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Spawn in two deep-sea volute gastropods (Neogastropoda: Volutidae) from southwestern Atlantic waters

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ABSTRACT

The gastropods *Odontocymbiola pescalia* and *Provocator corderoi* and their egg capsules were collected by the R/V Puerto Deseado from the Mar del Plata Submarine Canyon (~ 37°53′S, at depths of 291–1404 m) and from Burdwood Bank (~ 54°27′S, 128–785 m). *Odontocymbiola pescalia* egg capsules measured 15.67 ± 3.38 mm in diameter. They were subspherical in shape with an external calcareous layer. Each egg capsule contained 3–5 embryos and white material as extra embryonic food. Embryos grew to a size of up to 9.3 ± 1.1 mm in mean shell length before hatching as crawling juveniles. The spawn of *P. corderoi* consisted of a single dome shaped egg capsule of 14.17 ± 1.5 mm in diameter, attached to hard substrata by a basal membrane with a rounded outline. A curved semilunar furrow (seam) on one side of the capsules was always present. The number of embryos per capsule was 2–6. Embryos hatched as crawling juveniles with a shell length of 5.9 ± 0.6 mm.

The size and number of whorls in the hatchling shell suggested a slow rate of development, akin to many other deep-sea invertebrates. The egg capsules and reproductive development strategies of both species were compared with those from other congeneric representatives.

1. Introduction

Volutids encompass a group of large gastropods distributed all around the globe but the southern hemisphere reveals the higher number of species, particularly those from the Indo-Pacific Ocean. The southwestern Atlantic is especially rich in endemisms; however, the number of species is particularly low when compared with Oceania. About 25 species of Volutidae were described from Southwestern Atlantic coasts but the real number might change fast as several new species are being examined from recently explored deep water environments. Five species of this list are commercially exploited and represent an interesting economic resource (Cledón et al., 2005; Giménez et al., 2005; Bigatti and Ciocco, 2008). Most of the species play an important role in the food chain as top predators in the marine communities (Zabala et al., 2013).

The spawns of most shallow water gastropods of the family Volutidae from the Southwestern Atlantic coast have been previously studied in some detail. Several species of the genera *Adelomelon*, *Voluta*, *Zidona* and *Odontocymbiola* were characterized and illustrated since the first capsules described by d`Orbigny (1846) including their egg capsules and embryonic development (de Mahieu et al., 1974; Penchaszadeh and d Mahieu, 1976; Penchaszadeh, 1988; Penchaszadeh et al., 1999; Penchaszadeh and Miloslavich, 2001; Penchaszadeh and Segade, 2009; Matthews-Cascon et al., 2010; Zabala et al., 2015). Moreover, a detailed description of the morphology and biochemistry of the embryonic development and egg capsules was carried out for *O. magellanica* from Golfo Nuevo, Argentina (Bigatti et al., 2010, 2014). All these works established the basis for the study of the reproductive patterns of the family Volutidae in South America.

The species of these genera typically attach single egg capsules to hard substrates, with some exceptions as *V. ebraea* from sea grass beds of Northeast Brazil whose egg capsules are usually fixed to the algae *Udotia occidentalis* (Matthews-Cascon et al., 2010), and the enormous free demersal capsules of *Adelomelon brasiliana,* which lay on shallow sandy bottoms from Southern Brazil to Argentina (d'Orbigny, 1846; de Mahieu et al., 1974; Penchaszadeh and de Mahieu, 1976).

South American species of Volutidae are very uniform regarding their reproductive patterns. They generally spawn egg capsules with a variable number (2–33) of small eggs (90–450 μm in diameter, according to the species). All the species studied until now experience direct development and hatch as crawling juveniles. The embryos feed on substances (such as albumen, amino acids and carbohydrates) contained in the intracapsular fluid (de Mahieu et al., 1974; Penchaszadeh and Miloslavich, 2001; Bigatti et al., 2010). The same pattern of egg capsules was observed in *Provocator pulcher* from the Subantarctic Indian Ocean (Arnaud and Van Mol, 1979). No nurse eggs were found in

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Table 1
Summary of sampled stations with latitude, longitude and depths. Number of live (L) and dead (D) adults, number of egg capsules.

Latitude S	Longitude W	Depth (m)	Date	*O. pescalia*		*P. corderoi*	
				Adult	Egg capsules	Adult	Egg capsules
37°53.557′	54°42.941′	780	8/10/12	5(L)	0	2(L), 1(D)	0
37°53.557′	54°42.941′	780	5/26/13	4(L)	3	8(L)	4
37°55.184′	54°13.895′	1404	11/9/13	0	0	1(L)	0
37°57.182′	55°11.060′	291	8/8/12	1(L)	0	0	0
37°57.736′	55°8.456′	528.63	8/10/12	2(L)	0	0	0
37°57.857′	54°57.406′	647.22	8/10/12	12(L), 10(D)	0	13(L)	9
37°58.337′	55°8.915′	530	8/10/12	1(L)	0	0	0
37°58.698′	55°11.899′	308	8/17/12	1(L)	0	0	0
37°59.706′	54°41.854′	852	8/11/12	2(L), 5(D)	1	8(L)	10
37°59.800′	55°12.479′	319.29	8/17/12	1(L)	0	0	0
38°0.984′	54°30.326′	1006	8/11/12	1(L), 3(D)	0	3(L), 6(D)	16
38°01.631′	54°30.275′	997	5/26/13	2(L)	0	2(L)	0
54°23.424′	63°19.429′	293	4/11/16	5(L)	0	0	0
54°27.563′	59°13.21′	128	3/30/16	0	1	0	0
54°37.484′S	61°9.152′	202	4/15/16	0	0	1(L)	0
54°49.168′	60°42.466′	611	4/15/16	0	0	5(L)	0
54°53.218′	59°48.9′	785	4/13/16	2(L), 6(D)	0	0	0
54°81.24′	63°37.67′	585	11/13/14	1(L)	0	0	0

