Chapter 10

Discussion & Synthesis
DISCUSSION AND SYNTHESIS

Metazoan phylogeny and body plan evolution: potential pitfalls of a necessary interpretive framework

Phylogenetic systematics or cladistics has been instrumental in transforming a diversity of comparative or historical scientific disciplines into fully fledged evolutionary sciences, ranging from evolutionary paleobiology to evolutionary developmental biology. With these developments came the realization that a phylogenetic framework is a crucial tool for studying the evolutionary assembly and diversification of animal body plans. The molecular view of animal relationships that developed throughout the 1990s has been widely adopted to serve this role of interpretive framework. The spectacular findings of molecular developmental biologists that substantial parts of the genetic machinery underpinning the development of animal form in disparate phyla are apparently conserved, fueled intense interest into the big questions of animal macroevolution. During the mid-1990s the first molecular clock estimates of deep metazoan divergence dates based on different molecular data sets were published, which ushered in the interesting debate (continuing today) about the significance of these temporal estimates of deep time events. The combination of data from molecular developmental biology, molecular phylogenetics, and molecular clock estimates naturally led to the legitimate question as to what our deep ancestors looked like. The focal point of these inquiries quickly became apparent: Urbilateria, the elusive most recent common ancestor of the Bilateria.

In chapters 3 and 4, I attempted to separate some urbilaterian facts and fantasies by explicitly evaluating the phylogenetic foundations of several hypotheses of animal body plan evolution. In particular, I emphasized the theoretical and empirical inadequacies of the use of pruned or incomplete phylogenies for understanding body plan evolution. The selected examples discussed in these chapters are especially relevant for the numerous hypotheses of body plan evolution posed within a molecular phylogenetic framework, because earlier studies were necessarily confronted with the limited availability of sequence data for only a selection of higher level metazoan taxa. However, rather than considering pruned phylogenies as an important warning against advancing unsupportable and premature hypotheses of body plan evolution, instead they were enthusiastically embraced by many as a welcome alternative to morphological speculations. In fact, the failure to include all pertinent taxa (and sometimes even the lack of phylogenetic resolution) was rather effectively used to construct novel hypotheses of animal body plan evolution (see in particular the discussion of the roundish flatworm hypothesis by Gerhard & Kirschner in chapter 3, and Balavoine’s hypothesis for evolution of the platyhelminth body plan in chapter 4). Naturally, the excluded phyla
never ceased to exist, but for all practical purposes, lack of sequence data appeared to equal non-existence of the organisms.

The unjustifiable use of pruned trees is more widespread (see also chapter 6), however, and in some instances the problem is compounded by a detrimental bias in the selection of taxa even when more comprehensive sampling is possible. The phylogenetic frameworks marshaled in support of the hypothesis of platyhelminth body plan evolution and the set-aside cell hypothesis discussed in chapter 4, both independently exhibited exactly the same unwarranted bias in taxon selection: a bias towards coelomate, indirectly developing bilaterians. Given this bias, it is hardly surprising to learn that the respective conclusions of these studies reported that Urbilateria was a coelomate, and an indirect developer. In both cases, I used a more comprehensive phylogenetic framework to reinterpret the proposed hypotheses, not surprisingly leading to quite different conclusions.

A final curious and worrisome aspect of the current use of phylogenies relates to the use of history, in particular the alleged views of one of the most influential invertebrate zoologists of the 20th century, Libbie Henrietta Hyman. Invertebrate zoology textbooks, as well as primary research papers and reviews of metazoan phylogenetics in the current literature, frequently present the phylogenetic views of Libbie Hyman as an icon for the Anglo-Saxon view on animal relationships, and as a convenient starting point for the discussion of our current progress in understanding. However, as I outline in chapter 4, Hyman's views have been badly misrepresented in virtually all modern papers that cite her thoughts on metazoan phylogeny. Respect for our intellectual forebears amply justifies a proper reinstatement of Hyman's ideas on metazoan phylogeny.

Metazoan cladistics: epistemology and cladistic knowledge-claims, or practice what you preach

The first impression one will get from perusing the literature on morphological cladistics of the Metazoa published during the last decade will be that alternative phylogenetic hypotheses are abundant. The new millennium was inaugurated with the publication of no less than five new comprehensive cladistic analyses of metazoan morphology (including total evidence analyses) (Giribet et al., 2000; Sorensen et al., 2000; Nielsen, 2001; Peterson & Eernisse, 2001; Zrzavy et al., 2001). Some degree of topological congruence among these phylogenies is undeniable, but by far the most striking observation is that significant differences between these phylogenies prevail. This invites an obvious question: is it possible to nominate any of these phylogenies as a superior summary of morphological evidence? If we want to make reasonable inferences about the macroevolution of animal body plans, it is important that we select the most highly corroborated phylogeny. In order to identify this phylogeny, we need to confront the morphological data matrix.
The self-evident fact that the structure of the data matrix predominantly determines the outcome of a cladistic analysis hardly needs mentioning. Data matrix construction arguably is also the most difficult step of a cladistic analysis, and it is the only anchor that connects a cladogram to the empirical world. However, a remarkable paradox of cladistic practice then becomes apparent. This most important and difficult aspect of cladistic analyses has received strikingly little explicit attention, either theoretical or practical, especially when compared with the attention directed towards the extraction of phylogenetic signal from a given matrix. Typically we are presented with variations upon the minimally transparent statement that “the morphological matrix was compiled from various sources from the literature.” A larger section of the paper subsequently discusses aspects of cladogram construction, and finally the resulting topology is discussed with respect to topologies supported by other analyses. Despite the fact that an increase in understanding happens after discovering the most parsimonious cladograms (Kluge, 1997b), it is nevertheless clear that the matrix is never explicitly revisited after cladogram construction in recent cladistic studies of the Metazoa. However, as Wenzel (1997: 41) noted: “character reexamination should be an integral part of all phylogenetic studies...or the process of discovery will be crippled pointlessly.”

