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Book review

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A Hennigian monument on vertebrate phylogeny

Gerhard Mickoleit (2004) *Phylogenetische Systematik der Wirbeltiere* [Phylogenetic systematics of vertebrates]. Verlag Dr. Friedrich Pfeil, München, 671 pp., 676 figs. ISBN 3 89937 044 9. Price 98€.

When I was a postgraduate with the University of Tübingen more than 10 years ago, we all waited eagerly for the publication of 'his book'. Our teacher, Gerhard Mickoleit, had already produced, with Hennig's son Wolfgang, the fourth edition of Willi Hennig's Articulata volume in the series *Taschenbuch der Zoologie* (Hennig, 1986). The remaining invertebrates had been treated in the preceding volume of the series (Hennig, 1984). For us students, the clear presentation of the phylogenetic system of invertebrates in Hennig's *Taschenbüchern* was very appealing. Apomorphies and groundplans were clearly presented, and we could see why higher taxa were established and how we could diagnose them. However, a similar treatment of the vertebrates was missing since Hennig did not write the vertebrate parts of the series (Dathe, 1975). Other available text- and handbooks, valuable as they are (e.g. Fiedler, 1991; Starck, 1995; or the aged systematics volumes of the *Traité de Zoologie*; oddly enough, no appropriate English textbook exists), did not clearly and consistently present the phylogenetic system either; or if they intended to do so (e.g. the new textbook by Westheide & Rieger, 2004), they missed the didactic opportunity of consistently and clearly presenting the apomorphies of higher taxa. Willi Hennig did write a manuscript of a textbook on the phylogeny of chordates, but never finished it. His son Wolfgang published it posthumously (Hennig, 1983) but it remained a torso, with no illustrations and difficult to use. So we kept waiting for Mickoleit's book. Although Ax was a bit quicker with his third volume of his phylogenetic textbook of metazoan systematics (Ax, 2001) in which he deals with the Vertebrata in just over a hundred pages, he merely presents the system with a list of apomorphies extracted from literature, and with no detailed character discussion. The same is true of the recently published French textbook on the phylogenetic system of all organisms (Lecointre & Le Guyader, 2001) which treats the vertebrates in greater detail in just over 170 pages. Finally in February 2004, Mickoleit's *magnum opus* was published by the small but quality publisher Dr Friedrich Pfeil Verlag in Munich. For the first time, we have a complete presentation of the phylogenetic system of vertebrates with an account of all crucial morphological characters and their evolution.

Dr Gerhard Mickoleit worked as a senior scientific officer secluded in his Zoologische Schausammlung (zoological collections of the University of Tübingen) of which he had been the head since 1962, indefatigably supported by his wife Dr Erika Mickoleit to whom this book is dedicated. He never joined in the hustle and bustle of current science, focusing on writing the maximum number of papers about minimum publishable entities, selling himself at conferences, or investing substantial amounts of energy and time in grant proposals with only a maximum chance of 15% success. He simply taught and pursued his research. His insect and vertebrate courses were legendary in Germany. Admittedly, he was in the advantageous position of being employed by the rigid German civil service, secure from any danger of being sacked or promoted, and even better, he then retired in 1995. It is under such circumstances, that a monumental treatise of 671 pages can be produced. Mickoleit's personality, without any tendency to show-off or proselytise, was, if not a prerequisite, at least very helpful for this task. Another prerequisite is artistic talent. Mickoleit drew most of the 676 figures himself, many from original subjects, and those redrawn from the literature were mostly compared with specimens. Indeed, Mickoleit has evaluated an enormous amount of literature (more than 4000 papers), by rechecking with specimens from the Zoologische Schausammlung whenever possible. These rich research collections of the University of Tübingen, undervalued by the University management, were crucial for such a task. It took much longer than the author expected, 14 years in total, but it was worth it.

