

Arthropoda, Cirripedia: The Barnacles

Andrew J. Arnsberg

The Cirripedia are the familiar stalked and acorn barnacles found on hard surfaces in the marine environment. Adults of these specialized crustaceans are sessile. They are usually found in dense aggregations among conspecifics and other fouling organisms. For the most part, sexually mature Cirripedia are hermaphroditic. Cross-fertilization is the dominant method of reproduction. Embryos are held in ovisacs within the mantle cavity (Strathmann, 1987). Breeding season varies with species as well as with local conditions (e.g., water temperature or food availability). The completion of embryonic development culminates in the hatching of hundreds to tens of thousands of nauplii. There are approximately 29 species of intertidal and shallow subtidal barnacles found in the Pacific Northwest, of which 12 have descriptions of the larval stages (Table 1). Most of the species without larval descriptions (11 species) are parasitic barnacles, order Rhizocephala; a brief general review of this group is provided at the end of the chapter.

Development and Morphology

The pelagic phase of the barnacle life cycle consists of two larval forms. The first form, the nauplius, undergoes a series of molts producing four to six planktotrophic or lecithotrophic naupliar stages (Strathmann, 1987). Each naupliar stage is successively larger in size and its appendages more setose than the previous. The final nauplius stage molts into the non-feeding cyprid

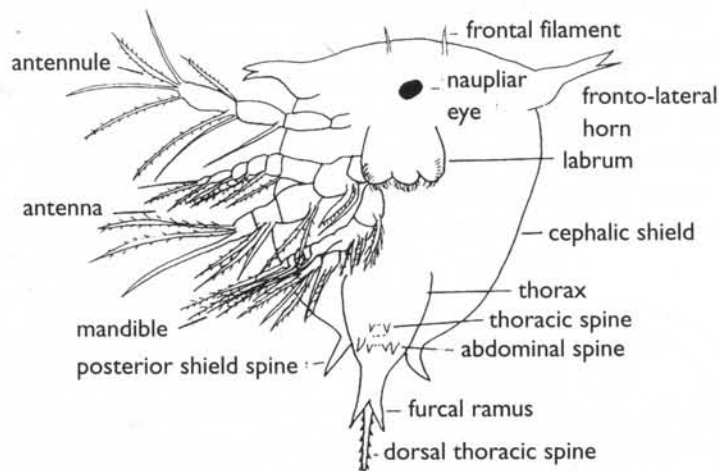


Fig. 1. Ventral view of a stage V nauplius larva. (From Miller and Roughgarden, 1994, Fig. 1)

Table 1. Species in the crustacean subclass Cirripedia from the Pacific Northwest

<i>Taxa</i>	<i>Larval Description</i>	<i>Reference</i>
Suborder Lepadomorpha		
<i>Mitella polymerus</i>	No	
<i>Scalpellum columbianum</i>	No	
<i>Lepas anatifera</i>	Yes	Moyse 1987
<i>Lepas fascicularis</i>	Yes	Bainbridge and Roskell, 1966
<i>Lepas hilli</i>	No	
<i>Lepas pacifica</i>	No	
<i>Pollicipes polymerus</i>	Yes	Lewis, 1975; Standing, 1980
Suborder Balanomorpha		
<i>Chthamalus dalli</i>	Yes	Korn and Ovsyannikova, 1979; Standing, 1980; Miller et al., 1989
<i>Semibalanus balanoides</i>	Yes	Pyefinch, 1949; Lang, 1980
<i>Semibalanus cariosus</i>	Yes	Standing, 1980; Branscomb and Vedder, 1982; Korn, 1989
<i>Solidobalanus engbergi</i>	No	
<i>Solidobalanus hesperius</i>	Yes	Barnes and Barnes 1959a
<i>Balanus balanus</i>	Yes	Barnes and Costlow, 1961; Lang, 1980
<i>Balanus crenatus</i>	Yes	Herz, 1933; Standing, 1980; Branscomb and Vedder, 1982; Ovsyannidova and Korn, 1984
<i>Balanus glandula</i>	Yes	Standing, 1980; Brown and Roughgarden, 1985
<i>Balanus improvisus</i>	Yes	Jones and Crisp, 1954; Standing, 1980
<i>Balanus nubilus</i>	Yes	Barnes and Barnes, 1959b; Standing, 1980; Miller and Roughgarden, 1994
<i>Balanus rostratus</i>	No	
Order Rhizocephala		
<i>Angulosasscus tenuis</i>	No	
<i>Clistosaccus paguri</i>	No	
<i>Brarosaccus callosus</i>	No	
<i>Peltogaster boschmae</i>	No	
<i>Peltogaster paguri</i>	No	
<i>Peltogaster gracilis</i>	No	
<i>Loxothylacus panopaei</i>	No	
<i>Sylon hippolytes</i>	No	
<i>Thompsonia</i> sp.	No	
<i>Trypetesa</i> sp.	No	
<i>Dendrogaster</i> sp.	No	

stage. The cyprid is responsible for finding a suitable habitat where it can settle and undergo a final metamorphosis into a juvenile sessile barnacle.

Both the nauplius and cyprid larval forms can be easily distinguished from other common zooplankters; there are, however, larval and adult forms of zooplankton that may create potential confusion for an inexperienced observer. Copepoda, another subclass of the subphylum Crustacea, also has a nauplius larval form. Figure 1 presents a generalized cirripede nauplius body form with distinguishing features noted. Figure 2 provides a comparison of the similar-looking copepod nauplius. The dorsal surface of the cirripede nauplius is covered with a cephalic shield (carapace) that is generally triangular or shield-shaped. Cirripede nauplii can be distinguished from copepod nauplii by the pair of conspicuous frontolateral horns on either side of the anterior end of the cephalic shield. A prominent naupliar eye present at the center of the anterior end may or may not be seen in other crustacean nauplii. Other cirripede naupliar characteristics include three pairs of biramous appendages and two prominent posterior structures, the dorsal thoracic spine and the ventral furcal ramus.

The cyprid larval form is unique to cirripedes. These are oblong, bivalved larvae with six pairs of thoracic appendages. A pair of compound eyes are present; both can be seen from the dorsal view, but only one is visible in the side view. This is a non-feeding larval form. Lipid reserves in the form of oil droplets are visible at the anterior end of the cyprids of some species. Ostracods are the organisms most easily confused with barnacle cyprids (Fig. 3). The easiest way to distinguish cyprids from ostracods is to note the compound eyes in the former.

Identification and Description of Local Taxa

A majority of this chapter deals with species of the order Thoracica. In addition there are two suborders in our estuaries and coastal waters, Lepadomorpha and Balanomorpha, with characteristics for the most part unique to each. Lepadomorphs have a unilobed labrum, whereas balanomorphs possess a trilobed labrum (see Fig. 1). The exception to this rule is found

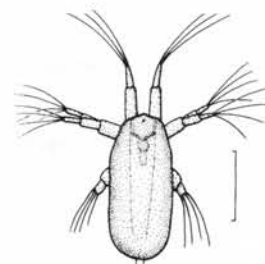
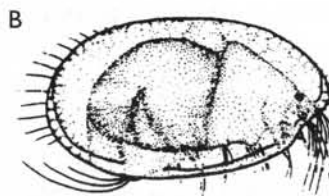
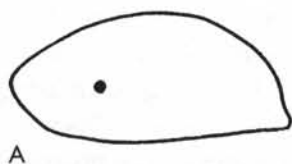


Fig. 2. Copepod nauplius. Scale = 100 μm . (From *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae*, Second Edition, by DeBoyd L. Smith and Kevin B. Johnson. Copyright 1996 by DeBoyd L. Smith and Kevin B. Johnson. Reprinted by permission of Kendall/Hunt Publishing Company.)

