

Research paper

Giant eggs in the gastropod *Aforia obesa* (Conoidea: Cochlespiridae) in Southwestern Atlantic deep-waters



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ABSTRACT

Egg capsules and adults of *Aforia obesa* Pastorino and Sánchez, 2016 were collected at the Mar del Plata Submarine Canyon in the Argentine continental slope at 780–1398 m depth during 2012 and 2013. Egg capsules were iridescent white, dome-shaped, solitary with tough and thick walls. The capsule diameter was 8.5–12 mm. The uncleaved eggs with a diameter of 1.6–1.9 mm ($X = 1.8 \pm 0.1$ mm) confirm a previous report for the genus and are by far the largest eggs known within Conoidea and, as far as we know, the largest ever described among Caenogastropoda from the Southwestern Atlantic. Embryos undergo complete intracapsular development with no evidence of oophagy, adelphophagy, late cannibalism, or other supplementary food. Young emerge as crawling juveniles throughout an elliptic and transparent exit hole in the top center of the egg capsule.

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1. Introduction

The gastropod genus *Aforia* Dall, 1889 comprises about 22 living species distributed in most worldwide seas. The most recent revision of the genus was made by Sysoev & Kantor (1987) who reviewed the species from the Pacific Ocean. *Aforia* was originally described in the family Turridae. In a thorough revision, Bouchet et al. (2011) established a new taxonomic arrangement of the old Turridae splitting it into 13 families. Among them the family Cochlespiridae includes the genus *Aforia*. The reproductive biology of 22 species of members of these families, previously included in Turridae have been studied so far. Many have free larval stages, i.e. *Ophiodermella inermis*, *Comarmondia gracilis*, *Ptychobela nodulosa*, *Bela nebula*, *Sorgenfreispira brachystoma*, *Pyrgocythara plicosa*, *Oenopota elegans*, *Oenopota levidensis*, *Kurtziella plumbea*, *Raphitoma linearis*, *Phymorhynchus buccinoides* and *Polystira barretti*, while other species emerge as crawling juveniles, i.e. *Clavus japonicus*, *Curtitoma violacea*, *Propebela exarata*, *Propebela nobilis*, *Oenopota pyramidalis* and *Obesotoma simplex*. Nurse eggs or any other food supplement have not been reported during development of any of these species.

Pastorino & Sánchez (2016) recorded two living species of this genus in Southwestern Atlantic Ocean, i.e. *Aforia goniodes* and *Aforia obesa*. Both species and egg capsules were collected during several cruises to the Argentine continental slope rendering an interesting opportunity to describe and compare them with other members of this group. The only previous reference of the spawn of a Cochlespiridae (*Aforia magnifica*) is from the Weddell Sea (Hain 1992). Here we describe the egg capsules and the different stages of intracapsular development of *A. obesa*. This is the first study of the spawn of the Superfamily Conoidea from Southwestern Atlantic deep water.

2. Materials and methods

Adults of *A. obesa* and their egg capsules were collected at 6 of 64 stations during three cruises to Mar del Plata Submarine Canyon, Argentina during 2012 and 2013 on the Argentine R/V "Puerto Deseado" (Table 1). The samples were obtained with a bottom trawl net from 780 to 1398 m depth. Adults were preserved in 96% ethanol and egg capsules in a 4% formalin-seawater solution, and later transferred to 70% ethanol. The egg capsules, eggs, embryos and juveniles were measured using a calibrated ocular micrometer. Radulae of embryos were obtained by dissolving the whole specimen in commercial bleach (sodium hypochlorite) and then coating

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Table 1Stations where adults and egg capsules of *Aforia obesa* Pastorino & Sánchez, 2016 were collected, SH: shell; SP: complete specimen.

