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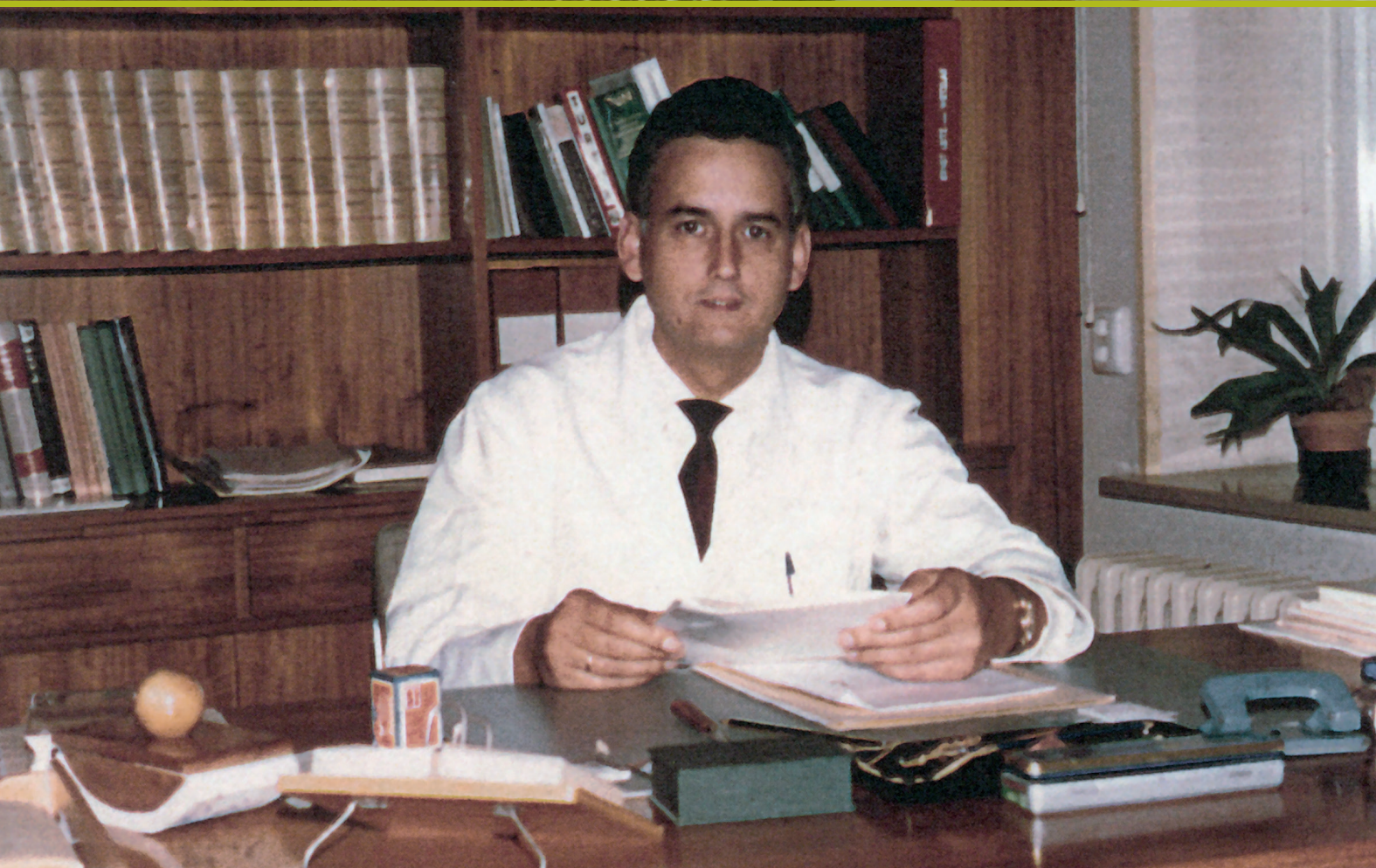
Peter Ax, the promotor of phylogenetic systematics
56th Phylogenetic Symposium 2014 in Hamburg, Germany

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Editorial

When Peter Ax died on May 2nd, 2013, we lost a great zoologist who left his mark in various areas. He was specialist on flatworms, an important researcher on the interstitial system and its particular fauna, a theoretical systematist who made Willi Hennig´s concept of phylogenetic systematics popular in Germany, and he possessed an excellent overview of metazoan morphology and phylogeny.

A number of obituaries were published in honour of Peter Ax (see references in the following articles) and on November 22, 2014 the Phylogenetic Symposium (Phylogenetisches Symposium), in which he had played a key role up until his retirement, was dedicated to 'Peter Ax and phylogenetic systematics'. The symposium was held in Hamburg.

During this symposium, five talks remembered the life of Peter Ax, each focusing on different aspects of phylogenetic systematics. All five authors have summarized their talks for this volume of Peckiana. We start with a list of publications by Peter Ax that was begun by Ax himself and finished by Rainer Willmann, his successor at the University of Göttingen. Willi Xylander looks back at the life of Peter Ax in an article entitled: 'From the interstitial to the phylogeny of the animal kingdom – Peter Ax as a scientist and academic teacher'. This is followed by an investigation by Andreas Schmidt-Rhaesa of the reasons that made Peter Ax write a three volume book on the phylogenetic relationships of metazoans ('Peter Ax and the system of Metazoa'). Michael Schmitt focusses at character polarization and outgroup comparison, contrasting the approaches taken by Willi Hennig, Peter Ax and current practice: 'Hennig, Ax, and present day mainstream cladistics, on polarizing characters'. Walter Sudhaus demonstrates for mammals how phylogenetic reconstruction, anagenesis and a functional explanation of character evolution complement each other: 'From the cladogram to an explanation of anagenesis in an evolutionary history perspective, exemplified by the mammals'. Finally, Stefan Richter compares the way(s) in which Adolf Remane, Willi Hennig and Peter Ax defined and used the term 'homology': 'Peter Ax's views on homology – a comparison with Remane and Hennig'.

Andreas Schmidt-Rhaesa
(Centrum für Naturkunde, University of Hamburg)
Stefan Richter
(Institute of Biosciences, Universität of Rostock)

Peter Ax (1927–2013)

List of scientific Publications compiled by Peter Ax & Rainer Willmann*

* Institut für Zoologie und Anthropologie, Universität Göttingen, Berliner Str. 28, 37073 Göttingen, Germany
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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
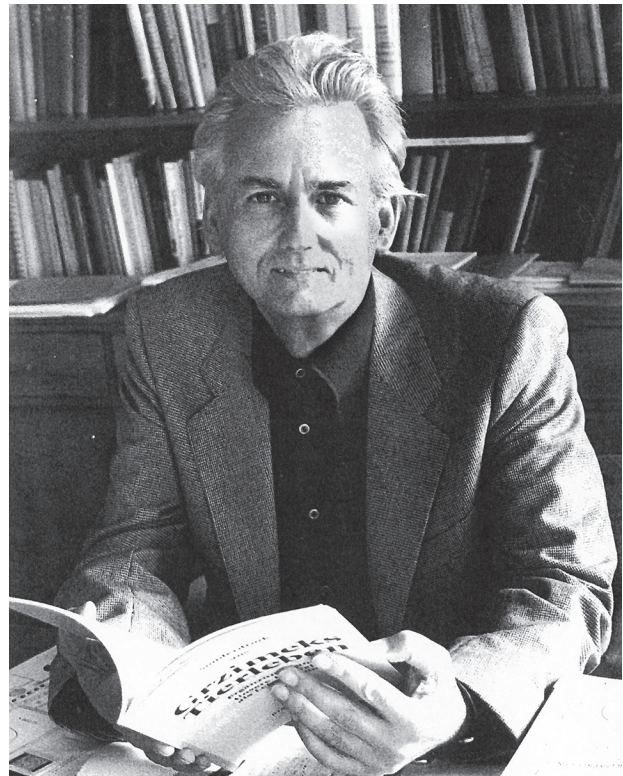
Figure 1. Prof. Dr. Peter Ax (March, 29th 1927 until May, 2nd 2013).

'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
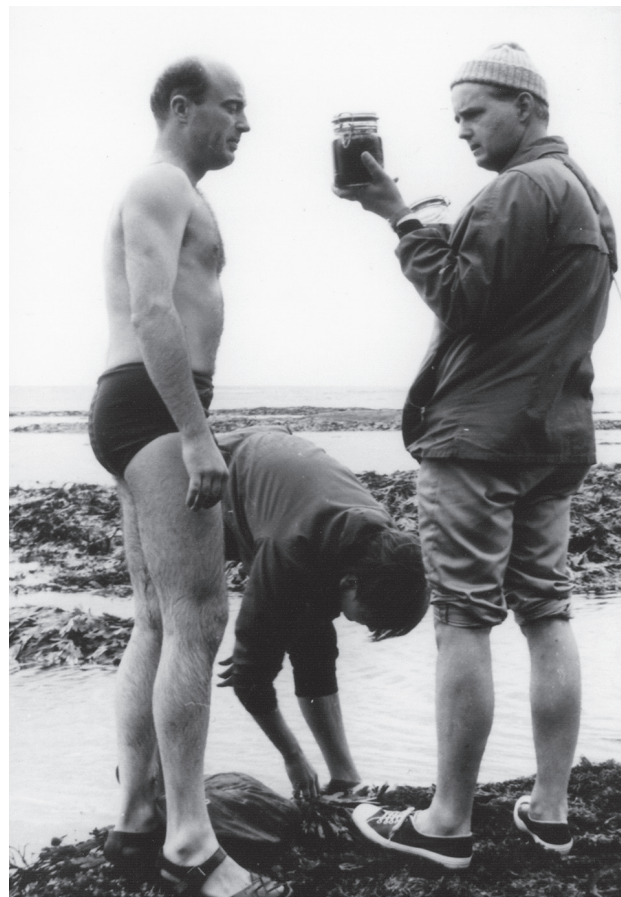

Figure 2. Sampling meiofauna in the Wadden Sea with doctoral students (around 1966).
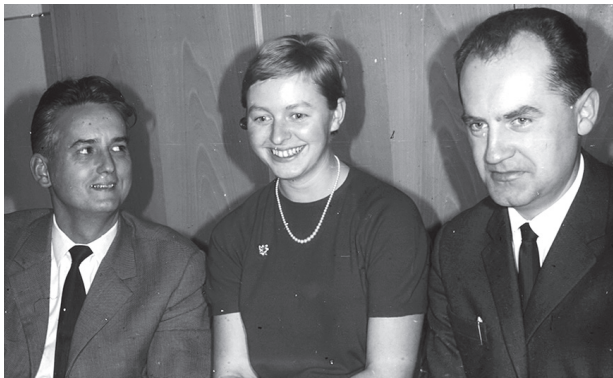
Figure 3. Peter Ax, Gertraud Teuchert and Siegfried Giesa (around 1966).

'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 the Hausstrand in List/Sylt from late 60s until the late 70s (or early 80s).

Name	Investigated Taxa
Hartwig, Eike	Ciliata
Blome, Dietrich	Nematoda
Tzschaschel, Gerd	Rotatoria
Mock, Herbert, Teuchert, Gertrud	Gastrotricha
Faubel, Anno	Macrostomida, Acoela
Sopott, Beate	Proseriata
Ehlers, Ulrich	Neorhabdocoela
Hoxhold, Siegmar	Kalyptorhynchia
Westheide, Wilfried	Polychaeta
Kossmagk, Klaus-Jürgen	Oligochaeta
Mielke, Wolfgang	Harpacticoidea
Schmidt, Peter	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).
2. 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 syn- and 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

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

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

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:

- 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
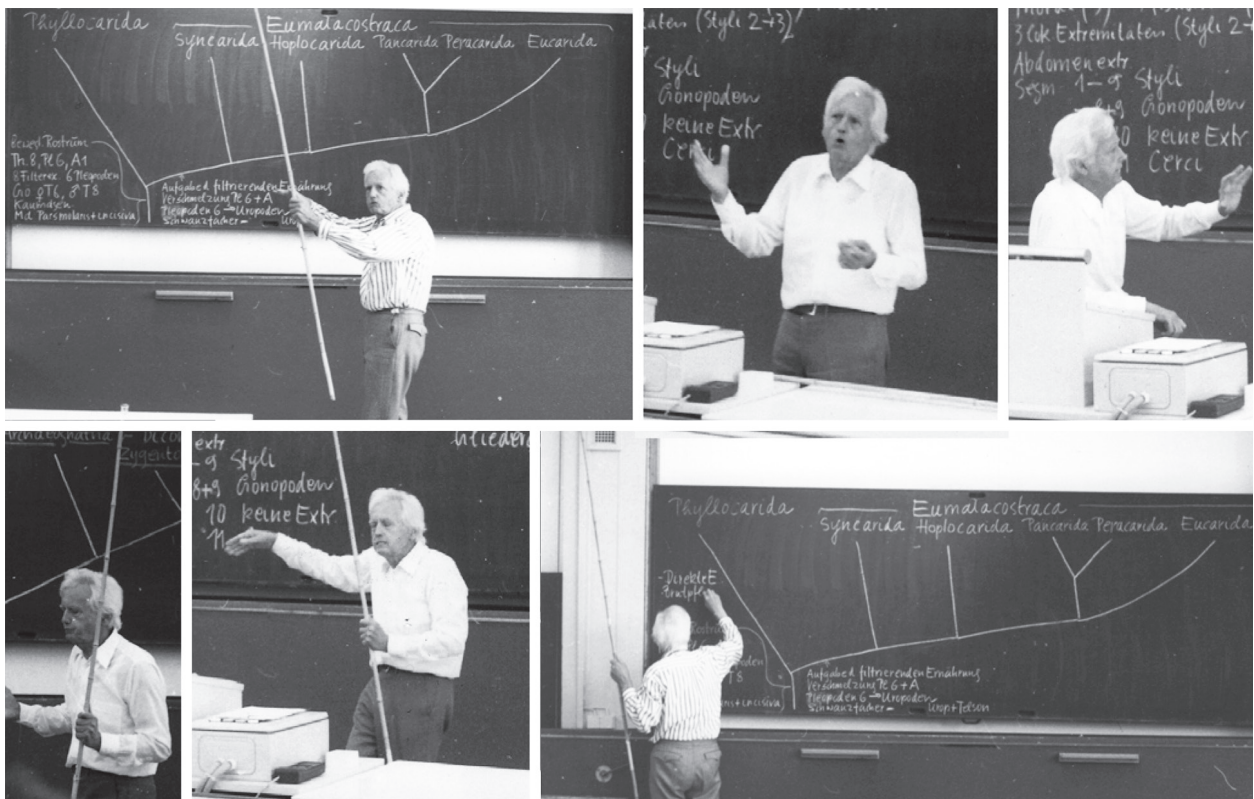

Figure 5. Peter Ax teaching his lecture on animal systematics in a characteristic enthusiastic style. Fig. from Schmidt-Rhaesa (2014), with permission from Elsevier.

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 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 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)

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.

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

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.

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.

Acknowledgement

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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.

(2) 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.

Peter Ax and the System of Metazoa

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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?

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

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

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Hennig, Ax, and Present-Day Mainstream Cladistics,
on polarising characters

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Abstract

The way in which Willi Hennig and Peter Ax substantiated hypotheses on character polarity are described and compared to the presently most common practice of polarising characters by rooting an unrooted network. Although Hennig applied the outgroup comparison method implicitly, and Ax regarded this method as the only general and reliable tool for determining character polarity, there is a crucial difference to the application of this method in present-day mainstream cladistics: Traditionally (Hennig, Ax), character polarity was assessed on a character-by-character basis, while in 'present-day mainstream cladistics' rooting replaced the a-priori-discussion of possible character transformations.

Keywords History of phylogenetics | outgroup comparison | character polarity | methodology | Willi Hennig | Peter Ax

Introduction

Since the foundation of Phylogenetic Systematics by Willi Hennig (Hennig 1950, 1966) it is agreed that 'monophyletic' is defined as 'comprising a stem species and all its descendants' and that establishing hypotheses on monophyly must be based on hypotheses on uniquely derived characters – syn- or autapomorphies. Consequently, the assessment of character polarity ('Lesrichtung der Merkmalsreihen', deciding on plesio- or apomorph states) is the core task in phylogenetic practice. It could, therefore, be of interest to compare how Willi Hennig, the founder, Peter Ax, the most prominent German propagator, and the practitioners of present-day cladistics, met or meet this task.

Willy Hennig
(20.04.1913–05.11.1976) (Fig. 1)

As described earlier (Schmitt 2001, 2013: 131ff.), Hennig had developed the basic idea that only relatively derived characters (or character states) can substantiate a hypothesis of closer relatedness (1936a: 552, 1936b: 170). However, how we can empirically identify such a derived state remained vague. In the *Grundzüge* (Hennig 1950: 172–178) he gave four rules for the evaluation of single morphological characters, repeated in *Phylogenetic Systematics* (Hennig 1966: 95ff., 1982: 98ff., see also Richter & Meier 1994): paleontological character precedence, chorological progression, ontological character precedence, and the correlation of transformation series. Interestingly, he presented these empirical tools originally not as 'criteria' to assess polarity, but rather neutrally as indications of closer relatedness.

The so-called 'criterion of paleontological character precedence' ('so-called' because it is strictly speaking not a logical criterion but an empirical indication) would, of course, yield information for determining character polarity, or phylogenetic (= genealogic) relationships in general, with absolute certainty if the fossil record would be complete. As this is not the case, fossils can lead to erroneous decisions, as Willmann (1989: 283) has pointed out. Nevertheless, there is a certain chance to reach the correct assessment by comparing fossil

and extant specimens. Normally, or at least mostly, the geologically older character state of a transformation series is plesiomorph as compared to younger states.

The 'chorological progression' means that an apomorph character state is expected to occur more frequently in populations near the edges of a distributional area than in the centre, whereas the respective plesiomorph state is said to occur close to the centre of origin of a species group with higher probability than towards the borders of the area covered by this group of species. Whether or not the underlying idea on dispersal of species and character transformation appear convincing, the whole 'criterion' suffers from the general drawback that the 'centre of origin' must be identified without reference to the putative state of the species considered, i.e. whether their character states are plesio- or apomorph. It is unclear how Hennig (or anybody else) would determine the centre of origin without circular reasoning.

