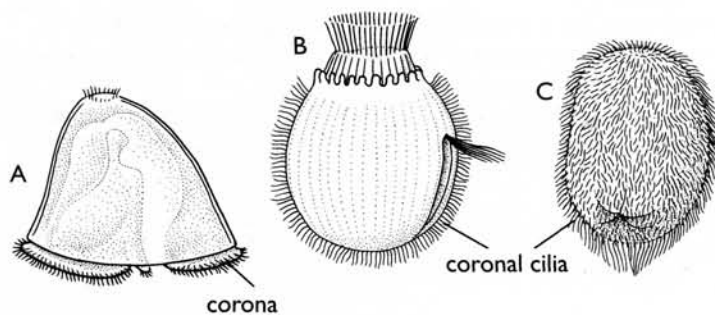


Two classes of Bryozoa are found in the marine environment, the Gymnolaemata and the Stenolaemata, with the majority of the marine species in the Gymnolaemata. Species descriptions, mostly from scientific collecting expeditions during the late 1880s and early 1900s, remain a primary source of information on bryozoan larvae. Many bryozoan species are found in the Pacific Northwest, but the larvae of only a handful have been described. Because of the limited number of larval descriptions, this chapter does not include a key to the larvae. Instead we offer a general description of the larvae of marine bryozoans, illustrations of a diversity of bryozoan larvae from around the world, and a brief account of local larvae for which we have published descriptions.

All stenolaemates and most gymnolaemates retain their embryos and release lecithotrophic larvae of short pelagic duration (Woollacott and Zimmer, 1978). A few gymnolaemate species release zygotes that develop into planktotrophic cyphonautes larvae (Fig. 1A); most, however, release lecithotrophic coronate larvae (Fig 1B). All species in the class Stenolaemata produce lecithotrophic coronate larvae (Fig. 1C). The pelagic duration of the lecithotrophic larvae in both classes is so brief that they seldom appear in zooplankton samples. The cyphonautes larvae, with their much longer pelagic duration, are common components of plankton samples collected in coastal waters.

Fig. 1. Bryozoan larval forms: (A) Planktotrophic cyphonautes larva (Gymnolaemata). (B) Lecithotrophic coronate larva (Gymnolaemata). (C) Lecithotrophic coronate larva (Stenolaemata). (A from Rupert and Barnes, 1994, Fig. 19-16; B from Hyman 1959, Fig. 131F; C from Nielsen 1970, Fig. 2A)



Class Stenolaemata

All stenolaemates release coronate larvae. The larvae are characteristically small, on the order of 100 μm wide by 150 μm long, ovoid, lecithotrophic, completely covered with cilia, and possess a pyriform gland (or pyriform complex) as well as an apical disc. Some gymnolaemates also release coronate larvae (see Figs. 1B, 5); they can be differentiated from stenolaemate coronate larvae by the presence of an apical tuft of longer cilia. Table 1 presents a list of the stenolaemate species present in the Pacific Northwest and indicates species for which a larval description is available; the larvae of only two (*Tubulipora pulchra* and *Disporella hispida*) of ca 33 local species have been described (Barrois, 1877; Nielsen, 1970). Drawings of representative coronate larvae are presented in Fig. 2.