Station	Latitude S	Longitude W	Depth (m)	Date	Gear	# Egg capsules	# Adult
10	37° 59.706'	54° 41.854'	852	11-Aug-12	Trawl	1	1 SH, 1 SP
14	38° 0.984'	54° 30.326'	1006	11-Aug-12	Trawl	11	10 SH, 6 SP
41	38° 01.631'	54° 30.275'	997	26-May-13	Trawl	2	4 SH, 3 SP
43	37° 53.837'	54° 30.458'	998	26-May-13	Trawl	2	3 SP
44	37° 53.557'	54° 42.941'	780	26-May-13	Trawl	2	2 SH, 1 SP
59	37° 49.688'	54° 5.236'	1398	10-Sept-13	Trawl	1	2 SH

the remaining radulae with gold-palladium. The radulae were then examined with a Philips XL30 scanning electron microscope (SEM) at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN). The different embryo stages and the egg capsules were dehydrated in graded ethanol series, critical point dried and observed using SEM. The egg capsules, eggs and embryos were photographed using a Nikon D100 camera with a 60 mm Micro Nikkor lens.

In order to produce a comparative scheme of the current knowledge of reproductive features in Conoideans once included in the old concept of Turridae, the information available was arranged in Table 2. All names were changed according to the current nomenclature (WoRMS 2018); however, in every case the name of the species used in the original source was also kept.

3. Results

3.1. Egg capsules

The egg capsules were iridescent white, dome-shaped, solitary and attached to the substratum (usually solitary scleractinians of

the genus *Flabellum*) by a flat base (Fig. 1). The walls were tough, smooth and thick (~0.74 mm) (Fig. 2A and B). The convex surface was covered by a thin and transparent membrane. Under SEM, hair-like fibers were seen to cover the entire surface (Fig. 2D and E). A suture that usually divided the capsule into two unequal parts is always visible (Figs. 1 and 2A). An elliptical, translucent preformed plug of 2.1–3.5 mm ($X = 3.1 \pm 0.2$ mm, $N = 16$) by 1.9–2.8 mm ($X = 2 \pm 0.1$ mm) was also clearly visible (Fig. 2A and D). The egg capsules measured 8.5–12 mm ($X = 10.3 \pm 0.9$ mm, $N = 18$) in diameter and 3.3–7 mm ($X = 6 \pm 0.6$ mm) in height.

3.2. Developmental stages

Each egg capsule contained 8 uncleaved bright yellow-orange eggs with a diameter of 1.6–1.9 mm ($X = 1.8 \pm 0.1$ mm) ($N = 2$) (Figs. 3A and 4A). The number of cleaved eggs per capsule varied from 6 to 8 with a diameter of 1.7–2.1 mm ($X = 1.8 \pm 0.1$ mm) ($N = 2$), corresponding to early cell divisions (Figs. 3B and 4B). Embryos developed synchronously within each egg capsule and no velum was observed. Embryos in early stages of development (Fig. 3C) with a diameter of 2.0–2.3 mm ($X = 2.2 \pm 0.1$ mm) were found in four egg

Table 2

Developmental features in the Conoideans included in the old concept of Turridae.