'Ontological character precedence' starts from the fact that organisms cannot 'close due to reconstruction' (wegen Umbau schließen, Osche 1966: 830). Therefore, evolutionarily more recent features can be integrated into the ontogeny of an organism by 'terminal addition' (Sewertsoff 1931: 266ff.). Consequently, this 'criterion' can be phrased 'If of two states of a character one occurs as a transitional state - an "interphaen" (Riedl 1975: 258) - in the ontogeny in one lineage and as a final state – a metaphaen - in another lineage, while the alternative character state occurs as a metaphaen only, then the first can be regarded apomorph'. Whether or not this line of argument is accepted or not, the fundamental drawback here is the general paucity of information on the ontogenetic development of the organisms under study. The ontogenetic development of neither fossils nor collection specimens can be observed. Even the study of the ontogeny of live organisms is a limited source of relevant information, although there are examples to the contrary, as was exemplified by Rudolf Meier (1997) in a critical study using sepsid larvae (Diptera). Possibly, numerous studies on the ontogeny of organisms could yield interesting data but have not yet been exploited by phylogeneticists.
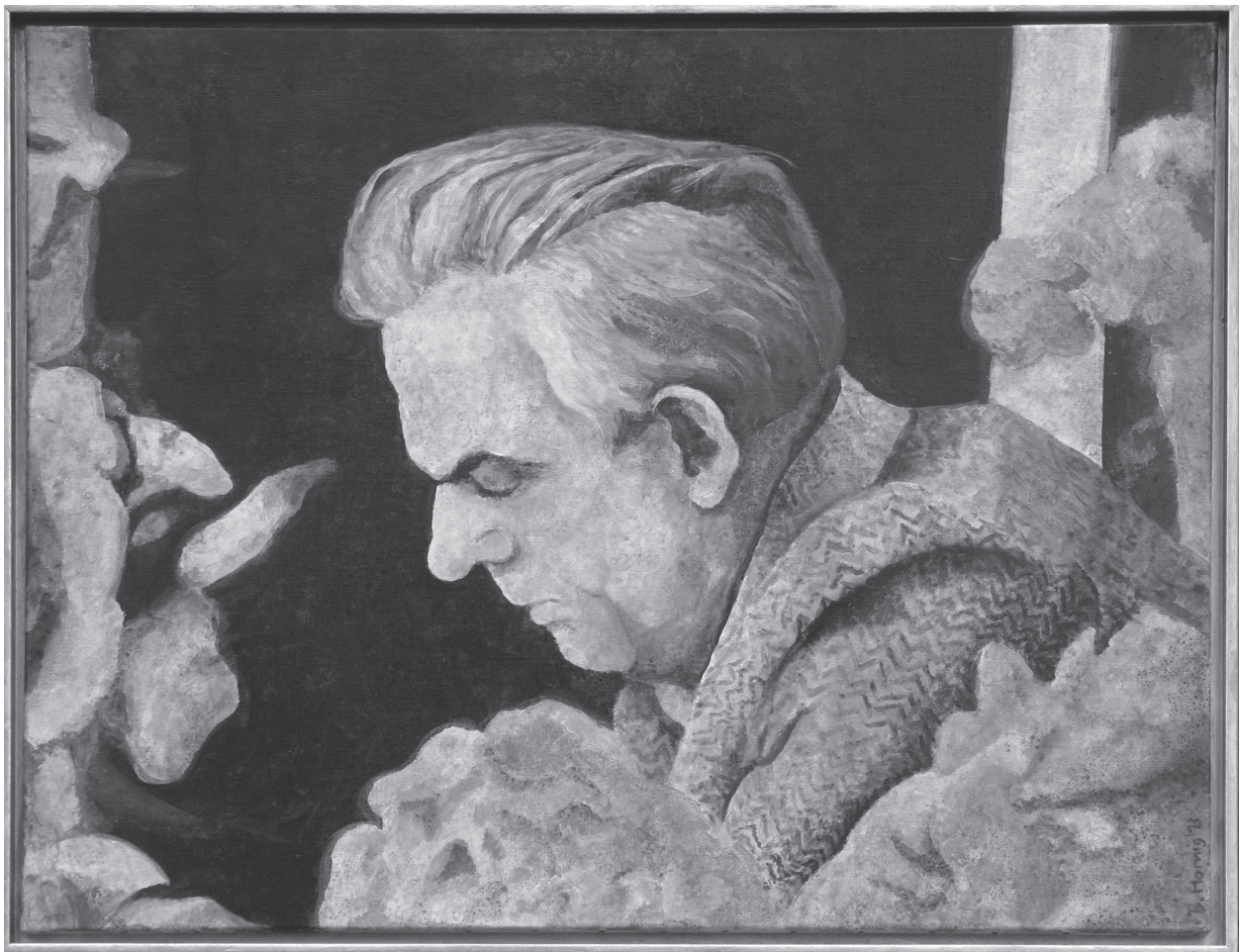

Figure 1. Willi Hennig in 1975. Painting by Adele Hornig (Oppach, Germany) after a photograph, with kind permission.

Theoretically, the 'correlation of transformation series' cannot establish a 'criterion' on its own. Already Lundberg (1972) has pointed out that this 'criterion' 'cannot be regarded as a very strong criterion nor a very useful one' (p. 400) when he discussed the three 'general criteria' presented by Kluge & Farris (1969). At most, it could enhance the reliability of an assessment of character polarity. The principal weakness of this tool is that all characters in a phylogenetic analysis must be regarded as varying independently, to avoid circularity. If two or more characters co-vary necessarily, they could actually be just one single character, possibly brought about by pleiotropy.

Hennig did not only not elaborate a concise and convincing method for polarising characters, he did, moreover, insist that it was not possible to provide such a method (Hennig 1984: 47). In his opinion, taxonomic experience and familiarity with the objects of study would teach the investigator how to decide. In his practical papers, he decided mostly on the basis of plausibility ('... es scheint mir .... durchaus plausibel', Hennig 1972:

25), or according to ideas on evolutionary processes, e.g. switch of hosts from reptiles and birds to mammals in phlebotomine flies (1972: 24). In some cases he simply relied on the statements of other authors: 'According to NN ....' (Hennig 1983, frequently).

In a posthumous paper (Hennig & Schlee 1978) we read that distinguishing plesiomorph from apomorph states of a character is easy and can be seen in most cases from the wide distribution of the characters outside the investigated group of species ('Die ... Entscheidung ist oft leicht und ergibt sich meist aus der weiten Verbreitung der Merkmale außerhalb der untersuchten Artengruppe', p. 5). Here, Hennig (and his last assistant Dieter Schlee) implicitly apply the method of outgroup comparison. We find examples of this approach very often in Hennig's publications. His usual argument for an assessment of character polarity is 'in comparison with the putative sister group' (e.g. 1968: 3), or 'since all other subfamilies of the Psychodidae have 2 spermathecae, ... the reduction of one of them is with certainty an apomorph character in the Bruchomyiinae', 1972: 19).

Figure 2. Peter Ax, during the discussion at the 31st Phylogenetisches Symposium, Freiburg im Breisgau (Germany), 26.11.1988. Photograph taken by Hannes Paulus, with kind permission.

Peter Ax (29.03.1927–02.05.2013) (Fig. 2)

In his early phylogenetic papers (e.g. Ax 1965), Ax followed the conventional line of reasoning, based on the methodological framework provided by Adolf Remane (10.08.1898–22.12.1976, e.g. 1952). Only later, e.g. in his analysis of systematics and phylogeny of the platyhelminth subfamily Trigonostominae (1971), he adopted Hennig's method of phylogenetic analysis. In his textbooks (Ax 1984, 1988), he described three arguments for polarising of characters ('directional arguments for evolutionary change', according to De Jong 1980): (1) Out-group comparison, (2) comparison with the stem-lineage of a taxon, and (3) in-group comparison. Ax stated that the outgroup comparison method, as formalised by Watrous & Wheeler (1981) is the only general and reliable method to determine character polarity. His argument was (1984: 125): If a character occurs within a putatively monophyletic group of species in alternatives, then the state also occurring outside this group is likely the plesiomorphy ('Tritt ein Merkmal in einer mutmaßlich monophyletischen Artengruppe in Alternativen auf, so ist jener Zustand, der auch außerhalb der Gruppe vorkommt, wahrscheinlich die Plesiomorphie'). He stated that the out-group can be any taxon showing the character in question in one of the alternatives occurring in the in-group – it is not required that it is the sister taxon nor that it is shown to be monophyletic. The 'comparison with the

stem-lineage' (p. 129) corresponds roughly to Hennig's 'criterion of paleontological character precedence': If a character occurs within a putatively monophyletic group of species in alternatives, then the state occurring in the stem-lineage of that taxon is likely the plesiomorphy ('Tritt ein Merkmal in einer mutmaßlich monophyletischen Artengruppe in Alternativen auf, so ist jener Zustand, der in der Stammlinie des Taxons vorkommt, wahrscheinlich die Plesiomorphie'). He discusses the weaknesses of this argument himself, i.e. due to the incomplete fossil record we can never be certain that a geologically older character state is plesiomorph as compared to a geologically younger, provided that they belong to the same transformation series. The latter point is especially relevant because we can only determine the putative members of the stem-lineage after conducting the phylogenetic analysis. Ax discussed as a third possible argument on p. 131 the 'in-group comparison' (common equals primitive) but stated on p. 132 that this argument is obsolete.

In the first volume of his opus magnum 'Das System der Metazoa' (1995: 27f.), he mentioned the outgroup comparison method as the only tool for polarising characters. He regarded a 'functional adaptive analysis' as a method that could yield possible additional considerations for the interpretation of character transformation but no proper argument for character polarity assessment. I find it remarkable that Ax had a fully operational concept of 'out-group', in contrast to all other contemporary phylogeneticists in Germany (e.g. Sudhaus & Rehfeld 1992: 105). An outgroup is a group of organisms exclusively chosen for the purpose of polarising a series of character states. Nothing is said and nothing has to be stated about phylogenetic relationships.

As far as I see, Peter Ax has never produced a character matrix, at least he never published one. He performed the outgroup comparison for each character individually, and he did rarey point to a concrete outgroup taxon when listing putative evolutionary novelties (aut- and synapomorphies). Very rarely he discussed alternative relationships in his system of the Metazoa (Ax 1995, 1999, 2001). This means that he composed the trees he presented on the basis of plausible ideas on character transformation and on comparison among a limited set of taxa. Considering that the number of possible dichotomous rooted trees increases exponentially with the number of taxa in the analysis – there are three possible trees for three taxa, 15 for four, 105 for five, and 34.459.425 for ten taxa – it is clear that neither Peter Ax nor anybody else could evaluate even a small proportion of the total number of possible trees. This means that Ax based his decisions on numerous tacit assumptions, on his personal experience and preferences.
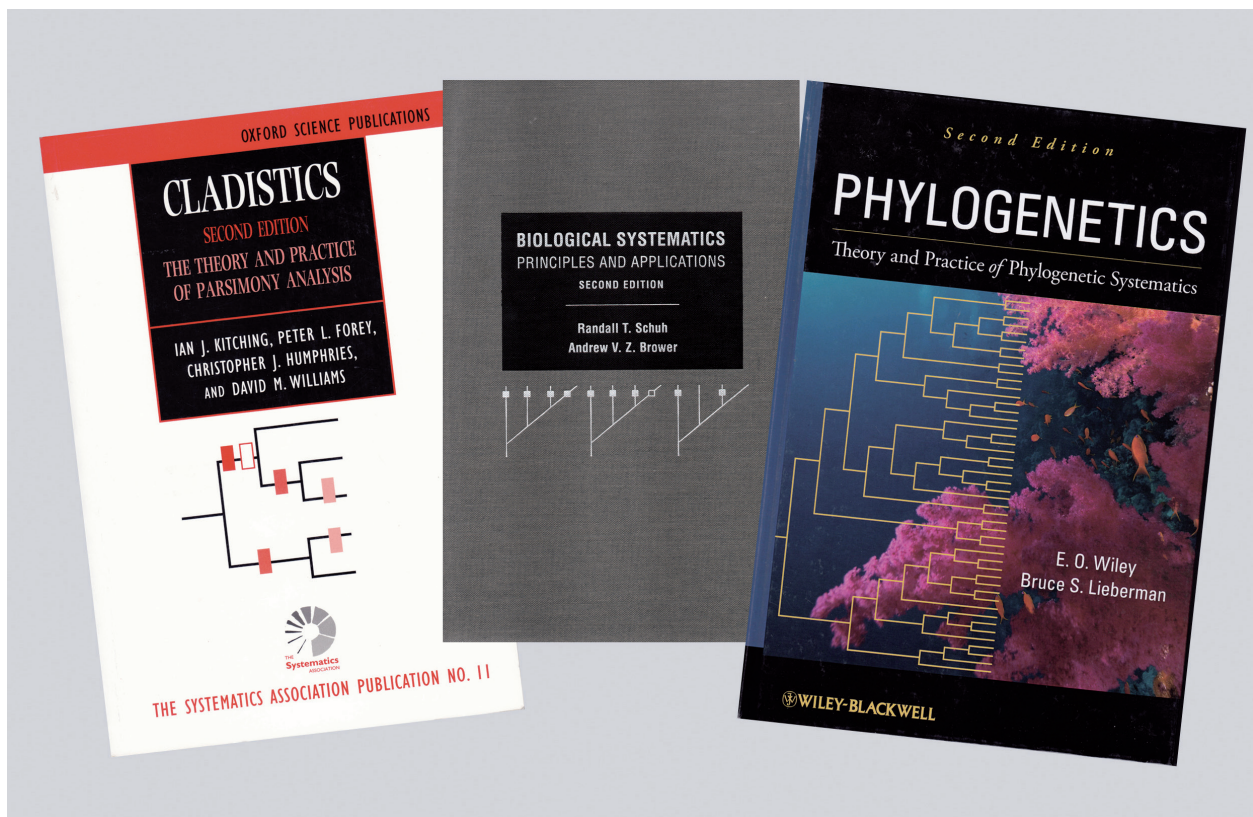

Figure 3. Covers of the three textbooks that I used as methodological sources for chapter on 'Present-Day Mainstream Cladistics'.

Present-Day Mainstream Cladistics

Especially since the 'transformation of cladistics' (Nelson 1979, Nelson & Platnick 1978, 1984, Patterson 1980, Platnick 1979), the landscape of approaches of phylogenetic analysis became diverse and nearly unintelligible, in spite of the analyses of Carpenter (1987) and Ebach et al. (2008). Here, I focus on 'mainstream cladistics' as practised in the papers published in *Systematic Zoology/Biology* and *Cladistics* during the past 40 years. As methodological sources I use the textbooks of Kitching et al. (1998), Schuh & Brower (2009), and Wiley & Lieberman (2011) (Fig. 3) that explain how to discuss character states individually. In practice, however, 'present-day mainstream cladists' polarise characters exclusively by 'outgroup addition' (Wägele 2000, p. 169), i.e. by rooting an unrooted network. Meier (1992, 1995) discussed extensively the implications of choice of the outgroup, rooting, and refraining from a-priori-determination of character polarity.

Throckmorton (1968) developed the method of outgroup comparison that was later explicitly described by Kluge & Farris (1969). Wiley published the 'out-group rule' (1981: 139): 'Given two characters that are homologous and found within a single monophyletic group, the character that is also found in the sister group is the plesiomorphic character whereas the character found only within the monophyletic group is the apomorphic character'. Strictly seen, this rule requires the assessment of monophyly of the ingroup and establishing its sister group prior to polarising the characters in question. Consequently, in the second edition (Wiley & Lieberman 2011), the 'outgroup rule' is slightly reworded: 'Given two (or more) homologous character states within a group studied, the state found outside this group in close relatives is the plesiomorphic state and the character found only within the group is the apomorphic state (p. 157). Watrous & Wheeler (1981) formalised the procedure of outgroup comparison and defined the 'outgroup criterion for polarity determination' as 'For a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic state (p. 5). Kitching et al. (1998) refer to Watrous & Wheeler (1981), stating that only from 1981 on a consistent set of operational rules for outgroup comparison was available.

The general rationale behind the outgroup comparison method (i.e. whether by rooting or on a character-by-character basis) is the principle of parsimony. William of Occam stated in his *Summa logicae* that 'pluralitas non est ponenda sine necessitate' (a plurality must not be supposed without necessity. Beckmann 1995: 43). William of Occam stated this principle ('Occam's razor') as a general rule of thinking, starting from the assumption that only individual things are real, and that we must aim at making the number of notions higher than the number of things only where necessary. In cladistics, the principle means that we should prefer the 'shortest' tree revealed by the cladistic analysis. The length of a tree is measured as the sum of transformational steps from one state of a character to another, calculated either (rarely) by a human scientist or (normally) by a computer algorithm.

In all four sources cited above, the method of outgroup comparison is explained in a way that polarity determination is done for each character separately and prior to the phylogenetic analysis. However, as Wiley and Lieberman bluntly state 'phylogeneticists rarely polarize characters a priori these days'. Schuh and Brower (2009) report that 'polarity was usually determined on a character-by-character basis during the data-gathering phase' by phylogeneticists following the 'traditional Hennigian approach'. The 'controversial interpretation of individual character polarities led to extended discussion in papers from the 1970s and early 1980s. Computer algorithms, such as the Wagner algorithm originally described by Farris, minimize the number of character-state changes among taxa without regard to the polarity … The orientation of the network created by the algorithm is then determined by specifying one taxon to identify the root. Under this formalization of cladistics, all of the literature describing methods to determine individual character polarity really addresses a non-problem. It is only the choice of the outgroup and the position of the root that matter' (p. 98f.).

Even if hardly any present-day cladist refers in publications to an explicit description of the outgroup comparison method, they all – with extremely few exceptions – polarise characters by rooting a posteriori, i.e. after running the respective cladistic computer programme. It is trivial to explain that a priori polarising is practically impossible when dealing with molecular sequence data exclusively. Also, all other arguments – ontogenetic, paleontological, functional-adaptive – are not applicable in these cases. But there are 'these days' only extremely few cladistics analyses based on non-molecular characters in which polarity is determined 'on a character-by-character basis'.

Discussion

From all discussions of the methodology of phylogenetic analysis it becomes clear that the outgroup comparison method is the most widely accepted and most frequently applied tool for polarising characters. Even Willi Hennig often used this method, however without explicit reference

or description. Nevertheless, Hennig stressed other, possibly additional, lines of evidence for the assessment of character polarity: ontogeny, palaeontology, chorology. Peter Ax discussed extensively the use of 'functional-adaptive analyses' and regarded them only a 'welcome supplement' (willkommene Ergänzung, Ax 1988: 84) to the outgroup comparison. Yet, we might think of cases in which such 'functional-adaptive' reasons could be helpful. For example, metacentric chromosomes can break and produce two acrocentric chromosomes, or two acrocentric chromosomes can fuse and form one metacentric or submetacentric chromosome. In the case of chromosome fission the centromere must be duplicated prior to fission, and the breakage must happen exactly between the two centromeres in order to reveal two functional acrocentric chromosomes. On the other hand, centric fusion can easily happen. Thus, it is much more likely that in the course of hominoid evolution the chromosome number decreased due to Robertsonian fusion than that it increased by fission (Yunis & Prakash 1982).

Outgroup comparison does not necessarily imply to determine character polarity globally for all characters in the matrix by choosing an outgroup or several outgroups. It is, of course, possible to choose an outgroup for each character individually (as, e.g., in Schmitt 1988). In this manner could a 'synthetic outgroup' be composed, consisting of character states in a number of different outgroup taxa (Meier, 1997, suggested a similar procedure; however, he did not explicitly state which taxa were used as outgroups). Naturally, the root can only be attached to this 'synthetic outgroup'. It would no longer make sense to 'play around' with re-rooting networks. Such an approach would circumvent a serious drawback of the 'outgroup addition' method: It cannot be expected that the organisms of a concrete taxon chosen as outgroup show *all* characters in the plesiomorph state. Possibly, the effect of this disadvantage could be minimised by using several outgroups, so that the resulting cladogram would possibly reflect the correct sequence of splitting events. However, if we aim at reaching a comprehensive picture of the phylogeny of a group of organisms, i.e. the evolutionary history consisting of cladogenetic events *and* anagenetic processes, then possible misinterpretations of character transformation will matter.

This is especially obvious when looking at cladistic analyses based on DNA sequence data exclusively, as, e.g. the one by Nardi et al. (2003). In this study the authors found that Hexapoda are paraphyletic, as Crustacea were closer related to insects than the Collembola. Ironically, they also found that Hymenoptera were sister to Acari, whitch they considered an artefact. Taking also non-molecular characters into consideration, e.g. morphological structures, would have demonstrated

that the presented cladogram is extremely unlikely, notwithstanding the high bootstrap values.

The principle of parsimony pertains to the economy of thinking only. It does not make any statements about nature. Parsimony does not necessarily reflect the economy of nature. We hardly do know anything about the real number of decisions, i.e. possible changes, in the regulation of the ontogenetic development of a character. Thus, just counting 'steps' does most probably not tell us anything about the number of non-synonymous mutations leading to a transformation of a character from one state to another. Anyway, there is no rational alternative to the procedure of outgroup comparison. All other ways of polarising characters suggested in the literature are either based on ad-hoc arguments and do, consequently, not provide general tools, or they are based on subjective ideas on plausibility, in the worst case they are nothing but 'just-so stories', and consequently are not scientific at all.

Comparing the approaches of Hennig, Ax and the 'present-day cladists' shows that there are strong correspondences but also differences (Schmitt in press). In my opinion, the most relevant difference is that the 'present-day cladists' no longer discuss character transformations a priori. Determining character polarity globally by rooting is, as far as I see, the crucial disagreement between the 'traditional Hennigian' approach and the 'present-day cladistics'.

Conclusion

Willi Hennig did not establish a method of polarising characters. He decided on the polarity of character states always individually on each character and each taxon. Often he exploited information on the 'distribution of the characters among the taxa', which means that he compared putatively closer related taxa, thus applying implicitly an outgroup comparison. Often he argued on the basis of an intuitively assessed plausibility, in some cases even by reference to certain authorities.

Peter Ax accepted the outgroup comparison as the only means to decide on plesiomorph or apomorph condition of a character. He discussed the polarity of characters each by each, and has never published – and probably never compiled – a character matrix.

Modern textbooks of cladistics (Kitching et al. 1998, Schuh & Brower 2009, and Wiley & Lieberman 2011) explain how polarity of characters can be assessed by analysing character by character (as Hennig and Ax proceeded). However, nearly all authors of recent cladistics polarise the characters of their matrices by 'outgroup addition' (or 'outgroup designation'). This

means that rooting between out- and ingroup is the only possibility to convert a network into a cladogram. In analyses based on molecular characters, polarity of characters cannot be assessed in any other way.

