# How ancient is the adult swimming capacity in the lineage leading to Euchordates?

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Current understanding of animal phylogeny has provided new insight on the evolution of the ancestors of the Euchordata (cephalochordates+vertebrates). Modern, adult euchordates possess a capacity for swimming, displacing themselves through water independently of currents. Swimming is achieved by the presence of a fin and axial body movements. However, the classic hypothesis on the origin of euchordates prescribes that their adult ancestors were sessile, and that axial swimming was only present in larvae that developed into sessile adults by metamorphosis, as in ascidian urochordates (Fig. 1). This implied that the free-living and swimming euchordate adults were paedomorphic (Garstang 1928). This hypothesis was compelling for several reasons. First, sessile adult lifestyles are present within every major group of deuterostomes (ascidian urochordates, pterobranch hemichordates, and crinoid echinoderms), raising the possibility that this was the primitive lifestyle of deuterostomes. In fact, sessile pterobranch hemichordates have been classically suggested to be representative of early deuterostomes. Furthermore, pterobranchs possess a motile, ciliated bilateral larva, similar to that of echinoderms. By modification of a similar larva, the notochord and dorsal nerve chord have been hypothesized to have evolved to facilitate habitat selection for the sessile adult, via an actively swimming stage (Fig. 1, Berrill 1955).

Second, it is likely that early chordates were ciliary mucus suspension feeders, as revealed by cephalochordates and the ammocoete larva of lampreys, a fact apparently more consistent with suspension-feeding in sessile lifestyles, rather than with free-living active predation. Third, lophophorates are sessile suspension-feeding invertebrates with motile ciliated larvae and a remarkable combination of traits found both in derived deuterostomes and protostomes. It was reasonable to consider that lophophorates could be representative of the lifestyle of the most recent common ancestors shared by the deuterostomes and protostomes, suggesting that even more remote ancestors of the chordates had also been sessile (Fig. 1).

Thus, a chordate ancestor with a motile larva and a sessile adult seemed an inescapable conclusion. It is therefore not surprising that the hypothesis of paedomorphosis has been repeatedly mentioned in college textbooks (Romer and Parsons 1977; Carrol 1987; Benton 2000).

However, suspension feeding and motile ciliated larvae can also be observed in burrowing, swimming or other nonsessile adult lifestyles, and in a strict sense cannot be considered as evidence for sessile ancestors. Furthermore, new molecular evidence indicates that the phylogenetic positions of ascidia, pterobranchia, lophophora, or echinodermata do not provide support for the presence of a sessile adult or of a process of paedomorphosis in the evolution of chordate ancestors (Wada and Satoh 1994; Wada 1998; Cameron et al. 2000). According to these analyses, chordates are not nested within any of these groups. Moreover, burrowing enteropneusts, rather than sessile pterobranchs, were found to be basal within hemichordates (Cameron et al. 2000), and appendicularians with an adult capacity for swimming, rather than the sessile ascidians, are basal within urochordata (Wada and Satoh 1994; Wada 1998). Thus, appendicularia, rather than ascidia, and enteropneusts, rather than pterobranchs, should be considered more closely representative of early urochordates and hemichordates, respectively. Importantly, according to molecular evidence, hemichordates and echinoderms do not represent successive outgroups to chordates, but rather, they make up a new group (hemichordata+echinodermata) that is the sister group of chordates (Turbeville et al. 1994). This implies that urochordates and euchordates are as relevant as echinoderms and hemichordates in order to infer the lifestyle of the most recent common ancestor of all deuterostomes. Considering this molecular evidence, the corrected inference is that adult early chordates were free-living ciliary mucus suspension-feeders, with axial swimming and a fin with iterated rays. Furthermore, early deuterostomes did not have a sessile adult lifestyle (Wada 1998; Cameron et al. 2000),
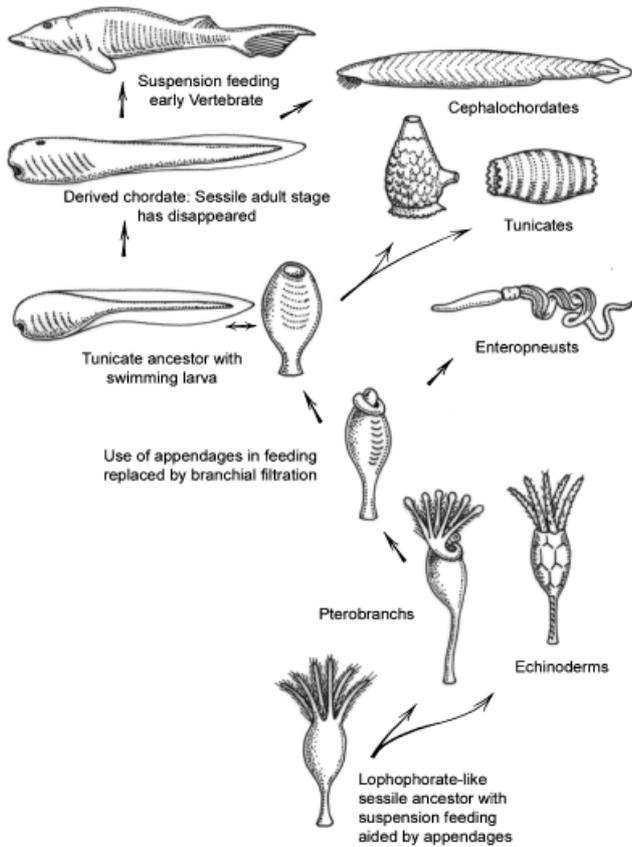
**Fig. 1.** The classic hypothesis of the sessile ancestors of chordates. A remote lophophorate-like sessile ancestor is considered to have given origin to the deuterostomes. Pterobranch hemichordates are taken to be representative of chordate ancestors. A free-living lifestyle is assumed to have involved paedomorphosis from sessile ancestors with motile larvae. Modified from Romer and Parsons (1977).