Species original names	Currently accepted names	Egg capsule size (mm)	Egg size (μ m)	Eggs per capsule	Embryos per capsule	Nurse eggs	Developmental stage at hatching	Family	Source
<i>Ophiidermella inermis</i>		4.7 \pm 1.0	222 \pm 15	208 \pm 61		No	“Veliger”	Borsoniidae	Shimek (1983a)
<i>Philbertia gracilis</i>	<i>Comarmondia gracilis</i>	3.4	160	40–80			“Larvae”	Clathurellidae	Lebour (1934, 1937)
<i>Aforia magnifica</i>		20	1700–1800	20–30				Cochlespiridae	Hain (1990, 1992)
<i>Aforia obesa</i>		8.5–12.0	1640–1920	6–8		No	“Crawling”	Cochlespiridae	This paper
<i>Clavus japonicus</i>		2.5	650	2–4		No	“Creeping stage”	Drilliidae	Amio (1963)
<i>Drillia crenularis</i>	<i>Ptychobela nodulosa</i>	6.0–7.0	230–300	150–170		No	“Pelagic stage”	Drilliidae	Thorson (1940)
<i>Bela nebula</i>	<i>Mangelia nebula</i>	1.6	160	60			“Larvae”	Mangeliidae	Thorson (1935)
<i>Bela bicarinata</i>	<i>Curtitoma violacea</i>	2.2–3.2			3–11		“Direct development”	Mangeliidae	Thorson (1935)
<i>Kurtziella plumbea</i>		2.3 \pm 0.3	137 \pm 8	180 \pm 43		No	“Veliger”	Mangeliidae	Shimek (1983c)
<i>Oenopota elegans</i>		3.02	150	250		No	“Veliger”	Mangeliidae	Shimek (1983b)
<i>Oenopota excurvata</i>		2.1	212 \pm 1	30				Mangeliidae	Shimek (1983b)
<i>Oenopota levidensis</i>		5.3 \pm 1.4	286 \pm 61	175 \pm 85		No	“Veliger”	Mangeliidae	Shimek (1983b, 1986)
<i>Bela pyramidalis</i>	<i>Oenopota pyramidalis</i>	3.5–6.0			4–20		“Direct development”	Mangeliidae	Thorson (1935)
<i>Bela exarata</i>	<i>Propebela exarata</i>	3.0–4.5			5–21		“Direct development”	Mangeliidae	Thorson (1935)
<i>Oenopota fidicula</i>	<i>Propebela fidicula</i>	2.2 \pm 0.3	371 \pm 10	20 \pm 1				Mangeliidae	Shimek (1983b)
<i>Bela nobilis</i>	<i>Propebela nobilis</i>				4.5–4.7		“Direct development”	Mangeliidae	Thorson (1935)
<i>Mangelia plicosa</i>	<i>Pyrgocythara plicosa</i>	30.1–33.0	160	60			“Larvae”	Mangeliidae	Perry & Schwengel (1955)
<i>Mangelia brachystoma</i>	<i>Sorgenfreispira brachystoma</i>	1.6	160	60			“Larvae”	Mangeliidae	Thorson (1946)
<i>Philbertia linearis</i>	<i>Raphitoma linearis</i>	1.5–2.0	140–150	60–80			“Larvae”	Raphitomidae	Lebour (1934, 1937)
<i>Phymorrincus buccinoides</i>		5.3–10.8	160–230	1098		No	“Veliger”	Raphitomidae	Watanabe et al. (2009)
<i>Bela simplex</i>	<i>Obesotoma simplex</i>	2–3			2–7 (5–6 usually)		“Direct development”	Turridae	Thorson (1935)
<i>Polystira barretti</i>		5.0–10.7	438	32–126			“Veliger”	Turridae	Penchaszadeh (1982)



Fig. 1. Egg capsules of *Aforia obesa* Pastorino & Sánchez, 2016 on *Flabellum* sp. Scale bar = 1 cm.

capsules (3–8 embryos per capsule). They were characterized by the presence of a visible foot. A second embryonic stage (3–8 embryos per capsule) with a diameter of 2.2–2.6 mm ($X = 2.4 \pm 0.1$ mm) was observed in two egg capsules, showing a small foot and a barely visible trace of thin and translucent shell (Figs. 3D and 4C) that would be more evident in the next stage. Three egg capsules presented 7–8 embryos each in late stage of development (third stage) with a diameter of 1.2–2.4 mm ($X = 1.9 \pm 0.4$ mm) (Fig. 3E). They were

characterized as embryo in torsion with a still not calcified organic matrix, translucent shell. Pre-hatching juveniles (Fig. 3F) with a length of 2.6–3.9 mm ($X = 3.2 \pm 0.4$ mm) were found in 6 egg capsules (from 4 to 10 per capsule); operculum, foot, eyes, cephalic tentacles and calcified shell were already developed. During the whole development, no nurse eggs, remains of free yolk, or any type of supplementary food were observed within the egg capsules.

