15
Phoronida

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Reproduction and Development

Phoronids reproduce primarily sexually and may be either hermaphroditic or dioecious. Asexual reproduction is well documented in only one species of *Phoronis* but reported present in all representatives of the genus. Internal fertilization is probably the dominant fertilization strategy in phoronids; fertilized primary oocytes are typically released into the water column, where larval development is completed.

Almost all phoronids produce a planktonic actinotroch larva. In some species (e.g., *Phoronis vancouverensis*) early embryos, attached to the female adult's tentacles, are brooded to an early actinotroch stage and then released. In others (e.g., *Phoronopsis viridis*, *Phoronis pallida*, and *Phoronis architecta*) all development takes place in the water column. Whether release into the plankton occurs shortly after fertilization or after a period of brooding, planktonic actinotroch larvae tend to be planktotrophic and reside in the plankton for extended periods.

The actinotroch larva bears a ring of tentacles arising from the cylindrical larval body just posterior to the hood, the most anterior major body region. It is propelled through the water by cilia lining the anterior tentacles and by a posterior telotrochal ciliary band. Additional details on the biology and development of the Phoronida are summarized in Brusca and Brusca (1990).

Identification and Description of Local Taxa

The actinotroch larvae illustrated herein are advanced stages approaching competence for metamorphosis. Early-stage larvae are morphologically simple and difficult to differentiate (see p. 258). As actinotroch larvae develop, their body size increases, the number of tentacles increases, they gain pigmentation, and blood corpuscle mass increases. A key based on the fully developed stages can be misleading if one attempts to apply it to earlier, less developed stages. It is recommended that the investigator collect plankton over a period of days or weeks to observe developmental changes in a cohort of actinotroch larvae. By maintaining actinotroch larvae in the laboratory, metamorphosis can be observed and an advanced

developmental state confirmed; see Strathmann (1987) for rearing techniques. Developmentally advanced actinotroch larvae can then be reliably compared to illustrations for identification. Phoronid actinotroch larvae are among the most beautiful and intriguing planktonic larval forms; with this guide one should be able to identify the advanced actinotroch larvae found in the Pacific Northwest.

This following list of phoronid species known or likely in the Pacific Northwest (USA) was compiled from a combination of published distributions (Austin, 1985; Kozloff; 1993), knowledge of the latitudinal distributions of West Coast phoronids (R. Zimmer, pers. comm.), and firsthand local observations. Including the previously undescribed *Actinotrocha D*, which has no known adult counterpart, there are five species of actinotroch larvae likely present in the Pacific Northwest plankton (Table 1). Descriptions are provided below for all five of these species.

Table 1. Species in the phylum Phoronida from the Pacific Northwest

Actinotrocha D
Phoronis architecta
Phoronis pallida
Phoronis vancouverensis
Phoronopsis viridis

Fully developed actinotroch larvae are most easily identified on the basis of larval size and number of tentacles. These attributes, however, change during development making it necessary to use all available information to identify an actinotroch larva of unknown developmental stage accurately. As mentioned previously, it is recommended that actinotroch larvae be raised through metamorphosis, ensuring that the most advanced larval stage possible is used for identification.

Phoronis vancouverensis. This species is known from along the North American west coast from British Columbia to southern California. It is commonly thought to be synonymous with the Japanese species *Phoronis ijimai* (e.g., Austin, 1985). This is likely incorrect, however, since there is no actinotroch larva in the region of Japan fitting the description of *P. vancouverensis* (R. Zimmer, pers. comm.).

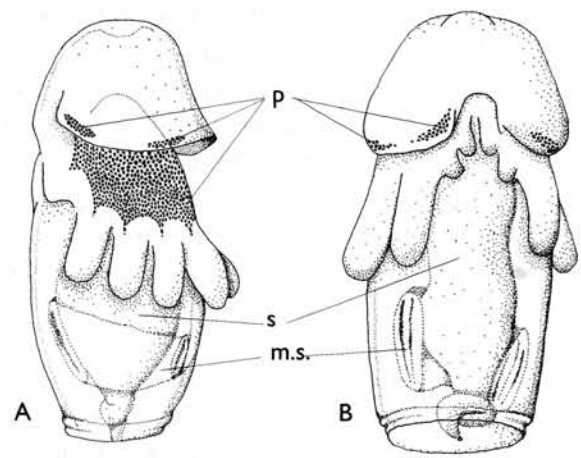

Fig. 1. Actinotroch larva of *Phoronis vancouverensis*, lateral (A) and dorsal (B) views. Pigment specks (p.) visible at the margin of the preoral hood and in the ventral collar region. s, stomach; m.s., metasomal sac. Length ca 600 µm. (Adapted from Zimmer, 1964)