As long as we are interested in phylogenesis, and as long as we accept 'phylogenesis = cladogenesis + anagenesis', any analysis without considering non-molecular characters is incomplete, if not irrelevant.

Acknowledgements

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From the cladogram to an explanation of anagenesis in an evolutionary history perspective, exemplified by the mammals[1]

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Abstract

The aim of this essay is to combine the anagenetic analysis of mammalian phylogeny with historical-narrative explanations. The methodology of reconstructing phylogeny and the relevant terms are recapitulated, while the significance of fossils in outgroup comparison and for reconstructing the sequence of evolutionary events or the transformation of complex structures is exemplified. In an evolutionary scenario of mammals, key innovations and their consequences are debated under eleven headings: endothermy and hair, sweat glands and chemical intraspecific communication, improvements in the locomotory apparatus for achieving higher agility and stamina, different improvements in the respiratory and circulatory systems, generation of a closed buccal cavity via the cheeks and lips and a masticatory apparatus for shearing arthropods, changes in dentition to accomplish a precise occlusion of opposing teeth that led to permanent molars, the synorganised evolution of secondary jaw articulation linked with the development of a prolonged chain of auditory ossicles, and other alterations. I also discuss the ways in which sensory organs provide arguments for a nocturnal life in ancestral species. A scenario is presented to elucidate the evolution of maternal care, incubation, lactation and the changes in ontogeny from nidifugous youth fending for themselves to nidicolous infants in a premature stage nourished on milk supplied by the mother. The stemspecies pattern of Mammalia is characterised, and some transformations in the ancestral lineages leading to both crown-monotremes and crown-therians are discussed. Special attention is paid in the essay to different modes of ossification of the secondary sidewall in the monotreme and therian braincase, as well as changes to viviparity and placentation in therians. It is suggested that the mode of reproduction in the stemspecies of therians was similar to that of marsupials, with 'clinging young' as an adaptation to a semi-arboreal mode of life. Some alterations in the ancestral lines of marsupials and placentals are portrayed. In placentals, epipubic bones were lost, the yolk-sac placenta was replaced, the gestation time extended, and a secondary nidicolous behaviour was established. For this anagenetic analysis, it is necessary to consider apomorphic features and how they are integrated into the organismic construction, what the sequence of evolutionary events was, and which transformation series can be specified. In doing so, there must be an attempt to elucidate causal relations in the evolutionary pathways of complex structures. The mechanisms in the restructuring are exemplified in the evolution of the skull and the pectoral girdle in mammals. Some examples are given for 'trait substitutions', parallelisms or 'alternative adaptations' and the emergence of new traits including synorganised complexes (like secondary jaw articulation). When it comes to criteria for evaluating anagenetic stages in the three main groups of mammals, only the number of apomorphies and the species diversity are unequivocal. Pinpointing gains in function, organismic licenses or preadaptations, changes of function, constraints, parallelisms, and limitations leads to a deeper understanding of the reorganisation of organisms over the course of evolution. Some examples are given for limitations in the organismic construction of marsupials.

Keywords Marsupialia | Monotremata | Placentalia | phylogeny | evolutionary morphology

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[1] Lecture on the 56th Phylogenetic Symposion 2014 in Hamburg in commemoration of Peter Ax, the promotor of phylogenetic systematics.

How to construct a cladogram

The discussion of phylogenetic relationships in biology today is predominantly based on the analysis of DNA sequences. With the exception of fossils, morphological characters are no longer used as primary sources, but they are mapped on the tree generated from molecular data. The heyday of phylogenetic systematics based on morphological data, which lasted in Germany from about 1970–2000, culminated in the three books covering the phylogenetic system of the Metazoa by Peter Ax (1996–2001). Nowadays, most universities no longer offer special courses in the methodology of phylogenetic systematics through compiling a character matrix, discussing the polarity of characters or reconstructing a phylogenetic tree by searching for synapomorphies to find sister taxa. That task requires a thorough examination of the characters in real organisms/objects or documentation in the literature. It questions their homology, and attempts to come to conclusions about the distribution of these characters across taxa. Constructing a cladogram in this way is a process of reciprocal illumination that rechecks preceding character analyses.

A short repetition of the method and the terms appears appropriate (Fig. 1). From the phylogenetic perspective, a 'species' is the sequence of populations between two subsequent splits of a lineage. A split is a speciation event, where the stemspecies is dispersed into two new species, which are considered sister species. A cladogram for several taxa represents all the dichotomous splits during the phylogenesis of these taxa, and thus is a diagram aimed at illuminating the relative relationships among them. How do you go about constructing such a cladogram? This is performed in reverse – against the direction of evolution – by searching for the sister taxon (B) to a terminal taxon (A), with sister taxon B a species or a monophyletic group. According to phylogenetic systematics, we can find B if we find a highly concordant feature that exists exclusively in A and B, and in all likelihood is apomorphic. This hypothesis is usually tested by an outgroup comparison (see contribution of Schmitt). This concordant feature is labeled a synapomorphy, a term restricted to use in sister taxa. It is the merit of Ax (1984) to define the term of Willi Hennig more precisely in this restriction. Claiming synapomorphy is a hypothesis aimed at establishing a sister taxon relationship between A and B. We infer that this feature has been evolved – as a novelty, by transformation or by complete reduction of a given character – in the ancestral line of their common stemspecies. It is an apomorphy of the monophylum or clade formed by this stemspecies plus its descendents A and B. The next step is to look for the sister taxon C of this AB-clade in search of a synapomorphy, which in turn is an apomorphy of the ABC-clade. Repeating this procedure yields a cladogram that unambiguously depicts a certain dataset in an apomorphy-based hypothesis of relationships between the examined taxa. – A character is only new or apomorphic at the moment of origin. If it is retained unchanged after a speciation event it is plesiomorphic. The term synapomorphy is needed for methodological reasons as explained before.

Ax (1988, see fig. 2) illustrated the methodology of phylogenetic systematics through the example of three extant species of the egg-laying Monotremata,
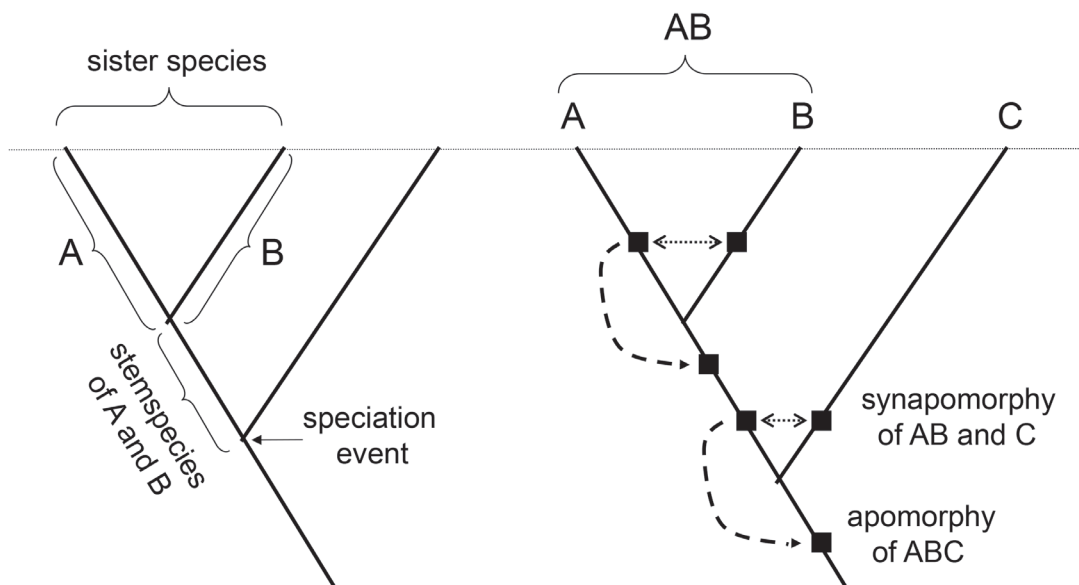

Figure 1. Explanation of terms of phylogenetic systematics.

Ornithorhynchus anatinus, Tachyglossus aculeatus and *Zaglossus bruijni* (Note: some authors differentiate three distinct *Zaglossus* species). In two of these species (the echidnas/spiny anteaters), the skin is covered with a spiny coat. This is interpreted as a synapomorphic character compared with the presence of hairs only, a character found in the platypus and most other mammals. The echidnas have another distinctive trait: they have long claws on the second and third toes for cleaning their spines. Based on these two synapomorphies, *T. aculeatus* and *Z. bruijni* can be hypothesised as sister species, under the assumption that spines and grooming claws evolved in the ancestral line of the latest common species of the echidnas, and were retained in the extant species. The sister taxon to this group would be *O. anatinus*, however not because of a venom gland and a poisonous spur on the hindlimb, as Ax suggested (1984, 1988). The following section will show that at least the spur is a plesiomorphic character. Ax (2001) stated that the side wall of the braincase closed by a dermal lamina, the loss of the jugal bone (a remnant exists) and the unique musculus detrahens mandibulae that functions as a depressor and retractor of the jaw are synapomorphies of these sister taxa, as well as apomorphic characters to constitute the monotremes as a monophylum. With hair and mammary glands as synapomorphies, the monophyletic Theria therefore becomes the sister group of the Monotremata. The Theria monophylum is established by apomorphic characters that include: viviparity, possession of teats (localised openings of the mammary glands), the separation of openings of the rectum and the urogenital system, and a fully coiled lagena (= cochlea) in the inner ear.

This cladogram could theoretically be substantiated with the help of many more characters. For example, the evolution of electro-receptors and the loss of vibrissae are further arguments for the monophyly of Monotremata. The task of systematics scholars is to continue working on cladograms constructed in this fashion, testing hypotheses of apomorphy of characters, and discovering new arguments in new characters to support or revise a cladogram. The cladogram is a statement about the relationships between taxa that provides a simple model of the phylogenetic history of a group. At the same time, it lists the distribution of characters among the taxa that give important support to this hypothesis on relationships, and documents differences in anagenetic processes in sister lineages (between e.g. Monotremata and Theria). It is important to mention here that with the exception of the grooming claws – which must have evolved in functional correlation with the spines in the echidna lineage – mentioned characters are in some ways listed incoherently. When several apomorphies are named for a lineage, it provides for example no information about the sequence in which they evolved.
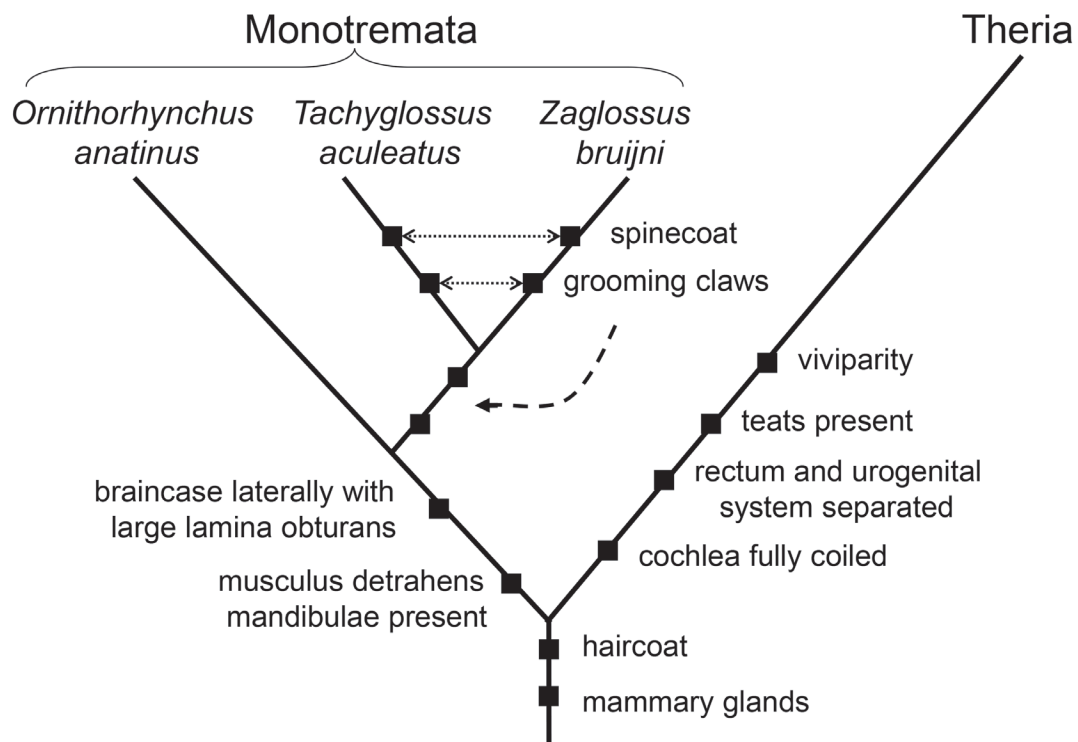
Figure 2. Cladogram of the species of Monotremata and Theria. The search for sister taxa by searching for synapomorphies, which concurrently are the apomorphies for the established monophylum, is exemplified for the echidnas.

Mammalia

Monotremata **Marsupialia** **Placentalia**

†*Barunlestes*

†*Zalambdalestes* — 20

†*Ukhaatherium* 23 — 19

†*Sinodelphys* †*Prokennalestes* — 18

†*Eomaia* — 18

22 17

18 δ

†*Vincelestes* — 16

Sauropsida †*Henkelotherium* — 15

†*Zhangheotherium* — 14

†*Maotherium*

†*Akidolestes*

†Multituberculata ?

? †*Gobiconodon*

21 13

γ

†*Castorocauda*

†*Haldanodon* 12

†*Morganucodon* 11

†*Sinoconodon* 10

†*Pachygenelus* 9

†*Diarthrognathus* 8

†*Probainognathus* 7

†*Chiniquodon* 6

†*Thrinaxodon* 5

†*Lycaenops* β 4

†*Estemmenosuchus* 3

†*Eocasea* 2

1

α

Pan-Mammalia

stem-lineage Mammalia

One outcome of a thorough character analysis attempting to construct a cladogram and to demonstrate the monophyly of each group is to clarify the anagenesis of a lineage (Fig. 3). Anagenesis comprises all apomorphic characters evolved *de novo*, via the transformation of an existing character or by its entire reduction. These were worked out by comparing the characters of extant vertebrate groups (data from various textbooks and tertiary literature). These characters evolved in the ancestral line of the last stemspecies of all extant mammal species, which together compose the crown-group. This ancestral line is the sequence of stemspecies after the branching off of the sister taxon with extant species (Sauropsida) until speciation of the stemspecies of the crown-group. In our example, this describes the segment between the stemspecies α of Crown-Amniota in the Middle Carboniferous and the stemspecies γ of Crown-Mammalia in the Late Trias or Early Jurassic (Fig. 3). The many apomorphies that evolved in the ancestral line are entangled with much more plesiomorphies. Together, they form a complex, three-dimensional mosaic of features that I describe as the stemspecies pattern. Instead Hennig used the term 'groundplan', while Ax (1984) suggested 'ground pattern'. 'The ground pattern of every individual descent community corresponds to the pattern of features of the stemspecies which gave rise to the community by splitting' (Ax 1996: 22). Through speciation, this pattern was passed to the two daughter species that respectively existed at the beginning of the ancestral line of Monotremata and Theria.

The Monotremata and Theria taxa both encompass the stem-lineage and the crown-group, which together form what, following Lauterbach (1989), we call the pan-monophylum (Pan-Monotremata = Prototheria, Pan-Marsupialia = Metatheria, Pan-Placentalia = Eutheria). Naming the sister group relationship depends on context. While actually sister groups are two Pan-groups, neontologists generally mean crown-groups when they use the term. To promote less ambiguity, in this case one might speak of 'extant sister groups' (which self-evidently also include extinct species). Only extant sister groups can have (and indeed usually do have) a different age. Geological history shows that the Monotremata and Theria crown-groups arose at different points in time (see below and Fig. 7).

◄ **Figure 3**. Cladogram of Pan-Mammalia to show the phylogenetic position of the extinct taxa that were mentioned in the text. The demarcated stem-lineage of Mammalia includes the ancestral line (between the stemspecies α and γ) and all side-branches. One daughter-species of α is the stemspecies of Pan-Mammalia. Crown-Mammalia is the monophylum encompassing the stemspecies γ plus exclusively all its descendants. – The branching pattern was adopted from Luo et al. (2007), complemented with some taxa that were not in that tree. Some apomorphies were mapped on this tree, showing the sequence of evolutionary acquisition of main characters. Sometimes characters belong to a neighboring branching point, because information was not available due to the fragmentary nature of the fossils. Characters compiled from various sources. (**1**) a) synapsid temporal fenestra behind the orbit present (indicating large and powerful adductor jaw musculature), b) postparietals fused, c) 'olfactory' turbinates (indicating enlarged olfactory epithelium), d) metacoracoid present, e) obturator foramen (between pubis and ischium) present; (**2**) a) thecodont (teeth in deep sockets), b) distinctive canine teeth in upper and lower jaw, c) double articulation of rib with head and tubercle; (**3**) a) teeth on primary palate (vomers, palatines, pterygoids) lost, b) vomers fused, c) immobility of basipterygoid articulation, d) cleithrum lost, e) ossified sternum, f) gastralia lost, g) lateral undulation of vertebral column lost, h) femur with trochanter major, i) joint between astragalus and calcaneum; (**4**) a) heterodonty (dentition differentiated into anterior incisors, enlarged canine, and laterally placed cheek teeth), b) closed secondary palate, c) expansion of nasal cavity, d) presence of respiratory turbinates, e) epipterygoid (= alisphenoid) expanded dorsally and broadened, constitutes part of the sidewall of the braincase, f) dentary with coronoid process, g) prominent masseter muscle present (indicated by enlarged masseteric fossa of dentary), h) double ball-and-socket joint between occipitale and atlas (allowed dorso-ventral movement; rotation between atlas and axis), i) 5 cervical vertebrae behind atlas and axis, j) differentiation of thoracic and lumbar regions, lumbar ribs shortened (indicative of the presence of a diaphragm?), k) incipient rotation of the limbs below the trunk, l) ilium extended forwards and pubis turned back, m) formation of a heel bone (tuber calcanei, on which the gastrocnemius inserts), n) tail much reduced; (**5**) a) pineal foramen disappeared (parietals became fused), b) musculus depressor mandibulae lost, c) phalangeal formula is 2-3-3-3-3 (unknown in †*Chiniquodon*); (**6**) sidewall of braincase consists of nearly equal-sized alisphenoid and anterior lamina of petrosal; (**7**) a) addition of second jaw joint between squamosal and dentary, b) loss of postorbital bar separating orbit and temporal fossa, c) pre- and postfrontale and postorbitale lost, d) sclerotic ring not ossified, e) dentary symphysis unfused, f) unilateral action between molars on one side of the jaw at a time; (**8**) a) quadratojugal lost, b) basipterygoid joint lost, c) postcanines with incipiently divided roots, d) loss of atlas postzygapophysis, e) axis with dens, f) segmentation of sternum, g) ilium cranially elongated, rod-shaped; (**9**) a) 4 upper incisors, b) single replacement of postcanines only, c) petrosal promontorium developed; (**10**) a) single replacement of antemolar teeth (diphyodonty), perhaps indicating determinate growth (growth restricted to the juvenile phase), b) precise occlusion between upper and lower molars (molars not replaced), c) postcanines have two roots, d) cochlear canal elongated (housed in enlarged promontorium), e) vertebrae platycoel (only a trace of the notochordal pits retained), f) procoracoid lost its contact to the shoulder joint, g) coracoid foramen (between both coracoids) present, h) remnants of lumbar ribs lost (fused to vertebrae), i) presumably facultative arboreal; (**11**) a) cervical ribs fused to vertebrae, b) epipubic bones and patella presumably present (patella cartilaginous in marsupials and other taxa), c) extratarsal spur present; (**12**) a) growth of limb bones in epiphyses, b) pelvic bones fused (in adults), c) restriction to one jaw joint: the squamosal-dentary joint, c) three ossicles in the middle ear, d) cribriform plate present; (**13**) supraspinous fossa of scapula and median scapular spine present (missing in †Multituberculata); (**14**) a) coiling of cochlear duct to ca. 270⁰, b) procoracoid and interclavicle lost, c) extratarsal spur lost; (**15**) molars 'pre-tribosphenic'; (**16**) a) squamosal expanded forward and contacts alisphenoid, b) anterior lamina in lateral wall of braincase strongly reduced, c) cochlear duct coiled 360⁰; d) tribosphenic molars (with a consistent pattern of wear facets); (**17**) dental formula I5/4-C1/1-P5/5-M3/3; (**18**) loss of the lamina obturans (completely replaced by alisphenoid); (**19**) a) only 7 postcanines (4 premolars, 3 molars) by loss of one premolar, b) superposition of astragalus on the calcaneum; (**20**) a) dental formula I3/3-C1/1-P4/4-M3/3, b) atlas forming a complete ring, c) loss of epipubic bones; (**21**) a) anterior lamina in sidewall of the braincase enlarged, reduced alisphenoid tiny, b) stapes unpierced; (**22**) reduced dental replacement: only one tooth generation, except the third premolar in both jaws; (**23**) a) medial inflection of angular process, b) atlas forming a complete ring (in †*Sinodelphys* unknown), c) dental formula I5/4-C1/1-P3/3-M4/4.

