Spawn and development of *Bulla striata* (Opisthobranchia, Cephalaspidea) from the Western Mediterranean

Puesta y desarrollo de *Bulla striata* (Opisthobranchia, Cephalaspidea) en el Mediterráneo occidental

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ABSTRACT

The egg masses of *Bulla striata* consist of very long gelatinous and cylindrical cords, irregularly coiled. The egg capsules are ovoid and measure about 161 x 137 µm. As a rule, each capsule contains a single embryo, but sometimes contains two, or rarely three. When freshly laid, the uncleaved eggs measure about 80 µm in diameter. The chronology and photographs of major developmental events are provided. Larval development is planktotrophic, and veligers hatch between the fourth and the fifth day after egg deposition. In the laboratory they could be reared up to ten days after hatching, but metamorphosis was not achieved. At this time, the globose larval shell of the veligers measured about 115 µm in diameter and they had a completely smooth surface.

RESUMEN

La puesta de *Bulla striata* consiste en un largo cordón, de consistencia gelatinosa y sección circular, arrollado irregularmente. Las cápsulas ovígeras son ovoides (de unas 161 x 137 µm) y contienen, generalmente, un único embrión. En ocasiones puede contener dos o, muy raramente, tres. Los huevos miden unas 80 µm antes de la primera división. Se aportan algunos datos sobre el desarrollo embrionario y larvario y su cronología. El desarrollo larvario es planctotrófico y las velígeras eclosionan entre el cuarto y quinto día después de la ovoposición. Dichas larvas se mantuvieron vivas en cultivo hasta diez días después de la eclosión, pero morían antes de realizar la metamorfosis. En este momento la concha larvaria era globosa, de superficie lisa y medía unas 115 µm de diámetro

KEY WORDS: Spawn, larval development, *Bulla striata,* Murcia, SE Spain.
PALABRAS CLAVE: Puesta, desarrollo larvario, *Bulla striata,* Murcia, SE España.

INTRODUCTION

The species *Bulla striata* Bruguière, 1792, is widespread along temperate and warm coasts of both sides of the Atlantic Ocean. Western Atlantic populations were once called *Bulla occidentalis* A. Adams, 1850, now universally recognized as a junior synonym of *B. striata*. Despite of its wide range of distribution, being very common in some areas, the life history of this species is poorly

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known. Only a few works give some data on its anatomy, chromosome number, chemical defenses or generalities of its egg masses (TCHANG-SI, 1931, MARCUS, 1957, BRACE, 1977a, b, VITTURI, CATALANO, MALACUSO AND PARRINELLO, 1985, WINNER, 1985, CIMINO, SODANO AND SPINELLA, 1987, ALVÁREZ, 1994, GOSLINER, 1994, MIKKELSEN, 1996), but neither complete morphological descriptions nor comparison of populations from both sides of the Atlantic have been done.

Bulla striata is the unique species of this genus in the western Mediterranean, where it is very common in sheltered muddy zones, mainly where beds of the seagrass *Cymodocea nodosa* (Ucria) Aschers, 1869, are present. A compilation of records of this species along the Spanish coasts can be seen in the catalog of CERVERA, TEMPLADO, GARCÍA-GÓMEZ, BALLESTEROS, GARCIA, ORTEA, LUQUE AND ROS (1988).

To facilitate future comparison of populations of *Bulla striata* from both sides of the Atlantic, data on its spawn and development in different localities along its wide geographical range are of great interest. The present work provides descriptions of the egg masses and larval development of *Bulla striata*, from specimens collected in the coast of Murcia, SE Spain.

A review of literature on cephalaspid reproduction and development was provided by SCHAEFER (1996a). Much attention has been paid to these aspects in species of the genus *Haminaea* (see references in SCHAEFER, 1996a). Data referring to *Bulla* were provided by OSTERGAARD (1950) on *Bulla* sp., from Hawaii, BANDEL (1976) on *Bulla solida* Gmelin, 1791, from the Caribbean Sea, and by ROBLES (1975) and FARFÁN AND BUCKLE RAMÍREZ (1988) on *B. gouldiana* Pilsbry, 1893, from the Western Pacific.