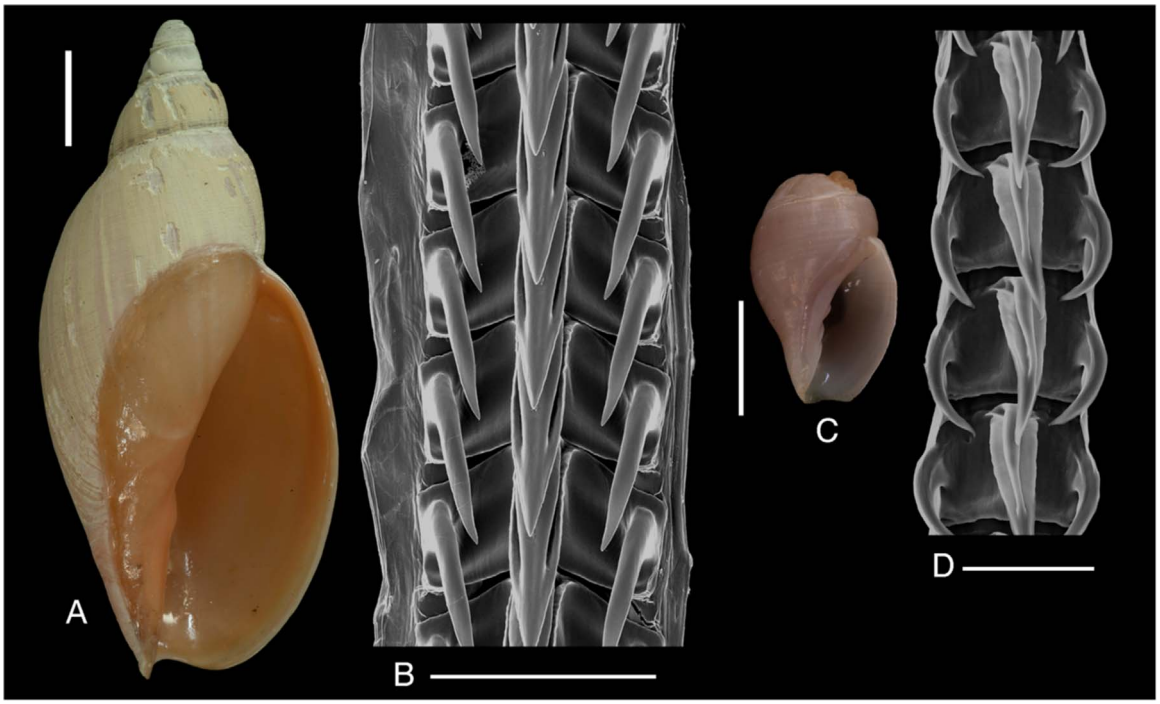

Fig. 1. *Odontocymbiola pescalia*: **A**- adult *Odontocymbiola pescalia* (MACN-In 41175); **B**- SEM photograph of adult radulae (from specimen in fig. **A**); **C**- ready-to-hatch embryo (MACN-In 41176); **D**- SEM photograph of radulae from ready-to-hatch embryo (from specimen in fig. **C**) Scale bars **A** 1 cm; **B** 500 μm; **C** 5 mm; **D** 100 μm.

South American species with the exception of *Voluta virescens* (according to Bandel, 1976, although never corroborated with live or preserved material).

When reproductive strategies of South American volutids are compared with West Africa and the majority of Indo Pacific species major differences became apparent. The spawn in the genus *Cymbium* Roding, 1798 consist on an egg capsule brooded by the female in a sac located on their foot. The egg capsules contained albumin and nurse eggs. Hatching take place as crawling juveniles (Marche-Marchad, 1980; Penchaszadeh et al., 1999). The morphology of several genera from tropical Indo-Pacific waters, as the species *Melo miltonis*, includes roughly cylindrical egg masses with a variable number of spirally arranged egg capsules. These egg masses have an empty central space connected to the exterior by a number of fontanels among the bands of egg capsules (Cotton, 1936, 1944; Allan and Middleton, 1946; Tokioka, 1962; Amio, 1963; Knudsen, 1993). They are attached to hard substrata by the base and may reach large sizes e.g., 20 cm in *Melo miltonis* and 25 cm in *M. ducale*. Only a single embryo develops inside each capsule. Hatchlings emerge as crawling juveniles.

Odontocymbiola pescalia Clench and Turner (1964) is distributed from ~ 36°S to 54°S from Buenos Aires Province to Tierra del Fuego Province, Argentina, at depths from 100 m to 1200 m (Castellanos and Landoni, 1992), while *Provocator corderoi* (Carcelles, 1947), is found from ~ 34°S to Tierra del Fuego (54°S) between 40 and 450 m depth (Carcelles, 1947; Kaiser, 1977; Castellanos and Landoni, 1992).

In this study, the spawns of two species deep sea volutid species, *O. pescalia* (subfamily Odontocymbiolinae) and *P. corderoi* (subfamily Zidoninae), from the Southwestern Atlantic are described for the first time, including the characterization of egg capsules and embryonic development. In addition, the capsules and embryo development of

