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, euctopics, and phoronids), long thought to lie either close to or within the deuterostomes (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” (10) are open to at least four criticisms: (i) premature introduction of a new taxonomic category, (ii) the need for a more cautious interpretation of euctoponct 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 prime 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 euctoponct Bryozoa 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 euctoponct 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 euctoponct are Ordovician (17). Moreover, all known euctoponct are colonial; possible solitary forms are not recognized in the fossil record until well after the first appearance of colonies (18), post-dating by perhaps 50 million years the Lower Cambrian appearance of brachiopods, annelids (polychaetes), and mollusks. Thus, a phylogeny (1) that places the origin of euctoponct 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 euctoponct have been overlooked, such a phylogeny (1) predicts that ancestral euctoponct 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 Glottidia 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 (24, 25), 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 setae in halkids suggest a more direct connection between this group and brachiopods (25).

REFERENCES AND NOTES

20. The most unambiguously missing sites, identified by reference to the sequence of Orchidella celtica (GenBank accession number X7021), include Glottidia pyriformata, 424, 476, 1639–1631, 1642, 167; Phoronis vanourensis, 380, 1397, 1356; and Plumatella repens, 1680.

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Science 272 (5259), 282-283.
DOI: 10.1126/science.272.5259.282