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Development of *Cerithiopsis gemmulosum* (Gastropoda: Cerithiopsidae) from Bocas del Toro, Panama

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ABSTRACT.—The relationships between the seven families in the Ptenoglossa and the relationships between the Ptenoglossa and other gastropod groups have been based on anatomical features associated with feeding, and on developmental characters. However the embryonic development of several of these families remains undescribed. Here I describe the development of *Cerithiopsis gemmulosum* from Bocas del Toro Province, Panama. This species lives on and lays its thin-walled egg capsules in *Halichondria melanadocia* sponges. The 79 µm eggs have equal cleavage with a polar lobe. The ciliated "trochophore" stage is followed by an encapsulated veliger which has distinct embryonic kidneys and large granular cells that cover the head vesicle. The black eyes are large and develop early, but there is no pigmented mantle organ. At hatching the brown larval shell is a single whorl and 127 µm long, and each semicircular velar lobe is unpigmented. The velar lobes are equal in size at hatching, but as the shell grows and becomes high-spired the right lobe grows to twice the size of the left lobe. The late larval shell is smooth but has a prominent beak flanked by two distinct notches that fit the velar lobes. After 3 weeks in culture the velum begins to shrink, and larvae with 500 µm shell length metamorphose when exposed to host sponge.

KEYWORDS.—Ptenoglossa, larvae, larval kidney, Halichondria melanadocia

INTRODUCTION

The biology of the seven gastropod families placed in the Ptenoglossa is not well-known. The Eulimidae, Janthinidae, Epitoniidae, Triphoridae, Triforidae, Aclididae and Cerithiopsidae have been linked by several features of the alimentry tract (e.g., ptenoglossate radula, and 2 pairs of salivary glands). However none of the proposed shared characters occur in all seven families (see Collin [2000] for a brief discussion) and Ponder and Lindberg (1997) stated that the Ptenoglossa is "an almost certainly paraphyletic or polyphyletic taxon."

Development and larval morphology have been suggested as useful sources of characters to further inform the discussion of ptenoglassate relationships. Various features of development have been used to argue for heterobranch affinities of epitoniids (Robertson 1985) and the epitoniid *Nitidiscala tincta* has been shown to possess developmental characters that have previously been thought to characterize only heterobranchs or only caenogastropods (Collin 2000). General larval morphology has been used to argue for the close relationship between the cerithiopsids and triphorids (Lebour 1933), which is also supported by adult shell morphology.

Despite the use of development in high-level systematic discussions of ptenoglossans, little is known about the embryology of most groups. Larval morphology has been described for several species, but embryology has been described only for a single epitoniid, *Nitidiscala tincta* (Collin 2000). Variation of developmental features both within and among the ptenoglossan families must be examined before their utility in systematics can be fully assessed. Here I describe the embryology and larval development of *Cerithiopsis gemmulosum* as a step towards this goal.

MATERIALS AND METHODS

Twelve adult *Cerithiopsis gemmulosum* (C. B. Adams, 1850) (Figure 1A) were collected

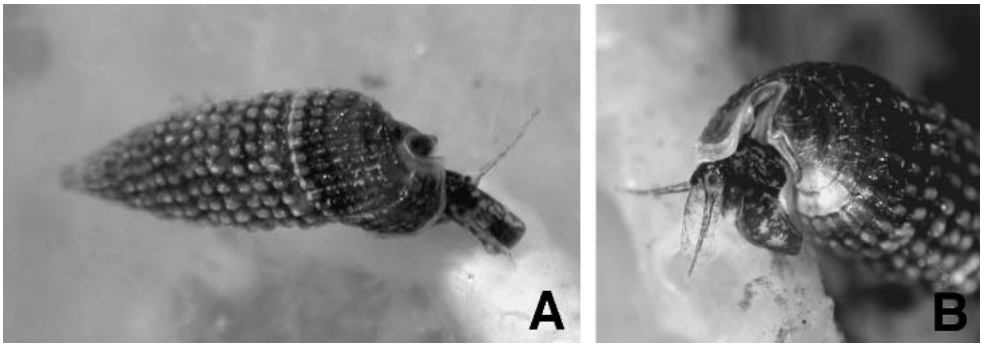

FIG. 1. Adult *C. gemmulosum.* **A.** crawling on the host sponge; **B.** feeding on the sponge. The proboscis excavates tissue forming a depression in the sponge. Shell length = 6.3 mm.

