Reference: *Biol. Bull.* **192:** 243–252. (April, 1997)

Morphology and Development of *Odostomia columbiana* Dall and Bartsch (Pyramidellidae): Implications for the Evolution of Gastropod Development

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Abstract. Although pyramidellid gastropods are a phylogenetically important group of diverse and abundant ectoparasites, little is known about their life histories. Herein, we describe the adult morphology and development of the pyramidellid *Odostomia columbiana,* which parasitizes the scallops *Chlamys hastata* and *C. rubida* in the Northeast Pacific. Anatomically, adult *O. columbiana* resemble other known pyramidellids although they lack the tentacular pads typical of other *Odostomia* species. Embryonic development is similar to that described for other pyramidellids: cleavage is unequal, gastrulation is partially by invagination, and considerable growth occurs before hatching. However, embryonic and larval development are much slower than for other described species. The planktotrophic larvae hatch after 19 days of intracapsular development and metamorphose about 2 months later. *O. columbiana* veligers have a large black pigmented mantle organ to the right of the midline, a distinct metapodial tentacle, and three or four long bristles that project over the operculum from behind the foot. Observations of newly metamorphosed juveniles suggest that previous disagreements regarding the development of heterostrophy are due to variation in the degree of heterostrophy among species. Our observations also generally corroborate certain scenarios explaining the evolution of gastropod cleavage type and larval heterochrony. Unequal cleavage and larvae that hatch without well-developed eyes and tentacles may be characteristic of the common ancestor of pyramidellids and opisthobranchs; however, late development of the larval heart is probably a derived condition of opisthobranchs.

Received 16 August 1996; accepted 17 December 1996.

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Abbreviations: PMO = pigmented mantle organ; bp1 = anterior buccal pump; bp2 = posterior buccal pump; VCSGL = ventral ciliated strip gland.

Introduction

Pyramidellids are common ectoparasites in many marine communities, but little is known about their biology and life histories (Haszprunar, 1988; Wise, 1996). In particular, data concerning their development and larval biology are lacking. As in many benthic marine invertebrates with limited adult dispersal, the duration of a planktonic larval stage may be a key factor influencing pyramidellid distribution and population dynamics. Long-lived planktonic stages may increase colonization of patchily distributed hosts, whereas species that hatch as crawling juveniles may have lower probabilities of local extinction (Thorson, 1950; White *et al.,* 1984; Cumming, 1993). Therefore, knowledge of pyramidellid development and larval biology is key to understanding their life histories and host-parasite interactions, and to planning effective pest-control strategies for aquaculture.

Pyramidellid development is also particularly informative when viewed in a phylogenetic context. Generally, pyramidellids are placed, with other families in the order Heterostropha, at the base of the heterobranch clade (Haszprunar, 1988). Although the relationships among these families are poorly resolved, pyramidellids clearly represent basal members of the clade that in-

cludes opisthobranchs and pulmonates, and which is the sister group of the Caenogastropoda (Haszprunar, 1988; Bieler, 1992; Mikkelsen, 1996). Knowledge of such basal groups can be useful in tracing evolutionary transitions, determining ancestral character states, and testing evolutionary scenarios. This knowledge may be particularly useful in gastropod development, where evidence for evolutionary scenarios is often available from derived representatives of only a few clades. For example, van den Biggelaar (1996) found a trend in cleavage type and D-quadrant specification from equal cleavage and late specification in "archaeogastropods" to unequal cleavage and early specification in opisthobranchs and pulmonates. Additionally, Page (1994) suggested that heterochronic shifts in gastropod development decelerated the formation of larval and adult structures in opisthobranch larvae relative to prosobranchs. These scenarios were generated primarily from observations of derived caenogastropods, opisthobranchs, and pulmonates. Moreover, detailed descriptions of pyramidellid development could be used to further support or refute these types of scenarios.

To date, accounts of pyramidellid reproduction and embryology are brief and limited to a small number of European (Lebour, 1932, 1936; Rasmussen, 1944, 1951; Fretter and Graham, 1949), eastern North American (Robertson, 1978; White *et al.*, 1985), and Indo-Pacific (Amio, 1963; Nishino *et al.*, 1983; Cumming, 1993) species (Table I). Although more than 50 species have been reported from western North America (Dall and Bartsch, 1909), there exists only a single account of pyramidellid development from the region (LaFollette, 1979). No detailed embryological studies of pyramidellids have been published, and larvae that do not metamorphose immediately after hatching are seldom reared through settlement (see Robertson, 1967, for an exception). Consequently, the details of early development, the duration of the planktonic period, and the events at metamorphosis have been the subject of much speculation (Thorson, 1946; Fretter *et al.*, 1982).