Fossils help in polarity decision

A unique character in extant mammals is the kidney-shaped venom gland in monotremes, which is located in the upper thigh connected with a hollow horny spur inside the ankle. In hindsight, it appears inevitable that this character complex would be described as apomorphic for monotremes (Ax 1988, Sudhaus & Rehfeld 1992, Westheide & Rieger 2004). In several fossil species, a rugose os calcaris could be established in the tarsus, which is a supporting bone for a spur and can be homologised with the os calcaris and a cornu calcaris of extant monotremes. Sometimes even remnants of a spur are fossilised. It must have existed at least in the segment of the mammalian stem-lineage between the branch to †*Castorocauda* and the branch to †*Henkelotherium* (evidence for †*Castorocauda lutrasimilis,* †*Gobiconodon ostromi,* †*Akidolestes cifellii,* †*Maotherium sinensis,* †*Zhangheotherium quinquecuspidens* and the multituberculates †*Catopsbaatar catopsaloides,* †*Chulsanbaatar vulgaris* and †*Kryptobaatar dashzevegi*: Hurum et al. 2006, Kielan-Jaworowska & Hurum 2006). The named authors suggested that the extratarsal spur could have been associated with a venom gland (like that found in monotremes), and possibly had a defensive function. This character, they said, could have been lost due to a possible change in the posture of the hindlimb or foot in the ancestral therian line. It had disappeared without a trace. Now, using different fossils for outgroup comparison, the spur in monotremes must instead be judged as plesiomorphic in Monotremata. – While the stapes is pierced in therians, it is columelliform in monotremes, which in comparison with other groups of tetrapods appears to be plesiomorphic. However, as the columella is pierced in representatives of the mammal stem-lineage (e.g. in the segment between †*Thrinaxodon* and †*Morganucodon*), the unpierced state can be viewed as apomorphic for Monotremata (Carroll 1993, Starck 1995).

How fossils help establish the sequence of character evolution

Although fossils do not play a part in the reconstruction of the relationships between extant taxa (Sudhaus 2007: 24), they are very important when it comes to refining an analysis of anagenesis in ancestral lines. As a prerequisite, this means that they can be precisely integrated into the cladogram based on synapomorphies that a fossilised species shares with a section of the ancestral line (an earlier stemspecies). This underlines the necessity for an analysis of morphological characters. Fossil documents like this are key to information about the evolutionary sequence of apomorphies in the ancestral line of crown-mammals, as well as the date when the character was at the latest present, and on the pathways and intermediates of transformations. For instance, what was the path that led to the final character 'temporal fossa confluent with the orbit'? Without fossils like †*Eocasea martini* (Late Carboniferous, Reisz & Fröbisch 2014) and many others, researchers would never have detected that the first step in this direction was a temporal fenestra directly behind each eye socket (a synapsid skull). – Only from fossils we know that the suppression of dental replacement towards diphyodonty evolved in two stages. In the first step, like in †*Sinoconodon rigneyi* from Early Jurassic, postcanines were replaced only once, and in a later step also the anterior teeth became diphyodont (Kielan-Jaworowska et al. 2004). It followed that the interdigitating upper and lower postcanine teeth were brought into precise occlusion. – In crown-mammals the lower jaw is only composed of the dentary. However, this state must have been reached independently within monotremes, marsupials and placentals by loss or displacement of the other bones, because in some extinct species vestigials of the coronoid still existed (Rowe 1988).

An important representative of the stem-lineage of mammals is the fox-sized †*Thrinaxodon liorhinus*, which lived during the Early Triassic. It provides information on mammalian characters that additively had evolved until it branched off from the lineage towards the crown-group. The bones forming the extinct species' snout exhibit numbers of small pits, indicating that vibrissae with well-innervated follicles might have existed. (This was debated by Estes (1961) and others, because similar pits were found in the lizard *Tupinambis,* where they have nothing to do with vibrissae.) Vibrissae are tactile devices for living in burrows (as documented in †*Thrinaxodon* fossils; Damiani et al. 2003) and/ or nocturnal foraging in a complex structured habitat with irregularly spaced surfaces. As vibrissae are specialised hairs, it can be inferred that this extinct species possessed fur. The main function of fur, in the end, is to retain the body heat. This suggests that it evolved together with endothermic characters, steadily improving the efficiency of both features. In this line of argument, the conclusion is therefore that †*Thrinaxodon* was warm-blooded and able to generate and regulate its body temperature internally, although it is unclear how efficiently it accomplished this. The hypothesis of (partial) endothermy in †*Thrinaxodon* is supported by skeletons that were found in curled-up positions, 'as if these animals had assumed this posture to conserve

body heat' (Colbert 1980: 134). A further argument is supported by indications of rudimentary nasal concha (Ruben & Jones 2000). Geist (1972) discussed the comparatively short tail as a means for considerably reducing the surface-to-mass ratio, thus delimiting heat loss. (By the way, this reduction of a massive tail impeded a bipedal movement like in archosaurs: Carroll 1993). Therefore, good arguments support the idea that the stemspecies (β) of †*Thrinaxodon* and Crown-Mammalia (Fig. 3) had high metabolic rates and was endothermic.

The †*Thrinaxodon* fossils exhibit several apomorphies of Crown-Mammalia, characters that must have existed in the last common stemspecies of both. These include: (1) A completely closed secondary palate formed by premaxillary, maxillary and palatine bones, which served to separate the nasal passage from the mouth and enabled breathing while food was retained in the oral cavity. This ensured that squeezing and chewing was possible, as opposed to swallowing food whole – a process facilitated by a tongue able to manipulate food against the rigid bony palate. This 'crunching' is believed to have ensured digestion that was both more efficient and quicker. The bony secondary palate is seen as preadaptive for the evolution of suckling infants.

(2) The leg structure of these animals demonstrates a gradual transition towards an erect stance similar to that found in therians. The sprawling posture – with the legs positioned to the sides of the body and the humerus and femur parallel to the ground – are changed to a semi-erect or semi-sprawling posture, with these bones projecting diagonally downwards. 'This intermediate posture results in an arc of femoral movement which is neither nearly horizontal, as in pelycosaurs, nor nearly vertical, as in *therians' (Jenkins 1971: 178). (*I have replaced 'mammals' with 'therians'.) As the legs were closer to the body, they could provide better support, and limb muscles were predominantly used in locomotion. It is assumed that the limbs worked effectively in tandem with propulsive force coming from the hindlimbs, which entailed changes in the pelvis. The forelimbs had to support the weight of the front part.

(3) It can be suggested that the possible conflict by movements of the hindlimb with the ribs favoured a shortening of the ribs in the lumbar region, which in any case are nearly reduced. For other authors the shortening of abdominal ribs should create the space for a bulging gut, which also initiated the separation of the gut space from the lung space by a muscular septum (Geist 1978). In this way the preconditions for diaphragmatic breathing were given, but it is speculative that a diaphragm already existed behind the chest in †*Thrinaxodon*. A distinct lumbar region and the typical regional differentiation of ribs and vertebrae was apparently reached at the latest in the ancestral species β. Through these and other changes in anatomy, curling the body to preserve warmth during sleep became an option.

(4) There are also indications of maternal care in †*Thrinaxodon liorhinus*. One tiny specimen was discovered in close contact with a skull of an adult, which by comparison of the two size-classes within this species is assumed to be a smaller female (Brink 1955). This indicates that eggs were at least protected, or possibly even incubated, and that hatchlings might have been cared for by the mother. It also suggests some intraspecific chemical signaling.

(5) One plesiomorphic situation should be mentioned: epipubic ('marsupial') bones were missing. They evolved later to support the abdominal wall, stiffen the body during locomotion, and serve as attachment points for muscles to the femur.

Fossils document the reorganisation of functional complexes

It was always clear that the secondary jaw joint of mammals could originate only via an intermediate stage of two jaw joints. Seemingly impossible in functional terms, creationists used this as an argument against evolution. Some evolutionists were only able to bridge the stages of a primary and a secondary jaw joint through saltation. Meanwhile various fossil species of the stem-lineage with double articulation between skull and jaw could be investigated: †*Diarthrognathus broomi*, †*Haldanodon exspectatus,* †*Morganucodon* spp., †*Pachygenelus* spp., †*Probainognathus jenseni,* †*Sinoconodon rigneyi.* They demonstrated that such transitional stages were fully functional for millions of years and were changed stepwise. In †*Probainognathus,* the quadrate bone was not only part of the primary jaw joint, but also articulated with the stapes of the middle ear and documented the initial transition to additional middle ear bones. Due to different fossils a complete chain of transitions to the secondary jaw joint – as well as the integration of the bones of the primary jaw joint in the sound-transmitting apparatus – can be demonstrated. The same holds true for the detachment of the angular from the lower jaw, which at that point in time apparently functioned as the tympanum. All the intermediates are functionally explicable (Takechi & Kuratani 2010). These are illustrious examples for change of function, where an earlier additional function becomes the primary function in the course of evolution.

An evolutionary scenario for Mammalia

Even with only these few landmarks in the attempts to reconstruct the anagenesis of mammals, we are now on solid ground when it comes to discussing and finding explanations for the following questions. In which ways can interdependent structures and functions change? What provided the impulses for transitions? And how could the efficiency of an organism be enhanced selectively through the corresponding transformations or emerging novelties? To find out, we have to search for key innovations in the ethological or physiological spheres that – after an adaptational process – are followed by key morphological innovations for improving the corresponding exploitation of resources in a new ecological zone. Thereby the interdependent network of causes and effects must be taken into consideration (Kemp 2005). In an evolutionary perspective an 'ecological zone' or ecozone by no means is a biogeographic realm, but it reflects the way of living and the ecological interrelationships of closely related species (Sudhaus 2002).

(1) Endothermy meets all the criteria for such a key innovation. The question is, 'how the various evolving characteristics are interrelated such that every stage in the transition from fully ectothermic organism to fully endothermic organism remained a viable, integrated entity' (Kemp 2005: 129). This author discussed the different hypotheses about the evolutionary origin of endothermy in mammals. Once evolved it was never given up. Regulated warm-bloodedness uses metabolic heat and novel mechanisms to control the body's temperature with accuracy. Emancipated from the temperature of the surrounding environment, animals were able to expand their active phases at night, avoiding competition with diurnal sauropsids. The costs of endothermy are higher metabolic rates and increased energy consumption. They in turn promoted improvements in insulation through hair, piloerection or pilodepression of the hairs, controlled vasodilation or vasoconstriction of skin capillaries and nervous mechanisms for body temperature regulation. Hair, formed by dead cells filled with keratin, might have originated with a holocrine gland secretion for repelling wetness, or one to protect the skin from drying out (Maier 1999). An argument for this is the existence
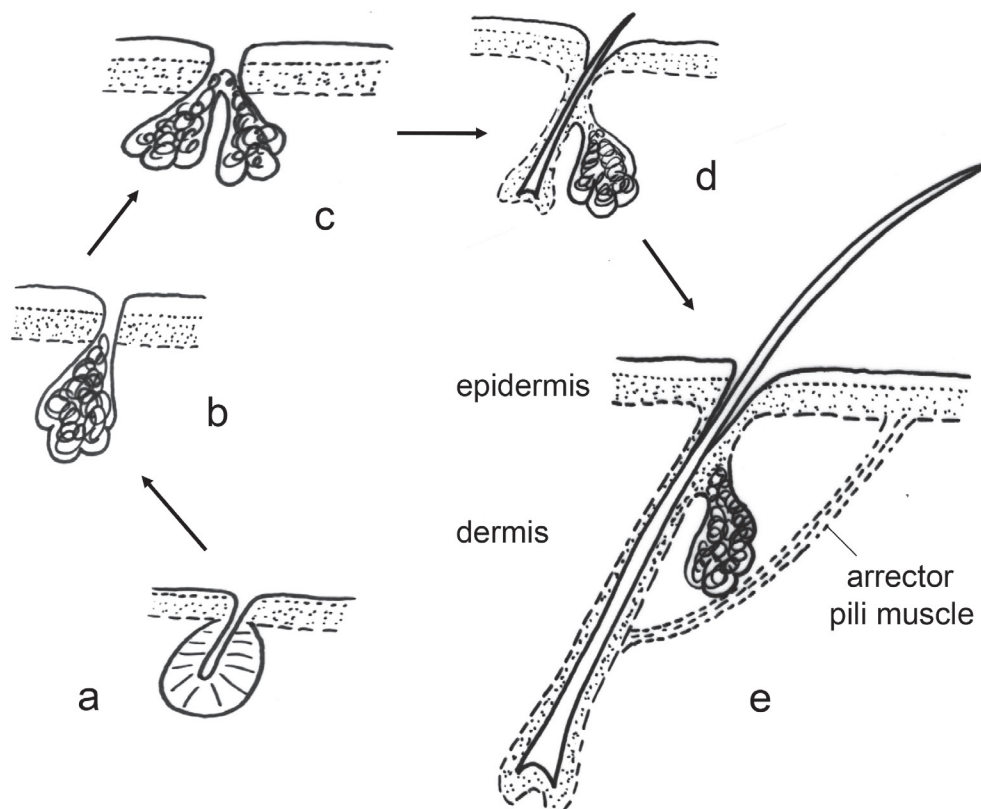

Figure 4. Hypothetical scheme for the evolution of hair in the ancestral line of mammals (stimulated by a sketch by Dhouailly 2009): (**a**) gland in the skin of an amniote ancestor; (**b**) transformation to a holocrine gland; (**c**) its duplication as prerequisite for a differentiation; (**d**) one gland converted into a hair-like structure, which serves as a wick to draw the oily secretion of the adjacent sebaceous gland to the skin surface; (**e**) the hair-sebaceous gland unit.

of holocrine sebaceous glands attached to hair follicles, which produce a secretion to lubricate and waterproof skin and hair (Fig. 4). Hair and sebaceous glands are developmentally coupled, so that Wagner (2014) speaks of a 'hair-sebaceous gland unit'. The pattern of rooting might indicate that individual hairs originated between still-existing scales before they adopted new functions and replaced them. Maderson (2003) suggested hair had a mechanical protection for the skin and mechano-sensory function, before permitting an insulation function. However, mechano-perception only needs sparsely scattered tactile bristles and not such a dense hairy coat to obtain any effect of insulation. In addition, insulating could have been supported by a layer of blubber below the skin (Geist 1972). The subcutaneous storage of fat is thought to have first been licensed by endothermy (ectotherms store fat internally).

(2) Tubular apocrine sweat glands are also associated with hair. Although they partly have a cooling function, scent glands are primarily for intraspecific communication. They secrete pheromones that transmit information about trails, territories, sex, age, kinship, dominance status, health, mood etc. Linked to the evolution of a sophisticated chemical communication system, the main olfactory system and the vomeronasal (Jacobson) organ developed progressively. The olfactory epithelium was enlarged, supported by cartilaginous and bony 'olfactory' turbinates (nasal conchae). The anterolateral 'respiratory' turbinates in the path of respired air assumed respiratory functions. In living mammals, inhaled air is warmed and moistened, while water and heat loss are reduced during exhalation on the extended surface of the mucous membrane in the nasal cavity (Ruben & Jones 2000). Since they are totally lacking in living ectotherms, respiratory turbinates in fossil animals are therefore viewed as indications of warm-bloodedness (see †*Thrinaxodon* above). The sense of smell, which primarily served a purpose in foraging, later became particularly important for social behavior. For the newly hatched young, the sense served to find the area where the mammary glands open. The dominance of the olfactory system stimulated the evolution of an enlarged telencephalon – the area where olfactory information is processed. That led to the ascension of the cerebrum as the superior region of the brain, accounting for the evolutionary success of mammals in coping with their environment.

(3) The increased metabolic rate needed for endothermy could not have evolved without adequate food acquisition and better digestion. On the other hand, higher agility and stamina in hunting arthropods to acquire energy required a high metabolic rate. These are the typical reciprocal dependencies we believe played a role in the evolution of these organisms. Higher agility was reached by abandoning the sprawling gait with splayed limbs. After Kemp (2005) the hindlimb was capable of two different gaits (dual-gait hypothesis). For slow movement it operated in a sprawling gait. For faster locomotion 'the knee was turned forwards, bringing the foot below the body, and the limb was operated in a mammal-like parasagittal mode' (p. 110). This initiated some reorganisation in the skeleton, changing the orientation of joints and the layout of leg muscles. Since the main propulsive force comes from the hindlimbs, apomorphic characters of Mammalia like the fusion of the pelvic bones, with the obturator foramen between pubis and ischium, the elongation of the ilium in front, and novelties like the paired endochondral epipubic bones, the greater trochanter on the proximal femur, the patella, and the caudad tuber of the calcaneus might be understood in this functional context. I view these features as arguments that show that monotremes did not retain a 'reptilian' sprawling posture in the hindlimb, but that instead the changes were adaptations due to the special exercises of that limb for swimming and digging. In the lineage leading to the stemspecies of Mammalia, the forelimbs in contrast might have retained a rather sprawled posture, so that monotremes retained ancestral bones in the shoulder girdle.

One consequence of the at least semi-erect hindlimbs and change in locomotion was presumably that the number of phalanges was brought to nearly the same length by the fusion of bones, so that (with the exception of the first finger or toe, which previously had only two phalanges) all subsequent digits possessed three phalanges. Related to a more upright pose and gait, that symmetrisation is revealed by parallels in species in the mammalian stem-lineage, among them †*Lycaenops ornatus*, which retained the plesiomorphic phalangeal formula of 2-3-4-5-4, but equalised the digits by reducing the length of certain phalanges (Hotton 1991).

In the more upright gait during quick movements, the body flexes vertically, forcing both lungs to expand and compress simultaneously. That meant, the animals could run and breathe at the same time – unlike sprawling animals, where during movement the body flexes from side-to-side. During lateral undulation one lung expands while the other compresses, passing its stale air to the expanding lung. Animals with this morphology need to pause during a quick run to breathe deeply. The semi-erect limb posture overcame this constraint, improving the animal's running ability and increasing its stamina (Carrier 1987).

(4) In the course of evolution, the increased oxygen demands for simultaneously higher metabolic rates and agility led to an improvement of both respiratory and

circulatory systems. Breathing was intensified by the new muscular diaphragm between the thorax and abdomen, as well as the intercostal muscles used to pull air into and out of the elaborate alveolar lungs. The erythrocytes are also unique, as they lack a nucleus. This is an advantage for several reasons. Without a nucleus, these red blood cells can contain more hemoglobin, which means they can carry more oxygen per cell. The absence of a nucleus also allowed the cell to assume a distinctive biconcave shape, so that its surface is high in relation to the volume. This makes diffusion more effective. The transport and release of oxygen is also more efficient, because denucleated erythrocytes are very deformable, and can pass through very narrow capillaries. Some hypotheses also claim that smaller and denucleated erythrocytes provided an evolutionary advantage in the hypoxic atmosphere of the Triassic Period (Blatter et al., online). A disadvantage was that they have a short lifespan (about 22 days in mice, 120 days in humans: von Buddenbrock 1967), which means permanent regeneration is necessary. In adults of a species, this takes place predominantly in the red marrow of large bones, which likewise is a novelty of mammals (Starck 1978). The circulatory system was also transformed. When the increasing lungs were able to receive a larger volume of blood from circulation in the body, the septum between the ventricles could be closed completely and the pulmonary and systemic circulatory systems were fully separated. The advantage of keeping arterial and venous blood entirely apart is obvious. However, one of the evolutionary singularities in the mammalian lineage was that the fourth artery on the right side was disconnected between the right subclavian artery to the forelimb and the descending aorta to the body. Now the carotid arteries to the head, like the subclavian arteries, diverged from the only existing left aortic arch.