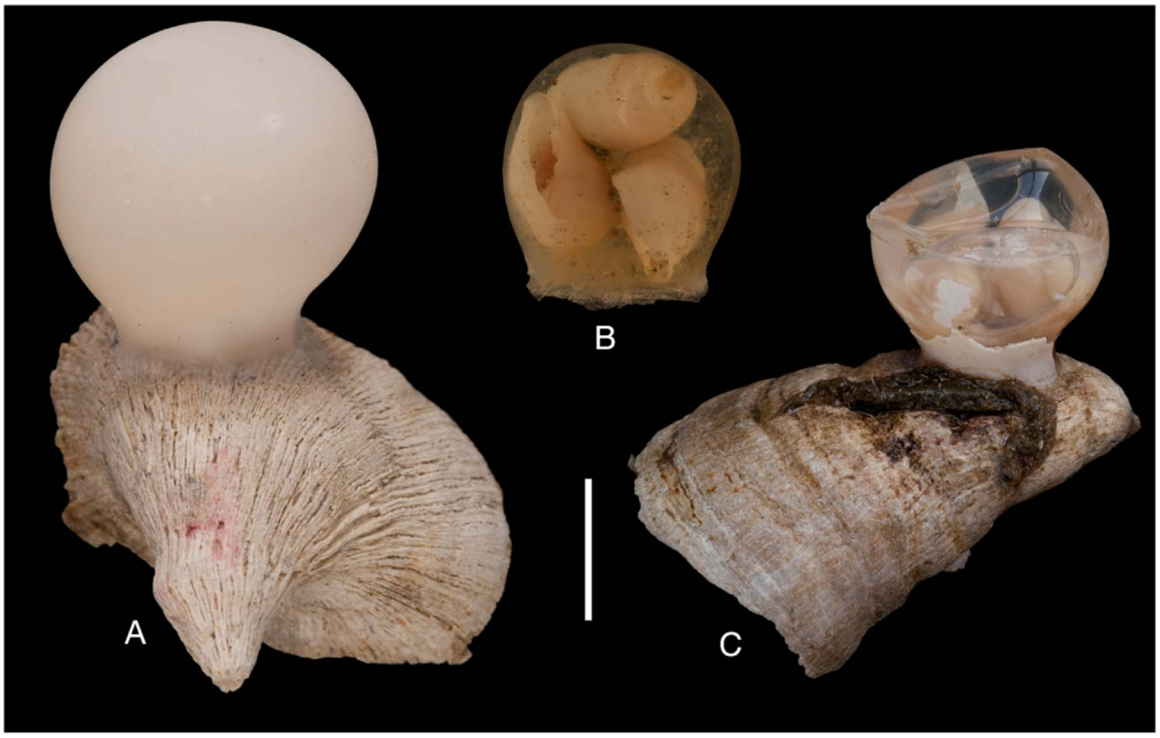

Fig. 2. *Odontocymbiola pescalia*: **A**- egg capsule attached to *Flabellum* sp. with its intact white calcareous cover (MACN-In 41177); **B**, **C**- egg capsules in which the external calcareous layer has been lost (MACN-In 41178). Scale bars **A-C** 1 cm.

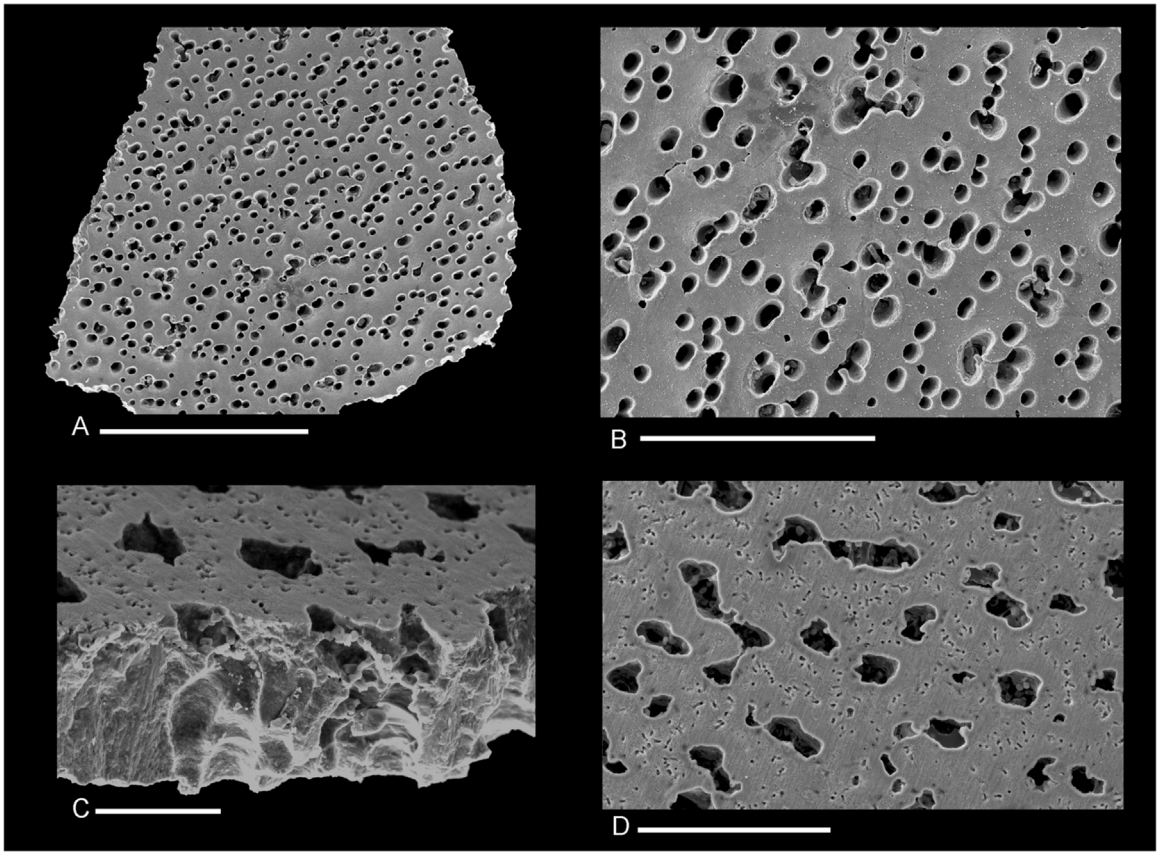

Fig. 3. *Odontocymbiola pescalia*: **A, B**- SEM images of the outer side of the external calcareous layer; **C, D**- SEM images of the inner side of the external calcareous layer. Scale bars **A** 1 mm; **B** 500 μm; **C** 100 μm; **D** 200 μm.