Fig. 3. (A) Generalized barnacle cyprid. (B) Ostracod. (A from Brown and Roughgarden, 1985; B from *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae*, Second Edition, by DeBoyd L. Smith and Kevin B. Johnson. Copyright 1996 by DeBoyd L. Smith and Kevin B. Johnson. Reprinted by permission of Kendall/Hunt Publishing Company.)

in *Chthamalus dalli*, a balanomorph with a unilobed labrum. Lepadomorph nauplii of the genus *Lepas* have distinct projections on their cephalic shield margin and a dorsal thoracic spine that is about twice as long as the carapace length (see Fig. 18). The cephalic shield of balanomorph nauplii, and those of the lepadomorph *Pollicipes polymerus*, is nearly as wide as long. Generally, lepadomorph cyprids are the largest in Pacific Northwest waters. *Pollicipes polymerus*, however, is an exception; its cyprids are small.

The identification of barnacle larvae is fairly difficult. A nauplius must be identified to stage before it can be differentiated to species. Species can be separated by examining the appendage setation, which requires a compound microscope (see Miller and Roughgarden, 1994, for species-specific setation patterns). The key to nauplii presented here is based on characteristics that can usually be distinguished through a good dissecting microscope, but it is usually much easier to stage and identify nauplii under a compound microscope.

Cyprid larvae are also difficult to identify to species. The separation of species is dependent on morphological differences such as pigmentation and variations in carapace margin outline. Overall cyprid size is useful in limiting possible species identification. Standing (1980) provides a comprehensive comparison of the cyprids of seven of the more common barnacles. Identification can be done under a dissecting microscope.

Nauplius Larvae

Balanomorph nauplii can be identified to stage based on the basis of the setation of their antennule and the presence of abdominal spines (Fig. 4) (Lang, 1979; Miller and Roughgarden, 1994). Lepadomorph nauplii may be staged similarly, as some characteristics used to stage balanomorph nauplii are conservative in lepadomorph nauplii. For example, in all naupliar stages of *Pollicipes polymerus*, a lepadomorph, antennule setation is identical to that of the balanomorphs (Lewis, 1975). Additionally, series two abdominal spine configurations for stage IV and VI *P. polymerus* nauplii are like that of the balanomorphs.

All stage I nauplii have folded frontolateral horns and are small in size. Because of the short duration of this stage, they are rarely present in plankton tows. The frontolateral horns of a stage II larva point away from the body approximately perpendicular to the long axis, and the tip of each horn is unsplit. There is one pair of abdominal spines and no preaxial setae on the antennule. Stage III nauplii are characterized by

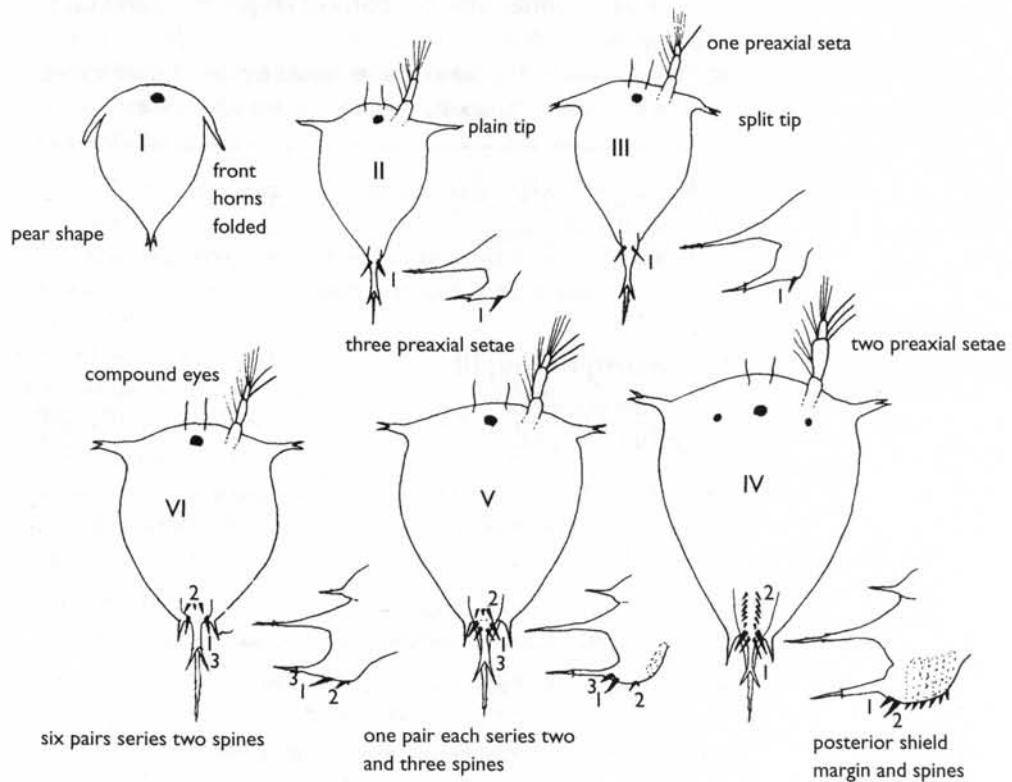


Fig. 4. Diagnostic morphological features, including lateral views of furcal ramus, for each of the six stages of balanomorph nauplii. Abdominal spines are grouped in three series, as noted by arabic numerals (Modified from Lang, 1979)

split frontolateral horn tips and one preaxial seta on the antennule. An additional preaxial seta and additional pair of abdominal spines are gained on the antennule and abdominal process, respectively, in stage IV nauplii. Stage V nauplii are distinguished by three preaxial setae on the antennule and three pairs of abdominal spines. Compound eyes are rarely present in stage V nauplii. Compound eyes are, however, a diagnostic characteristic of stage VI nauplii. Additionally, there are six pairs of abdominal spines on stage VI nauplii.

Key to cirriped naupliar stages (modified from Lang, 1980)

- 1a. Frontolateral horns extended; furcal ramus well developed 2
- 1b. Frontolateral horns folded against body; furcal ramus rudimentary spine Stage I
- 2a. Posterior shield spine absent 3
- 2b. Posterior shield spine present 4
- 3a. Frontolateral horns with plane tips; antennule without preaxial setae Stage II
- 3b. Frontolateral horns with split tips; antennule with 1 preaxial seta Stage III

- 4a. Furcal ramus with 1–2 pairs of large spines and up to 3 small spines 5
- 4b. Furcal ramus with 2 pairs of large spines, 6 pairs of small spines, antennule with 3 preaxial setae; compound eyes present Stage VI
- 5a. Furcal ramus with 1 pair of large spines, antennule with 2 preaxial setae Stage IV
- 5b. Furcal ramus with two pairs of large spines, antennule with three preaxial setae, compound eyes not present Stage V

Key to cirriped nauplii

- 1a. Labrum unilobed 2
- 1b. Labrum trilobed 4
- 2a. Cephalic shield outline smooth 3
- 2b. Cephalic shield outline with projections, frontal horns long in stages I and II (page 171) *Lepas* spp.
- 3a. Dorsal outline round (page 170) *Chthamalus dalli*
- 3b. Dorsal outline goblet-shaped (page 172) *Pollicipes polymerus*
- 4a. Anterior margin flat between frontolateral horns (stages III–VI) 5
- 4b. Anterior margin rounded between frontolateral horns 7
- 5a. Bulky outline, wide triangular or goblet-shaped 6
- 5a. Slender outline, long and narrow, triangular; relatively long frontolateral horns pointed anteriorly (page 169) *Solidobalanus hesperius*
- 6a. Frontolateral horns curved laterally; cephalic shield triangular (page 164) *Balanus glandula*
- 6b. Frontolateral horns straight; cephalic shield square or goblet-shaped (page 166) *Balanus nubilus*
- 7a. Larger nauplii (all stages $\geq 450 \mu\text{m}$), width less than cephalic shield length 8
- 7b. Smaller nauplii (all stages $\geq 500 \mu\text{m}$), width nearly equal to length; anterior margin between frontolateral horns slightly curved (page 163) *Balanus improvisus*
- 8a. Anterior margin between frontolateral horns prominently curved 9
- 8b. Anterior margin between frontolateral horns slightly curved, smaller; narrower, more triangular shape, frontolateral horns anteriorly directed in all stages (page 165) *Balanus crenatus*
- 9a. Nauplius with rudimentary furcal ramus and small abdominal spines, frontolateral horns perpendicular to shield axis in stages I–III and swept back in stages IV–VI 10
- 9b. Nauplius with distinct well-formed furcal ramus and abdominal spines, frontolateral horns swept back in all stages (page 167) *Balanus balanus*

