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Hemichordate models

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Hemichordates are marine animals with two different lifestyles. The solitary, free-living enteropneusts or acorn worms resemble polychaetes or earthworms, while the tiny, colonial, sessile pterobranchs are similar to bryozoans and phoronids. Hemichordates, together with echinoderms, comprise the clade Ambulacraria and are a sister group to the Chordata. As adults, they exhibit cardinal chordate characters, such as gill slits. Their embryogenesis and dipleurula-type (tornaria) larvae are very similar to those of echinoderms. Recent advances in comparative genomics and molecular developmental biology of hemichordates, especially the vermiform enteropneusts, have shed light on deuterostome ancestors. This paper briefly reviews the numerous recent studies on the Phylum Hemichordata.

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Introduction

Hemichordates are deuterostome animals with bilateral body plans based on three developmental features: radial, indeterminate cell cleavage in the early embryo, enterocoelous formation of the body cavity, and a blastopore that forms the anus. They are generally dioecious, and each sex is distinguishable by its gonads (genital wings or genital ridges) during the spawning season. The Phylum Hemichordata contains two classes that have very different lifestyles, the solitary Enteropneusta (acorn worms) and the sessile, colonial Pterobranchia (tube worms). We began working on molecular developmental biology of hemichordates, using a Hawaiian acorn worm, *Ptychodera flava*, more than twenty years ago. At that time, only a few people worldwide were working on these rarely encountered animals. Currently at least four species of the Class Enteropneusta (*Ptychodera flava*, *Saccoglossus kowalevskii*, *Balanoglossus misakiensis*, and *Balanoglossus shimodensis*) and two species of the Class Pterobranchia (*Rhabdopleura compacta* and *Cephalodiscus gracilis*) are used for comparative developmental biology and/or phylogenetic studies by various laboratories in Japan, Taiwan, the U.S., Canada, and Europe [1–8].

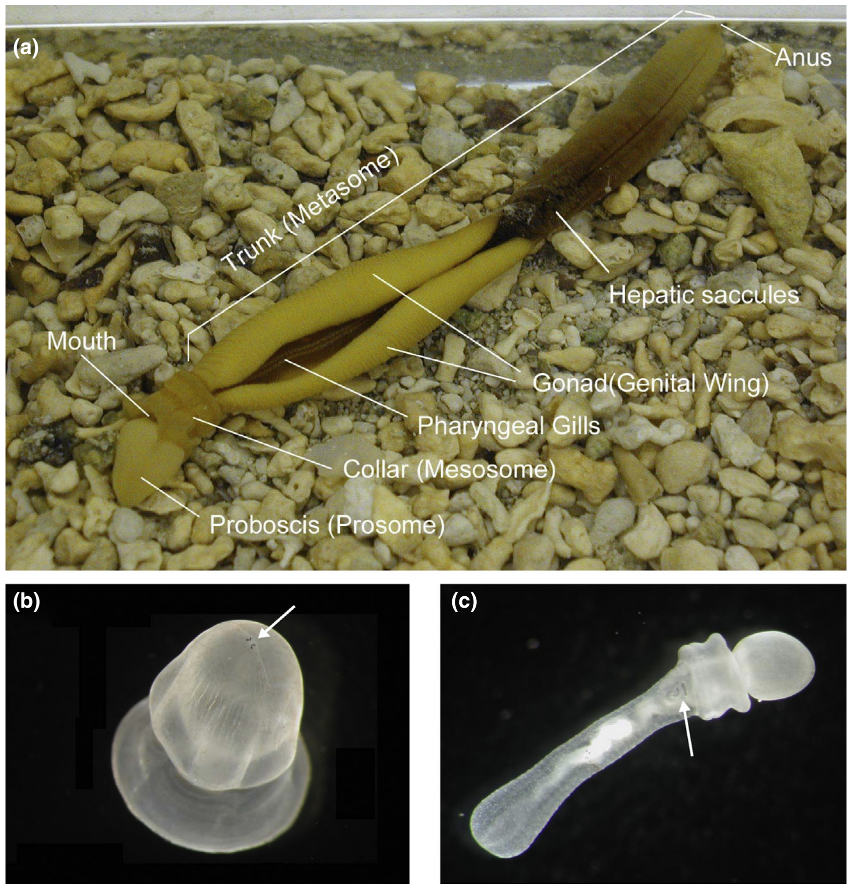
Hemichordates represent the closest phylogenetic nexus between extant chordates and invertebrates; therefore, it is necessary to study these animals carefully in order to garner additional insights into the evolution of developmental mechanisms of deuterostomes and bilaterians [9]. The adult enteropneust body is divided into three parts: an anterior prosome or proboscis, a mesosome or collar, and a metasome or trunk (Figure 1). The mouth opens on the ventral side of the collar and the anus opens at the posterior end of the trunk. Each part of the worm's body exhibits cardinal chordate-like structures. Such homology was originally proposed by Bateson more than a century ago [10••,11••]. According to Bateson, the stomochord in the proboscis corresponds to the notochord of chordates. He thought that the dorsal hollow nerve cord or collar cord in the collar is comparable to the chordate neural tube, and that the pharyngeal gill slits in the anterior dorsal trunk correspond to chordate pharyngeal gill slits (originally described by Kowalevsky, 1886). However, recent progress in comparative molecular developmental biology to verify these classical hypotheses has shown that only the pharyngeal gill slits constitute a conserved ancestral character in the last common ancestor of deuterostomes [10••,11••,12].

