



Brooding comatulids from the Southwestern Atlantic, Argentina (Echinodermata: Crinoidea)

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Abstract

Isometra vivipara and *Phrixometra nutrix* are two brooding feather stars (order Comatulida) that are widely distributed along the southern tip of South America to the Antarctic. We examined 210 specimens of *I. vivipara* and 38 specimens of *P. nutrix* collected during five cruises in the southwestern Atlantic between 91 and 642 m depth. Specimens were analyzed and deposited in the National Invertebrate collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. *Isometra vivipara* reaches an arm length of 49 mm long and shows two stages of brooding: in the female genital pinnules and on the cirri of the mother. In this paper, we propose that spermatozoa reach the ovary via the ambulacral groove. By contrast, *P. nutrix* is smaller with a maximum recorded size of 26.8 mm, and brooding occurs only inside the female genital pinnules. Here, we record, for the first time for *P. nutrix*, spermatozoa shape and a cleaved egg attached externally to a genital pinnule of a female. The distributions of both species and their abundances in some areas could be related to their doliolaria larval stage. In addition, we extend the bathymetric range of *P. nutrix* to 512 m in Marine Protected Area Namuncurá/Burdwood Bank and distribution to the Mar del Plata Submarine Canyon area. We also propose mode of reproduction and developmental patterns as attributes for identification and possible explanations for their differences in distribution.

Keywords Crinoids · *Isometra vivipara* · *Phrixometra nutrix* · Malacodium · Southern Ocean · MACN

Introduction

Feather stars, members of the crinoid order Comatulida that lose the stalk after a stalked postlarval stage, are the dominant group of living crinoids with 561 species in six genera (Hemery et al. 2013; Roux et al. 2002; WoRMS Editorial Board 2021). While some species show external and internal brooding (Hyman 1955; Messing 1984; Mladenov 1987; Haig and Rouse 2008; Obuchi et al. 2010), their most common reproductive mode is broadcast spawning (Messing 1984; Holland 1991; Balser 2002; Eléaume et al.

2001). Two species of Argentina were described as brooders (Mortensen 1920; Pertossi et al. 2019).

Crinoids have six distinct life-history stages; among them, the doliolaria larvae play a key role in dispersion (Chia et al. 1986; Hendlar et al. 1995; Balser 2002). The distribution of species and their abundances in some areas may be related to the planktonic doliolaria larval stage which could enable the specimen to drift long distances, far from the adult habitats (McClintock and Pearse 1987; Helgen and Rouse 2006).

Among brooding comatulids, Mortensen (1918) described two species from Argentina: *Isometra vivipara* Mortensen, 1917, and *Phrixometra nutrix* (Mortensen, 1918), both currently placed in family Antedonidae (Brogger et al. 2013a), although the family is polyphyletic, and the placement of both genera is currently uncertain (Hemery et al. 2013; Rouse et al. 2013). *Isometra vivipara* exhibits two stages of brooding: as doliolaria in the female genital pinnules, and as cystidean and pentacrinoid attached to the cirri of the mother (Clark and Clark 1967; Pertossi et al. 2019). In *P. nutrix*, brooding occurs inside the female genital pinnules, until the juvenile stage is released as a young free feather star that sheds its stalk and swims away (Andersson 1904; Mortensen 1917, 1918; Messing 1984).

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Isometra vivipara has separate sexes, internal fertilization, and intraovarian sperm storage preceding the development of embryos in the mother's brood pouches (Holland 1991). Andersson (1904) proposed that males transferred sperm via copulation, although without any direct observation. Holland (1976) discussed the unlikelihood of copulation and suggested that sperm might be transferred through seawater. He noted that the sperm head is "modified" (flattened, oval, and with an acrosome displaced to one side, unique among crinoids), which might reflect packaging in spermatophores or a modification, allowing them to pass from the exterior through the female's brood pouch cavity and into the interior lumen of the ovary. Although the so-called primitive sperm, with a spherical head and free flagellum, is characteristic of external fertilization, recent studies indicate that the sperm shape does not always match fertilization mode. *Eumorphometra marri* John, 1938 and *Phrixometra longipinna* (Carpenter, 1888) both internal brooders (John 1939) have "primitive" sperm, which is thought to use the external fertilization mode, whereas *Antedon bifida* (Pennant, 1777) has a "modified" sperm but external fertilization (Holland 1976, 1991). Sperm morphology remains unknown for the brooding species *P. nutrix*, *Aporometra wilsoni* (Bell, 1888), and *Notocrinus virilis* Mortensen, 1917.

The purpose of this study was to introduce brooding as an attribute for identification. We add new information for *I. vivipara* and *P. nutrix*. Finally, we discuss the brooding and distribution of both crinoids with reference literature.

Material and methods

Five cruises were carried out aboard the R/V Puerto Deseado from 38° S to 61° S between 2009 and 2017 (Fig. 1). Samples were collected using bottom trawls and fishing nets at depths between 91 and 642 m and included 38 specimens of *P. nutrix* and 210 of *I. vivipara* (Pertossi et al. 2019). All samples were preserved in ethanol 96%, analyzed, and deposited at the National Invertebrates collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In).

In addition to the samples collected, specimens previously deposited at the MACN-In were studied. Observations were carried out under a stereoscopic microscope; images were taken with a Stereo Discovery V20 and an Axiocam HRc digital camera. All diagnostic characters were analyzed in detail, including the cirri, oral pinnules, genital pinnules, arm number, and segments of the cirri and arms. Feather star size measurements were taken from the tip of an arm to the centrodorsal. A study on sperm morphology was carried out for both species. For *I. vivipara*, fixed genital pinnules were dehydrated, embedded in Leica Historesin®, sectioned with a RM2155 Leitz microtome (5–6 µm sections), and then

stained in hematoxylin and eosin. Slides were photographed and measured with a Zeiss Axio Imager Z1 light microscope and an Axiocam HRc digital camera. In the case of *P. nutrix*, genital pinnules of the male were dehydrated in graduated series of ethanol, critical point dried, and observed under a SEM.

Results

Family Antedonidae Norman, 1865

Remarks: Molecular data have recently rendered this family as polyphyletic, and the relationships among its traditional subfamilies and genera remain to be worked out in detail (Hemery et al. 2013; Hemery et al. 2013).

Subfamily Isometrainae Fet & Messing, 2003.

Remarks: This subfamily, which includes only *Isometra*, was renamed from Isometrinae to remove homonymy with a subfamily of scorpions (see Hess and Messing 2011). Hemery et al. (2013) reported that it is weakly supported by nonparametric bootstrap but well supported by posterior probabilities.

Isometra A. H. Clark, 1908

Remarks: The genus occurs along southeastern South America and around Antarctica and currently includes seven accepted species. However, two are known only from one specimen each, and several are distinguished only on the bases of differences in proportions of proximal pinnules (Clark and Clark 1967).

Isometra vivipara Mortensen, 1917 (Fig. 2a, b, c, d, e).

Antedon hirsuta (non Carpenter, 1888); Andersson 1904: 1–8; Wilton et al. 1908: 21, 61.

Isometra sp. A. H. Clark 1915: 106.

Isometra angustipinna (non *Antedon angustipinna* Carpenter, 1888); A. H. Clark 1915: 146.

Isometra vivipara Mortensen 1917: 208; 1918: 10–15; 1920: 1, 13, 14, 29, 31–48, 49, 52, 53, 60–65, 69, 75, 81, 92; Clark 1921: 23, 153, 230, 281, 292, 365, 367, 369, 375, 409, 410, 510, 528, 582, 613; 1931: 59; John 1937: 86–88; 1938: 123–126, 128, 131, 132, 178–181, 191, 192, 211; Clark 1937: 5, 17, 18; Vaney 1938: 661; Clark 1941: 18, 29, 35, 1947: 308, 310; Hyman 1955: 75, 86, 87; Marr 1963: 339, 342, 345, 347–349, 352, 356, 360, 361; Clark and Clark 1967: 8, 9, 632–644, 645; Holland 1976: 147–152; Afzelius 1977: 277; Speel and Dearborn 1983: 2–11, 47; Messing 1984: 88; McClintock and Pearse 1987: 382; Healy et al. 1988: 308, 309; McEdward et al. 1988: 11; Eckelbarger et al. 1989: 267; Bishop and Ryland 1991: 116; Giese et al. 1991: 259, 260, 272, 275, 286; Jamieson 2000: 178, 179, 182; McEdward and Miner 2001: 1132, 1157; Balser 2002: 463–482; Haig and Rouse 2008: 466, 467; Bohn 2009: 795, 798; Mironov and Pawson 2010: 50; Obuchi et al. 2010: 1199; Haig et al. 2012: 7; Brogger et al. 2013a: 367;

