Verlag, Stuttgart: 317 pp.

Ehlers, U. (1993): Ultrastructure of the spermatozoa of *Halammohydra schulzei* (Cnidaria, Hydrozoa): the significance of acrosomal structures for the systematization of the Eumetazoa. – Microfauna Marina **8**: 115–130.

Ehlers, U. & P. Ax. (1974): Interstitielle Fauna von Galapagos. VIII. Trigonostominae (Turbellaria, Typhloplanoida). – Mikrofauna des Meeresbodens **30**: 1–33.

Ehlers, U. & J. Dörjes (1979): Interstitielle Fauna von Galapagos. XXIII. Acoela (Turbellaria). – Mikrofauna des Meeresbodens **72**: 1–75.

Ehlers, U. & B. Ehlers (1981): Interstitielle Fauna von Galapagos. XXVII. Byrsophlebidae, Promesostomidae, Brinkmanniellinae, Kytorhynchidae (Turbellaria, Typhloplanoida). – Mikrofauna des Meeresbodens **83**: 1–35.

Ehlers, U. & B. Sopott-Ehlers (1989): Interstitielle Fauna von Galapagos. XXXVIII. *Haloplanella* Luther and *Pratoplana* Ax (Typhloplanoida, Plathelminthes). – Microfauna Marina **5**: 189–206.

Ehlers, U., K. Reise & W. Armonies (1995): *Scoliopharyngia arenicola* nov. spec. (Plathelminthes, Rhabdocoela) from burrows of the lugworm *Arenicola marina* on intertidal flats near the island of Sylt (North Sea). – Microfauna Marina **10**: 143–146.

Ehlers, U., W. Ahlrichs, C. Lemburg & A. Schmidt-Rhaesa (1996): Phylogenetic systematization of the Nemathelminthes (Aschelminthes). – Verhandlungen der Deutschen Zoologischen Gesellschaft **89.1**: 8.

Eitel, M., W. Jakob, H.-J. Osigus, O. Paknia, K. von der Chevallerie, T. Bergmann & B. Schierwater (2014): Phylogenetics and phylogenomics at the root oft he Metazoa. – In: Wägele, J.W. & T. Bartolomaeus (eds): Deep metazoan phylogeny: the backbone oft he tree of life. – De Gruyter, Berlin: 23–47.

Erséus, C. (1984): Interstitielle Fauna von Galapagos. XXXIII. Tubificidae (Annelida, Oligochaeta). – Microfauna Marina **1**: 191–198.

Faubel, A. (1974a): Die Acoela (Turbellaria) eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **32**: 1–58.

Faubel, A. (1974b): Macrostomida (Turbellaria) von einem Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **45**: 1–32.

Faubel A. (1976a): Interstitielle Acoela (Turbellaria) aus dem Litoral der nordfriesischen Inseln Sylt und Amrum (Nordsee). – Mitteilungen aus dem Hamburgischen Zoologischen Institut und Museum **73**: 17–56.

Faubel, A. (1976b): Populationsdynamik und Lebenszyklen interstitieller Acoela und Macrostomida (Turbellaria. Untersuchungen an einem mittel-lotischen Sandstrand der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **56**: 1–107.

Fernholm, B., K. Bremer, L. Brundin & H. Jörnvall (1989): The hierarchy of life. – Excerpta Medicac, Amsterdam: 499 pp.

Field, K. G., G. J. Olsen, D. J. Lane, J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace & R. A. Raff (1988): Molecular phylogeny of the animal kingdom. – Science **239**: 748–753.

Gottwald, J. (1983): Interstitielle Fauna von Galapagos. XXX. Podocopida 1 (Ostracoda). – Mikrofauna des Meeresbodens **90**: 1–187.

Gruner, H.-E. (1982): Lehrbuch der Speziellen Zoologie. Part 3: Mollusca, Sipunculida, Echiurida, Annelida, Onychophora, Tardigrada, Pentastomida. – Gustav Fischer Verlag, Stuttgart: 608 pp.