In order to achieve some progress in understanding higher level metazoan relationships we need to pry open this most prominent black box of cladistic analyses. Chapters 5, 7, and 8 specifically focus on these neglected aspects of cladistic analyses of the Metazoa. Chapter 5 reports a first attempt to explicitly evaluate alternative phylogenetic hypotheses of the Metazoa in terms of the various contributions of acknowledged ingredients of any cladistic study to the conclusions, ranging from character coding to taxon selection. The general conclusion was that morphological cladistic analyses of the Metazoa should become more experimental in order to better evaluate the robustness of the phylogenetic conclusions, both with regard to the data matrix used, and other published analyses. There is reason to believe that “playing” around with data sets is a common procedure among phylogeneticists, but it is never done in print, despite the fact that it may yield important insights into the robustness of the results. For example, it is important to understand the differential effects that variations in the assumptions feeding into the construction of the data matrix may have on the outcomes of a cladistic analysis. In studies of molecular phylogenetics, experimental manipulations of the data sets are commonly employed to assess the robustness of the outcomes of an analysis in terms of varying input parameters and assumptions. For example, it is commonplace to assess the effects of various weighting schemes for transitions/translations, or insertions/deletions costs on the results of the analysis. As the various experimental manipulations of morphological data sets reported in chapters 5 and 8 show, introduction
of such an explicit experimental approach would also be a major asset in morphological phylogenetics.

It is an acknowledged dictum of cladistics that all pertinent information should be included into an analysis, lest the results are unjustifiably biased towards reaching certain conclusions. Therefore, as a rule of thumb, it appears reasonable to use sheer size of the morphological data sets to select among available cladistic hypotheses. The analysis based on the largest data matrix embodies the largest amount of empirical information, and high empirical content is widely considered to be a desirable epistemic value of scientific hypotheses (Kluge, 1997a; Siddall & Kluge, 1997). When faced with the choice of two phylogenetic hypotheses that differ solely in the amount of character information embodied in their matrices, then from an epistemological perspective, the choice for the hypothesis based on the largest data set is better justified. The phylogeny based on the larger matrix is more strongly corroborated because it is most severely tested, i.e., by a larger number of potential falsifiers.

The largest morphological data matrix compiled for the Metazoa is that of Zrzavy et al. (1998), with 276 characters scored for all major extant metazoan taxa. With high empirical content as a much desired epistemic value, it is not surprising to learn that this phylogenetic analysis (also incorporating molecular sequence data) has become widely cited. However, as is discussed in detail in chapters 7 and 8, large matrix size in Zrzavy et al. (1998) was attained at the expense of the quality of the morphological data matrix, thereby critically compromising the phylogenetic results of this study, and those of subsequent works that recycled the same matrix.

As explained in chapter 9, Popperian testability is at the heart of cladistic knowledge-claims, and this is a view widely endorsed by cladists. It is embodied within the term “sophisticated falsification,” which is currently used to label this philosophy of phylogenetic inference. Central to an understanding of the strength of sophisticated falsification is a notion of competing hypotheses, available for testing. In cladistics, testing is done through a character congruence or parsimony test. For an effective test, the data set should be so structured that potentially corroborating and falsifying evidence for all competing hypotheses is included, so that all alternatives could in principle be vindicated or refuted. The most parsimonious cladogram resulting from the cladistic analysis then embodies the most highly corroborated, most severely tested hypothesis, with the highest explanatory power. This points to the importance of careful data matrix construction, because only unbiased selection of input data allows an efficient cladistic test.

Given the importance of careful data matrix compilation to allow cladistic testing of competing phylogenetic hypotheses, and given the presence of research cycles within an effective sophisticated falsification research program which take the results from previous analyses into explicit consideration, the question presents itself whether current practices of metazoan phylogenetics reflect these considerations. The
answer is no. Apart from attempts to maximize the efficacy of cladistic analyses through compilation of bigger matrices, I detect no clear signs of an integrated research program in morphological cladistics of the Metazoa. With the exception that several studies simply recycle unchanged or slightly modified versions of existing data sets (see chapter 7), current "progress" is best characterized as parallel lines of research based in different laboratories yielding largely independent and different morphological data sets, without any explicit attempt to critically test available alternative data sets and phylogenies. Even the largest data sets published to date differ in their selection of characters without making it clear why this is so. It should be noted that even a large, error free, but uncritically compiled data matrix still compromises the unique strength of a cladistic analysis to test conflicting hypotheses.

