

The development of three heterobranch mollusks from California, USA

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ABSTRACT

The development of *Odostomia altina*, *Turbonilla* sp., and *Williamia peltoides* from California, is typical of heterobranch mollusks. They all produce small eggs (about 60 μm) that are individually encapsulated and embedded in gelatinous egg masses. The capsules are connected by chalazae. Cleavage is unequal and gastrulation occurs by invagination. Planktotrophic larvae hatch at shell lengths of 120–150 μm .

Additional key words: Pyramidellidae, *Turbonilla*, *Odostomia*, gastropod development, *Williamia*.

INTRODUCTION

Although lower heterobranchs and marine pulmonates are common in shallow marine waters, their development remains largely undescribed. Knowledge of their development may be useful and important because developmental features such as the structure of egg masses, cleavage type, presence of the larval pigmented mantle organ (PMO), and hydrophobic larval shells may be important characters for phylogenetic studies (Robertson, 1985; van den Biggelaar, 1996; van den Biggelaar and Haszprunar, 1996; Collin, 1997). Additionally, there are a variety of interesting trends in the evolution of cleavage patterns (Freeman and Lundelius, 1992; van den Biggelaar and Haszprunar, 1996) and heterochronies in larval morphologies (Page, 1994) whose documentation could benefit from more extensive phylogenetic sampling.

Herein I describe the development of two pyramidellid and one siphonariid pulmonate species from the Californian coast. All animals were collected by hand in the summer of 1997 and kept in small dishes in the laboratory where they laid egg masses. Egg masses were observed daily until hatching, but no attempt was made to raise the larvae to metamorphosis.

RESULTS

Odostomia altina Dall and Bartsch, 1909
(Table 1)

Large numbers of *Odostomia altina* were found on the shells of *Haliotis corrugata* collected at a depth of 10 m from Point Loma, California (29°40'N, 117°20'W). Specimens are deposited at the Field Museum of Natural History (FMNH 282369 and 282370) and were identified by comparison with the original species description and illustrations in (Dall and Bartsch, 1909). There were as many as 50 adult pyramidellids and numerous egg masses on one abalone. Egg masses were typical of other pyramidellids: Single eggs are enclosed in albumin-filled oval capsules that are embedded in a clear sticky gelatinous mass. The capsules are connected by thin extensions of the capsular covering called chalazae (see Robertson, 1985; Collin and Wise, 1997 for detailed description). A timetable of development is given in Table 1.

The round, white eggs are 60 μm in diameter (mean = 60.83 μm ; sd = 1.39 μm ; n = 31; eggs from 3 egg masses) the inner capsule diameter is 150 μm (sd = 8.11 μm ; n = 19) and the outer capsule diameter is 176 μm (sd = 6.992 μm ; n = 10). First cleavage is unequal and at the 4-cell stage the two largest cells are adjacent, as are the two small ones. Several embryos were observed in a 3-cell stage, which suggests that second cleavage is not synchronous. There is no polar lobe and third cleavage is unequal. The round blastula gradually flattens and invaginates to form a horseshoe shaped gastrula. During subsequent development the embryo grows to fill the capsule and the larval organs differentiate. Planktotrophic larvae hatch after about 7 days (Table 1) with 130 μm (mean = 130.33 μm ; sd = 8.55 μm ; n = 15; egg masses from two females) smooth, left-handed, hydrophobic shells. Each larva has a well-developed metapodial ten-

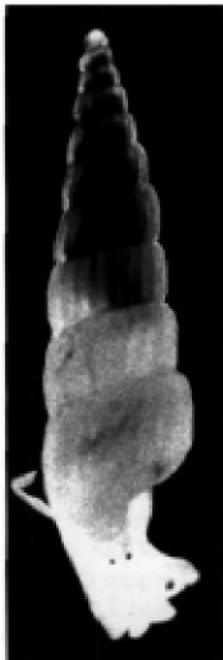
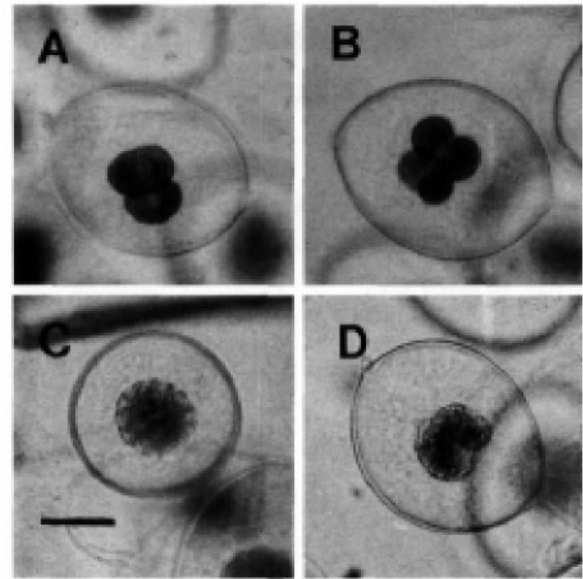
Table 1. Development schedule for *Odostomia altina* at 22–24°C.

Age	Stage
>3 hours	2-cells
5 hours	4-cells
12 hours	64-cells
1 day	blastula
1.5 days	gastrulation by invagination
3 days	just moving, foot and velum anlagen visible
5 days	red-yellow PMO visible, shell operculum and statocysts
~7 days	hatching at 130 μm

tacle and statocysts, but no detectable heartbeat, and no eyes. The larval PMO consists of two parts: A round red central part and an additional semi-transparent yellow lobe on one side. Observation of the yellow lobe under the dissecting microscope is difficult, but the structure can be seen easily under a compound microscope.