Gruner, H.-E. (1984): Lehrbuch der Speziellen Zoologie. Part 2: Cnidaria, Ctenophora, Mesozoa, Plathelminthes, Nemertini, Entoprocta, Nemathelminthes, Priapulida. – Gustav Fischer Verlag, Stuttgart: 621 pp.

Halanych, K. M., J. D. Bacheller, A.M.A. Aguinaldo, S. M. Liva, D.M. Hillis & J.A. Lake (1995): Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. – Science **267**: 1641–1643.

Hankeln, T., A. R. Wey-Fabricius, H. Herlyn, A. Witek, M. Weber, M. P. Nesnidal & T. H. Struck (2014): Phylogeny of platyzoan taxa based on molecular data. – In: Wägele, J.W. & T. Bartolomaeus (eds): Deep metazoan phylogeny: the backbone oft he tree of life. – De Gruyter, Berlin: 105–125.

Hartwig, E. (1973a): Die Ciliaten des Gezeiten-Sandstrandes der Nordseeinsel Sylt. I. Systematik. – Mikrofauna des Meeresbodens **18**: 1–69.

Hartwig, E. (1973b): Die Ciliaten des Gezeiten-Sandstrandes der Nordseeinsel Sylt. II. Ökologie. – Mikrofauna des Meeresbodens **21**: 1–171.

Haszprunar, G. (1996): Plathelminthes and Plathelminthomorpha - paraphyletic taxa. – Journal of Zoological Systematics and Evolutionary Research **34**: 41–48.

Hellwig, M. (1987): Ökologie freilebender Plathelminthen im Grenzraum Watt - Salzwiese lenitischer Gezeitenküsten. – Microfauna Marina **3**: 157–248.

Hennig, W. (1950): Grundzüge einer Theorie der phylogenetischen Systematik. – Deutscher Zentralverlag, Berlin: 370 pp.

Hennig, W. (1966): Phylogenetic Systematics. – University of Illinois Press, Urbana: 263 pp.

Hennig, W. (1984): Taschenbuch der Speziellen Zoologie. Wirbellose I. 5. Edition. – Verlag Harri Deutsch, Thun: 392 pp.

Hennig, W. (1986): Taschenbuch der Speziellen Zoologie. Wirbellose II. 4. Edition. – Verlag Harri Deutsch, Thun: 335 pp.

Herbst H.V. (1974): Drei interstitielle Cyclopoinae (Crustacea, Copepoda) von der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **35**: 1–17.

Herlyn, H. (2000): Zur Ultrastruktur, Morphologie und Phylogenie der Acanthocephala. – Logos Verlag, Berlin: 131 pp.

Jékely, G., J. Paps & C. Nielsen (2015): The phylogenetic position of ctenophores and the origin(s) of nervous systems. – EvoDevo **6**:1, doi: 10.1186/2041-9139-6-1.

Kaul-Strehlow, S., M. Urata, T. Minokawa, T. Stach & A. Wanninger (2015): Neurogenesis in directly and indirectly developing enteropneusts: of nets and cords. – Organisms Diversity & Evolution (online version).

Kristensen, R. M. & P. Funch (2000): Micrognathozoa: A new class with complicated jaws like those of Rotifera and Gnathostomulida. – Journal of Morphology **246**: 1–49.

Kossmagk-Stephan, K. J. (1983): Marine Oligochaeta from a sandy beach of the Island of Sylt (North Sea) with description of four new enchytraeid species. – Mikrofauna des Meeresbodens **89**: 1–28.

Lemburg, C. (1999): Ultrastrukturelle Untersuchungen an den Larven von *Halicryptus spinulosus* und *Priapulus caudatus*. Hypothesen zur Phylogenie der Priapulida und deren Bedeutung für die Evolution der Nemathelminthen. Cuvillier-Verlag, Göttingen: 393 pp.

Lorenzen, S. (1985): Phylogenetic aspects of pseudocoelomate evolution. – In: Conway Morris, S., J. D. George, R. Gibson & H. M. Platt (eds): The origins and relationships of lower invertebrates. – The Systematics Association Special Volume 28, Clarendon Press, Oxford: 210–223.