(5) The high basic metabolism required a much greater quantity of food, as well as more efficient and rapid digestion. The morphology of the teeth of the animals at this stage indicates that they were mainly insectivorous. Captured arthropods were not swallowed whole, but instead their hard cuticles were sheared and the prey was scrunched. The new chewing motions were accompanied and promoted by various morphological changes and/or entailed such changes. One of them was the development of new glands producing saliva for the oral cavity. With the immobilisation and later the loss of the basicranial joint, the skull had become akinetic. A bony secondary palate allowed uninterrupted breathing while masticating and processing food with the tongue against it. It evolved for mechanical reinforcement associated with jaw function. Initially there were separate shelves projecting medially from each premaxilla and maxilla that served to resist bending and torsion of the snout during biting (Thomason & Russell 1986). The masticatory apparatus allowed three movements of the jaws: up and down, forward and backward, and transverse movement. During mastication only one side of the dentition was used at a time. Important for feeding was the formation of soft cheeks and lips able to flexibly seal the buccal cavity and narrow the mouth, preventing the loss of shredded food (Fig. 5). (Lips and cheeks were also preadaptive for licking and sucking milk.) In the most posterior region, this sealing action was assisted by the jaw muscles, which allowed the complex chewing movements. Their insertions on the lower jaw shifted forward, raising the chewing pressure, and aiding in precise movements of the jaw for tooth occlusion. The food was broken down into small pieces, enhancing digestive efficiency and the rate of digestion, which were in turn additionally increased by endothermy.

(6) Catching insects with a strong bite and chewing the food required that the teeth remain firmly embedded.
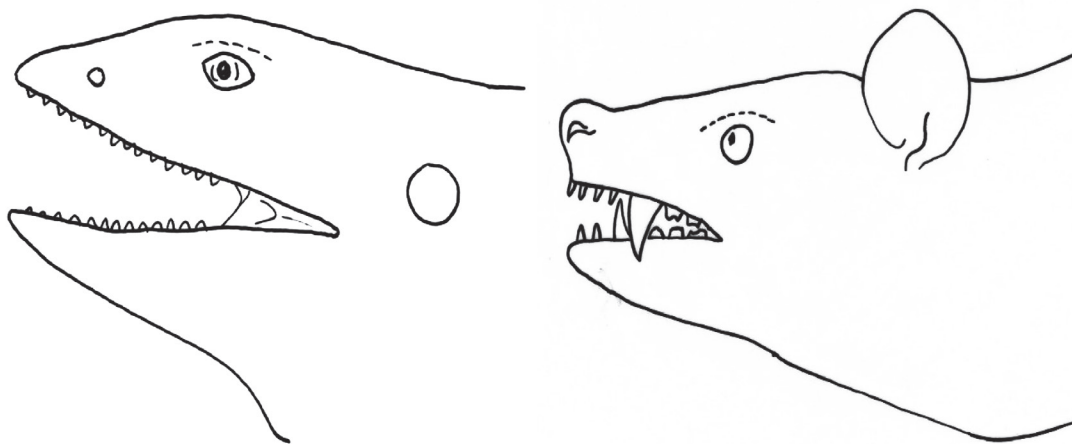

Figure 5. In comparsion with sauropsids, in mammals the oral fissure is narrowed and the corners of the mouth are shifted anteriorly. Cheeks and lips allow chewing while the mouth is closed.

This necessary anchorage was provided by implanting them in deep sockets in the jawbones (thecodont). The teeth became differentiated into separate functional units (heterodonty), with a large canine for puncturing and tearing and a series of postcanine teeth for cutting the prey into smaller particles. The postcanines also evolved grinding functions, and overall multi-cusped teeth began to fit into one another accurately, interlocking with their counterparts on the opposed jaw. Double roots arose to withstand lateral forces during mastication. The occlusion improved over time, and was very precise in the rather complicated 'tribosphenic' dentition of therians. Occluding edges and surfaces of upper and lower molars combined shearing and chewing. The accurate fitting in this form-function complex would be destroyed if one of the complementary teeth were replaced. Thus arose a selective force not to replace molars, although possibly diphyodonty (only two generations of teeth) had already evolved. A relationship between only one or no tooth replacement, determinate growth and lactation is worth a discussion in its own right.

(7) Initiated by chewing motions to fracture prey, the jaw mechanics and masticatory apparatus were reorganised. In the course of evolution, the jaw muscles shifted and found new attachment sites on the skull and on the jaw. The primary jaw muscle divided into the masseter and temporalis muscles. Both inserted on the dentale, which gradually enlarged, while the postdentary bones shrank. The braincase and the dentary bone expanded for completely different reasons, but finally this led to direct contact between the upwardly extended dentale and the squamosum. Though both are dermal bones, an articulation surface could be created between them via secondary cartilage as a synovial joint (Anthwal et al. 2013). From the beginning, this attachment must have been advantageous, so that a new articulation could arise just lateral to the plesiomorphic endochondral quadrate-articular joint. During food processing, the different motions could be performed by one or the other jaw joint. The fossil record documents a progressive emphasis of the squamosal-dentary joint, indicating that it adopted most of the functions. This might have constrained further evolutionary transformations, so that the squamosal-dentary joint repeatedly and in parallel to the ancestral line of crown-mammals replaced the double articulation between skull and jaw. The existing demands of the quadrate and articular in their second function (sound transmission) could have selectively promoted the joint replacement, and otherwise might have hindered a reversal back to a quadrate-articular jaw joint. In the end, the dentaries took over all jaw functions, and the bones of the primary jaw joint were co-opted for hearing.

(8) 'Changes in the jaw joint are so closely associated with the development of the mammalian middle ear that it is hardly possible to discuss one without considering the other' (Ungar 2010: 95). Early in the ancestral line of mammals, the quadrate was in direct contact with the stapes (see †*Probainognathus* above). The joint bones also functioned in transmitting ground-borne vibrations to the inner ear. Hand-in-hand with this, the secondary jaw joint was optimised to take over the various functions of double-jointed jaws, and the bones of the primary jaw joint were completely detached. Freed from their functions in the feeding apparatus, the articular and quadrate (now called malleus and incus) shrank in size, and their flexibility was increased. (Also detached, the prearticular became included in the malleus. It forms a relatively large anterior process in monotremes.) The transmission of airborne sounds improved in the chain with the stapes in the middle ear, and a shift towards hearing in a higher frequency range was possible. In connection with the detachment of the articular, the angular bone supporting the tympanic membrane also became released from the lower jaw and formed the tympanic ring. Thus, the mammalian ear apparatus to transmit vibrations from the tympanic membrane via three auditory ossicles to the oval window of the inner ear was complete.

(9) The arguments for a mainly nocturnal mode of life in ancestral mammals over millions of years mostly come from insights about their sensory organs. In early mammalian evolution, olfaction was emphasised in the search for food, and aided in nocturnal activities. With the transformations described above, the sense of hearing was enhanced, allowing small animals to be hunted in the dark (Hülsmann & von Wahlert 1972). The elongation of the cochlear duct correlated with an extension in the hearing range and in frequency discrimination. Novel flexible pinnae (echidnas have remnants) and the sensitivity to higher frequencies improved the acoustic location of active arthropods. The tactile sense became well developed, particularly due to long and highly moveable facial whiskers actively used during thigmotaxis, locomotion, exploration and predation (Anjum et al. 2006). By integrating information from sound, smell and touch, the animals could be agile foragers in the dark. 'A keen olfactory sense would also warn of predators close by, while permitting the animal to follow its own scented trail system' (Geist 1972: 4). The importance of chemical communication in mammals is in accord with a primarily nocturnal lifestyle. In contrast to the mostly diurnal birds, optical signals were irrelevant. Fur colour was grey or brown. ('All cats are grey by night.') Some degenerative changes in photoreception are adaptations to dim light (Gerkema et al. 2013). The

circadian pacemaker system no longer needed input from the parietal eye, so the foramen could be closed (in †*Chiniquodon* spp. it is absent). With the loss of cone photopigments (in parallel with other vertebrates that lived under low light intensities) the colour visual system became dichromatic. This even may have improved the discrimination of colours in dim light (Vorobyev 2006). Further adaptations were larger eyes and pupil and a high ratio of rods with respect to cones (Gerkema et al. 2013, and references therein). In correlation with the developing sensory organs, the forebrain enlarged and the neocortex expanded. 'The requirements of nocturnal life would select increasingly for an improvement in learning and memory capacity, and for a better neural mechanism to handle the increased flow of sensory data from olfactory, tactile, and kinesthetic senses' (Geist 1978: 163).

(10) Did the evolution of endothermy force parental care, or was it the other way round? Because of the way the tubular mammary glands are associated with hair follicles, it can be deduced that the evolution of hair – and therewith endothermy – preceded lactation. Therefore, against the idea that enhanced parental care was the driving force for the evolution of endothermy in mammals (Farmer 2000, Koteja 2000), the reversed scenario is preferable. It appears that the process comprised several steps, beginning with already endothermic species that laid their eggs into substrates with saturated humidity, and had juveniles that fended for themselves. Like the sauropsids, their eggs had probably had parchment-like shells, and still had to absorb moisture from the surroundings. In a next step, the clutch could have been laid in the occupied cavity or burrow to guard it, which would have enhanced the survival of developing eggs. Another advantage was when the mother protected the eggs from drought by moistening them with water transported in wet hair (adopted from Haldane 1965) and later or directly with secretions of apocrine sweat glands (Oftedal 2012). This was a gain in function for these glands, so that some of them on the ventral side of the body were selected to provide water to the eggs. Egg survival could also be enhanced if the fluid was enriched with antimicrobial or other substances. Eventually, these secretions evolved into 'milk' as nutrients for offspring, and the glands that provided it into mammary glands. But this happened in concert with incubation of the eggs, perhaps initiated by the contact of the mother to the eggs for watering.

The mortality of developing embryos could be even further reduced by brooding. The hatched young could at that point be classified as nidifugous. At this stage, hunting efforts must have remained unchanged. The next step could have been an extension of the contact with the mother, perhaps to be warmed, reducing thermoregulatory costs. This indicates repeated returns of mother and offspring to the shared breeding burrow. In this close contact, the sympathetic innervated apocrine glands of the mother could have been stimulated, and the young licking the liquid secretion could have obtained valuable
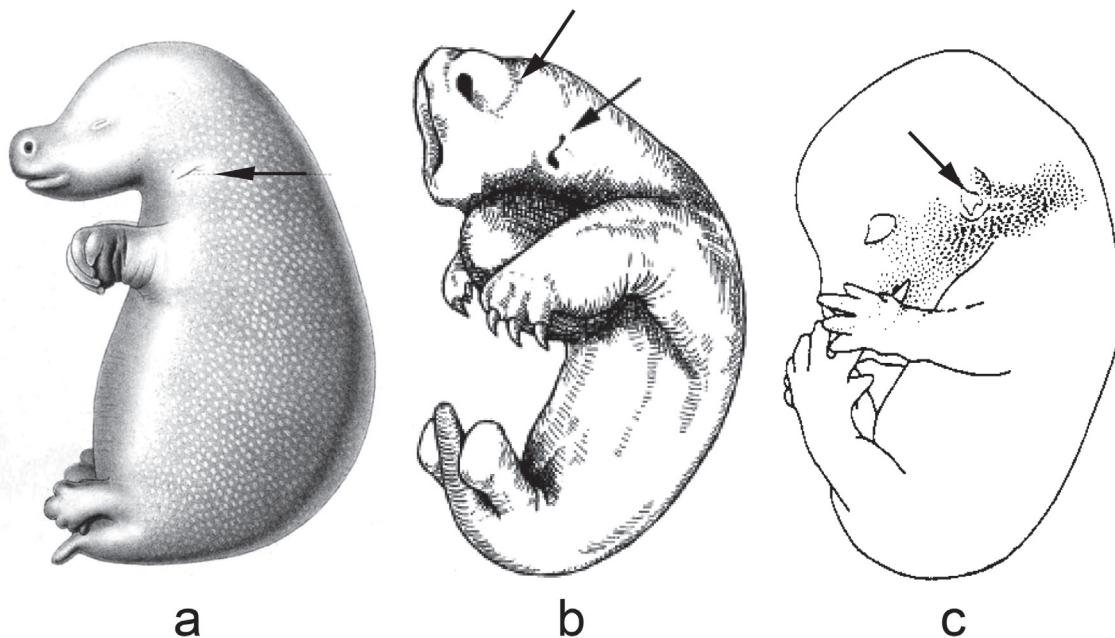

Figure 6. Comparison of neonates of the three major groups of Mammalia: (**a**) the monotreme *Tachyglossus aculeatus* (after Semon 1894); (**b**) the marsupial *Dasyurus viverrinus* (after Hill & Hill 1955); (**c**) the placental *Tupaia javanica* (after Maier 1999). Notice the strongly developed forelimbs and the open nose in the first two species. Arrows point to closed eye or external ears. The stippled area in c marks the posterior anlagen of the facial muscles in the ear region. *D*rawings not to scale.

substances from her like electrolytes, or lysozyme for defence against infections. At this point, evolution would have been canalised to produce specialised glands derived from the sweat glands, producing a more substantial secretion. Antimicrobial compounds against pathogenic microorganisms were recruited as an energy source (Messer & Urashima 2002). The transfer of nutrition to the young grew increasingly important. In coevolution with enzymatic changes for production and digestion (ancestors were lactose-intolerant), this milk was enriched with unique sugars (lactose) and proteins (casein). A novelty of mammals is also α-lactalbumin, which is a component of the enzyme lactosynthetase derived from lysozyme. A high concentration of lactose in the milk is apomorphic for placentals. The sugar appears in low amounts in monotremes and marsupials, and the corresponding low intestinal lactase activity only allows for a slow rate of lactose digestion (Messer & Urashima 2002, Jackson 2003).

In a sketch on the evolution of lactation Haldane (1965) thought about how the sucking by the young and the presentation of the underside by the adult to be sucked could have evolved. He suggested 'that it began by water transport to the young by wet hairs in a hot dry climate' (p. 47) to offer drink to their offspring. Later this was substituted by a watery fluid from the sweat glands, and even later nutritive substances were added and mammary glands arose.

Though feeding the juveniles required a higher rate of food acquisition for the mother, it increased her fitness by reducing mortality among her offspring. Finally, the young were nidicolous and nourished purely on nutrient-rich milk. That meant their ontogeny could be transformed dramatically; egg size and amount of yolk diminished. As we see it in extant Mammalia, they hatched from the egg in a premature stage – naked, with closed eyes and ears and retarded dentition (Fig. 6). The nakedness improved heat transmission in direct contact with the mother. Only the forelimbs with claws were functional, in order to drag the hatchling through the mother's fur. To find the mammary patch, which was made up of diffuse gland openings and hairs on the belly, the hatchling's olfactory sense was also fully developed. For cutting the leathery shell, they also retained a median egg tooth on the premaxillary sutur and a caruncle. This true tooth is surely not an apomorphy of monotremes, as ontogenetic relics of homologous teeth and caruncles have also been found in various marsupial species (Hill & de Beer 1950).

(11) Offspring survival was enhanced by lactation and intense maternal care. This care stimulated the progressive evolution of the telencephalon, which in positive feedback allowed a higher level of social behavior and learning. A novelty in mammals is also that growth is determinate. Infants grow rapidly to the mature adult size. Determinate growth might be stated in extinct species if many adult fossils of a species are present which are of the same size (reported for †*Morganucodon*). Many changes also took place in other organ systems, e.g. the alimentary tract or the kidney. Nitrogenous metabolic waste products were converted mainly into urea, which is soluble in water (and blood), but requires a lot of water to be excreted. Ancestral mammals therefore developed the novel loop of Henle in the kidney to reabsorb much of it. The conversion to urea as the chief nitrogenous substance might have been energetically advantageous. Otherwise, it was ecologically licensed in an environment where water was not limited. However, it was one physiological precondition for the evolution of viviparity in Theria, where it could easily be exchanged across the placenta. In egg-laying mammals, uric acid was retained as a waste product during development, and stored in the allantois.

From the stemspecies pattern of Crown-Mammalia to monotremes and therians

The stemspecies pattern comprises all the characters of the last common species of extant mammals. Several of these were described in the analysis above. They evolved in an interrelated fashion with key innovations like endothermy, chewing, vigorous exercise, incubation and lactation in a nest. Most of the characters of the stemspecies remained plesiomorphic. Here I will only mention the heavily yolked eggs, their meroblastic discoidal cleavage, the uptake of uterine secretions by the yolk-sac of the embryo through the shell membrane, and the existence of a cloaca. Because of this mosaic of characters, this species can be loosely described as an 'egg-laying, wool-milk beast'. Starting from this character mosaic, the stemspecies patterns of Monotremata as well as of Theria must be derived.

A few apomorphies that accumulated in the ancestral line of Crown-Monotremata were mentioned in the first chapter. Remarkable are the electro-receptors located on the horny beak that are innervated by the trigeminal nerve, which helped them to detect prey in moist substrates or water. Six large pairs of autosomes – along with several smaller ones and multiple sex chromosomes – are characteristic (McMillan et al. 2007). A few other derived characters are shown by the skull. Of particular interest is that the secondary sidewall of the braincase is largely formed by the anterior dermal lamina of the prootic bone (lamina obturans). The alisphenoid is greatly reduced

in size (Starck 1978). By the same formation of this sidewall, e.g. †Multituberculata could be representatives of the stem-lineage of Monotremata. It differs from crown-therians, where the sidewall of the cranial cavity was completed by expansion of the squamosal and the endochondral alisphenoid (= epipterygoid, that traces back to the palatoquadratum of an early vertebrate jaw and lost an earlier function when the mammalian skull became akinetic). The plesiomorphic condition appears to be represented by the stem-mammalian †*Morganucodon* and the stem-therian †*Vincelestes neuquenianus,* which possessed both a large alisphenoid and a prominent anterior lamina. It can be deduced that in the ancestral line towards crown-monotremes the lamina was enlarged and the alisphenoid became vestigial, whereas within therians the alisphenoid expanded and finally completely replaced the anterior lamina (Hopson & Rougier 1993). As a remnant of this lamina was detected in †*Prokennalestes trofimovi*, which is regarded as a stem-placentalian, the complete reduction of this bone must have occurred independently in marsupials and placentals after the branching of †*Prokennalestes* (Wible et al. 2001).

As described above, monotremes have a rather sprawling posture. So the 'typical' mammalian upright stance – with the all legs turned directly beneath the body – appears to have been reached first in the therian line, possibly independently in some extinct lineages. The elbows finally point backward and the knees forward, while the radius and distal end of the ulna became crossed in pronation position. This significantly changed locomotion, and improved efficiency in running, the more so as limb muscles no longer had to support the body. The animal could remain on standing on its legs with little difficulty, and the joints and legs took over cushioning functions. The complex of pectoral girdle and forelimb muscles was profoundly restructured and reoriented, while the interclavicle and procoracoid were lost, the scapula reshaped. It obtained a new part (the supraspinatous fossa) and a big spine for the muscles. Convincing evidence for postures comes from taphonomy of specimens preserved in lacustrine sediments. Animals in sprawling postures are generally embedded in the dorso-ventral position, whereas those in an erect posture are preserved in a lateral position. The passive positions of skeletons of multituberculates and stem-therians (†*Akidolestes cifellii,* †*Maotherium sinensis,* †*Zhangheotherium quinquecuspidens*) were dorso-ventral, indicating a sprawling stance, whereas †*Sinodelphys szalayi* (stem-marsupial) and †*Eomaia scansoria* (stem-placental) having parasagittal limbs were lying on their flanks (Kielan-Jaworowska & Hurum 2006). The upright gait of therians – with the limbs rotated under the body – can be discussed regarding their supposed semi-arboreal mode of life. Inferred from digit morphology, †*Sinodelphys* and †*Eomaia* were mainly climbing with their claws (Kümmel 2009).

