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REVIEW

ANIMAL PHYLOGENY AT LAST IN THE MAINSTREAM


Any successful treatment of the phylogeny of the animal kingdom these days should have three things: (1) a solid knowledge of all the groups, (2) a cladistic approach, and (3) a love of the myriad diversity of the creatures themselves. Claus Nielsen’s new book has all three of these. First, he has had a productive and noteworthy career involved in the zoomorphology of various animals groups, especially among the lophophorates. Second, Nielsen utilizes in a most effective way cladistic techniques, and in this respect joins the efforts of Brusca and Brusca (1990) and Eernisse et al. (1992), who only analyzed some of the animal phyla, and Meglitsch and Schram (1991) and Schram and Ellis (1995), who have analyzed, as has Nielsen, all the phyla with a single data base. Third, it is clear from the way he handles details and from the layout of the book figures themselves that Nielsen has a special affection for his study matter.

Treatments of the phylogeny of the animal phyla usually occupy the final chapter of text-books on invertebrate zoology. This opus of Nielsen is noteworthy in that an entire volume is devoted to the subject. However, the casual reader should not be mislead into thinking that this is just another book on invertebrate zoology. In fact, if you don’t know your phyla already, you may find this treatise not to your taste. This volume harkens back to a time, not all that long ago, when everyone considered a solid knowledge of the animal phyla essential to a well-founded education in zoology. If you do not have this kind of background, you will be disappointed because you will not be able to really appreciate the wealth of information and insight this book contains.

The work opens with an introductory chapter that nicely illustrates phylogenetic speculations characteristic of the past, of which Haeckel’s famous 1866 tree is such an example. Nielsen then poses his own conclusions, formulated as a cladogram, side by side with cladograms from the text-books of Brusca and Brusca (1990) and Meglitsch and Schram (1991).

However, these other two references are rather theory free, in that neither set of authors had preconceived notions as to how the tree should look before the data were put into the computer. With Nielsen’s effort this is not the case. This book is rather theory laden. Nielsen is right up front about this, quite literally. Chapter two recapitulates for those not in the know his trochea theory of animal evolution. The heart of this theory is that a series of holoplanktonic ancestors gave rise to pelagobenthic ancestors that developed sessile or bottom-locomotory adults. The central line of reasoning of this theory revolves around a series of modifications of larval structures that supposedly gave rise to adult features.

Nielsen clearly states his position (p. 222), which applies equally well in his system to any phylum. "It should be clear that the phylogenetic position of [a] phylum cannot
be deduced directly by comparisons with other phyla in the hope of finding decisive synapomorphies defining sister-group relationships . . . Understanding the position of [a phylum] is intimately connected with the choice of phylogenetic theory." In a sense, the dice are loaded; and to Nielsen it is a good thing that they are. Now I want to make clear that I see nothing wrong with developing scenarios of animal evolution. I believe, however, that this should occur after the cladistic analysis rather than before.

Despite my misgivings about theory laden analyses, occasional glimmers of insight emerge from Nielsen's hypothetical diagrams that caused me to pause. As one example, his chart of functional steps in chordate evolution (Fig. 51.2: 401) at first glance struck me as just another theory laden, a priori, scenario. However, as I stared at the pleasing arrangement of real and paper animals, I found myself focusing on the presumed "Ancestor of NEORENALIA" at the base of the chart. I suddenly realized that the little vignette bore a striking resemblance to a problematic fossil from the Carboniferous of America, *Etacystis communis* Nitecki and Schram, 1976, whose affinities have been long debated (e.g. Foster, 1979; Schram, 1991). Then too, I admired the way Nielsen broke up certain traditional groupings of animal phyla to see how they might re-sort. For example, his fragmentation of the traditional Hemichordata and Chordata enabled him to display the polyphyletic nature of the former while reconforming the monophyly of the latter. In fact, I wished he had maintained that approach in regard to some of the "worm" phyla instead of deciding to merge gnathostomulids, echiurans and pogonophorans into Annelida. If these groups had emerged from the analysis in a clade which poly-chaetes and clitellates, rather than been arbitrarily assigned there, I would have felt more comfortable with the results. That failure, however, results automatically from theory driven analyses. The positions of taxa cannot emerge from the analysis when most of the placement of phyla is effectively predetermined before the analysis actually begins.