Marlowe, H. & D. Arendt (2014): Evolution: Ctenophore genomes and the origin of neurons. – Current Biology **24**: R757-R761.

McKirdy, D., P. Schmidt & M. McGinty-Bayly (1976): Interstitielle Fauna von Galapagos. XVI. Tardigrada. – Mikrofauna des Meeresbodens **58**: 1–43.

Menker, D. & P. Ax (1970): Zur Morphologie von *Arenadiplosoma migrans* n.g.n.sp., einer vagilen Ascidien-Kolonie aus dem Mesopsammal der Nordsee (Tunicata, Ascidiacea). – Zeitschrift für Morphologie der Tiere **66**: 323–336.

Mielke, W. (1973): Zwei neue Harpacticoidea (Crustacea) aus dem Eulitoral der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **17**: 1–14.

Mielke, W. (1975): Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **52**: 1–134.

Mielke, W. (1976): Ökologie der Copepoda eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **59**: 1–86.

Mielke, W. (1979): Interstitielle Fauna von Galapagos. XXV. Longipediida, Canuellidae, Ectinosomatidae (Harpacticoida). – Mikrofauna des Meeresbodens **77**: 1–107.

Mielke, W. (1981): Interstitielle Fauna von Galapagos. XXIX. Darcythompsoniidae, Cylindropsyllidae (Harpacticoida). – Mikrofauna des Meeresbodens **87**: 1–52.

Mielke, W. (1982): Interstitielle Fauna von Galapagos. XXVIII. Laophontinae (Laophontidae), Ancorabolidae (Harpacticoida). – Mikrofauna des Meeresbodens **84**: 1–106.

Mielke, W. (1984): Interstitielle Fauna von Galapagos XXXI. Paramesochridae (Harpacticoida). – Microfauna Marina **1**: 63–147.

Mielke, W. (1989a): Interstitielle Fauna von Galapagos XXXVI. Tetragonicipitidae (Harpacticoida). – Microfauna Marina **5**: 95–172.

Mielke, W. (1989b): Interstitielle Fauna von Galapagos XXXVII. Metidae (Harpacticoida). – Microfauna Marina **5**: 173–188.

Mielke, W. (1997a): Interstitielle Fauna von Galapagos XXXIX. Copepoda, part 7. – Microfauna Marina **11**: 115–152.

Mielke, W. (1997b): Interstitielle Fauna von Galapagos XXXIX. Copepoda, part 8. – Microfauna Marina **11**: 153–192.

Mock, H. (1978): *Ototyphlonemertes pallida* (Keferstein, 1862) (Hoplonemertini, Monostilifera). – Mikrofauna des Meeresbodens **67**: 1–14.

Mock, H. (1979): Chaetonotoidea (Gastrotricha) der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **78**: 1–107.

Mock, H. & P. Schmidt (1975): Interstitielle Fauna von Galapagos. XIII. *Ototyphlonemertes* Diesing (Nemertini, Hoplonemertini). – Mikrofauna des Meeresbodens **51**: 1–40.

Moroz, L. L., K. M. Kocot, M. R. Citarella, S. Dosung, T. P. Norekian, I. S. Povolotskaya, A. P. Grigorenko, C. Dailey, E. Berezikov, K. M. Buckley, A. Ptitsyn, D. Reshetov, K. Mukherjee, T. P. Moroz, Y. Bobkova, F. Yu, V. V. Kapitonov, J. Jurka, Y. V. Bobkov, J. J. Swore, D. O. Girardo, A. Fodor, F. Gusev, R. Sanford, R. Bruders, E. Kittler, C. E. Mills, J. P. Rast, R. Derelle, V. V. Solovyev, F. A. Kondrashov, B. J. Swalla, J. V. Sweedler, E. I. Rogaev, K. M. Halanych & A. B. Kohn (2014): The ctenophore genome and the evolutionary origins of neural systems. – Nature **510**: 109–114.