Published accounts of pyramidellid reproduction and development are often obscured by taxonomic confusion within the group. Criteria used to identify species are often not explicitly stated in published reports, or the taxonomy is so conjectural that species cannot be identified with much certainty. For example, Clark (1971) and Hoffmann (1979) did not state how they identified their snails as *Odostomia columbiana*, and Cumming (1993) was unable to definitely identify "*Turbonilla* sp." to genus or species. This taxonomic uncertainty makes it difficult to interpret comparative reproductive and developmental data.

Reports of poecilogony, a rare condition in gastropods (Hoagland and Robertson, 1988; Bouchet, 1989) in which two or more developmental modes occur in one species, may be an example of such taxonomic confusion. *Boonea impressa* has been reported to have planktotrophic development in North Carolina and lecithotrophic development in Texas. However, these populations may not represent the same species (Bouchet, 1989). Both small eggs that develop into planktotrophic larvae and large eggs with direct development have also been reported for *Brachystomia rissoides* in areas of different salinities in Europe (Pelseneer, 1914; Rasmussen, 1944, 1951; Thorson, 1946).

This paper adds to the data on pyramidellid development while avoiding the taxonomic confusion of previous studies by describing both the adult morphology and the development of the pyramidellid *Odostomia columbiana* Dall and Bartsch, 1907. This new information is discussed in the context of the general characteristics of pyramidellid development and its implications for the evolution of development within the gastropods.

Materials and Methods

Mature *Odostomia columbiana* were found on the scallops *Chlamys hastata* and *C. rubida* dredged from 90–130 m in San Juan Channel, Washington (48°34′10″ N, 123°2′0″ W) during March 1995. Both the snails and their hosts were kept at ambient sea temperature (8°–12°C) in flow-through sea-tables at Friday Harbor Laboratories, Washington. Snails ranged from 5 to 8 mm in length and were identified as *O. columbiana* on the basis of the original description of the shell provided by Dall and Bartsch (1907) and by comparison with the holotype and five syntypes on deposit at the National Museum of Natural History (lot #126658). Voucher specimens have been deposited at the Field Museum of Natural History (FMNH 293334: dry shells; FMNH 293334: formalin-fixed animals).

Adult morphology

Adult snails were extracted for dissection by first cracking their shells with a vise. Snails were dissected whole, and structures of the gut and reproductive tract were routinely stained with toluidine blue (Wise, 1993, 1996).

Development

Egg masses were present on the scallops when they were collected, and adult snails continued to produce egg masses in the laboratory until May 1996. Scallop shells were checked for new egg masses several times a month to determine whether reproduction was seasonal. Individual egg masses were removed from the scallop shells and kept in small glass dishes while their development

was observed. Although we did not observe egg laying, several egg masses were collected before the beginning of first cleavage. Observations of these egg masses were used to produce a developmental timetable. Eggs and egg capsules were measured prior to first cleavage, and measurements were taken in the plane of the chalazae. After hatching, larvae were transferred to filtered (0.45 μm) seawater in small glass dishes. They were fed *Isochrysis galbana* and *Rhodomonas* sp. *ad libitum,* and the water was changed every 2 to 3 days. Because the larval shells are hydrophobic, flakes of cetyl alcohol were added to the surface of the cultures to prevent larvae from becoming trapped in the surface tension. When the veligers began to spend time crawling, juvenile scallops were added to the cultures to induce metamorphosis and as food for newly metamorphosed juveniles. All observations reported are of animals reared or maintained in the laboratory.

Larval shells were prepared for scanning electron microscopy by rinsing them in dilute bleach and distilled water following the procedure of Hickman (1995). They were mounted on stubs with double-sided tape, coated with gold and palladium, and examined with a JEOL JM35 scanning electron microscope.

Results

Adult morphology

The following is given in the concise style of a species description.

Shell: Relatively thin, elongate conical, chalky white, 5–8 mm in length, composed of 5 to 6 adult whorls. Adult whorls with numerous fine spiral growth lines. Whorl shoulders rounded, with moderately deep sutures. Shell etched and pitted, particularly above body whorl. Lenticular aperture, with flared lower portion. Single, short, acute columellar fold on upper half of columella perpendicular to columellar axis. Smooth, sinistrally heterostrophic protoconch oriented 130 degrees to teleoconch axis, with 40% submerged within first adult whorl. Operculum brown, lenticular, with subcentric nucleus.

Head-Foot: White to yellow, with numerous scattered white cells. Propodium with slight medial indentation and rounded lateral edges. Foot narrows posterior to propodium, then widening to gradually taper to a blunt apex. Pedal gland opens in middle of groove extending along posterior half of ventral surface of foot. Attachment thread present. Tentacles subtriangular, connate, ventrolaterally folded; tentacular pads apparently absent. Black round eyes beneath epithelium on median side of tentacles. Mentum unnotched, not bifurcate.

