

## On the origin of the Lophophorata

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Brachiopoda, Bryozoa (= Ectoprocta), and Phoronida are closely related; they share together a large proportion of common structures, overall an archimerate (= oligomeric, trimerous) body plan around which are developed all Lophophorates and the same kind of food-gathering apparatus known as the lophophore, recently redefined by EMIG (1976 a). And for these reasons are believed by most recent authors to form a close-knit phylogenetic group, named Lophophorata, even three separate phyla have been preferably retained. Nevertheless, it is my guess (EMIG 1976 b, 1977, 1982) that the three lophophorate phyla constitute not only a phylogenetic assemblage but also a natural systematic unit, and in this way the Lophophorata as a taxon deserves the status of a phylum, the Brachiopoda, Bryozoa, and Phoronida being classes. The directionality argued here suggests a monophyletic origin of the Lophophorata phylum, possessing an ancestral stem from which each class arose via radiation and anatomical modifications by independent and quite dissimilar ways.

Brachiopoda are known from the early Cambrian, some supposed Precambrian. Inarticulates are represented unequivocally in the Lower Cambrian, but probably the earliest Articulates occurred at the same period. Both Inarticulates and Articulates become then expansion in the late Cambrian, precursors of the great Ordovician radiation, where the Brachiopoda attained their evolutionary climax (WILLIAMS and HURST 1977). On their origin, there are two views, whether they arose monophyletically or polyphyletically. But more evidence is presently for a monophyletic radiation, perhaps from a prototypic brachiopod ancestor as described by WILLIAMS and HURST (1977). Thus the Articulates are derived from primitive Inarticulates during the late Precambrian and have evolved independently and significantly radiated in different lines. The radiation of the encapsulation of the Brachiopod body is clearly of cardinal interest, that needs furthermore studies to assert a monophyletic origin.

Bryozoa appeared in the early Ordovician, possibly become evident in the Cambrian, and they underwent rapidly a great burst of evolution into the major taxa.

Fossil Phoronida are only known by their burrows that seem to have been present since the Devonian (cf. EMIG 1982) and no evidence exists of their occurrence before this period. In regard to the other Lophophorata classes either Phoronida first appear during the Devonian peak of diversification or in absence of hard-skeleton fossils are unknown but the radiation occurred in the early Cambrian, even late Precambrian as suggested by FARMER (1977).

The first primitive Brachiopoda, Bryozoa and Phoronida appeared abruptly and were organised and differentiated. In this way the first appearance of brachiopod and bryozoan skeletons indicates the time of their origin, not necessarily those of their body plan. But such acquisitions in relation to divergent anatomical plans, as exemplified by lophophore adaptations and life modes, open to exploit broad opportunities which may explain, as in other phyla, the occurrence of rapid radiations in new directions, particularly during late Precambrian and early Cambrian (see Fig.). The fact that Phoronida remain an ancestral