- 10a. Large, bulky, slightly rounded outline, stages II and III with long dorsal thoracic spine, frontolateral horns perpendicular to long axis in stages II and III and anteriorly directed in stages IV–VI; maximum size of stage II–VI, respectively, ca 350, 350, 450, 550, and 650 μm (page 165) *Semibalanus cariosus*
- 10b. Same general characters as above; maximum size of stage II–VI, respectively, 400, 500, 600, >700, and >800 μm (page 169) ..
..... *Semibalanus balanoides*

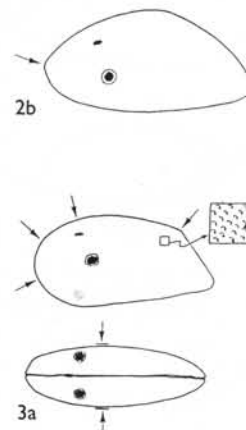
Cyprid Larvae

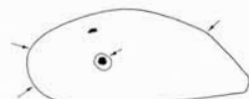
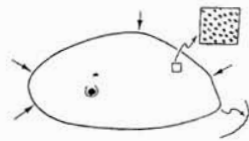
Cyprid larvae can be identified by carefully comparing shape, size, carapace texture, and carapace pigmentation. The location of the collection site may be of some help in excluding possible species; for example, *Balanus improvisus* cyprids are not likely to be collected outside an estuary. Any cyprid belonging to the genus *Lepas* should rarely be found within an estuary, since they are strictly oceanic species; adults are only found attached to floating objects.

In the following key, size ranges are from animals collected by Standing (1980) at Bodega Harbor, California, except where noted. Although size ranges may be different for specimens collected farther north, the relative size differences should be conservative. Length refers to the long axis (anterior to posterior), depth refers to dorsal–ventral distance, and breadth refers to length from left to right side at the widest point of the cyprid. Note that the shape of the carapace margin is visible only in a side view.

Key to cirriped cyprids (adapted from Standing, 1908)

- 1a. Small, length <625 μm 2
- 1b. Medium to large, length >625 μm 4
- 2a. Anterior end broadly rounded in side view; posterodorsal margin with break in curve 3
- 2b. Anterior end angular in side view (arrow in figure 2b); posterodorsal margin evenly curved, relatively translucent when preserved, no special pigmentation when fresh, carapace surface shiny under low magnification, smooth under high magnification, length 440–580 μm (page 170) *Chthamalus dalli*
- 3a. Carapace depth greatest about one-third of the way from anterior end; carapace breadth narrow in dorsal view, surface of carapace sculptured under high magnification, posterior margin triangular; mainly found on outer coast; length from 420–540 μm (page 172) *Pollicipes polymerus*

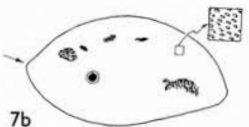




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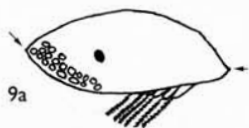
7a



7b



8b



9a



9b

3b. Carapace depth greatest ca halfway from anterior end; carapace breadth wide in dorsal view, anterior end rounded, slight break in shell outline near posterior end; surface of carapace sculptured under high magnification; estuarine dependent species; length 540–610 μm (in San Francisco) (page 163) *Balanus improvisus*

4a. Medium size, 625–1,200 μm 5

4b. Large, length >1,200 μm , ventral margin straight, angular at posterior end; sometimes retaining signs of frontolateral horns at anterior end; usually on open coast (page 171) *Lepas* spp.

5a. Anterior end angular 6

5b. Anterior end broadly rounded, posterior end narrowly rounded, break in posterodorsal margin, median and paired eyes visible in side view, length 800–1,000 μm (page 166) *Balanus nubilus*

6a. Posterior end rounded or broadly angular; ventral margin curved 7

6b. Anterior and posterior ends angular 8

7a. Posterior end rounded, ventral margin relatively straight, median and paired eyes visible in side view, 1 pair of black pigment spots just posterior to midlength and eyes; white in color when preserved, with pigment spots persisting; carapace shiny under low magnification and smooth under high magnification; length 700–960 μm (larger in Alaska) (page 165) *Balanus crenatus*

7b. Distinct golden color (rarely brown), pigmentation absent when preserved; carapace profile high in side view, large carapace depth; carapace surface dull under low magnification, sculptured with papillae under high magnification; median and paired eyes visible, 4 pigment patches, length 640–780 μm (page 164) *Balanus glandula*

8a. Dorsal and ventral surfaces rounded, posterior end sharply pointed and turned slightly upward; length >900 μm 9

8b. Dorsal and ventral surfaces rounded, anterior end sharply pointed and turned slightly upward; length ca 800 μm (in Scotland) (page 167) *Balanus balanus*

9a. Translucent when fresh; white to pink when preserved, without distinguishing pigment spots; medium carapace depth; only one eye visible in side view, length 960–1,200 μm (page 165) *Semibalanus cariosus*

9b. Typically brown in color but with high degree of variation, without distinguishing pigment spots; medium carapace depth; only one eye visible in side view, length 960–1,200 μm (in England) (page 169) *Semibalanus balanoides*

Order Thoracica, Suborder Balanomorpha

Balanus improvisus. Adults live in low intertidal and subtidal areas within estuaries and some enclosed bays on rocks, pilings, and hard-shelled animals. This cirripede is particularly tolerant of brackish waters; high numbers of cyprids and adults have been found in low salinity (3.4 PSU) water in the San Francisco Bay estuarine system (Standing, 1980). Adults and larvae of this species are found in the upper portions of Coos River and South Sough estuary, Oregon (R. Emlet, pers. comm.). *B. improvisus* ranges from the Columbia River, Washington, to the Salinas River, California, and occasionally farther south. This species was introduced, probably from the North Atlantic.

The nauplius is similar in appearance to other balanoids. Figure 5 shows outlines for the six stages of *B. improvisus* collected in British estuaries. Jones and Crisp (1954) reported that the paired eyes are present in the stage V nauplius, although unpigmented. This is earlier than in other cirripede species. A table of larval dimensions and additional comparative drawings can be found in Jones and Crisp (1954).

