Lophophorate Phylogeny

Four new gene sequences presented in the report by Kenneth M. Halanych et al. (1) reinforce earlier conjectures (2–5) that the lophophorates (brachiopods, euctroctects, and phoronids), long thought to lie either close to or within the deutrostomes (6, 7), cluster with other protostomes. Although largely neglected by mainstream zoology, such a conclusion actually has a long pedigree (8, 9). While we agree that evidence from a nuclear-encoded small subunit (SSU) ribosomal RNA gene sequence strongly supports the association of lophophorates with protostomes, the proposed phylogeny (1) and its expression in a new taxonomic category, the “Lophotrochozoa” (1) are open to at least four criticisms: (i) premature introduction of a new taxonomic category, (ii) the need for a more cautious interpretation of euctroctect molecular phylogeny, (iii) the incongruence of the proposed phylogeny with paleontological data, and (iv) questions about sequence reliability.

1) For anyone attempting to reconstruct a phylum-level phylogeny from an alignment of the many currently available protostome SSU sequences (10), a cautious approach is advisable. Caution is also necessary when choosing an outgroup. As no unambiguous evidence yet identifies the sister group (or groups) of protostome phyla collectively or individually, it is probably premature to root phylum-level trees, especially with distant taxa (as Halanych et al. have done). Because the role of molecular phylogenies as a primary basis for animal classification is controversial, and because the complex relationship between molecular phylogenies and taxonomic practice is still evolving (11), major taxonomic changes should not be proposed on the basis of a single gene sequence; congruent evidence from multiple, independent genealogical sources is needed.

2) The euctroctect byssoco are a highly diverse phylum (12, 13), yet their phylogenetic relationships have been inferred from the SSU sequence of a single species, Plumatella repens (1). However, the class to which Plumatella belongs is not typical of the phylum (14), and the wide range of extant euctroctect diversity is not reflected in available sequences, one of which (15) has unusual apomorphies and might not be representative. No decision about the phylogenetic relationships of the whole phylum is yet firm enough to justify its place in a new taxonomic category (1).

3) Excluding some highly questionable Cambrian examples (16), the first convincing euctroctects are Ordovician (17). Moreover, all known euctroctects are colonial; possible solitary forms are not recognized in the fossil record until well after the first appearance of colonies (18), postdating by perhaps 50 million years the Lower Cambrian appearance of brachiopods, annelids (polychaetes), and mollusks. Thus, a phylogeny (1) that places the origin of euctroctects basal to the origins of these phyla is inconsistent with present knowledge of the fossil record. As it is unlikely that fossils of hard-bodied, Lower Cambrian euctroctects have been overlooked, such a phylogeny (1) predicts that ancestral euctroctects were soft-bodied. There is currently no evidence from Cambrian faunas such as the Burgess Shale that such forms existed, although the possibility cannot be dismissed. This incongruence between paleontological and molecular evidence emphasizes the need for a cautious approach to the use of molecular phylogenies in classification.

4) When we compared the four new lophophorate SSU sequences (1) with homologous sequences from many other protostomes, including another phoronid (GenBank accession number U36271) and another inarticulate brachiopod (GenBank accession number X81631) (15 and 19, respectively), we found that nucleotides were missing at several sites that are otherwise completely or almost completely conserved (20). The Glotiaida sequence (GenBank accession number U12647) also had an unusual deletion affecting only one strand of a helical stem region, whose general form is also widely conserved (21–23). These results call into question the reliability of the data in, and the conclusions of, the report by Halanych et al.

The ultimate value of molecular biology in understanding early metazoan evolution is not in dispute, but without data from a sufficiently wide range of genes and species and from other data sources such as the fossil record, progress may be delayed or diverted. Paleontological information can throw light on apparent inconsistencies in a phylogeny or, alternatively, reveal intermediate states between what we choose to call phyla (24). For example, the fossil record may display unexpected, phylogenetically informative combinations of character states directly relevant to the evolution of lophophorates; in particular, the “shells” and precursors of the seata in halkierids suggest a more direct connection between this group and brachiopods (25).

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20. The most unambiguously missing sites, identified by reference to the sequence of Ochridella cetica (GenBank accession number X72231), include Glotiaia pygmaea, 424, 475, 1259–1261, 1541, 1567, 1577, 3900, 1387, 1395; and Plumatella repens, 1680.
The purpose of our report (1) was to determine the phylogenetic placement of the Lophophorata. Specifically, we wanted to know whether lophophorates are protostomes, deuterostomes, or an independent groupage of metazoan evolution. Conway Morris et al. agree with our major conclusion, that the Lophophorata are a part of the deuterostome radiation. However, they do mention some specific issues about our report.

... To emphasize our major conclusion, we must decide whether the node-based theory of evolution (that is, byoschekans, brachiopods, and phoronids), gastropods, and all of the descendants of that common ancestor. The utility of node-based names has been thoroughly discussed in previous papers and is reviewed in (4) evidence 

... In our original report, it is suggested to be inconsistent with paleontological evidence. Other reports by Conway Morris (3) show that our results agree well with the fossil record. The fact that a solitary, soft-bodied, ancestral bryozoan fossil has not been discovered is not unexpected given the incompleteness of the fossil record.

... The most serious issue raised by Conway Morris et al. is that of data reliability and its effect on our conclusions. The presence of indels in conserved regions of the 18S rDNA does occur across metazoan taxa (6). Since our publication, we have reexamined our results and have found a few minor errors in some of our sequences (7). The GenBank submissions have been appropriately updated. Also, Conway Morris et al. were correct in pointing out the mistake in the Glottida helical stem region. However, this region is not conserved across triploblast metazoans, and therefore most of it was excluded from the original analysis because it cannot be aligned unambiguously. We have reanalyzed our data incorporating these corrections, and our original phylogenetic tree, bootstrap trees, and conclusions are unaffected. Additionally, an independent study (5) has confirmed our major conclusions.

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6. 18S rDNA sequences often exhibit indels in highly conserved regions. Below are a few examples: Strongylocentrotus purpuratus (echinoderm), GenBank accession number L26095; six indels in conserved regions when aligned to our own data set; Arctica islandica (echinoderm), D14357; five indels; Limcola kamtschatica, K56476; three indels; Artemia salina (crustacean), K01723; two indels; Pleurobrachia luteostoma (bryozan), K56899; two indels; and two Euryepa californica (chelicerate), X13457, one indel.
7. Updates have been reported for the Plumatella repens (GenBank accession number U12649), Terebratalia and transversa (U12650), Phoronis vancouverensis (U12648) sequences. In addition to minor changes, the Glottida pyramidalis (U12647) contained a mistake in a helical stem region. Most of these mistakes were originally reported as gaps and occurred at phylogenetically uninformative positions. Because they were originally scored as gaps, they were considered as missing information in the analyses, and therefore had no bearing on our conclusions.

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