Polar Biology (2019) 42:807–816
https://doi.org/10.1007/s00300-019-02477-5

ORIGINAL PAPER

Reproduction and developmental stages in the crinoid *Isometra vivipara* Mortensen, 1917 from the southwestern Atlantic

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Received: 5 July 2018 / Revised: 7 January 2019 / Accepted: 25 February 2019 / Published online: 7 March 2019

Abstract

Isometra vivipara Mortensen, 1917, which was described one hundred years ago, represents a particular case within the feather stars of the southwestern Atlantic Ocean. This is a dioecious species in which the oocytes are fertilized in the ovary and not externally as in other species. Some authors have pointed out that *I. vivipara* stores spermatozoa in the genital pinnules of the female, although there is still no detailed data on how they reach the pinnule. Besides, this species is characterized by possessing a second sexually dimorphic trait and presents two incubation stages: one in the genital pinnules, and the second one attached in the cirri of the mother. In the present work, the reproduction and developmental stages of the *I. vivipara* were studied. Samples were taken from two cruises aboard the B/O "Puerto Deseado" to Burdwood Bank/MPA Namuncurá at 84–642 m depth, during March/April 2016 and April/May 2017. Four developmental stages were recognized: Embryo, Doliolaria larvae (inside the brood pouches), Cystidean, and Pentacrinoids (attached in the cirri of the mother). In addition, histological analysis showed that fertilization in *I. vivipara* could occur between the ovary and the marsupium. The egg measurements reached 0.35 mm in diameter—on of the largest egg size within South America and Antarctica comatulids—whereas for the larvae the largest registered diameter was 0.77 mm. These results are compared and discussed with all the available information of comatulids from South America and Antarctica.

Keywords Echinodermata · Crinoidea · Southern Ocean · Marsupium · Brooding · Burdwood Bank/MPA Namuncurá

Introduction

There are several reproductive studies on asteroids, ophiuroids, echinoids, and holothuroids from the Southern Ocean (Gil et al. 2009, 2011; Brogger et al. 2010, 2013; Martinez et al. 2011; Berecoechea et al. 2017; Martinez and Penchaszadeh 2017; Rivadeneira et al. 2017), but little is known about crinoids (McClintock and Pearse 1987; Holland 1991; Haig and Rouse 2008; Haig et al. 2012). As a general characteristic, crinoids possess pinnules on each side of the arms giving to the animal a jointed appearance. These pinnules are differentiated along the arms into three types: the proximal or oral pinnules, the genital pinnules, and the distal pinnules. Genital pinnules, which are distributed in the middle area of the arms, contain the gonads (Hyman 1955; Hendler et al.1995).

Almost all non-brooding species of crinoids spawn ova that are fertilized externally (Holland 1976). Within the comatulids (feather stars), there are two brooding modes, one external and another internal that usually occurs inside marsupium (Holland 1976; Messing 1984). A unique case within crinoids is the comatulid *Isometra vivipara* Mortensen, 1917, a dioecious species in which the oocytes are fertilized in the ovary and not externally. Some authors have pointed out that this species stores spermatozoa in the genital pinnules of the female (Andersson 1904; Mortensen 1920), although there are still no precise data on how they reach the pinnule (Holland 1976). In addition, *I. vivipara* presents two stages of incubation: the embryos (in the marsupium) and the cystideans (attached in the cirri of the mother).

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Isometra vivipara is distributed from southern Brazil (33°S) to the Southern Ocean (64°S), between 75 and 340 m depth (Mortensen 1920; Clark and Clark 1967). In order to study the reproduction and development of *I. vivipara,* we used optical modern techniques such as stereomicroscopy, light, and scanning electron microscopy. Additionally, egg and larval size were compared within Subantarctic and Antarctic comatulids. This is the first detailed study on the reproduction of Crinoidea for the Southwest Atlantic and broadens the knowledge of a typical South American species.

Materials and methods

Samples were collected using a dredge trawl or fishing nets during two cruises on board the B/O "Puerto Deseado" to Burdwood Bank/MPA Namuncurá at 91–642 m depth in March/April 2016 (BB-2016) and April/May 2017 (BB-2017) (Fig. 1). Specimens were analyzed and deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In). In addition, specimens previously deposited in the MACN-In were studied (Table 1).

A total of 22 genital pinnules from five females and 21 genital pinnules from six males were separated for histological examinations. Afterward, they were decalcified for 60–90 min using a non-diluted solution of Histodecal Extra® Leica. They were then embedded in plastic resin (Historesin® Leica) and sectioned at 5–6 µm with a RM2155 Leica microtome. They were stained with eosin and hematoxylin. Gonad sections were examined with a Zeiss Axio Imager Z1 microscope and photographed using an Axiocam HRc digital camera.