Cyprids of this species can usually be found low in the water column in estuaries and some enclosed bays. Standing (1980) found a mean length and width of *B. improvisus* cyprids collected in San Francisco Bay of 584 μm (range, 540–610 μm) and 285 μm , respectively (Fig. 6). Cyprids collected by Jones and Crisp (1954) from the east coast of England were smaller, with a mean length of 523 μm . This cyprid is most similar to *Chthamalus dalli*, *Balanus glandula*, and *Pollicipes polymerus*, but it can be differentiated by its size and carapace texture. *Chthamalus dalli* has a smooth carapace, whereas *B. improvisus* possesses a carapace sculptured with rounded pits. *Balanus improvisus* cyprids have a more rounded anterior end (in side

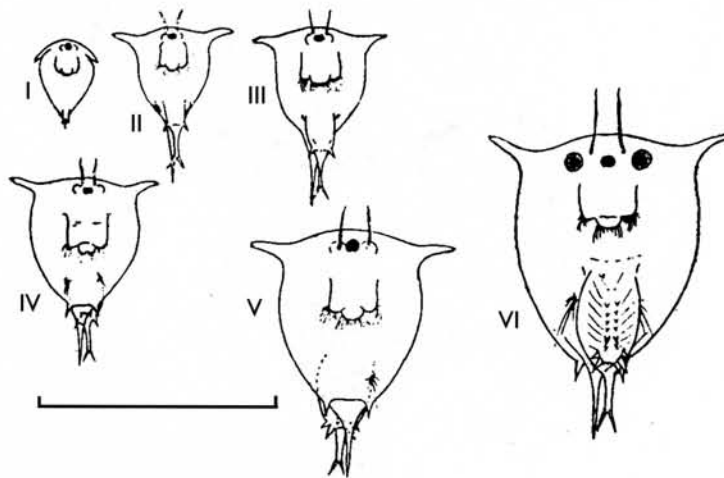
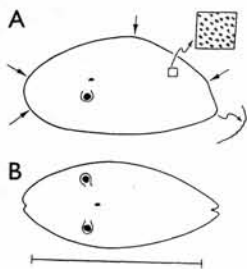


Fig. 5. *Balanus improvisus* nauplii. Stages I, II, III, and VI in ventral view; stages IV and V in dorsal view. Scale = 500 μm (From Jones and Crisp, 1954, Fig. 1)

Fig. 6. *Balanus improvisus* cyprid, (A) lateral and (B) dorsal views; carapace sculpturing inset. Scale = 500 μ m. (From Standing, 1980, Fig. 3)



view) than do the cyprids of *C. dalli*. Further, the posterodorsal margin of *B. improvisus* cyprids breaks just in front of the posterior end (see Fig. 6). *Balanus improvisus* cyprids are usually smaller than *B. glandula* cyprids but larger than those of *P. polymerus*. For additional distinctions between *B. improvisus* and other cyprids, see Standing (1980).

Balanus glandula. Adults of this species live in the upper and occasionally lower intertidal zone on both exposed and protected shores (Standing, 1980). *Balanus glandula* is found from the Aleutian Islands south to Bahía de San Quintín, Baja California. Like all other local balanomorph nauplii (except *Chthamalus dalli*), this one has a three-lobed labrum. The first naupliar stage is ephemeral; 99% molt to stage II within one hour (Brown and Roughgarden, 1985). A table of naupliar and cyprid sizes of specimens collected from Monterey Bay, California, is provided in Brown and Roughgarden (1985). In addition to their larger size, stage IV, V, and VI nauplii can be distinguished from earlier stages by the presence of a pair of well-developed posterior shield spines at the posterior margin of the dorsal shield (Brown and Roughgarden, 1985). Outline drawings of stage I–VI nauplii are shown in Fig. 7 (see also Fig. 9).

Live *B. glandula* cyprids are translucent or brown (Brown and Roughgarden, 1985) and are usually found high in the

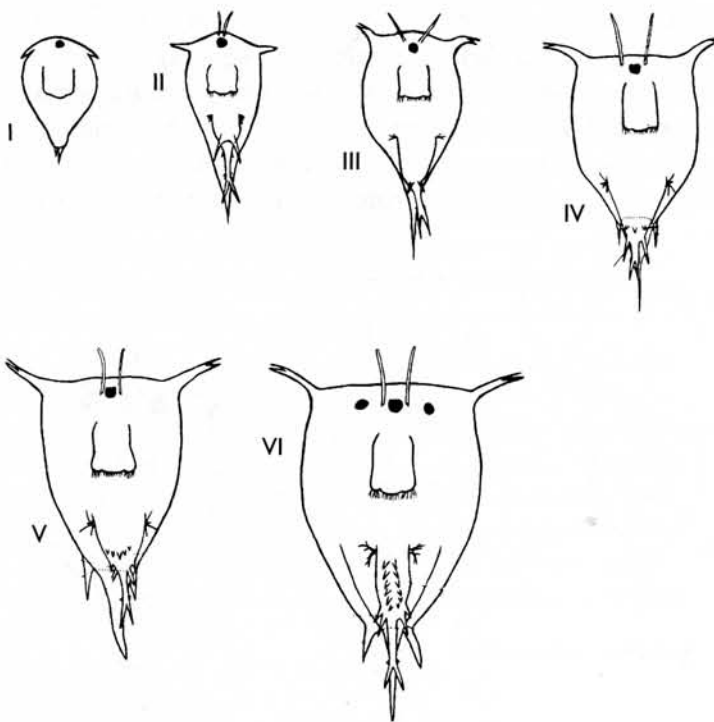


Fig. 7. Stage I–VI *Balanus glandula* nauplii as seen from ventral aspect. (From Brown and Roughgarden, 1985, Fig. 3)

water column and mainly during the non-winter months (Standing, 1980). They range in size from 640 to 780 μm (Fig. 8). Chartreuse pigmentation on live specimens is distinctive. See Standing (1980) for a detailed description of pigmentation and other unique characteristics. Preserved specimens are pale brown or, more commonly, golden. Similar to the smaller *P. polymerus* cyprid, the carapace of *B. glandula* is sculptured with papillae (Standing, 1980).

Balanus crenatus (Bruguere). Adults are found in the low intertidal and subtidal to depths of 182 m. They live on pier pilings, hard-shelled animals, and occasionally seaweed. They range from Alaska to Santa Barbara, California (Morris et al., 1980; Standing, 1980). Herz (1933) was one of the first to describe *B. crenatus* development, though he incorrectly described eight naupliar stages. Ovsyannidova and Korn (1984) provide a detailed description of differences between the six naupliar stages in specimens collected from the Sea of Japan. Branscomb and Vedder (1982) describe the naupliar stages of *B. crenatus* as well as those for *B. glandula* and *Semibalanus cariosus* (Fig. 9). Early stage *B. crenatus* nauplii are roughly triangular (Pyefinch, 1948). The last three naupliar stages are more shield-shaped. *B. crenatus* nauplii have a shape similar to that of *S. cariosus*, but they tend to be smaller. *Balanus crenatus* nauplii are similar in shape and size to those of *B. glandula*; comparison of the frontolateral horns can be used to differentiate between the species. At each naupliar stage, the frontolateral horns of *B. glandula* are angled more strongly to the anterior than they are in *B. crenatus*.

Fig. 8. *Balanus glandula* cyprid, (A) lateral and (B) dorsal views; carapace sculpturing inset. Scale = 500 μm . (From Standing, 1980, Fig. 4)

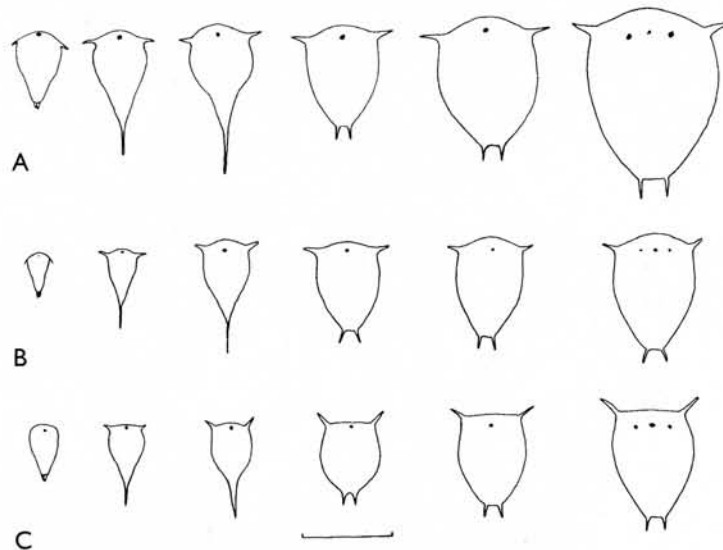
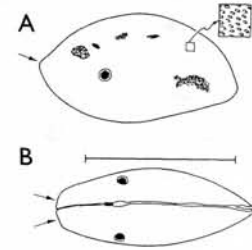
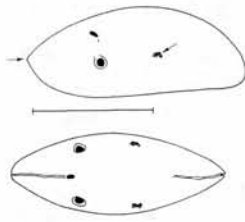