Müller, U. & P. Ax (1971): Gnathostomulida von der Nordseeinsel Sylt mit Beobachtungen zur Lebensweise und Entwicklung von *Gnathostomula paradoxa* Ax. – Mikrofauna des Meeresbodens **9**: 1–41.

Nesnidal, M. P, M. Helmkampf, A. Meyer, A. Witek, I. Bruchhaus, I. Ebersberger, T. Hankeln, B. Lieb, T. H. Struck & B. Hausdorf (2013): New phylogenomic data support the monophyly of Lophophorata and an Ectoproct-Phoronid clade and indicate that Polyzoa and Kryptrochozoa are caused by systematic bias. – BMC Evolutionary Biology **13**: 253.

Nielsen, C. (1995): Animal evolution. 1st edition. – Oxford University Press: 467 pp.

Nielsen, C. (2012): Animal evolution. 3rd edition. – Oxford University Press: 402 pp.

Noldt, U. (1989a): Kalyptorhynchia (Plathelminthes) from sublittoral coastal areas near the island of Sylt (North Sea). I. Schizorhynchia. – Microfauna Marina **5**: 7–85.

Noldt, U. (1989b): Kalyptorhynchia (Plathelminthes) from sublittoral coastal areas near the island of Sylt (North Sea): II. Eukalyptorhynchia. – Microfauna Marina **5**: 295–329.

Noldt, U. & S. Hoxhold (1984): Interstitielle Fauna von Galapagos. XXXIV. Schizorhynchia (Plathelminthes, Kalyptorhynchia). – Microfauna Marina **1**: 199–256.

Peterson, K. J. & D. J. Eernisse (2001): Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S rDNA sequences. – Evolution & Development **3**: 170–205.

Philippe, H., H. Brinkmann, R. R. Copley, L. L. Moroz, H. Nakano, A. J. Poustka, A. Wallberg, K. J. Peterson & M. J. Telford (2011): Acoelomorph flatworms are deuterostomes related to Xenoturbella. – Nature **470**: 255–258.

Pisani, D., W. Pett, M. Dohrmann, R. Feuda, O. Rota-Stabelli, H. Philippe, N. Lartillot & G. Wörheide (2015): Genomic data do not support comb jellies as the sister group to all other animals. – Proceedings of the National Academy of Sciences of the USA **112**: 15402–15407.

Potel, P. & K. Reise (1987): Gastrotricha Macrodasyida of intertidal and subtidal sediments in the northern wadden sea. – Microfauna Marina **3**: 363–376.

Reise, K. (1984): Free-living Platyhelminthes (Turbellaria) of a marine sand flat: an ecological study. – Microfauna Marina **1**: 1–62.

Reise, K. (2014): Nachruf auf Prof. Dr. Peter Ax (29. März 1927 bis 2. Mai 2013). – Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin **50**: 205–207.

Remane, A. (1924): Neue aberrante Gastrotrichen I. *Macrodasys buddenbrocki* nov. gen. nov. spec. – Zoologischer Anzeiger **61**: 289–297.

Remane, A. (1925a): Diagnosen neuer Archianneliden. – Zoologischer Anzeiger **65**: 15–17.

Remane, A. (1925b): Neue aberrante Gastrotrichen II: *Turbanella cornuta* nov. spec. und *T. hyalina* M. Schultze 1853. – Zoologischer Anzeiger **64**: 309–314.

Remane, A. (1925c): Organisation und systematische Stellung der aberranten Gastrotrichen. – Verhandlungen der Deutschen Zoologischen Gesellschaft 1925: 121–128.

Remane, A. (1926a): Protodrilidae aus Ost- und Nordsee. – Zoologischer Anzeiger **67**: 119–125.

Remane, A. (1926b): Marine Gastrotrichen aus der Ordnung Chaetonotoidea. – Zoologischer Anzeiger **64**: 243–252.

Remane, A. (1926c): Morphologie und Verwandtschaftsbeziehungen der aberranten Gastrotrichen. I. – Zeitschrift für Morphologie und Ökologie der Tiere **5**: 625–754.

