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BOOK REVIEW

Multicellular Animals. PETER AX. Springer Verlag, Berlin, 1996/2000/2003, 225 + 396 + 317 pp. (cloth ISBN 3-540-60803-6, 3-540-67406-3, 3-540-00146-8; € 96.25 + 245.03 + 193.55). Translation (by M. POWER, S. KINSEY, and R. E. DUNMUR) of:

Das System der Metazoa I–III. Ein Lehrbuch der phylogenetischen Systematik. Peter Ax. Gustav Fischer Verlag, Stuttgart/Spektrum Akademischer Verlag, Heidelberg, 1995/1999/2001, 226 + 384 + 283 pp. (cloth, ISBN 3-8274-0972-1, 3-8274-0973-X, 3-8274-1179-3; as set, 3-8274-1186-6; € 29.95 + 44.95 + 44.95; as set, € 109.00).

In these gene-centered days, Peter Ax's three-volume treaty on the phylogeny of the Metazoa is refreshing reading. More than once while teaching systematics courses, I have been frustrated by the genetic reductionism uncritically adopted by some graduate students. I use to spend some time discussing the pros, cons, and mutually complementing nature of different kinds of characters. Nevertheless, in exam answers I keep being told by my students that, in phylogenetics, molecular data are to be preferred ''because genes don't lie.'' One starts wondering indeed whether something is wrong with the textbooks students are exposed to during their undergraduate studies.

Frank as ever, Ax uses several opportunities to put genetic chauvinism in place. In many cases he has good reason to do so. The number of articles, even in well-reputed journals, that attempt to overthrow well-founded ''traditional'' phylogenies with bold statements built on molecular evidence that turns out to be little more than statistical noise, is not insignificant and still increasing (*e.g.,* Christen *et al.,* 1991; Rasmussen and Arnason, 1999).

More important than his witty sarcasms against molecular naivete is that Ax gives an example of what the morphological data base is good for. *Multicellular Animals* illustrates that the days of ''classical'' traits are anything but gone. In several cases he arguably pays *too* little attention to genetic results. Recent advances in research on rare genomic changes, for instance, are exactly the sort of evidence morphologists like Ax should appreciate. They are virtually irreversible, unambiguous to diagnose, and sufficiently infrequent to rule out convergence—in short, they fulfill all requirements of ''good'' morphological characters.

Some of those advances support the morphology-based phylogenetic hypotheses put forward by Ax (*e.g.,* paraphyly of Pisces, placement of Strepsiptera). However, in other cases, rare genomic changes do not support the hypotheses favored by Ax. Examples are the Atelocerata (or Tracheata; *i.e.,* Myriapoda + Hexapoda), which now, with more evidence still accumulating, have been superseded by the Tetraconata concept (or Pancrustacea; *i.e.,* Crustacea + Hexapoda). Another of Ax's hypotheses, which is so elaborate that it deserves to be true, concerns the ''Hemichordata.'' Morphological evidence has long been equivocal as to the monophyly and position of the hemichordates, some characters favoring a Hemichordata + Echinodermata relationship (together forming the Ambulacralia), some a Hemichordata + Chordata grouping (Pharyngotremata), an Enteropneusta + Chordata taxon (Cyrtotreta), and/or a Pterobranchia + Echinodermata clade. Ax favors the Pharyngotremata hypothesis, but compiles evidence that not only the hemichordates but also the pterobranchs are paraphyletic grades. Unfortunately, a change in the genetic code of the mitochondrial genome in both enteropneusts and echinoderms strongly rejects chordate affinities of the hemichordates (Castresana *et al.,* 1998).

However, I do not see these conflicting findings as a severe critique of Ax's book. Rather they illustrate the pleasant fact that new phylogenetic evidence is accumulating rapidly: the evidence against Atelocerata from rare genomic changes (Boore *et al.,* 1998) was published while the second volume of *Das System der Metazoa* was in print. The Ambulacralia hypothesis, being published in the same year, could have made it into the third volume, however.

A final example is the Ecdysozoa (Arthropoda + Nematoda and allies). This hypothesis—which is devastatingly incompatible with the Articulata concept (Annelida + Arthropoda) embraced by Ax—was originally proposed in 1997 by Aguinaldo *et al.,* and has since been widely (and, as I would maintain, often overly uncritically) accepted in research articles and textbooks. Corroboration of the Ecdysozoa hypothesis would invalidate large parts of the first two volumes, as it would turn ''Articulata'' into a paraphylum. This taxon's paraphyly would then ''trickle down'' the phylogeny and affect Pulvinifera, Trochozoa and Euspiralia. Aguinaldo *et al.*'s paper was published too late to be discussed in *Das System der Metazoa.* In the English translation, a footnote was added which briefly mentions the Ecdysozoa concept and Wägele *et al.*'s (1999) critique of it.