The support for these conclusions is elaborated in chapters 5, 7, and in particular in chapters 8 and 9. Chapter 8 is a first attempt to comprehensively reconcile the differences between competing phylogenetic hypotheses for a selected set of phyla, namely the 'acoelomate' worms. This chapter comprehensively evaluates all synapomorphies proposed as diagnostic of competing sister group relationships of Platyhelminthes, Nemertea, and Gnathostomulida. Naturally, these are merely preliminary first steps towards a complete evaluation of the morphological character support for competing phylogenetic hypotheses for all phyla, but the conclusions resulting from this study emphasize the usefulness of this approach for providing a first explicit synthesis of alternative cladistic hypotheses of higher level metazoan relationships. Chapter 9 clearly illustrates that several recent cladistic analyses that were specifically performed to test hypotheses of character evolution and phylogenetic branching order, are in fact no tests at all. The exclusion from these analyses of readily available evidence incongruent with the proposed results fatally cripple their testing power and leads to inescapable circularity.

Interestingly, despite the widespread view that cladistics is philosophically predicated upon Popperian falsificationism, current practices in the field of higher level metazoan cladistics in fact show rather strong signs of verificationism/justificationism. Only that explains why recent studies, for example the five comprehensive analyses published over the last two years as cited above, generally fail to incorporate pertinent information from available older studies. I believe that verificationist approaches to reconstructing evolutionary history stymie true progress in understanding, by merely fostering change of opinion. Following the logic of verificationism, it will be exceedingly difficult to distinguish the relative merits of competing hypotheses, which is a particular strength of falsificationist approaches. Similar concerns were already expressed in 1970s for other evolutionary disciplines such as adaptive reasoning in evolutionary biology in general, and sociobiology in particular (Gould & Lewontin, 1979; Wilson, 2000: 28).
Telling tales and spinning stories: narrative devices and the Great Chain of Being

The two parts of this thesis, part one on using trees, and part two on choosing trees, can be connected through what appears to be a common psychological attitude and resulting scientific practice: our preference for telling stories with a clear story line, and our fundamental discomfort with entertaining multiple alternative hypotheses at any given time. O’Hara (1992) drew attention to the frequent use of narrative devices that reflect the influence of the human standpoint on our representations of the evolutionary past. Narrative devices, such as unequal attention to all data, and the putting into sequence of contemporary taxa either in text or pictures, allow the formulation of a clear story line. Within evolutionary narratives the Great Chain of Being has played a prominent role in times past, and I believe its influence lingers on in modern metazoan phylogenetics, as embodied in the quote that I chose as the motto for this thesis. Our desire to tell clear, linear stories may explain our willingness to use pruned trees for studying body plan evolution (chapters 3, and 4), the presence of unjustifiable biases in the selection of taxa and characters in the reconstruction of phylogenetic relationships, and during the supposed testing of competing hypotheses of body plan evolution and phylogenetic relationships (chapters 5, 7, 8, and 9). Additionally it might explain our apparent uneasiness with entertaining multiple equally plausible hypotheses at any given time (see also chapter 6). We rather select a “preferred” cladogram from among the multiple equally corroborated most parsimonious trees, for example in Nielsen et al. (1996), and Sorensen et al. (2000), with the attendant invention of novel names for supraphyletic taxa, even if their monophyly is not supported (Acanthognatha in Zrzavy et al., 2001). These practices are easily accommodated under a verificationist perspective concerned with advocating “novel” hypotheses. However, it is difficult to explain these findings within a framework of falsificationism.

Avenues for further research

I believe it is currently impossible to nominate any published morphological cladistic analysis as an effective synthesis of all available evidence. Further studies of their relative merits are necessary before we can make any well-founded statements. This introduces a problem for comparative biologists in search of a morphological (or total evidence) phylogenetic framework. Without understanding the relative merit of alternative phylogenies, the selection of a phylogeny at this time amounts to little more than an exercise in random coin flipping. A temporary solution is the use of multiple alternative phylogenetic frameworks.

There is ample room for progress in the field of higher level metazoan morphological cladistics.
In summary:

1) There is room for several theoretical contributions, principally with respect to the logic of character coding, and the choice of semaphoronts (life cycle stages) for cladistic analysis. Studies on character coding logic are already undertaken in the theoretical literature, but a practical evaluation in the context of metazoan phylogeny has scarcely begun.

2) Continual re-evaluation of data matrix quality. This includes attempts to reduce ambiguity in the scoring of ground patterns for variable higher level taxa, for example, through phylogenetic analyses within terminal taxa.

3) Careful compilation of data sets so as to fully exploit the testing power of cladistics.

References