Alimentary Tract: Retracted introvert-proboscis extending posteriorly from its aperture on ventral side of head, dorsal to mentum base and entering cephalic hemocoel (Fig. 1). Introvert joining buccal sac (containing buccal sucker, stylet, and stylet bulb), which is connected to buccal pump. Buccal pump divided into anterior (bp1) and posterior (bp2) sections, with bp2 one-third longer than bp1; bp1 narrow, round in cross-section; bp2 wider, laterally flattened, distally rounded. Short, straight anterior esophagus originating on ventral surface of alimentary tract at bp1–bp2 juncture, extending posteriorly to join posterior esophagus and paired salivary glands, forming a four-way junction. Long, highly coiled posterior esophagus extending posteriorly to enter visceral mass and join stomach. Long, narrow salivary glands equal to bp2 in length. Salivary gland ducts highly folded and attached to anterior esophagus. Ducts penetrating alimentary tract just anterior to bp1–bp2 juncture, extending parallel to one another within walls of bp1 and entering stylet bulb without exiting gut. Salivary glands not attached distally to esophagus.

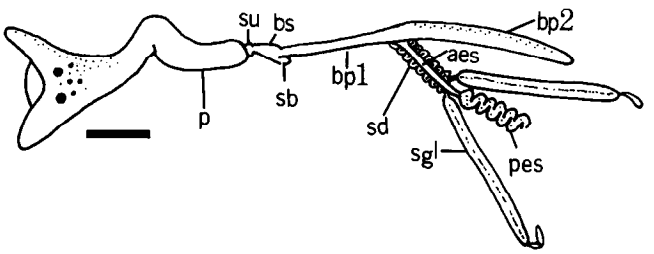

Figure 1. Diagram of alimentary tract of *Odostomia columbiana.* aes = anterior esophagus, bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, p = proboscis, pes = posterior esophagus, sb = stylet bulb, sd = salivary gland duct, sgl = salivary gland, su = sucker. Scale bar is 500 μm.

Pallial Cavity: Mantle and mantle organs typical of members of the Odostominae, with exception of position of ventral ciliated strip gland (=VCSGL). Small, spherical, yellow VCSGL underlying 20% of ventral ciliated strip about halfway from anterior edge of mantle floor. Ventral and dorsal ciliated strips joining on mantle roof posterior end of mantle cavity. Small, round-to-oblong pigmented mantle organ (=PMO), composed primarily of cells containing a bright yellow exudate, framed by numerous brown cells. A thick, bright yellow exudate is released when snail is disturbed.

Reproductive System: Opaque-to-transparent reproductive organs located on columellar side. Common pallial gonoduct extends anteriorly from visceral mass to open on right side of head just anterior and beneath the right tentacle.

Reproduction and development

Our observations of reproduction and larval development of *O. columbiana* generally agree with previous accounts of pyramidellid development (Pelseneer, 1914;

Table I

Review of pyramidellid development

Species	Egg size (μm)	Capsule size (μm)	Days to hatching	Larval duration (days)	Temp. (°C)	Reference
Boonea impressa	130*	180–280*	3–5	7	~25	White *et al.*, 1985
Brachystomia rissoides	120	500	25	0	?	Rasmussen, 1951
Brachystomia rissoides	60	200	?	?	?	Thorson, 1946
Brachystomia rissoides	70	200	6	?	~20	Rasmussen, 1944
Brachystomia rissoides	100	380	25	0	?	Pelseneer, 1914
Chrysallida cincta	?	320	22–27	0	20	LaFollette, 1979
Chrysallida decussata	90–120†	240–350	?	?	?	Lebour, 1936
Menestho diaphana	80*	200	16	?>8	11	Kristensen, 1970
Odostomia acuta	~80*	160 × 200	a few	?	?	Høisæter, 1989
Odostomia columbiana	**72–74**	**153–178**	**19**	**~70**	**12**	**this study**
Odostomia desimana	80	130 × 160	14	?	?	Amio, 1963
Odostomia eulimoides	?	?	10–12	3–4	18	Fretter and Graham, 1949
Odostomia eulimoides	90*	160	?	?	?	Lebour, 1932
Odostomia fujitaii	?	?	15–16	8–12	15	Minichev, 1971
Odostomia sp.	~100*	~200*	7	3 (?)	22	Nishino *et al.*, 1983
Odostomia omaensis	60	120 × 150	8	?	?	Amio, 1963
Turbonilla sp.	130	300 × 400	10–11	3–5 or 0	23	Cumming, 1993

* Measured from figures.
† 4–8 eggs per capsule.