3.3. Identity of egg capsules

Juveniles found in the egg capsules presented the same protoconch features of those described in the adult shells (Fig. 5D), including the characteristic “wrinkles” in the first whorl and the typical “turrid” notch in the aperture (Fig. 5A–C). In addition, radular characters in the juveniles as weak denticles at both sides of the central cusp in the rachidian tooth described for the adults of *A. obesa* by Pastorino & Sánchez (2016) (Fig. 5E and F), allowed identification. The presence of radula in juveniles inside de capsule suggests that the embryo has already functional digestive apparatus, although it is not conclusive about the presence of the venom gland. The radula of the embryo as far as we can see 5 rows of rachidian teeth while the adult dissected showed at least 14.

4. Discussion

Among the different ways for direct encapsulated development in caenogastropods, the most common ones are: oophagy, adelphophagy (nurse eggs), late cannibalism or, intracapsular white as supplementary food for the embryo. In all these cases, hatchlings are crawling juveniles. Few species producing large eggs containing

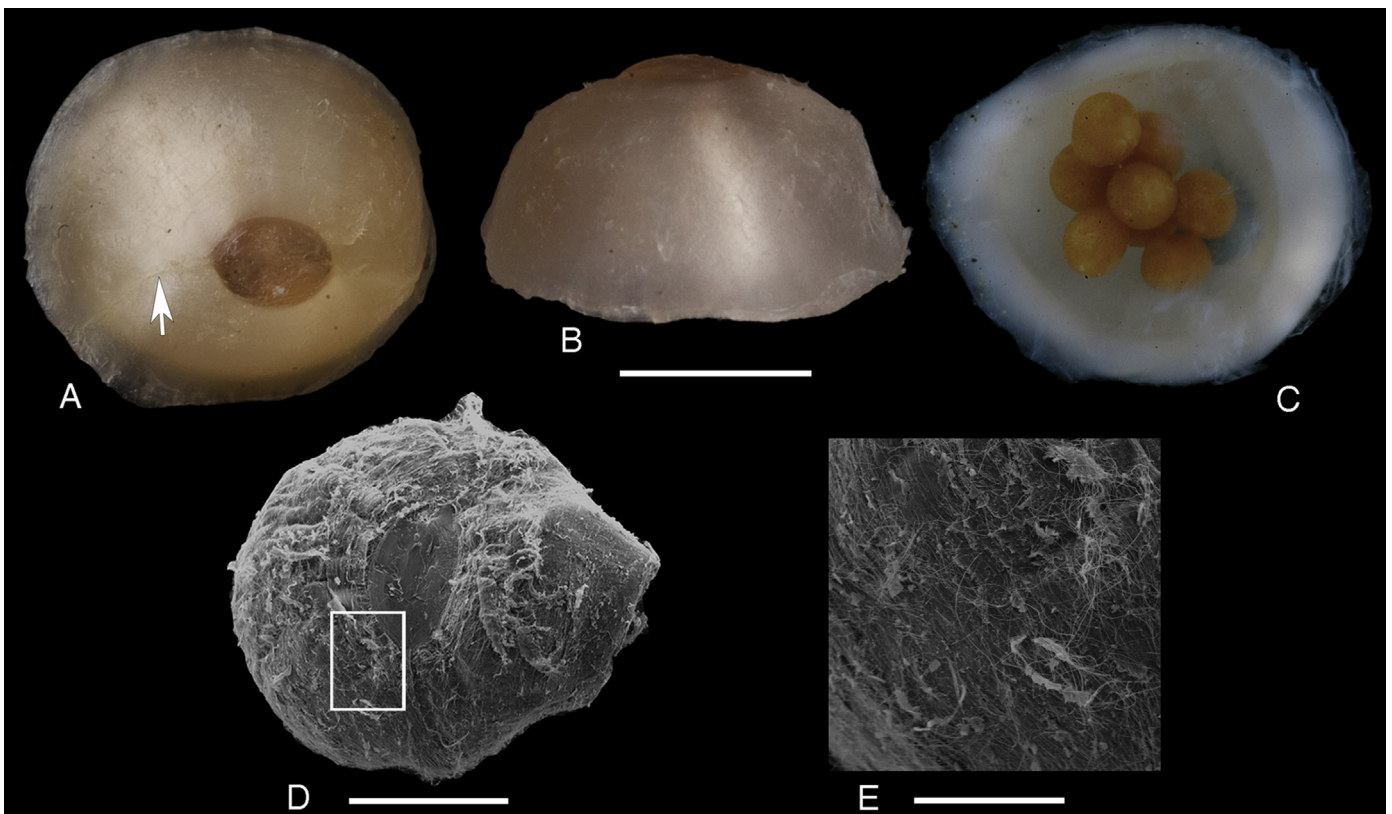


Fig. 2. Egg capsules of *Aforia obesa* Pastorino & Sánchez, 2016. (A) Dorsal view, arrow head suture (B) lateral view and (C) ventral view with eggs. (D) SEM photograph of critical point dried egg capsule and (E) detail of surface. Scale bars: (A–C) = 5 mm; (D) = 3 mm; (E) = 1 mm.

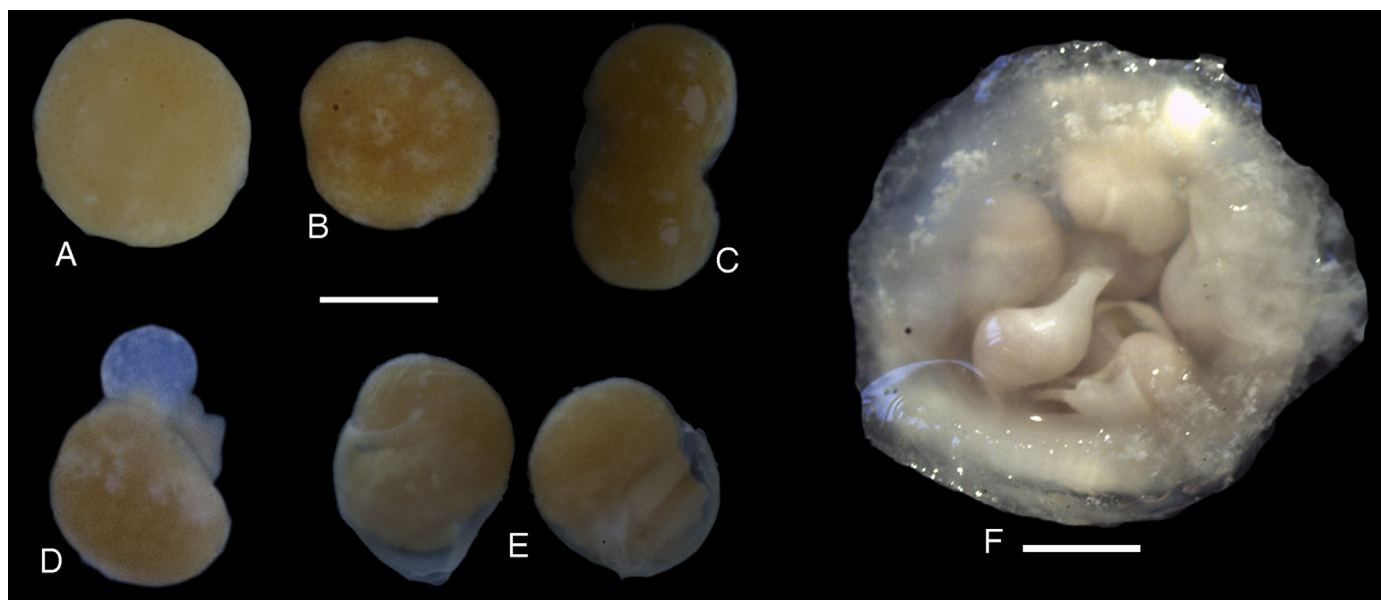


Fig. 3. Developmental stages of *Aforia obesa* Pastorino & Sánchez, 2016. (A) Uncleaved egg. (B) Cleaved egg. (C) Embryo in early stage of development. (D) Second embryonic stage. (E) Two views of embryo in late stage of development and (F) Egg capsule with pre-hatching juveniles, ventral view. Scale bars: (A–E) = 1 mm; (F) = 2 mm.