Remane, A. (1926d): Zur Frage der Sommereier der Gastrotrichen. – Zoologischer Anzeiger **69**: 54–56.

Remane, A. (1927a): *Halammohydra*, ein eigenartiges Hydrozoon der Nord- und Ostsee. – Zeitschrift für Morphologie und Ökologie der Tiere **7**: 643–678.

Remane, A. (1927b): Gastrotricha. – In: Grimpe, G. & E. Wagler (eds): Tierwelt der Nord- und Ostsee. – Akademische Verlagsgesellschaft, Leipzig: 2–56.

Remane, A. (1928a): *Nerillidium mediterraneum* n. sp. und seine tiergeographische Bedeutung. – Zoologischer Anzeiger **77**: 57–60.

Remane, A. (1928b): Kinorhyncha. – In: Grimpe, G. & E. Wagler (eds): Tierwelt der Nord- und Ostsee. – Akademische Verlagsgesellschaft, Leipzig: 57–84.

Remane, A. (1928c): Neue Gastrotricha Macrodasyoidea. – Zoologische Jahrbücher, Abteilung Systematik **54**: 203–242.

Remane, A. (1928–1933a): Kinorhyncha. – In: Krumbach, T. (ed.): Handbuch der Zoologie. Zweiter Band, erste Hälfte: Vermes Amera – Walter de Gruyter & Co, Berlin: 187–248.

Remane, A. (1928–1933b): Gastrotricha. – In: Krumbach, T. (ed.): Handbuch der Zoologie. Zweiter Band, erste Hälfte: Vermes Amera – Walter de Gruyter & Co, Berlin: 121–186.

Remane, A. (1929–1933): Rotatoria. – In: Bronn, H. G. (ed): Dr. H. G. Bronn´s Klassen und Ordnungen des Tier-Reichs. Band 4, Abteilung 2 – C. F. Winter´sche Verlagshandlung, Leipzig: 1–576.

Remane, A. (1929): Rotatoria. – In: Grimpe, G. & E. Wagler (eds): Tierwelt der Nord- und Ostsee. – Akademische Verlagsgesellschaft, Leipzig: 1–156.

Remane, A. (1932): Archiannelida. – In: Grimpe, G. & E. Wagler (eds): Tierwelt der Nord- und Ostsee. – Akademische Verlagsgesellschaft, Leipzig: 1–36.

Remane, A. (1933): Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. – Wissenschaftliche Meeresuntersuchungen **21**: 163–221.

Remane, A. (1934a): *Diurodrilus subterraneus* nov. spec., ein Archiannelide aus dem Küstengrundwasser. – Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein **20**: 479.

Remane, A. (1934b): Die Gastrotrichen des Küstengrundwassers von Schilksee. – Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein **20**: 473–479.

Remane, A. (1936a): Kinorhyncha. – In: Bronn, H. G. (ed): Dr. H. G. Bronn´s Klassen und Ordnungen des Tier-Reichs. Band 4, Abteilung 2: Askhelminthes, Trochhelmithes – C. F. Winter´sche Verlagshandlung, Leipzig: 243–372.

Remane, A. (1936b): Gastrotricha. – In: Bronn, H. G. (ed): Dr. H. G. Bronn´s Klassen und Ordnungen des Tier-Reichs. Band 4, Abteilung 2: Askhelminthes, Trochhelmithes – C. F. Winter´sche Verlagshandlung, Leipzig: 1–242.