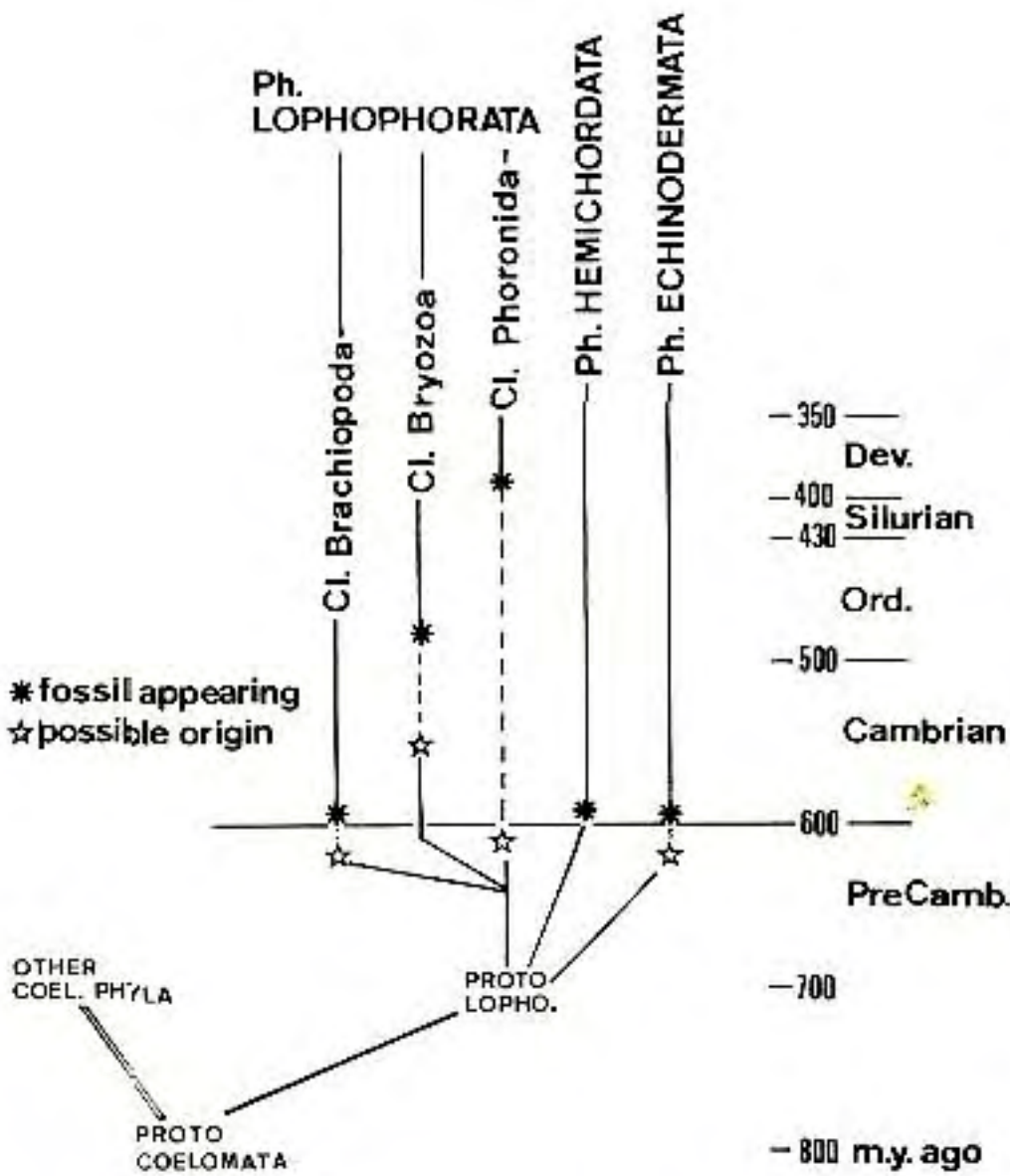


Fig. Diagram illustrating the phylogenetic connections of the Archimerata phyla (Chordata are not shown) with possible timing of appearance

So the remote ancestry can only be reconstructed by phylogenetic way. The features present in the ancestral lophophorate stock can be established on the basis of the possession of a common body plan (EMIG 1982): the archetypal form is a small soft-bodied animal, with three distinctive regions, each with its own coelom separated by a septum and charged with separate functions. However, a distinctive archimerate adult body plan, although modified in some brachiopods and bryozoans, occurs in each three classes according to their particular range of life modes, but also in their larval body. The archetypal form had: — a trunk or metasome, unsegmented with a pair of metanephridia (coelomoducts and gonoducts), an U-shaped digestive tube bringing the anus outside of the lophophore. The trunk was employed primitively for burrowing and to sustain the animal in its infaunal mode of life. The evolution to an epifaunal mode by Bryozoa and Brachiopoda leads to reduce the functional importance of the metacoelom, but in both modes this coelom is a functional necessity. The trunk wall was capable of secreting mucopolysaccharides to shape an exoskeleton, probably a tube as in Phoronida, to become a pair of unarticulated valves in Brachiopoda and different types of exoskeleton in Bryozoa. — A lophophore or mesosome, oval shaped around the mouth with a single row of tentacles. Its main functions may be feeding, respiratory, and protective (EMIG 1976 a). This lophophore had probably the possibility to be retracted in the anterior trunk part. The lophophore of all three classes is easily derived from such a type, including Brachiopoda, which involved the single trocholophe. — A small poorly developed protosome, represented by

plan and form, adapted to their infaunal mode of life, may explain the small variety of phoronid species (10 species, 2 genera). The Ordovician radiation represents merely the acquisition of mineralized skeletons by Brachiopoda and Bryozoa (HYMAN 1959; VALENTINE 1977), when also bony structures were just emerging in other organisms (JOPE 1967), whilst both classes developed also epifaunal adaptations, except some taxa as Lingulida which remained mainly infaunal. During this period the Lophophorata as other suspension-feeding lineages shared in the thorough exploitation of marine habitats.

According to the some supporting evidence for timing the coelomate phyla origin given by VALENTINE (1977), the Lophophorata ancestor appeared well before the Precambrian-Cambrian boundary, i. e. between about 800 and 700 m. y. ago (Fig.), and the earliest evolutionary stages as well as direct paleontological evidence are not preserved.

the epistome as a mere fold above the mouth with probable functions in feeding (particle sorting) and lophophore sustaining.