Besides the braincase structure and the apomorphies mentioned in the first chapter, several further novelties arose in the ancestral line to the stemspecies of Crown-Theria, which by comparison are hypothesised as synapomorphic for Marsupialia and Placentalia. Two embryonal milk lines were generated along the underside between the bases of fore and hind limbs, giving rise to the mammary glands and several nipples to suckle multiple newborns per litter. As development starts in the uterus and the embryo begins to acquire nutrition from secretions of uterine glands in monotremes, the same can be assumed for the stemspecies of crown-mammals in the first step to viviparity. Due to a longer egg retention in the ancestral line to therians the next step then is very likely to have been ovoviviparity, demonstrated by a transitory, thin eggshell membrane of the marsupial fetus as an ontogenetic recapitulation. One advantage of being ovoviviparous is that eggs no longer cooled down when the female animal left the nest to feed. It could 'incubate its own eggs within the oviduct' (Geist 1972: 11).

Constituted by two completely different circulatory systems, the yolk-sac placenta characteristic for marsupials and the chorioallantoic placenta in placentals cannot be derived from either one or the other. Despite these alternatives, most likely is a placentation in the stemspecies of therians. We cannot rule out that this ancestral species might have simultaneously had a yolk-sac placenta and a chorioallantoic placenta, from which one daughter lineage (Marsupialia) retained the yolk-sac placenta (or primarily both, as suggested by Freyer et al. 2003) and the other (Placentalia) the chorioallantoic placenta. Some placentals develop a transitory yolk-sac placenta in early pregnancy that later is completely replaced by the chorioallantoic placenta. This recapitulation is compatible with both placenta types in the stemspecies of therians, as well as with just a yolk-sac placenta.

It is likely that with absorption of uterine gland secretions, lactation and hatching of juveniles in an earlier stage of development in ancestral Mammalia, the amount of yolk and egg size were reduced considerably. In correlation with placentotrophy, this reduction proceeded in the lineage to Theria to an egg-diameter of about one third of a millimeter, allowing cleavage to become secondarily holoblastic. We can reconstruct that the stemspecies of crown-therians, after a short gestation period, gave birth to tiny young. Like marsupials, the newborns were at a very early stage of development, but able to cling to their mothers' fur and crawl with well-developed forelimbs to the nipples. (Quite likely a pouch was missing, corresponding to the first branches

of marsupials to *Didelphis* or *Caenolestes.*) After seizing a nipple, they anchored according to the push-button principle by narrowing the oral opening and fusing the lips. This permanent anchoring mechanism was essential, because in this stage the primary jaw joint had not yet transformed to middle ear bones, although it was not functional as a joint. We observe this situation only in marsupials, but it must also be assumed for the stemspecies of therians. Otherwise, the reversion to a primary jaw joint in marsupial neonates must be shown to be an adaptational process. I entirely agree with Szalay (1994: 52): 'It appears nearly certain that the primitive marsupial condition of development and reproduction, birth, and post-neonate nipple-attachment and growth of an "embryo" was closely similar to that which was antecedent to the eutherian common ancestor.' The same holds for the recapitulatory development of the double jaw joint, and detachment of middle ear bones after birth.

Fixed in a permanent grip on a nipple, the young were carried about by the mother for an extended period. As the evolution of 'clinging young' is typical in arboricolous mammals – and since adaptations for an arboreal life are postulated for several extinct species of the therian stem-lineage (Kümmel 2009) – a partial or semi-arboreal mode of life can be assumed for the stemspecies of Theria. In coevolution with the nipples in the adult, the newborns sucked instead of licking or slurping milk. The new facial musculature in mammals that developed from muscles in the neck and throat region (Fig. 6c) was a preadaptation that served this purpose. Suction was allowed by an early closure of the secondary palate during development, prolonged by the soft palate (velum), and an advanced developed oro-muscular apparatus – including the tongue – before birth (Smith 2006). On the other hand, milk consumption presupposing that this structural complex was already in existence.

From the stemspecies pattern of Crown-Theria to marsupials and placental mammals

We believe Marsupialia retained plesiomorphic characters such as a thin shell membrane around the fertilised egg that disintegrates at a late stage, a yolk-sac placenta, and epipubic bones – also existing in monotremes – that are an integral part of the abdominal wall and independent of a pouch. We assume that these characters first arose in relation to locomotion, and then became adaptive to maternal marsupials carrying several developing young attached to the nipples. However, we still miss detailed investigations on the muscle-apparatus involved. Only two conspicuous apomorphic Marsupialia characters need be mentioned here: the dentary has an inwards-inflected angular process, and the fact that one generation of dentition is suppressed in all teeth except for the last premolar, which is replaced by a permanent tooth. The functional relevance of these features remains unclear. A similar medial inflection of the angular process occurred independently in some cretaceous stem-placentals (Sánchez-Villagra & Smith 1997), but is missing in the stem-marsupial †*Sinodelphys szalayi* (Luo et al. 2003).

In the lineage to Crown-Placentalia, epipubic bones were lost, and were only present in certain representatives of the stem-lineage (e.g. †*Barunlestes butleri, †Eomaia scansoria*, †*Ukhaatherium nessovi, †Zalambdalestes lechei)*. It would be practical if this loss – perhaps correlated with an enhancement of the angle at which the two sides of the pelvic girdle meet ventrally – possibly indicated the replacement of the ancestral, marsupial-similar reproductive mode by young birthed after a longer gestation period (Novacek et al. 1997). The shell membrane and nutrition by uterine secretion were also lost. The yolk-sac placenta was reduced and replaced, although it is recapitulated. During a transitional period in the ancestral line of placental mammals, both a yolk-sac placenta and a chorioallantoic placenta must have been involved in respiration and metabolic exchange before the chorioallantoic placenta assumed all related functions. A further potent trophoblast (Lillegraven 1985) and different additional mechanisms that helped provide an immunological barrier between mother and embryo were pivotal features for prolonging the period of intra-uterine development. They allowed young that were more fully developed, even though eyes and ears remained closed (Fig. 6c). This extended the vulnerable gestation period for the foraging mother. From birth on, however, infants could be temporarily left behind in a nest. The production of more advanced young is a secondary specialisation (Hopson 1973).

In ecological terms, nesting in burrows or holes during the period of lactation was a significant evolutionary step in this lineage. It is not unlikely that it was related to a change from a more arboreal to a more terrestrial lifestyle, possibly within a complex, structured habitat. The animals involved must have been small, which is in accord with the fossil record. A convincing argument that the stemspecies of crown-placentals was nidicolous is a recapitulatory development in mammals that are nidifugous (guinea pigs, artiodactyls or cetaceans) or have clinging young (primates). In these species, the eyes and ears are open at birth, but their foetuses undergo transitory eye and ear closures within the uterus just like their nidicolous ancestors (Portmann 1976). It is

thought that this nidicolous behaviour required a complex reorganisation in the behaviour of mother and infant, as well as in their communication system. One could term it 'secondary nidicolous', emphasising that Mammalia were primarily nidicolous – as discussed above – and then developed clinging young in the lineage to Theria. This was perpetuated in the Marsupialia, and for a certain period in the ancestral line of Placentalia, before the line evolved 'secondary nestlings'. – The stemspecies of crown-placentals was reconstructed very realistically not only in the skeleton and the dentition, but also in brain, uterus and sperms by O'Leary et al. (2013). This example should act as a precedent. One conspicuous novelty in the brain of placental mammals is the corpus callosum, which connects the cerebral hemispheres.

Topics in the discussion on anagenesis

(1) **Special characters** in a group are recognized. The focus is thereby not on their relevance as apomorphies that allow us to establish monophyletic relationships within the group, but on how they are integrated in the existing construction. All species have a mosaic of apo- and plesiomorphic features, and these must be harmonious. Individual changes must also be advantageous with respect to the preceding structural complex. Labelling taxa as 'primitive' or 'derived' appears ineradicable, and not only in more popular literature – although such terms should be restricted to characters. Monotremes, for instance, are not 'primitive' mammals, and do not at all resemble species on the ancestral therian lineage. Instead, they represent the first branch of extant mammal taxa, and possess plesiomorphic characters like a cloaca, shoulder girdle with interclavicle and two coracoids, a heart with a distinct sinus venosus, a venom gland opening in a spur in the ankle region and the incubation of eggs. Apomorphic characters include horny snouts without teeth in the adult, electro-reception, and a relatively large body compared with ancestral species. Modern monotremes furthermore exhibit very special attributes in morphology and ecological behaviour at the species level. By the way, it is worth a mention here that the crown-monotremes are much younger than the crown-groups of marsupials or placentals (Fig. 7).

(2) The **sequence** of evolutionary events in a lineage has to be established using different sources of information. The best source for postulating chronological orders is features documented in fossil remnants, if an extinct species can be placed in a cladogram (Fig. 3). Some indications for the sequence might be derived from ontogeny (in placentals, a yolk-sac placenta preceded the chorioallantoic placenta) and verisimilar functional analyses (some authors suggest a relationship between determinate growth, lactation and diphyodonty).

(3) One must consider evolutionary **transformation series** – including reductions and reversals. Such a series must be subdivided into small steps that were all functional, although the function may have changed more or less during the transformation process. As much as possible, the projected steps should be based on real documents, even if some cautious deductions on intermediates are inevitable. For example, epipubic bones are believed to have evolved as a novelty in Mammalia, and were lost in the ancestral line of crown-placentals. In the evolution of Theria we assume a transition from oviparity to viviparity, and have postulated ovoviviparity as a transitional stage that results from the retention of segmenting eggs in the uterus. A natural next assumption is for a transition from birth at an early stage of development to birth at a more advanced stage in placentals.

(4) The **evolutionary pathways** towards complex structures/apparatuses must be elucidated. A dramatic reorganisation took place in the skull when the primary jaw joint was finally replaced, and its bones became auditory ossicles. It is ambitious to come to a satisfying, functional understanding of this synorganised restructuring, which affected the bones of the jaws and the cranial cavity as well as the masticatory muscles and the middle ear. Remind that all changes had to have a selective advantage over the previous stages. In the passages above, respective occurrences were described one-dimensionally, although they are of course intimately connected, and can actually only be understood within the framework of permanent feedback loops between the different systems. Many questions are not satisfyingly answered. For example, which processes led to an appositional joint between the squamosum and dentale, which assumed a joint function? How did a sound-transmitting apparatus for high frequencies between a primary jaw joint and one middle ear bone (stapes) evolve? What was the advantage of two jaw joints, and how could these multiple functions in the end be fulfilled by one joint – the secondary jaw joint?

(5) A remarkable reshaping in organisms during phylogeny takes place through '**trait substitution**'. This means that a special organ or form-function unit is substituted by a different one, with both existing side by side during a longer transitional period. (The term substitution is also used in describing ontogenetic processes: Schmidt 1966.) There are many examples of this phenomenon. The list includes – the replacement of epidermal scales by fur or the replacement of the primary by the secondary jaw joint in mammals, and replacement of a yolk-sac placenta by the chorioallantoic placenta

in therians. – Adult *Ornithorhynchus anatinus* possess horny grinding plates instead of teeth (like the young), while the fossil †*Obdurodon dicksoni* still had molars. – In the ancestral line of mammals, the musculus depressor mandibulae, which inserts on the articular and in tetrapods is responsible for opening the jaw, was functionally replaced by the new musculus digastricus, which inserts on the dentale (Frick & Starck 1963, Starck 1982). Through this substitution, the articular was freed up, licensing the transformation to an auditory ossicle (the malleus). – The angular (later transformed to the tympanicum) formed the frame for a new eardrum (in contact with the articular). The structure included the ancestral tympanic membrane (communicating with the columella), and later replaced it (Shute 1956). Homologous vestiges of the primary tympanic membrane are present in the dorsal part of the new mammalian eardrum. – Whereas primarily light signals received from the dorsal eye were necessary to regulate circadian rhythms, in the course of mammalian evolution only a chain from the lateral eye retina via the suprachiasmatic nucleus in the hypothalamus influenced the release of melatonin by the pineal gland. That meant the photoreceptors in the pineal complex could wither away, and the parietal foramen could be closed. – When in the evolution of mammals the projections to transmit visual information switched in the thalamus entirely to the telencephalon, the optic tectum could be considerably reduced towards the lamina tecti. – In †*Kayentatherium wellesi* and †*Oligokyphus* spp. 'canines are absent but have been functionally replaced by an enlarged pair of second incisors' (Kemp 2005: 72).

(6) When comparing closely related groups, characters that arose independently are of particular interest. They can be so similar that they might be regarded as homologous, but must be interpreted as **parallelisms** in resolving conflicts in the phylogenetic reconstruction. A frequent occurrence, parallelisms result from a very similar construction inherited from the common ancestor, plus selection forces acting in the same direction. – The descent of the testicle in Marsupialia and within Placentalia appears to be equal. But the testes were independently displaced caudally from the primary
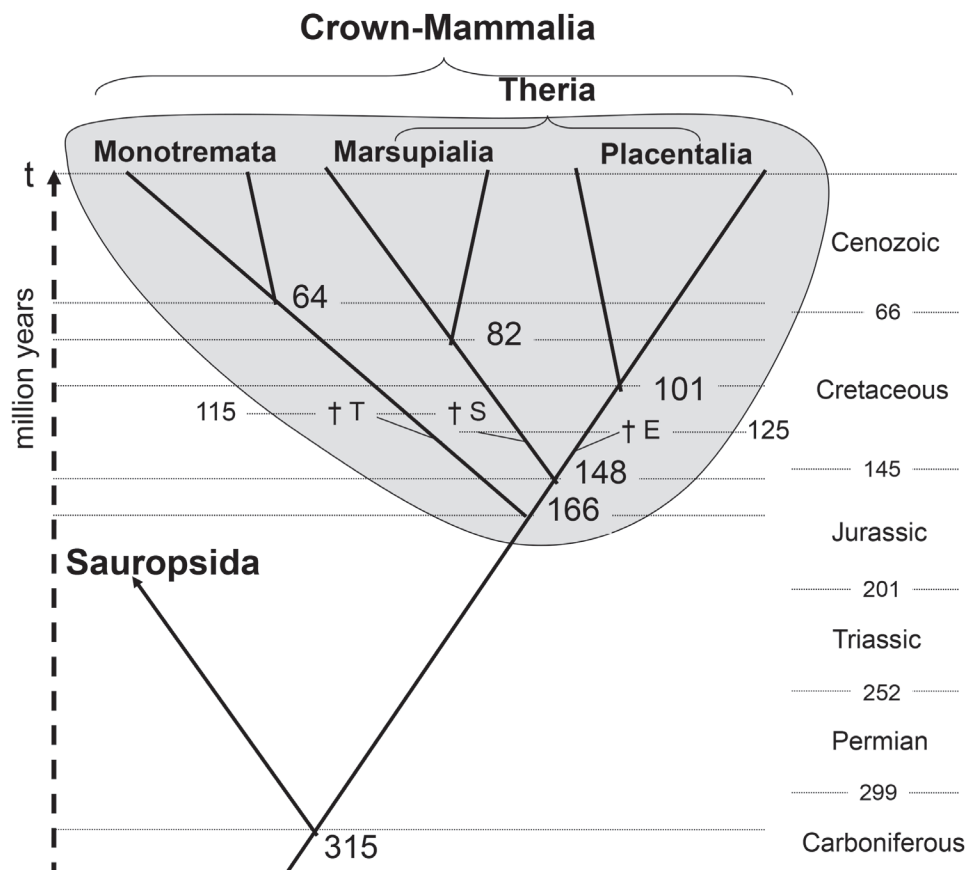

Figure 7. Timescale of estimated origin of the crown-groups of Monotremata, Marsupialia, Placentalia, Theria, Mammalia and Amniota (= Mammalia + Sauropsida) in million years. †E = †*Eomaia scansoria*, †S = †*Sinodelphys szalayi*, T = †*Teinolophos trusleri*. Data for mammal groups from Bininda-Emonds et al. (2007), date for the split into mammals and sauropsids after Reisz & Fröbisch (2014). – By the 160 million years old stem-placental †*Juramaia sinensis* the marsupial–placental split is extended into Middle Jurassic and the monotremes–therians split into Early Jurassic (Luo et al. 2011).

position behind the kidney (where they are still found in monotremes) through the abdominal wall into a scrotum, which is differently positioned with respect to the penis in these groups. It is believed that this descensus evolved due to faster modes of locomotion that culminated in gallops (Frey 1991). Why is this so? During fast locomotion, the constant pressure within the testis required for the unimpaired process of spermiohistogenesis is only guaranteed in an extra-abdominal location. In the primary site within the abdominal cavity, fluctuations of intra-testicular pressure would occur, because the powerful vertebral column flexions and extensions during a gallop cause intense fluctuations of intra-abdominal pressure, affecting the drainage in abdominal veins and impacting on testicular function. The descent of the testes was thus the organismic license for galloping. The parallel evolution of the descensus allows to infer that this effective mode of locomotion also evolved in parallel, and that the stemspecies of therians – and presumably also the stemspecies of placentals – could not gallop.

Apart from parallelisms resulting in the same evolutionary solutions, we often also observe '**alternative adaptations**' in closely related taxa, a phenomenon called 'multiple evolutionary pathways' (Bock 1959). As mentioned above, monotremes and therians used different bones to close the sidewall of the cranial cavity. This dichotomy allows to conclude that in the last stemspecies of these sister-groups, the sidewall still had unossified areas like those found in †*Morganucodon oehleri*. The alternative solutions of completion of the side wall of the skull in the sister lineages is a nice example of the opportunistic character of evolutionary processes. Alternative adaptations thus demonstrate the degree of freedom in evolution. – In addition to the primary jaw joint a contact between a bone of the lower jaw and the squamosal was achieved, apparently to stabilise the jaw articulation. In †*Probainognathus* and related taxa this happened with the surangular behind the dentary (Luo & Crompton 1994, Kemp 2005), whereas in the ancestral line of mammals the squamosal-dentary articulation was established. These are different solutions, even if the surangular-squamosal contact might have been a forerunner and in a later step was replaced by a dentary-squamosal joint, as it was suggested by palaeontologists (Kemp 2005, Benton 2014). – The stemspecies of Theria had 8 postcanines, which were reduced in different ways to 7 in the crown-groups of Marsupialia and Placentalia, respectively (see fig. 3, characters 19 and 23).

(7) A serious problem in understanding evolution is the **emergence of new traits**. Here I do not mean those novelties (like auditory ossicles) that result from a transformation of already existing structures. To understand such changes of function and structure

by gradual evolution is hard enough. But how could absolutely new structures like hair or sweat glands arise? Ernst Mayr thought that incipient structures originate as pleiotropic by-products, upon which selection can act. 'Yet the problem remains of how to push a structure over the threshold where it has a selective advantage' (Mayr 1997: 95). To think about incipient structures like hairs or tubular glands, one must first determine the structure of skin in the stemspecies of Amniota. The usual view is that the corneal epithelium of the skin in this species was thickened, and made up of multiple layers of dead cells entirely filled with keratin to protect the animal against water loss in a terrestrial environment. A kind of epidermal scale like those found in Sauropsida might also have existed to protect against abrasion. But what is essential is whether the skin retained a glandular quality comparable to that in amphibians from the stemspecies of tetrapods, as suggested by Dhouailly (2009), which then would have been lost first in the ancestral line of sauropsids. Well-preserved integument impressions from the huge early stem-lineage mammal †*Estemmenosuchus uralensis* (Middle Permian) revealing a smooth skin do not help answer this question for different reasons. Even if the amniote stemspecies skin retained the potential to produce gland secretions, when they appeared the precursors of hairs or tubular glands must have been useful from the beginning, perhaps in addition to scales. For hair, an early function as a holocrine gland is conceivable (Fig. 4). Or 'hair first arose as a 'wick' that served to draw the oily secretion out from the gland and onto the external skin surface' (Wagner 2014: 306). Stenn et al. (2008) indicated possible intermediates with initial wick function.

(8) Based on the cladistic analysis within a certain range of characters, different **anagenetic stages** can be ascertained between the three main groups of Mammalia using different benchmarks (Sudhaus & Rehfeld 1992: 132).

- First, the number of apomorphies in each lineage can be compared. In the previous text and legend of fig. 3, ca. 13 apomorphies were listed for Monotremata. For the other groups, around 19 Theria apomorphies have to be added. Marsupialia then have about 26 apomorphies, while Placentalia have ca. 33. Lots of further apomorphic characters could be added without changing the proportions.
- Second, the complexity of apomorphic characters can be evaluated. This is problematic for instance if we compare apomorphic features for marsupials with those of placentals.
- Third, the number of retained plesiomorphies in the groups can be estimated.
- Fourth, the rate of divergence with respect to number of species and different 'types' can be compared, although

the latter is hard to delimit. Montremata includes 3–5 species in two 'morphotypes', Marsupialia 331 species in 7 order-taxa (Bennett 2012) and Placentalia about 4370 species in 18 order-taxa (Archibald 2001).
• Finally, the ages of the crown-groups can be compared. Often taxa that represent an early branch are called 'primitive'. The first branch in mammals is the Pan-Monotremata. But the Crown-Monotremata is the youngest group, followed by Crown-Marsupialia. Crown-Placentalia is the oldest (Fig. 7).
• Taking the number of apomorphies and the diversity of species in our time frame as criteria for anagenetic stages, the ranking would be conform with the general view: Monotremata < Marsupialia < Placentalia.