Lebour, 1932, 1936; Rasmussen, 1944, 1951; Fretter and Graham, 1949; White *et al.*, 1985). However, both embryonic (used here to refer to development prior to hatching) and larval development are much slower than reported for other species (Tables I and II). Although we searched for spermatophores like those described by Robertson (1978), at no time did we find any attached to the shells or bodies of these snails. Egg masses each containing up to several hundred eggs were deposited on the hosts' shells continually from March 1995 until May 1996 when the last of the snails died. Irregular egg masses are often deposited in groups, making it difficult to distinguish individual masses. Each snail generally produced several egg masses per week.

Table II

Developmental time table for O. columbiana *at 10–12°C*

Age	Stage
~6 h	First cleavage
18 h	4 cells
24 h	8 cells
48 h	Round blastula
2–3 days	Gastrulation: blastula flattens and then forms a horseshoe-shaped gastrula
3–7 days	Gastrula
8 days	Foot and head rudiments begin to differentiate, some trochal ciliary motion; the shell is not yet present
10 days	Shell, cilia, and foot with operculum and statocysts present, light red PMO just visible
17 days	Heartbeat and ciliary motion in gut visible
19 days	Veligers hatch, PMO is black
72–80 days	Veligers begin to crawl
~90 days	Settlement and metamorphosis

Individual eggs are white and range from 71 to 77 μm in diameter (mean = 74.5; SD = 1.61; n = 23). Egg size did not differ between summer (July) and winter (January). Each round egg, surrounded by an oval layer of opaque albumin, is enclosed in a thick transparent gelatinous capsule (Fig. 2A–F). The length of the space enclosing the albumin is 154–170 μm (mean = 162.5; SD = 4.6; n = 23) and the outer length of the capsule is 193–222 μm (mean = 211; SD = 6.9; n = 23). In some previous accounts of pyramidellid development (*e.g.*, White *et al.*, 1985), capsular length has been reported as egg size, whereas other studies measure the egg cell. In this paper "egg" is used to denote the actual egg cell, and "capsule" refers to the egg and the albumin contained in one gelatinous covering. The capsules are connected to one another by thin strands called chalazae. In *O. columbiana*, chalazae are composed of a thin extraembryonic layer that surrounds the albumin layer beneath the capsule, traverses the capsule, and continues between capsules as a thin tubular strand (Fig. 2C). The egg, albumin, and capsular covering are embedded in a transparent gelatinous matrix that is often covered with diatoms.