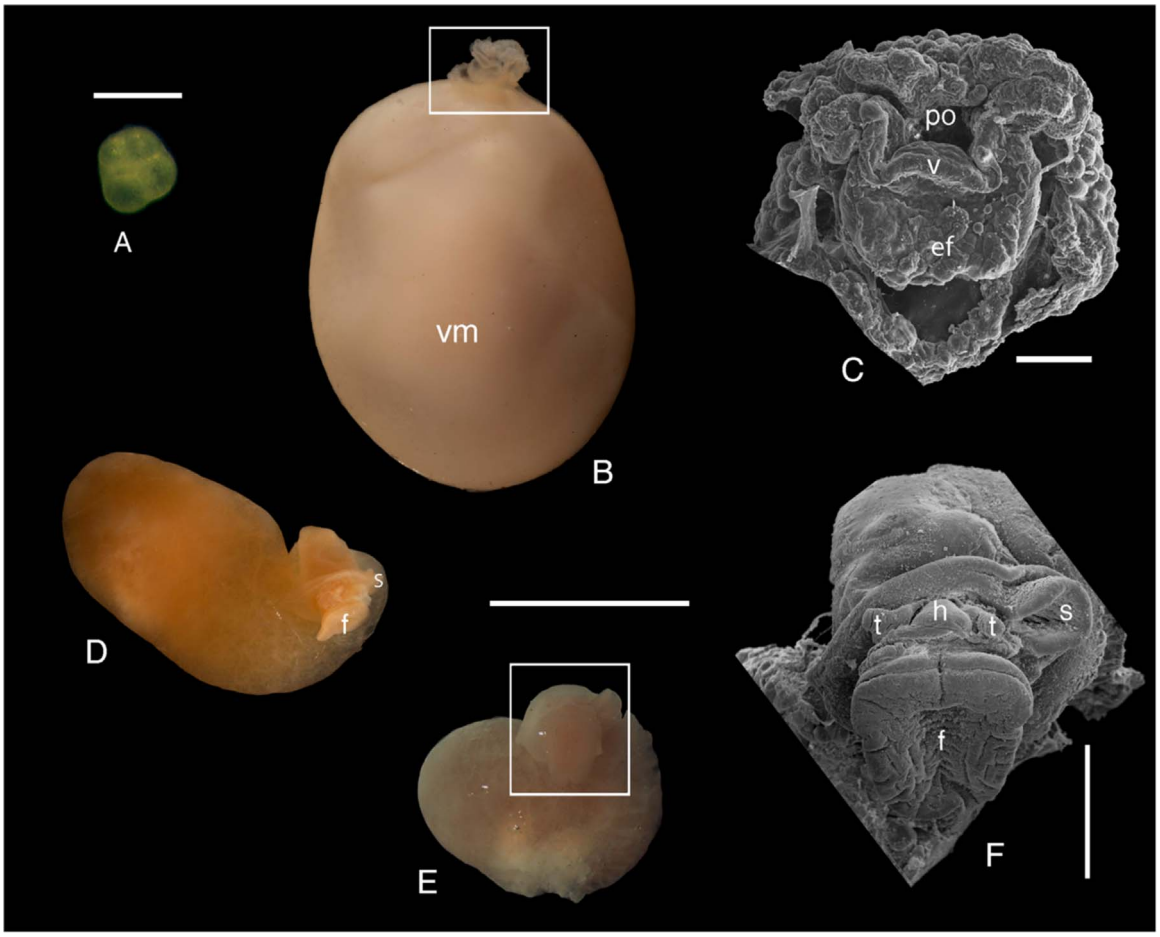

Fig. 4. *Odontocymbiola pescalia´s* developmental stages: **A**- four-cell stage; **B**- ball-shaped embryos; **C**- SEM detail of the cephalopodium ball embryos, area in the square of figure **B**; **D**- early pediveliger embryo; **E**-coiling embryo stage; **F**- SEM detailed photograph of coiling embryo stage, area in the square of figure **E**. Scale bars **A, C** 200 μm; **B, D-E** 5 mm; **F** 1 mm. *ef* early foot, *f* foot, *h* head, *po* oral pouch, *s* siphon, *t* tentacle, *v* velum, *vm* visceral mass.

both species were compared with other members of the same and different subfamilies.

2. Materials and methods

Adults and egg capsules of *Odontocymbiola pescalia* and *Provocator corderoi* were collected from 15 stations during three cruises on board of the Argentine R/V "Puerto Deseado" to the Mar del Plata Submarine Canyon area and from six stations nearby Burdwood Bank (Table 1). A total of 44 egg capsules of both species were collected, providing the chance to study these rare, gastropods. All the material obtained was collected using a bottom net and a modified Agassiz dredge (Table 1). The egg capsules were preserved in a 4% formalin-seawater solution, which is most suitable for histology and preservation of egg and embryos. The capsules were measured with a 0.1 mm precision caliper and the embryos using a 0.01-mm precision ocular micrometer. Volume of each egg capsule was measured in a graduated cylinder according to the method used by Bigatti et al. (2010). In order to confirm the species correspondence of the capsules, radulae of embryos, juveniles and adults were dissected for comparisons. These radulae were cleaned with Clorox and sonicated in an ultrasonic cleaner. Embryos were critical point dried. All samples were mounted and coated with gold and observed using a Philips XL 30 scanning electron microscope at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires. The specimens and egg capsules of both species were preserved in the gastropod spawn collection of the MACN-In. All shells and capsules were photographed using a Nikon D100 camera with a 60 mm Micro Nikkor lens and a Leica IC 80 HD camera for those items smaller than 5 mm. Photographs were digitally processed with the appropriate software (Adobe suite). The calcareous composition of the external wall of the egg capsules of *O. pescalia* was corroborate with **HISTODECAL®** -decalcify (Biopack) during four hours. This decalcifying is successfully used on bone or hard tissues with histopathological purposes because the nature of the cells and nucleus remain unaffected. The whole technique is as simple as observing the disappearance of the calcareous layer.

3. Results

3.1. Odontocymbiola pescalia

This is a representative of the subfamily Odontocymbiolinae living in depth ranges of 128–1000 m along the Argentine platform and continental slope, according to the material obtained in this study (~ 37°S to ~ 55°2′S) (Fig. 1A). It was first described after a single complete specimen and later confirmed by several more (Kaiser, 1977). The radula extracted from an adult of *O. pescalia* was uniserial, with a tricuspid rachidian tooth with fang-like cusps (Fig. 1B), characteristic of the genus. The embryo radulae showed already developed lateral cusps, somewhat curved and smaller than the central cusp (Fig. 1D). The central cusp was still keeping the size and shape of the keel in the medium of the cusp, that becomes wider and lower later in the adult.