In addition, six genital pinnules of males and females were dissected longitudinally and transversely, with a razor blade to expose the gonads. These pinnules were critical point dried, coated with 60% gold 40% palladium, and mounted on a stub for observation with a scanning electron microscope (SEM). Images were taken using an XL30 Phillips microscope at the MACN.

For the identification of the different stages of embryonic development, 17 genital pinnules of sexually mature females were dissected under a stereoscopic microscope. The oocytes in the ovary, as well as the embryos and doliolaria larvae in the pouch, were then counted. Photographs were taken with an IC80 LEICA and an Axiocam HRc digital camera. The different embryonic stages were dehydrated in graduated series of ethanol, critical point dried, and then observed under a SEM.

The maximum full-grown oocyte (in diameter) size of *Isometra vivipara* was recorded and compared with bibliographic data of Subantarctic and Antarctic comatulid egg sizes. Finally, egg volumes $\left(43\pi R^3\right)$ were calculated.

Results

Ecology and morphology of adults

A total of 210 specimens of *Isometra vivipara* were collected between 82–642 m depth, with samples from 91 to 263 m, and from 483 to 642 m (Table 1). Samples were collected between 6 and 9 °C and in the stations where more specimens were found the registered temperature was

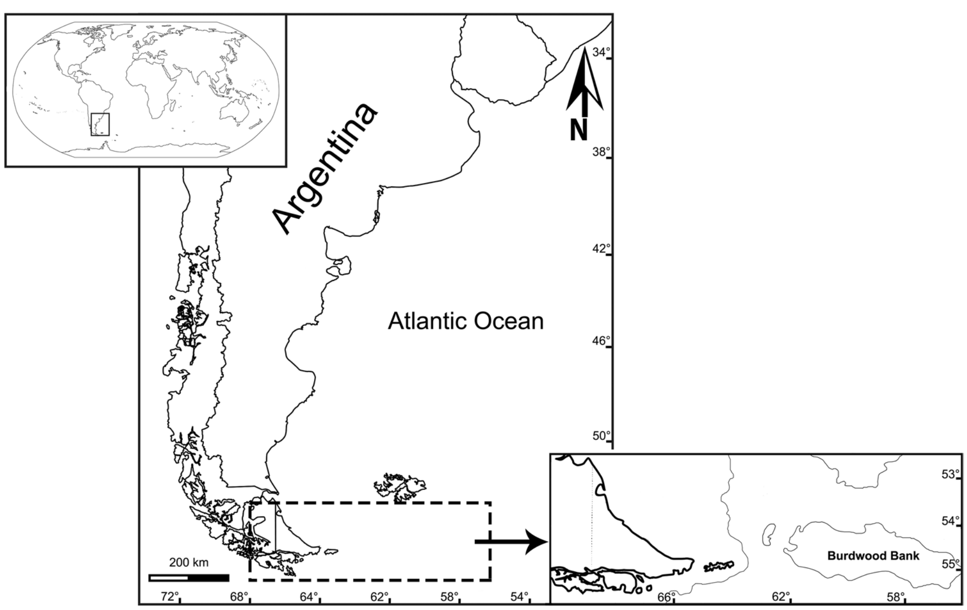

Fig. 1 Map showing the location of the collected samples

Table 1 Specimens examined from the Museo Argentino de Ciencias Naturales (MACN)

Cat. no.	St. code	Latitude (S)	Longitude (W)	Number of specimens	Depth (m)
MACN-In 22821	–	54°50′	64°01′	1	151
MACN-In 22822	–	54°57′	64°42′	12	265
MACN-In 42367	BB2016 E26L27	54°25′	58°31′	27	137
MACN-In 42368	BB2016 E39L140	54°51′	60°0′	25	159
MACN-In 42369	BB2016 E32L77	54°32′	60°1,2′	3	98
MACN-In 42370	BB2016 E27L11	54°10′	58°16′	2	100
MACN-In 42371	BB2016 E27L12	54°11′	58°19′	1	95
MACN-In 42372	BB2016 E31L197	54°30′	59°52′	8	109
MACN-In 42373	BB2016 E17L282	54°37′	61°9′	4	202
MACN-In 42374	BB2016 E28L52	54°28′	59°13′	4	128
MACN-In 42375	BB2016 E35L89	54°32′	61°26′	20	125
MACN-In 42376	BB2016 E38L38	54°35′	58°38′	1	140
MACN-In 42377	BB2016 E13L172	54°36′	62°51′	3	608
MACN-In 42378	BB2016 E26L24	54°24′	58°28′	8	95
MACN-In 42379	BB2017 E5L9	55°6′	65°44′	9	263
MACN-In 42380	BB2017 E9L50	54°52′	64°16′	36	151
MACN-In 42381	BB2017 E10L349	54°39′	63°49′	2	143
MACN-In 42382	BB2017 E14L118	54°24′	62°49′	4	483
MACN-In 42383	BB2017 E21L157	54°26′	58°32′	13	138
MACN-In 42384	BB2017 E23L173	54°26′	59°30′	6	91
MACN-In 42385	BB2017 E31L269	53°40′	61°38′	3	642
MACN-In 42386	BB2017 E35L236	53°34′	63°58′	2	263
MACN-In 42387	BB2017 E34L249	53°34′	62°58′	2	516
MACN-In 42388	BB2017 E30L273	53°49′	61°28′	4	209
MACN-In 42389	BB2017 E29L283	53°49′	61°19′	8	197
MACN-In 42390	BB2017 E10L349	54°39′	63°49′	2	143