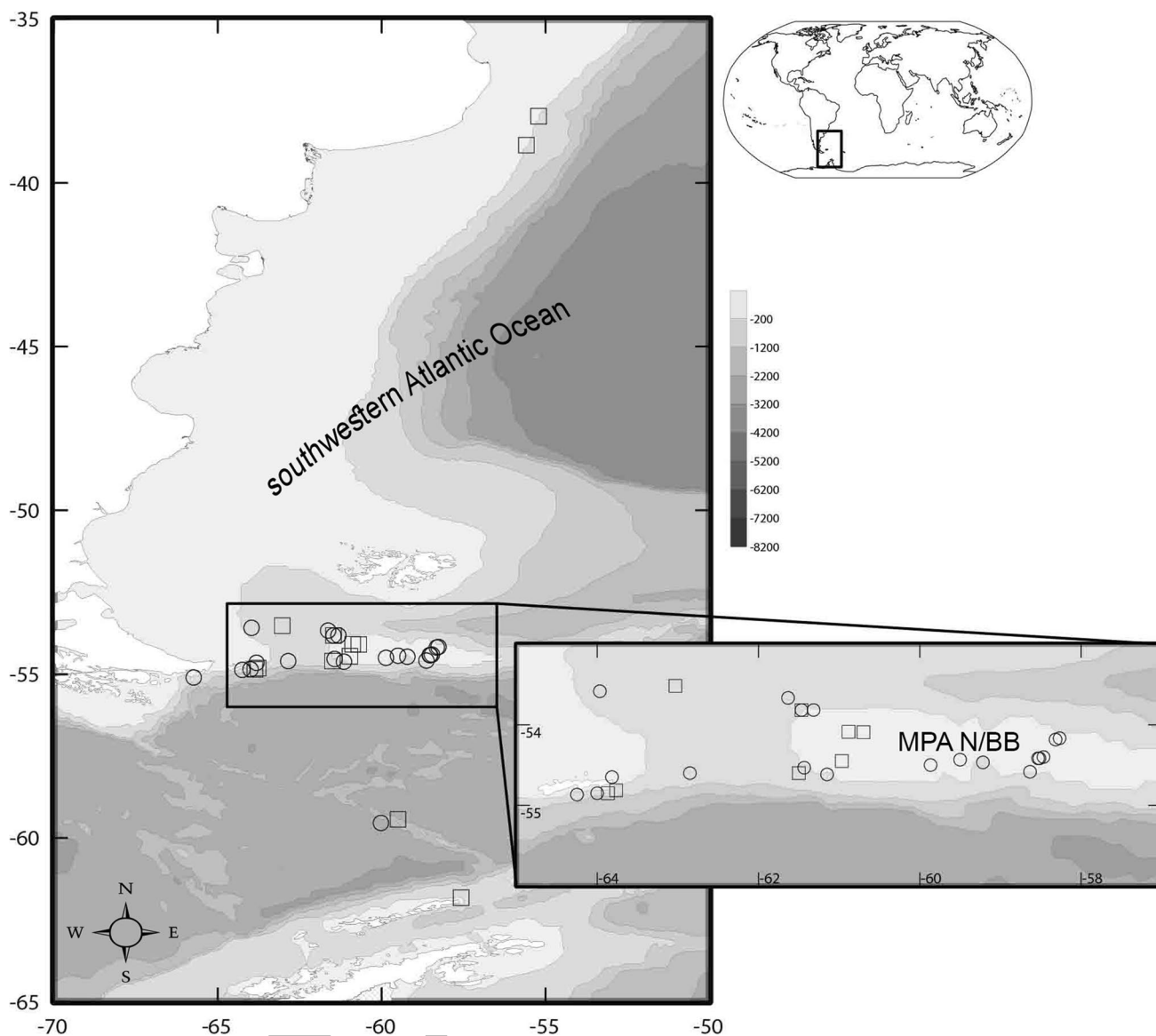


Fig. 1 Map showing the location of the collected samples, square: *Isometra vivipara*; circle: *Phrixometra nutrix*

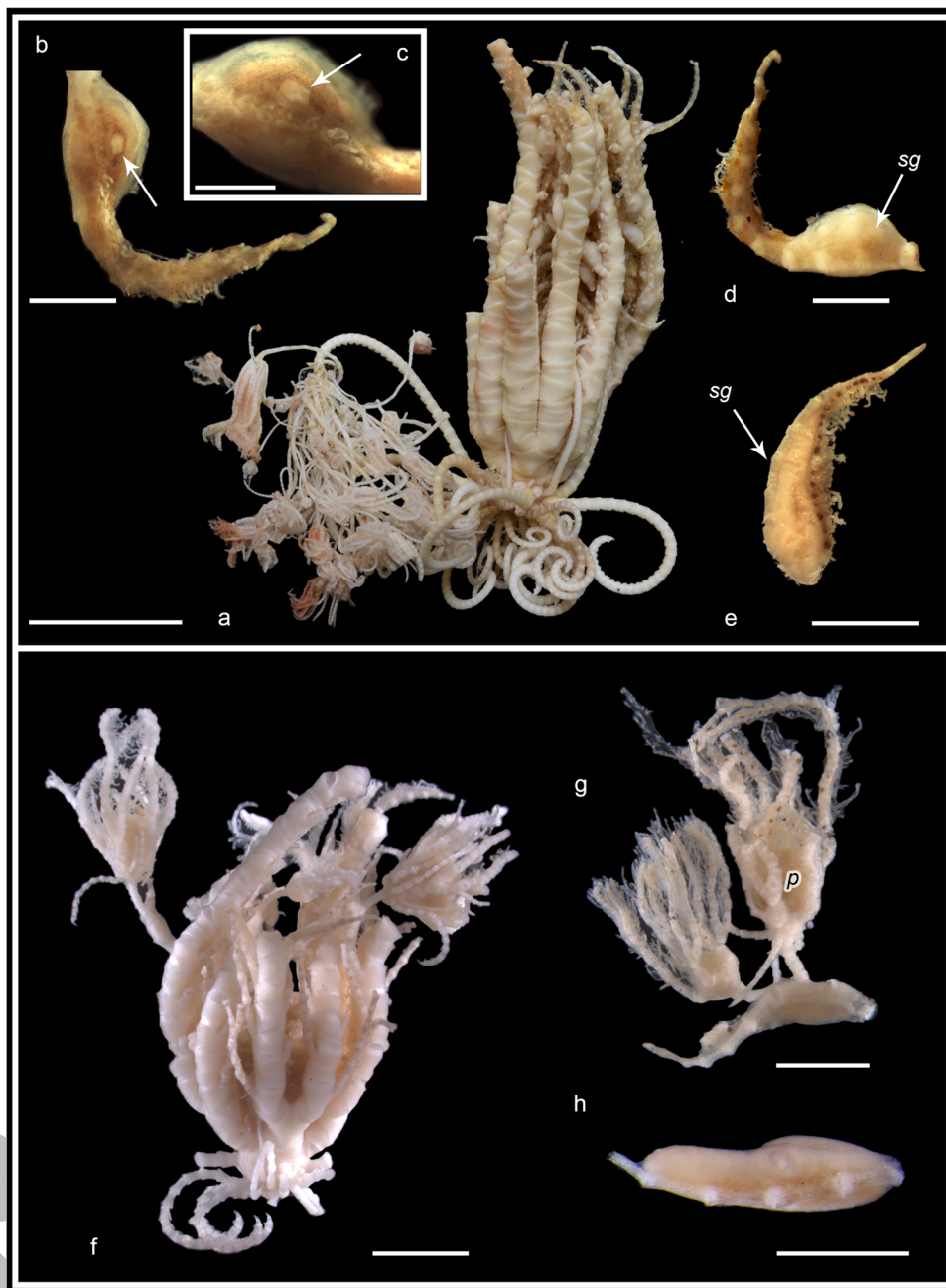
Eckelbarger and Riser 2013: 277; Hemery et al. 2013: 513; Solís-Marín et al. 2013: 544; Eléaume et al. 2014: 210, 211; Souto et al. 2014: 279; Clouse et al. 2015: 4; Kammer et al. 2015: 309,310; Hays 2016: 8, 16, 58, 82, 89, 104–106, 108, 132, 192, 193, 206, 250; Jones et al. 2016: 2, 3, 5; Pandia 2018: 55, 56; Hasan et al. 2019: 4, 18; Pertossi et al. 2019: 807, 808, 810, 811, 812, 815.

Diagnosis (modified from Clark and Clark 1967): A species of *Isometra* with 26–43 cirri, the longest segments hardly, if at all, longer than wide; P1 is up to 8 mm long with 14 segments while P2 is usually 5.5 mm shorter with 12 segments; P5 is usually the first genital pinnule.