A total of five egg capsules of *Odontocymbiola pescalia* were found attached to dead specimens of the corals *Flabellum* cf. *curvatum* and *F. areum* (Fig. 2), four of them between 780 and 850 m depth in the Mar del Plata Submarine Canyon (~ 37°53′S, 54°42′W) and another one at

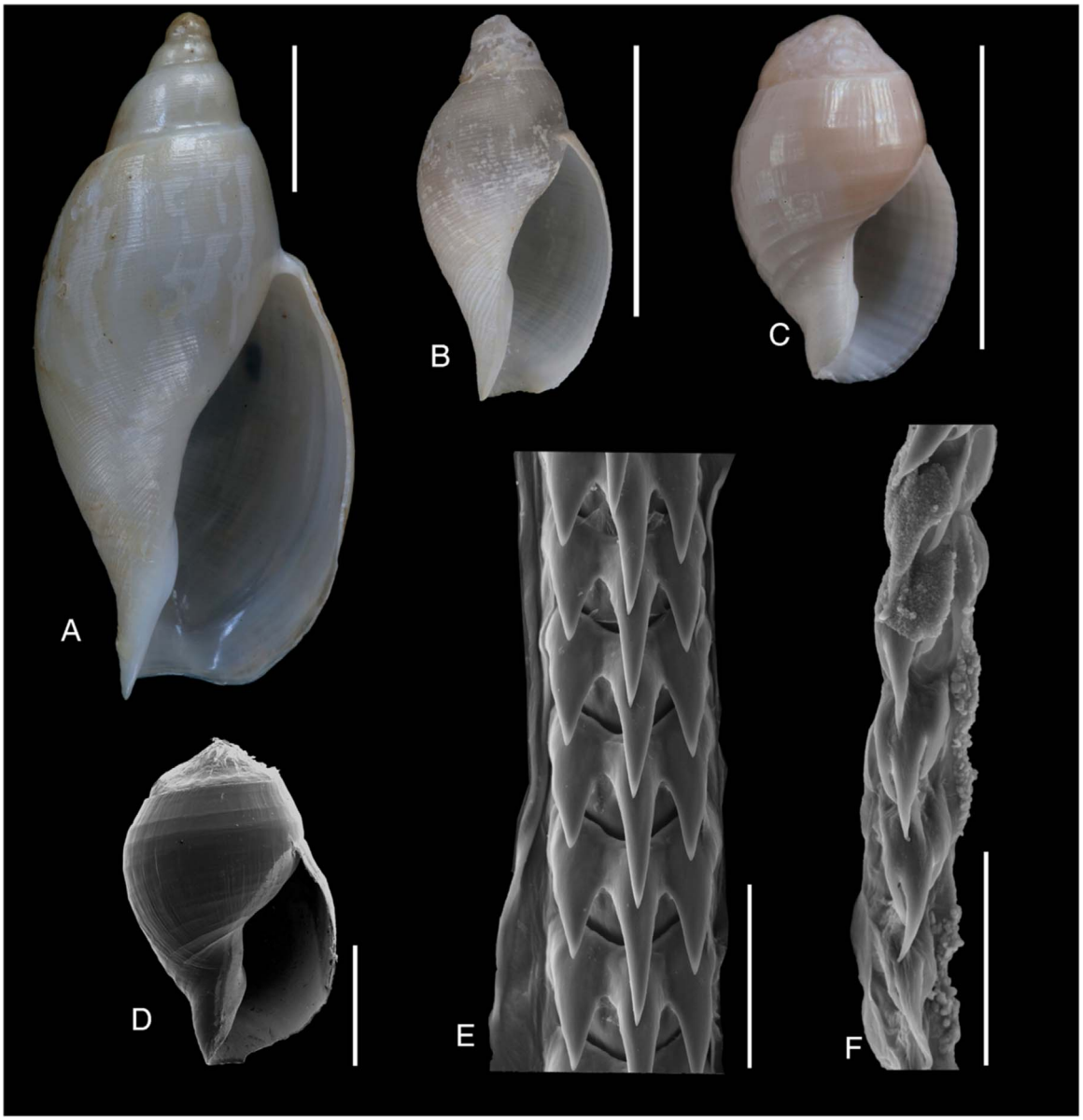

Fig. 5. *Provocator corderoi*: **A-** adult (MACN-In 41179); **B-** young from nature (MACN-In 41180); **C**- embryo (MACN-In 41181); **D**- SEM photograph of embryo; **E**- radulae from young (specimen in fig. **B**); **F**- radulae from ready-to-hatch embryo (specimen in fig. **C**). Scale bars **A** 1 cm; B 1 mm; **C** 5 mm; **D** 2 mm; **E** 100 μm; **F** 50 μm.

128 m depth in the Burdwood Bank (~ 54°27′S, 59°13′W).

The egg capsules were subspherical in shape (Fig. 2A-C). An external calcareous, brittle layer, chalky white in color, was present. SEM images of the outer side of this external calcareous layer showed regularly spaced oval holes with rounded edges (Fig. 3A-B) that became irregular and confluent internally. In addition, very small pits surrounding larger holes were present (Fig. 3C-D). Mean capsular height and width were 16 ± 3.4 mm and 15.67 ± 3.38 mm, respectively. A constricted area of about 8.3–12.7 mm was observed right above the base of the egg capsule. The volume of the capsule was 1.5–4.5 ml (mean ± SD: 2.42 ± 1.8 ml). No pre-formed escape aperture, plug or suture lines were found in any capsule. Prior to hatching, the calcareous external wall fall to small pieces exposing the membranous wall towards the end of intracapsular development (Fig. 2B-C). No nurse eggs were observed.