Remane, A. (1949a): Archianneliden aus der Familie Nerillidae aus Südwest-Afrika. – Kieler Meeresforschungen **6**: 3–8.
Remane, A. (1949b): Die psammobionten Rotatorien der Nord- und Ostsee. – Kieler Meeresforschungen **6**: 3–11.
Remane, A. (1950): *Macrodasys africanus* nov. spec., ein Gastrotrich von der Küste Südwest-Afrikas. – Kieler Meeresforschungen **7**: 35–37.
Remane, A. (1951): *Mesodasys*, ein neues Genus der Gastrotricha Macrodasyoidea aus der Kieler Bucht. – Kieler Meeresforschungen **8**: 102–105.
Remane, A. (1952a): Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. – Verhandlungen der Deutschen Zoologischen Gesellschaft 1951: 327–359.
Remane, A. (1952b): Zwei neue *Turbanella*-Arten aus dem marinen Küstengrundwasser. – Kieler Meeresforschungen **9**: 62–65.
Remane, A. (1956): Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. – Zweite Auflage. – Akademische Verlagsgesellschaft, Leipzig: 364 pp.
Remane, A. (1957): Fortschritte und heutige Probleme der Stammesgeschichte. Makro- und Mikroevolution. Naturwissenschaftliche Rundschau **10**: 163–169.
Remane, A. (1961a): Gedanken zum Problem: Homologie und Analogie, Praeadaption und Parallelität. – Zoologischer Anzeiger **166**: 447–465.
Remane, A. (1961b): *Neodasys uchidai* nov. spec., eine zweite *Neodasys*-Art (Gastrotricha Chaetonotoidea). – Kieler Meeresforschungen **17**: 85–88.
Remane, A. & E. Schulz (1934): Die Tierwelt des Küstengrundwassers bei Schilksee (Kieler Bucht). I. Das Küstengrundwasser als Lebensraum. – Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein **20**: 399–408.
Remane, A. & E. Schulz (1964): Die Strandzonen des Roten Meeres und ihre Tierwelt. – Kieler Meeresforschungen **20** (Sonderheft): 5–17.
Riedl, R.J. (1969): Gnathostomulida from America. – Science **163**: 445–452.
Rieger, R.M. & S. Tyler (1995): Sister-group relationship of Gnathostomulida and Rotifera-Acanthocephala. – Invertebrate Biology **114**: 186–188.
Ruiz-Trillo, I., M. Riutort, H. M. Fourcade, J. Baguna & J. L. Boore (2004): Mitochondrial genome data support the basal position of Acoelomorpha and the polyphyly of the Platyhelminthes. – Molecular Phylogenetics and Evolution **33**: 321–332.
Ruppert, E. E. & R. D. Barnes (1994): Invertebrate Zoology. 6th edition. – Saunders College Publishing, Fort Worth: 1056 pp.
Ryan, J. F. (2014): Did the ctenophore nervous system evolve independently? – Zoology **117**: 225–226.
Ryan, J. F., K. Pang, C. E. Schnitzler, A.-D. Nguyen, R. T. Moreland, D. K. Simmons, B. J. Koch, W. R. Francis, P. Havlak, NISC Comparative Sequencing Program, S. A. Smith, N. H. Putnam, S. H. D. Haddock, C. W. Dunn, T. G. Wolfsberg, J. C. Mullikin, M. Q. Martindale & A. D. Bauxevanis (2013): The genome of the ctenophore Mnemiopsis leidyi and its implications for cell type evolution. – Science **342**: 6164.
Schaefer, M. (2014): Nachruf auf Peter Ax. – Jahrbuch 2013 der Akademie der Wissenschaften und der Literatur Mainz. – Franz Steiner Verlag, Stuttgart: 82–85.
Schierwater, B., S.-O. Kolokotronis, M. Eitel & R. DeSalle (2009): The Diploblast-Bilateria sister hypothesis. – Communicative & Integrative Biology **2**: 403–405.
Schmidt, P. (1974a): Interstitielle Fauna von Galapagos. IV. Gastrotricha. – Mikrofauna des Meeresbodens **26**: 1–76.
Schmidt, P. (1974b): Interstitielle Fauna von Galapagos. X. Kinorhyncha. – Mikrofauna des Meeresbodens **43**: 1–15.
Schmidt, P. (1978): Interstitielle Fauna von Galapagos. XXI. Lebensraum, Umweltfaktoren, Gesamtfauna. – Mikrofauna des Meeresbodens **68**: 1–52.
Schmidt, P. & B. Sopott-Ehlers (1976): Interstitielle Fauna von Galapagos. XV. *Macrostomum* O. Schmidt, 1848 und *Siccomacrostomum triviale* nov. gen. nov. spec. (Turbellaria, Macrostomida). – Mikrofauna des Meeresbodens **57**: 1–45.
Schmidt, P. & W. Westheide (1977): Interstitielle Fauna von Galapagos. XVII. Polygordiidae, Saccocirridae, Protodrilidae, Nerillidae, Dinophilidae (Polychaeta). – Mikrofauna des Meeresbodens **62**: 1–38.
Schmidt-Rhaesa, A. (1996): Zur Morphologie, Biologie und Phylogenie der Nematomorpha – Untersuchungen an *Nectonema munidae* und *Gordius aquaticus*. – Cuvillier Verlag, Göttingen: 276 pp.
Schmidt-Rhaesa, A. (2013): Gastrotricha, Cycloneuralia and Gnathifera: general history and phylogeny. – In: A. Schmidt-Rhaesa (ed.): Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera. Vol. 1: Nematomorpha, Priapulida, Kinorhyncha and Loricifera. – De Gruyter, Berlin: 1–10.
Schmidt-Rhaesa, A. (2014): Obituary: Peter Ax (29.03.1927-02.05.2013). – Zoologischer Anzeiger (published online).
Schram, F. R. (1991): The early evolution of Metazoa and the significance of problematic taxa. – In: Simonetta, A. & S. Conway Morris (eds): The early evolution of Metazoa and the significance of problematic taxa. – Cambridge University Press, Cambridge: 35–46.
Sibley, C. G., J. E. Ahlquist & B. L. Monroe (1988): A classification of the living birds of the world based on DNA-DNA hybridization studies. – Auk **105**: 409–423.
Siewing, R. (1985): Lehrbuch der Zoologie. Vol. 2: Systematik. 3rd. edition. – Gustav Fischer Verlag, Stuttgart: 1107 pp.
Smith, J. P. S., S. Tyler & R. M. Rieger (1986): Is the Turbellaria polyphyletic? – Hydrobiologia **132**: 13–21.
Sopott, B. (1973): Jahreszeitliche Verteilung und Lebenszyklen der Proseriata (Turbellaria) eines Sandstrandes der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **15**: 1–106.