Tübingen was Willi Hennig's university from 1970 (Schmitt, 2001). Although he was employed as a researcher with the natural history museum in Stuttgart, Hennig held his university seminars as honorary professor in Tübingen. Gerhard Mickoleit and Willi Hennig had met several years before when Hennig's eldest son Wolfgang joined the 'Zoologisches Großpraktikum' (principal zoological practical) in which Mickoleit taught the vertebrate part. However, Phylogenetic Systematics came to Tübingen much earlier. Mickoleit had already become familiar with Hennig's ideas and methodology in the mid-fifties when he read the *Grundzüge* (Hennig, 1950) and met a delegation of East German zoology students from Jena who visited the Schausammlung in 1957. They knew of Hennig's ideas and their implications for systematics. Although Phylogenetic Systematics came to Tübingen very early, phylogenetic approaches were considered 'dubious' in zoological circles of that time, and 'should best be kept for one's retirement' (Mickoleit, pers. comm.). Therefore, Mickoleit turned to phylogeny only after he became employed as assistant in 1960, but from then on, he forcefully advocated phylogenetic systematics in his courses and used it as the foundation of his entomological studies, and now of his monumental treatise of vertebrate systematics.

Mickoleit refrains from lengthy methodological introductions, giving just some clarifications on the relevance of fossil taxa. His book is about extant vertebrates. The sister group relationships presented here are between extant taxa. Fossils are only considered when necessary for the assessment of homologies and the understanding of phylogenetic relationships of extant taxa. Fossil taxa were treated as members of (paraphyletic) stem groups, not as terminal taxa. Mickoleit states unassumingly that the matter of his book consists of an overview about the structural diversity (*Formenfülle*) of the extant vertebrates, with the consistently phylogenetic system as the framework. In fact, this is no less than the first complete in-depth presentation of the phylogenetic system of vertebrates according to Hennig's principles. If we see Ax's (2001) textbook as a succinct skeleton, Mickoleit's monograph is the complete body, working and functioning as a didactic handbook. The Hennigian methodology is the state of the art for both of these textbooks, and Mickoleit sees no necessity to defend it.

Since Hennig's times, cladistics has developed rapidly, but mainly as a numerical methodology, which Hennig's Phylogenetic Systematics never was (Schlee, 1969). Actually, the approach and procedure of modern cladistics differ substantially from Hennig's methodology, a fact that is not widely recognized though occasionally explained (Ridley, 1986; Sæther, 1986; Schmitt, 1989;

Meier, 1995; Wägele, 1996, 2001, 2004; Disney, 2003). It has even been shown (Wägele, 2001, p.185f) that cladistic methods did not derive primarily from Hennig's methodology, but from the Numerical Taxonomy of Sokal & Sneath (1963) a procedure that Hennig and his collaborators rigorously rejected (Hennig, 1971; Schlee, 1975). Modern cladistics generally follows a numerical approach (considered 'objective'), distinct from Hennig's methodology, the step-by-step 'search for the sister group' with a priori character weighting (considered subjective, naïve, old-fashioned or not considered at all). 'Nowadays, Cavalli-Sforza and Edwards's view that phylogeny reconstruction should best be considered as a statistical estimation problem is well accepted' (Yang, 2003). This is undoubtedly true in numerical cladistics, particularly in molecular phylogenetics. If the phylogeny is to be reconstructed on the basis of ambiguous characters (simple characters with high probability of homoplasy like nucleotides or the length of setae) statistical procedures are the only way to deal with the data. The evolution of those trivial characters in itself, however, is rather uninteresting. Moreover, as Quicke (1993, p. 7) frankly stated 'Computers [. . .] are not yet able to re-examine characters and so have to accept the input given to them by their operators', leading to the widely accepted solution that a formal algorithm has to be applied (e.g. parsimony) to cope with homoplasious characters rather than re-examining characters during the process of reconstructing the phylogeny. Character matrices and their (quantitative) analysis (tree statistics) have become the central point in phylogenetic research rather than (qualitative) iterative character analyses (Rieppel & Kearney, 2002), which are crucial for the Hennigian approach. Mickoleit's book profits from its author coming from this more qualitative tradition. He discusses key characters (apomorphies with a low probability of convergence and parallelism) and their evolution, rather than presenting matrices of all definable characters. Character matrices are a didactic nightmare, whereas key apomorphies can be easily memorized. Mickoleit discusses the evolution of morphological structures in the framework of a consistently phylogenetic system, considering competing hypotheses. Major morphological structures are at the centre of the argument, rather than tree topologies or statistics of quantitative analyses, or matrices of essentially trifling characters.