Fig. 9. Cephalic shield outlines of the six naupliar stages of (A) *Semibalanus cariosus*, (B) *Balanus crenatus*, and (C) *Balanus glandula*. Scale = 500 μm . (From Branscomb and Vedder, 1982, Fig. 1)

Fig. 10. *Balanus crenatus* cyprid, (A) lateral and (B) dorsal views. Scale = 500 μ m. (From Standing, 1980, Fig. 5)



Standing (1980) provides a description of *B. crenatus* cyprids—their size, vertical distribution in the water column, and characteristics that can be used to differentiate them from other cyprids. This species produces a medium-sized cyprid with a mean length of 852 μ m (range, 700–960 μ m). Standing (1980) found that on the west coast of North America cyprid size increases with latitude. These cyprids are generally found low in the water column. *Balanus crenatus* cyprids are most similar to cyprids of *B. nubilus* but differ in having a narrow, angular anterior end and an evenly curved posterodorsal margin (Fig. 10). An important distinguishing characteristic is the presence of a single pair of black pigment spots, somewhat smaller than the compound eyes, just posterior to midline of the cyprid. These spots persist after preservation. See Standing (1980) for additional details on differentiating balanomorph cyprids.

Balanus nubilus. Adults occur in the lower intertidal and subtidal zones of exposed coasts from southern Alaska to Bahía de San Quentín, Baja California (Barnes and Barnes, 1959b; Standing, 1980). There are six naupliar stages (Fig. 11). From stage II onward, the cephalic shield is funnel-shaped. Stage III–VI nauplii are recognizable by the nearly flat, noncurved anterior margin between the relatively large and anteriorly oriented frontal horns (Miller and Roughgarden, 1994). A median naupliar eye is present in all six stages, and compound eyes are apparent at stage VI although they are not always deeply pigmented (Barnes and Barnes, 1959b). The boxy angular outline of these nauplii distinguishes them from all other Pacific Northwest barnacle nauplii.

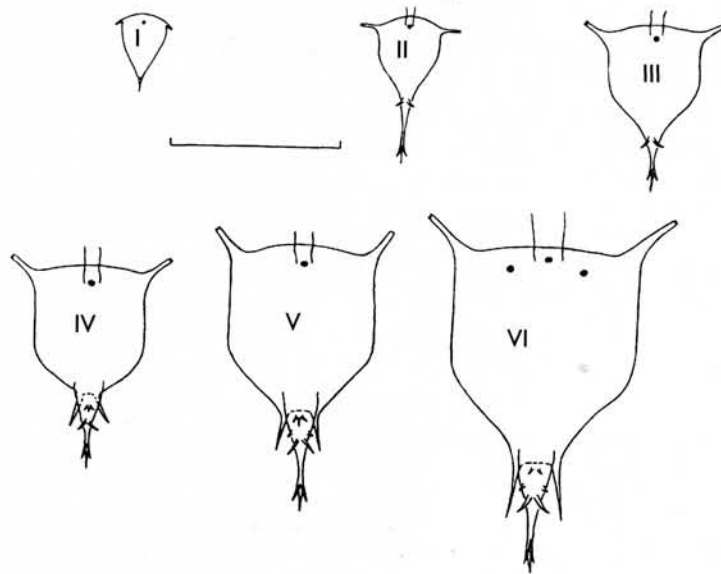


Fig. 11. Stage I–VI *Balanus nubilus* nauplii. Scale = 500 μ m. (From Barnes and Barnes, 1959b, Fig. 1)

Standing (1980) provides the best description of *B. nubilus* cyprids. Cyprids are medium-sized (mean length, 932 μm ; range 800–1,000 μm). Like the nauplii of this species, the cyprid poses a distinctive profile. Viewed from the side, there is a break in the posterodorsal margin and a sharply curved posterior end (Fig. 12). The anterior end is rounded. This cyprid is most similar to that of *B. crenatus* but can be differentiated from it by the break in the posterodorsal margin and the lack of a posterior pigment spot. The rounded anterior end separates this cyprid from *Semibalanus cariosus*. All of the above-mentioned characteristics as well as a smooth carapace separate this cyprid from that of the smaller *B. glandula*. An additional description is provided by Miller and Roughgarden (1994).

Balanus balanus. This subtidal species is rare in the San Juan Archipelago (Strathmann, 1987). The carapace of the first three naupliar stages is triangular (Fig. 13), and the frontolateral horns are turned slightly to the posterior. The carapace of naupliar stages IV–VI is roughly goblet-shaped, with the frontolateral horns perpendicular to the long axis of the carapace. The cyprid is ca 800 μm in total length, with sharply pointed ends (Fig. 13). The anterior end turns slightly upward (Barnes and Costlow, 1961; Lang, 1980).

Semibalanus cariosus (= *Balanus cariosus*). *Semibalanus cariosus* adults are found in the lower midtidal and sometimes low intertidal zones of wave-exposed shores on rocks and hard-shelled animals; they range from Alaska south to Morro Bay, California (Standing, 1980). Nauplii of this species are shield-shaped like those of *Balanus glandula* and *B. crenatus*, but they

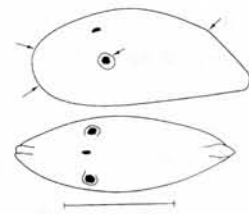


Fig. 12. *Balanus nubilus* cyprid, (A) lateral and (B) dorsal views. Scale = 500 μm . (From Standing, 1980, Fig. 6)

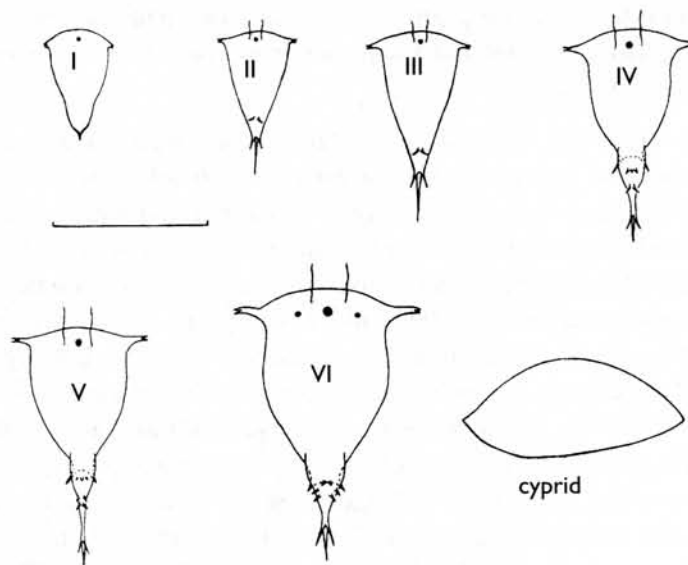
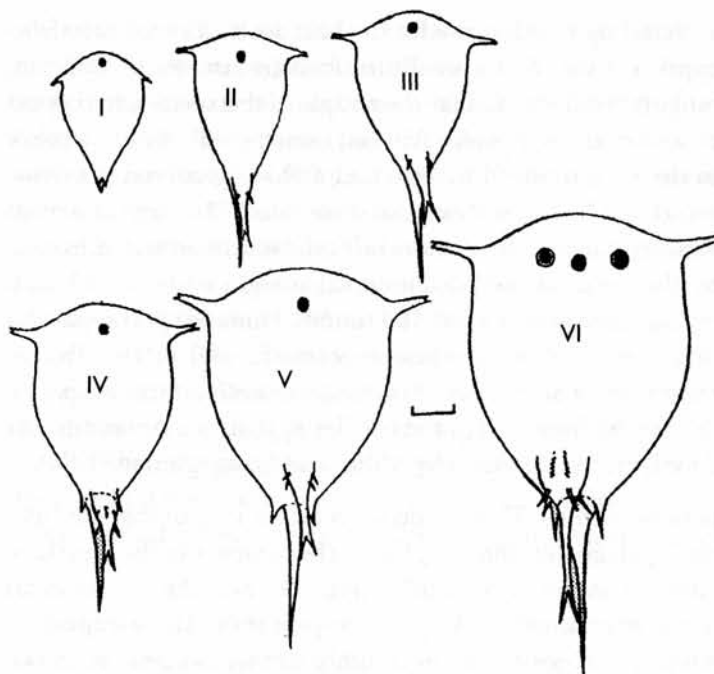


