

## Prof. Dr. Peter Ax

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On 2 May 2013 Prof. Dr. Peter Ax passed away in Göttingen at the age of 86 after a brief illness. The German community of systematic zoologists thereby lost one of its outstanding representatives.

Peter Ax was born in Hamburg on 29 March 1927. He went to school there and visited the “Oberschule für Jungen” until 1944. Afterwards, he was a soldier in World War II. As of 1946, he studied biology at the University of Kiel and worked on his doctoral thesis on the faunistics and ecology of turbellarians of the eulittoral in the Bay of Kiel. Under supervision of the famous evolutionary biologist Adolf Remane, he submitted his thesis in 1950 at the age of 23 (published in 1951). Ax’s fellow students were, e.g., Otto Kinne (who later became the director of the Biologische Anstalt Helgoland), Rolf Siewing (professor in Erlangen) and Hermann Remmert (professor in Marburg). From 1952 to 1961, Ax worked as a scientific assistant at the Zoological Institute of the University in Kiel; at that time, he met his wife, Renate, whom he married in 1954. In 1955, he submitted his habilitation thesis on the taxonomy and biogeography of Otoplanidae, a species-rich group of Proseriata from the

littoral mesopsammon. During his time in Kiel, Peter Ax described the Gnathostomulida, a new enigmatic taxon from the littoral, the phylogenetic relationships of which had remained uncertain for decades. Inspired by this discovery, he wrote a book on recently discovered “missing links” (such as the Neopilina, Hutchinsoniella, Latimeria and Gnathostomula) entitled “Die Entdeckung neuer Organisationstypen im Tierreich” (The discovery of new body plan types in the animal kingdom). This popular book showed his broad zoological interests, and, with his authorship, Ax received attention beyond that of systematists.

His two major fields of research (the ecology of the meiofauna of coastal beaches and the systematics of Plathelminthes) held much of his interest also during the following decades. Holding the chair at the II Zoological Institute and Museum of the University in Göttingen (since 1961), he built up a large work group and investigated the various meiofaunal groups of sandy beaches, especially from the North Sea around the island of Sylt. The systematic breadth that this group of eco-taxonomists worked on ranged from ciliates over the various groups of “Turbellaria” and “Nemathelminthes” (Gastrotricha, Rotatoria, Nematoda), to Annelida and crustaceans (Harpacticoidae, Ostracoda), and even interstitial tunicates and cnidarians. In most cases a single doctoral student investigated the biodiversity and species’ distribution and described taxa new to science. Altogether about 15 graduate students and postdoctoral students worked on this project, which lasted for more than 2 decades. Peter Ax’s close personal friendship with Otto Kinne made possible the installation of a large work group at the littoral station of the Biologische Anstalt Helgoland in List/Sylt for such a long period. Furthermore, as a consequence of the taxonomical and long-term faunistic studies the interstitial communities of the sandy beaches of Sylt are the best known worldwide.

From 1972 until 1973, a grant from the Volkswagen Foundation and the Academy of Science and Literature in Mainz (of which Peter Ax was a member from 1969 until he retired) financed the ‘Galapagos Project,’ which he realized

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together with several colleagues from Göttingen, including his wife Renate (who permanently supported his scientific work) and his former doctoral student, Peter Schmidt (later Aachen). This project focused on the alpha taxonomy, biogeography and evolution of the mesopsammon, and many new species could be described.

When research on the biodiversity and faunistics of the interstitial fauna of sandy beaches was most fruitful (in the late 1960s and early 1970s), Peter Ax began to turn away from alpha taxonomy and mesopsammon ecology and to focus on a new field of research that fascinated him until the end of his life: phylogenetic systematics. Over the following years, he developed what was later called the “Göttinger Schule,” which consequently used the systematization principles developed by Willi Hennig to elucidate phylogenetic relationships. His co-workers and former doctoral students Wilfried Westheide (later professor of zoology in Osnabrück and senior editor of the most important German textbook for zoological systematics) and Ulrich Ehlers followed his change in direction and, since the mid/late 1970s, together built up another large work group investigating the phylogenetic relationships of lower metazoa (e.g., Plathelminthes, Annelida, Nemertinea, Gnathostomulida, Kinorhyncha) using ultrastructural characters and Hennigian methodology. Although Peter Ax never worked with the electron microscope himself, under his supervision important new insights on “invertebrate” phylogeny and functional morphology arose from this group.