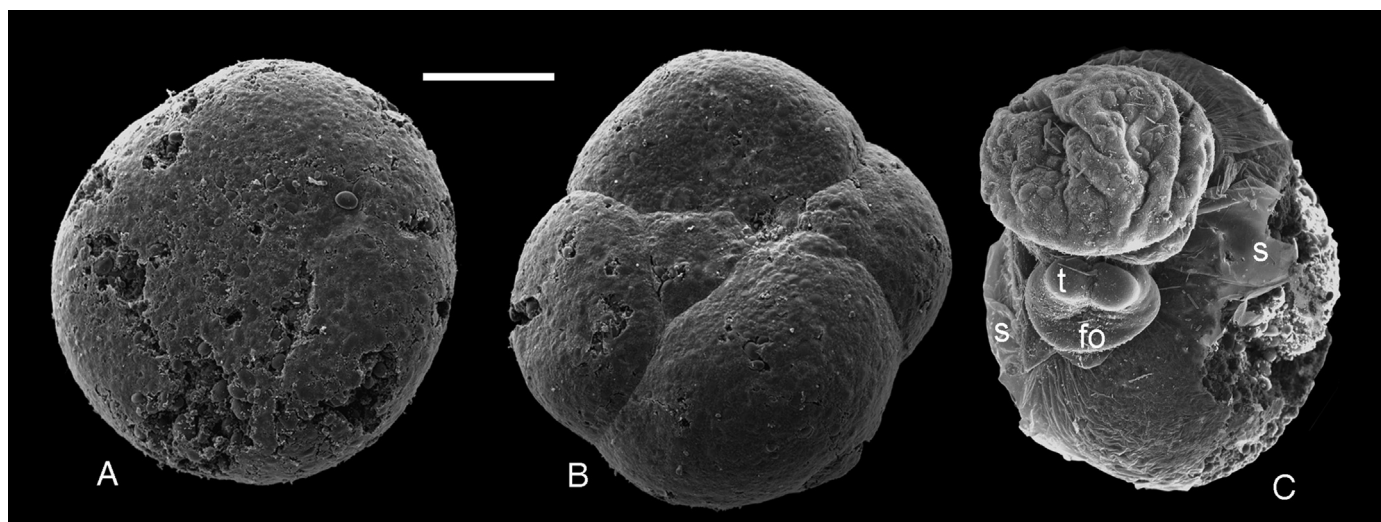


Fig. 4. SEM photographs of critical point dried developmental stages of *Aforia obesa* Pastorino & Sánchez, 2016. (A) Uncleaved egg. (B) Cleaved egg and (C) Second embryonic stage with traces of shell. Abbreviations: fo foot; s shell traces; t tentacles. Scale bar: (A–C) = 400 μm .

considerable amount of yolk have been reported. Penchaszadeh & Rincón (1966) reported the egg size of the marginellid *Prunum prunum* (895–1075 μm diameter) and Cipriani & Penchaszadeh (1993) those of the columbellids *Strombina francesae* (571 \pm 35 μm) and *S. pumilio* (616 \pm 48 μm).

Most Conoidea species registered small uncleaved egg diameters (~100–286 μm). *C. japonicus* (Drillidae) has an uncleaved egg size with 650 μm , while in *P. barretti* (Turridae) uncleaved eggs measured 438 μm . The family Conidae is probably the largest family in the superfamily Conoidea with a reasonably knowledge of development. It includes many species with large eggs up to 1 mm diameter, *Conus pennaceus* of 460 μm (Kohn 1961a, b), *C. spurius* of 690 μm (Penchaszadeh 1984), *C. achatinus* of 854 μm (Kohn & Perron 1994) and one series of endemic species from Cape Verde (Duda & Rolán 2005). Although about of 75% of the species of Conidae develop obligate planktonic larval stage (Kohn

& Perron 1994), all species of the so call “species flock” of *Conus* from Cape Verde Archipelago have direct development (Duda & Rolán 2005).

A. obesa, with an uncleaved egg of 1640–1920 μm are by far the largest uncleaved eggs known within Conoidea and, as far as we know, the largest ever recorded in Caenogastropoda. This confirms a previous report of eggs of 1.7–1.8 mm diameter for the genus by Hain (1992) and Hain & Arnaud (1992).