Fig. 2 Images under stereoscopic microscope. **a** Female of *Isometra vivipara*, collection material MACN-In 22822; **b** *I. vivipara* incubating young (cystideans and pentacrinoids) in its cirrus; **c** oral view of female genital pinnules, with marsupium (ma) and embryos (em); **d** aboral view of female genital pinnules, third and fourth segments widened (sg); **e** dorsal view of male genital pinnule; **f** Lateral view of male genital pinnules, gradual widening of the segments (sg). Scale bars **a**, **b** 5 mm; **c**–**f** 2 mm

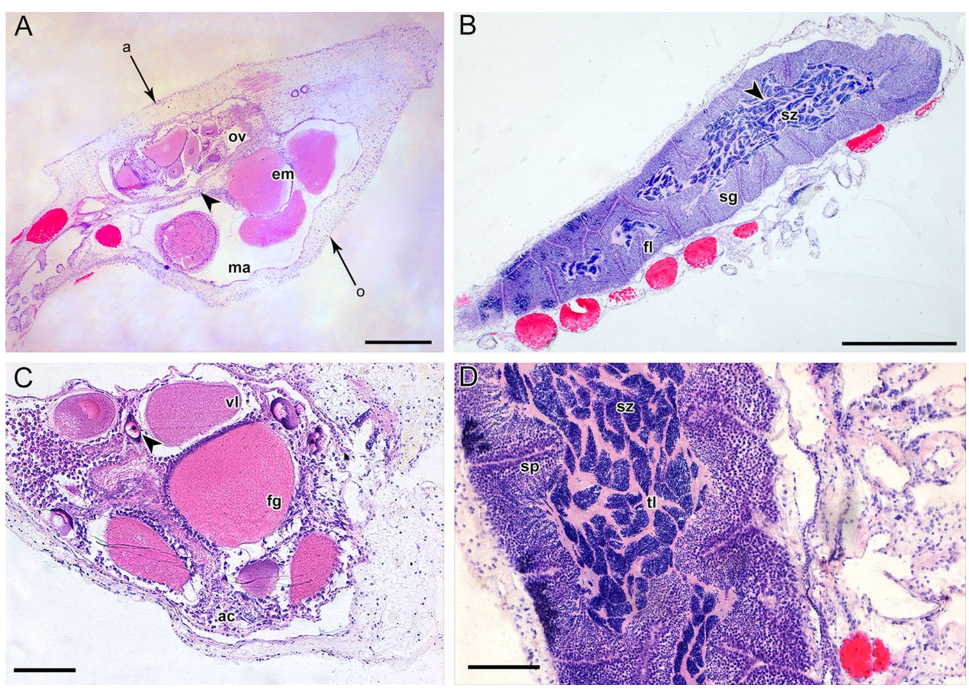

Fig. 3 Histology of *Isometra vivipara*. Microscope images **a** Longitudinal section of female genital pinnules with ovary (ov), membrane which separates the ovary and marsupium (arrow), embryos (em) and marsupium (ma), aboral (a), oral (o); **b** Longitudinal section of male genital pinnules, showing a testicular lumen (arrow) with spermatozoa (sz) and folds (fl) of the gonadal wall with spermatogonia (sg); **c** Ovarian enlargement with previtellogenic oocytes (arrow), vitellogenic oocytes (vl), full-grown oocytes (fg) and accompanying cells (ac); **d** Longitudinal enlarged section of male genital pinnules, showing spermatogenic columns (sp), testicular lumen (tl) with spermatozoa (sz). Scale bars **a** 200 μm; **b** 500 μm; **c**, **d** 100 μm

7 °C. For these sampling stations, only a few species of echinoderms were found.

The number of cirri in *I. vivipara* varied between 26 and 43 being cirral segments longer than wider. P1 is up to 10.5 mm long with 10–17 segments, while P2 is generally 1.5–2.0 mm long and not more than 8.5 mm, with 9–14 segments. The first genital pinnule is P4 or P5, usually P5. Broods were found attached in the cirri of the mother (Fig. 2a, b). *Isometra vivipara* has separate sexes. One hundred and twelve females, thirty-nine males, and 23 juveniles were identified; added to this 23 specimens were not sexed because samples were not in good conditions because the arms were incomplete. The females were distinguished from the males by a greater expansion of their genital pinnules in the third and fourth segments. In males, the broadening of the segments was gradual (Fig. 2d–f). Besides, color differences between ripe ovaries and ripe testes could be visible through the body wall (Fig. 2c–e). Also, a marsupium with early embryos (0.42 ± 0.12 mm in diameter) was observed in the pinnule of the females (Fig. 2c).

