19

Hemichordata, Class Enteropneusta: The Acorn Worms

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The Enteropneusta are marine, benthic, bilateral, enterocoelous vermiform invertebrates. They are common components of the infauna of all soft-bottom benthic habitats and can be locally abundant (Hadfield, 1975). Their burrowing and feeding mix the sediment and alter benthic biochemistry. Adults accumulate toxic halogenated organics, which are used in predator defense, fouling control, burrow conditioning, and bacteriostasis (reviewed in King et al., 1995).

The class Enteropneusta includes about 70 species distributed into four families, the Protoglossidae, Harrimaniidae, Spengelidae, and Ptychoderidae (Benito and Pardos, 1997). Kozloff (1996) points out that acorn worms, as they are known, can be found at a half a dozen or more locations around the Pacific Northwest. At some of these sites the worms are abundant. At least several enteropneust species are present in the Pacific Northwest, though only two species have been described (Table 1).

Table 1. Species in the class Enteropneusta from the Pacific Northwest

Family Ptychoderidae
Glossobalanus berkeleyi (Wiley, 1931)

Family Harrimaniidae
Saccoglossus bromophenolosus (King, 1994)
Saccoglossus spp. (Kozloff, 1996)

Enteropneusts are broadcast spawners with external fertilization. In the spawning events that have been observed, females initiate spawning, releasing their eggs in long strings of mucus. Males follow, releasing sperm also bound in mucus. The mucus surrounding sperm fairly rapidly dissolves, releasing the sperm. Observed spawning events have been epidemic. In some species, eggs in a "cocoon" of mucus are retained in the burrow, where fertilization occurs (Hadfield, 1975).

Direct development has been observed in several *Saccoglossus* species. Species with large eggs in the genera *Harrimania* and *Protobalanus* may also be direct developers. In some *Saccoglossus* species, larvae hatch out of the egg after one to two days. The embryos are rounded, with the anterior end bearing an apical tuft and a broad telotrochal ciliar band that provides propulsion (Fig. 1A). These larvae swim briefly before settling to the bottom. During this period the anterior end of the larvae elongates into a proboscis (Fig. 1B). Other *Saccoglussus* species settle immediately to the bottom after hatching (Hadfield, 1975).

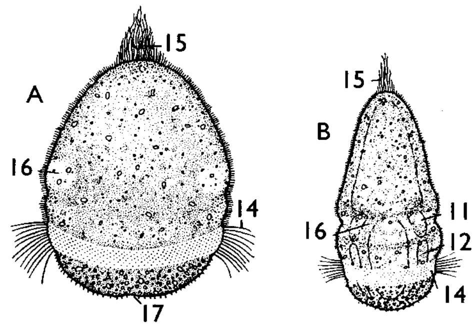
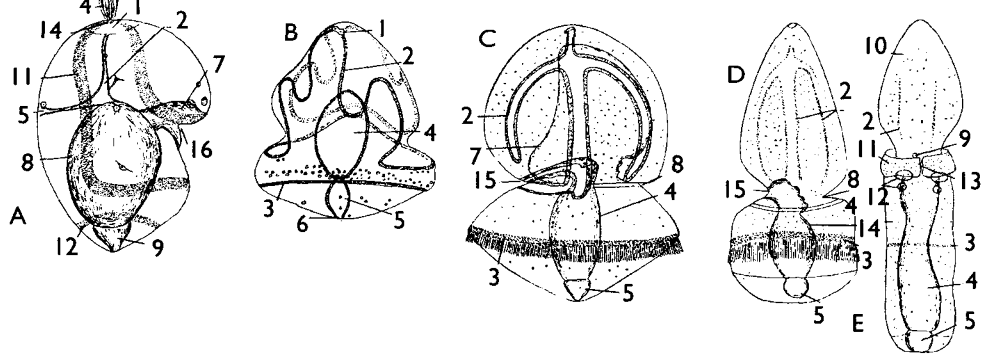


Fig. 1. Direct development in the enteropneust species *Saccoglossus horsti.* (A) Newly hatched larva. (B) Later stage showing elongation of the body anterior to a developing constriction. Locally, there are probably at least two species of *Saccoglossus.* 11, mesocoel; 12, metacoel; 14, telotroch; 15, apical tuft; 16, location of future collar; 17, anal indentation. (From Hyman, 1959. Fig. 47)