According to the available data most of the species belonging to superfamily Conoidea have free swimming larvae (Lebour 1934, 1937; Thorson 1940, 1946; Perry & Schwengel 1955; Penchaszadeh 1982; Shimek 1983a, b, c, 1986; Watanabe et al. 2009). Thorson (1935), Amio (1963) and Hain (1992) reported the only cases of crawling juveniles. The species *C. japonicus* has several features closely related to *A. obesa*, such as a very large egg size, few eggs per egg capsule (2–4), and no nurse eggs (Amio 1963).

The only previous citation of the spawn of a member of the family Cochlespiridae is reported by Hain (1990) who illustrated an egg capsule of *A. magnifica* from shelf area of Weddell Sea. Later, in a table (1992, Table 1) the same author mentioned diameters of 20 mm for the egg capsule and 20–30 eggs of 1700–1800 µm of diameter from material spawned in aquarium of the same species. Hain provided no description of the egg capsule, but an illustration (Fig. 8C, p. 135, 1990). According to this the shape of the capsule is very different from the egg capsules of *A. obesa* described here. It is not dome shaped, no exit hole is visible, and have a thin, apparently flexible stalk. Neither has he described the intracapsular development or the presence of any type of supplementary food. All these reproductive characteristics, lead us to think that *A. magnifica* could be assigned to a different genus.

Differences in the growth of the velum are present in the intracapsular development of many caenogastropods that hatch as crawling juveniles, e.g. *Pleuroploca audouini* (as *Fasciolaria audouini* in Gohar & Esawy 1967), *Fusinus ansatus* (as *Fusinus closter* in Miloslavich & Penchaszadeh 1997), *Hexaplex (Trunculariopsis) trunculus* (Vasconcelos et al. 2004), *Voluta musica* (Pencaszadeh &

Miloslavich 2001) and *Odontocymbiola magellanica* (Bigatti et al. 2014), among others. We did not record any trace of velum in any of the intracapsular stages observed in *A. obesa* a character that is truly different from *C. japonicus* that develops a conspicuous velum, resorbed prior to hatch as a crawling juvenile. Embryos of *A. obesa* grew only consuming the yolk provided by the original eggs. This is a remarkable difference compared to some of the previously mentioned species, which feed on nutritive eggs (e.g. *P. audouini*, *F. ansatus* and *Hexaplex trunculus*) or, have proteins in the intracapsular fluid as extra-embryonic food (e.g. *V. musica* and *O. magellanica*).

The presence of an almost complete series of intracapsular stages collected in the same stations at the same dates could give support for a year-round breeding for *A. obesa*. This is probably correlated with the fact that the deep sea is frequently considered a constant environment, presenting almost no seasonal variation (Tyler & Young 1992) where embryonic development rates are among the slowest of all animal life, and its generally include direct development without a larval stage (Robison et al. 2014).

The genus *Aforia* has significant morphological and reproductive characteristics that make it distinctive among all conoideans. This is