Towards a deeper understanding of the history of organismic diversity

The aim of an analysis in evolutionary history is to gain an understanding of different ways transformations happen in phylogeny, and to find historical narrative explanations (Bock 2000). The first task is to argue on hypotheses for phylogenetic relationships among taxa by using a cladogram to illustrate said argument. This was what Peter Ax was endeavoring to do when he wrote his influential books. A well-established cladogram is the backbone for all discussions and statements on phylogeny, evolutionary morphology, evolutionary ecology, coevolution or historical biogeography. This should be a matter of course, though there were deficits in the literature on mammals until the fairly recent past. The identification of anagenetic events in ancestral lines – and in part determining their succession over time – is a by-product of a careful cladistic analysis based on extant and fossil species. The same holds for the ordering of apomorphic features in a stem species on any branching point of the cladogram. When many fossils from the stem-lineage of mammals can be integrated in the cladogram, it sheds light on the alterations in bauplan from the stem species of Amniota to that of Mammalia (Fig. 3). In constructive additive and regressive typogenesis, new characters were acquired, others were transformed, and yet others were either reduced or lost. This gradually led to a reorganisation of the organisms in a lineage.

The relevant plesiomorphies of the stemspecies pattern must be reconstructed by ingroup comparison. A significant part of the work in the field of phylogenetics revolves around trying to make clear-cut statements about stemspecies of groups, particularly of crown-groups. If there are two succeeding stemspecies in an ancestral line, e.g. of therians, the differences between the patterns must

be elucidated. There are several primary questions that have to be answered. What was new in the more recent species? What was retained? And how do plesiomorphic and apomorphic elements interlock to form a properly functional apparatus? To bridge the gap between these patterns, recognised transformations in different organ systems and in behaviour must then be dissected into successive anagenetic steps, and each such step must attempt to show an adaptive process. The entire analysis also has to be conducted in a functional-constructive and ecological context. If fossil documents are not available, the sequence of changes might be elucidated in a fragmentary way on functional and other feasible reasons. Needless to say, all statements remain hypotheses that must be rechecked over and over and – if indicated by new material – revised.

Just in a group like mammals with a satisfying fossil record with about 4,000 fossil species, it is exciting to trace the gradual changes in the organs and in the entire organisms. A little alteration in one element of a well-proven structure or function chain affects separate features, and at some point leads to an innovation, which in turn has a feedback impact on other characters. This was shown above for the descensus testis, which taken alone appears disadvantageous, but is caused by a selectively advantageous faster mode of locomotion (Frey 1991). It is always a compromise. Through the steady process of coadaptation, the interlocking of apomorphic and plesiomorphic parts in whole organisms, in organs and in the genome (designated 'heterobathmy' by Takhtajan 1959) describes the general course of evolution. To understand the evolution of morphologies, we have to find explanations for the sequence of alterations, and uncover why certain features are retained. Plesiomorphies have to be considered, because they also demonstrate organismic licenses or preadaptations for evolutionary innovations. Through phylogenetic substitution, the functional role of an organ could be taken over by a completely different one, with both operating simultaneously during a transitional period (e.g. the jaw joints). When an older structure loses its main function in this way, selection either promotes an improvement of an additional function (primary jaw joint had auditory function), or the structure is no longer required and undergoes reduction (some bones of the lower jaw finally disappeared). Alternatively, it is freed up to assume a new function, as we saw with the epipterygoid changing to the alisphenoid. When all of the masseter attachments migrated forwards to the dentary, the angular was left free, and could be transformed into the tympanicum.

A fundamental reconstruction occurred in the pectoral girdle when the forelimbs migrated beneath the body and gait changed. The adductor between the coracoid

and humerus (the musculus supracoracoideus), which supported the pectoral region in the sprawling posture, became superfluous in this function. As a result, the attachments of this muscle shifted to the scapula, the muscle divided (into supraspinatus and infraspinatus) and changed function to stabilise the shoulder joint (Starck 1979). The coracoids were no longer really required, and were reduced in therians. In monotremes, which retained sprawling forelimbs, the plesiomorphic supracoracoideus and both coracoids still exist.

A significant aspect of typogenesis is the realisation of synorganised complexes. Gain of function and change of function in structures plays a role in that process, combining different pieces and getting them to act together to fulfill a novel biological role. This was shown for mammalian jaw articulation under point (7) of the evolutionary scenario chapter. 'This secondary jaw articulation is an almost ideal illustration of the formation of a new structure as a result of a coming-together of two structures formed for entirely independent reasons' (Mayr 1997: 108).

Limitations that have to be uncovered exist in every organismic construction. Severe limitations can preclude adaptations for a special mode of life. An often-cited example is the fact that no marsupial (not even an extinct species) has wings like bats or flippers like dolphins. That is because the forelimbs and special shoulder girdle of neonate marsupials must be developed sufficiently to climb and crawl from the birth canal to a nipple. Because of this demand made by ontogeny, the forelimb evolution is rather constrained (Kelly 2011). – A 'constructional fault' in Marsupialia is the female reproductive system, where the ureters pass between the lateral vaginae and the transitory birth canal or median vagina to open into the ventral bladder. A large single median uterus like that found in placentals could not possibly evolve, because it would pinch the ureters. 'This may be one of the reasons that marsupial offspring are so remarkably small at birth' (Renfree 1993: 5). The existing immunological problems should not be forgotten. – The birth of underdeveloped young has been a major barrier to marsupials in the evolution of water-living life-forms like sirenians or cetaceans. On the other hand, a semi-aquatic lifestyle is possible with special adaptations. In the water opossum (*Chironectes minimus*) the young are born and enter the pouch in a nest. During a dive, the pouch can be kept watertight by closing a sphincter muscle, retaining an air bubble, while the young can tolerate low oxygen levels for some time. – Limitations might explain why certain evolutionary events have not occurred in a species-rich group. They could be surmounted by trait substitutions.

The other side of the coin is that the organismic construction provided morpho-functional preadaptations for future development. These preadaptations allowed changes in behaviour or physiology, which are general pacesetters in selection pressure to change structures. Chewing food was such a key invention in the phylogeny of mammals, and it had major consequences in the skull, teeth, musculature and nervous system. The formation of a masseter and of cuspid teeth were preadaptations for the accurate occlusion of opposed cheek teeth, needing a fine control over the movements of the jaw. – In placentals, the ability of the trophoblast to block immunological attacks on the embryo provided the license for birth at an advanced stage. – Among other factors, an efficient placenta depended on the conversion of nitrogenous waste products to urea. – A syndrome of features associated with endothermy was also preadaptive for animals in undertaking a shift to a new ecological zone, for example having their active phase at lower temperatures during nightfall or in the night. – Lactation and modes of reproduction had an ecological impact, even though the ecological zones for marsupials or placentals cannot be characterised. The stemspecies of crown-monotremes were semi-aquatic, as is indicated by electro-sensory capability and members of the stem-lineage. This means that the stemspecies of echidnas reinvaded terrestrial habitats (Phillips et al. 2009).

Special insights can be gained by studying parallelisms, underlying synapomorphies and convergences. 'Several mammalian features (e.g. dentary-squamosal jaw articulation, loss of alternate tooth replacement, complex occlusion, and double-routed cheek teeth) are known to have evolved independently in several phyletic lines' (Crompton & Jenkins 1973: 137). Especially the parallel evolution of a secondary jaw joint in the stem-lineage of mammals has been frequently discussed (Frick & Starck 1963). The independent occurrence of features showing a high degree of similarity illustrates accordant selective forces, though their origins in similar initial structures might have some channeling effect. Differences in solutions like the formation of the secondary sidewall in the Monotremata and Theria braincase illustrate the opportunism of evolution, and how flexible it can be. The uniqueness of one or the other of these solutions is even confirmed, as it has been demonstrated that there were different ways to solve the problem. If different evolutionary solutions exist, a sort of benchmarking can be conducted to assess the advantages and the weaknesses of one version in comparison to the other.

Acknowledgment

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Peter Ax's views on homology
– a comparison with Remane and Hennig

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Abstract

Peter Ax's major theoretical contribution, the book 'Das Phylogenetische System' (The phylogenetic system) (1984; English 1987) is compared with Remane's 'Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie der und Phylogenetik' (The foundations of the natural system, of comparative anatomy and of phylogenetics) published in 1952, and Hennig's (1950) 'Grundzüge einer Theorie der phylogenetischen Systematik' (Introduction to the theory of phylogenetic systematics). While Hennig and Ax's goal was plead the case for a 'phylogenetic system', Remane's objective was to describe how to establish a 'natural system'. For Remane, homology is the core of the 'natural system'. His 'systematic type' is based on the distribution of homologous correspondences, and his 'homology criteria' are still in use today. In Hennig's book (1950), homology is only mentioned peripherally. Later (1953), he would emphasize the importance of distinguishing synapomorphies from symplesiomorphies, which both constitute homologies. Ax very much followed Willi Hennig's view, and certainly helped to clarify how phylogenetic systematics should be applied. He referred to Remane's 'homology criteria' too, but rejected the term 'criterion' on the grounds that what Remane described were just 'pointers' on how to look for similarity or correspondences. In doing so, however, he may have failed to have acknowledged sufficiently that identifying 'correspondence/ sameness' is indeed an independent empirical method.

Keywords homology criteria | synapomorphy | typology | convergence | Ockham's razor

Peter Ax, Adolf Remane, Willi Hennig

Most zoologists and systematists will remember Peter Ax (1927–2013) for the role he played in phylogenetic systematics. Participants in the Phylogenetic Symposium from the 1960s to the early 1990s (Ax stopped participating the Symposium after his retirement in 1992, with the exception of the one held in Göttingen in 2005; Fig. 1) will recall Ax's lively and stringent contributions to the discussion. His major theoretical contribution is a 350-page book published in 1984 (English in 1987) whose concise title 'Das Phylogenetische System' characterizes his personality very well (see Xylander, this volume).

My task is to compare Ax's book, and particularly his views on homology, with books on the same topic and with comparable intentions written by authors of the previous generation: Remane's 'Die Grundlagen des Natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik' (The foundations of the natural system, of comparative anatomy and of phylogenetics) published in 1952, and Hennig's 'Grundzüge einer Theorie der Phylogenetischen Systematik' (Introduction to the theory of phylogenetic systematics) published in 1950 (see also Richter 2013).

The books by Hennig and Remane are based on the same (mainly German) scientific tradition and were written at almost the same time. It is known that Hennig's book was written in 1945 when he was a prisoner of war

(Schmitt 2013: 56), and Remane's book was also at least partly written long before it was published. His chapter on evolutionary theories was written seven years earlier (i.e. around 1945), and the latest citation in his book is from 1949. It is probable that Remane was not aware of Hennig's book. Neither was ever translated into English. Hennig's very influential 'Phylogenetic Systematics', published in 1966, which laid the foundation for phylogenetics/cladistics worldwide, is a translation of a fundamentally revised version of the 1950 book, which Hennig finished around 1962. The German version was only published in 1982.

Adolf Remane (1898–1976), certainly for decades one of the most influential zoologists in Germany, was the PhD supervisor (1950) and scientific advisor of Ax until 1961, when Ax obtained a full professorship in Göttingen. Willi Hennig (1913–1976) is generally seen as the founder of phylogenetic systematics (e.g., Schmitt 2013). It is not clear when Hennig and Ax met for the first time. Hennig only rarely attended the annual (Northern German) Phylogenetic Symposia. Westheide (2014) remembers several visits by Hennig to Göttingen during the 1970s, where he discussed the theory of phylogenetic systematics with Ax. Ax (1984: 47) mentions that personal discussions with Hennig resulted in the introduction of the concept of 'adelphotaxon'.

In this article I will focus on the importance to Ax and his predecessors of the concept of homology in identifying phylogenetic relationships. The article is not intended to give a full account of this topic, which is one of the most discussed in systematics, but aims to contribute to the history of phylogenetics by comparing the three key books mentioned. The differences between them become visible almost immediately. Alone the titles

Figure 1. Peter Ax at the Phylogenetic Symposium in Göttingen 2005. Behind Ax Profs. Kraus and Götting. Photo: Rainer Willmann

of the books speak volumes. While Remane's focuses on the 'natural system', both Hennig and Ax place the 'phylogenetic system' at the heart of their contributions. While it can easily be said that homology forms the core of Remane's entire book, Hennig (1950) only mentions the term homology when he compares 'true homologies' with the concept of homoiology (p. 176). Ax's account of homology is fairly detailed (20 pages), but doesn't start until page 166, by which point he has already discussed methods of reconstructing phylogenetic relationships.

Natural system or phylogenetic system

In his 1952 book, Remane accepts the importance of pre-phylogenetic morphology but rejects the metaphysical (Platonic) interpretation of the type and suggests the term 'pure morphology' to replace 'idealistic morphology.' He also rejects the idea (p. 11) that the natural system should be based on phylogenetic insights, arguing that it precedes and is therefore independent of phylogenetics. Phylogenetics, on the other hand, has no research method of its own but usurps findings from systematics and morphology and interprets them in an evolutionary way. 'Phylogenetic trees are primarily nothing other than a historical interpretation of the natural system.'[1] And two pages later: 'Phylogeny does not dictate the structure of the natural system, the natural system forms the basis of phylogeny.'[2] A few years later (1955: 171–172), this was rephrased as: 'Phylogeny does not dictate homology, homology dictates phylogeny.'[3] It appears obvious that Remane used the term 'phylogeny' here to mean phylogenetic hypothesis (Schmitt 1989), which actually corresponds very well to the way the English term 'phylogeny' is used today. Nevertheless, for Remane, the natural system and identification of homologies had priority over phylogenetic hypotheses. Furthermore, following the tradition of idealistic morphology, the term type (typus) played an important role in his argumentation: 'the independence of homologous type characters from analogous structural and functional correspondences is the most important principle of morphology.'[4] Later in the book, Remane (p. 163) describes the main

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[1] „Stammbäume sind zunächst nichts weiter als historische Interpretationen des Natürlichen Systems."

[2] „Nicht die Phylogenie entscheidet über den Aufbau des natürlichen Systems, sondern dieses bildet die Grundlage für die Phylogenie."

[3] „Nicht die Phylogenie entscheidet über die Homologie, sondern die Homologie über die Phylogenie."

[4] „… gerade die Unabhängigkeit der homologen Typusmerkmale von den analogen Struktur- und Funktionsübereinstimmungen [ist] wichtigster Grundsatz der Morphologie."

method of phylogenetics as 'identifying homologous correspondences, on whose distribution the natural system and, at the same time the systematic type and the pure stem form [in the sense of ancestor] are – simply and clearly – based.'[5] Remane's 'systematic type' (which he contrasts with other kinds of types; see also Rieppel 2013) corresponds closely to a real ancestor. He describes how the systematic type can be reconstructed and then transformed (Umformung) into the ancestor. Here, Remane is rooted firmly in the tradition of empirical idealistic (pure) morphology, postulated, for example, by Adolf Naef (1883 – 1949) (see also Rieppel 2012, 2013).

Naef (1919: 5) described Haeckel's phylogenetics as 'naïve' and criticized the older, pre-Darwinian, idealistic morphology in the same way for its failure to provide an explicit methodology. Naef's goal was a natural system and his main methodology was the reconstruction of the type (as in the case of Remane). 'Johannes Müller just takes the type as a given; we look for it'[6] (p. 27). 'I have come to realise that the natural system is nothing other than an expression of the typical correspondences actually identified or presumed to exist'[7] (p. 19). For Naef (1919: 35) it was clear that the 'typical correspondence (or form-relatedness) of organic species is the result of phylogenetic relatedness (or "Stammesverwandtschaft"), and that the morphological characters of the ideal type correspond with those of a real stem form (ancestor).'[8]

Neither Naef nor Remane were essentialists, and any attempt to equate idealistic morphology, typology and essentialism would be entirely misplaced. Platonic types were considered to be constant and timeless, and sharply delineated from other types, but in no sense are they the kind of types favored by Naef or Remane. Mayr (1999: 24) saw Remane's book as promoting the 'typological (idealistic-morphological) tradition, following Goethe', mainly because of its lack of 'population thinking' (a complaint Mayr did not limit to Remane's work). However, typology is conceptually neutral with respect to hypotheses of evolutionary mechanisms and there is no contradiction between 'population thinking' and 'typological thinking', as convincingly shown by Levit & Meister (2006). Remane was, without doubt, a true 'phylogeneticist' (Schmitt 1989, Zachos & Hosfeld 2006).

Hennig (1950) is well known for arguing that a phylogenetic system should be preferred over all other kinds of potential biological system, and that only phylogenetic relatedness should be considered in the establishment of such a system. He also gives a clear definition of what 'phylogenetic relatedness' actually means (Richter & Meier 1994, Schmitt 2013). In particular, he argues against all kinds of systems which are based solely on general similarity (Gestaltähnlichkeit), though as we have seen this would not really apply to Naef or Remane. Hennig (p. 108–110) compares three figures (fig. 24a–c; here Fig. 2A–C) representing different approaches to typological/phylogenetic relatedness. Whereas Fig. 2A is clearly based on similarity only, Figures 2B and 2C represent some kind of phylogenetic relationship. Interestingly, only Figure 2C shows phylogenetic relationships as sister group relationships, and for Hennig, this is the only true way of representing a phylogenetic system. Figure 2B is considered to be somehow typological. Twenty years later, Günther (1971) suggested several synonyms for the word pair natural vs. phylogenetic system (reflecting Figs 2B and 2C), including typological vs. phylogenetic system, patristic-phylogenetic vs. cladistic-genealogical system and paraphyletic vs. consequent-phylogenetic system. This implies that Ernst Mayr's (e.g. 1990) evolutionary classification is actually a typological system.

Hennig also rejects on several grounds the idea that phylogenetic systematics is historical and logically founded in non-phylogenetic systems (i.e. in idealistic morphology) (see also Rieppel 2012, who compares Naef's and Hennig's thoughts). Hennig writes (p. 26) that the argument that idealistic morphology must precede a phylogenetic system for logical reasons would only be true if morphological correspondences were the only basis on which phylogenetic relationships were recognizable.[9] He admits that in many cases, phylogenetic systematics starts with morphological correspondence and in this way does indeed go back to idealistic morphology, but argues that phylogenetic systematics is not restricted to a new interpretation of morphological findings and actually embodies the 'principle of reciprocal illumination' (see Schmitt 2013: 163–164 for general comments), which also needs to include zoogeography, ecology and genetics. However, if we consider that phylogenetic systematics/ cladistics was, for decades, effectively nothing other than using morphological correspondences to reconstruct phylogenetic relationships (see for example Ax's approach), this argument might be seen in a new light (see also Rieppel 2012). Later on, Hennig (p. 147–149) deals

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[5] „Sie besteht aus der Feststellung der homologen Ähnlichkeiten. Aus ihrer Verteilung ergibt sich das natürliche System und gleichzeitig in einfacher und klarer Weise der systematische Typus oder die reine Stammform."

[6] „Joh. Müller setzt den Typus einfach voraus; wir suchen ihn!"