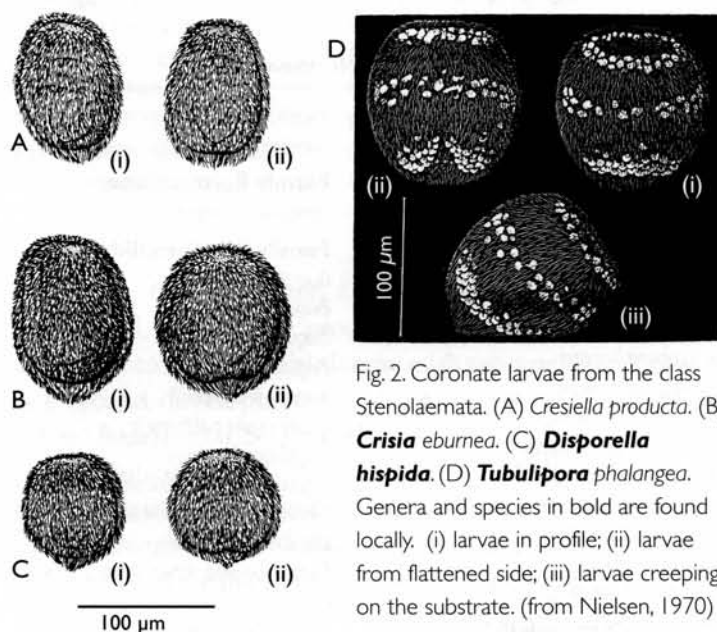


Fig. 2. Coronate larvae from the class Stenolaemata. (A) *Cresiella producta*. (B) *Crisia eburnea*. (C) *Disporella hispida*. (D) *Tubulipora phalangea*. Genera and species in bold are found locally. (i) larvae in profile; (ii) larvae from flattened side; (iii) larvae creeping on the substrate. (from Nielsen, 1970)

Class Gymnolaemata

Although there are obvious gross morphological differences between coronate and cyphonautes larva of the Gymnolaemata, there are consistent structural characteristics common to both types of larva in this class (Fig. 3). The larvae all have a ciliated girdle (the corona), an anterior tuft of long cilia and the external (or metasomal) sac (Zimmer and Woollacott, 1977).

The type of larva released (feeding or non-feeding) is dependent on the development mode of the species. Because of their long pelagic duration, they are usually the most abundant bryozoan larvae in plankton tows. Local genera displaying this pattern of development include *Membranipora*,

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

Family

Oncousoeciidae

Stomatopora granulata

Proboscina incrassata

Family Diastoporidae

Diaperoecia californica

Diaperoecia intermedia

Diaperoecia johnstoni

Diaperoecia obelium

Plagioecia patina

Family Tubuliporidae

Tubulipora flabellaris

Tubulipora pacifica

Tubulipora tuba

*Tubulipora pulchra**

Family Fondiporidae

Fulifascigera fasciculata

Family Crisiidae

Bicrisia edwardsiana

Crisidia cornuta

Crisia elongata

Crisia occidentalis

Crisia operculata

Crisia serrulata

Crisia pugeti

Filicrisia franciscana

Filicrisia geniculata

Family Cytididae

Discocytis canadensis

Family

Heteroporidae

Heteropora alaskensis

Heteropora magna

Heteropora pacifica

Family

Lichenoporidae

*Disporella hispida**

Disporella fimbriata

Disporella separata

Lichenopora verrucaria

Lichenopora novae-zelandiae

Oncousoecia ovoidea

Diaperoecia californica

Diaperoecia major

*Published larval description available.

Fig. 3. Hypothetical gymnolaemate larva, showing the components common to both coronate and cyphonautes larval forms. (Zimmer and Woollacott, 1977, Fig. 1)

