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Brachiopoda

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The brachiopods are a small phylum of sessile filter feeders with bivalved shells. Superficially they look like clams, but they can easily be distinguished from clams by noting that the brachiopod is attached to the substratum by a peduncle that passes through one of the valves. Brachiopods are composed of three distinct regions: the mantle, which secretes the bivalved shells and encloses the internal mantle cavity; the lophophore, a ciliated tentaculate feeding organ found within the mantle cavity, and the pedicle, which attaches the brachiopod to the substratum. The phylum is composed of two classes, the Articulata, without shell or cirri, and the Inarticulata, with both shell and cirri. Locally there are four species of articulate and only one species of inarticulate brachiopod (Table 1). More detailed descriptions of the Brachiopoda can be found in Hyman (1959) and Brusca and Brusca (1990).

Class Articulata

The Articulata have indirect development. Their larvae are lecithotrophic, demersal, and generally have a short free-swimming stage. Brachiopod larvae are divided into three body regions: the apical (or anterior) lobe, the mantle lobe, and the pedicle lobe (Fig. 1A). When articulate larvae are competent to settle, the apical lobe is uniformly ciliated with an apical tuft. An annular band of long locomotory cilia surrounds the posterior margin of the apical lobe (Fig. 1A, B). The mantle lobe extends like a skirt over the pedicle lobe. Early in development, the mantle lobe is evenly ciliated, but this ciliation is lost during development. At competence, ciliation on the mantle lobe has been reduced to a ventromedial longitudinal band of cilia and a pair of ciliated pits near the apical lobe. The posterior margin of the mantle lobe bears four bundles of long chaetae (Fig. 1A). When disturbed, these chaetae are splayed out. At settlement, the larva attaches to the substratum via the pedicle, and the mantle lobe folds up and over the apical lobe, enclosing it (Fig. 1C). The mantle lobe loses its ciliation and secretes the bivalve shell. After settlement, the tentacles (cirri) develop on the lophophore.

In the four local species, larvae are retained in the mantle cavity and released as demersal non-feeding larvae. Meta-

Table 1. Species in the phylum Brachiopoda from the Pacific Northwest (from Kozloff, 1996)

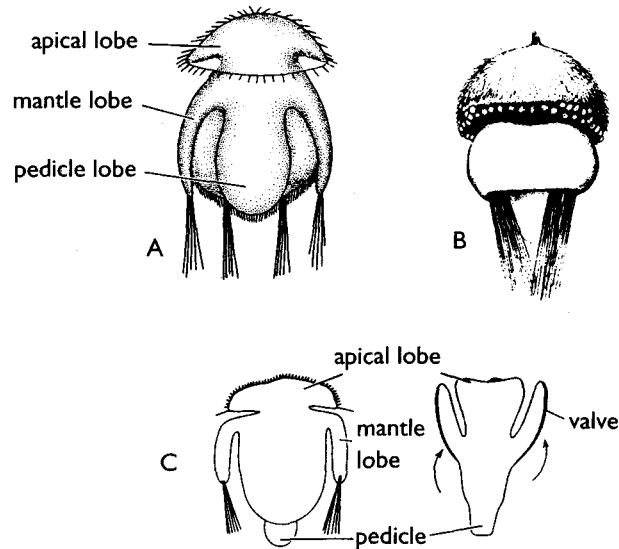
Class Articulata

Hemithiris psittacea
Terrebratulina unguicula
Terebratalia transversa
Laqueus californianus

Class Inarticulata

Crania californica

Fig. 1. Articulate brachiopod larvae.
 (A) Larva of *Waltonia*.
 (B) Larva of *Terebratalia*; there is one species in this genus locally.
 (C) Schematic of metamorphosis in articulate brachiopods; the mantle lobes flex up to cover the apical lobe, and the pedicle attaches to the substratum. (A,C from Brusca and Brusca, 1990, Fig. 21; B from Nielsen, Fig. 19)



morphosis occurs within 100 hours (*Hemithiris psittacea*, *Terrebratulina unguicula*, and *Laqueus californianus*) to 200 hours (*Terebratalia transersa*).

