INARTICULATA, BRACHIOPODA, LOPHOPHORATA: WHAT DO THEY SIGNIFY?

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Higher taxonomic ranks typically distinguish morphologically disparate groups whose within-group common ancestry is assumed to be more recent than that between groups. Because in practice this assumption is rarely tested, common wisdom now advocates that the relationship between traditional classifications and phylogenies be made more explicit. Classifications of organisms were established originally to serve a variety of purposes, which may or may not have had an evolutionary rationale. Thus, if named superspecific taxa are to play an interpretable role in macroevolutionary studies, their status as clades should at least be investigated, if not demonstrated unambiguously.

The monophyly of the Brachiopoda is supported by a large number of synapomorphies, both morphological and embryological. Within the Brachiopoda, systematists have focused historically on single character ("key innovation") definitions of higher taxa (e.g., attitude of the pedicle relative to the valves, nature of articulation between the valves, valve mineralogy); this procedure has resulted in intraphylum divisions whose evolutionary significance is uncertain. For example, monophyly of the Inarticulata continues to be debated vigorously; the position of the calcareous inarticulates (craniaceans) is particularly contentious. The traditional classification, based largely on the presence or absence of teeth and sockets, has been challenged recently by the following arguments: lack of articulation is primitive for brachiopods and, as a symplesiomorphy, cannot define a major clade; valve mineralogy is a more reliable indicator of phylogenetic affinity because phosphatic and calcareous-shelled brachiopods both appear very early in the fossil record.

To test these arguments in the broader context of metazoan phylogeny, I chose to investigate not only relationships among brachiopod higher taxa, but also of brachiopods to other lophophorates and selected protostome and deuterostome taxa. I analyzed (using PAUP 3.0) the phylogenetic relationships among the seven Recent brachiopod superfamilies (assuming each to be monophyletic), using 119 characters of soft and hard anatomy and embryology. Four outgroup taxa were used: Phoronida, Bryozoa, Sipunculida, Pterobranchia. One most parsimonious cladogram of length 219, C.I. = .722, resulted. In this cladogram, Inarticulata and Articulata are each monophyletic, with 9 and 32 synapomorphies, respectively. Calcareous skeletal mineralogy is clearly primitive for metazoans; there is no justification for claiming it as a synapomorphy of a clade within the Brachiopoda. Outgroup analysis has no power, in this instance, to determine the polarity of articulation, since no outgroups possess two valves (molluscs and other animals have evolved the bivalved condition independently, based on numerous other characters); thus, the lack of valve articulation is not unambiguously primitive, by this polarity criterion.

Although many textbooks continue to refer to Lophophorates as a group distinct from other metazoans, presumably by virtue of common ancestry, "lophophorates" do not appear to be monophyletic unless the possession of a lophophore is selectively weighted; among the outgroups in this cladogram, bryozoans cluster with sipunculids, and phoronids with pterobranchs. The notion that lophophorates, as a group, are in some sense "intermediate" between protostomes and deuterostomes must be investigated in greater detail, phylogenetically.