All eggs within a single egg mass develop synchro-

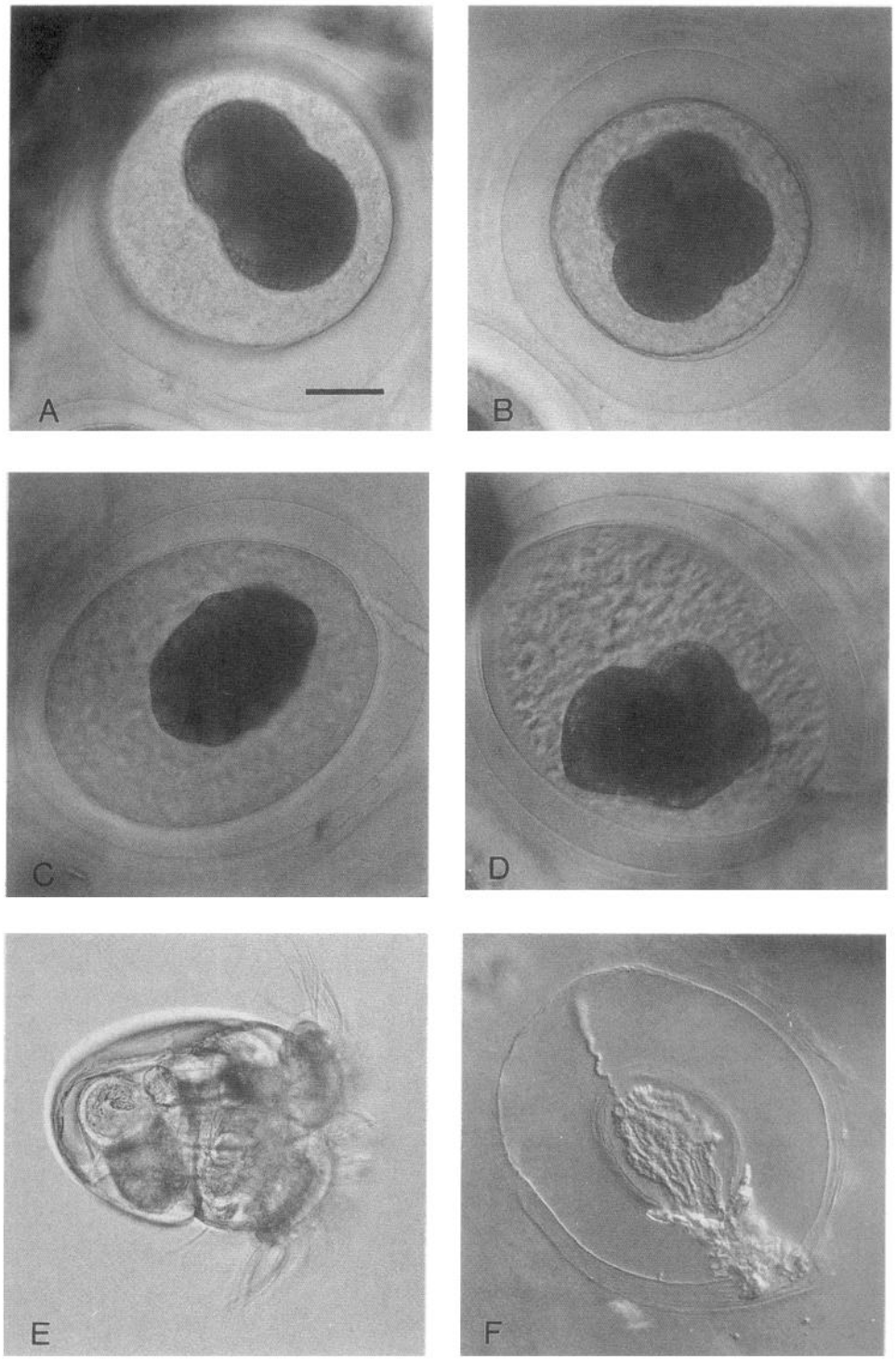

Figure 2. Stages in *Odostomia columbiana* development. (A) Two-cell stage; (B) four-cell stage; (C) blastula; (D) begining of differentiation of the foot, velum, and shell; (E) hatchling veliger; (F) empty egg capsule. In A and B the capsule appears round because it is viewed end on. Chalazae are clearly visible in the upper right of C and the upper left of F. All figures are to the same scale, and scale bar is A is 40 μm.

nously, and the initial cleavages are simultaneous. First cleavage is clearly unequal (Fig. 2A), but the second cleavage appears to be more-or-less equal. This results in a four-cell stage with two relatively large cells and two small cells (Fig. 2B). Third cleavage is also unequal. Because the polar bodies are initially obscured by the

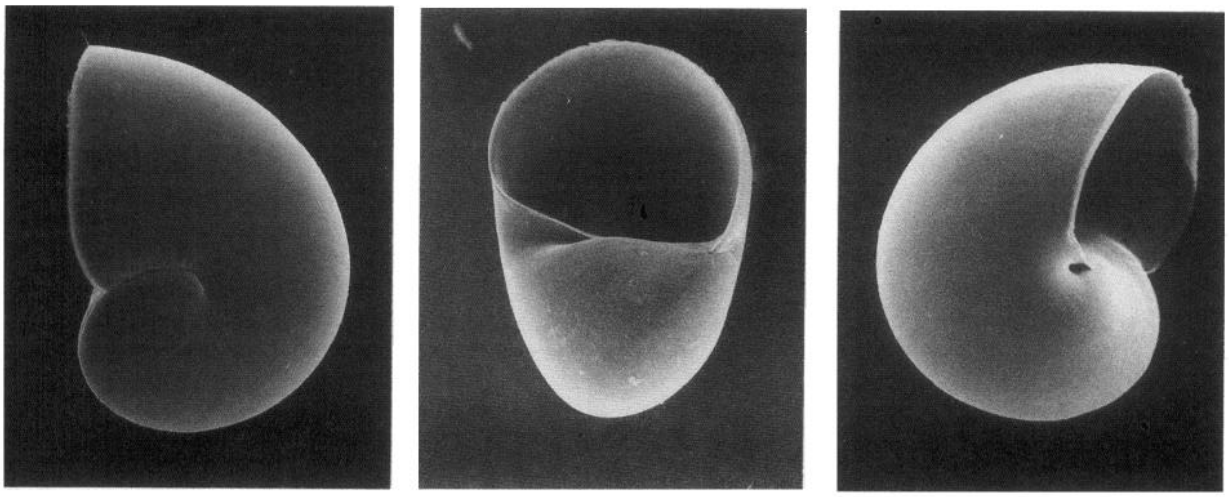

Figure 3. Scanning electron micrograph of *Odostomia columbiana* larval shell at hatching. Apical, apertural, and umbilical views, from left to right. Shell length is 150–160 μm for these three shells.

opaque albumin, the polarity and direction of this division could not be determined.