Examined material: 54° 50' S–64° 01' W 151 m MACN-In22821, 54° 57' S–64° 42' W 265 m MACN-In

22,822, 54° 25' S–58° 31' W 137 m MACN-In 42,367, 54° 51' S–60° 0' W 159 m MACN-In 42,368, 54° 32' S–60° 1' W 98 m MACN-In 42,369, 54° 10' S–58° 16' W 100 m MACN-In 42,370, 54° 11' S–58° 19' W 95 m MACN-In42371, 54° 30' S–59° 52' W 109 m MACN-In42372, 54° 37' S–61° 9' W 202 m MACN-In42373, 54° 28' S–59° 13' W 128 m MACN-In42374, 54° 32' S–61° 26' W 125 m MACN-In42375, 54° 35' S–58° 38' W 140 m MACN-In42376, 54° 36' S–62° 51' W 608 m MACN-In42377, 54° 24' S–58° 28' W 95 m MACN-In42378, 55° 6' S–65° 44' W 263 m MACN-In42379, 54° 52' S–64° 16' W 151 m MACN-In42380, 54° 39' S–63° 49' W 143 m MACN-In42381, 54° 24' S–62° 49' W 483 m MACN-In42382, 54° 26' S–58° 32' W 138 m MACN-In42383, 54° 26' S–59°

Fig. 2 Crinoids of Argentina. **a** Female of *Isometra vivipara* with cystidean and pentacrinoids attached in the cirri; **b** oral view of female genital pinnules, with marsupium and larva emerging (arrow); **c** detail of **b** showing the marsupium and larva emerging (arrow); **d** aboral view of female genital pinnules showing, widened third and fourth segments (*sg*); **e** lateral view of male genital pinnules showing gradual widening of the segments (*sg*); **f** Female of *Phrixometra nutrix* with cystidean and pentacrinoids in the genital pinnule; **g** lateral view of female genital pinnules with two pentacrinoids (*p*); **h** lateral view of male genital pinnules. Scale bars **a**, **c**, **g**, **h** 1 mm; **b**, **d**, **e**, **f** 2 mm



30' W 91 m MACN-In42384, 53° 40' S–61° 38' W 642 m MACN-In42385, 53° 34' S–63° 58' W 263 m MACN-In42386, 53° 34' S–62° 58' W 516 m MACN-In42387, 53° 49' S–61° 28' W 209 m MACN-In42388, 53° 49' S–61° 19' W 197 m MACN-In42389, 54° 39' S–63° 49' W 143 m MACN-In42390.

Type locality: Marine Protected Area Namuncurá/Burdwood Bank (MPA N/BB) (52° 29' S–60° 36' W) and Antarctic station 58, 197 m.

Geographic range: In South America, from off SW Chile to Cape Horn in the Pacific, and in the Atlantic, from 33° S off the southern tip of Brazil to the south of Argentina,

including Marine Protected Area Namuncurá/Burdwood Bank and Tierra del Fuego. In Antarctica, reported for the northwest area of the Weddell Sea (Bohn 2009).

Bathymetric range: From 79 to 845 m (Speel and Dearborn 1983).

Reproduction

In this study, we found sperm inside the females' ovaries. In general, they are found in the center of the ovary, surrounded by oocytes. We observed a possible connection between the ambulacral groove and the ovary, where sperm could have

access (Fig. 3a). According to these observations, fertilization occurs within the ovary. *Isometra vivipara* exhibits secondary sexual dimorphism: the third and fourth segments of the genital pinnules in females are greatly expanded, whereas in males, the broadening of the segments is weaker and gradually tapered distally (Fig. 2d, e) (Mortensen 1918; Pertossi et al. 2019).

Remarks Adults of *Isometra vivipara* attain a size of 49 mm long. This species shows two stages of brooding. The first stage takes place in the brood pouches and involves doliolaria larvae that have three perpendicular ciliated bands and two depressions (adhesive pit and vestibule). Also, the doliolaria was covered by eight well-differentiated plaques on both sides (see Fig. 5 of Pertossi et al. 2019). The second stage occurs on the cirri of the mother and involves two

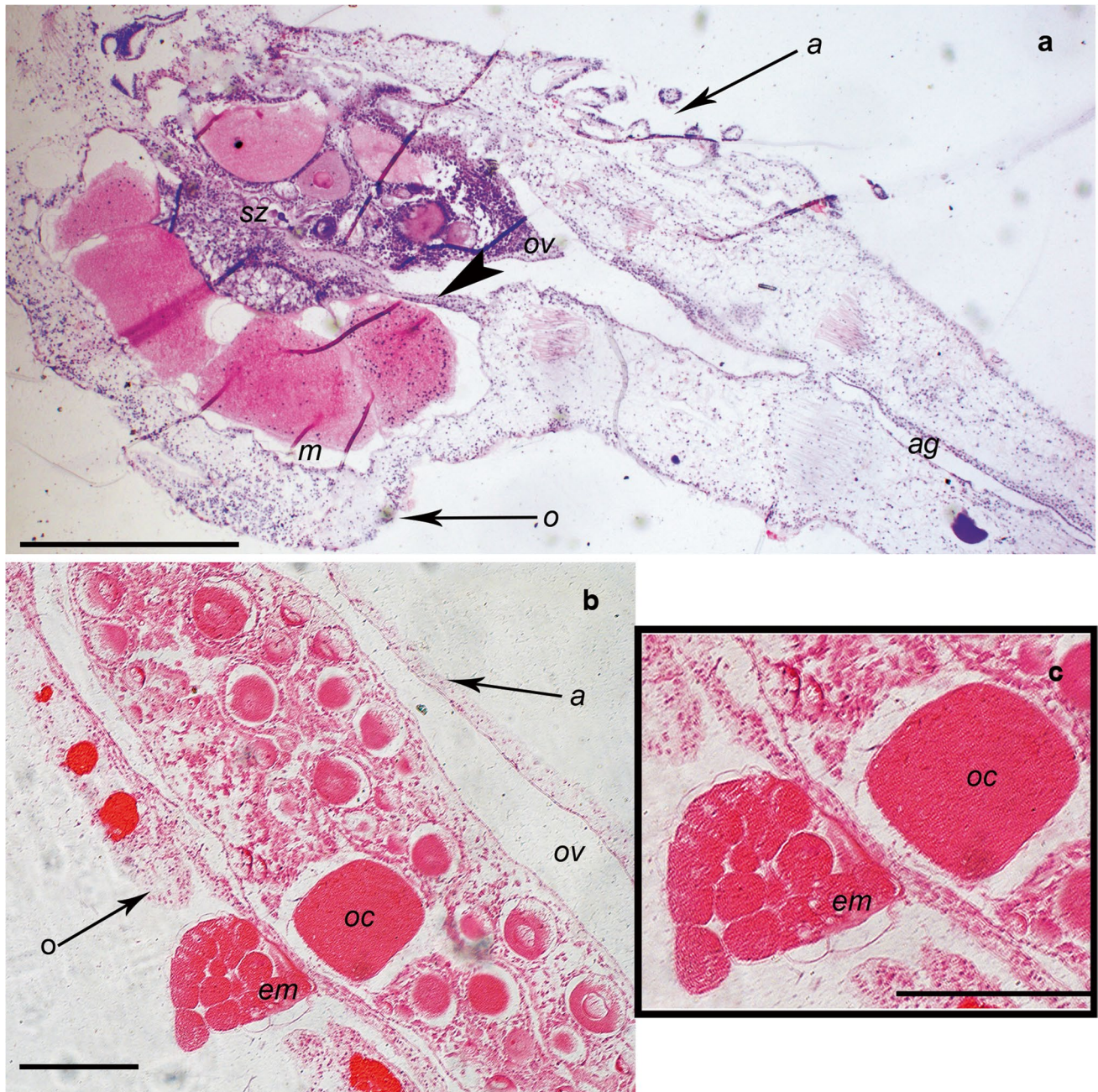


Fig. 3 a, b Microscope images of a longitudinal section of female genital pinnules. a *Isometra vivipara*; b *Phrixometra nutrix*; abbreviations: aboral (a), oral (o), ovary (ov), spermatzoa (sz), marsupium (m), ambulacral groove (ag) membrane which separates the ovary and

marsepium (arrow); oocytes (oc), embryo (em); c details of female genital pinnules of *Phrixometra nutrix* with oocytes (oc), embryo (em). Scale bars a 0.5 mm; b, c 200 μm

developmental stages, the cystidean and pentacrinoid larvae (also sometimes called postlarvae) that precede the juvenile stage when the stalk detaches. The cystidean has a globular head composed of oral plates, basal plates, a stalk, and an attachment disk. In the pentacrinoid, which remains attached by its stalk to the female's cirri, the arms separate from the head, and radial and brachial plates appear (Clark and Clark 1967, see Fig. 6 and 7 of Pertossi et al. 2019).

Phymetrinae A. H. Clark, 1909a

Remarks: The diagnosis of the subfamily in Hess and Messing (2011) incorporates a wide range of variation, e.g., cirri “crowded or not, in alternating, irregular rows with tendency to form as many as 30 columns in some species,” and not enough molecular data is available to determine whether the subfamily is a monophyletic clade, or not.