**Fig. 2.** A possible phylogeny of animals. The presence of a capacity for swimming as hypothesized here is represented by blue-colored branches. Further molecular evidence is required to confirm if the Ctenophora are actually the sister group to protostomes+deuterostomes. Other aspects of this tree are based on well-accepted results from molecular phylogenetic analysis.

and were probably capable of swimming and/or burrowing (Fig. 2).

Additional molecular evidence reveals that the sessile lophophorates are protostomes (Adoutte et al. 1999; Mallatt and Winchell 2002) and that they do not necessarily represent the lifestyle or the morphology of the common ancestor of protostomes and deuterostomes. Importantly, lophophorates are not the only group bearing a combination of traits present in derived deuterostomes and protostomes. The swimming, pelagic Chaetognatha are another group that in the past, has been classified as either protostomes or deuterostomes (Brusca and Brusca 1990). Recent sequencing of the mitochondrial genome of a chaetognath has confirmed the hypothesis that the Chaetognatha are the sister group to all other protostomes (Fig. 2, Peterson and Eernisse 2001; Helfenbein et al. 2004). If this is correct, the Chaetognatha may represent the lifestyle of the earliest protostomes. Both chaetognaths and basal chordates share an
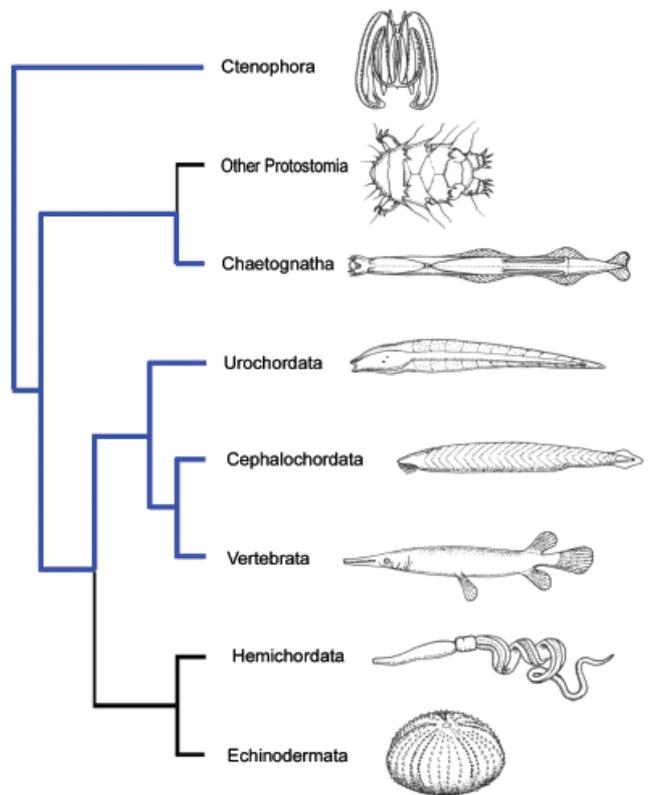
adult fin with iterated rays and swim by body movements. It is possible that this trait was present in the ancestors they shared at the basis of the protostome–deuterostome divergence (Fig. 2).