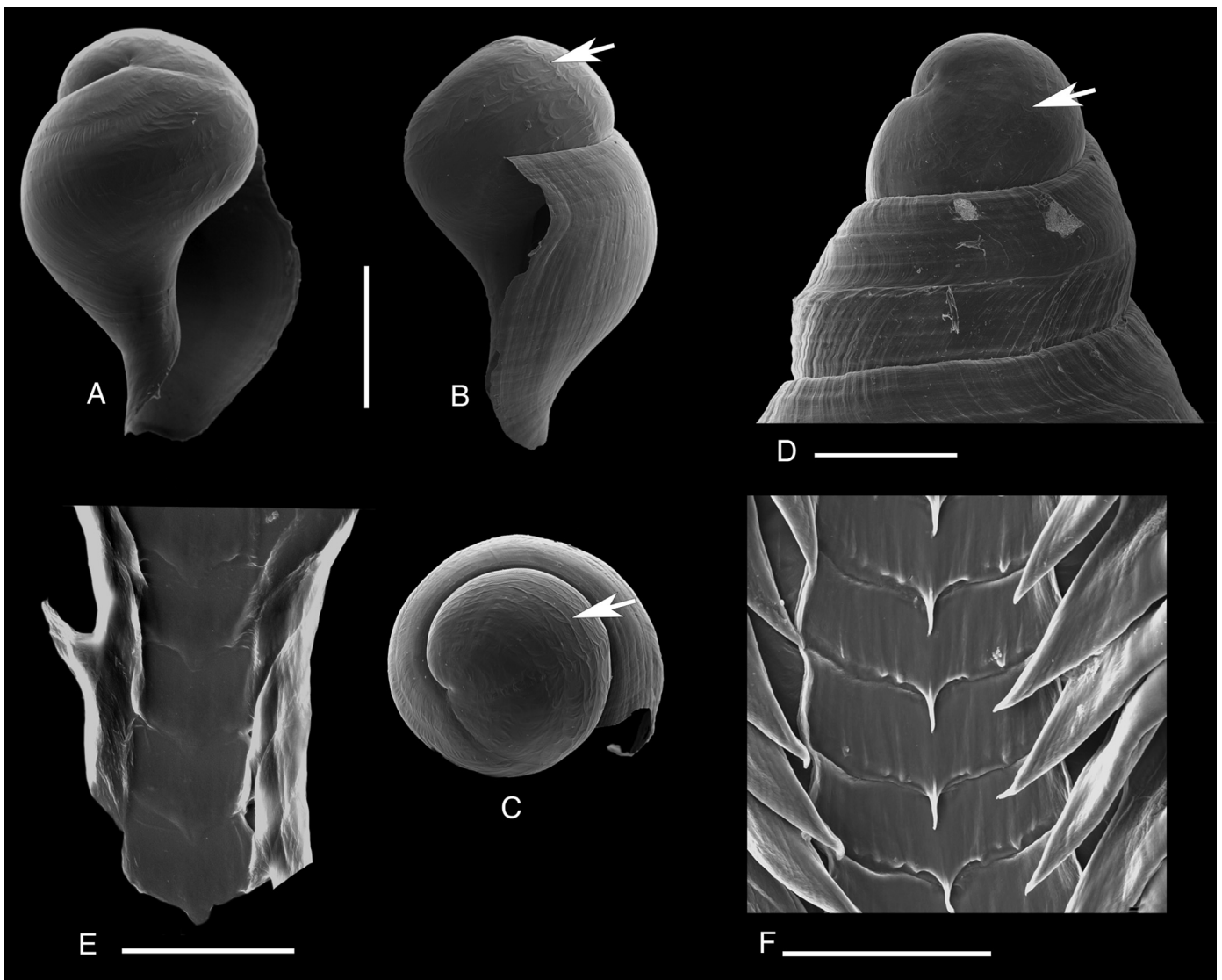


Fig. 5. SEM photographs of *Aforia obesa* Pastorino & Sánchez, 2016. (A–B) Pre-hatching juvenile, (A) apertural, (B) lateral view and (C) apical view. (D) Detail of protoconch of juvenile, MACN-In 40479, arrows in B, C and D head characteristic “wrinkles” on shell surface. (E) Radula of pre-hatching juvenile of similar size of figure A and B. (F) Radula of adult. Scale bars: (A–D) = 1 mm; (E) = 50 µm; (F) = 100 µm.

supported in part by the phylogeny proposed by Puillandre et al. (2011) where Cochlespiridae constitutes a single clade that is the sister group of a larger one where Drilliidae (*Clavus*) and Turridae (*Polystira*) among others are included. The knowledge of the reproductive way of the different families of Conoideans included in the old concept of Turridae could be of help when searching for relationships among them.

Compliance with ethical standards

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Conflict of Interest: Noelia Sánchez declares that she has no conflict of interest. Guido Pastorino declares that he has no conflict of interest. Pablo E. Penchaszadeh declares that he has no conflict of interest.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Ethical approval: This article does not contain any studies with human participants performed by any of the authors.

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