

From the interstitial to phylogeny of the animal kingdom

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Abstract

The biography of Peter Ax is resumed reflecting the significant steps in his research focus and orientations to new fields.

Peter Ax was student of Adolf Remane in Kiel and took his doctoral and habilitation thesis on free living Platyhelminthes of sandy beaches. In 1961 he became the director of the II. Zoological Institute of the University of Göttingen and built up a group of doctoral students working on the mesopsammon especially from the North Sea. The research in this first phase (until about 1968) concentrated on the description of biodiversity in this habitat whereas later on his doctoral student also dealt with the distribution and abundance of species in space and time (until about 1975). In the early 70s he investigated together with Peter Schmidt and several others the mesopsammon of the Galapagos Islands.

His interest in phylogeny of the animal kingdom which already was recognizable during his postdoctoral studies in Kiel brought him in contact with Willi Hennig and phylogenetic systematics. So from the late 70s his scientific interests shifted towards the phylogenetic system of metazoa and the majority of his doctoral students worked on gross morphology and ultrastructure of lower invertebrates, the so-called 'Göttinger Schule'. The research of this group provided a huge amount of new data for the understanding phylogeny and evolution of the taxa investigated and the 'deep phylogeny' of Metazoa. Ax summarized his view on the principles and theory of systematization 1984 in his textbook 'Das Phylogenetische System' by which he gained a broad attention of the scientific community.

Peter Ax also was a charismatic academic teacher and his lectures, on the phylogenetic system were attractive to students. He was co-editor of several international scientific journals and responsible for the 'Mikrofauna des Meeresbodens' as Editor-in-Chief.

After his retirement in 1992 he went on working and published a multivolume textbook on 'Multicellular Animals' as well as a comprehensive monograph on free living flatworms of brackish waters.

Peter Ax passed away on the 2nd of May 2013.

Keywords Phylogenetic systematics | mesopsammon research | Turbellaria | Plathelminthes | Peter Ax

Introduction

The scientific community honored Peter Ax in the obituaries as a outstanding pioneer of phylogenetic systematics in Germany who contributed with his so-called 'Göttinger Schule' significantly to the development of the principals of systematization according to Willi Hennig (s. Hennig 1950, 1966) in theory and practice. He thereby created conditions for the acceptance of this systematics approach in science as well as in academic education (Schaefer 2013, Xylander 2013a,b, Bartoloaeus 2014, Reise 2014, Schmidt-Rhaesa 2014, Westheide 2014).

Besides his merits in establishing phylogenetic systematics Peter Ax (Fig. 1) also was taxonomist, zoologist, morphologist and marine biologist. He was a gifted academic teacher, author of several text books, editor-in-chief of various scientific journals and monographs. This contribution reflects his biography and important phases of his scientific work. It will also consider turning points in his research focus and stress out his contribution for zoology in Germany and internationally.



Family, childhood and youth

Peter Ax was born in Hamburg on March 29th, 1927 as the second son of a banker. He visited the high school for boys (Oberschule für Jungen) where he finished his exams in 1944. He was called up for military service in the last days of World War II and became prisoner of war by the Russians troups. Due to the fact that he was considered as 'too weak for forced labor', he was not brought to a prisoners' camp in Russia, but was set free and could return to the completely destroyed city of Hamburg (Bartolomaeus 2014).

Studies in Kiel

The young Peter Ax took up his studies in biology in Hamburg in 1946, but soon changed to the University of Kiel. There he got in contact with his later academic teacher and supervisor of his doctoral thesis, Prof. Dr. Adolf Remane, who was one of the leading German morphologists and systematists at that time. During these years Adolf Remane worked intensively on marine interstitial fauna, the biodiversity of which he investigated with a high number of doctoral students (among others Sebastian Gerlach, Wolfram Noodt and Gesa Hartmann) scrutinizing the sandy beaches of Schilksee at the Kiel Bay and at the French Mediterranean coast (remark 1, see also Schmidt-Rhaesa, this volume). As soon as 1950 (at the age of 23) Peter Ax passed his doctoral exams with a thesis on the turbellarians of the eulittoral of the Kiel Bay ('Die Turbellarien des Eulitorals der Kieler Bucht') (Ax 1951). Doctoral students of Adolf Remane at his time were Otte Kinne (later director of the Biologische Anstalt Helgoland), Hermann Remmert (later professor for ecology in Erlangen and Marburg), Rolf Siewing (later professor in Erlangen) and Sebastian Gerlach (later professor in Hamburg and Kiel).