Indirect development via a tornaria larva occurs in the families Ptychoderidae and Spengelidae. At hatching, the larvae of species in these families are generally in the late gastrula stage of development and are uniformly covered with cilia. With development, ciliation becomes concentrated into a single band that loops above the mouth and connects at the apical plate (Fig. 2A). A ventral loop of cilia runs posteriorly on each side of the body and meets across the ventral surface between the mouth and the anus. A telotroch with long cilia develops, encircling the anus (Fig. 2A). These cilia provide most of the propulsion of the larva. The larva at this stage of development is know as a tornaria and, depending on the species, is achieved after several days to several weeks. Tornariae are generally small, a millimeter or less in length, but some species have tornariae up to a centimeter in length. They are highly transparent, allowing clear inspection of internal structures (Hadfield, 1975).

With continued development, the ciliar band becomes increasingly more complex (Fig. 2B), looping extensively about the body of the larva. In *Ptychodera* species, small freely projecting lappets develop on the ciliar band (see Hyman, 1959, Fig 43E; Strathmann and Bonar, 1976, Fig. 1). These larvae are referred to as tentaculate tornariae. In the next stage of development, the ciliary band begins to regress, a circular constriction forms about the middle of the larva, and the body elongates anterior to the constriction (Fig. 2C, D). Metamorphosis begins in the plankton just prior to settlement. During this process, the ciliary band vanishes, the circular constriction develops into a collar, and the animal elongates posterior and anterior to the collar (Fig. 2E). Anterior to the collar, the body develops into a proboscis. A long trunk develops posterior to the collar. At this stage, the larvae remain mobile due to the ciliated telotroch. Culture in the laboratory suggests that the development of tornariae can be quite long, up to several months.



(A) 1, apical thickening; 2, protocoel; 4, apical tuft; 5, hydropore; 7, esophagus; 8, stomach; 9, intestine; 11, ciliary band; 12, telotroch; 14, eye; 15, muscle fibers. (B–E) 1, eye; 2, ciliary band; 3, telotroch; 4, stomach; 5, intestine; 6, anus; 7, protocoel; 8, proboscis-collar groove; 9, hydropore; 10, proboscis; 11, collar; 12, first and second gill pores; 13 groove of invagination of collar cord; 14, truck; 15, mouth.

Fig. 2. Indirect development in the enteropneusts, as exemplified by the tornaria larva of *Balanoglossus clavigerus* (family Ptychoderidae). (A) Beginning development of the ciliary bands. (B) Fully developed tornaria. (C) Ciliary bands regressing, midbody circular constriction forming, and elongation of the body anterior to the constriction. (D) Ciliary band disappearing as collar develops. (E) Larva just prior to settlement; ciliary band nearly gone, collar developed, and body elongated. (From Hyman, 1959, Figs. 42, 43)

References

Hadfield, M. G. (1975). Hemichordata. In: Reproduction of Marine Invertebrates Vol. II, A. C. Giese and J. S. Pearse (eds.). Academic Press, New York. pp. 1–42.

Hyman, L. H. (1959). The Invertebrates: Smaller Coelomate Groups. McGraw-Hill, London and New York.

King, G. M., C. Giray, and I. Kornfield (1994). A new hemichordata, *Saccoglossus bromophenolosus* (Hemichordata: enteropneusta: Harrimaniidae) form North America. Proc. Biol. Soc. Wash. 107:383–90.

King, G. M., C. Giray, and I. Kornfield (1995). Biogeographical, biochemical, and genetic differentiation among North American saccoglossids (Hemichordata; Enteropneusta; Harrimaniidae). Mar. Biol. 123:369-77.

Kozloff, E. N. (1996). Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle.

Strathmann, R. and D. Bonar (1976). Ciliary feeding of tornaria larvae of *Ptychodera flava* (Hemichordata: Enteropneusta). Mar. Biol. 34:317–24.

Willey, A. (1931). *Glossobalanu berkeleyi*, a new enteropneust from the west coast. Trans. Ro. Soc. Canada, Sect. 5, Ser. 3, 24:19–28.