A major result of his lasting research on the theory and practice of phylogenetic systematics was his book “Phylogenetic Systematics” (first published in its German version in 1984), which became internationally acknowledged. Here he explained for a wide scientific audience the principles of systematization according to Hennig, but also the practical procedure when searching for “adelphotaxa relationships” and genealogy (and not similarity). Just one year later, Ulrich Ehlers published the first complete phylogeny of a large group of invertebrates: *Das Phylogenetische System der Plathelminthes* (Ehlers 1985). As a consequence of his decade-long struggle to understand the phylogenetic relationships in the animal kingdom, Peter Ax came out with his three-volume opus “*Das Phylogenetische System der Metazoa*” (Ax 1995–2001), which was later also published in English.

In spite of his focus on animal phylogeny in his later years, Peter Ax never lost his interest in coastal ecology, as indicated by numerous research stays from the 1960s to the 1980s at marine biological stations such as Kristineberg, Naples, Banyuls sur Mer, Arcachon, Friday Harbor Laboratories/Seattle, the Darwin station/Galapagos and the Bermuda Biological Station. In the early 1980s, his former doctoral student, Karsten Reise, established a group of ecologists at the Litoralstation of the BAH in List/Sylt, which focused on

Wadden Sea ecology and long-term community changes—including the mesopsammon. Peter Ax visited this group for many years for a week or two in late summer/early autumn. Every morning was reserved for a few hours of discussion on the work progress and recent results of his undergraduate and doctoral students.

Peter Ax was not only an outstanding scientist, but also an engaged and charismatic academic teacher and supervisor of more than 100 doctoral and diploma theses. His lecture “*Das Phylogenetische System des Tierreichs*” (“The Phylogenetic System of the Animal Kingdom”), which presented the morphology and phylogeny of animals from protozoa to man, was the first comprehensive approach to biodiversity for thousands of young students in Göttingen. He always started with an introduction on the principles and procedure of phylogenetic systematics. During the following presentation of taxa, he consequently ignored the Linnean categories, instead showing cladograms explaining the phylogeny and referring to the aut- and synapomorphies of the groups considered. The clear structure of his lectures, his rhetoric talent and his clever use of media helped students to understand the interrelationships and evolutionary development of the different animal groups—and to structure the unexpected complexity of scientific terms, the varieties of body plans and taxa specific developmental stages as well as evolutionary trends. In his seminars and colloquia, Peter Ax discussed with his students phylogeny in general as well as the evolution, systematics and apomorphies of specific taxa—with amazing expertise, vividly and sometimes controversially. For his students, these discussions were a permanent orientation, inspiration and motivation.

Peter Ax was editor in chief, co-editor and a member of the editorial boards of various international scientific journals such as *Zoomorphology*, the *Journal of Zoological Systematics and Evolutionary Research*, and *Mikrofauna Marina*. He especially developed *Zoomorphology* (together with Otto Kraus in Hamburg) into one of the outstanding morphological journals and to a forum (one of the first worldwide) in which all results and systematic considerations had to be discussed using the criteria of Hennigian phylogenetic systematics.

Over all these years, Peter Ax contributed significantly to the development of “his” institute that he chaired for more than 30 years until he retired on 31 March 1992. He refused three professorships at other universities (Giessen 1966, Bochum 1969 and Kiel 1976) and thus made the University of Göttingen install a professorship for animal ecology. He received numerous awards, e.g., becoming a fellow of the *Wissenschaftskolleg Berlin* and in 2003 an Honorary Member of the *Gesellschaft für Biologische Systematik*.

In his free time, Peter Ax was a passionate horseman, a hobby that he shared with his wife, and a member of the local Rotary Club. Even after he retired in 1992, Peter Ax regularly

worked at the zoological institute and remained in contact with many of his former colleagues and students.

His extremely straightforward thinking, broad taxonomic and morphological expertise, clearness in the written and spoken word and engagement in systematic questions—with which he

argued and discussed with his typical Hanseatic distance—will be unforgotten by his students, colleagues and all who met him.

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