Each egg capsule showed 3–5 embryos with a mean number of 3.6 ± 0.89 mm. The following stages were recognized: four-cell stage (192.0 ± 6 μm in diameter, n = 3) (Fig. 4A); late veliger stage with ball-shaped embryos, in which the visceral mass had grown much larger than the cephalopodial structures and the velum (11.0 ± 0.6 mm in maximum length, n = 4) (Fig. 4B-C); early pediveliger embryos (8.5 ± 0.6 mm in maximum length, n = 4) (Fig. 4D); and coiling embryo stage with well-developed foot, tentacles, head and siphon (10.1 ± 0.9 mm in maximum length, n = 5) (Fig. 4E-F). Developed ready-to-hatch embryos (according to juvenile shell length) ranged from 10.3 to 10.6 mm in shell length (n = 3) (mean ± SD: 10.4 ± 0.2 mm) (Fig. 1C).

3.2. *Provocator corderoi*

The radulae extracted from the embryos and adults of *P. corderoi* had a tricuspid single rachidian tooth (typical for the subfamily Zidoninae), with the central cusp larger than the two lateral denticles (Fig. 5E-F), which characterizes the genus. This feature was remarkable in the embryo radulae, where the central tooth was about three times larger than the lateral cusps (Fig. 5F). The radula and shell of the embryos were characteristic of the family Volutidae living in South America (Fig. 5).

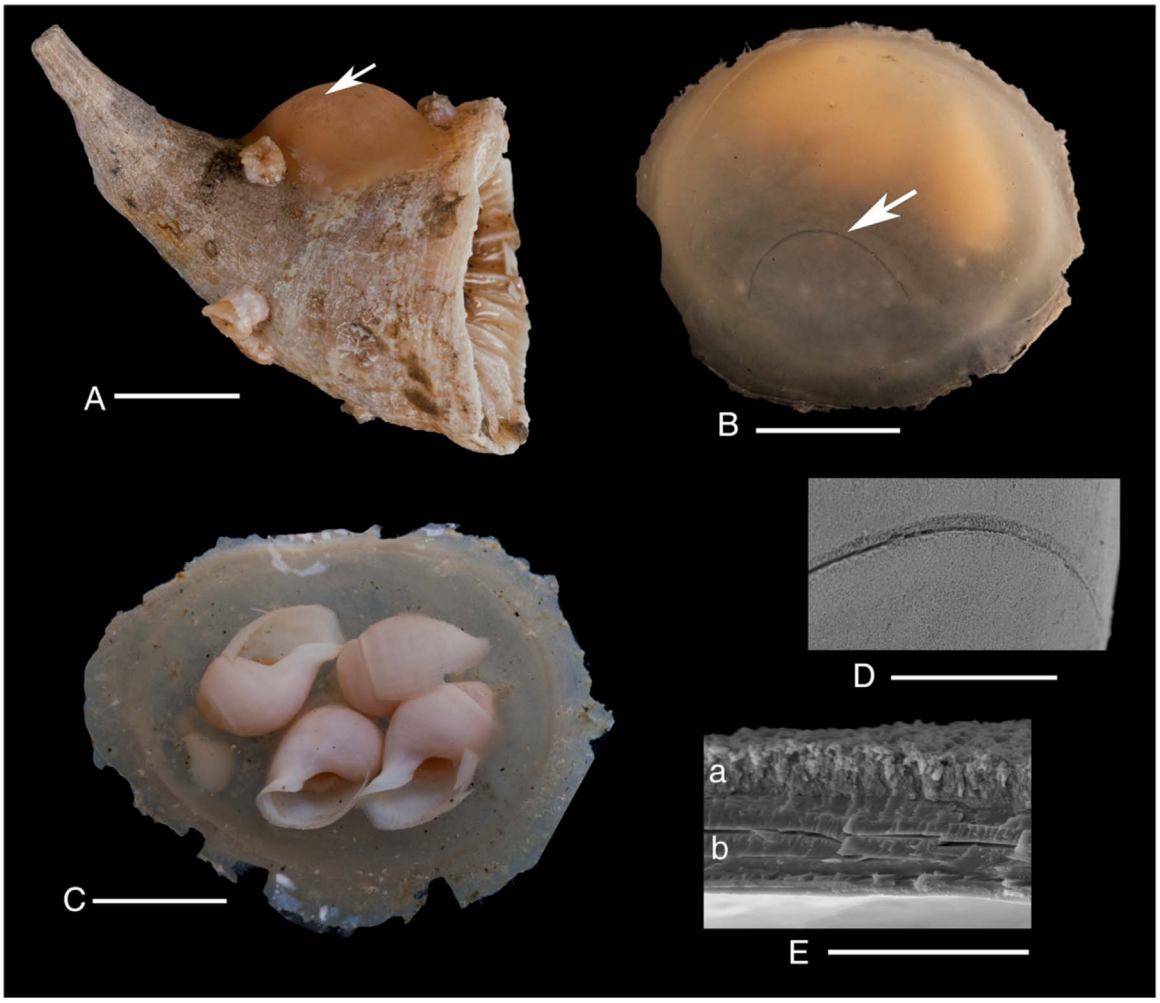

Fig. 6. *Provocator corderoi*: **A**- egg capsule attached to the coral *Flabellum curvatum*, lateral view (MACN-In 41186); **B**- dorsal view of an egg capsule with a curved semilunar line (arrowhead); **C**- egg capsule prior to hatching, basal view; **D**- SEM detail of the curved semilunar line egg capsule prior to hatching, basal view; **E**- SEM images of the egg capsule with two large layers. Scale bars **A** 1 cm; **B-C** 5 mm; **D** 500 μm; E 100 μm.

Spawns were collected at 647–1000 m depth and consisted of a single dome-shaped egg capsule attached to hard substrata (as the corals *Flabellum curvatum* and *F. areum*) with a rounded outline and a basal membrane (Fig. 6). The capsules measured 14.2 ± 1.5 mm diameter in width (mean ± SD) and 5.6 ± 1.25 mm diameter in height (mean ± SD). No pre-formed escape aperture was found in any capsule. However, a curved semilunar line on one side of the capsules was always present (Fig. 6A-B). A detailed SEM on this part of a critical point dried capsule showed a deep furrow on the capsule (Fig. 6D). A transverse section of the egg capsule differentiated two conspicuous layers (Fig. 6E) with a distinct disposition of smaller layers. A total of 39 egg capsules were studied of which 18 contained embryos and the rest were broken and empty. The number of embryos per capsule ranged from 2 to 6, with a mean of 2.81 ± 1.8.

