
Preface

A recent paper by Dunn *et al.* in *Nature* presents a phylogenetic tree of the metazoans based on a newly increased sample of molecular sequences for 77 representative species. The results support many phylogenetic hypotheses that have been consolidating during the last couple of decades in the context of an increasingly heated debate on the interrelationships among the main animal lineages. For example, the clade of moulting animals, the Ecdysozoa, is supported, which groups together animals as different as arthropods (spiders, crabs, millipedes, and flies) and nematodes (the roundworms, e.g. the filarias and the model species *Caenorhabditis elegans*). Also supported are the Lophotrochozoa, a very diverse assemblage including molluscs, annelids, flatworms, and a diversity of smaller or less familiar groups. Supported too are other groupings the reader will find in this book, such as the Ambulacraria (echinoderms plus hemichordates) and the Tetraconata (crustaceans and insects, to the exclusion of myriapods). However, the phylogeny of Dunn *et al.* (2008) also suggests a number of unexpected and arguably controversial hypotheses. First, the deepest split in the new metazoan tree is one between the Ctenophora (the fragile comb-jellies) and all remaining groups, rather than the traditional contrast between the sponges (or, probably better, a subset of the former Porifera) and all other animal groups. Second, sponges and cnidarians (hydras, medusae, corals, and sea anemones) appear to form, together, a lineage sister to all other animals to the exclusion of the ctenophores. Third, the acoels, a group of small marine worms traditionally classified with the flatworms but recently acknowledged to occupy to a very basal position in the tree, is found in the *Nature* tree in

the odd company of little-known groups such as myzostomids and gnathostomulids, in a branch which is deeply nested within the thick crown of the tree.

Will these three phylogenetic hypotheses eventually replace those presented in this book, which have been distilled from the evidence available until last week? And, if so, how robust will they prove to the challenges of future investigations?

No later than June 2007, an international conference on animal phylogeny held at the Royal Society of London left the general impression of a growing convergence of molecular, morphological, developmental, and palaeontological evidence towards a reconstruction of animal interrelationships different from the new tree now presented in *Nature*. Interestingly, some of the 18 authors of the *Nature* paper were among the contributors or the discussants at the Royal Society's conference. This circumstance shows how much our trees are still dependent on a body of evidence that is obviously growing, and thus changing, rapidly, so that we must be cautious before accepting this or that grouping as definitive.

An obvious implication is that a book is not the best place to look for the best tree of the day. On the one hand, phylogenetic research is such a lively branch of science that a serious update on its output can only be found by checking the most recent issues of pertinent journals. On the other hand, at the moment there is, arguably, nothing like a single best tree for the metazoans. Some trees are probably more useful, or more reliable, in delineating the main branching of the animal tree, rather than the internal phylogeny of annelids, molluscs, or chordates, whereas

others are more accurate in this respect, but less informative at the level of deeper branchings. Much depends, of course, on the set of representative species included in the analysis. Thus, irrespective of its merits in suggesting the interrelationships between, say, sponges, cnidarians, and bilaterians, the paper by Dunn *et al.* (2008) is probably not the best place to look for the internal phylogeny of molluscs or arthropods, which are represented by only eight and nine species respectively. Therefore, I refrain from expressing my scepticism with respect to the Cephalopoda (squids and octopuses) branching with the shellless, worm-like Chaetodermatida (=Caudofoveata) rather than with some group of shell-bearing molluscs. Correspondingly, I must refrain from manifesting my satisfaction with the suggested branching of myriapods (actually, of the only myriapod in the sample) with the Chelicerata (spiders, scorpions, and mites) rather than with the Tetraconata (insects and crustaceans), in agreement with the phylogenetic relationships suggested in this book.

Thus, taking the expected ephemeral lifespan of so many current hypotheses of phylogenetic interrelationships among animal lineages for granted, what is this book about? As promised by the title, I only aim to offer an articulated set of perspectives on animal phylogeny and evolution. Forty years ago, animal phylogenetics was a Cinderella who could not dream to have its discoveries published in the most important scientific journals. Many causes have contributed to its eventual progress to a much higher status. Some of these causes are environmental rather than structural, but are anyway important; others are more technical and specific. First, whatever the nature of the characters considered and the principles according to which the analysis is performed, reconstructing the tree of life only makes sense in the context of an evolutionary view of life. Developments in phylogenetics have been largely independent from advance in the other provinces of evolutionary biology; nevertheless, the increasingly positive reception of phylogenetic studies has certainly benefited from a generally growing interest in evolution in the community of biologists.