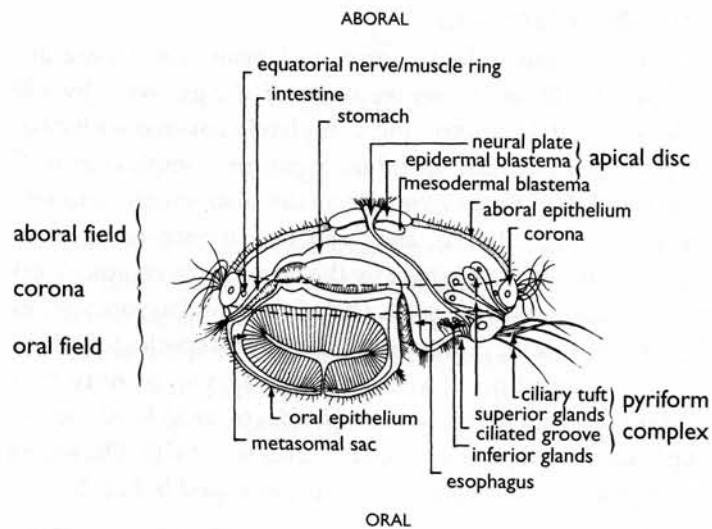


Table 2. Species in the class Gymnolaemata from the Pacific Northwest

Family Flustrellididae <i>Flustrellidra corniculata</i>	<i>Cauloramphus spiniferum</i> <i>Ellisina levata</i>	<i>Tricellaria ternata</i> <i>Tricellaria praescuta</i>
Family Alcyonidiidae <i>Alcyonidium mammilatum</i> <i>Alcyonidium parasiticum</i> <i>Alcyonidium pedunculatum</i> <i>Alcyonidium polyoum</i>	<i>Hincksina alba</i> <i>Hincksina pallida</i>	Family Epistomiidae <i>Synnotum aegyptiacum</i>
Family Clavoporidae <i>Calvopora occidentalis</i>	Family Alderiniidae <i>Callopora circumclathrata</i> <i>Callopora corniculifera</i> <i>Callopora horrida</i> <i>Callopora lineata</i> <i>Callopora armata</i> <i>Alderina brevispina</i> <i>Copidozoum protectum</i> <i>Copidozoum tenuirostre</i> <i>Doryporella alcornis</i> <i>Tegella aquilirostris</i> <i>Tegella armifera</i> <i>Tegella robertsonae</i>	Family Bicellariellidae <i>Bugula californica</i> <i>Bugula pugeti</i> <i>Bugula cuclifera</i> <i>Bugula pacifica*</i> <i>Bugula flabellata*</i> <i>Caulibugula californica</i> <i>Caulibugula ciliata</i> <i>Caulibugula occidentalis</i> <i>Dendrobeania curvirostrata</i> <i>Dendrobeania laxa</i> <i>Dendrobeania lichenoides</i> <i>Dendrobeania longispinosa</i> <i>Dendrobeania murrayana</i>
Family Triticellidae <i>Triticella pedicellata</i>	Family Chapperiellidae <i>Chapperiella condylata</i> <i>Chapperiella patula</i>	Family Cribrilinidae <i>Cribrilina radiata</i> <i>Cribrilina annulata</i> <i>Cribrilina corbicula</i> <i>Colletosia radiata</i> <i>Lyrula hippocrepis</i> <i>Puellina setosa</i> <i>Reginella furcata</i> <i>Reginella nitida</i>
Family Arachnidiidae <i>Nolella stipata</i>	Family Microporidae <i>Micropora coriacea</i> <i>Microporina borealis</i>	Family Hippothoidae <i>Hippothoa divaricata</i> <i>Hippothoa hyalina</i> <i>Trypostega claviculata</i>
Family Immergentiidae <i>Immergetia</i> sp.	Family Cellariidae <i>Cellaria diffusa</i> <i>Cellaria mandibulata</i>	Family Umbonulidae <i>Umbonula arctica</i>
Family Vesiculariidae <i>Bowerbankia gracilis</i>	Family Scrupocellariidae <i>Caberea boryi</i> <i>Caberea ellisi</i> <i>Scrupocellaria californica</i> <i>Scrupocellaria varians</i> <i>Tricellaria gracilis</i> <i>Tricellaria occidentalis*</i>	
Family Buskiidae <i>Buskia nitens</i>		
Family Penetrantiidae <i>Penetrantia</i> sp.		
Family Aeteidae <i>Aetea</i> sp.		
Family Membraniporidae <i>Conopeum reticulum*</i> <i>Membranipora membranacea*</i>		
Family Electridae <i>Electra crustulenta*</i>		
Family Hincksinidae <i>Cauloramphus brunea</i> <i>Cauloramphus echinus</i>		