From 1951 to 1961 Peter Ax was assistant of Adolf Remane in Kiel. During his post-doctoral period Peter Ax undertook several expeditions e.g. to the marine biological stations of Archachon, Banyuls-sur-Mer and Tvärminne as well as to the North Sea, accompanied by his wife Renate, who took her doctoral degree on ciliates and whom he married in 1954. On these expeditions he investigated the different groups of the mesopsammon and focused especially on the platyhelminth group of Otoplanidae, a species-rich taxon of Proseriata, mainly distributed in high-energy beaches, where they may reach high abundances (e.g. Sopott 1973, Xylander & Reise 1984). Peter Ax submitted his habilitation thesis on this species-rich taxon in 1955. It was published in the



Figure 1. Prof. Dr. Peter Ax (March, 29th 1927 until May, 2nd 2013).

'Schriftenreihe der Akademie der Wissenschaften und der Literatur in Mainz' (Ax 1956a), the first of a long series of contributions which Peter Ax published with the academy over the next decades.

In the same year Peter Ax described two species of Gnathostomulida for the first time (Ax 1956b), which had already been discovered and drawn by Remane and Josef Meixner. But their manuscript had not been published due to World War II and the death of Meixner in 1946. Peter Ax found representatives of this taxon during his investigations in the sands of the Kiel Bay, on the Island of Sylt and later in the Mediterranean. He published his results under the title 'Gnathostomulida - eine rätselhafte Tiergruppe aus dem Meeresstrand' ('Gnathostomulida an enigmatic animal group from marine beaches', Ax 1956b). The first two species of this taxon he assigned (as a subtaxon) to the platyhelminthes (with some doubt due to their monociliarity and the specific jaw structures). Riedl (1969) raised the rank of Gnathostomulida within the zoological system to a 'phylum' and stressed out its position and relevance for the system of Bilateria. So Peter Ax, who discovered this taxon, also received international acknowledgement. But due to the following phylogenetic, taxonomic and ultrastructural research of the Vienna group around Rupert Riedl (with Wolfgang Sterrer and Reinhard M. Rieger) he lost some of the exclusivity on this animal group, what he lifelong regretted (1).

Inspired by the public attention Peter Ax wrote a book in the series of 'Die Neue Brehm-Bücherei' named 'Die Entdeckung neuer Organisationstypen im Tierreich' (The discovery of new body plan types in the animal kingdom, Ax 1960) on his findings with references to many new unusual life forms and rediscovered living fossils. In this book he presented recent results on groups such as Monoplacophora (Neopilina) and Actinistia (Latimeria) which were up to that time only known from the fossil record. But he described also various representatives of the meiofauna of marine sands and stressed out the relevance of the mesopsammal as habitat of primitive as well as highly derived life forms. This small book was widely disseminated. Only one year later he became director of the II. Zoological Institute and Museum of the University of Göttingen and ordinary professor for zoology.

At the II. Zoological Institute in Göttingen

When in 1961 Peter Ax took over the II. Zoological Institute he was accompanied by his second doctoral student Siegfried Giesa, who worked at the institute in Göttingen as lecturer until he retired. Immediately after his start in Göttingen Peter Ax set up a working group, which investigated the marine meiofauna of sandy beaches, especially on the Island of Sylt. The lasting friendship to Otte Kinne was very useful as he made the labs at the litoral station of the BAH available for undergraduate and doctoral students of Peter Ax for the next decades (Fig. 2).

In the following 30 years Peter Ax worked on four major fields of research:

- 1. The biodiversity and ecology of marine interstitial fauna
- 2. The taxonomy, morphology and phylogeny of Platyhelminthes and Gnathostomulida
- 3. The morphology and phylogeny of animals in general
- 4. The theory and practice of phylogenetic systematics

Additionally, he supervised successfully several developmental investigations on Platyhelminthes (by Giesa), Gastrotricha (by Gertraud Teuchert, Teuchert 1968, see Fig. 3) and Acoela (by Gieselbert Apelt, Apelt 1969). Much later he supervised the theses of Thomas Bartolomaeus and was co-author of papers on the transition of the coelom and nephridia during metamorphosis of Polychaeta and Phoronida (Bartolomaeus & Ax 1992). He was very interested in developmental biology, although he never worked in this field himself.