with a section of host *Halichondria melanadocia* sponge from red mangrove roots fringing Isla San Cristobal, Bocas del Toro Province, Panama (9°13.375′N, 82°12.555′W). The snails were identified with a review of Caribbean cerithiopsids (Rolán and Espina 1995), and consultation with Dr. E. Rolán. The taxonomy of cerithiopsids is very difficult and this identification should be considered provisional. Ethanol preserved adults and juveniles were deposited at the Swedish Natural History Museum (lot number SMNH 55977).

The snails and some host sponge were kept in a custard dish at 21-23 C. The water was changed every day, and both the snails and the sponge survived for over a month under these conditions.

After hatching the larvae were transferred to finger bowls with 1 μm filtered water. The water was changed every 2-3 days and larvae were fed *Isochrysis galbana*.

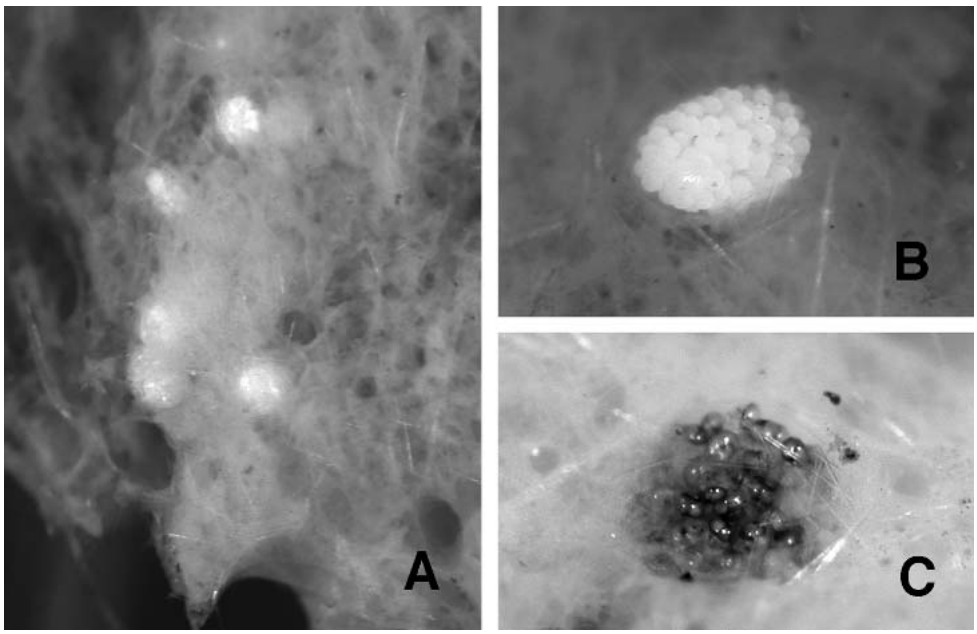

FIG. 2. Egg capsules of *C. gemmulosum* embedded in the sponge. **A.** several capsules in the sponge; **B.** An early stage capsule excavated from the sponge; **C.** Capsule of *C. gemmulosum* near hatching, the brown larval shells are clearly visible.

After 3 weeks in culture, the largest larvae were placed in a dish with a 3 mm fragment of sponge host to test for competence to metamorphose. After metamorphosis they were kept on the sponge fragment for a month, until the sponge died.

RESULTS

In the laboratory, the adult *Cerithiopsis gemmulosum* remained closely associated with the sponge and were frequently observed feeding on the sponge (Figure 1B). Immediately after collection it was clear that the sponge had numerous egg capsules embedded in it (Figure 2A). The capsules were completely surrounded by the sponge tissue and did not appear to be deposited in natural chambers in the sponge. No connection was visible from the egg capsules to the surface of the sponge. The adult snails continued to deposit egg capsules in the sponge in the laboratory.