MATERIAL AND METHODS

Adults and egg masses of *Bulla striata* were collected from two localities of Murcia, SE Spain: Cabo de Palos (37° 43′ N - 00° 42′ W), and Mar Menor lagoon (37° 43′ N - 00° 49′ W). For this study, sixteen specimens were collected at the first locality, and twenty-seven from the second one. All the specimens were collected in *Cymodocea nodosa* beds at 1 m deep, during July of 1996. All were obtained in the late evening, because this species shows nocturnal activity, remaining burrowed into the mud during daylight hours. Specimens from both localities were almost identical, and their shell lenght ranged from 17.5 mm to 21.6 mm ($\bar{x}$= 19.0 ± 1.9 mm, n= 43).

Groups of six specimens were maintained in aerated aquaria at seawater temperature of 23 ± 1°C. After 24 h, some egg masses were laid. Some spawns were removed immediately after ovoposition and maintained in glass dishes at the same seawater temperature. Culture water was replaced daily with 1-µm filtered seawater.

A few complete egg masses obtained directly from Mar Menor and some of those deposited in the aquaria were measured with a simple rule. Segments of the eggs masses were taken to measure egg and capsule dimensions, count number of embryos per capsule, and stimate number of capsules per unit length of cord. Measurements of eggs and egg capsules were taken with the aid of an ocular micrometer under a stereomicroscope. All developmental events were recorded on videotape, and some embryonic and larval stages were selected to be photographed using an optical microscope. Hatched veligers were removed and maintained in a culture of unicellular algae of the genus *Nanocloropsis* until they died. Then, some larval shell were removed and prepared for SEM.

Material of adults and egg masses have been deposited in the malacological collection of the Museo Nacional de Ciencias Naturales, Madrid, Spain (catalogue numbers 15.05/29212- 15.05/29219).

RESULTS

In the collecting area egg masses had been only found in late spring and early summer. They are long gelatinous

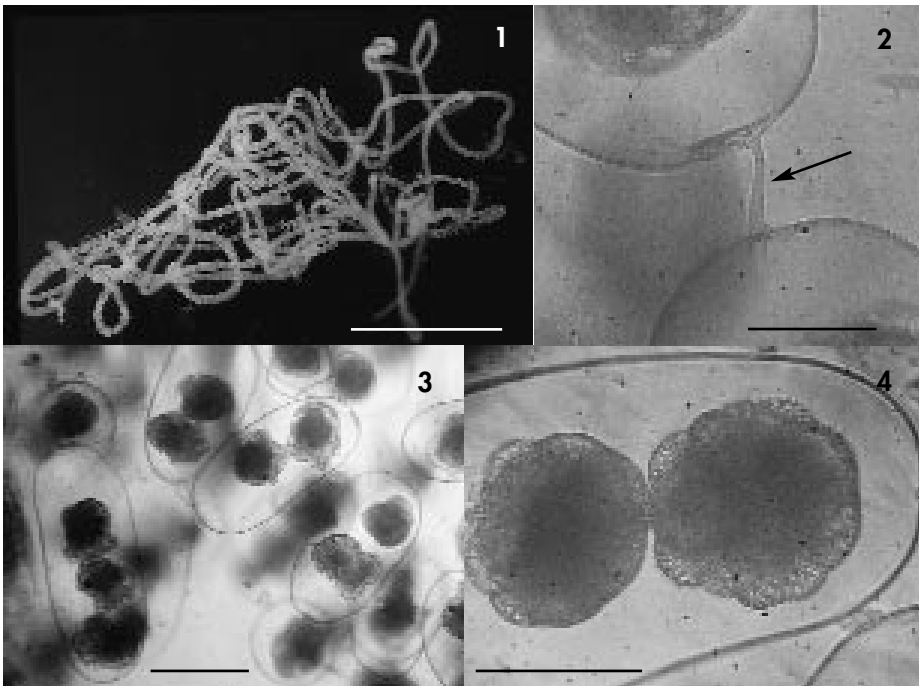


Figure 1. Egg mass of *Bulla striata.* Figure 2. Two egg capsules inter-connected by a chalaza (indicated by the arrow). Figure 3. Egg capsules containing two or three embryos. Figure 4. Egg capsule containing two embryos. Scale bars, 1: 1 cm; 2: 50 µm; 3: 100 µm; 4: 75 µm.
Figura 1. Puesta de Bulla striata. *Figura 2. Chalaza (señalada por la flecha) entre dos cápsulas ovígeras. Figura 3. Cápsulas con dos y tres embriones. Figura 4. Cápsula con dos embriones. Escalas, 1: 1 cm; 2: 50 µm; 3: 100 µm; 4: 75 µm*

capsule-filled cords, circular in cross-section, and irregularly coiled (Fig. 1). They can be found entwined in seagrass as loose tangles. Each cord consists of two egg strings closely spiralled, and embedded within a colourless jelly cord. The capsules are interconnected by a chalazae (Fig. 2), which is hardly visible.