Mesopsammon I – the qualitative record of a biocenosis

During the 1960ies Peter Ax investigated with the first cohort of his mesopsammon group different taxa from marine sands and many new species and their biology were discovered (s. review in Ax 1969; Schmidt-Rhaesa, this volume). These investigations included also taxonomically difficult groups such as the Acoela (by Jürgen Dörjes, Dörjes 1968 and Gieselbert Apelt, Apelt 1969), Polychaeta (e.g. Wilfried Westheide 1967, see also Westheide & Ax 1965) and Gastrotricha (Teuchert 1968). Together with his group Peter Ax recorded the biodiversity of the marine sands of the North Sea qualitatively and he himself focused on different groups of Platyhelminthes (Ax 1966, Fig. 2).

First quantitative investigations of the meiofauna of sandy beaches at List/Sylt by Wilfried Westheide turned out to be extremely difficult and insufficient regarding the results (1). The major problem at that time was the lack of a method to extract meiofauna quantitatively from marine sand samples (s. Noldt & Wehrenberg 1984). Such a method was 'invented' and published by Gottram Uhlig as



Figure 2. Sampling meiofauna in the Wadden Sea with doctoral students (around 1966).



Figure 3. Peter Ax, Gertraud Teuchert and Siegfried Giesa (around 1966).

'seawater-ice-method' (Uhlig 1964, Uhlig et al. 1973, see also Westheide & Schmidt 1969, Schmidt & Westheide 1971). Thereby, for the first time marine meiofauna could be investigated quantitatively and the results could be used for ecological approaches. Wilfried Westheide together with Peter Schmidt and Peter Ax established a simple quantitative method which was used for the next 25 years for investigations of meiofauna (1). Schmidt (1968) simultaneously recorded the abiotic factors of the sandy beach of Sylt and made first comprehensive quantitative investigations on its total meiofauna by extracting more than 350.000 specimens and addressing them to further systematic investigations.

Mesopsammon II – the 'Hausstrand'

From the late sixties until the end of the seventies more than a dozen doctoral students worked at the 'Hausstrand' in front of the litoral station in List/Sylt. In their theses they investigated the biocenosis of this sandy beach covering a broad spectrum of meiofauna groups. During their doctoral studies (which lasted between 3 and 6 years) they investigated the biodiversity, the species composition and abundances, population dynamics, developmental cycles and habitat demands. The result of this scientific program was a 'complete record of biodiversity' (with 652 recorded species, s. Reise 2014) and made the Hausstrand the best investigated beach of the world (Tab. 1).

The results of the theses were published mostly in 'Mikrofauna des Meeresbodens', a journal of the Academy of Sciences and Literature in Mainz, of which Peter Ax was Editor-in-Chief. In most cases the authors published in a first paper their results to morphology, taxonomy and autecology (including descriptions of new species). This was followed by a second publication on the ecology, e.g. abundances in space (horizontal and vertical distributions within this beach) and time (seasonal variation as well as distribution of developmental stages) (e.g. Blome 1974, Ehlers 1973, 1974, Faubel 1974a,b, 1976, Hartwig 1973a,b, Hoxhold 1974, Kossmagk-Stephan 1985, Mielke 1975a,b, Sopott 1972, 1973).

Table 1. Doctoral students working on the meiofauna of theHausstrand in List/Sylt from late 60s until the late 70s (or early 80s).

Investigated Taxa
Ciliata
Nematoda
Rotatoria
Gastrotricha
Macrostomida, Acoela
Proseriata
Neorhabdocoela
Kalyptorhynchia
Polychaeta
Oligochaeta
Harpacticoidea
all groups quantitatively

The investigations showed a) which unexpected biodiversity could be found in a single sandy beach, b) that a big portion of the species found was still unknown to science and c) that the distribution of species and their abundances varied with the regard to seasonal cycles and the habitat specificities. This was principally known but the complexity of the biocenosis and biodiversity was shown for the meiofauna of a marine sandy habitat for the first time. As a consequence of these investigations in the Wadden Sea, there was the wish for comparative surveys of sandy beaches that were expected to differ significantly with regard to the habitat parameters as well as to the biogeography.