Histological analysis of female genital pinnules

Histological analyses revealed that *I. vivipara* pinnules were formed by external calcium carbonate segments followed by the ovary, which was separated from the marsupium by a membrane (Fig. 3a). Inside the ovary, previtellogenic and vitellogenic oocytes were observed, being the largest egg size recorded of 0.35 mm. In one case, an embryo of 0.4 mm in diameter was observed within the membrane that separated the ovary from the marsupium (Fig. 3c). Regarding the marsupium, generally between five and six embryos and doliolaria larvae were found inside. Except for two cases, in which up to 14 embryos and doliolaria larvae were found inside the marsupium.

Histological analysis and SEM examination of male genital pinnules

A central lumen with spermatozoa was differentiated in the histological sections (Fig. 3d). In the baseline of the testicular wall folds, spermatogonia were observed in male gonads (Fig. 3b). In the lumen, SEM images showed spermatozoa that consisted of a flattened oval head (~3.05 µm) connected to a flagellar tail (Fig. 4a, b).

Stages of larval development

Doliolaria larvae were found inside and outside the marsupium (Fig. 5a). In histological sections, these larvae were observed at different growth stages. Besides, different structures such as the archenteron, blastocoel, and epidermis were distinguished (Fig. 5b). Larvae presented three perpendicular ciliated bands, and two depressions: a rounded apical one on the anterior ventral surface (adhesive pit), and another one elongated in the posterior surface (vestibule) (Fig. 5). SEM images showed that these doliolaria larvae were formed by four well-differentiated plates of calcium carbonate (Fig. 5f). The largest size recorded for larvae was 0.77 mm in diameter.

Broods (cystidean and pentacrinoids) were found in thirty-four females, 1 male, 2 juveniles, and on hard substrates. The cystideans ($n = 23$, in $N = 5$ adult individuals) were formed by plates in the globular head, a columnar ossicle, and an attachment disk (Fig. 6a, b). More developed stages of cystideans presented oral, basal, radial, and brachial ossicle and a stalk. This stalk only possessed rings in the first part after the globular head, followed by well-marked septa (Fig. 6c, d). Farther stages (around 0.68 ± 0.1 mm in length) were formed by a more elongated stalk, arms more opened, and oral ossicles.

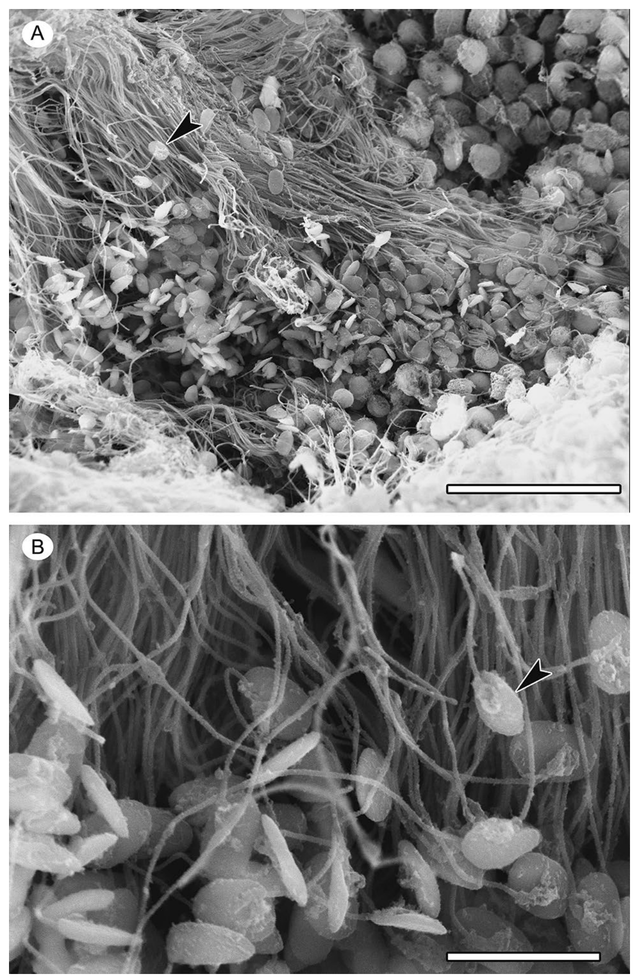

Fig. 4 Sperm in the male gonad. SEM images. **a** Male gonad lumen where spermatozoa are observed (arrow); **b** details of sperms (arrow). Scale bars **a** 20 µm, **b** 5 µm