The total length of untwined egg masses was variable and ranged from 26 to 82 cm ($\bar{x}$= 58.3, n= 15). The longest one was laid by and specimen of 32 mm shell length. The diameter of the cord was about 1 mm (from 0.8 to 1.2 mm). The egg mass in its natural arrangment (as a tangle) measured 1.8 cm to 3.4 cm in length and 0.9 cm to 1.8 cm in width (n= 15).

The egg capsules are 160.8 ± 22.6 µm long and 137.1 ± 9.5 µm wide (n= 80). As a rule, each capsule contains a single embryo. In egg masses obtained directly from the sea, almost all egg capsules contained one embryo, but in egg masses laid in the aquaria about 1% of the capsules contained two embryos (Figs. 3, 4). In one of these egg masses, five capsules containing three embryos were observed (Fig. 3). The capsules containing two embryos were larger than those containing a single one. No nurse eggs or auxiliary yolk-like material is present. The number of capsules per millimeter of the string is 87-90, being fairly constant. The number of eggs per egg mass is highly variable and can reach near 75.000.

Development is almost synchronous within each egg mass, with a slight difference between the two ends of the

Table I. Chronological sequence of development of *Bulla striata* cultured at 23°C.
Tabla I. Secuencia cronológica del desarrollo de Bulla striata *cultivada a 23°C.*

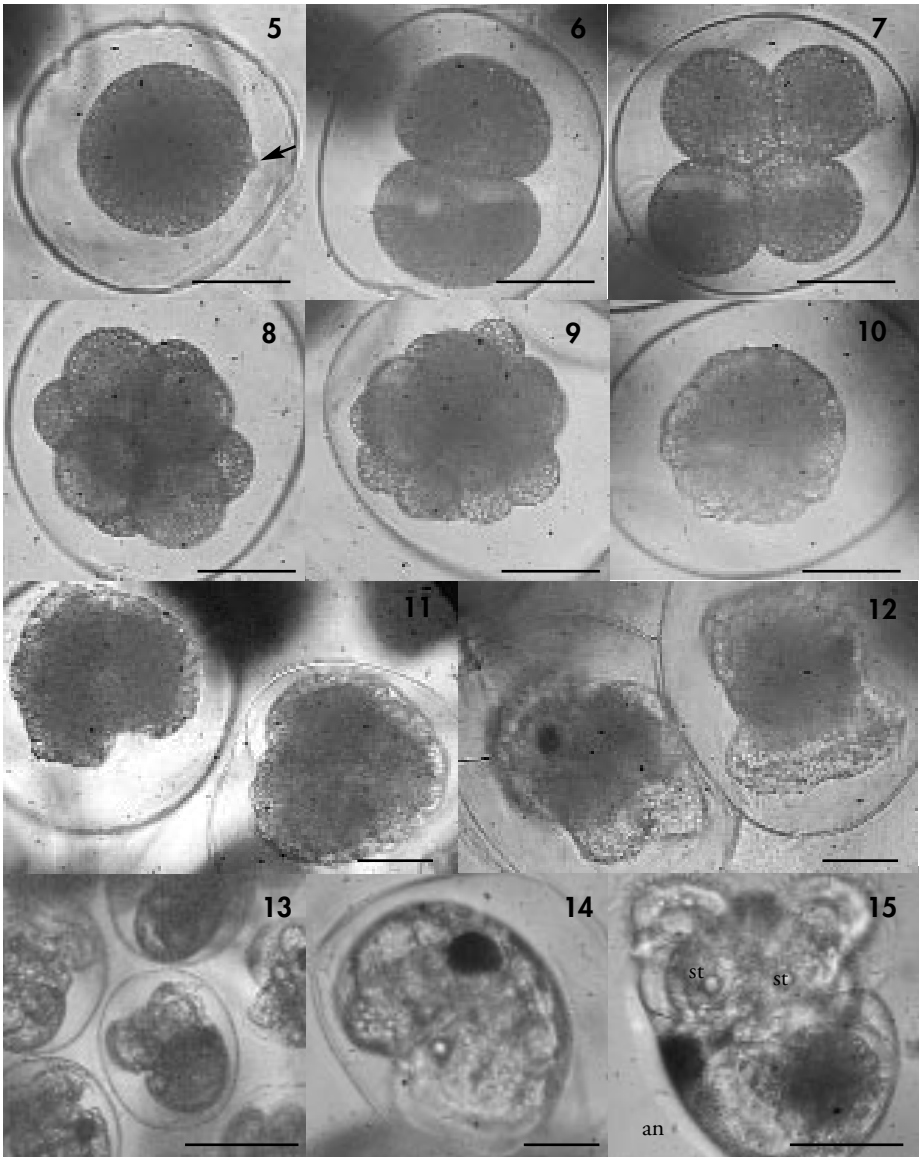
Time	Developmental stage
0	Oviposition
1 h	2-celled
2 h	4-celled
3 h	8-celled (four macromeres and four micromeres)
5 h	16-celled
12 h	Morula
18 h	Blastula
25 h	Gastrula
35 h	Preveliger (rotation by ciliary activity)
55 h	Early veliger
80 h	Veliger (pigmentation of eyes)
115 h	Hatching veliger