So Peter Ax decided together with Peter Schmidt to start another comprehensive comparative investigation at Galapagos. Peter Ax applied for a DFG-project (DFG = Deutsche Forschungsgemeinschaft, German Science Foundation) to investigate the marine meiofauna of Galapagos and simultaneously for support by the Academy of Sciences and Literature in Mainz. Both applications were approved and the project was realized in 1972 and 1973.

Mesopsammon III – Galapagos

A total of seven scientists from the II. Zoological Institute in Göttingen took part in the Galapagos-project. Peter Ax was project leader, Peter Schmidt was the coordinator and the responsible scientist at place. Schmidt spent more than a year together with his wife on Galapagos, took over the regular sampling at the different sampling sites (at various places on islands, which were more than 100 kilometers away from each other) and recorded the abiotic parameters (Schmidt 1978). Furthermore, Schmidt organized the research visits of Peter and Renate Ax, Ulrich Ehlers and Wilfried Westheide (Ax & Schmidt 1973).

During this investigation various meiofauna groups were recorded quantitatively and qualitatively and in the run more than 20 publications were published (mostly in Mikrofauna des Meeresbodens from 1973 to 1984). Many new species, their biology and ecology were described. An international team of acknowledged specialists for various taxonomic groups (of which the scientists from Göttingen had no expertise) were included in working up the samples. And several biologists at Göttingen investigated material which was brought back and deposited in the zoological museum of the University (e.g. Wolfgang Mielke, Jochen Gottwald, Uwe Noldt). Nevertheless, some of the requirements of the project could not be met: The knowledge on biodiversity of the meiofauna of the region was low at the start of the project and the habitat types investigated were very heterogeneous. Furthermore, the intention of the project was to cover alpha taxonomy as well as ecology and evolutionary biology.

Although the project was extremely successful from a scientific point of view and comprehensive (mainly taxonomic) data were generated it never came to a sufficient end. Soon after he returned from Galapagos, Peter Schmidt left Göttingen to take over the education of medical students in zoology at the University of Aachen. Peter Ax failed to convince him to publish his comprehensive ecological data e.g. within a habilitation thesis or a larger monograph (1). Only Wilfried Westheide published a longer review on the Galapagos project (Westheide 1991).

At this period (at the end of the 70s) there was a change in the points of interests of Peter Ax from the mesopsammon to the phylogenetic research.

Phylogeny and ultrastructure – new research fields and the start of the 'Göttinger Schule'

Peter Ax had already published several articles on the evolution of Platyhelminthes in the 60s (Ax 1961, 1963). These articles were influenced by Adolf Remane with regard to their presentation and character evaluation and did not match the principles of phylogenetic systematics (according to Hennig). However, Ax already used cladograms in the late 50s in Kiel to present the systematic

interrelationships of animal taxa when he eventually substituted Adolf Remane during his lectures (2). Why the major field of research of Peter Ax moved to phylogenetic questions in the 70s and 'the items of the past' did not show up for nearly two decades remains at least partly speculative. Presumably, however, several factors may have been of relevance:

- 1. During his lectures Peter Ax successively dealt with the systematic interrelationships of higher taxa of the animal system and realized the demand for new approaches of systematization (see 3, Schmidt-Rhaesa, this volume).
- The son of Willi Hennig (Bernd Hennig) worked as scientific assistant at the Max-Planck-Institute for Biochemistry in Göttingen from 1974 to 1976. Visiting his son, Willi Hennig met Peter Ax several times for scientific discussions in the II. Zoological Institute (s. Westheide 2014).
- 3. Willi Hennig and Adolf Remane met 1971 on a symposium in Erlangen (on which Peter Ax must have been present) and discussed their significantly differing positions regarding systematization and modern systematics. This quite emotional discussion, which Willi Hennig led convincingly, may have let Peter Ax consider the ideas of Willi Hennig on how to develop and set up a natural system.
- 4. Wilko Ahlrichs reported that Peter Ax told him that he realized the problems to order the many new taxa which he and his co-workers had found in the mesopsammon into the Linnaean 'drawer-like' categories (4). So Ax searched for alternatives.
- 5. In the middle of the 1970s Ulrich Ehlers (and later Wilfried Westheide) started their electron microscopical (EM) investigations and discussed with Ax the potential of this method for phylogenetic systematics. The EM-investigations became a major field of research in the institute and there was a demand for tools to assess the phylogenetic relevance of the new tissue and subcellular characters for the animal system.
- 6. After 25 years of mesopsammon research (from his doctoral thesis in 1949/50 until the end of the Hausstrand-investigations) Peter Ax may have felt that it was time for a new orientation.
- 7. Moreover, the insufficient results of the Galapagos-project may have been an additional impulse to turn away from mesopsammon research for some time.