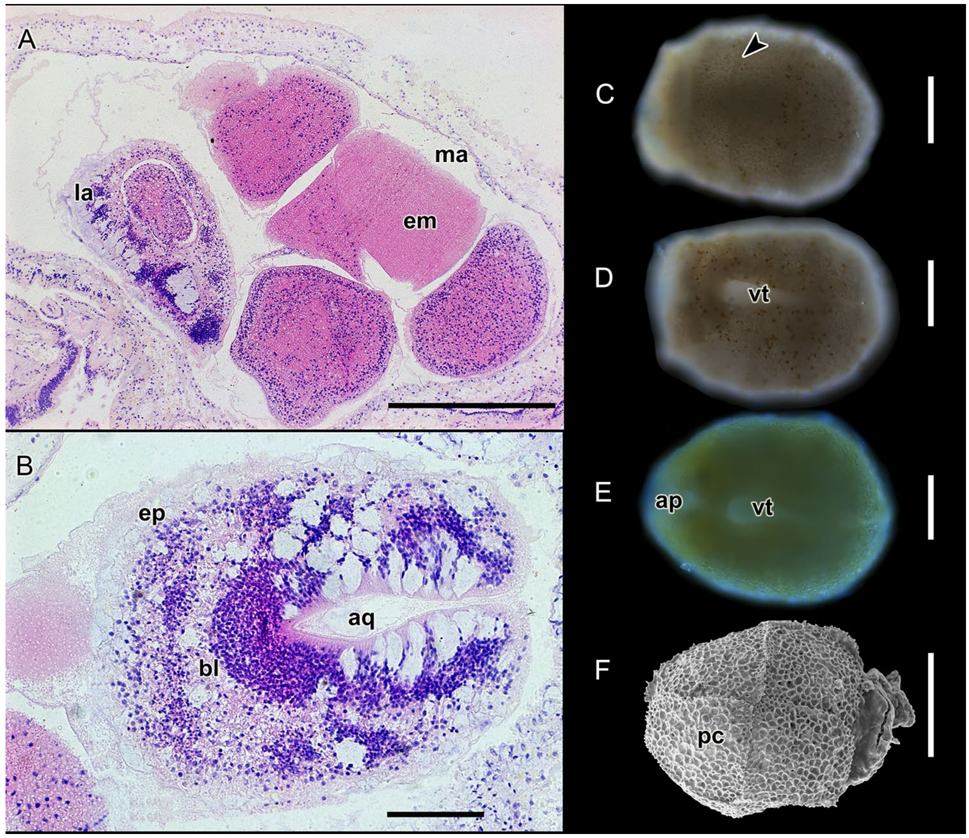

Fig. 5 Doliolaria larvae from *Isometra vivipara.* **a** Details of the marsupium (ma) with embryos (em) differentiating into doliolaria larvae (la); **b** cross-section of larva inside the pouch, showing the archenteron (aq), blastocoel (bl), and epidermis (ep); Stereoscopic microscope **c** Larva with three transverse bands (arrow); **d** Larva with a central ovoid fossa that differentiates into vestibule (vt); **e** Larva with two pits, a rounded apical, adhesive pit (ap), and the central vestibule (vt); **f** SEM image, where four plates of calcium carbonate (pc) are differentiated. Scale bars **a**, **f** 200 µm, **b** 100 µm, **c**–**e** 300 µm

Pentacrinoids ($n=26$, in $N=4$ adults individuals) presented several sub-stages of development. The less-developed stage had a stalk and arms that began to separate from the oral ossicle (Fig. 7a, b). At the following stages, some pentacrinoids showed their arms already with podia and well-separated from the calyx. Finally, pentacrinoids around 5.25 ± 2.9 mm in length were found with cirri and pinnules (Fig. 7c).

Discussion

Isometra vivipara Mortensen, 1917, has one of the largest eggs (0.35 mm in diameter) of the Southern Ocean. *I. vivipara* presents more specimens in stations at 7 °C, despite the species of echinoderms in these stations are few. The depth range of *I. vivipara* is quite particular as they come up to approximately 600 m, with a gap between 300 and 600 m where specimens were not observed. The presence of this gap could be due to their patchy distribution and the particularity of the habitat; probably, with more samplings, the absence of specimens would not be observed. *Aporometra wilsoni*, as *I. vivipara*, has a particular distribution because of its habitat characteristics. Both southern crinoids possess sexual dimorphism, internal fertilization, and protected development (Haig and Rouse 2008; Haig et al. 2012). The reproductive biology of both species reinforces the idea of the peculiar distribution of these crinoids.

In this study, the histological analyses of the females revealed that their genital pinnules have two compartments: the ovary and the marsupium. Inside the ovary, oocytes at different stages of development can be found, while the eggs and doliolaria larvae are protected inside the marsupium, as previously observed (Andersson 1904; Mortensen 1920; Clark and Clark 1967). Besides, the presence of oocytes at different stages of development may indicate that *I. vivipara* has a continuous reproduction, i.e., the oocytes are continuously released to the marsupium. A different strategy was reported for *Antedon bifida* that has a seasonal reproduction (Nichols 1994).