Phrixometra A. H. Clark, 1921

Remarks: *Phrixometra* currently includes three species: *P. nutrix* from Uruguay to Antarctic; *P. longipinna* (Carpenter, 1888) off the coast of Uruguay; *P. exigua* (Carpenter, 1888) off Marion Island and *P. rayneri* John, 1938 Shag Rocks.

Phrixometra nutrix (Mortensen, 1918) (Fig. 2f, g, h).

Thaumatometra nutrix Mortensen, 1918: 15, 16, 17, 18; A. H. Clark 1923: 43, 56; Gislén 1924: 28, 195; A. H. Clark 1937: 5, 6, 8; John 1937: 86, 87, 88; Cuénot 1948: 55; Dawidoff 1948: 353.

Phrixometra nutrix John, 1938: 123, 125, 126, 128, 129, 132, 170, 171, 172; Hyman 1955: 69, 75; Marr 1963: 339, 342, 345, 349, 359; Clark and Clark 1967: 8, 548, 661, 665, 836; Speel and Dearborn 1983: 3, 5, 6, 7, 9, 10, 17, 50, 52; Messing 1984: 88, Holland 1991: 286, 287; Pearse and Bosch 1994: 10; McEdward and Miner 2001: 1157; Haig and Rouse 2008: 466, 467, 468; Bohn 2009: 795, 798; Mironov and Pawson 2010: 50; Solís-Marín et al. 2013: 367; Eléaume et al. 2014: 210, 211; Souto et al. 2014: 279; Clouse et al. 2015: 4; Pandia 2018: 56; Hasan et al. 2019: 4, 18; Pertossi et al. 2019: 812, 815.

Diagnosis (modified from Clark and Clark 1967): A species of *Phrixometra* with about 45 cirri, with less than 18 segments; P1 has about 14 segments; P3 is usually the first genital pinnule and is similar in length and number of segments to P1.

Examined material: 38° 51' S–55° 35' W 145 m MACN-In39870, 38° 51' S–55° 35' W 140 m MACN-In43242, 38° 51' S–55° 34' W 140 m MACN-In43243, 61° 49.6' S–57° 34.4' W 210 m MACN-In43244, 37° 58' S–55° 12.73' W 201 m MACN-In43245, 54° 27' S–60° 58' W 100 m MACN-In43246, 53° 49' S–61° 28' W 209 m MACN-In43247, 54° 36' S 61° 30' W 294 m MACN-In43248, 54° 51' S–63° 52'

W 330 m MACN-In43249, 55° 6' S–60° 41.9' W 122 m MACN-In43250, 54° 49' S–63° 45.91' W 278 m MACN-In43251, 59° 26' S–59° 30' W 91 m MACN-In43252, 54° 5' S–60° 53' W 132 m MACN-In43253, 53° 31' S–63° 2' W 512 m MACN-In43254.

Type locality: To the northwestern side of the Marine Protected Area Namuncurá/Burdwood Bank (MPA N/BB) (53° 41' S–61° 10' W).

Geographic range: In South America, from the Magellanic Region, in the Pacific, to the Marine Protected Area Namuncurá/Burdwood Bank in the Atlantic. Also occurs around Antarctica, including the Antarctic Peninsula and near islands, i.e., South Shetlands and South Orkneys (Speel and Dearborn 1983). Herein, we expand the distribution to the north, near the Mar del Plata Submarine Canyon area (38° 51' S–55° 35' W, MACN-In38970).

Bathymetric range: From 91 to 512 m. The previous report was from 150 to 200 m (Clark and Clark 1967), extended herein.

Reproduction

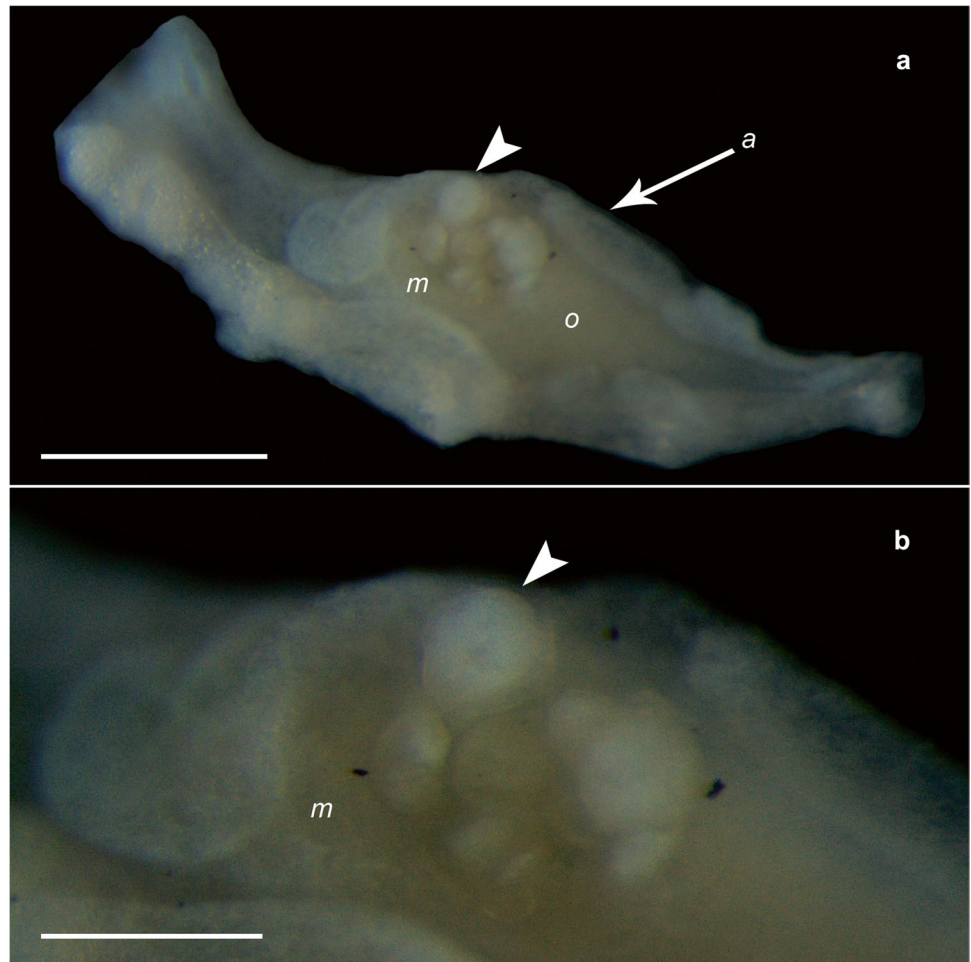
We found accumulated eggs (up to 200 µm) on the outside of the marsupium in some specimens (Fig. 4a, b) and a cleaved egg attached to a genital pinnule (up to 234 µm) in one specimen (Fig. 3b, c). We found no fertilized oocytes inside the genital pinnule. For males, the external morphology is similar to the females, and spermatozoa consist of a spherical head (up to 4 µm) and free flagellum shown here for the first time in SEM images of the male genital pinnule (Fig. 4a, b).

Remarks *Phrixometra nutrix* reaches an arm length of 26.8 mm. This species shows only one stage of brooding inside of a pocket-like groove (marsupium) on the side of the genital pinnule. The offspring do not leave the marsupium when the doliolaria is ready to metamorphose into a cystidean and then to a pentacrinoid; only the cystidean head and the upper part of the pentacrinoid stalk extend out of the opening of the marsupium; they still use the marsupium as the substratum (Mortensen 1918). Also, *P. nutrix* exhibits no secondary sexual dimorphism (Fig. 2g, h).

Discussion

Few taxonomists and researchers currently focus on crinoids, and those who study other echinoderm classes tend to publish little about crinoids (Messing 1977). However, Mortensen, who was an expert on multiple groups of echinoderms, was the first to record several features of the two species of crinoids from Argentina (Mortensen 1917, 1918, 1920). For *Isometra vivipara* and *Phrixometra nutrix*, all

Fig. 4 Genital pinnule of *Phrixometra nutrix* without treating. **a** with aboral (*a*), oral (*o*), marsupium (*m*) with eggs (arrow); **b** details of marsupium (*m*) and eggs (arrow). Scale bars a 0.5 mm, b 0.2 mm



the information related to their reproduction (Andersson 1904; Mortensen 1917, 1918, 1920; Clark and Clark 1967; Pertossi et al. 2019) has been confirmed here (with the exception of the means by which sperm enter the ovary of *I. vivipara*). These features contribute to distinguish these species along with the morphological characters presented in Table 1. These differences are important for taxonomic purposes and have been indicated as important in phylogenetic studies too, in other groups of echinoderms (Bohn and Heß

2014, Martinez et al. 2020). This information could help in comatulid studies, taking into account the difficulties associated with species identifications in this group (Eléaume et al. 2014, Messing 1977).