cord. The uncleaved eggs (Fig. 5) are pale yellowish and they measure 79.2 ± 2.9 µm (n= 15) in diameter. The chronology of major developmental events is summarized in Table I and illustrated in Figures 5-15.

A small polar body are visible before first cleavage (Fig. 5). First and second cleavages are holoblastic and equal (Figs. 6, 7), leading to four equal blastomeres. The third cleavage takes place about 3 h after egg deposition. It is unequal, giving rise to four large micromeres (almost equal in size than macromeres) in the animal pole (Fig. 8), situated interradially relative to the macromeres (typical spiral cleavage begins). The 16-celled stage (Fig. 9) occurs at about 5 h after egg deposition. After sucessive divisions, a typical stereoblastula is attained at about 18 h (Fig. 10), with the micromere cap covering a large part of the macromeres. Gastrulation occurs by partial invagination of the vegetal field followed by the epibolic downward growth of micromeres. The gastrula stage is reached about 25 h after egg deposition and shows a typical triangular bilobed shape, with a depression at the posterior end (Fig. 11).

After 35 h the embryo passes a preveliger stage, in which a thin larval shell begins to cover its posterior end and the cilia of the prototroch are clearly evident. The preveligeres rotate irregularly within the capsule. An early veliger is reached at about 55 h. The velar and pedal anlage are now distinct, and the veligers rotate regularly by metachronic beating of cilia. Soon after, the larval shell covers the visceral mass, the velum becomes bilobed, the foot is fully developed, and an opercular rudiment is formed on its dorsal side. During the veliger stage (Fig. 12) the eye spots, rudiment of tentacles, and the digestive tract become evident. About that time the cardiac pulsation appears at a right dorsal site near the alimentary canal, and a conspicuous bright red anal gland (Figs. 14, 15) is also evident at right latero ventral position. A pair of statocysts also become clearly visible (Fig. 15).

By the fourth day of development the veligers (Figs. 13, 14) move actively inside the capsules, and finally they began to hatch approximately 115 h after egg deposition. The planktotrophic larvae (Fig. 15) could be maintained for a further nine or ten days after hatching, but metamorphosis was not achieved. At this time, the larval shell of the veligers measured about 115 µm in diameter, with a completely smooth surface (Fig. 16).



Figures 5-15. *Bulla striata* developmental stages: 5: Uncleaved egg, just after egg deposition; a small polar body can be observed (indicated by the arrow); 6: Two-celled stage; 7: Four-celled stage; 8: Eight-celled stage; 9: Sixteen-celled stage; 10: Blastula stage; 11: Gastrula stage; 12: Veliger stage; 13: Late veligers; 14: Late veliger just before hatching, in which the pigmented anal gland is very evident; 15: Veliger five days after hatching; the conspicuous anal gland (an) and a pair of statocysts (st) are clearly visible. Scale bars 50 µm.