The actinotroch (Fig. 1) is relatively small compared to many other species (~600 µm) and opaque. There are blackish-brown pigment specks on the margin of the preoral hood and the ventral side of the body between the tentacles and the hood margin. Tentacles number 12–14 at metamorphic competence.

Phoronis pallida. This phoronid, first described from Europe, is well known in central and southern California (Austin, 1985). It has also been observed in the waters of British Columbia (R. Zimmer, pers. comm.) and is known to be abundant in Coos Bay, Oregon.

Like *Phoronis vancouverensis*, *P. pallida* is smaller than many other actinotroch larvae (~600 µm) and opaque (Fig. 2). It is easily distinguished from *P. vancouverensi* by a girdle of yellowish-brown pigmentation just posterior to the tentacles, and by the circumesophageal blood corpuscle mass, appearing bow tie–shaped from a ventral, or frontal, view. Also, refractile globules highlight the wall of the stomach, which extends from the bow tie–shaped blood corpuscle mass to slightly posterior of the point at which the tentacles connect to the body. Larval tentacles number 10 at metamorphic competence. In addition to Zimmer (1994), information on the larval development of *P. pallida* is available in Silén (1954).

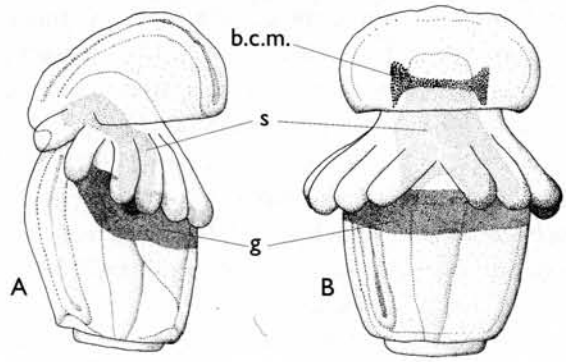

Fig. 2. Actinotroch larva of *Phoronis pallida*, lateral (A) and dorsal (B) views. Bow tie–shaped blood corpuscle mass (b.c.m.), refractile globules lining stomach wall (s.), and girdle (g.) of yellowish-brown pigmentation are visible. Length ca 600 µm. (Aadapted from Zimmer, 1964)

Phoronis architecta. This species was first described from the east coast of North America but is common along the coast of southern California. Less known north of California, the actinotroch larva of this species has been observed in plankton samples taken in Puget Sound, and *P. architecta* adults have been identified from near Tacoma, Washington (R. Zimmer, pers. comm.). *Phoronis architecta* has been lumped with *Phoronis muelleri* but is better treated as a separate species. *Phoronis muelleri*, found only rarely in California (Zimmer, pers. comm.), is not known from the Pacific Northwest coast.

The average length of the actinotroch larvae of *P. architecta* is 1.03 mm. The larva bears a pointed apical sense organ that adorns the preoral hood and can be quite pronounced as

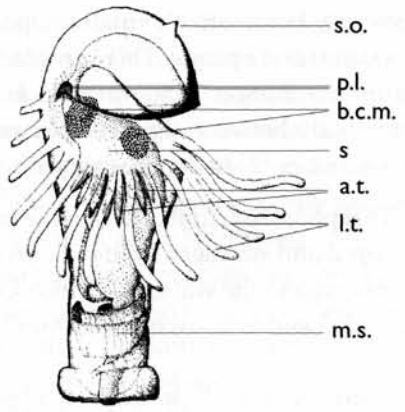

Fig. 3. Actinotroch larva of *Phoronis architecta*, lateral view. s.o., apical sense organ; p.l., pigmented lobe of the stomach; b.c.m., blood corpuscle masses; s., stomach; a.t., adult tentacles; l.t., larval tentacles; m.s., metasomal sac. Length ca 1 mm. (Drawn from photographs supplied by R. Zimmer)