After 2 days the initially spherical blastula flattens (Fig. 2C) and in the next few days develops into a heart-shaped or cup-shaped gastrula. Thus gastrulation occurs at least partially by invagination, as is typical of many opisthobranchs. After 8 days the foot, head, and velum anlangen appear (Fig. 2D), and short cilia present on the velar lobes beat weakly. Even after the cilia are fully formed the embryos rotate very slowly, if at all, within the capsules. After 10 days the shell and statocysts are clearly visible, and the pigmented mantle organ begins to develop. As the PMO grows it darkens and changes from dark red to black before the larvae hatch. At 17 days the beating heart is visible, and the cilia of the gut are active. The embryo continues to absorb the surrounding albumin and grows until it eventually fills the capsule. At no time during development did we observe paired larval kidneys similar to those described by Pelseneer (1914). Additionally, methods used to demonstrate protein uptake in morphologically similar caenogastropod larval kidneys (Collin, unpubl. data) did not detect protein uptake in decapsulated embryos. Inspection of capsules, after hatching, shows that larvae hatch through an opening in the capsule along one of the chalazal strands (Fig. 2F).

At hatching the smooth, sinistral protoconch comprises nearly an entire whorl (Fig. 3) and is 150–160 μm in length (n = 7; Fig. 3). Newly hatched larvae have a black PMO just to the right of the midline, a small bilobed velum, and no eyes, tentacles, or obvious apical tuft (Fig. 2E). Except for the PMO and the stomach and digestive gland, whose color reflects larval diet, the veliger is entirely transparent. Although larvae retracted into their shells when placed under the microscope, the foot points slightly to the animal's right when they swim. As the foot grows, the metapodial tentacle, the posterior protuberance of the foot (distinct from adult metapodial tentacles) and its terminal cilia, which extend over the operculum, become more obvious. On each side of the foot, three or four bristles, which seem to originate behind the foot, project radially over the edge of the operculum. Veligers develop eyes within 18–23 days of hatching. After 2 months, the velum shrinks and the larvae, which are about 290 μm in shell length, begin to crawl. Larvae at this stage settle and metamorphose within days of the addition of juvenile scallops to the culture. Larvae that were the same age but had not begun to crawl did not settle in response to scallops. Water in which scallops had been kept overnight did not induce metamorphosis in crawling larvae. The PMO remained dark for at least 1 month after metamorphosis (Fig. 4), but had turned yellow after 6 months.

Discussion

Taxonomic note

The snails used in this study were identified as *O. columbiana* on the basis of the original description of the shell (Dall and Bartsch, 1907, 1909) and by comparison with the type specimens. All animals were collected attached to *Chlamys* spp. However, previous papers have described *O. columbiana* found on *Trichotropis cancellata* in Puget Sound, but did not state how the snails were identified (Clark, 1971; Hoffmann, 1979). Pyramidellid snails on *T. cancellata* are much smaller (2–4 mm, pers. obs., RC) than the snails used in this study and those described by Dall and Bartsch (up to 8 mm). The differences in size and host suggest that these may be two

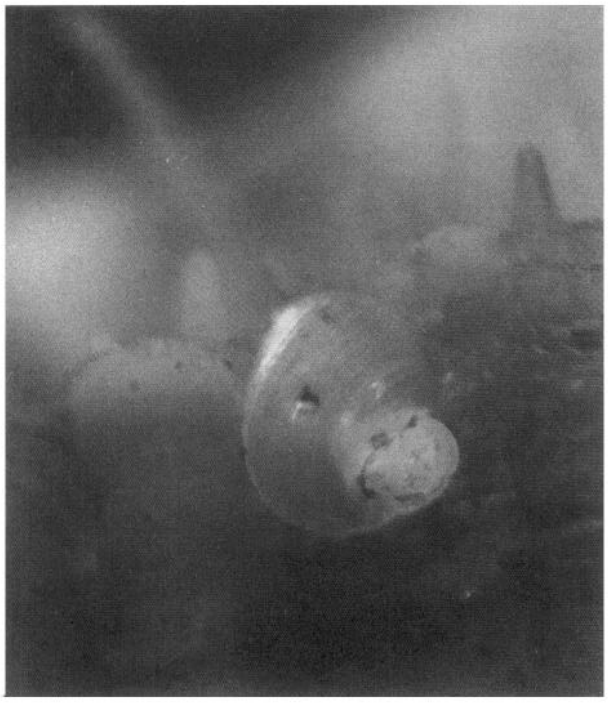

Figure 4. Juvenile *Odostomia columbiana* at the edge of a scallop shell about 1 month after settlement. The black PMO is visible through the shell in the middle of the body whorl. Shell length is about 700 μm.

different species. Nevertheless, the adult shell shape, sculpture, protoconch morphology, and adult anatomy are quite similar.