Figuras 5-15. Estadios de desarrollo de Bulla striata. *5: Huevo sin dividir, justo después de la ovoposición; puede observarse un pequeño corpúsculo polar (señalado por la flecha); 6: Estadio de dos blastómeros; 7: Estadio de cuatro blastómeros; 8: Estadio de ocho blastómeros; 9: Estadio de dieciseis blastómeros; 10: Estadio de blástula; 11: Estadio de gástrula ; 12: Velígeras; 13: Velígeras avanzadas; 14: Velígera a punto de eclosionar, en la cual se aprecia claramente la glándula anal conspicuamente pigmentada; 15: Velígera cinco días después de la eclosión; se aprecian claramente la conspícua glándula anal (an) y los dos estatocistos (st). Escalas 50 µm.*

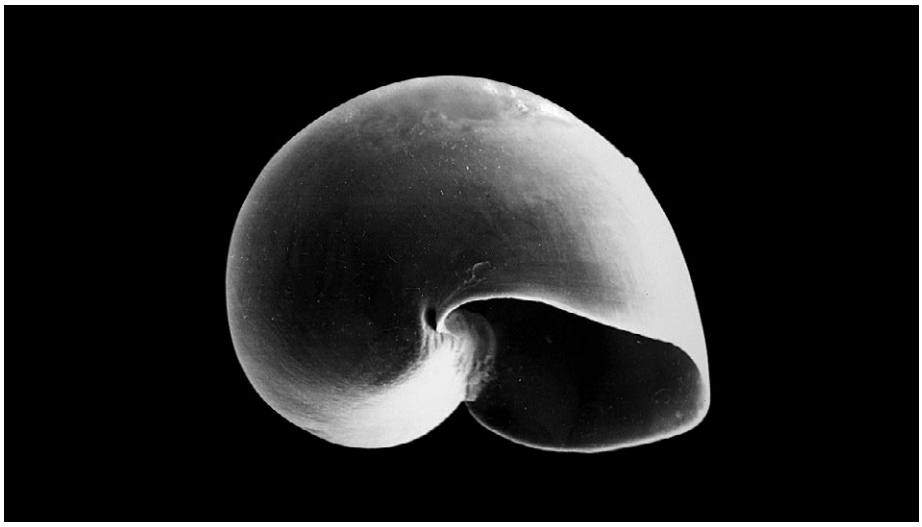


Figure 16. Larval shell (under SEM) ten days after hatching. Scale bar 20 µm.
Figura 16. Concha larvaria (al MEB) diez días después de la eclosión. Escala 20 µm.

DISCUSSION

While tropical species are commonly active for reproduction throughout the year, those distributed in temperate areas normally present a seasonal reproductive cycle, closely associated with the pronounced changes in the sea surface temperature, as occurs in the Mediterranean Sea. Spawning season in *B. striata* is similar to that reported for other mediterranean caphalaspideans that live in the same habitat, as *Haminaea navicula* and *H. hydatis* (BERRILL, 1931, SCHAEFER, 1996a).

Types of egg masses in Opisthobranch have been categorized by HADFIELD AND SWITZER-DUNLAP (1984) and SOLIMAN (1987). Three different forms of the egg masses described by these authors were considered by MIKKELSEN (1996. p. 419) to be present in Cephalaspidea: a) elongated string (round in cross-section), b) flattened ribbon, and c) gelatinous ball. In *Bulla* the egg mass consists of an elongated string, as occurs in the anaspid genera *Aplysia* or *Akera* and in the shelled sacoglossans *Volvatella* and *Cylindrobulla* (MIKKELSEN (1996), while in the related genus *Haminaea* consist of a flattened ribbon (SCHAEFER, 1996a). Therefore, the form of the egg mass does not seem to be a good phylogenetic character within lower opisthobranchs.

The data given by ÁLVAREZ (1994) and MIKKELSEN (1996) on the spawn of *B. striata* agree with our observations. Nevertheless, the egg mass shown by BARASH AND ZENZIPER (1980) as belonging to *B. striata* are like those of species of the genus *Haminaea,* and probably corresponds to *Haminaea navicula*, a species that lives in the same habitat. The egg masses of *Bulla gouldiana* described by FARFÁN AND BUCKLE RAMÍREZ (1988) and those of *B. quoyii* shown by WELLS AND BRYCE (1993, lowest figure on page 8) are quite similar in form to those of *B. striata*.

The presence of chalazae connecting the eggs has been used as a synapomorphic character of the heterobranch clade within gastropods (ROBERTSON, 1985, HASZPRUNAR, 1985, 1988). Therefore, this character should be present in the egg masses of all Cephalaspidea, and is confirmed here for *B. striata*.