metamorphosis approaches (Fig. 3). A pair of pigmented evaginations, termed stomach lobes, arise from the dorsolateral surface of the stomach's extreme anterior. The stomach may span most of the length of the trunk cavity, with a relatively short intestine connecting it to the posterior anus. Two pairs of blood corpuscle masses are present in mature larvae on the ventrolateral and dorsolateral surfaces of the stomach, anterior to the tentacles. At metamorphosis, this actinotroch usually has 26 larval tentacles (13 pairs). Adult tentacles, numbering eight pairs and usually arising after all 26 larval tentacles are present, appear as laterally paired fans of separate tentacles underneath and posterior to the larval tentacles (similar to an actinotroch larva described in Ikeda, 1901). Adult tentacles tend to be more pointed at the distal end compared to the rounded larval tentacles. For more information on the early development of *P. architecta*, see Brooks and Cowles (1905). The larva of *P. architecta* is similar to the actinotroch larva of *P. muelleri* (= *Actinotrocha branchiata*), which is well described from the coast of northern Europe (Selys-Longchamps, 1902, 1903, 1907; Silén, 1954; Siewing, 1974; Hay-Schmidt, 1989).

Brooks and Cowles (1905) examined development in *P. architecta*. Their Fig. 34 illustrates an actinotroch larva they label "Species A," which they identify as the larva of *P. architecta*. This animal is not the larva of *P. architecta*, however, for it lacks the apical sense organ, the pigmented stomach lobe, and adult tentacles separate from the larval tentacles, and it has the wrong number of tentacles and blood corpuscle masses. Only this one illustration of *Actinotrocha* Species A is offered and compared to an unidentified *Actinotrocha* Species B, which ironically is probably what we now know to be *P. architecta*.

Phoronopsis viridis. This species is known from British Columbia to southern California (Austin, 1985). Although it is generally considered synonymous with *Phoronopsis harmeri*, there is a

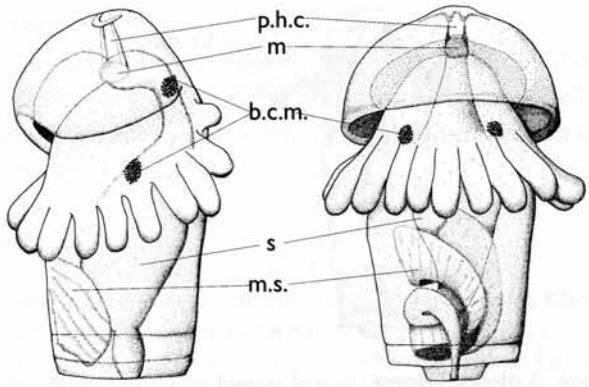

Fig. 4. Actinotroch larva of *Phoronopsis viridis*, lateral (A) and dorsal (B) views. p.h.c., preoral hood coelom; m., mouth; b.c.m., blood corpuscle masses; s., stomach, m.s., metasomal sac. Length ca 1.1. (Adapted from Zimmer, 1964)

distinct phenotypic basis for the separation of these two species. Adult phoronids described as *P. viridis* are green and generally occur south of an otherwise similar white phoronid occurring near British Columbia and originally described as *P. harmeri*. Though this issue is unresolved, these are currently considered the same species.

In *P. viridis*, the preoral hood coelom (the anterior space between the coelomic lining and the epidermis) is a rather obvious boxlike space between the brain and the esophagus (Fig. 4). This actinotroch larva may be as large as 1 mm or slightly larger, and the body wall is relatively transparent. There are two pairs of blood corpuscle masses. One pair is in the posterior "flange" or "corner" of the preoral hood and is most easily visible from the dorsal view. The other mass is on either side of the "collar," slightly anterior to the larval tentacles. When ready to metamorphose, this larva has ca 20 tentacles (10 pairs). Several studies deal with the development of *P. viridis*, including a comparison of its development with a *Phoronis* species from Monterey Bay (Rattenbury, 1951), observations of early development (Fairfax, 1977), and detailed descriptions of "*Actinotrocha A*" (Zimmer, 1964).