Turbonilla sp.
(Figures 1, 2, table 2)

One adult of an unknown species of *Turbonilla* was collected on the high mid-intertidal zone at Alegria, California (34°28'N, 120°17'W) in July 1997. The species identification is uncertain because *Turbonilla* taxonomy is especially difficult and the single specimen could not be unambiguously assigned to any Californian species. The current taxonomy of Californian pyramidellids assigns all species with axial-ribbed shells to the genus *Turbonilla* (Dall and Bartsch, 1909). This snail laid one egg

**Figure 1.** Adult *Turbonilla* sp. Shell length is 6 mm.**Figure 2.** Early developmental stages of *Turbonilla* sp. A. 2-cell stage at the beginning of second cleavage, the cells are clearly not equal in size, B. 4-Cell stage, C. blastula, D. gastrula, showing the invagination typical of heterobranch development. Scale bar = 50 μm .

mass of about 100 eggs in the laboratory and development was followed until hatching (table 2 and figure 2). The egg mass consisted of capsules containing one white egg surrounded by clear albumin, connected together by chalazae and embedded in a clear sticky gel. The egg diameter was 65.5 μm ($n = 10$, $sd = 1.97 \mu\text{m}$) and the capsule length was 187.8 μm ($n = 10$, $sd = 6.67 \mu\text{m}$). The chalazae are thicker and less twisted than in *O. columbiana* Dall and Bartsch 1907 (Collin and Wise, 1997). First cleavage is slightly unequal but by the 4-cell stage the blastomere inequality is very subtle. The early cleavages do not produce a polar lobe. The polar bodies are clearly visible throughout development because the albumin is transparent. After 24 hours the embryos form flattened blastulas, which begin to invaginate at about 40 hours. Gastrulation continues by invagination for the next day. By the fourth day the foot and velum anlagen are visible. On the fifth day the embryos begin to move

Table 2. Developmental schedule for *Turbonilla* sp. at 16–18°C.

Age	Stage
7 hours	2-cells
24 hours	blastula
2–3 days	gastrulation by invagination
4 days	just moving, foot and velum anlagen visible
5 days	shell and velum differentiated. Embryo fills 1/4 of the capsule
6 days	black PMO visible
9 days	embryo fills the capsule
11 days	hatching at 152 μm

and they fill about a quarter of each capsule. By the next day the black PMO is visible on the right side just posterior to the velum. The embryo grows to completely fill the capsule, before hatching. Shell length at hatching is 152 μm ($n = 14$; $sd = 2.37 \mu\text{m}$; from a single egg mass). The shell is hydrophobic, left-handed and the larva has no heart or eyes but has a well-developed metapodial tentacle on the foot. The planktotrophic larvae swim actively.

Williamia peltoides (Carpenter, 1864)

Several adult *W. peltoides* (Carpenter, 1864) were collected in the subtidal zone (~ 10 m), on hard substrates, in the vicinity of Santa Barbara, California ($34^{\circ}28'N$, $120^{\circ}17'W$). Voucher specimens are deposited at the Bailey-Matthews Shell Museum, Sanibel, Florida (BMSM 4999). *Williamia* species are unusual among marine pulmonates because they are predominately subtidal. Adults produced several egg masses in dishes in the laboratory.

The structure of the egg masses is very similar to those of the pyramidellids. The eggs are each individually enclosed in a coating of albumin inside an oval capsule. The capsules are connected with chalazae and are embedded in a gelatinous mass. The capsules are 147 μm in length (mean = 147.7 μm ; $sd = 3.4 \mu\text{m}$; $n = 11$). Unfortunately uncleaved eggs and early cleavage stages were not observed. Gastrulation occurs via invagination forming a horseshoe-shaped gastrula that is 69 μm in diameter ($d = 69.28 \mu\text{m}$; $sd = 3.4 \mu\text{m}$; $n = 7$; from one egg mass). Further development progressed as in the pyramidellids. However, no pigmented PMO develops: I could not determine if there was no PMO or if the structure was present but not pigmented. There is some reddish pigmentation along the suture of the larval shell, but the larval body was pigmentless. After 9 days at 18–22 $^{\circ}\text{C}$ the larvae hatch at a length of 126 μm (length = 126.0 μm ; $sd = 5.58 \mu\text{m}$; $n = 10$). The planktotrophic larvae have a hydrophobic smooth left-handed shell. There is still no pigmented PMO, no eyes, and no metapodial tentacle but the statocysts are clearly visible.

DISCUSSION

These observations are the first descriptions of intracapsular development for species in the genera *Williamia* and *Turbonilla*.

The features of pyramidellid development described here generally agree with previous descriptions of pyramidellid development. Because *Turbonilla* and *Odosstomia* are distantly related genera within the Pyramidellidae (Wise, 1996), characters shared by the species described here and *O. columbiana* (Collin and Wise, 1997) may be typical of pyramidellid development in general. All three species have small eggs, unequal cleavage, gastrulation by invagination, and hatch with smooth, left-handed, hydrophobic shells, a metapodial tentacle, distinct PMO, but without eyes or a larval heart. The color

of the larval PMOs varies among species as does the color of the adult PMO (Robertson, 1985).

The development of *Williamia peltoides* is strikingly similar to pyramidellid development. The structure of the egg masses is indistinguishable from that of the pyramidellids. Hatching larvae are distinct in their lack of a metapodial tentacle and pigmented PMO and the small area of shell pigment. These results are in agreement with Robertson's (1985) conclusion that larval PMOs are not present in pulmonates while chalazae and heterostrophy are common. The reddish pigment along the shell suture is also found in larvae of *Siphonaria* sp. from New Zealand (pers. obs.).

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