The egg size of *B. striata* (about 80 µm in diameter) is within the range pre-

Table II. Summary of data on spawn and development of three species of *Bulla* from the literature and present work. Data for *B. gouldiana* from ROBLES (1975) and FARFÁN and BUCKLE RAMÍREZ (1988), data for *B. solida* from BANDEL (1976), and data for *B. striata* from the present work.
Tabla II. Cuadro comparativo sobre la puesta y desarrollo en tres especies de Bulla. *Los datos de* B. gouldiana *proceden de ROBLES (1975) y FARFÁN AND BUCKLE RAMÍREZ (1988), los datos de* B. solida *de BANDEL (1976), y los de* B. striata *del presente trabajo.*

	Bulla gouldiana	*Bulla solida*	*Bulla striata*
Spawning period	Spring-summer		Late spring-summer
Substrate	Free; *Zostera*	Plants, stones covered witn silt or sand	Leaves of *Cymodocea*
Shape of the mass	"Meters"	5-25 mm	26-82 cm
Diameter of the cord	4 mm	1-1,5 mm	0,8-1,2 mm
Number of egss/egg mass		2000-200000	18000-73800
Number of eggs/mm of string	326±50	75	85±10
Length x width of capsule in µm	247x209	60	160x137
Eggs/capsule	1-12	1-2	Normally 1; sometimes 2-3
Egg diameter in µm	84,5		79,2
Color of eggs	Bright-yellow	Yellowish	Yellowish
Developmental type	Planktotrophic	Indirect, pelagic	Planktotrophic
Time until hatching	5-6 days	6 days	4-5 days
Pelagic life observed	15 days		10 days
Length larvar shell	250 µm		115 µm
Temperature	24±1°C		23°C

sented for other species of Cephalaspidea (or opisthobranchs, in general) with planktotrophic larvae (see SCHAEFER, 1996a). Cleavage pattern and ontogenetic details are quite similar to that described in other species of cephalaspids, as *Bulla gouldiana* (FARFÁN AND BUCKLE RAMÍREZ, 1988), *Haminaea vesicula* (GIBSON AND CHIA, 1989), *H. callidegenita* (BORING, 1989), or *H. navicula* (SCHAEFER, 1997), but remarkable differences exist concerning the duration of the total developmental process and in its different phases. According to SCHAEFER (1997), the differences observed in timetable of cleavage and in further stages up to hatching may be explained by different egg sizes and different developmental types (planktotrophic *vs*. lecithotrophic) or by different temperatures of their cultures. For instance, *Haminaea vesicula* or *H. navicula* spent much more time to complete the development (GIBSON AND CHIA, 1989, SCHAEFER, 1997) than *B. striata*. *Haminaea vesicula* and *B. striata* have similar egg size (90 and 80 µm in diameter respectively), and both present planktotrophic larval development. Nevertheless the temperature of culture of *H. vesicula* was lower (12-15° C) than that of *B. striata* (23° C). On the other hand, *H. navicula* (reared at 19-22° C) spawn larger eggs (180 µm in diameter) than those of *B. striata* and it has a lecitotrophic development (SCHAEFER, 1997). It must be noted the large size of the micromeres in embryos of *B. striata* at the 8-celled stage, only slightly smaller than the macromeres. This may indicate a relatively low yolk content in the eggs. CHIA (1971, fig. 10) and BRIDGES AND BLAKE (1973, fig. 2b) showed 8-celled embryos of the opisthobranchs *Limapontia depressa* and *Coryphella trilineata* with large micromeres as in *B. striata*.

A dark red anal gland was also reported in veligers of *Bulla striata* by MIKKELSEN (1996). FARFÁN AND BUCKLE RAMÍREZ (1988) mentioned a bright red anal gland (as nephrocyst) in *Bulla gouldiana*. The development and homologies

of the anal gland (also called in the literature: pigmented mantle organ, larval kidney, secondary kidney, or nephrocyst) was studied and discussed by SCHAEFER (1996b), and it was claimed to be a synapomorphic character of all heterobranch gastropods (ROBERTSON, 1985, HASZPRUNAR, 1985 and 1988). However, the value of the anal gland as synapomorphic of the heterobranchs was doubted by SCHAEFER (1996b) (see also PONDER AND LINDBERG, 1997).

Comparative data on spawn and development of three species of *Bulla* are summarized in Table II, *B. gouldiana* (from ROBLES, 1975, and FARFÁN and BUCKLE RAMÍREZ, 1976), *B. solida* (from BANDEL, 1976), and *B. striata* (present work).

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