The maximum size of oocyte found in *I. vivipara* was 0.35 mm in diameter. The oocytes of comatulids such as *Phrixometra nutrix* (Mortensen, 1918) and *Promachocrinus kerguelensis* (Carpenter 1888) have up to 0.2 mm in diameter (McClintock and Pearse 1987; Holland 1991). Also, these two species are 88% and 70% smaller in egg volume than *I. vivipara*. This indicates that *I. vivipara* presents one of the largest egg sizes within this region. In addition, it is

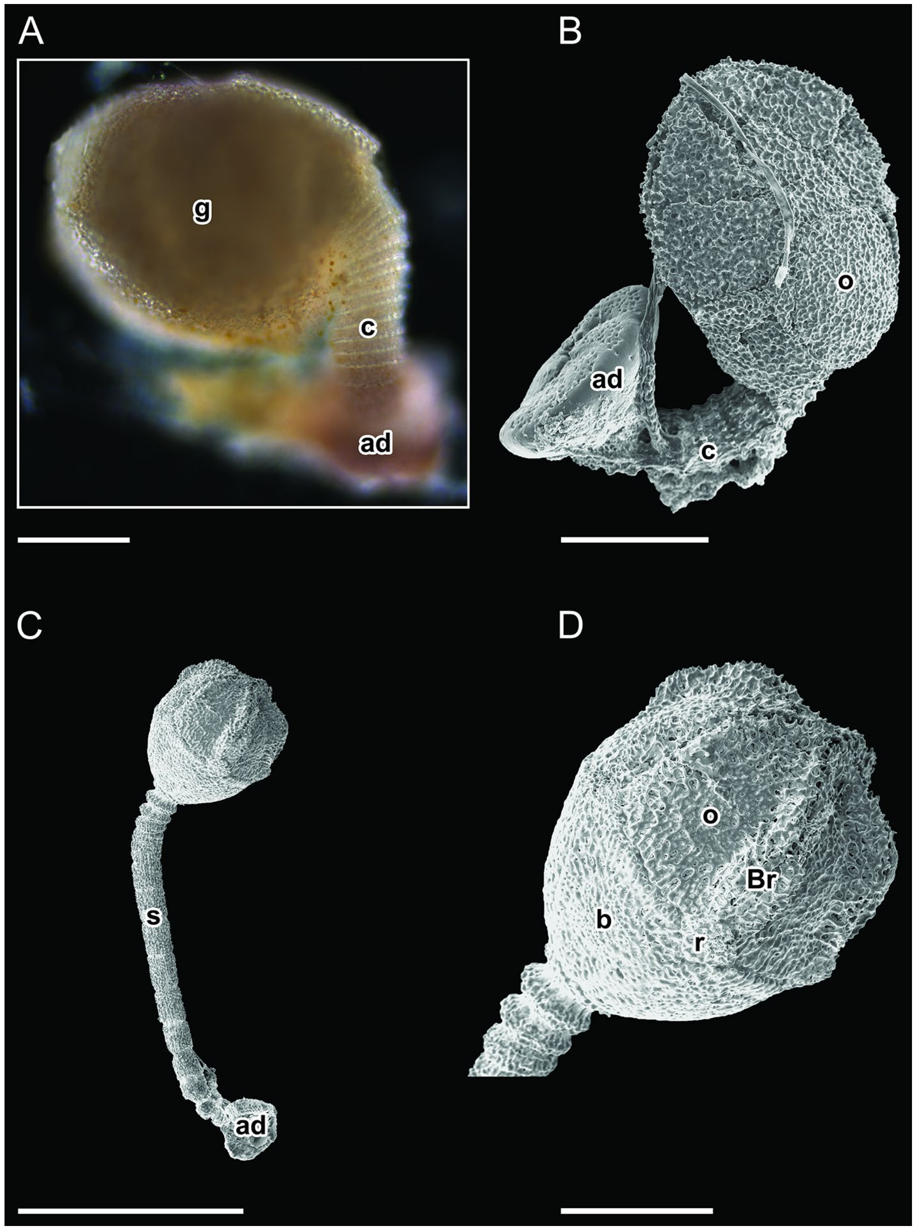

Fig. 6 Cystidean stage. Microscope images **a** Cystidean with globular head (g), columnar ossicle (c), from distal to proximal zone, and attachment disk (ad); SEM images **b** Cystidean with globular head with oral plate (o), columnar ossicle (c), and attachment disk (ad); **c** well-developed cystidean stage with stalk (s) and attachment disk (ad); **d** details of the globular head where oral (o), basal ossicle (b), radial ossicle (r), and brachial ossicle (Br) plates are differentiated. Scale bars **a** 250 µm, **b** 200 µm, **c** 1 mm, **d** 250 µm

the second largest egg in the Southern Ocean, after *Aporometra wilsoni* Bell, 1888 which has 0.42 mm in diameter (Eléaume et al. 2003; Haig and Rouse 2008) (Table 2).