Actinotrocha D. An unidentified actinotroch larva, referred to here as *Actinotrocha D*, is commonly found in plankton samples from Coos Bay, Oregon. Development has been observed in all known adult phoronid species in the Pacific Northwest. Since *Actinotrocha D* resembles no previously described larva, it is likely the larva of an undescribed species.

Actinotrocha D is easily recognized by its enormous size, commonly 2–3 mm and as large as 4 mm (Fig. 5). There are three pair of blood corpuscle masses. Two sets are paired laterally and located at the base of the tentacles. One pair lies within the oral hood (Fig. 6). Larvae approaching metamorphosis may have 30 or more tentacles. The stomach of this larva is distended and fluid-filled, taking up most of the body

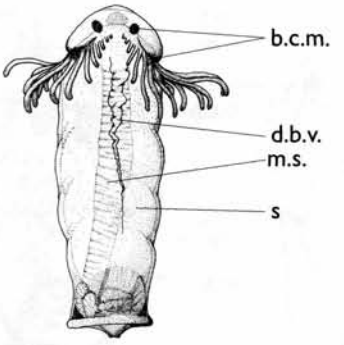

Fig. 5. *Actinotrocha D*, dorsal view. The metasomal sac (m.s.) is situated on the ventral side of the animal, running between the large fluid-filled stomach (s.) and the body wall. b.c.m., blood corpuscle masses; d.b.v., dorsal blood vessel. (Drawn from video and live observations, Coos Bay, Oregon)

Fig. 6. *Actinotrocha D*, anterior dorsolateral view.

volume. A pleated dorsal blood vessel extends posteriorly from the base of the tentacles to the telotroch. Because the stomach is transparent and nearly the same diameter as the body itself, it is not the most obvious structure in the body posterior of the tentacles. Rather, the metasomal sac, a flattened tube extending the length of the body and coiling upon itself several times at the posterior end, is located on the ventral side of the animal and may be mistaken for the stomach.

Early Pelagic Stages in Phoronida

Postembryonic phoronid stages preceding the actinotroch stage have fewer distinguishing features than an advanced actinotroch larva. Consequently, identifying early developmental stages to genus or species is difficult. Many earlier stages are distinctly phoronid, however, and generalized diagrams of early developmental stages (Fig. 7) can aid identification of larvae as phoronids.

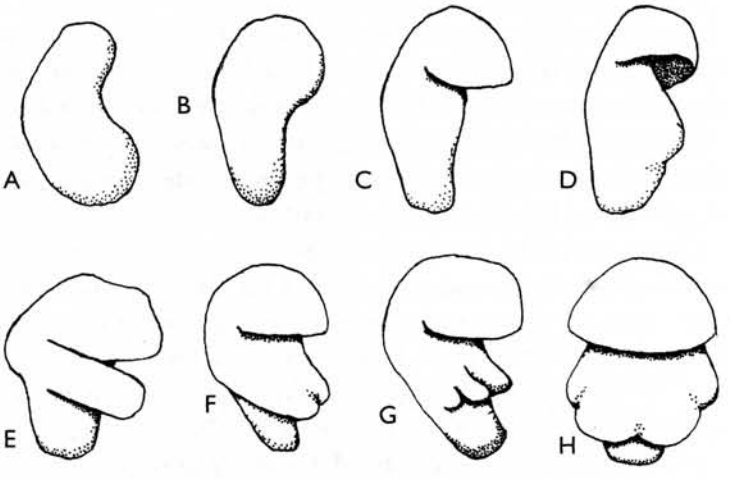

Fig. 7. Generalized phoronid developmental stages following gastrula but preceding the advanced actinotroch larva. Phases G and H represent an early actinotroch with small tentacles. All stages are presented in lateral view except phase H, which is shown in ventral view. Size varies with species and stage of development but generally ranges from <100 to >1,000 mm. (Adapted from Rattenbury, 1951, 1954; Silén, 1954; Forneris, 1957; Zimmer, 1964)

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