Little evidence exists about how sperm get inside the genital pinnules of brooding female feather stars (Holland 1976). Previous reports show that *I. vivipara* sperm can be found within the ovary (Andersson 1904; Mortensen 1918) and in the marsupium (Andersson 1904), which suggests

Table 1 Comparison establishes between *Isometra vivipara* and *Phrixometra nutrix*, based on morphological and reproductive characteristics. *Feather star size measurements were taken from the tip of an arm to the centrodorsal

Species	Sexual dimorphism	Brooding stages	Larger size* (mm)	N° of cirri	N° segments P1	P1 and P2	First genital pinnule
<i>Isometra vivipara</i>	Secondary	Two stages: inside the brood pouches and attached to the cirri of the mother	49	26–43	14	P1 longer than P2	P5
<i>Phrixometra nutrix</i>	None	One stage: in the female genital pinnules until the juvenile stage is attained	26.8	45	14	Similar in length	P3

that spermatozoa reach the ovary through the marsupium (Andersson 1904; Holland 1976). Here, we propose that spermatozoa could also get inside the ovary via a possible connection between the base of the ambulacral groove and the lumen of the ovary (Fig. 3a). Haig and Rouse (2008) noted that another brooding feather star, *Aporometra wilsoni* (Bell, 1888), must exhibit internal fertilization, but that the sites of fertilization and possible sperm storage remained unknown. Female *A. wilsoni* collected sperm, possibly via filter feeding, and either stored the sperm internally or used the sperm to fertilize eggs as they were collected. Internal fertilization followed by brooding also occurs in several other crinoids (Mortensen 1920; Holland 1991), such as *Comatilia iridometrififormis* A.H. Clark, 1909b, *Phrixometra* spp., and *Notocrinus* spp., although the means of entry of sperm into the genital pinnule and the fertilization process remains a mystery (Messing 1984; Haig and Rouse 2008; Haig et al. 2012). For *P. nutrix*, we observed for the first time, as far as we know, a cleaved egg attached to the genital pinnule, although we found no fertilized oocytes inside the genital pinnules (Fig. 3b). The same occurs in *Dorometra sesokonis* Obuchi, Kogo & Fujita, 2009 and *Antedon bifida* (Pennant, 1777) (Lahaye and Jangoux 1985; Obuchi et al. 2010). The embryos pass from the ovary into the marsupium, which is a pocket-like groove on the side of the genital pinnule, and are fertilized there (Mortensen 1918). We report here for the first time that *P. nutrix* sperm has a spherical head (up to 4 μm) and free flagellum (Fig. 5a, b). Although Franzen (1956) and Hodgson et al. (2009) proposed a correlation between sperm shape and method of fertilization, e.g., the spherical head with external fertilization, in which shed eggs and sperm are released into the seawater, Holland (1991) and Haig and Rouse (2008) pointed out inconsistencies between sperm shape and fertilization method in other feather stars, e.g., a sperm shape characteristic of external fertilizers in the brooding species *Aporometra wilsoni* (Haig and Rouse 2008), *Phrixometra longipinna* (Carpenter, 1888), and *Eumorphometra marri* John, 1938 (John 1939). Although *P. nutrix* is a brooding species, the fact that its sperm do not cross any membrane to fertilize eggs may eliminate possible selection for any specialized morphology, as is the case with *I. vivipara* (Holland 1976; Pertossi et al. 2019). Several *Antedon* species, although these are external brooders, have sperm that is “arguably” of the primitive type, characteristic of external fertilization (Haig and Rouse 2008). So, this is similar to the case of *P. nutrix*.

Crinoids have seven distinct life stages, embryo, uniformly ciliated larvae, auricularia, doliolaria, cystidean, pentacrinoid, and the adult (Chia et al. 1986; Holland 1991; Balser 2002; Nakano et al. 2003). The doliolaria is a barrel-shaped larva with four or five bands of locomotory cilia (Hendler et al. 1995; Balser 2002). The time interval from hatching (in free-spawning species) or larval release (in brooding

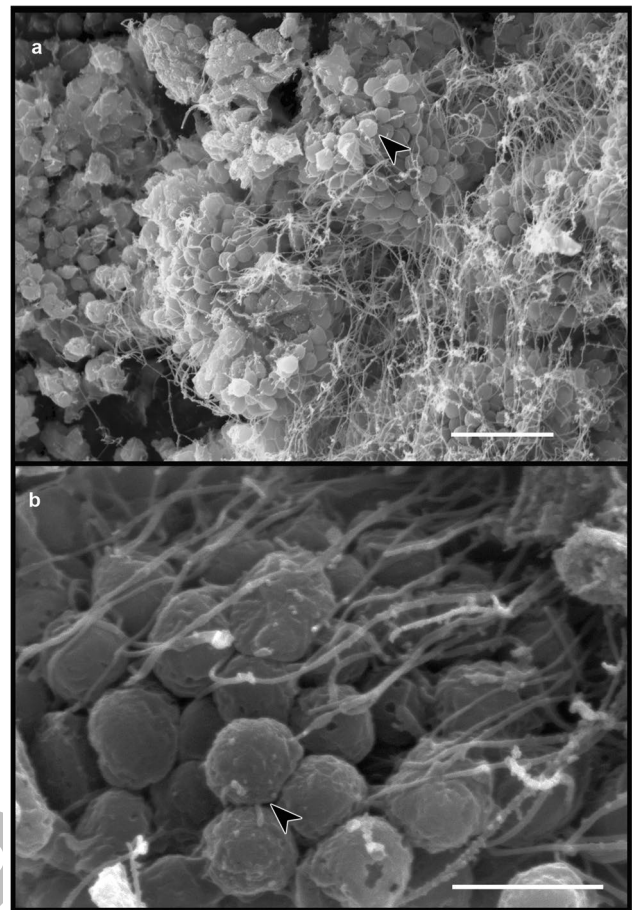


Fig. 5 Sperm in the male gonad of *Phrixometra nutrix*. SEM images. **a** Male gonad lumen, arrow indicates spermatozoa; **b** details of sperm (arrow). Scale bars a 20 μm , b 5 μm

species) to settlement spans a wide range from hours to days or months. The pelagic stage in *Florometra serratissima* (Clark, 1907) (Mladenov and Chia 1983) lasts 2 weeks, in *Antedon serrata* Clark, 1908 (Kotsuka 2001) 3 weeks, and in *Promachocrinus kerguelensis* Carpenter, 1879 (McClintock and Pearse 1987) up to 3 months. Although *P. kerguelensis* reflecting maybe the widest geographical distribution of any Antarctic crinoid likely consists of at least two cryptic species, and that, although all are sympatric and circumpolar, they exhibit variations in genetic connectivity (Mortensen 1920; Dearborn and Rommel 1969; McClintock and Pearse 1987; Hemery et al. 2012). Although the distribution of *Isometra vivipara* and *Phrixometra nutrix* extends from southern South America to the Scotia Arc, they may be cryptic species as have been found in other crinoids (Eléaume et al. 2014). For the Marine Protected Area Namuncurá/Burdwood Bank (MPA N/BB), we found both species in gregarious form but *I. vivipara* in greater abundance ($N=197$) than *P. nutrix* ($N=23$) (see Fig. 1, Table 1). The two final larval stages (cystidean and pentacrinoid) of *I. vivipara* were found

attached to several surfaces, including the cirri of the mother, juveniles, males, and on hard substrates (Pertossi et al. 2019). This suggests an extended free-swimming larval period, which reflects its wider distribution, from southern Brazil to the current study area. Conversely, *P. nutrix* brooding its larvae to the juvenile stage in the genital pinnule, without releasing doliolaria larvae, could also support the differences observed in the distributions and abundances of both species in MPA N/BB.

Lawrence (1987) defined brooding as the association of embryos and juveniles with the females. For some years now, some authors have proposed vicariance as a key factor for the unusually high number of benthic marine invertebrate species in the Southern Ocean with non-pelagic development (brooding). For class Crinoidea, one of the major taxa in Comatulidina, in terms of extant species richness, is Antedonidae. Most brooding species, including *I. vivipara* and *P. nutrix*, belong in this family (Mortensen 1920; Haig et al. 2012; Obuchi et al. 2009). The results of several studies have suggested Antedonidae as polyphyletic. Brooding species such as *Isometra* spp. are structured into distinct genetic lineages, restricted to specific areas. This could be the result of population isolation during glacial events, and poor recolonization potential during interglacial periods (Hemery et al. 2013; Rouse et al. 2013; Eléaume et al. 2014). Reports of parental care in various phyla in SWA and Antarctic waters have been increasing for several years (Gil et al. 2009; Brogger et al. 2010; Gil et al. 2011; Martínez et al. 2011; Brogger et al. 2013a; Eléaume et al. 2014; Berecoechea et al. 2017; Lauretta and Penchaszadeh 2017; Martínez and Penchaszadeh 2017; Rivadeneira et al. 2017; Pérez et al. 2017; Averbuj et al. 2018; Fraysse et al. 2018; Martínez et al. 2018; Sánchez et al. 2018; Flores et al. 2019; Pertossi et al. 2019; Teso and Penchaszadeh 2019; Fraysse et al. 2020; Lauretta et al. 2020; Martínez et al. 2020). Given this, it would not be surprising to find more cases of parental care among crinoids in the SWA. Brooding is a feature that contributes to the identification of species. All the information above shows that, although plenty of data exists for both species, much remains to be learned about these species and crinoids worldwide.