Previous studies have reported that some pyramidellids may not be host specific, or their preference may change as they grow (Boss and Merrill, 1965; Powell *et al.*, 1987), suggesting that the association of small animals with *T. cancellata* and large animals with *Chlamys* spp. may represent an ontogenetic host shift. This is unlikely because juvenile *O. columbiana* raised in this study did not move onto *T. cancellata* when given the choice between juveniles of *Chlamys* spp. or *T. cancellata*. No egg masses were discovered on *T. cancellata*, so it is unclear whether the pyramidellids from these hosts were sexually mature. Our preliminary results suggest that these are closely related species.

Adult morphology

The morphology of *O. columbiana* is very similar to that of other members of the family. However, it differs in several ways from the morphology of known species of the genus *Odostomia*. *Odostomia columbiana* lacks tentacular pads, and its gut arrangement is similar to that found in members of the genus *Boonea* except that the salivary gland ducts are attached to the anterior esophagus, which with the posterior esophagus and paired salivary glands form a four-way junction (Fig. 1). *Odostomia columbiana*, as well as other members of the subfamily Odostominae, will ultimately be relegated to other genera (Wise, in prep.).

Pyramidellid development

The reproduction and development of *O. columbiana* is similar to that previously described for other pyramidellids (Lebour, 1932, 1936; Rasmussen, 1944, 1951; Fretter and Graham, 1949; White *et al.*, 1985), although most of these descriptions are brief and small differences may have been overlooked. Eggs of *O. columbiana* are relatively small, but not unusually so (Table I). Because embryos grow to fill the capsule before hatching, capsule size is a good predictor of larval size in pyramidellids. *O. columbiana* deposits a single egg per capsule, as do other pyramidellids except *Chrysallida decussata* (Table I). Development of *O. columbiana* is slower than in other species with comparable egg size; only species with large eggs and direct development have a similarly long embryonic period (Table I). Because water temperatures were either not reported or varied considerably in several previous studies, it is difficult to determine whether these differences in development rate were due to temperature.

In *O. columbiana* the long embryonic period is followed by an unusually long planktonic larval stage. Although times to metamorphosis may be different in the laboratory than in nature, veligers in two non-overlapping cultures settled at the same age. Furthermore, recent improvements in larval culture technique and larval diet have reduced the time to metamorphosis in cultures of other invertebrate larvae (Strathmann, 1987). This suggests that the longer larval period of *O. columbiana* in comparison to other laboratory-reared pyramidellid species from previous studies is real (Table I). Unfortunately these studies did not indicate if the larvae studied were planktotrophic or if food was added to the larval cultures. A distinctive characteristic of the *O. columbiana* veligers is the presence of bristles extending over the operculum from the side of the foot. These are not figured or mentioned in any other description of pyramidellid larvae.

Our observations increase the data on the distribution of several developmental characters that are used in heterobranch systematics. Robertson (1985) suggested that chalazae may be a useful synapomorphy shared by pyramidellids, architectonicids, and opisthobranchs. Chalazae are clearly present in egg masses of *O. columbiana* and many other pyramidellids. Høisæter (1989), however, suggests that some pyramidellids lack chalazae and that their presence may be a useful systematic character within the pyramidellids. He did not find chalazae in *O. acuta*, and they were not mentioned in descriptions of egg masses from *Brachystomia eulimoides* (Lebour,

1932) and *Odostomia* sp. (Nishino *et al.*, 1983). Additionally, the shape and thickness of the chalazae of *O. fujitanii* figured by Minichev (1971) are clearly different from those in *O. columbiana* and other pyramidellids. Spermatophores have also been used as a systematic character within pyramidellids to define the genus *Boonea* (Robertson, 1978). *O. columbiana* apparently lacks spermatophores; however, this character has been observed in some other species occurring in the northeastern Pacific (A. J. Kohn, pers. comm.).

Our observations of pyramidellid development from hatching to metamorphosis illuminate several points that have been the subject of much conjecture. At hatching, veligers of *O. columbiana* are morphologically similar to veligers of other planktotrophic pyramidellid species, all of which seem to have small, nonpigmented velums. Previous studies that failed to rear larvae to metamorphosis often concluded that the larval period is short because the velum is small (*e.g.*, Thorson, 1946). This is not the case for *O. columbiana,* which has a long planktonic period during which its velum remains small. Small velar lobes are also typical of planktotrophic opisthobranch larvae (pers. obs., RC), although caenogastropods with long-lived feeding larvae often have large complex velar lobes (Thorson, 1946).