Table 2 continued. Species in the class Gymnolaemata from the Pacific Northwest

Family Stomachetosellidae	<i>Microporella californica</i>	Family Cheiloporinidae
<i>Stomachetosella cruenta</i>	<i>Microporella ciliata</i>	<i>Cheilopora praelonga</i>
<i>Stomachetosella limbata</i>	<i>Microporella setiformia</i>	<i>Cryptosula pallasiana</i>
<i>Stomachetosella sinuosa</i>	<i>Microporella umbonata</i>	Family Phylactellidae
Schizoporellidae	<i>Microporella vibraculifera</i>	<i>Lagenipora punctulata</i>
<i>Dakaria dawsoni</i>	Family Eurystomellidae	<i>Lagenipora socialis</i>
<i>Dakaria ordinata</i>	<i>Eurystomella bilabiata</i>	Family Celleporidae
<i>Dakaria pristina</i>	Family Smittinidae	<i>Holoporella brunnea</i>
<i>Hippodiplosia insculpta</i>	<i>Codonellina cribriformis</i>	<i>Costazia costazia</i>
<i>Hippodiplosia reticulato-punctata</i>	<i>Mucronella ventricosa</i>	<i>Costazia robertsoniae</i>
<i>Schizomavella auriculata</i>	<i>Parasmittina collifera</i>	<i>Costazia ventricosa</i>
<i>Schizoporella cornuta</i>	<i>Porella columbiana</i>	Family Myriozoidae
<i>Schizoporella unicornis</i>	<i>Porella concinna</i>	<i>Myriozoum coarctatum</i>
<i>Schizoporella linearis</i>	<i>Porella porifera</i>	<i>Myriozoum subgracile</i>
Family Hippoporinidae	<i>Rhamphostomella cellata</i>	<i>Myriozoum tenue</i>
<i>Gemelliporella inflata</i>	<i>Rhamphostomella costata</i>	
<i>Hippomonavella longirostrata</i>	<i>Rhamphostomella curvirostrata</i>	
<i>Hippoporella nitescens</i>	<i>Smittina cordata</i>	
<i>Lacerna fistulata</i>	<i>Smittina landsborovi</i>	
<i>Stephanosella vitrea</i>	Family Reteporidae	
Family Microporellidae	<i>Lepraliella bispina</i>	
<i>Fenestulina malusii</i> *	<i>Phidolopora labiata</i>	
	<i>Rhynchozoon tumulosum</i>	

*Published larval description available.

Alcyonium, *Conopeum*, and *Electra* (Atkins, 1955a, b; Ryland, 1965; Reed, 19917). The production of a few large eggs that develop into lecithotrophic larvae with short pelagic durations is a second developmental pattern. It is seen locally in the genera *Bowerbankia*, *Schizoporella*, and *Hippodiplosia* (Reed, 1978, 1980; Nielson, 1981). A third pattern of development is characterized by extraembryonic nutrition of larvae reared in a brood chamber. These larvae are also lecithotrophic and reside only briefly in the plankton. Species in the genus *Bugula* display this developmental pattern (Reed, 1987). Few of the larvae of species in the Gymnolaemata have been described; of ca 128 local species in this class, only eight have been described (Table 2).

Cyphonautes Larvae

The most obvious diagnostic features of cyphonautes larvae (Fig. 4) are their triangular shell and extreme lateral compression (Ryland, 1964). Food particles are removed from a continuous current of water that the ciliary action drives through the mantle cavity or vestibule (Atkins, 1955b).

Fig. 4. Cyphonautes larvae. (A)

Membranipora membranacea. (B)

Electra pilosa. (C)

Electra crustulenta. (D)

Conopeum reticulum.

(E) **Flustrellidra hispida**;

1, apical organ; 3,

adhesive sac; 5, shell; 12,

vibratile plume; 14,

pyriform organ; 15,

ciliary girdle; 17, muscle strands.