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Declarations

Conflict of interest The authors declare no competing interests.

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. The study is compliant with CBD and Nagoya protocols.

Author contribution RP and MM conceived and designed research. RP conducted experiments. RP and MM analyzed data. RP wrote the manuscript. PP and MM contributed in writing the manuscript. All authors read and approved the manuscript.

References

- Andersson KA (1904) Brutpflege bei *Antedon hirsuta* Carpenter. In: Lithographisches Institut des Generalstabs (eds). Wiss Ergeb Schwedische Südpolar-Exped 5(1):1–7.
- Averbuj A, Penchaszadeh P, Pastorino G (2018) Egg masses and development of *Falsilunatia eltanini* (Mollusca: Gastropoda): A deep-sea naticid from southwestern Atlantic Canyon. Mar Biol. <https://doi.org/10.1007/s00227-018-3337-8>
- Balser EJ (2002) Phylum Echinodermata: Crinoidea. In: Young CM (ed) Atlas of Marine Invertebrate Larvae. Academic Press, London, pp 463–483
- Bell FJ (1888) Notes on echinoderms collected at Port Phillip by Mr. J Bracebridge Wilson Ann Mag Nat Hist 6:401–406
- Berecoechea JJ, Brogger MI, Penchaszadeh PE (2017) New evidence of brooding in the deep-sea brittle star *Astrotoma agassizii* Lyman, 1876 from a South Western Atlantic Canyon. Deep Sea Res 127:105–110. <https://doi.org/10.1016/j.dsr.2017.08.007>
- Bishop JDD, Ryland JS (1991) Storage of exogenous sperm by the compound ascidian *Diplosoma listerianum*. Mar Biol 108:111–118. <https://doi.org/10.1007/BF01313478>
- Bohn J (2009) Crinoidea - Sea lilies and feather stars. In: Häussermann V, Försterra G (eds) Marine Benthic Fauna of Chilean Patagonia. Nature in Focus, Santiago, pp 793–800
- Bohn JM, Heß M (2014) The Antarctic holothurian genus *Echinopso-lus* Gutt, 1990 (Dendrochirotida, Cucumariidae): brood pouches, spermatozoa, spermatozeugmata and taxonomic implications. Zootaxa 3841:573–591
- Brogger MI, Martínez MI, Penchaszadeh PE (2010) Reproduction of the sea urchin *Arbacia dufresnii* (Echinoidea: Arbaciidae) from Golfo Nuevo, Argentina. J Mar Biol Assoc UK 90:1405–1409. <https://doi.org/10.1017/S0025315410000445>
- Brogger MI, Gil DG, Rubilar T, Martínez MI, Díaz de Vivar ME, Escollar M, Epherra L, Pérez AF, Tablado A (2013a) Echinoderms from Argentina: biodiversity, distribution and current state of knowledge. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderm Research and Diversity in Latin American. Springer-Verlag, Berlin, pp 359–402
- Brogger MI, Martínez MI, Zabala S, Penchaszadeh PE (2013b) Reproduction of *Ophioplocus januarii* (Echinodermata: Ophiuroidea):

- a continuous breeder in northern Patagonia. *Argentina Aquat Biol* 19:275–285. <https://doi.org/10.3354/ab00537>
- Carpenter PH (1888) Report on the Crinoidea. Second Part—Comatulæ. Report on the Challenger Expedition, London. 26: 1–357
- Chia FS, Burke RD, Koss R, Mladenov PV, Rumrill SS (1986) Fine structure of the Doliolaria Larva of the Feather Star *Florometra serratissima* (Echinodermata: Crinoidea), With Special Emphasis on the Nervous System. *J Morphol* 189:99–120
- Clark AH (1907) New genera of recent free crinoids. *Smithson Misc Collns* 50:343–365
- Clark AH (1908) New genera of unstalked crinoids. *Proc Biol Soc Wash* 21:125–136
- Clark AH (1909a) *Comatilia*, a remarkable new genus of unstalked crinoids. *Proc US natn Mus* 36:361–367
- Clark AH (1909b) New genera and higher groups of unstalked crinoids. *Proc Biol Soc Wash* 22:173–178
- Clark AH (1915) A monograph of the existing crinoids. Vol. 1. The comatulids. *Bull US Natl Mus.* 82(1):1–406
- Clark AH (1917) A revision of the crinoid family Antedonidae, with the diagnoses of nine new genera. *J Wash Acad Sci* 7(5):127–131
- Clark AH (1921) A monograph of the existing crinoids. Vol. 1. The comatulids. *Bull USA Natl Mus.* 82(2):1–795
- Clark AH (1923) Crinoidea The Danish Ingolf-Expedition Copenhagen 4(5):1–60
- Clark AH (1931) A monograph of the existing crinoids. Vol. 1. The comatulids. *Bull USA Natl Mus.* 82(3):1–816
- Clark AH (1937) Crinoidea. *Sci Rep Aust Antarct Exped.* 8(a):5–18
- Clark AH (1941) A monograph of the existing crinoids. Vol. 1. The comatulids. *Bull US Natl Mus* 82(4a):1–603
- Clark AH, Clark AM (1967) A monograph of the existing crinoids, Volume 1. The comatulids. Part 5 Suborders Oligophreata (concluded) and Macrophreata. *Bull US Natl Mus* 82:1–860
- Clouse RM, Linchangco GV, Kerr AM, Reid RW, Janies DA (2015) Phylotranscriptomic analysis uncovers a wealth of tissue inhibitor of metalloproteinases variants in echinoderms. *R Soc Open Sci* 2:1–14. <https://doi.org/10.1098/rsos.150377>
- Cuénot L (1948) Anatomie, éthologie et systématique des échinodermes. In: Grassé PP (ed) *Traité de zoologie*. Paris, Masson. 11: 32–75
- Dawidoff C (1948) Embryologie des échinodermes. In: Grassé PP (ed) *Traité de zoologie*. Paris, Masson. 11: 277–363
- Dearborn JH, Rommel JA (1969) Crinoidea. *Antarctic Map Folio Ser* 11:35–36
- Eckelbarger KJ, Riser NW (2013) Derived sperm morphology in the interstitial sea cucumber *Rhabdomolgus ruber*, with observations on oogenesis and spawning behavior. *Invertebr Biol* 132(3):270–281. <https://doi.org/10.1111/ivb.12030>
- Eckelbarger KJ, Young CM, Cameron JL (1989) Ultrastructure and development of dimorphic sperm in the abyssal echinoid *Phrisocystis multispina* (Echinodermata: Echinoidea): Implications for deep sea reproductive biology. *Biol Bull-US* 176:257–271
- Eléaume M, Baumiller TK, Améziane N (2001) Developmental mode, egg size, larval size and some evolutionary considerations in comatulids (Crinoidea; Echinodermata). In *Echinoderm research 2001*. Proc 6th Eur Conf, Banyuls-sur-mer. 3–7
- Eléaume M, Améziane N, Park YH (2004) Re-evaluation of the systematics of two deep-sea species of *Thalassometra* (Echinodermata: Crinoidea) and its biogeographical implications. *J Nat Hist* 38:1949–1968. <https://doi.org/10.1080/0022290310001613566>
- Eléaume M, Bohn JM, Roux M, Améziane N (2012) Stalked crinoids (Echinodermata) collected by the R/V Polarstern and Meteor in the south Atlantic and in Antarctica. *Zootaxa* 3425:1–22. <https://doi.org/10.11646/zootaxa.3425.1.1>
- Eléaume M, Hemery LG, Roux M, Améziane N (2014) Southern ocean crinoids. In: Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz Cd, Van de Putte AP, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y (eds) *Biogeographic atlas of the southern ocean*. SCAR, Cambridge, pp 208–212
- Flores JN, Brogger MI, Penchaszadeha PE (2019) Reproduction and development of the brooding sea urchin *Austrocidaris canaliculata* from deep-sea off Argentina. *Deep-Sea Res I* 143:35–42. <https://doi.org/10.1016/j.dsr.2018.11.012>
- Franzen A (1956) On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool Bidr Upps* 31:355–482
- Frayse CP, Calcagno JA, Pérez AF (2018) Asteroidea of the southern tip of South America, including Namuncurá Marine Protected Area at Burdwood Bank and Tierra del Fuego Province. *Argentina Polar Biol* 41:2423–2433
- Frayse CP, Boy CC, Becker YA, Calcagno JA, Pérez AF (2020) Brooding in the Southern Ocean: The Case of the Pterasterid Sea Star *Diplopteraster verrucosus* (Sladen, 1882). *Biol Bull* 239:000–000. <https://doi.org/10.1086/709664>
- Giese AC, Pearse JS, Pearse VB (1991) Reproduction of marine invertebrates. The Boxwood Press 6:247–292
- Gil DG, Zaisso HE, Tolosano JA (2009) Brooding of the sub-Antarctic heart urchin, *Abatus cavernosus* (Spatangoida: Schizasteridae), in southern Patagonia. *Mar Biol* 156:1647–1657. <https://doi.org/10.1007/s00227-009-1200-7>
- Gil DG, Escudero G, Zaisso HE (2011) Brooding and development of *Anasterias minuta* (Asteroidea: Forcipulata) in Patagonia. *Argentina Mar Biol* 158:2589–2602. <https://doi.org/10.1007/s00227-011-1760-1>
- Gislén T (1924) Echinoderm studies. *Zool Bidrag från Uppsala* 9:330
- Haig JA, Rouse GW (2008) Larval development of the featherstar *Aporometra wilsoni* (Echinodermata: Crinoidea). *Invertebr Biol* 127(4):460–469. <https://doi.org/10.1111/j.1744-7410.2008.00134.x>
- Haig JA, Gillanders BM, Rouse GW (2012) Live fast, die young: the life cycle of the brooding feather star *Aporometra wilsoni* (Echinodermata: Crinoidea). *Invertebr Biol* 131:235–243. <https://doi.org/10.1111/j.1744-7410.2012.00270.x>
- Hasan I, Gerdol M, Fujii Y, Ozeki Y (2019) Functional characterization of OXYL, a SghC1qDC LacNac-specific lectin from the crinoid feather star *Anneissia japonica*. *Mar Drugs*. 17:136. <https://doi.org/10.3390/md17020136>
- Hays B (2016) Can skeletal morphology support new molecular phylogenies of Antedonidae (Crinoidea: Comatulida)? Master's Thesis. Nova Southeastern University. 1–268
- Healy JM, Rowe FWE, Anderson DT (1988) Spermatozoa and spermiogenesis in *Xyloplax* (Class Concentricycloidea): a new type of spermatozoon in the Echinodermata. *Zool Scr* 17:308–309. <https://doi.org/10.1111/j.1463-6409.1988.tb00105.x>
- Helgen LE, Rouse GW (2006) Species delimitation and distribution in *Aporometra* (Crinoidea: Echinodermata): endemic Australian featherstars. *Invertebr Syst* 20:395–414. <https://doi.org/10.1002/ejoc.200500775>
- Hemery LG, Eléaume M, Roussel V, Améziane N, Gallut C, Steinke D, Cruaud C, Couloux A, Wilson NG (2012) Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid species *Promachocrinus kerguelensis* (Echinodermata). *Mol Ecol* 21(10):2502–2518. <https://doi.org/10.1111/j.1365-294X.2012.05512.x>
- Hemery LG, Roux M, Ameziane N, Eleaume M (2013) High-resolution crinoid phyletic inter-relationships derived from molecular data. *Mar Biol* 54:511–523
- Hendler G, Miller JE, Pawson DL, Kier PM (1995) Sea stars, sea urchins and allies. Echinoderms of Florida and the Caribbean. Smithsonian Institution Press, Washington, pp 43–56
- Hess H, Messing CG (2011) Articulata. In: Seldon, P. (ed.) and W.I. Ausich (Coordinating Author). *Treatise on Invertebrate*