Another southern comatulid, *Notocrinus virilis* Mortensen, 1917 presents a larvae size of 1.8 mm in diameter. This species has an egg size of 0.2–0.3 mm in diameter and a 42% volume egg smaller than *I. vivipara* (Table 2). Mortensen (1920) inferred that the larvae of *N. virilis* consume granulated eggs with a yellow substance that would have somehow migrated from the ovary to the marsupium, but he did not see real evidence of this. Something similar has been reported by Messing (1984) for *Comatilia iridometriformis* Clark AH, 1909 which has larvae up to 1.6 mm long. This author saw larvae accompanied by a yellow sphere of about 400 µm wide that could be an egg or an embryo in the process of absorption. The difference in the larvae and egg size of these two species and *I. vivipara* could indicate that *I. vivipara* would not need additional food. The larger egg size of *I. vivipara* would allow it to develop with its reserves and survive up to the free stage, outside the marsupium. The same would occur with the larvae of the *Aporometra wilsoni* (0.6 mm long) that is not markedly larger than the mature oocytes (Haig and Rouse 2008).

Doliolaria larvae are followed by cystidean and pentacrinoids stages. These pentacrinoids have open arms with pinnules and well-developed cirri, which was described by

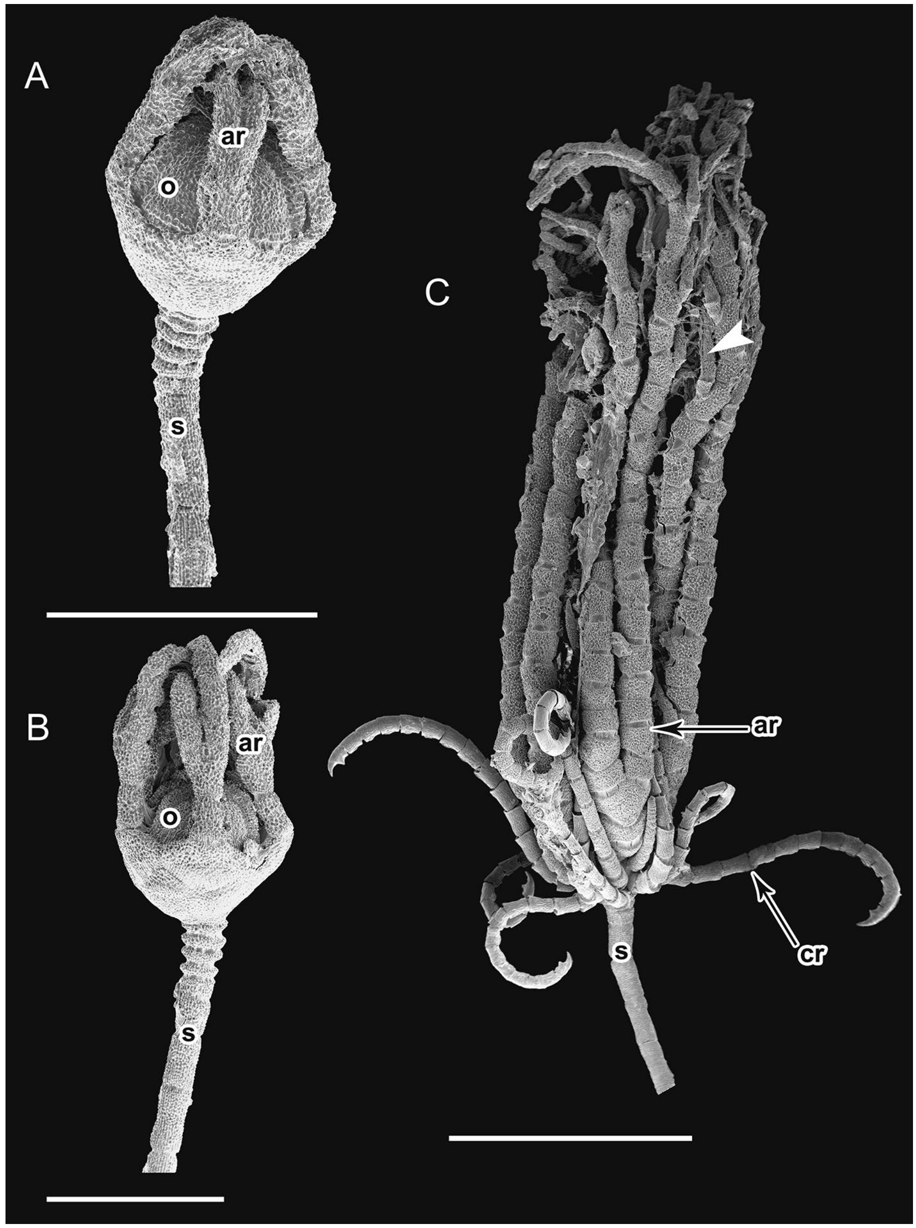

Fig. 7 Pentacrinoid stage. SEM images **a**, **b** Sub-stages of development of pentacrinoids by open the arms (ar) with oral ossicle (o) and stalk (s); **c** pentacrinoid with cirri (cr), stalk (s) and well-developed arms (ar), where pinnules (arrow) are distinguished. Scale bars **a**, **b** 1 mm, **c** 3 mm