Second, phylogenetic analyses are performed with the help of dedicated software. This is very important, not simply because of the computational power of the machines, but most of all because it demonstrates that phylogenetic inference is obtained by applying a set of explicitly formulated rules. This does not mean that today we must completely dispose of the perceptive but informal insights of specialists with a lifelong experience with a taxonomic group, but their precious experience is required in the selection of the taxa and the characters on which the analysis will be performed, and in the subsequent interpretation of the results, but not in the actual phylogenetic analysis. To be sure, we cannot expect 'objectivity' from a machine-run analysis, which obviously depends on the quality of the input data and the rules embodied in the software, but the very fact that these data and rules are made explicit in every analysis will always allow for that recursive process of challenge and revisitation that is vital to science.

Third, phylogenetics has become molecular. Filling a data matrix with numerical codes to be used for a phylogenetic analysis has proved to be a very critical and often controversial step. This is particularly true in the case of the traditional kind of evidence, mostly from morphology, but also from embryology. Things are generally less controversial with molecular data; that is, essentially, with the nucleotide or amino acid sequences that currently represent the single largest source of data available for phylogenetic analyses. By increasingly moving from morphological to molecular, phylogenetics has not simply obtained a much larger body of evidence. Additionally, it has got a chance of sharing a little bit of the unique visibility of molecular biology, something morphology-based phylogenetics would have never enjoyed. There is a place for phylogenetics even at that frontier of molecular biology, genome sequencing, which has satisfied the media that, similar to other disciplines such as physics and astronomy, biology is able to develop real 'big science' projects.

Thus, phylogenetics has its credentials: it uses algorithms, it analyses molecular (including genomic) data, and it aims to comprehensively

reconstruct the whole tree of life. But the next questions are: how successful is this enterprise? And, perhaps more important, what is it actually for? Why are we so keenly interested in reconstructing phylogeny? Is this a target per se, or just a necessary step towards a less immediate, but more interesting and rewarding research target? These questions are introduced in the first two chapters of this book and revisited again in the final chapter. I only anticipate here that I do not see phylogeny as a final aim. Otherwise, I would not have written the last three chapters of this book, those where I dare to express my personal and sometimes idiosyncratic views more extensively.

With Chapter 3 we abandon these mainly conceptual and methodological questions to circumscribe the context within which we will move. The chapter deals with the relationships of the animals (Metazoa) to other lineages of living beings, as well as with the palaeontological evidence on the earliest animals, including some fossils whose animal nature is possible but not certain. Chapters 4 to 6 summarize the main hypotheses of phylogenetic relationships among major animal groups. Some nodes of the tree will deserve a more articulated discussion, especially in a few cases where in recent times alternative hypotheses have been defended that have major consequences for our reconstruction of the evolution of animal morphology and development. Some aspects of this evolution are highlighted in the next two chapters, against the background of the provisional consensus phylogeny emerging from the previous pages. Chapter 7 focuses on evolutionary aspects of reproduction and development, Chapter 8 on the evolution of the most general traits of animal morphology, such as body axes and segmentation, as well as the main organ systems. Finally, Chapter 9 summarizes the main lessons that I have learned from this short walk through animal phylogeny and evolution. The core message is that evolution is not simply one of origin of species or, indeed, of clades, but also one of origin of rules, to such an extent that the very concept of origin becomes problematic.

As often happens with books, *Perspectives on Animal Phylogeny and Evolution* has evolved extensively since I first tentatively drafted its contents, in replying to stimulating input from Ian Sherman, who eventually become my editor at Oxford University Press and, no less important, a good friend of mine. Since then, Ian has been supporting me by all means, including a well-justified strong reaction to my continuous delays in delivering the manuscript. Together with him, Helen Eaton has also let me appreciate how much attention Oxford University Press pays to authors, even the most recalcitrant. More recently, I have experienced also friendly, fruitful interaction with Nik Prowse, the best copy editor I ever met, and with Carol Bestley, sensible and accurate production editor. My most sincere thanks to all of them.

I should add here a list of colleagues and friends from whom I have learned most of what is summarized in these pages. But this list would be too long: to some extent, it would duplicate the list of references. Therefore, I only mention here Ron Jenner (Bath), whose papers have been my single best and most critical source of information about the current phylogenetic debates, and Andreas Schmidt-Rhaesa (Hamburg), to whose excellent book on the evolution of animal organ systems, published by Oxford University Press in 2007, I refer the reader for a subject area I could never dream to cover in this book as accurately as he did. My young research associates at the University of Padova have helped me with healthy discussion and literature search: my sincere thanks to Massimo Bernardi, Lucio Bonato, Leandro Drago, Giuseppe Fusco, Diego Maruzzo, and Marco Uliana. Renzo Mazzaro and Matteo Simonetti have assisted me in preparing or editing the illustrations. Most of the images in this book have been very kindly offered by a huge number of old and new friends worldwide: their names are given individually in the figure legends. To all of them I extend here my warmest thanks for an extremely prompt and sympathetic reply to my shameless request for help.

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