In a curious way, and without intention or even awareness of the authors themselves, Scotland *et al*. (2003) reconcile current cladistics to Hennigian phylogenetics in a currently much discussed paper. These authors have given up on the statistical treatment of highly homoplasious morphological characters and suggest that we should concentrate on fewer, rigorously studied morphological structures in a molecular framework. However, they do not recognize (and they probably cannot recognize from a numerical-cladistic viewpoint), that rigorously studied anatomical characters are not necessarily subordinate to molecular analyses, but may have primacy in the Hennigian method of phylogenetic reconstruction, or even in all cladistic procedures, as stressed by Rieppel & Kearney (2002) around the same time. This is precisely what Mickoleit has done so masterfully here. He did not simply copy and compile from the original literature. He checked and tried to grasp the characters in depth; and this is probably the only didactically sensible way to present the phylogenetic system in a text- or reference book. Highly homoplasious characters are not discussed in this book, because they are of minor heuristic interest. They might (e.g. Wiens, 2004) or might even not (see Nelson, 1996, 2004) be of analytical interest if no complex characters with a lower probability of convergence are present, but fall outside the scope of Mickoleit's book anyway. Of course, he has considered the relevant results of numerical analyses, but focuses on the phylogeny of taxa explained through the transformation of anatomical structures. Apomorphies of each monophylum are listed (marked by a black dot) and discussed. Other diagnostic characters of unknown or uncertain polarity, and major diagnostic plesiomorphies are also listed, but not marked. The complete phylogenetic tree of vertebrates precedes the text in an unexpected, but very user-friendly way: it is used as the table of contents and easily found on pp. 5–10. Additionally, succinct trees of extant Vertebrata and Tetrapoda (including important fossil stem group taxa) conclude the book on the two final pages.

It is probably a shortcoming of the book that when morphological structures do not provide any robust data to discuss, Mickoleit does not consider phylogenetic hypotheses exclusively based on molecular results, e.g. the hypothesis that turtles and crocodiles are sister groups (see Meyer & Zardoya, 2003). Molecular results are not mentioned, even if they support the morphological hypotheses expounded by the author (e.g. Venkatesh *et al*., 2001 who also reject some unorthodox molecular hypotheses on fish phylogeny; Zardoya & Meyer, 2001 who support the monophyly of Batrachia; or van Tuinen *et al*., 2000 who confirm the monophyly of neognath birds). However, the scope of the book is the discussion of morphological characters, which makes it difficult to include the rapidly fluctuating molecular hypotheses (e.g. palaeognath birds sister to chicken and duck, or the 'Is the guinea pig a rodent?' debate). As we see in Meyer & Zardoya's (2003) review, competing molecular hypotheses are often difficult to discuss. 28S rDNA sequence data support hypothesis A, whereas recent molecular studies based on complete mitochondrial genome support hypothesis B. That's it. The simple nature of the data forming the basis for these analyses often prevents qualitative interpretation of results. It allows only statistical justification, and generally, this does not help the development of a deeper understanding of organismic evolution that might enable us to judge competing evolutionary hypotheses.

Gerhard Mickoleit's *Phylogenetische Systematik der Wirbeltiere* is a unique compendium of vertebrate phylogeny and morphology, an original, critical revision rather than a mere compilation, well written and illustrated. Although the author explicitly intended to produce a working foundation (facilitating growth of knowledge) rather than a textbook (that cements knowledge), the result is easily usable as a textbook. As with so many leading textbooks of zoological systematics, and even more classical papers on vertebrate morphology, it is written in German. However, the predominantly telegraphic style of character descriptions and the clear international morphological terminology certainly helps to surmount a possible language barrier. The phylogenetic system of vertebrates will be refined, and will change in time. However, the fundamental facts presented in this book will be valuable for a long time. Perhaps some courageous publisher might think about an English translation. It would be very welcome.

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