- Paleontology, Part T, Echinodermata 2 Revised, Crinoidea 3. University of Kansas Press, Lawrence, Kansas. xxix + 261 p
- Hodgson AN, Eckelbarger KJ, Young CM (2009) Sperm ultrastructure and spermatogenesis in the hydrothermal vent gastropod *Rhynchopelta concentrica* (Peltospiridae). *J Moll Stud* 75:159–165. <https://doi.org/10.1093/mollus/eyp014>
- Holland ND (1976) Morphologically specialized sperm from the ovary of *Isometra vivipara* (Echinodermata – Crinoidea). *Acta Zool* 57:147–152. <https://doi.org/10.1111/j.1463-6395.1976.tb00221.x>
- Holland ND (1991) Echinodermata: Crinoidea. In: Giese AC, Pearse JS, Pearse VB (eds) *Reproduction of Marine Invertebrates. Echinoderms and Lophophorates*. Boxwood Press, London, pp 247–299
- Hyman LH (1955) *Echinodermata*. McGraw-Hill Book Company, New York. 4: 34–118
- Jamieson BGM (2000) Echinodermata. In: *Reproductive Biology of Invertebrates*. 356
- John DD (1937) Antarctic Comatulids. *Proceedings Linnean Society London*. 149 (2) 85–89. <https://doi.org/10.1111/j.1095-8312.1937.tb01188.x>
- John DD (1938) Crinoidea. *Discov Rep* 18:121–222
- John DD (1939) Crinoidea. *Br Aust NZ Ant Res Exp Ser B* 4:189–212
- Jones CE, Zandawala M, Semmens DC, Anderson S, Hanson GR, Janies D, Elphick MR (2016) Identification of a neuropeptide precursor protein that gives rise to a “cocktail” of peptides that bind Cu (II) and generate metal-linked dimers. *Biochim Biophys Acta* 1860:57–66. <https://doi.org/10.1016/j.bbagen.2015.10.008>
- Kammer TW, Bartels C, Ausich WI (2015) Presumed postlarval pentacrinoids from the Lower Devonian Hunsrück Slate, Germany, Lethaia 49:307–311. <https://doi.org/10.1111/let.12147>
- Kotsuka H (2001) Observations on spawning behavior, eggs, and larvae of the comatulid, *Antedon serrata* in aquarium tanks. *J Jap Assoc Zool Aqua* 42:124–132
- Lahaye MC, Jangoux M (1985) Post spawning behavior and early development of the comatulid crinoid, *Antedon bifida*. In: Keegan BF, O'Connor BDS (eds) *Echinodermata: proceeding of the fifth international echinoderms conference*. Balkema, Rotterdam. 181–184. <https://doi.org/10.1201/9781003079224-38>
- Lamarck JBM (1816) Histoire naturelle des animaux sans vertèbres. In: Troisième T (ed) *Les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s’y rapportent*. Deterville/Verdière, Paris, pp 1–586
- Lauretta D, Penchaszadeh PE (2017) Gigantic oocytes in the deep sea black coral *Dendrobathypathes grandis* (Antipatharia) from the Mar del Plata submarine canyon area (southwestern Atlantic). *Deep Sea Res Part I* 128:109–114. <https://doi.org/10.1016/j.dsr.2017.08.011>
- Lauretta D, Vidos C, Martinez MI, Penchaszadeh PE (2020) Brooding in the deep-sea sea anemone *Actinostola crassicornis* (Hertwig, 1882) (Cnidaria: Anthozoa: Actiniaria) from the southwestern Atlantic Ocean. *Polar Biol* 43:1353–1361. <https://doi.org/10.1007/s00300-020-02713-3>
- Lawrence JM (1987) *A functional biology of Echinoderms*. The Johns Hopkins University Press, Baltimore
- Marr JWS (1963) Unstalked crinoids of the Antarctic continental shelf, notes on their natural history and distribution. *Philos Trans R Soc Lond B Biol Sci* 246:327–379. <https://doi.org/10.1098/rstb.1963.0009>
- Martinez M, Alba-Posse E, Lauretta D, Penchaszadeh PE (2018) Developmental stages in the brooding sea cucumber *Cladodactyla crocea* (Lesson, 1830) in the Southwestern Atlantic Ocean. *Polar Biol* 41:1237–1244. <https://doi.org/10.1007/s00300-018-2280-y>
- Martinez M, Alba-Posse E, Lauretta D, Penchaszadeh PE (2020) Reproductive features in the sea cucumber *Pentactella perrieri* (Ekman, 1927) (Holothuroidea: Cucumariidae): a brooding hermaphrodite species from the southwestern Atlantic Ocean. *Polar Biol* 43:1383–1389
- Martinez MI, Penchaszadeh PE (2017) A new species of brooding *Psolidae* (Echinodermata: Holothuroidea) from deep-sea off Argentina. *Southwestern Ocean. Deep-Sea Res II* 146:13–17. <https://doi.org/10.1016/j.dsr2.2017.05.007>
- Martinez MI, Giménez J, Penchaszadeh PE (2011) Reproductive cycle of the sea cucumber *Psolus patagonicus* Ekman, 1925, off Mar del Plata, Buenos Aires, Argentina. *Invertebr Reprod Dev* 55:124–130. <https://doi.org/10.1080/07924259.2011.553423>
- McClintock JB, Pearse JS (1987) Reproductive biology of the common Antarctic crinoid *Promachocrinus kerguelensis* (Echinodermata: Crinoidea). *Mar Biol* 96:375–383
- McEdward LR, Carson SF, Chia F (1988) Energetic content of eggs, larvae, and juveniles of *Florometra serratissima* and the implications for the evolution of crinoid life histories. *Invertebr Reprod Dev* 13:9–22. <https://doi.org/10.1080/01688170.1988.10510338>
- McEdward LR, Miner BG (2001) Larval and life-cycle patterns in echinoderms. *Can J Zool* 79:1125–1170. <https://doi.org/10.1139/z00-218>
- Messing CG (1977) Living Comatulids. *Paleontological Society* 3:3–30. <https://doi.org/10.1017/S1089332600000188>
- Messing CG (1984) Brooding and paedomorphosis in the deep-water feather star *Comatilia iridometrifomis* (Echinodermata: Crinoidea). *Mar Biol* 80:83–91. <https://doi.org/10.1007/BF00393131>
- Meyer DL, Macurda DB (1977) Adaptive radiation of the comatulid crinoids. *Paleobiology* 3:74–82. <https://doi.org/10.1017/S0094837300005121>
- Mironov AN, Pawson DL (2010) A new genus and species of Western Atlantic sea lily in the family Septocrinidae (Echinodermata: Crinoidea: Bourgueticrinida). *Zootaxa* 2449:49–68. <https://doi.org/10.5281/zenodo.195174>
- Mladenov PV (1987). Phylum Echinodermata, Class Crinoidea. In: Strathmann MF (ed) *Reproduction and Developmental in Marine Invertebrates of the Northern Pacific Coast*. Seattle and London, 597–606.
- Mladenov PV, Chia FS (1983) Development, settling behaviour, metamorphosis and pentacrinoid feeding and growth of the feather star *Florometra serratissima*. *Mar Biol* 73:309–323
- Mortensen TH (1917) *Notocrinus virilis* n.g., n.sp., a new viviparous crinoid from the Antarctic Sea. *Vidensk Medd fra Dansk naturh Foren* 68:205–208
- Mortensen TH (1918) The Crinoidea of the Swedish Antarctic Expedition. *Wiss Ergebn Schwed Südpolar Exp* 8:1–23
- Mortensen TH (1920) Studies in the development of crinoids. *Pap Dep Mar Biol Carnegie Inst Wash* 16:1–94
- Mutschke E, Rios C (2006) Distribución espacial y abundancia relativa de equinodermos en el estrecho de Magallanes. *Chile Ciencia y Tecnología del Mar* 29(1):91–102
- Nakano H, Hibino T, Oji T, Hara Y, Amemiya S (2003) Larval stages of a living sea lily (stalked crinoid echinoderm). *Nature* 421:158–160. <https://doi.org/10.1038/nature01236>
- Norman AM (1865) On the genera and species of British Echinodermata. 1. Crinoidea, Ophiuroidea, Asteroidea. *Ann. mag. nat. hist.* (series 3) 15:98–129
- Obuchi M, Fujita Y, Nakano Y, Uehara T, Motokawa T (2010) Reproductive biology and early life history of the hermaphroditic feather star *Dorometra sesokonis* (Echinodermata: Crinoidea). *Mar Biol* 157:1191–1201. <https://doi.org/10.1007/s00227-010-1399-3>
- Obuchi M, Ichizo K, Yoshihisa F (2009) A new brooding feather star of the genus *Dorometra* (Echinodermata: Crinoidea: Comatulida: Antedonidae) from the Ryukyu Islands, southwestern Japan. *Zootaxa* 2008:61–68. <https://doi.org/10.5281/zenodo.185734>