Class Inarticulata

The Inarticulata have direct development. Their larvae are planktotrophic, pelagic, and the free-swimming stage can be quite long. Brachiopods are rare in plankton samples and, when they are present, it is usually larvae from the Inarticulata. The lophophores, mantle, and shell develop early in the inarticulate brachiopods and the pedicle develops late or after settlement. The lophophore consists of a variable number of ciliated tentacles, or cirri. The cirri are added in pairs at the anterior edge of the lophophore (Fig. 2B, C). After the acquisition of two pairs of cirri, the lophophore becomes a trocholophe. The trocholophe can be everted for feeding or locomotion or retracted between the valves of the shell (Fig. 2B). There is considerable variation in the number of cirri present at the time of settlement. For example, in *Lingula*, if a suitable settlement substratum is encountered early in the pelagic phase, settlement can occur with as few as eight cirri, but settlement can be delayed until a suitable substratum is encountered during which time the larva adds cirri (Chuang, 1990). At settlement, *Lingula* larvae can have as many as 20 cirri. See Reed (1987) and Chuang (1990) for a more detailed presentation of the characteristics of larval brachiopods.

Crania californica is the single local inarticulate species. Its eggs are freely shed. The larvae are bilobed, demersal, and non-feeding.

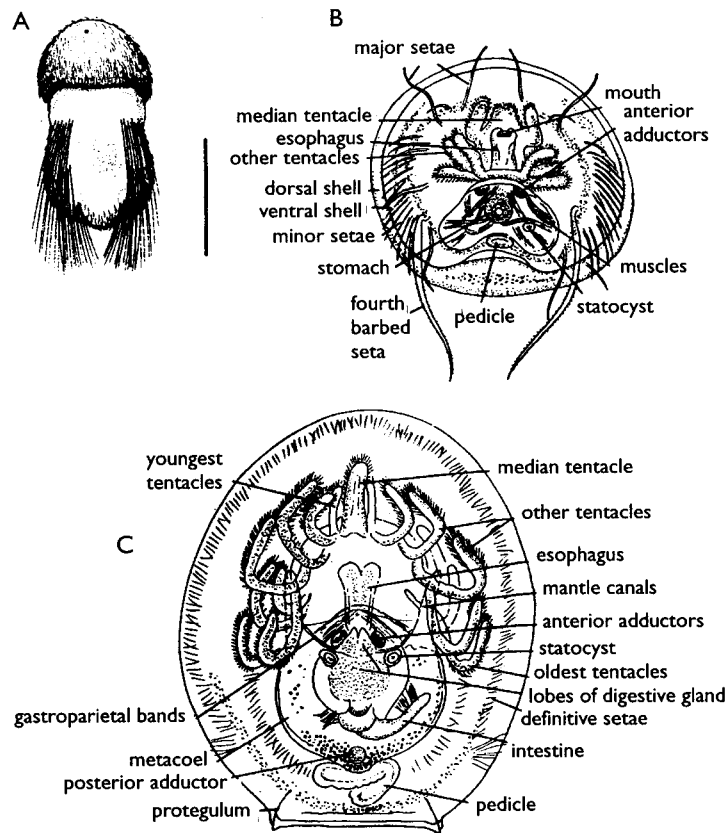


Fig. 2. Inarticulate brachiopod larvae. (A) Larva of *Crania*; there is one species in this genus locally. Scale = 100 mm. (B) Late-stage larva of *Pelagodiscus atlanticus*. (C) Late-stage larva of *Lingula* (A from Nielsen, 1990, Fig. 19; B, C from Hyman, 1959, Fig. 207)

References

- Brusca, R. C. and G. J. Brusca (1990). Invertebrates. Sinauer Associates, Inc., Sunderland.
- Chuang, S. H. (1990). Brachiopoda. In: Reproductive Biology of Invertebrates. Vol. IV, Part B. Fertilization, Development, and Parental Care, K. G. Adiyodi and R. G. Adiyodi (eds.), pp. 212–54. John Wiley & Sons, New York.
- Hyman, L. H. (1959). The Invertebrates: Smaller Coelomate Groups. McGraw-Hill, London and New York.
- Kozloff, E. N. (1996). Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle. 539 pp.
- Nielsen, C. (1990). The development of the brachiopod *Crania* (*Neocrania*) *anomala* (O. F. Müller) and its phylogenetic significance. Acta Zool. Stockh. 72:7–28.
- Reed, C. G. (1987). Phylum Brachiopoda. In: Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast, M. F. Strathmann (ed.), pp. 486–93. University of Washington Press, Seattle.