So in the second half of the 70ies and the beginning of the 80ies three former (Ehlers, Sopott-Ehlers and Westheide) and six new doctoral students of Peter Ax investigated ultrastructural characters of invertebrates considering the results mainly from a phylogenetic view point (Tab. 2).

The members of this group followed two approaches: a) comparative investigations on organ systems (sensory organs and receptors, protonephridia, reproductive organs, coelom: Sopott-Ehlers, Bartolomaeus, Kunert, Brüggemann) or b) investigations of taxa with regards to different tissues and celltypes (Platyhelminthes, Gnathostomulida, Kinorhyncha: e.g. Ehlers 1985, Xylander 1986, Lammert 1986, Neuhaus 1988)

During his discussions with colleagues and students, Peter Ax realized that there was need for a text book comprising the principles of phylogenetic systematics in an updated and easy to read form using clear examples for illustration. Such a book should help to make systematization according to the Hennigian principles also usable for academic teaching and for transfer of the principles into the practice of systematization. So since about 1980 he worked on the manuscript of his book 'Das Phylogenetische System'. This book ended up with the most recent system of the Platyhelminthes to demonstrate (pars pro toto) how to use characters of taxa when setting up a cladogram. He used many of the new characters and taxon names (such as 'Neodermata' or 'Trepaxonemata') set up by Ulrich Ehlers a year before in his habilitation thesis (Ehlers 1984, 1985).

At that time Peter Ax had already stopped to use the Linnaean categories in his lecture 'Stämme des Tierreichs'. Even earlier he had used cladograms to visualize interrelationships of taxa and to address synand autapomorphies when setting up the system of the different taxa.

Ulrich Ehlers published his habilitation thesis nearly unchanged under the title 'Das Phylogenetische System der Plathelminthen' (Ehlers 1985) presenting numerous ultrastructural characters from his own research and a comprehensive overview on the literature on Plathelminthes. Thereby Ehlers showed the high relevance of TEM for phylogenetic systematics of lower invertebrates.

Wadden sea ecology – a new old field

In the late 70s, Karsten Reise who had worked in the United States on community ecology joined the group of Peter Ax. He came with a solid theoretical background in animal ecology and convinced Peter Ax to supervise his thesis on the ecological interrelationships of macrofauna using cage exclusion experiments, a field of research

Name	Animal group	Organ system
Westheide, Wilfried	Polychaeta	several
Ehlers, Ulrich	Plathelminthes	several
Sopott-Ehlers, Beate	Seriata	receptors, vitellaria
Lammert, Volker	Gnathostomulida	receptors, nephridia
Xylander, Willi	Gyrocotylidea, Amphilinidea	several
Bartolomaeus, Thomas	Nemertini, Polychaeta, Mollusca	nephridia, coelom
Neuhaus, Birger	Kinorhyncha	several
Brüggemann, Jochen	Plathelminthes	genital hard structures
Kunert, Tamara	Macrostomida	photoreceptors

Table 2. The TEM/Lower Invertebrates-working group at the

II. Zoological Institute.

that obviously interested Peter Ax. Reise became a postdoctoral student working at the Litoralstation of the BAH (= Biologische Anstalt Helgoland) in List. At the University of Göttingen he gave undergraduate courses on taxonomy and evolutionary biology. Interested students joined his group and their theses were officially supervised by Peter Ax, e.g. Bernd Scherer, Werner Armonies, Monika Hellwig, Sabine Dittmann and me. Peter Ax met his 'Sylt-students' during his traditional visits at Sylt every late summer.