Fig. 13. *Balanus balanus* nauplii stages I–VI and cyprid. Scale = 500 μm . (From Barnes and Costlow, 1961).

Fig. 14. Ventral view of stage I–VI nauplii of *Semibalanus cariosus*. The abdominal process is slightly displaced to show the dorsal spine. Scale = 100 μm . (From Korn, 1989, Fig. 4)



are wider, larger, and possess a more pronounced anterior curvature between the frontolateral horns (Fig. 14; see also Fig. 9). The naupliar stages are similar in shape to those of *Semibalanus balanoides*, but they are smaller in size. Approximate maximum size of stage II–VI, respectively, is 350, 350, 450, 550, and 650 μm (Korn, 1989).

Standing (1980) reports that *S. cariosus* cyprids tend to be found mainly in the spring and summer and low in the water column. These cyprids tend to be large, with a mean length of 1,111 μm (range, 960–1,200 μm). They are opaque when preserved except for a translucent area along the dorsum, and they lack unique pigmentation. The carapace is smooth, angular at both anterior and posterior ends, and has no pigment spots (Fig. 15).

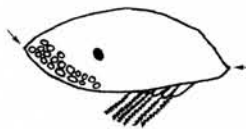


Fig. 15. *Semibalanus cariosus* cyprid. (Drawn from color slide provided by R. Emlet)

Semibalanus balanoides (= *Balanus balanoides*). Adults are intertidal with a large vertical range and do not occur south of Washington state. The anterior of the nauplii is strongly curved. The frontolateral horns are roughly perpendicular to the long axis of the body in the first three stages and are tilted anteriorly in the last three stages (Fig. 16). The carapace is shield-shaped. The nauplii are similar in shape to those of *S. cariosus* but larger at each stage. Approximate maximum size of stage II–VI, respectively, is 400, 500, 600, >700, and >800 μm (Lang, 1980). The cyprid stage is typically brown but with a high degree of variation. There is no distinguishing pigmentation. In a side view, only one eye is visible. In samples collected off England, sizes range from 960 to 1,200 μm (Pyefinch, 1948; Lang, 1980).

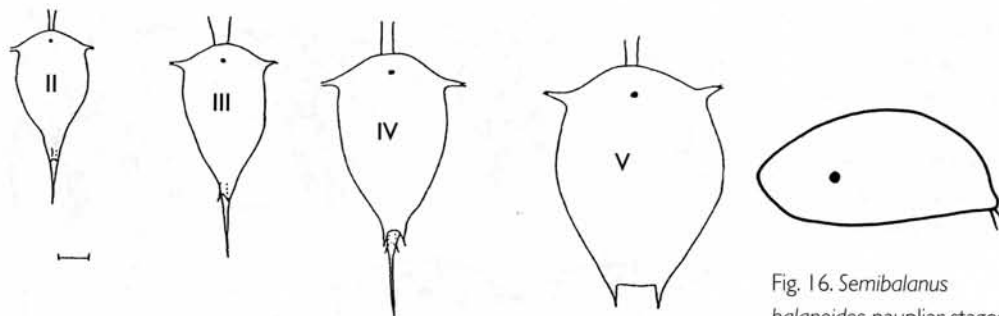


Fig. 16. *Semibalanus balanoides* naupliar stages II-V and cyprid. Scale = 0.1 mm and applies to the nauplii; the cyprid is ca 0.9 mm total length. (Nauplii from Lang, 1980; cyprid from Pyefinch, 1948)

Solidobalanus hesperius (Pilsbry). This species is not well studied. Adults of what Pilsbry (1916) called the *laevidomus* form of *Solidobalanus hesperius* are found from Alaska south to Monterey, California. Pilsbry separated a unique form of this animal after thorough examination of the cross sections of calcareous plates of adults from different eastern Pacific locations; species variation based on these findings is, however, seldom considered in recent literature.

Barnes and Barnes (1959a) described the six naupliar stages but did not provide a description of the cyprid (Fig. 17). Stage I nauplii are pear-shaped. The later stages are characteristically triangular; their length is about two and a half times greater than their width. Stage III nauplii and beyond possess a prominently flat anterior margin between the frontolateral horns. The frontolateral horns are long. In naupliar stages V and VI the posterior shield spines are long, extending more than half the length of the furcal ramus. There is no published description of the cyprid form of this species.

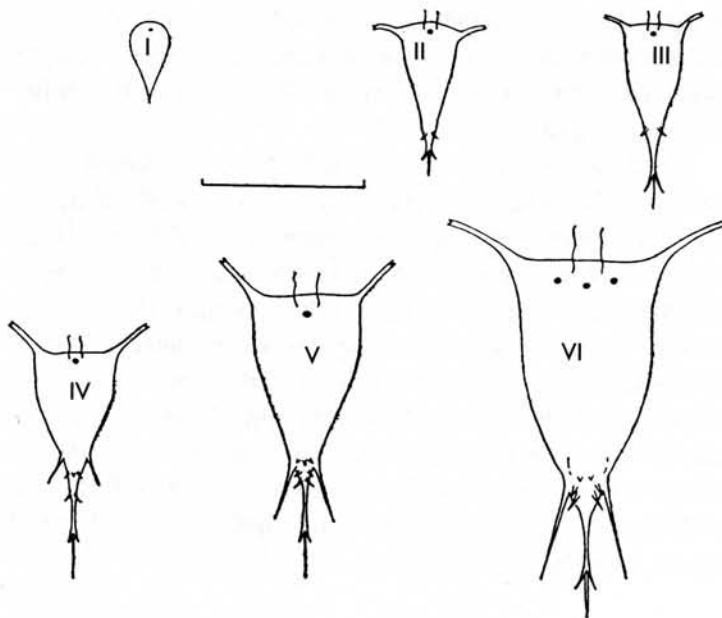
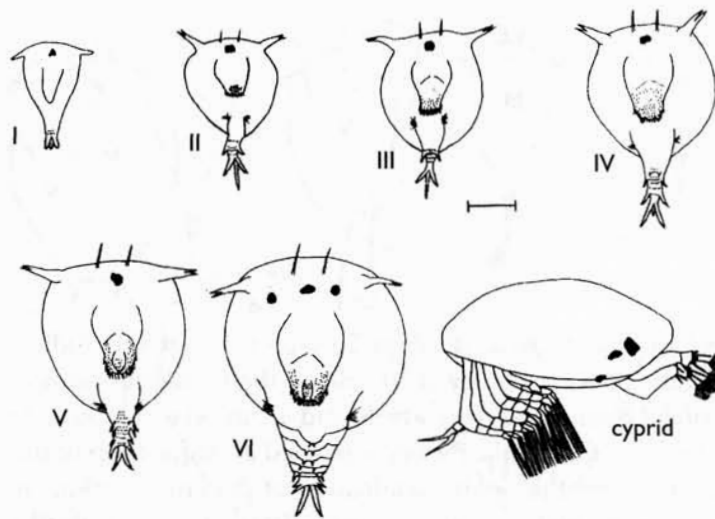


Fig. 17. *Solidobalanus hesperius* naupliar stages I-VI. Scale = 500 μ m. (From Barnes and Barnes, 1959a, Fig. 1)

Fig. 18. *Chthamalus dalli* naupliar stages I–VI and cyprid. Note that the anterior end of the cyprid is on the left. Scale = 100 μm . (From Miller et al., 1989, Fig. 5)



Solidobalanus engbergi. There are no descriptions of the larvae of this species. Adults live in the littoral zone from Alaska to Oregon (Austin, 1985).