[7] „Ja, ich stelle fest, dass das natürliche System nichts anderes ist als der Ausdruck für die erkannten oder angenommenen typischen Ähnlichkeiten"

[8] „Die typische Ähnlichkeit (oder Formverwandtschaft) organischer Arten sei die Folge ihrer "phylogenetischen Verwandtschaft" (oder "Stammesverwandtschaft") und die morphologischen Charaktere des idealen Typus stimmen mit denen einer realen Stammform überein."
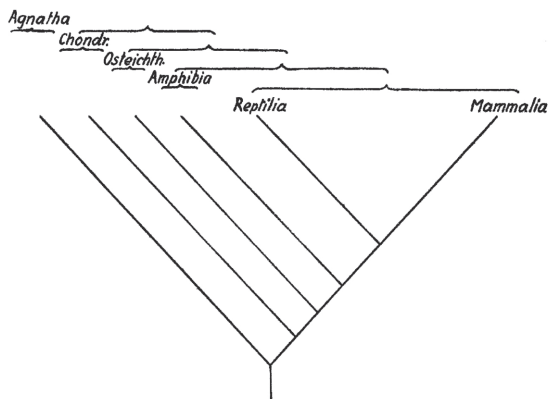
[9] „Sie wäre das nur, wenn der phylogenetischen Systematik zur Aufdeckung der Abstammungsbeziehungen keine anderen Mittel zur Verfügung stünden als die Analyse der morphologischen Ähnlichkeitsbeziehungen."
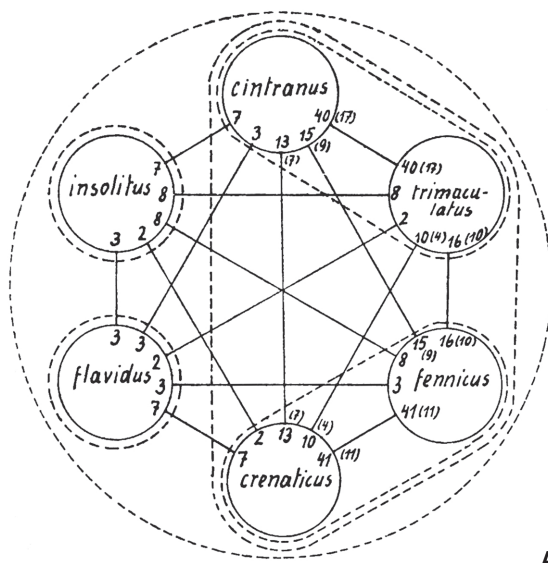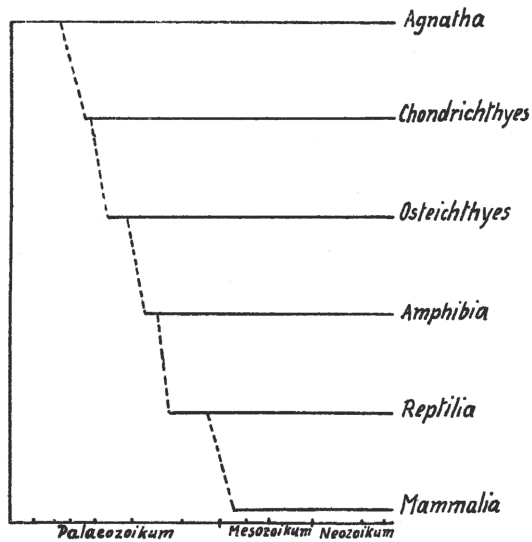
with Naef's take on of idealistic morphology and clearly shows that Naef's approach is a mixture of typological and phylogenetic systematics. This leads Hennig (p. 149) to suggest that phylogenetic systematics should adopt many of the results of idealistic morphology, particularly the kind advocated by Naef (Naefscher Prägung) 'with regard to the morphological primacy of certain character types.'[10]

Ax (1984: 39) is very clear in his preference for the term phylogenetic system: 'The object of our particular science is to uncover the products of phylogenesis and to arrange them on the basis of the chronology of speciation. Logically, we call this science phylogenetic systematics and its aim the establishment of a phylogenetic system.'[11] And later (p. 41): 'It is only consistent to refrain from using the enigmatic term 'natural system'.'[12]

Homology and Methodology

As already mentioned, the chapter on homology in Ax's book appears as a kind of addendum without homology being allotted any particular importance for the reconstruction of phylogenetic relationships. He writes (p. 166): 'The definitions of the terms symplesiomorphy, synapomorphy and convergence cover – in a clear and complete way – all possible kinds of evolutionary correspondence between different evolutionary species. The meaning of the term homology and that of its supposed counterpart analogy are insufficient for the goals of phylogenetic systematics.'[13] He provides a definition of homology which only refers to characters shared between evolutionary species (this was later extended to all kinds of supra-individual taxa, Ax 1988), ignoring other aspects of homology such as serial homology (see e.g. Schmitt 1995). Homologous characters go back to the exact same character and are either unchanged or transformed (p. 167). Because his definition includes

Figure 2. Representations of different appraoches to typological/ phylogenetic relatedness (A–C). From Hennig (1950) fig. 24 a-c.

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[10] „…hinsichtlich des morphologischen Primats bestimmter Merkmalstypen."

[11] „Der Forschungsgegenstand unserer Wissenschaft ist die Aufdeckung der Produkte der Phylogenese sowie ihre Ordnung entsprechend der zeitlichen Abfolge von Speziationen. Logischerweise nennen wir sie eine phylogenetische Systematik und das Ziel ihrer Bestrebungen ein phylogenetisches System."

[12] „…ist es nur konsequent, auch von dem buntschillernden Begriff „Natürliches System" Abstand zu nehmen."

[13] „Mit den Definitionen der Wörter Symplesiomorphie, Synapomorphie und Konvergenz verfügen wir über einen Begriffsapparat, der die prinzipiell möglichen Formen evolutiver Übereinstimmungen zwischen verschiedenen evolutionären Arten einwandfrei und vollständig erfasst. Die Bedeutungsinhalte des Wortes Homologie und seines vermeintlichen Wortpartners Analogie sind dagegen für die Ziele der phylogenetischen Systematik unzureichend."

no reference to similarity or correspondence, Ax argues that no term which expresses similarity, e.g. analogy, can be regarded as the antonym of homology. For Ax, the antonym of homology is simply non-homology. Ax also refers to Remane's 'homology criteria' but rejects the term 'criterion' on the basis that what Remane proposes are simply 'pointers' (Anregungen) on how to look for similarity or correspondences.

The term 'homology criterion', however, does not stem from Remane but from the earlier author Bertalanffy (1936). For Bertalanffy (p. 164), 'typological homology', i.e. the identification of a correspondence in position, is the 'most important criterion for phylogenetic homologization'. The phylogenetic homology concept did not replace the typological concept for Bertalanffy, who actually discusses the importance of the typological concept. 'Homology in a typological sense, i.e. based on a correspondence in position, is open to direct testing; if we define homology on the basis of shared ancestry following Haeckel, we push the criterion of homology back into an unknowable past.'[14] It was also Bertalanffy who characterized phylogenetic relationships as an 'explanation' of typological homology. What can be regarded as a typological homology concept can clearly be seen in Naef's work (1919). Naef (p. 10, 11) compared 'typical similarity' (typische Ähnlichkeit) with geometrical figures. Two rectangles possess corresponding, i.e. homologous, parts. Homology means 'morphological equivalent', which presupposes the typical similarity of the whole.[15] Naef (p. 70) concluded that 'the identification of homology is based on comparable spatial and temporal correlation (…) between the parts of the compared whole.'[16] Here, identification of homology is clearly independent from the historical explanation for such homology.

When we now turn to Remane, we must first remember that for him, homology was the obvious core of the natural system. His main method of phylogenetics, the identification of homologous correspondences, has already been cited above. It should be noted that Remane always refers to correspondences, although he admits that homologous correspondences might exist 'regardless of their apparent similarity or dissimilarity'[17] (p. 30).

Before Remane discusses in detail his three main and three auxillary criteria, he criticizes the previous use of 'homology definitions' because their sheer disparity might indicate that different homology concepts exist (p. 32).[18] For Remane (p. 33) it is very clear that this is not the case: what differ are, at most, subcriteria (Teilkriterien) of a uniform and impartible concept of homology.[19] Clearly, Remane uses the term 'criterion' not to mean a necessary condition, but more loosely. Only after a detailed discussion of his six criteria does Remane (p. 67–68) discuss phylogeny as part of the homology definition. For Remane, however, common descent is not part of the 'definition' but the 'explanation' for homology. In 1955 (p. 172), this term was replaced by 'explication'. Interestingly, Remane (p. 65–66) accepts that decisions on homology might be driven by probability, with some homologies being more likely than others, which shows that in his view too, not every detailed correspondence (sameness) is necessarily a true homology. Hennig (1953) criticized Remane for not distinguishing clearly between definition and criteria, and Mayr (1984: 187) objected that 'Remane used the criteria which serve as the proof of homology as part of the definition of homology.'[20] Indeed, Remane used the terms criteria and definition almost interchangeably and used explanation/explication for what Hennig and Mayr would call definition. Remane might well be criticized for a lack of precision in his terminology, but this does not mean that his general concept is flawed.

Remane (1952: 163) also suggests what can be considered a methodology for establishing a natural system. The systematic type (i.e. the stem form) can be reconstructed on the basis of the distribution of homologies, and the 'order of types in the branching of the phylogenetic tree shows us an essential aspect of phylogenesis.'[21]

To explain what the 'distribution of homologies' really means, the term 'homology circles' (Homologiekreise) is introduced (p. 106). *Sciurus*, for example, is part of the homology circle of rodents (steht im Homologiekreis der Nagetiere), the rodents together with other mammal orders are part of the homology circle of mammals, and mammals together with reptiles and birds part of the homology circle of amniotes, etc. In his summary

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[14] „Die Homologie im alten typologischen Sinn, auf Grund der Übereinstimmung der Lage, ist direkter Nachprüfung zugänglich; definieren wir aber mit Haeckel als homologe Organe, die durch gemeinsame Abstammung erhalten sind, so verlegen wir das Kriterium der Homologie in eine unkontrollierbare Vergangenheit."

[15] „Es entsteht damit der Begriff der "Homologie" oder "morphologischen Gleichwertigkeit", der, wie man sieht, die typische Ähnlichkeit des Ganzen voraussetzt, ohne die ein solcher Vergleich überhaupt wegfällt."

[16] „Die Feststellung der Homologie gründet sich auf den Nachweis gleicher räumlicher (und zeitlicher) Korrelation (…) zwischen den Teilen der verglichenen Ganzen."

[17] „…ungeachtet ihrer äußeren Ähnlichkeit oder Unähnlichkeit."

[18] „Diese Vielfältigkeit der Definitionen, die z.T. gar nichts Gemeinsames aufwiesen, ließen schließlich den Verdacht aufkommen, es gäbe mehrere ihrem Wesen nach verschiedene Homologiebegriffe."

[19] „Was in verschiedene "Homologiebegriffe" zerspalten wurde, sind in Wirklichkeit nur Teilkriterien des einen einheitlichen und unteilbaren Homologiebegriffs."

[20] „…dass Remane die als *Beweis* für Homologie dienenden Kriterien zur *Definition* von Homologie erhob."

[21] „Die Typenfolge wiederum im Geäst des Stammbaums übermittelt uns einen wesentlichen Teil der Stammesgeschichte."

(p. 379), he very clearly states that 'when two or more species share homologous structures the structure already existed in their common ancestor.'[22] Remane (p. 106) argues that if this kind of encaptic system (this is not the term he uses, however) of homologies were always valid, the resulting grouping would be an exact and correct system. However, this is not the case. Monotremes, for example, exhibit both mammalian and reptile characters. Here, he introduces the term 'homology bridges' (Homologiebrücken) to describe the phenomenon where certain homologies overlap 'typical groups' (most homologies are restricted to typical groups). Remane (p. 106) even suggests a law (Gesetzmäßigkeit) by which 'if two natural groups are connected by a homology bridge with a third group, they themselves are not connected by homology bridges.'[23] When discussing homology bridges, Remane does not distinguish between primitive and derived characters, though Dohle (1965) clearly showed that when symplesiomorphies are used, the homology circles enclose completely different taxa. It is difficult to imagine how this methodology (even without the problems Remane himself discusses later) can lead to anything like a natural/phylogenetic system without additional instructions.

It is interesting to note that Hennig (1950: 176–177) used the term homology only to distinguish it from homoiologies, which have a 'curious intermediate position between true homologies and convergences.'[24] If his avoidance of the term homology had been intended as a real critique of the concept, Hennig would surely have emphasized the fact. In his critical remarks on insect phylogeny (Hennig 1953), Hennig refers to Remane (1952) and uses the term homology without hesitation, insisting, however, that Remane's homology criteria are clearly subordinated to the phylogenetic definition of homology (p. 11). This work is the first in which Hennig (1953: 16) writes about the relationship of the term homology to the terms he himself introduced: 'Homologies are not only the true synapomorphies but also the symplesiomorphies. The concepts of synapomorphy and homology, therefore, do not coincide. Of course, the homology criteria form the starting point of any systematic work which uses morphological methods. Only correspondences in homologous characters can be compared. But not all homologies are important for systematics: symplesiomorphies are not.'[25]

In his revised book, Hennig (1966: 93) provides a very specific definition of homology. 'Different characters that are to be regarded as transformation series of the same original character are generally called homologous.' Here, the concept of homology becomes incorporated into Hennig's ideographic character concept, where characters are transformation series (see Grant & Kluge 2004). The fact that Hennig actually emphasized that 'transformation' refers to the real historical process and not to any formal process, as in idealistic morphology, makes the definition even more interesting for us.

In his discussion of Remane's criteria, Hennig (p. 94) states: 'But with respect to defining the concept "homology", all three of his "principal criteria" are only accessory criteria that we have to use because the real principal criterion – the belonging of the characters to a phylogenetic transformation series – cannot be directly determined.' It is interesting to note that Hennig here is also guilty of mixing up definition and criterion, at least when he uses the term 'real principal criterion.' Comparing Remane's three main criteria, Hennig suggests that the first – 'criterion of sameness of position' – must take priority, for without it the other criteria are unusable.

When Hennig (1966: 95) discusses 'character phylogeny' it again becomes clear that for him, the starting point for the reconstruction of phylogenetic relationships is indeed the identification of homology. 'If it can be shown that a character is homologous in a series of species, the question arises: in which direction is this transformation to be read.' In other words, which character state is apomorphic, which plesiomorphic. Hennig (p. 94–95) also noted that 'the concepts of symplesiomorphy and synapomorphy go somewhat beyond what are ordinarily called 'homologous characters' because 'a "character" may also be the absence of an organ but generally we speak only of the homology of organs.' Ax (p. 181) discusses this point under the heading of 'negative characters' (Negativmerkmale). For him it is 'simply impossible to hypothesize whether something which does not exist is homologous or non-homologous.'[26]

Ax rejects in a footnote Hennig's posthumously published idea (1984: 38–39) of extending the term 'homologous character' to the absence of structures when a particular position on the body is considered (e.g. the wings or lack of wings in insects), because for

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[22] „Wenn zwei oder mehrere Arten homologe Strukturen aufweisen, so ist die homologe Struktur bereits bei dem gemeinsamen Ahnen vorhanden."

[23] „Sind zwei natürliche Gruppen des Systems durch eine Homologiebrücke mit einer dritten verbunden, so sind sie untereinander nicht durch weitere Homologiebrücken verbunden."

[24] „…eine merkwürdige Zwischenstellung zwischen echten Homologien und Konvergenzen."

[25] „Homologien sind ja nicht nur die echten Synapomorphien,

sondern auch die Symplesiomorphien. Die Begriffe Synapomorphie und Homologie decken sich also nicht. Natürlich stehen die Kriterien der Homologie am Anfange der systematischen Arbeit, soweit sie morphologische Methoden benutzt. Verglichen werden können überhaupt nur Übereinstimmungen in homologen Merkmalen. Aber nicht alle Homologien sind für die Lösung einer systematischen Frage von Bedeutung: die Symplesiomorphien sind es nicht."

[26] „… man kann schlechterdings nichts als homolog oder auch als nicht-homolog hypothetisieren, was gar nicht existiert."

certain characters (e.g., amnion, allantois, serosa), no corresponding position exists.

It is clear that Ax (1984, 1988) adopted most of Hennig's (1966) ideas. However, the chronological principle of identifying homologous characters first before making a decision on the direction of transformation is apparently missing in Ax's approach (but see also Hennig 1969). Ax (1984: 66–67; 151) suggests first deciding between plesiomorphy and apomorphy, and then between synapomorphy and convergence. He does not recognize any specific 'empirical measure' (Maßstab) to help with the latter decision, but refers to the principle of parsimony (Ockham's razor). This is odd, because the decision between plesiomorphy and apomorphy requires a previous decision to have been taken that both states belong to the same transformation series (i.e are homologous characters/character states if we follow Hennig). Ax clearly avoids using the term homology here. When discussing homology explicitly, he writes (p. 170): 'This does not mean that homologies can only be identified by deduction based on previously accepted phylogenetic hypotheses. The logic of the decision-by-probability between homology and non-homology corresponds exactly to the logic of the decision-making procedure between synapomorphy and convergence.'[27] This point could also be argued the other way round, starting with the decision between homology and non-homology. Ax continues: 'if characters are very similar or identical in their spatial and/or temporal structure, the principle of parsimony requires an *a priori* assumption of homology, unless this conflict with the distribution of characters in the organisms being compared.'[28] Contrary to what Ax claims, the identification of similar or identical spatial or temporal structures (interestingly, Ax uses Naef's phrase) does indeed require its own 'empirical measure', which in turn corresponds with Remane's first and second homology criteria.

It is not the intention of this contribution to discuss the current view on homology and phylogenetics. In Germany in particular there is still a tradition which emphasizes an empirical *a priori* criterion for identifying homologies which is often referred to as the 'complexity criterion' (Dohle 1976, 1989, Scholtz 2005; see also Riedl 1975). The cladistics community, on the other

hand, argue that homology identification is a two-step approach, resulting in what often has been called primary and secondary homology (de Pinna 1991). For some decades the identification of secondary homology by character congruence was considered more important (Farris 1983). Although Ax never used a computer to analyze phylogenetic relationships, his writings appear to tend towards the second approach. Although these two approaches are not really contradictory (de Pinna 1991 quotes Remane on the identification of primary homologies; see also Richter 2005), their emphasis is clearly different. Patterson's (1982) equation of homology and synapomorphy is still defended by some (Brower & de Pinna 2012), but rejected by others (Nixon & Carpenter 2012, Farris 2014) - the latter position representing Hennig's view, as we have seen. Ax (1984: 183) is explicit in his rejection of Patterson's view, emphasizing that synapomorphy refers to a very specific hierarchical level and that this needs to be stated unambiguously. Ax in this respect is more precise than Hennig in his use of the term synapomorphy to refer exclusively to sister group relationships. The problem of applying the concept of homology to the absence of organs remains. One final aspect of Ax's view on the relationship between homology and synapomorphy should be mentioned. Ax (1984: 184) cites Bock's 'conditional phrasing', e.g. 'the wings of birds and the wings of bats are homologous *as the forelimbs of tetrapods*' (Bock 1973: 387) and not, in Bock's opinion, as wings. For Ax this conditional phrase is just a circuitous way of expressing the hierarchical level on which a homology is relevant to systematics as a synapomorphy. Wagner (2014) recently phrased this slightly differently, incorporating Hennig's character concept: 'In fact bird wings and bat wings are homologous, but what is not synapomorphic is their character state as a wing'. While all these approaches refer to the contribution of the homology concept to phylogenetics, it has long been considered that homology also needs to have some kind of mechanistic cause (Riedl 1975, 1978). However, this goes beyond the focus of the present contribution (see Wagner 2014).

Peter Ax strictly rejected the evolutionary but still typological approach (a term which in my view should have no negative connotation) advocated by Adolf Remane. He was a keen follower of Willi Hennig's view, and certainly helped to clarify the way in which phylogenetic systematics should be applied. When Ax degraded Remane's criteria to mere 'pointers', he may have failed to acknowledge sufficiently that identifying 'correspondence/ identity' is indeed an independent empirical method. Peter Ax will be remembered as a great advocate of phylogenetic systematics, particularly in Germany. Even if I do not agree with all of his writings,

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[27] „Das allerdings bedeutet keineswegs, dass Homologien nur deduktiv anhand vorab akzeptierter Verwandtschaftshypothesen „festgestellt" werden können. Die logische Situation der Wahrscheinlichkeitsentscheidung zwischen Homologie und Nicht-Homologie entspricht vielmehr exakt dem Procedere bei der Entscheidung zwischen Synapomorphie und Konvergenz."

[28] „Bei einer sehr ähnlichen oder identischen Raum- und/oder Zeitstruktur verlangt das Prinzip der sparsamsten Erklärung von uns, Merkmal für Merkmal solange der Hypothese einer homologen Beziehung zu verfechten, solange sie mit der Merkmalsverteilung bei den verglichenen Organismen nicht in Konflikt gerät."

it remains a pleasure to read him and I remember that I felt the same when I listened to him. He was a champion of the maxim that clear thoughts require clear language.

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