Karsten Reise investigated at that time the impact of the oxygenation of normally anoxic strata of the wadden seafloor by macrofauna (e.g. *Arenicola marina*). He found that meiofauna used the oxygenated layers alongside the burrows as habitat and occurred there in significantly increased numbers. These findings led to a controversy with Pat Boaden who had described a 'Thiobios' from anoxic wadden areas as relict representatives of primitive precambrian life forms (Boaden 1975, 1977) – a thesis which was vehemently contradicted by Reise and Ax in a sequence of theses and negations (Boaden 1975, 1977, 1980, Reise & Ax 1979, 1980).

After his habilitation (1982) Reise worked at Sylt, originally as Heisenberg-fellow, later as an employee of the BAH. Briefly after his habilitation (see Reise 1984) he returned to macrofauna ecology again with a special focus on long-term changes in the Wadden Sea. After 1982, Peter Ax had only a few candidates taking their doctoral degrees at the island of Sylt, as Reise supervised such theses by himself. Short time later Reise became honorary professor at the University of Oldenburg.

Academic teaching in Göttingen – 'The Phylogenetic System of Animals'

Since he became professor at Göttingen, Peter Ax gave lectures on zoosystematics. The lecture was originally entitled 'Stämme des Tierreichs' ('Phyla of the Animal Kingdom') but Ax consequently changed the title into 'Das Phylogenetische System der Tiere' ('The Phylogenetic System of Animals') omitting completely all Linnean categories and concentrating on cladograms and autapomorphies. This lecture comprised two semesters and was embedded in a number of additional courses: In the summer semester:

- 3 hours lecture 'Das Phylogenetische System der Tiere I' (starting with an introduction into systematization according to Hennig and the protozoa, ending with the annelids)
- 1 hour films on invertebrates many of them had been produced by his doctoral students and published by the institute of scientific film (IWF = Institut für den Wissenschaftlichen Film)
- 5–6 'demonstrations' in the afternoon, during which Peter Ax showed his students plankton and meiofauna alive using a so-called micro projection.
 In the winter semester:

In the winter semester:

- 5 hours lecture 'Das Phylogenetische System der Tiere II', starting in October with the arthropods and ending before Christmas with the mammals
- In parallel: the morphological part of the undergraduate course.

In any case, the two lectures were the heart of the academic teaching of Peter Ax. He updated them permanently with new results. His elaborated black board presentations, daily changing objects from the museum collection (which comprised more than 500 selected samples from nearly all taxa of the animal kingdom), informative slides of animals (for recapitulation at the end of the lecture) as well as a presentation of cladograms with the aut- and synapomorphies of the groups presented were typical for his lecture (see also Schmidt-Rhaesa 2014). Many of his students took over his way of teaching, speaking, formulating and thematical structuring, sometimes even his gestures (Fig. 5).

Beside these lectures Peter Ax was responsible for the undergraduate course in morphology (where he, however, showed up rather sporadically at my time), for the morphological, systematic and an ecological seminar (together with Matthias Schaefer), where diploma and doctoral students had to present their results. Furthermore, Peter Ax organized together with Ulrich Ehlers a phylogenetic seminar for doctoral students and the zoological colloquium with the other colleagues from the zoological institutes.

Establishing Phylogenetic Systematics in Germany in the 80s

After the death of Willi Hennig in 1973 Peter Ax and Otto Kraus became Editors-in-Chief of the journal Zoomorphology. Both required that the authors consequently applied the Hennigian principles. Especially the increasing number of publications with electron microscopical investigations and phylogenetic profile developed Zoomorphology into one of the leading journals in this field worldwide (Bartolomaeus 2014). Ax also was member of the editorial board of 'Zeitschrift für Zoologische Systematik und Evolutionsforschung' as well as Editor-in-Chief of 'Mikrofauna Marina' (formerly 'Mikrofauna des Meeresbodens').

Peter Ax presented his consideration of the development of lower Bilateria to an international audience first 1983 during the symposium 'On the Origin of Lower Metazoa' at the Natural History Museum in London. There he presented the Plathelminthomorpha, comprising Gnathostomulida and Platyhelminthes as sister groups, as the sister group of Eubilateria. All taxa were grouped according to the Hennigian criteria. Ax's lecture led to a vivid public discussion with Rolf Siewing, who supported a view based on Remane's archicoelomate theory. At that time Ax had nearly finished the manuscript of 'Das Phylogenetische System' and after a quite critical review



Figure 4. Peter Ax during the welcome address of the annual meeting of the German Zoological Society in Göttingen 1966.

of the German edition by Siewing, Ax broke completely with his former fellow from PhD times.