Sopott-Ehlers, B. & P. Schmidt (1974a): Interstitielle Fauna von Galapagos. IX. Dolichomacrostomidae (Turbellaria, Macrostomida). – Mikrofauna des Meeresbodens **34**: 1–20.

Sopott-Ehlers, B. & P. Schmidt (1974b): Interstitielle Fauna von Galapagos. XII. *Myozona* Marcus (Turbellaria, Macrostomida). – Mikrofauna des Meeresbodens **46**: 1–19.

Sopott-Ehlers, B. & P. Schmidt (1975): Interstitielle Fauna von Galapagos. XIV. Polycladida (Turbellaria). – Mikrofauna des Meeresbodens **54**: 1–32.

Sterrer, W. & M.V. Sørensen (2015): Phylum Gnathostomulida. – In: Schmidt-Rhaesa, A. (ed.): Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera. Vol. 3: Gastrotricha and Gnathifera. – De Gruyter, Berlin: 135–196.

Tzschaschel, G. (1979): Marine Rotatoria aus dem Interstitial der Nordseeinsel Sylt. – Mikrofauna des Meeresbodens **71**: 1–64.

Tzschaschel, G. (1980): Verteilung, Abundanzdynamik und Biologie mariner interstitieller Rotatoria. – Mikrofauna des Meeresbodens **81**: 1–56.

Wallace, R. L., C. Ricci & G. Melone (1995): Through Alice´s looking glass: a cladistic analysis of pseudocoelomate anatomy. – Selected Symposia and Monographs U.Z.I. **8**: 61–67.

Wallace, R. L., C. Ricci & G. Melone (1996): A cladistic analysis of pseudocoelomate (aschelminth) morphology. – Invertebrate Biology **115**: 104–112.