Extensive molecular analysis, especially of two hemichordates, *P. flava* and *S. kowalevskii*, during the past quarter century has accumulated new data and stimulated evo-devo studies to understand evolution of bilateral animals and the emergence of chordates [13,14••,15–19]. Acorn worms have become model organisms because they occupy a pivotal position to elucidate the origin and evolution of deuterostomes. The aim of this review is to summarize recent advances in comparative molecular developmental biology and comparative genomics of hemichordates, in the context of present evolutionary understanding (Figure 2).

Phylogeny of hemichordates

Hemichordates have been placed in the clade Deuterostomia of the Bilateria. They are less closely related to chordates than to echinoderms, with which they comprise the clade Ambulacraria, a name coined by Metschnikoff [20] (Figure 2). However, the question of whether colonial tube-dwelling pterobranchs are sister to vermiform enteropneusts or whether they should be nested within

Figure 1



(a) *Ptychodera flava*, a model enteropneust hemichordate with indirect development. This female acorn worm is an Indo-Pacific species and shows a characteristic body plan. The picture shows a dorsal view of *P. flava*, illustrating the anterior proboscis or prosome, the collar or mesosome, and the trunk or metasome. The stomochord is located in the proboscis and the dorsal hollow nerve cord is located at the dorsal side of the collar, while the pharyngeal gills reside in the anterior trunk along the dorsal midline. Gonads or genital wings full of eggs cover both sides of the gills. The mouth opens at the ventral side of the collar and anus opens at the posterior end of the trunk. Using the muscular proboscis, enteropneusts dig readily in the sand. They are about 15 cm in length. **(b)** An unidentified species of enteropneust larva during metamorphosis. This 5-mm larva is larger than the same stage of *P. flava*. Two pigmented eye spots, evident at the anterior tip of the future proboscis, are indicated by an arrow. The swelling protocoel can be observed under the epidermis. **(c)** A young juvenile *P. flava*, several days after metamorphosis. The definitive deuterostome feature, pharyngeal gill slits, is evident on the dorsal side of the anterior trunk posterior to the collar. The length is about 5 mm.

them has been much debated [21–24]. Also, enteropneust phylogeny requires revision in light of recent investigations of deep-sea acorn worms [25–27]. Phylogenetic analysis based on morphology split the solitary enteropneusts into four families: the direct developing Harrimaniidae, two groups of indirect developers, the Spengelidae and Ptychoderidae, and the deep-sea spaghetti worms of the Family Saxipendiidae [28]. More recently, one more family, the deep-sea Family Torquaratoridae was added [29].

Previous phylogenetic studies based on 18S ribosomal DNA sequences showed that enteropneusts were paraphyletic with pterobranchs, and sister to the harrimaniids [21,22]. Cannon *et al.* (2009) updated the phylogeny with expanded taxonomic sampling and mitochondrial DNA sequences and showed that the Saxipendiidae should be included in the Family Harrimaniidae, while the Torquaratoridae is allied with the Family Ptychoderidae, comprising three families of enteropneusts [30]. They also showed that pterobranchs (Cephalodiscida and Rhabdpleurida) are sister to the harrimaniids. Recent phylogenomic comparisons of transcriptomes for all hemichordate families revealed the reciprocal monophyly of the Enteropneusta and Pterobranchia and placed the deep-sea family Torquaratoridae within the Ptychoderida [31,32,33•]. Our current analysis, based on comparative