Especially in the early 80s Peter Ax developed further the principles of phylogenetic systematics, including philosophic and epistemological approaches (Schaefer 2013). Consequently rejecting the Linnean categories, Ax only accepted the 'evolutionary species' and the 'closed descendantship' (Ax 1984). He presented and discussed his position on symposia (Fig. 6), but mainly in Germany, especially on the 'Phylogenetisches Symposium'. Many other colleagues like Otto Kraus in Hamburg, Wolfgang Dohle and Walter Sudhaus in Berlin, Wolfgang Wägele in Bielefeld, later in Bochum and Bonn, Ulrich Ehlers (in Göttingen) and Wilfried Westheide (later in Osnabrück) as well as Günther Peters in East-Berlin, Bernhard Klausnitzer in Leipzig, Reinhard Rieger in Innsbruck and Rainer Willmann in Kiel (who became the follower of Peter Ax in Göttingen) applied the principles of phylogenetic systematics in research, publication and education. For them Peter Ax was a valuable discussion partner and often the ultima ratio in cases of conflict.

Most important for establishing phylogenetic systematics in Germany, however, was his persuasiveness as academic teacher and supervisor. From his students he consequently demanded the application of the principles of phylogenetic systematics and trained his

students in the use of the tools for systematization. His 'Göttinger Schule' spread to many German universities establishing phylogenetic systematics in research and education: Wilfried Westheide in Osnabrück, Thomas Bartolomaeus in Bielefeld, Berlin und Bonn, Birger Neuhaus in Berlin, Andreas Schmidt-Rhaesa in Bielefeld and Hamburg, Willi Xylander in Gießen, Leipzig and Görlitz, just to name a few. Many colleagues at other places had a similar impact e.g. Stefan Richter from Berlin in Rostock, Gerhard Haszprunar from Innsbruck in Munich. So a net of Hennigian systematists and morphologists spread over Germany transferring the theory and practice of phylogenetic systematics into academic teaching, developing and adapting the theory and helping to establish it.

Peter Ax as the director of the II. Zoological Institute

Peter Ax remained director of the II. Zoological Institute of the University of Göttingen from 1961 until his retirement in 1992. During these years he received three calls from other universities (Gießen: 1966, Bochum: 1969 and Kiel: 1976). During tenure negotiations he



Figure 5. Peter Ax teaching his lecture on animal systematics in a characteristic enthusiastic style. Fig. from Schmidt-Rhaesa (2014), with permission from Elsevier.

succeeded to transfer the position of Ulrich Ehlers into a permanent position and later he could certify that Matthias Schaefer stayed in Göttingen as professor for ecology, as his position was changed to a C4-professorship.

As a member of the Academy of Sciences and Literature in Mainz Peter Ax had access to financial resources for a position of an executive editor of 'Mikrofauna des Meeresbodens' (held by Beate Sopott-Ehlers), research expeditions, consumables and partly large-scale facilities. So in 1981/1982 he successfully applied for a transmission electron microscope (Zeiss EM 10 B) together with Winfried Schürmann from the I. Zoological Institute.

Peter Ax organized or co-organized several national and international symposia (Figs 4 and 7), e.g. the annual



Figure 6. Peter Ax during the discussion on the contribution of Ernst Mayr (annual meeting of the German Zoological Society in Frankfurt 1990; bottom left: Prof. Dr. Wilfried Westheide)

meeting of the German Zoological Society (1966), the workshop symposium 'The Meiofauna Species in Time and Space' (1975 at the Bermuda Biological Station) or the 5th International Symposium on the Biology of 'Turbellarians' (1987). Normally, the contributions to the symposia were published in monographs or journals edited by Peter Ax (e.g. Ax et al. 1988, Sterrer & Ax 1977).