(F) **Alcyonidium mytili**; 5,

apical organ; 6, groove; 7,

ciliary girdle; 8, vibratile

plume; 9, ciliated cleft; 10,

adhesive sac. Genera and

species in bold are found

locally. A, B present

lateral, apical, and

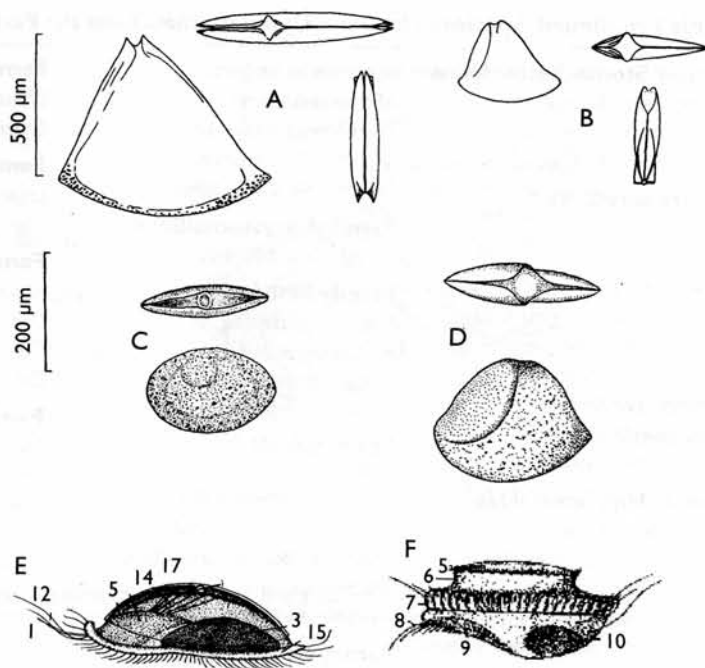
anterior views (clockwise

from left). C, D present

lateral and apical views.

(A–D from Ryland, 1965;

E, F from Hyman, 1959)



Membranipora membranacea. This species produces a large cyphonautes with an ornamented shell (Fig. 4A). The shell outline is roughly triangular. Faint striations (growth lines) may show near the apex and down the posterior margin. The anterior and posterior margins of the valves are of equal length, or sometimes the anterior margin is slightly longer. The posterior flange is narrow. The notch for the apical organ is deep and flared but relatively small. The shell and internal organs are transparent. The larvae reach a basal width of 440 μm . They are most abundant in coastal waters that have nearby rocky shores and are found in the plankton throughout the year, most abundantly in May through September (Atkins, 1955b; Ryland, 1964, 1965; Yoshioka, 1982).

Conopeum reticulum. The small cyphonautes measures ca 250–290 μm in length and 180–200 μm high. The shell is roughly bell-shaped (Fig. 4D). The valves are flat, truncated, and strongly flared at the apical organ. The anterior and posterior margins are asymmetrical and proportionally taller than in most other small cyphonautes. There is a broad flange bordered by a prominent ridge running from the apex toward the posterior margin. The shell is gray and lightly encrusted with small dark particles. The internal organs are not visible (Ryland, 1965).

Electra crustulenta. The larvae measure 160–200 μm long by 120–170 μm tall. The shell outline is roughly oval (Fig 4C). The shell is encrusted with fine particles that give it a brownish or gray, granular appearance. The internal organs are barely visible, often only the stomach showing clearly (Ryland, 1965).