The capacity for adult swimming can go as far back as the ancestors shared with Ctenophora or with medusoid Cnidarians. On morphological grounds, the Ctenophora have been repeatedly argued to be the sister group to protostomes+deuterostomes (Fig. 2, Brusca and Brusca 1990; Peterson and Eernisse 2001). Molecular evidence has been yet unable to conclusively support or reject this hypothesis (Collins 1998; Peterson and Eernisse 2001). Ctenophores swim by the beating of lengthwise ciliary ctene rows, which are composed of longitudinally iterated comb plates bearing the ctenes or ciliary "combs." The use of ciliary rows in swimming can be found in the small motile larvae or in the early stages of several protostomes and deuterostomes (Nielsen 1987). However, ctenophores demonstrate that ciliary swimming is not restricted to larval stages or small body sizes (Brusca and Brusca 1990). Finally, the iterated rays encased within the

swimming fins of urochordate and cephalochordate larvae have been found to be made up of ciliary structures (Flood 1975; Crowther and Whittaker 1994). These rays have been argued not to be homologous to those of the fins of modern vertebrates because of their structural differences (Holland and Chen 2001). However, the fin rays of the early fossil vertebrate *Haykouichthys* were not like the endoskeletal fin rays of agnathan vertebrates such as the myxinoids and lampreys, but rather are preserved as faint stains of soft structures that were not preserved, despite preservation of other soft and skeletal tissues (Zhang and Hou 2004). Here we propose that the fins of chordates evolved from longitudinal swimming rows of iterated ciliary structures, and that there was a continuity in swimming function in all intermediate structures, from the ciliary rows of ctenophore-like ancestors, to the iterated ciliary rays of basal chordates (Fig. 2). If ctenophores are the sister group to bilateria, it can be argued that adult ciliary swimming at a large body size preceded swimming with a fin and body movements. The cydippid larva of ctenophores also swims by ciliary rows, a condition that has also been argued to be present in the larvae of early eubilateria. The presence of ciliary larvae has been argued to be secondarily lost in forms with direct development (Arendt et al. 2001). Axial swimming in the larval stages of urochordates that metamorphose into sessile adults does not imply that axial swimming is as old as ciliary swimming, because early urochordates may have already lost the ciliated larva and could have been appendicularian-like, with direct development in which early stages resembled the adult, both free-living with axial swimming. In sessile urochordates, axial swimming was secondarily restricted to only early stages.

Fossil traces claimed to be as old as 1.1 billion years indicate the presence of burrowing and benthic lifestyles for early metazoa (Seilacher et al. 1998). Authors favoring a benthic scenario for the evolution of early bilateria have described hypotheses of a pelagic–nectonic lifestyle as "conveniently escaping our attention" (Collins and Valentine 2001). However, preservation of early benthic activity cannot be considered as evidence to reject the importance of a swimming capacity in the common ancestors of protostomes and deuterostomes. It remains conceivable that the use of body movement within a swimming lifestyle may have preceded and allowed exaptation to burrowing or creeping benthic lifestyles. Secondary acquisition of creeping–burrowing from a swimming lifestyle is exemplified by the benthic platyctenid ctenophores (descended from swimming cyddipid-like ancestors, Podar et al. 2001), and also by benthic chaetognaths such as *Spadella*. Here we wish to emphasize that it is possible to propose a scenario suggesting that a capacity for swimming was important in the lifestyle of the most recent common ancestors of deuterostomes and protostomes.

Although taxon sampling for molecular phylogenetic analysis is limited to extant species, the fossil record can provide

further insights. In this context, the earliest fossil vertebrates known were clearly capable of swimming (Shu et al. 2003). No fossils providing support for a sessile stage in the lineage of euchordates have yet been found, such as basal sessile euchordates. Regarding the early Eubilateria (protostomes+deuterostomes), the Precambrian *Kimberella* is considered to be a mollusc and as such does not reveal much about the appearance of early eubilaterians (Martin et al. 2000). Nonetheless, the reconstructed body shape of the microscopic *Vernanimalcula*, a possible sister taxon to the Eubilateria (Chen et al. 2004), suggests that it was not sessile, and could have had a capacity for swimming, perhaps by the use of cilia. Finally, the phylogenetic relationships among acoel flatworms, ctenophora, cnidaria, and the eubilateria remain controversial. Whether the Ctenophora are closer to the Eubilateria than the benthic acoel flatworms is of special interest here but unfortunately, few studies include both groups. Nevertheless, Eubilateria are not nested within the acoel flatworms (Ruiz-Trillo et al. 2004), and it is therefore possible that the latter became secondarily benthic and structurally simplified from a more complex swimming ancestor shared with the Ctenophora. If, as suggested by morphology, the Ctenophora are found to be closer to Eubilateria, the best inference may support the presence of an adult capacity for swimming predating the divergence of protostomes and deuterostomes (Fig. 2).

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