The thin-walled, transparent capsules were 500-650 μm across and were not connected to each other. Capsules could not be separated from the sponge without rupturing them and therefore development could not be observed without removing the embryos from the capsule, which arrests further development. Each capsule contained 30-60 eggs which are pale early in development (Figure 2B). Later in development brown pigment from embryonic shells show through the capsule wall (Figure 2C).

The 78.7 μm (n = 21, s. d. = 3.1) eggs are cream colored. The polar bodies remain associated with the eggs and the first polar body is cone-shaped (Figure 3A). The first two cleavages are equal and synchronous and there is a small but distinct polar lobe (Figure 3B). Later, cleavage becomes asynchronous and one macromere can clearly be seen rounding up out of synch with the other three macromeres. Gastrulation is by epiboly. A trochophore-like stage with a

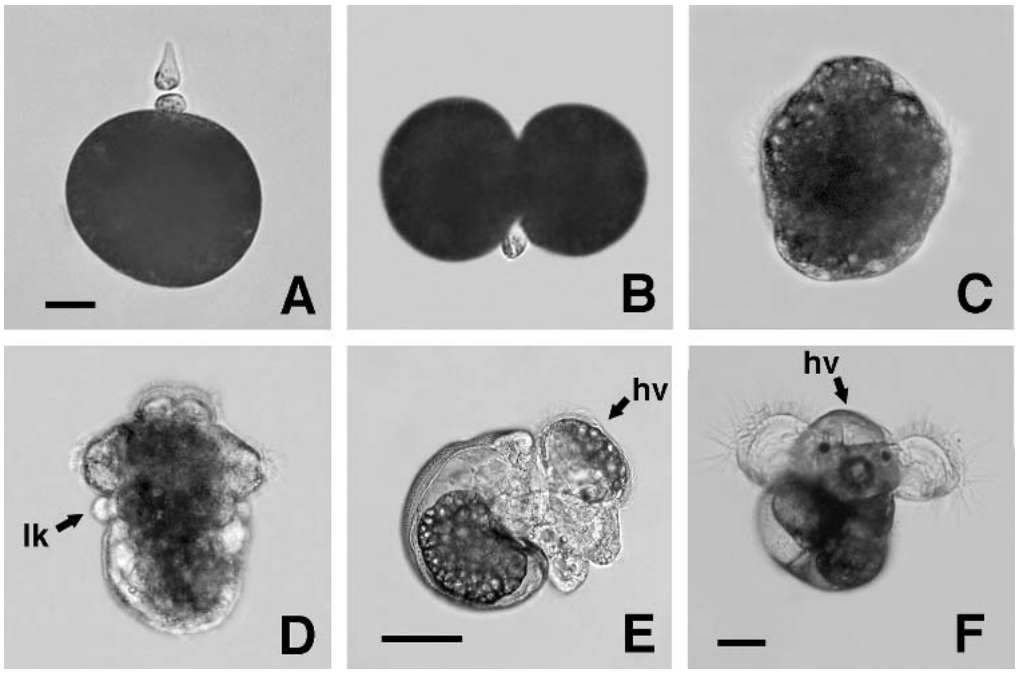

FIG. 3. Developmental stages of *C. gemmulosum*. **A.** Uncleaved egg showing polar bodies at the top; **B.** First cleavage with polar lobe visible below; **C.** "Trochophore" stage; **D.** pre-veliger stage showing the larval kidneys (lk) below the velum; **E.** Pre-hatching veliger stage with large opaque cells on head vesicle; **F.** 3-day old larva, showing the large eyes and well-developed right tentacle. **A-D** are the to the same scale: scale bar = 20μμm; **E**: scale bar = 50 μm; **F**: scale bar = 50 μm.

distinct unraised ring of cilia towards the anterior end (Figure 3C) follows gastrulation. As the velum Anlagen extend out from the body, a single small round embryonic kidney can be seen below the velum (Figure 3D) on each side and the ciliated head vesicle begins to develop. The prehatching veliger shows a well developed foot with an operculum and pair of statocysts, dark eyes, and a distinct round head vesicle covered with opaque granular cells (Figure 3E). All of these features are well-developed before the velum reaches its hatching size.