Coronate Larvae

The morphology of coronate larvae is more diverse than that of the cyphonautes. The structures common to all coronate larvae are (see Fig. 3) the corona, the apical disc, the blastema (or pallial sinus) associated with the apical disc, the pyriform complex, and the metasomal (or internal) sac (Zimmer and Woollacott, 1977; Reed, 1980). Zimmer and Woollacott (1977) group coronate larvae into five categories based on the size

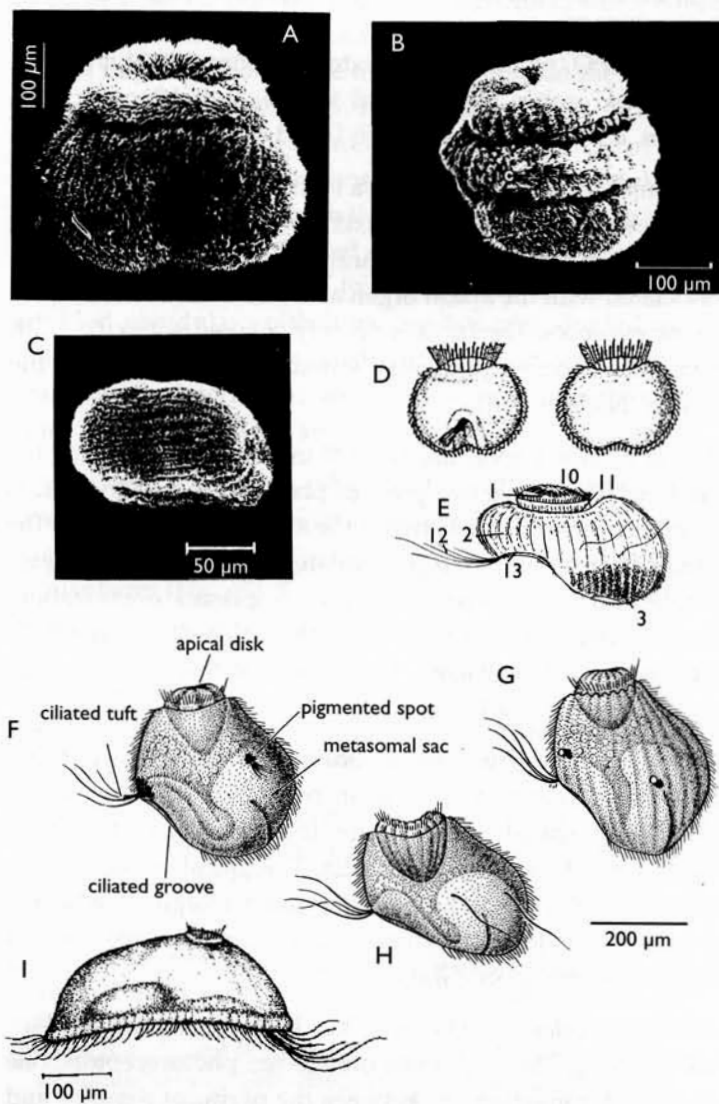


Fig. 5. Coronate larvae in the class Gymnolaemata. (A) **Hippodiplosia insculpta**. (B) *Watersipora arcuata* (type E larva). (C) **Bowerbankia gracilis** (type AEO/PS larva). (D) **Bugula flabellata** (type AEO/ps larva). (E) *Cellepora* sp. (Type AE larva); 1, apical organ; 2, coronal cells; 3, adhesive sac; 10, sensory bristles; 11, groove; 12, vibratile plume; 13, ciliated cleft. (F) **Scrupocellaria reptans** (Type AEO/ps larva). (G) **Bugula plumosa** (Type AEO/ps larva). (H) *Bicellariella ciliata*. (I) *Scruparia* sp. (Type O larva). Genera and species in bold are found locally. (A from Nielsen, 1981; B from Reed, 1991; C from Reed and Cloney, 1982; D from Grave, 1930; E from Hyman, 1959; F–H from Woollacott and Zimmer, 1978; I from Barrois, 1877)

and position of the corona, and the size of the pallial sinus. The categories are as follows (definitions from Reed, 1980); examples of each category are presented in Fig. 5.

Type O. Larva with narrow corona located orally, e.g., *Scuparia* sp. and *Alcyonidium duplex* (Zimmer and Woollacott, 1977).