This remote ancestor was a burrowing vermiform suspension-feeder of infaunal mode of life, such an ancestor all suggests a phoronid-like form we call Proto-Lophophorate. Because the latter shares several features overall the body plan in common with the other Archimerata phyla, i. e. the Hemichordata and the Echinodermata both considered as lower Deuterostomes, it is logical to expect their close affinity with Lophophorata, to which the Hemichordata bears most resemblance (EMIG 1982). VALENTINE (1977) stated that epi-faunal mode of life imply descent from infaunal precursors and that the appearance of epi-faunal descendants may be considered as an importante episode of genome growth.

The offshoot of the Protolophophorates has probably arisen directly from a flatworm-like coelomata, with addition of a mesodermal body space through modification within the genome leading to a re-ordering of organ systems to create novel body plans, and presumably the primitive lophophorate stem evolved without metameric stage (HYMAN 1959; EMIG 1976 b; VALENTINE 1977). In view of this opinion, the speculative hypothesis of GUTMANN et al. (1978) to derive the Lophophorates from an annelid-like metamerous ancestral form seems highly unlikely, and the Lophophorates do not represent a central group in the coelomata phylogenetic system leading to Spiralia and Chordata as was proposed by SIEWING (1976, 1980). The resemblance between Spiralia (or Gastroneuralia or Protostomia) and Lophophorata have proven to be incorrect (EMIG 1962; SALVINI-PLAWEN 1982) as well as to consider the larval body plan of Lophophorata as deriving from a trochophore type.

### Summary

Brachiopoda, Bryozoa, and Phoronida may be considered not only as a phylogenetic assemblage but also as a systematic unit, the phylum Lophophorata. They may therefore be regarded as different lines of evolution which have diverged from a common ancestor in very early times, during the Precambrian. Phylogenetic speculations lead to describe the main features of the soft-bodied, tri-regionated coelomic Protolophophorate and its similarities deserve reassessment as ancestor from which the other Archimerata phyla, i. e. Echinodermata and Hemichordata, have evolved.

### Zusammenfassung

#### *Über die Entstehung der Lophophoraten*

Brachiopoda, Bryozoa und Phoronida können nicht nur als Gruppen mit gewissen phylogenetischen Beziehungen betrachtet, sondern als Stamm Lophophorata zusammengefaßt werden. Die drei Gruppen dürften sich im Praecambrium aus einer gemeinsamen Ahnenform differenziert haben. Es wird versucht, die wesentlichen Organisationszüge des „Protolophophoraten“ zu rekonstruieren, der als eine in drei coelomhaltige Körperregionen gegliederte Weichkörperorganisation aufgefaßt wird. Von einer derartigen Organisation können auch die anderen Archimerata Phyla, so die Echinodermata und Hemichordata abgeleitet werden.

### Literature

- EMIG, C. C., 1976 a: Le Lophophore – structure significative des Lophophorates (Brachiopoda, Bryozoa, Phoronida). *Zool. Scripta* 5, 133–137.  
 – 1976 b: Phylogenèse des Phoronida. Les Lophophorates et le concept des Archimerata. *Z. zool. Syst. Evolut.-forsch.* 14, 10–24.  
 – 1977: Un nouvel embranchement: les Lophophorates. *Bull. Soc. zool. Fr.* 102, (4) 341–344.  
 – 1982: The Biology of Phoronida. *Adv. mar. Biol.* 19, 1–89.  
 FARMER, J. D., 1977: An adaptative model for the evolution of the ectoproct life cycle. In: *Biology of Bryozoa*. (Ed. by R. M. WOLLACOTT, R. L. ZIMMER). London and New York: Academic Press. 487–517.  
 GUTMANN, W. F.; ZORN, H.; VOGEL, K., 1978: Brachiopods: biomechanical interdependences governing their origin and phylogeny. *Science* 199, 890–893.  
 HYMAN, L. H., 1959: *The Invertebrates: Smaller Coelomates Groups*. New York: McGraw Hill.

- JOPE, M., 1967: The protein of brachiopod shell. I. Amino-acid composition and implied protein taxonomy. *Comp. Biochem. Physiol.* 20, 593–600.
- SALVINI-PLAWEN, L. VON, 1982: A pedomorphic origin of the oligomeric animals? *Zool. Scr.* 11, 77–81.
- SIEWING, R., 1976: Probleme und neuere Erkenntnisse in der Grosssystematik der Wirbellosen. *Verh. Deutsch. Zool. Ges.* 1976, 59–83.
- 1980: Das Archicoelomatenkonzept. *Zool. Jb. Anat.* 103, 439–482.
- VALENTINE, J. W., 1977: General patterns of Metazoan evolution. In: *Patterns of Evolution as illustrated by the fossil record*. Ed. by A. HALLAM. *Develop. Palaeontol. Stratigr.* 5, 27–57.
- WILLIAMS, A.; HURST, J. M., 1977: Brachiopod evolution. In: *Patterns of Evolution as illustrated by the fossil record*. Ed. by A. HALLAM. *Develop. Palaeontol. Stratigr.* 5, 79–121.

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