Confusion exists as to how differential shell growth around the aperture results in heterostrophy (the change of coiling direction from a left-handed protoconch to a right-handed teleoconch). Thorson (1946) illustrated several pyramidellid shells near metamorphosis and stated that the outer apertural margin of the larval shell thickens to become a new columella at metamorphosis. Fretter *et al.* (1982) disagreed and suggested that the protoconch's outer lip is continuous with the outer lip of the teleoconch. In *O. columbiana,* the position of the columella shifts clockwise around the aperture as the coiling direction changes, but not to the extent described by Thorson (1946). These conflicting observations of changes in shell shape at metamorphosis may be due to variation in degree of heterostrophy among pyramidellid species. Although the coiling direction reverses in all cases, there is considerable variation in the displacement of the coiling axis of the teleoconch relative to that of the protoconch. In most of the species figured by Thorson (1946), the protoconch is offset roughly perpendicular to the teleoconch. However, in *O. columbiana* and *Brachystomia eulimoides* (one species studied by Fretter and Graham, 1949), the angle between the coiling axes of the protoconch and teleoconch often appears to be closer to 140 degrees (Fretter *et al.*, 1982).

Evolution of gastropod development

Detailed studies of embryology and larvae of "archaeogastropods," caenogastropods, and opisthobranchs reveal several trends in gastropod development. Among gastropods there is a trend in both caenogastropods and opisthobranchs toward unequal cleavage and early D-quadrant specification (Freeman and Lundelius, 1992; van den Biggelaar, 1996; van den Biggelaar and Haszprunar, 1996). Equal cleavage with 4d cell formation at the 64-cell stage as in "archaeogastropods" is assumed to be the ancestral condition. In opisthobranchs, the first one or two cleavages are unequal, and the 4d cell is produced by the 24-cell stage. Intermediate conditions occur in the Architaenioglossa and the Valvatoidea, and there is considerable variation in basal opisthobranchs (van den Biggelaar, 1996). Although Pelseneer (1914) and van den Biggelaar and Haszprunar (1996, citing Pelseneer) report equal cleavage in pyramidellids, first cleavage in *O. columbiana* is clearly not equal. In addition, White *et al.* (1985) figured an unequal two-cell stage of *Boonea impressa* in the process of division. This suggests that either cleavage varies among pyramidellids (an unusual occurrence in gastropod groups) or Pelseneer's account is inaccurate. Regardless, it is interesting that early cleavage divisions in pyramidellids are similar to those in anaspideans and some other opisthobranchs.

Page (1994) suggested that heterochronic shifts in the timing of development of larval and adult organs account for some of the variation in gastropod larval development. In "archaeogastropods" the adult organs develop directly from the embryo, whereas in caenogastropods the larva hatches with well-formed larval organs and subsequently develops the definitive adult structures. Development is retarded in opisthobranchs, and they hatch at a stage of morphogenesis similar to that of unhatched caenogastropods: some larval organs develop after hatching, and the definitive adult organs develop during late larval life or at metamorphosis (Page, 1994). Page (1994) paid particular attention to the stage of formation of the eyes, tentacles, and larval heart. Caenogastropod veligers hatch with well-formed eyes and tentacles, and the larval heart develops long before hatching (Page, 1994, and pers. obs). In opisthobranchs, the larvae hatch before the eyes or tentacles have formed, and the larval heart usually forms during the last half of the planktonic stage (Page, 1994). The observations of *O. columbiana* reported here suggest that pyramidellid larval development may combine characters of opisthobranch and caenogastropod development. As in opisthobranchs, the eyes and tentacles did not appear until well into larval development; as in caenogastropods, the heart began to beat well before hatching.

These observations support recognized trends in the evolution of gastropod development and suggest ancestral character states. Unequal cleavage is characteristic of pyramidellids and some basal opisthobranchs, whereas caenogastropods have a polar lobe; thus unequal cleav-

age may be a heterobranch synapomorphy. However, additional groups at the base of this clade must be examined to rule out parallel evolution of unequal cleavage from an equally cleaving ancestor, because many other opisthobranchs and pulmonates have equal cleavage. Additionally, larvae that hatch before the development of eyes and tentacles were probably ancestral for pyramidellids and opisthobranchs. On the other hand, early appearance of the larval heart relative to hatching in pyramidellids and caenogastropods suggests that late development of the heart is a derived feature of the opisthobranchs. It is clearly necessary to have detailed descriptions of more phylogenetically intermediate groups and to formulate robust phylogenetic hypotheses before any firm conclusions regarding the evolution of these characters can be drawn.

Acknowledgments

We thank A. Kabat (US National Museum of Natural History) for lending us the type specimens of *O. columbiana,* R. Bieler (Field Museum of Natural History, Chicago) for accepting the voucher specimens, E. Kozloff for translating Minichev (1971), and D. Willows and the staff of Friday Harbor Laboratories for their support. B. Pernet and R. Strathmann made useful comments on the manuscript. This research was supported by a National Science Foundation Graduate Fellowship and a Pacific Northwest Shell Club Scholarship to RC, and grant OCE 9301665 to R. Strathmann.

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