Type E. Larva with narrow equatorial corona, e.g., *Alcyonidium polyoum* (Zimmer and Woollacott, 1977).

Type AE. Larva with expanded corona that is aboral and equatorial in position, e.g., *Cellepora pumicosa* (Zimmer and Woollacott, 1977).

Type AEO/ps. Larva with extensive corona that is aboral, equatorial, and oral in position and with small pallial sinuses. This type is characteristic of all cellularioid cheilostome larvae, e.g., all *Scrupocellaria* and *Bugula* species (Woollacott and Zimmer, 1978).

Type AEO/ps. Larva with extensive corona that is aboral, equatorial, oral in position and with well-developed pallial sinuses, e.g., *Bowerbankia gracilis* (Reed and Cloney, 1982).

Hippodiplosia insculpta. The larva is roughly spherical (slightly compressed along the apical axis) and 330–350 μm diameter (Fig. 5A). It is light reddish orange with darker coloration associated with the apical organ and below the corona. There are no eyespots. The larva is densely covered with cilia, with two pairs of compound cilia located laterally just below the corona (Nielsen, 1981).

Bugula pacifica. Larvae are 110–120 μm diameter and 150–165 μm long. They have two pairs of photoreceptors. One pair is anterolateral, midway between the aboral epithelium and the equator. The other pair is posterolateral at the equator. *Bugula simplex* and *B. pacifica* have identical cytoplasmic organization. The sensory cells are flush with the adjacent coronal cells (Hughes and Woollacott, 1980). Typical *Bugula* larvae are depicted in Fig. 5D, G.

Bugula flabellata. The larva is almost spherical (170–190 μm) and transparent to yellowish in color (Fig. 5D). There is a prominent apical organ at the anterior end of the larva surrounded by a "cirlet" of cilia. The apical organ is often delimited by a circular groove the outer margin of which is frequently scalloped (Hyman, 1959). There are two pairs of pigmented eye spots (Grave, 1930).

Tricellaria occidentalis. The larva is ca 135 μm diameter and 140–160 μm long. There are three orange-red photoreceptors, one on the anteromedian line between the pyriform complex and

the vesiculated epithelium and the other two on the larval equator about 135 degrees on either side of the anteromedian line (Hughes and Woollacott, 1980).

Fenestrulina malusii. The larvae are small and yellowish white. They swim rapidly and settle within an hour of liberation (Nielsen, 1981).

Scruparia sp. This larva is known from a single illustration (Barrois, 1877). It is similar to *Flustrellidra hispida* (shelled lecithotrophic larva) but lacks a shell (Fig. 5I). No other *Scruparia* has been examined (Zimmer and Woollacott, 1977).

Bowerbankia gracilis. The larvae are coronate type AEO/PS described by Reed and Cloney (1982). They lack pigment spots and are light yellow in color. They are barrel-shaped, elongated along their aboral-oral axis (Fig. 5C). The corona, which covers most of the larval surface, consists of 32 long, narrow cells that extend from the aboral pole to the oral pole on the posterior and lateral sides of the larva. The coronal cells on the anterior side are shorter and extend from the aboral pole to the pyriform organ. The pyriform organ consists of a superior glandular field with a glandular pit, a papilla that bears a ciliary tuft, an inferior glandular field, and a ciliated cleft. A glandular region of the oral epithelium is infolded to form a small internal sac. The infolded glandular epithelium consists of a single layer of columnar cells virtually filled with large bipartite secretory granules. The internal sac opens as a narrow slit in the median plane of the larva (Reed and Cloney, 1982).

Alcyonidium gelatinosum. The corona on the free-swimming larvae of *Alcyonidium gelatinosum* forms a narrow equatorial band of ciliated cells that separates the aboral and oral hemispheres (Fig. 4F). The apical disc is large, covering most of the aboral hemisphere (Reed 1991).

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