The following developmental stages were observed (Fig. 6): uncleaved egg of about 256.0 ± 6.4 μm in diameter (n = 6), spiral and holoblastic cell cleavage with presence of polar bodies (Fig. 7A); four cells 348 μm in diameter (n = 1); late embryo without shell in which the visceral mass had grown much larger than the foot and velum (4.6 ± 0.9 mm n =13) (Fig. 7B-C); coiled shell embryo (5.3 ± 0.8 mm n = 14) (Fig. 7D) and pre-hatching juveniles (5.4 ± 1.2 mm n = 6) (Fig. 7E). Ready to hatch developed embryos ranged from 5 to 7 mm in shell length (n = 11) (mean ± SD: 5.9 ± 0.6 mm) (Fig. 5C-D).

4. Discussion

The identification of both species is based on the adult shells and radulae which are very characteristic and present no doubts. The original descriptions are clear and well-illustrated (Clench and Turner, 1964; Carcelles, 1947).

4.1. Egg capsules

The egg capsules of *O. pescalia* are comparable to those of its shallow-water congener *O. magellanica*. The general shape and the presence of an external calcareous layer with a similar perforation arrangement confirm the same pattern. In addition, the capsules are also attached to hard substrates. The notorious constriction area right above the base of the capsule is an apparently morphological difference with *O. magellanica*, in which no reduction in capsule diameter are usually observed. Moreover, the capsule size is another main difference. The egg capsules of *O. pescalia* are smaller than those of *O. magellanica* (15.7 ± 3.4 mm vs. 30.0 ± 5.2 mm, respectively; Bigatti et al., 2010), and also the capsule internal volume is about 10 times smaller in *O. pescalia* than in *O. magellanica* (4.5 ml vs. 29.7 ml, respectively). In addition, the number of embryos were 3–5 and 4–18, respectively.

Heavily calcified egg capsule external walls such as those of *O. pescalia* and *O. magellanica* appear only rarely among the Neogastropoda. *Alcithoe arabica* (Volutidae) from New Zealand is

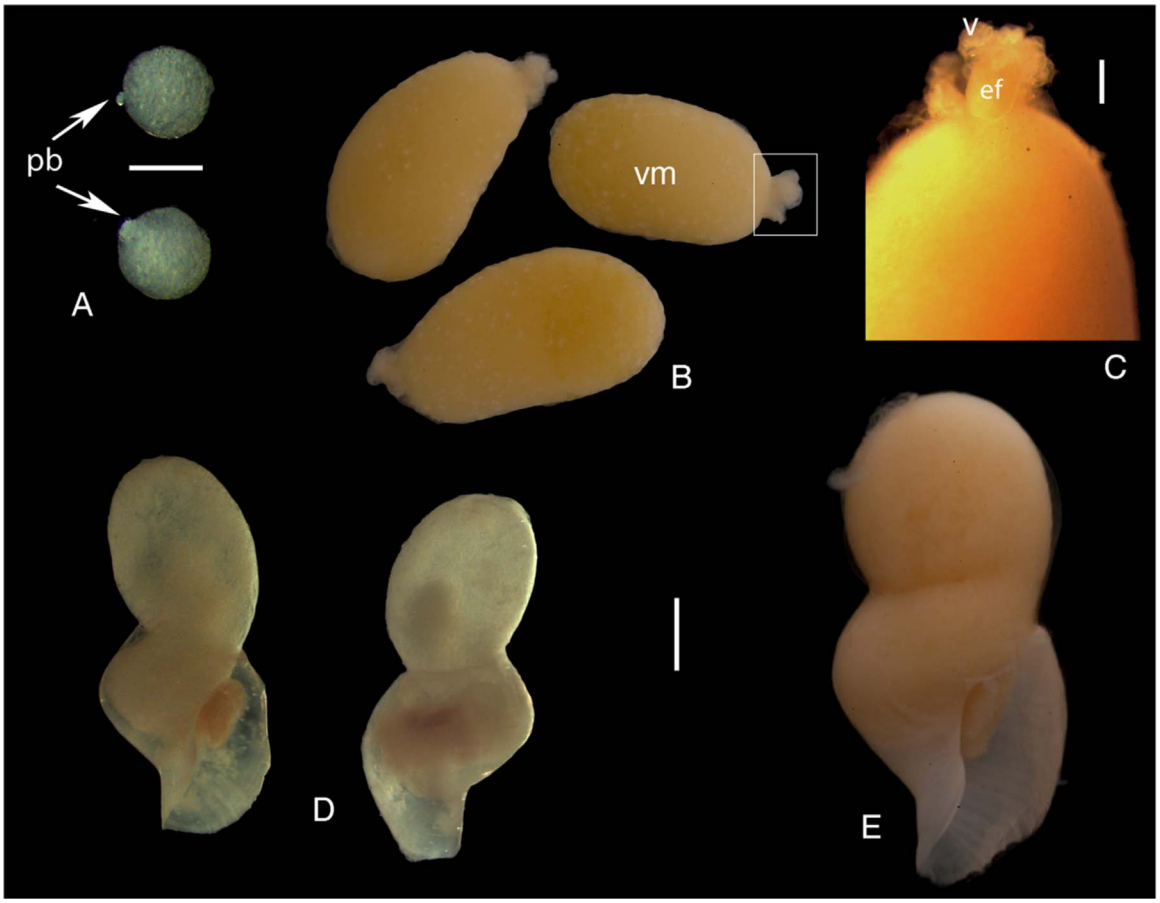

Fig. 7. *Provocator corderoi´s* developmental stages: **A**- uncleaved eggs with polar bodies; **B**- late embryo without shell; **C**- detail of late embryo without shell, area in the square of figure **B**; **D**- coiled shell embryo; **E**- pre-hatching juveniles. Scale bars **A** 200 μm; **B, D-E** 1 mm; **C** 250 μm. *ef* early foot, *pb* polar bodies, *v* velum, *vm* visceral mass.

another example in which this particular calcareous layer protecting the egg capsules can be observed (Graham, 1942; Ponder, 1970). The egg capsules containing ready-to-hatch embryos were found partially or almost completely free from the calcareous layer as it was observed in *O. magellanica* (Bigatti et al., 2014).