Mortensen (1920) as feeding stage. Although the greatest number of broods was found in females, we were also able to find one male, two juveniles, and broods in solid substrates. It seems that *I. vivipara* broods mostly in females, but when the environmental conditions become hostile, broods can adhere to other specimens or substrates.

Andersson (1904) and Mortensen (1920) observed sperm within the ovary of *I. vivipara* and concluded that that was the place where fertilization occurs. In this study, we did not find spermatozoa within the female genital pinnules, nor embryos in the ovary, but we did observe cleaved eggs inside the membrane that separates the ovary from the marsupium. These results may indicate that internal fertilization would occur between these two compartments.

Holland (1976) described the morphology of the sperm head of *I. vivipara* as flattened and oval, which was confirmed in this study by SEM images of the testicular lumen. Additionally, SEM analysis enabled us to observe broods between ovary and marsupium, which may support the idea of internal fertilization. The particular morphology of the sperm might be related to its passage through the female genital pinnules, as was also suggested by Holland. However, it is not known how this passage occurs, yet.

Table 2 Comparison between *Isometra vivipara* and species of Subantarctic and Antarctic comatulids

Species	Egg diameter (mm)	Larval (mm)	Volume (mm^3)	Relationship between volumes (%)[a]	Distribution	Depth (m)[b]	References
Promachocrinus kerguelensis	0.2	ND	0.0042	3.33	Antarctic continent, Graham Land peninsula, South Shetland Islands and South Sandwich Islands, South Georgia, Bouvet and Heard and Kerguelen Islands	20–2100	McClintock and Pearse (1987, 378 pp.)
Notocrinus virilis	0.2–0.3	1.8[c]	0.0082 0.0141	3.33 1	Antarctic continent and adjacent islands	80–1120	Mortensen (1920, 49 pp.)
Kempometra grisea	0.25	ND	0.0082	1.71	South Shetland Islands	660–1120	John (1938, 163 pp.)
Phrixometra nutrix	0.15	ND	0.0017	8	Burdwood Bank, near Falkland Island and Bransfield Strait	137–485	Mortensen (1918, 17 pp.)
Aporometra wilsoni	0.45	0.6	0.046	0.30	Witton Bluff, Christies Beach, Adelaide, South Australia	< 3	Haig and Rouse (2008, 467 pp.) Haig et al. (2012, 2 pp.)
Isometra vivipara	0.35[d]	0.77[d]	0.0141		South of Brazil (33°S) to the northwest of the Weddell Sea (64°S)	78–845	Present study

ND no data

[a]Relationship between volumes of the *Isometra vivipara* and species of Subantarctic and Antarctic comatulids (volumes of *I. vivipara*/volumes of other comatulids)

[b]From Speel and Dearbon (1983)

[c]Dololiaria larvae with supplementary feed, Mortensen (1920, 50 pp.)

[d]Present study

Finally, this research not only extends the knowledge of the reproductive biology of *I. vivipara,* but also the limited knowledge of crinoids from Argentina. Future studies of these groups will provide clarity in taxonomy and reproduction, reopening the doors of an almost forgotten world, i.e., Southwestern Atlantic crinoids.

Acknowledgements The authors would like to express their gratitude to the colleagues on board the B/O *Puerto Deseado* for assistance during the 2016–2017 expedition. We thank Alejandro Tablado, curator of the Invertebrate Collection of the MACN and Fabian Tricarico for assistance with the SEM. We also would like to thank all the technical and scientific staff of the Laboratorio de Ecosistemas Costeros, Plataforma y Mar Profundo-Malacología for their assistance, support, and contributions to this work, especially to Carlos Sánchez Antelo, Juan José Berecoechea, Pamela Rivadeneira, and Jonathan Flores. In addition, we would like to thank Sonia M. Landro and John Lawrence for their contributions with the English. Finally, we would like to thank Jodie A. Haig and two anonymous reviewers for their valuable suggestions and comments that improved this manuscript. This is the contribution number 24 to the Area Marina Protegida Namuncurá (Ley 26.875).

Funding This study was funded by PICT 2013-2504, PICT 2015-0428, PICT 2016-0271 from the *Agencia Nacional de Promoción Científica Tecnológica* and PIP 11220170100643CO from the *Consejo Nacional de Investigaciones Científicas y Técnicas*.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

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