Chthamalus dalli. Adults of this common northern barnacle inhabit the high intertidal zone from Alaska to San Diego, California (Standing, 1980; Miller et al., 1989). Miller et al. (1989) provide a complete description of distinctive characteristics of *C. dalli* nauplii. Unique features include a rounded dorsal shield outline and a unilobate labrum (Fig. 18). In addition, *C. dalli* nauplii are small; the only similarly sized nauplii are those of *Pollicipes polymerus*. The nauplii of the two species can be differentiated by noting the following differences: the cephalic shield of *C. dalli* nauplii is round, whereas that of *P. polymerus* nauplii is goblet-shaped; *C. dalli* nauplii have large spines on the furcal ramus which are not present in *P. polymerus* nauplii. See Miller et al. (1989) for further discussion of the differentiation of *C. dalli*.

Standing (1980) states that *C. dalli* cyprids are found at the surface and mid-depths of the water column. Like the nauplius stage, the cyprid is small, with a mean length of 529 μm (Figs. 18, 19). Live specimens are translucent, and when preserved they become a bit more opaque at the anterior end. They lack unique pigmentation. The carapace is completely smooth, distinguishing this cyprid from that of the similarly sized *P. polymerus*. Both the nauplii and cyprid of this species are identical in appearance to the more southern *C. fissus* (Miller et al., 1989). Korn and Ovsyannikova (1979) provide an additional resource with detailed descriptions of naupliar and cyprid features of *C. dalli*.

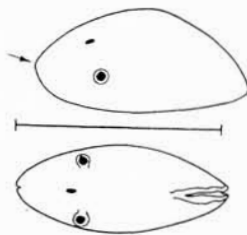


Fig. 19. *Chthamalus dalli* cyprid, lateral (a) and dorsal (b) views. Scale = 500 μm . (From Standing, 1980, Fig. 2)

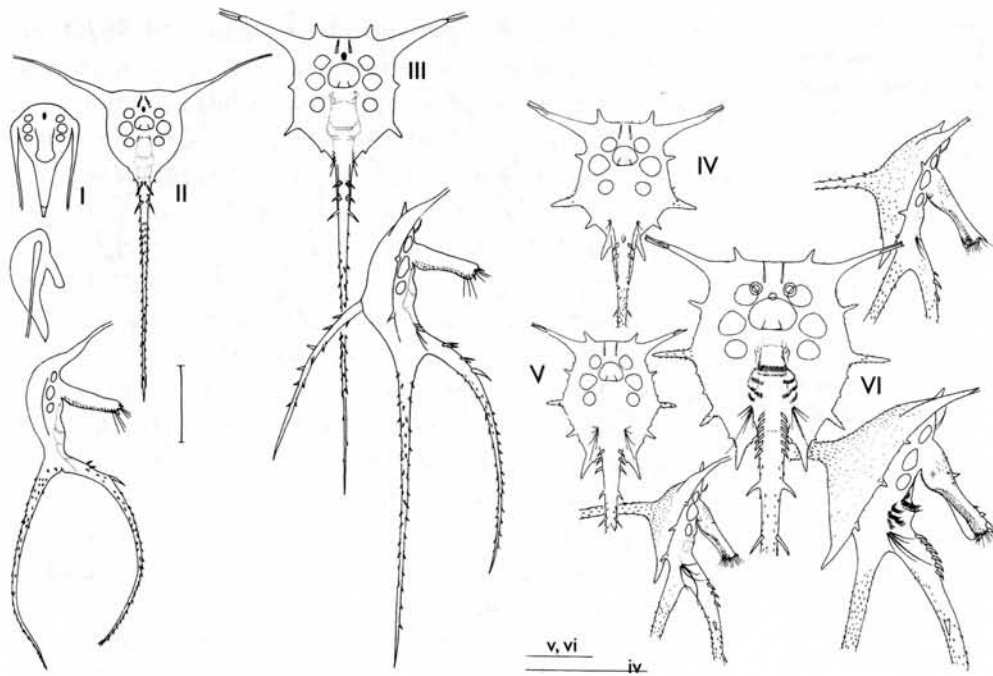


Fig. 20. *Lepas anatifera* naupliar stages I–VI. Scale = 200 μm for stages I–III and 500 μm for stages IV–VI. (Modified from Moyses, 1987, Figs. 4, 5)

Order Thoracica, Suborder Lepadomorpha

Lepas anatifera. Like all adults of the genus *Lepas*, these are found on open-ocean flotsam such as logs and glass fishing floats. Moyses (1987) provides detailed illustrations of *L. anatifera*. The unique shape of the nauplii of these lepadomorph barnacle larvae easily distinguishes them from other Pacific Northwest cirripedes (Fig. 20). The stage I nauplii have frontolateral horns folded back against the body as in the balanomorph stage I nauplii, but these horns are nearly as long as the entire nauplius. In stage II and all later stages, the dorsal thoracic spine is more than twice the body length. With each stage, the cephalic shield gains projections around its edges. As in all lepadomorphs, the nauplii have a single-lobed labrum.

Moyes (1987) gives little information on the cyprid. *Lepas* cyprids are large and translucent. In a side view the ventral margin is relatively straight, with a uniformly rounded dorsal margin. The anterior end is broadly rounded, sometimes showing signs of retaining the naupliar frontolateral horns (anterior arrow, Fig. 21). The posterior ventral end is angular (posterior arrow, Fig. 21). *Lepas pacifica* and *L. fascicularis*, two other members of the genus, may be present off our coastline; little has been published on the appearance of the larvae of these two species. Additional information can be found in Bainbridge and Roskell (1966) and Darwin (1851).