Peter Ax as personality

Peter Ax was characterized by a balanced mood and a 'hanseatic aloofness', especially with regard to his co-workers and employees at the institute. Peter Ax normally did not allow a closer view into his private live. Even long-term co-workers knew little on his interests, hobbies or friends. Personal talks were rare. Only if one had the luck for a longer common trip by car, a colleague could get a glance into 'a more private Peter Ax'. He offered his students and doctoral students a significantly leeway: Approaches and methods could be developed or determined by the students themselves. But when students or doctoral students presented their results or drafts of the manuscript of their thesis he discussed critically the data and their phylogenetic relevance. Here he kept to some extent the interpretive. In later years he refused to give up once formulated phylogenetic considerations and not always included recent results (e.g. from ultrastructural research, but even more from molecular investigations) (see Schmidt-Rhaesa, this volume). Peter Ax was not a personality



Figure 7. Congress photo of the 5th International Symposium on the Biology of 'Turbellarians' in Göttingen in August 1987.

who introduced his students to other colleagues on symposia and congresses so he incited the initiative of his doctoral students. On the other side he was willing to inform his students about his assessment on a new place of work, e.g. at another university (as he did with me when I changed from Göttingen to Giessen).

His diction was extremely clear, verbal as well as written, and he avoided ambiguity and potential (mis-) interpretations of his consideration by third parties. This demand for clarity Peter Ax also extended to the illustrations in his publications.

Horse-riding played an important role in his live and he build up close friendships to other riders on a horseback in the Solling mountains. In the 70s and 80s Peter Ax was an active member of the Göttinger Rotary Club and many knew him for years as an enthusiastic BMW-driver. He was interested in arts and an engaged museum visitor (Schaefer 2013). The visits of his working group in Sylt did not only result from professional interests but were the expression of a personal close relation to the North Sea and the Wadden Sea.

Shielding off his private live increased during his time in Göttingen. In the 60s until the middle of the 70s Renate and Peter Ax regularly intended parties in the institute (Fig. 8), what was not the case anymore in the 80s. Until about 1975 Renate Ax took actively part in research projects and worked in the institute during the afternoons and evenings.

The late Peter Ax

Peter Ax retired in 1992 and his companions, colleagues and students, especially Wilfried Westheide und Thomas Bartolomaeus, organized a 'farewell colloquium' during



Figure 8. Renate and Peter Ax during a carnival party at the institute in Göttingen 1963.



Figure 9. Peter Ax at the age of 74 in July 2001.

which Peter Ax finally thanked his collaborators. There he said with a wink that he would have worked on interstitial polychaetes if he only had known what a fascinating group this turned out to be.

When his follower Rainer Willmann started, Peter Ax (Fig. 9) moved from his office in the second floor to rooms in the ground floor of the institute. There he worked on the volumes of his text book 'Multicellular Animals' (in German 'Das System der Metazoa'), which were successively published in a German as well as in an English version (Ax 1996a,b, 1999, 2000, 2001, 2003). Furthermore, he wrote a comprehensive, nearly 700 pages strong opus on free-living flatworms of brackish waters (Ax 2008), a group which fascinated him since his post-doctoral stay in Tvaerminne. From the 342 species listed in this compendium Ax had described more than a third (Reise 2014). These animals also inspired the few biogeographic articles he wrote (Ax 1959, 2008, Ax & Armonies 1987, 1990). Even his last publication led him back to the roots: He described three new species of marine interstitial platyhelminthes from the Bay of Biskaya (Ax 2011).

Peter Ax died on the 2nd of May 2013 on his way back from Sylt, a place which had a significant impact on his life and work and which he was cordially connected to for decades.

Resume

Peter Ax is nowadays perceived as an outstanding invertebrate zoologist, as the initiator of the 'Göttinger Schule' as well as important for establishment of phylogenetic systematics. But he was also a marine biologist, taxonomist, morphologist, editor of various scientific journals, author of several text books and a gifted academic teacher.

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Further references and sources

- (1) Notes of the author regarding two long telephone calls with Wilfried Westheide in October 2014 and June 2015.
- Remark by Mr Rempe, student of Peter Ax in Kiel (about 1957).
- (3) Remark of Rainer Willmann during the Phylogenetic Symposium in Hamburg (22.11.2014).
- (4) Remark by Wilko Ahlrichs during the Phylogenetic Symposium in Hamburg (22.11.2014), in which Wilko Ahlrichs stated, that Ax in the 80ies and 90ies neglected to some extent recent results on ultrastucture and phylogeny of Nemathelminthes from his institute in Das System der Metazoa.

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