Even so, I find that the author has done a remarkable job of making sense of invertebrates. Although his conclusions do not always agree with my own, they are nevertheless framed in terms of clearly defined characters with matching cladograms for each and every clade within the animal kingdom. Each clade gets its own chapter. At the end of each chapter is a list of research problems yet to be resolved relevant to that clade. Finally, each chapter has a list of references that can quickly immerse the readers into the group at hand should they wish to explore that part of the kingdom on their own. Sometimes these chapters are no more than a few pages, e.g. that on Placozoa is 2½ pages long, but they are often longer and accompanied by clear line drawings and/or micrographs.

Although Nielsen's trocha theory drove his analysis, I found it fascinating that, in comparison to the efforts of other currently active invertebrate phylogenists, certain patterns of relationships seem to occur in each work giving strength to, what traditionalists will consider, unorthodox ideas. For example, Nielsen finds, as did Meglitsch and Schram (1991), that Ctenophora are not in a clade with Cnidaria, that Chaetognatha group in among the pseudocoelomates, and that pseudocoelomates form a coherent clade and are "lower" in the scheme of things than "acoelomates". Nielsen also locates at least some of the lophophorates as an integral part of the deuterostomes, as did Meglitsch and Schram (1991) and Brusca and Brusca (1990), although the latter treated these as a solitary lophophorate clade while Nielsen and the former discovered that these separate phyla occupy a
paraphyletic position in the tree. Nielsen, and Meglitsch and Schram (1991), perceive hemichordates as a polyphyletic group, and also develop a considerable amount of resolution within the pseudocoelomate clade. Nielsen along with Meglitsch and Schram (1991), and Brusca and Brusca (1990) reveal molluscs, annelids and other phyla as part of a transition series to arthropods, while Eernisse et al. (1992) and Schram and Ellis (1995) distinguish distinct clades of trophophorates (molluscs, annelids and relatives) and panarthropods (arthropods, tardigrades and onychophorans). It would seem, therefore, that a fair amount of agreement between different authorities is beginning to emerge.

One problem some people will have with Nielsen’s treatment is that the trees were derived by an application of strict Hennigian methods, i.e. essentially using paper and pencil and foregoing the use of any of the current computer programs. The question we should then be entitled to ask is whether Nielsen’s cladogram is in fact the most parsimonious one. This is especially important since a few of his phyla do end up in startling positions. For example, Nielsen places Ctenophora as part of the deuterostome clade, and the Ectoprocta and Entoprocta appear within a protostome or spiralian clade—albeit in an unresolved status—and rather far away from the other lophophorates. Are these positions in the tree due to real historical events, or are they the consequences of the theory that drove the analysis? A computer derived investigation of the same data base, which I understand Nielsen and his colleagues will publish soon, should provide us an answer.

So what are we left with? In short, this book still stands as a fine piece of work in my opinion. I’ve given up long ago believing any of us has the inside track on the truth. All we can effectively do is organize knowledge, and Nielsen has done an excellent job at that task. I wish that he would have done this within the framework of computer derived parsimony. However, Nielsen’s logic is clear enough for anyone to follow. His results also confirm in part the conclusions of others as mentioned above. Most importantly, however, Nielsen’s book immediately demands that speculations about the relationships of animal phyla cease unless they also occur within a cladistic framework. Animal phylogeny now sits securely at the high table of the science of systematics.—Frederick R. Schram, Institute for Systematics and Population Biology, University of Amsterdam, Postbox 94766, 1090 GT Amsterdam, The Netherlands.

REFERENCES