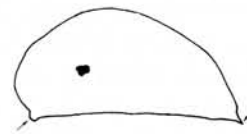


Fig. 21. Outline of an unidentified *Lepas* cyprid. Overall length is 2,200 μm . (Drawn from color slide provided by R. Emler)

Fig. 22. *Pollicipes polymerus* naupliar stages I–VI, dorsal view. Scale = 50 μm . (From Lewis, 1975, Fig. 2)

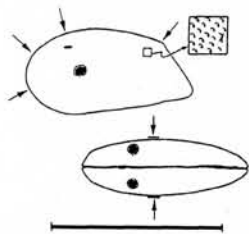
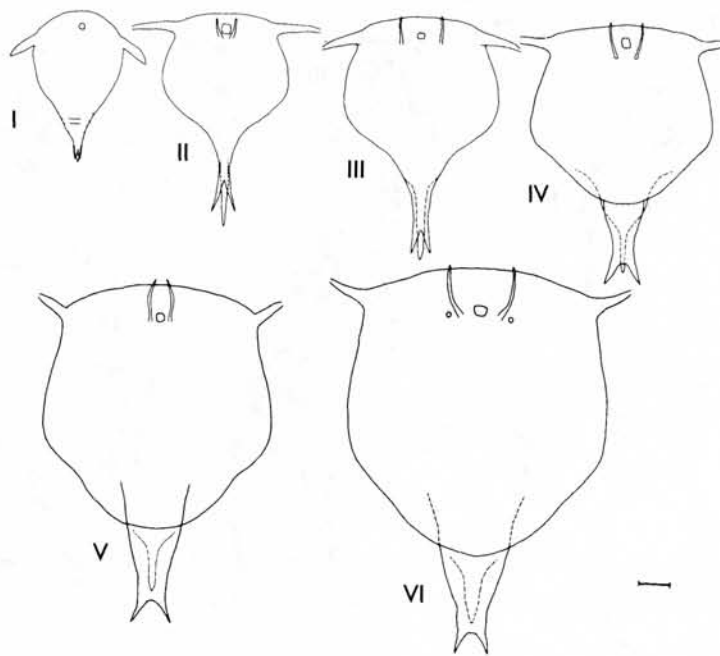


Fig. 23. *Pollicipes polymerus* cyprid, lateral (a) and dorsal (b) views; carapace sculpturing inset. Scale = 500 μm . (From Standing, 1980, Fig. 1)

Pollicipes polymerus (= *Mitella polymerus*). Aggregations of adults occur in the upper rocky intertidal zone in areas of surge or wave action from British Columbia to Cabo San Lucas, Baja California (Lewis, 1975; Strathmann, 1987). The naupliar carapace is a rounded and shaped like a goblet (Fig. 22). The frontal horns move progressively anterior with each successive stage. The furcal ramus exceeds the length of the dorsal thoracic spine in stage V and VI nauplii, unlike that in all other Pacific Northwest cirripedes (see Lewis, 1975, for illustrations of this feature).

The cyprid larvae do not possess the characteristic oil cells of other cirripedes, suggesting that they either feed in the plankton or settle out of the water column rapidly (Lewis, 1975). The entire carapace is sculptured with uniform, rounded, regularly spaced papillae (ca 4.5 μm diam. by 1.5 μm high) (Fig. 23). Transparent when fresh, this cyprid differs from other species in having a broadly rounded anterior end in the side view, a break in the posterodorsal margin, a narrow dorsal carapace profile and small papillae (Standing, 1980).

Lewis (1975) provides a description of *P. polymerus* embryological development and larval growth. Standing (1980) provides a detailed comparison of *P. polymerus* larvae to other common Pacific Northwest cirriped larvae.

Order Rhizocephala

The Rhizocephalan barnacles are parasites on decapod crustaceans particularly hermit crabs and other anomurans.

There are two suborders, the Kentrogonida and the Akentrogonida, and at least eleven local species (Table 2). A detailed description of the amazing life cycle of the rhizocephalan barnacles can be found in Høeg (1992).

Most species in the Kentrogonidae release propagules at the naupliar stage. Several Kentrogonidae species and all Akentrogonidae species release propagules that develop to the cyprid stage.

The nauplii are small lecithotrophic, and there are only four stages. Depending on the species and ambient water temperature, development takes from four to twenty days. Consistent with their being non-feeding, the nauplii lack gnathobases (paired endites, inwardly directed lobes, used to manipulate or move food) on their limbs (Høeg 1992). Most nauplii possess pigmented eyes and all contain numerous large yolk cells (Fig. 24). In some species in the family Peltogastridae nauplii stages II – IV are enclosed in a hollow annulus consisting of very thin cuticle reinforced by a mesh of thicker ribs (Høeg, 1992). This hollow annulus may aid in floatation of the larvae.

Rhizocephalan cyprids are small, ranging in size from 60 μm to as much as 400 μm . In the Kentrogonidae, the male cyprid tends to be smaller and morphologically different from the female (Høeg 1992); after the molt from the naupliar to the

Table 2. Species in the order Rhizocephala from the Pacific Northwest (from Kozloff, 1996)

Suborder	Kentrogonida
Family	Clistrosaccidae
	<i>Angulosaccus tenuis</i>
	<i>Clistrosaccus paguri</i>
Family	Peltogastridae
	<i>Briarosaccus callosus</i>
	<i>Peltogaster boschmae</i>
	<i>P. paguri</i>
	<i>P. gracilis</i>
Family	Sacculinidae
	<i>Loxothylacus panopaei</i>
Family	Sylonidae
	<i>Sylon hippolytes</i>
Suborder	Akentrogonida
Family	Akentrogonidae
	<i>Thompsonia</i> sp.

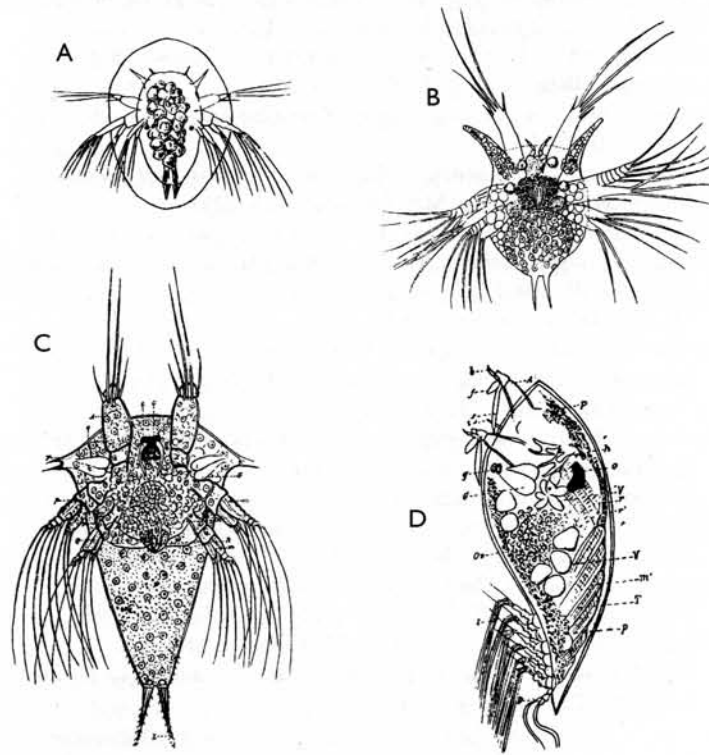
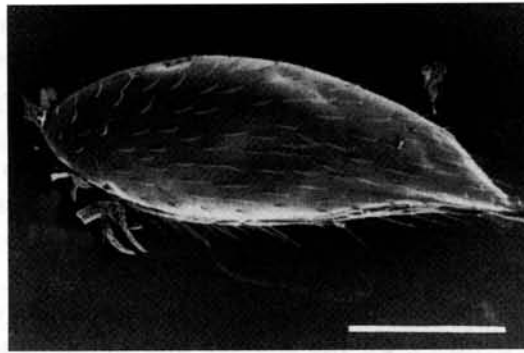


Fig. 24. Larvae of rhizocephalan barnacles. (A, B) *Peltogaster* sp., total length about 0.3 mm. (C, D) *Sacculina carcini*, total length about 0.2 mm. The numerous small circles in the nauplii represent yolk cells. (From Høeg, 1992, Figs. 48–50, 52)

Fig. 25. *Peltogaster paguri* cyprid. Note the numerous setae covering the carapace, a characteristic of rhizocephalan cyprids. Scale = 25 μm (From Høeg 1992, Fig. 13A)



cyprid stage, the cyprid must go through several days of development before it is competent to settle. Rhizocephalan cyprids may be distinguished by their small size, most lack a compound eye associated with the frontal filament (except the genus *Thompsonia*), most species have a naupliar eye (except some species in the genus *Peltogaster*), and the carapace is covered with setae (Fig. 25).

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