Very few studies recorded *Provocator corderoi* after the original description by Carcelles in 1947. Despite this fact, it becomes a common representative of this family between 200 and 1000 m depth, reaching records of up to 1400 m. Adult snails of this species are easily recognized because they are the only ones among the species of Volutidae of the southwestern Atlantic Ocean showing a bright white, very thin shell with spiral ornamentation consisting of subtle wavy threads throughout the whole shell (Fig. 5A-B). Arnaud and Van Mol (1979) described the capsules of *P. pulcher* (from 3 samples), the only congeneric species endemic from Kerguelen and Crozet Island in the Subantarctic Indian Ocean (~ 48°S, at 200–360 m depth). They were 17–18 mm in diameter, almost hemispherical, with 4 embryos per capsule. The egg capsules of *P. corderoi* are similar in shape, size and general features to those described for *P. pulcher*.

Arnaud (1978) examined the egg capsules of *Harpovoluta charcoti*, another typical volute species from subantarctic waters. He mentioned some similarities with those of *Adelomelon ancilla*, wrongly identified and described as *O. magellanica* by Dall (1890). The egg capsules of *H. charcoti* studied by Arnaud (1978) (26 × 29 mm in diameter and 10–12 mm in height) doubled the size of those from *P. corderoi*, despite the similar size of the adults (57 mm according to Arnaud, 1978). Although Hain (1990, 1992) reported one egg capsule of *H. charcoti* of about 12 mm and another of 16 mm diameter supporting the similarity between the egg capsules of the genera *Provocator* and *Harpovoluta,* both belonging to subfamily Zidoninae.

Neither Arnaud (1978) nor Hain (1990) mentioned the presence of a curved semilunar line at both sides of the capsules of *H. charcoti*, described in this study for *P. corderoi* and also observed in *O. magellanica* (Bigatti et al., 2014). This curved semilunar line, suture line, or seam (according to Rawlings, 1999) was observed in other species belonging to the family Volutidae. For example, in the subfamily Volutinae i.e. *Voluta musica* (Penchaszadeh and Miloslavich, 2001) and *V. ebraea* (Matthews-Cascon et al., 2010), and in the subfamily Zidoninae i.e. *A. ferussacii* (Penchaszadeh and Segade, 2009) and *A. ancilla* (Zabala et al., 2015). All these species showed a similar structure in the capsule wall. In *P. corderoi*, this structure was always closed in the collected material; therefore, its role in the embryos hatching is still to be determined.

4.2. Embryos

The stages of development found in *O. pescalia* (late veliger stages with ball-shaped embryos) were similar to those found in *O. magellanica* and highly different from those of the rest of the known Volutidae species. The number of embryos per egg capsule in *O. pescalia* was lower than that recorded for *O. magellanica* [3–5 embryos, 3.6 ± 0.89 (mean ± SD) vs. 4–18 embryos, 9.6 ± 0.4 (mean ± SD)] (Bigatti et al., 2014). No opercula were present in any stage of development of *O. pescalia* or *O. magellanica*. Ponder (1970) mentioned the presence of opercula in 5 mm hatching juveniles of *A. arabica*, a character that lack in adults.

The intracapsular fluid of recently laid capsules of *O. pescalia* showed uncleaved eggs or early embryos glued into a white sticky content from which they could only be separated laboriously in fixed material. This white content constitutes the supplementary food resource for the embryos, which can develops from a 192 μm egg

diameter to a juvenile of 10.4 mm of shell length. Supplementary food as albumen, amino acids and carbohydrates contained in the intracapsular fluid enable volute embryos from southwestern Atlantic to grow and hatch as crawling juveniles with shell sizes between 4.2 and 18.6 mm (de Mahieu et al., 1974; Penchaszadeh and Miloslavich, 2001; Bigatti et al., 2010), as in other Neogastropoda (Miloslavich, 1996; Miloslavich, 1999; Penchaszadeh and Rincon, 1996). At the pediveliger stage, only a translucent fluid remained, as was observed in other southwestern Atlantic Volutidae (Bigatti et al., 2014).

The number of embryos per egg capsule in *P. corderoi* was similar to that recorded for *P. pulcher* (2–6 vs. 2–4) and *H. charcoti* (3–5) (Arnaud, 1978; Arnaud and Van Mol, 1979; Hain, 1992). According to Dell (1990), the protoconch of *Harpovoluta charcoti*, only seen in the embryos, is of the "scaphelloid" type (Finlay, 1931). The same feature can be seen in the embryos of *Provocator corderoi*.

The presence of a heavily calcified egg capsule external wall and a late veliger stage with ball-shaped embryos, in which the visceral mass had grown much larger than the cephalopodial structures and the velum was incipient is known in two species of the subfamily Odontocymbiolinae, i.e. *O. magellanica* and *O. pescalia*, (Bigatti et al., 2010 and the present work). In Zidoninae (i.e. *Adelomelon*, *Zidona*, *Provocator*) the late veliger stage show a well-developed velum (e.g. 2.60 mm ± 0.14 in *Adelomelon ancilla*, Zabala et al., 2015). The stage of intracapsular veliger was not found in the analyzed samples of *P. corderoi*. In the subfamily Volutinae, embryos at the late veliger stage had a large bilobed velum that were equal or larger than the visceral mass (e.g. > 8 mm in *V. musica* and ~ 5.7 mm in *V. ebraea*) (Penchaszadeh and Miloslavich, 2001; Matthews-Cascon et al., 2010). The studies of these two species (i.e. *O. pescalia* and *P. corderoi*) contribute to the knowledge of the reproductive modalities of the family Volutidae in the Southwestern Atlantic. In all currently known species, the spawn consists of a single egg capsule with a variable number (2–33) of small eggs (90–450 μm in diameter) and no nurse eggs (except for *Voluta virescens,* Bandel, 1976).

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