Wehrenberg, C. & K. Reise (1985): Artenspektrum und Abundanz freilebender Plathelminthen in sublitoralen Sänden der Nordsee bei Sylt. – Microfauna Marina **2**: 163–180.

Weigmann, G. (1973): Verzeichnis der wissenschaftlichen Schriften von Prof. Dr. Dr. h.c. Adolf Remane. – Faunistisch-Ökologische Mitteilungen **4**: 275–281.

Wellner, G. & K. Reise (1989): Plathelminth assemblages from an exposed and a sheltered sandy beach of the island of Sylt in the North Sea. – Microfauna Marina **5**: 277–294.

Westheide, W. (1974): Interstitielle Fauna von Galapagos. XI. Pisionidae, Hesionidae, Pilargidae, Syllidae (Polychaeta). – Mikrofauna des Meeresbodens **44**: 1–146.

Westheide, W. (1977): Interstitielle Fauna von Galapagos. XVIII. Nereidae, Eunicidae, Dorvelleidae (Polychaeta). – Mikrofauna des Meeresbodens **63**: 1–40.

Westheide, W. (1981): Interstitielle Fauna von Galapagos. XXVI. Questidae, Cirratulidae, Acrocirridae, Ctenodrilidae (Polychaeta). – Mikrofauna des Meeresbodens **82**: 1–24.

Westheide, W. (2014): Nachruf auf Peter Ax 29.3.1927-2.5.2013. – Mitteilungen der Deutschen Zoologischen Gesellschaft 2014: 55–58.

Westheide, W. & P. Ax (1965): Bildung und Übertragung von Spermatophoren bei Polychaeten (Untersuchungen an *Hesionides arenaria* Friedrich). – Verhandlungen der Deutschen Zoologischen Gesellschaft 1965: 196–203.

Westheide, W. & R. Rieger (1996): Spezielle Zoologie. Teil 1: Einzeller und wirbellose Tiere. – Gustav Fischer Verlag, Stuttgart: 909 pp.

Westheide, W. & P. Schmidt (1974): Interstitielle Fauna von Galapagos. VI. *Aeolosoma maritimum dubiosum* nov. ssp. (Annelida, Oligochaeta). – Mikrofauna des Meeresbodens **28**: 1–11.

Wey-Fabrizius, A. R., H. Herlyn, B. Rieger, D. Rosenkranz, A. Witek, D. B. Mark Welch, I. Ebersberger & T. Hankeln (2014): Transcriptome data reveal syndermatan relationships and suggest the evolution of endoparasitism in Acanthocephala via an epizoic stage. – PloS ONE **9**:e88618.

Willmer, P. (1990): Invertebrate relationships. Patterns in animal evolution. – Cambridge University Press, Cambridge: 400 pp.

Witek, A., Herlyn, H., Ebersberger, I., Mark Welch, D.B. & Hankeln, T. (2009) Support for the monophyletic origin of Gnathifera from phylogenomics. – Molecular Phylogenetics and Evolution **53**: 1037–1041.

Wörheide, G., M. Dohrmann, D. Erpenbeck, C. Larroux, M. Maldonado, O. Voigt, C. Borchellini & D. V. Lavrov (2012): Deep phylogeny and evolution of sponges (phylum Porifera). – Advances in Marine Biology **61**: 1–78.

Wörheide, G., T. Nosenko, F. Schreiber & B. Morgenstern (2014): Progress and perspectives oft he deep non-bilaterian phylogeny, with focus on sponges (phylum Porifera). – In: Wägele, J. W. & T. Bartolomaeus (eds): Deep metazoan phylogeny: the backbone oft he tree of life. – De Gruyter, Berlin: 9–21.

Xylander, W. (2013): Prof. Dr. Peter Ax. – Organisms, Diversity and Evolution **13**: 665–667.

Xylander, W. E. R. & K. Reise (1984): Free-living Plathelminthes (Turbellaria) of a rippled sand bar and a sheltered beach: a quantitative comparison at the Island of Sylt (North Sea). – Microfauna Marina **1**: 257–277.