At hatching the larvae have a round, brown shell about 127.5 μm (n = 12; s. d. = 7.0) across with a single right-handed whorl. With the light microscope the shells appears smooth. The head vesicle is still distinct, although somewhat smaller, and the large cells are no longer visible. The embryonic kidneys also disappear before hatching. The velum is unpigmented and consists of two small, equal, semicircular lobes (Figure 3F). The right tentacle, just medial to the eye, is well-developed but the left tentacle is not visible (Figure 3F).

Within 3 or 4 days of hatching the larval shell begins to show high-spired coiling but continues to appear smooth. The beak begins as a point on the outer aperture of the shell and develops distinct flanges as it grows (Figure 4A). The velum gradually becomes more asymmetrical until the right lobe is at least twice the size of the left lobe. The velar lobes remain round and unpigmented throughout development (Figure 4B). The large diamond-shaped foot retains the operculum.

After 3 weeks in culture, larvae with a shell length of 500 μm metamorphose when placed in a dish with a fragment of host sponge. Three weeks after metamorphosis the juvenile shell reaches a length of 2 mm with 6-7 whorls (3 of which are the protoconch). After a month the juveniles reach 2.6-2.8 mm.

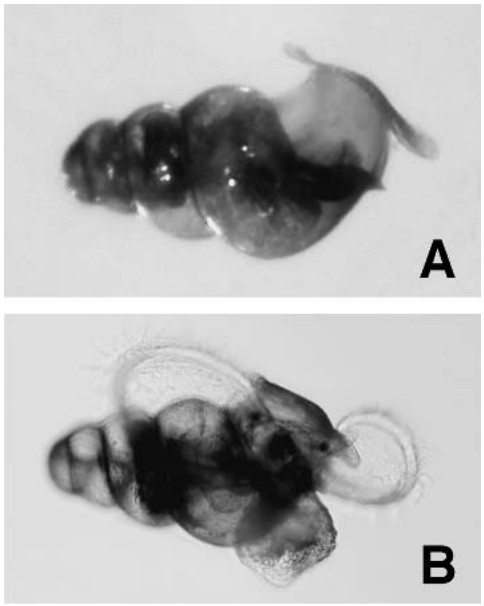

FIG. 4. Three-week old larva of *C. gemmulosum* **A.** A larva retracted into the shell showing the beaked aperture; **B.** The same larva extended showing the asymmetrical velum and large foot typical of a larva that is near metamorphosis. The beak of the shell is visible directly above the eyes. Shell length = 500 μm.

DISCUSSION

As previously noted by Robertson (1985), developmental features have the potential to contribute useful data to understand high-level gastropod relationships. The main drawback to using developmental features is that few data are available on the development of many groups. Previous descriptions of cerithiopsid development include the following observations. *Cerithiopsis tubercularis*, *C. barleei* and *C. flavum* deposit egg capsules in sponges (Lebour 1933, 1936; Cipriani et al. 1994). Cipriani et al. (1994) did not describe the embryology of *C. flavum* but did note that embryonic kidneys are present. The larvae of cerithiopsids are relatively well known, with published descriptions of *C. tubercularis*, and *C. barleei* (Lebour 1933, 1936, 1937) and several un-identified species (Lebour 1944). In all cases the larvae have highspired, beaked shells, and asymmetric, circular velar lobes. These larvae are similar to the larvae of triphorids (Lebour 1933; Richter and Thorson 1975) except that triphorid larval bodies and shells are left-handed while cerithiopsid larvae are right handed.

Among the Ptenoglossa, cerithiopsid,

TABLE 1. Developmental characters of cerithiopsids and epitoniids in comparison to other caenogastropods and heterobranchs.