- Pandia TJ (2018) Reproduction and development in mollusca (reproduction and development in aquatic invertebrates), vol 2. CRC Press, TaylorandFrancis Group, pp 1–320
- Pawson DL (2007) Phylum Echinodermata. *Zootaxa* 1668:749–764. <https://doi.org/10.5281/zenodo.180113>
- Pearse JS, Bosch I (1994) Brooding in the Antarctic: ostergren had it nearly right. In: David B, Guille J, Féral P, Roux M (eds) *Echinoderms through time*. Balkema, Rotterdam, pp 111–120
- Pennant T (1777) Crustacea. Mollusca. Testacea. London. *British Zoology*. 4: 1–154
- Pérez AF, Fraysse C, Boy CC, Epherra L, Calcagno J (2017) Reproductive biology and energetics of the brooding sea star *Anasterias antarctica* (Echinodermata: Asteroidea) in the Beagle Channel, Tierra del Fuego, Argentina. *Rev. Biol. Trop.* 65: S221–S232. <https://doi.org/10.15517/RBT.V6511-1.31690>
- Pertossi RM, Brogger MI, Penchaszadeh PE, Martinez MI (2019) Reproduction and developmental stages in the crinoid *Isometra vivipara* Mortensen, 1917 from the southwestern Atlantic. *Polar Biol* 42:807–816. <https://doi.org/10.1007/s00300-019-02477-5>
- Rivadeneira PR, Brogger MI, Penchaszadeh PE (2017) Aboral brooding in the deep water sea star *Ctenodiscus australis* Lütken, 1871 (Asteroidea) from the Southwestern Atlantic. *Deep Sea Res I* 123:105–109. <https://doi.org/10.1016/j.dsr.2017.03.011>
- Rouse GW, Jermiin LS, Wilson NG, Eeckhaut I, Lanterbecq D, Oji T, Young CM, Browning T, Cisternas P, Helgen LE, Stuckey M, Messing CG (2013) Fixed, free, and fixed: the fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian-Triassic origin. *Mol Phylogenetics Evol* 66(1):161–181. <https://doi.org/10.1016/j.ympev.2012.09.018>
- Roux M, Messin CG, Améziane N (2002) Artificial keys to the genera of living stalked crinoids (Echinodermata). *Bull Mar Sci* 70(3):799–830
- Sánchez N, Pastorino G, Penchaszadeh PE (2018) Giant eggs in the gastropod *Aforia obesa* (Conoidea: Cochlespiridae) in Southwestern Atlantic deep-waters. *Zool Anz* 276:94–99
- Solís-Marín FA, Alvarado JJ, Abreu-Pérez M, Aguilera O, Alió J, Bacallado-Aránega JJ, Barraza E, Benavides-Serrato M, Benítez-Villalobos F, Betancourt Fernández L, Borges M, Brandt M, Brogger MI, Borrero-Pérez GH, Buitrón-Sánchez BE, Campos LS, Clemente S, Cohen-Renfijo M, Coppard S, Costa-Lotufu LV, Del Valle-García R, Díaz Y, Díaz de Vivar ME, Díaz-Martínez JP, Durán-González A, Epherra L, Escolar M, Francisco V, Freire CA, García-Arrarás JE, Gil DG, Guarderas P, Hadel VF, Hearn A, Hernández JC, Hernández-Delgado EA, Herrera-Moreno A, Herrero-Pérezrul MD, Hooker Y, Honey-Escandón MBI, Lodeiros C, Luzuriaga M, Manso CLC, Martín A, Martínez MI, Martínez S, Moro-Abad L, Mutschke E, Navarro JC, Neira R, Noriega N, Palleiro-Nayar JS, Pérez AF, Pérez-Ruzafa A, Prieto-Ríos E, Reyes J, Rodríguez R, Rubilar T, Sancho-Mejía T, Sangil C, Silva JRM, Sonnenholzner JI, Ventura CR, Tablado A, Tavares Y, Tiago CG, Tuya F, Williams SM (2013) Appendix. In: Alvarado JJ, Solís-Marín FA (eds) *Echinoderm Research and Diversity in Latin America*. Springer, Berlin, p 116
- Souto V, Escolar M, Genzano G, Bremec C (2014) Species richness and distribution patterns of echinoderms in the southwestern Atlantic Ocean (34–56°S). *Sci Mar* 78(2):269–280. <https://doi.org/10.3989/scimar.03882.26B>
- Speel JA, Dearborn JH (1983) Comatulid crinoids from the R/V Eltannin cruises in the Southern Ocean. *Antarct Res Ser* 38:1–60
- Teso V, Penchaszadeh PE (2019) Development of the gastropod *Trochita pileus* (Calyptraeidae) in the sub-Antarctic Southwestern Atlantic. *Polar Biol* 42:171–178
- Vaney C (1938) Scientific Results of the Voyage of SY Scotia, 1902–04: The Crinoidea. Department of Zoology, BNMH, XXVI 1: 661
- Wilton DW, Pirie JHH, Brown RNR (1908) Zoological Log. *Sci Res Voy “Scotia”*. 4(1): 105
- World Register of Marine Species (2021) Available from <http://www.marinespecies.org> at VLIZ. <https://doi.org/10.14284/170>
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