One obvious criticism of *Multicellular Animals* is that numerical analyses are entirely absent. There is not a single bootstrap value or other measure of branch support in the book, and you will not find any appendices containing character matrices. However, I hesitate to see this as a disadvantage. It might be exactly one of the book's strengths that Ax illustrates that cladistic analysis doesn't need to be numeric. Obviously this opens up arguments about interpretation and weighting of characters. It might seem that this contradicts Ax's own determined attempts to ban arbitrariness from phylogenetics. This contradiction may be purely superficial, however. Michael Ghiselin (1997, p. 204) has remarked that ''we often encounter the expression 'character weighting' when one would hope that what weight is being attached to is arguments.'' On the one hand it is naïve to believe that weighting schemes are not arbitrary. On the other hand functional reasoning need not be arbitrary at all. My point is not that all or even most of Ax's judgments are correct. They might or might not be. What *Multicellular Animals* illustrates, however, is that profound knowledge of functional morphology is invaluable in choosing between competing sister group hypotheses. Leaving judgments of homology to algorithms rather than to mortals does not make those judgments less arbitrary, only less obviously so.

However, in two places I was surprised to find that Ax—who earlier has exposed himself as a pronounced skeptic against pattern cladism (*e.g.,* Ax, 1988)—argues like a transformed cladist. In dismissing the doubts of paraphyly directed against the ''Polychaeta'' as unparsimonious, he seems to implicitly remove functional reasoning from the realms of phylogenetics (cf. Westheide *et al.,* 1999). Also his statement that resolving the phylogenetic position of the Tardigrada is beyond the reach of phylogenetics, is somewhat surprising. Obviously some questions may not yet be answerable with the evidence available. But resolvability comes in degrees, and it is not at all obvious why the Tardigrada + Euarthropoda hypothesis should be so much less supported than some of the hypotheses endorsed by Ax.

In the absence of severe criticisms, I close with three minor remarks. The motivation for the variation in the subtitles of the English translation remains unclear, especially as none of them reveals the contents of its volume (*A new approach to the phylogenetic order in nature; The phylogenetic system of the Metazoa;* and *Order in nature—system made by man*). While the subtitle of Volume III quite aptly expresses the author's low opinion of arbitrariness in systematics, it is in the introduction to the *first* volume that he exposes his systematic philosophy: Ax's system is strictly phylogenetic (cladistic) and bifurcating, and avoids all Linnean categories except species. Unfortunately, Ax abandons his earlier conviction (*e.g.,* Ax, 1987) that species and higher monophyletic taxa are ontological individuals, and replaces it by a muddled argument in favor of Mahner and Bunge's (1997) ontology.

A matter Ax does not discuss is how he decided where to terminate the branches of his cladograms. Laudably, and in contrast to many other treatments of the topic, such as Nielsen's (2001) *Animal Evolution,* Ax avoids terminating branches at some mysterious ''phylum'' level, which only introduces an aspect of seeming objectivity where there is none. However, some cases of further subdivisions of taxa could have been discussed, especially among the vertebrates (*e.g.,* Condrichthyes, Teleostei, Amphibia). On the other hand, the great detail with which cestode relationships are covered can be justified by little more than the fact that they represent Ax's

personal research interests. These choices of cladogram termination are exactly as defensible as any other. They just might have deserved a few words of comment.

Ax argues lively against using different names for taxa that differ only in the fossil groups included. His arguments, exemplified by the ancestral lineages of mammals and birds, are (for my part) convincing. One can wonder, however, why Ax's aversion against redundant nomenclature does not extend to other taxa such as *Amia calva*, *Latimeria chalumnae* and *Sphenodon*, which he introduces under the synonyms Halecomorphi, Actinistia, and Rhynchocephalia, respectively.

However, those final remarks are comments rather than criticisms. To summarize, *Multicellular Animals* is an important publication for at least three reasons. It gives morphology the weight it deserves (though it gives molecular evidence less weight than it deserves). It illustrates that cladistic analysis does not need to mean absence of functional reasoning. Finally, I think that the heuristic value of plotting evolutionary novelties directly onto the phylogeny is considerable for students of biology. One may argue that the book is too advanced for undergraduates. However, my experience is that being able to place evolutionary novelties in a tree makes learning both easier and more intellectually rewarding than ''simply'' cramming properties phylum- or class-wise. To date, *Multicellular Animals* is still the only introduction to metazoan morphology that is strictly organized in this way.

I highly recommend the three volumes to all interested in zoology and/or phylogenetics. More specifically, I recommend the *German* edition—at least if you are able to read it: you do not only get all photographs in colors, you also save 426 Euros (*i.e.*, 80% off!).

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ERRATUM

Due to a typesetting error, the page numbers of *Integrative and Comparative Biology* 43(6) start on p. 771, instead of p. 671, the number following the ending page of the previous issue.