	Epitoniidae	Cerithiopsidae	Caenogastropoda	Heterobranch
Species	*Nitidiscala tincta*	*Cerithiopsis gemmulosum*		
Reference	Collin (2000)	This study		
Cleavage	polar lobe	polar lobe	polar lobe	unequal
Gastrulation	epiboly	epiboly	epiboly	invagination
Embryonic kidney	yes	yes	yes	no
Head vesicle	no	yes	common	no
Larval PMO	yes	no	no	yes
Hydrophobic larval shell	yes	no	no	yes
Left handed larval shell	no	no	no	yes
Well-developed larvae at hatching	no	yes	yes	no
Beaked larval shell	yes	yes	sometimes	no

triphorid, and aclid larvae all have a beak on the high spired shell, and a colorless bilobed velum which is usually reported as asymmetrical (Lebour 1933; Throson 1946; Fretter and Pilkington 1970; Richter and Thorson 1975). Eulimid veligers lack the beak on the larval shells but are otherwise also similar. The protoconchs of *Janthina* and epitoniids show that the larvae have high-spired shells, but the shells are not beaked and are much smoother than larval shells of cerithiopsids or triphorids (Richter and Thorson 1975). Late stage larvae of *Epitonium clathrus* and *Eulima polita* are figured in Richter and Thorson (1975) and also show an asymmetrical bilobed velum. As far as I know the larvae of triforids have not been described.

This is the first published account of the embryology of a cerithiopsid species. Comparisons of developmental features observed during this study with a description of the embryology of the epitoniid *Nitidiscala tincta* show few similarities. Both species have equal cleavage with a polar lobe, gastrulation by epiboloy, embryonic kidneys, and a right-handed larval shell (Table 1). These features are all characteristic of caenogastropods and therefore do not address the idea that these families are closely related beyond both being caenogastropods. The three typically heterobranch characters of *N. tincta* (absence of head vesicle, larval pigmented mantle organ, and hydrophobic larval shell) are not shared by *C. gemmulosum*, which show the typical caenogastropod states of these characters (Table 1). Overall, these observation of embryology and larval morphology do not offer additional strong support for the monophyly of the "Ptenoglossa", but observations of the embryology of other ptenogloassan families are necessary before firm conclusions are reached.

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LITERATURE CITED

Cipriani, R., S. M. Pauls, and F. Losada. 1994. Observations on the egg-capsules of *Cerithiopsis flavum* (C. B. Adams, 1850) (Gastropoda: Cerithiopsidae) from Venezuela. *J. Moll. Stud.* 60:200-203.

Collin, R. 2000. Development and anatomy of *Nitidiscala tincta* (Carpenter 1865) (Gastropoda: Epitoniidae). *Veliger.* 43(3):302-312.

Fretter, V., and M. C. Pilkington. 1970. Prosobranchia veliger larvae of Taenioglossa and Stenoglossa. Sonseil International Pour L'Exploration de la Mer. Zooplankton sheets. 129-132.

Lebour, M. V. 1933. The life-histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.). *J. Mar. Biol. Assoc. U.K.* 18: 491-498.

Lebour, M. V. 1936. Notes on the eggs and larvae of

some Plymouth prosobranchs. *J. Mar. Biol. Assoc. U.K.* 20:547-565.

Lebour, M. V. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *J. Mar. Biol. Assoc. U.K.* 22:105-166.

Lebour, M. V. 1944. The eggs and larvae of some prosobranchs from Bermuda. *Proc. Zool. Soc. London*. 114:462-489.

Ponder, W. F., and D. R. Lindberg. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zool. J. Linn. Soc.* 119: 83-265.

Richter, G., and G. Thorson. 1975. Pelagische Prosobranchier-Larven des Golfes von Neapel. *Ophelia.* 13:109-185.

Robertson, R. 1985. Four characters and the higher category systematics of gastropods. *Am. Malacol. Bull.,* Special Edition 1:1-22.

Rolán, E., and J. Espinosa. 1995. The family Cerithiopsidea (Mollusca: Gastropoda) in Cuba 3. The genus *Cerithiopsis* s. l., species with brown shells. *Iberus* 13(2):129-147.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Oresund). Medd. Komm. Danmarks Fisk. Havunders., Ser. Plancton 4:1-523.