Polar Biology (2018) 41:1237–1244
https://doi.org/10.1007/s00300-018-2280-y

ORIGINAL PAPER

Developmental stages in the brooding sea cucumber *Cladodactyla crocea* (Lesson, 1830) in the southwestern Atlantic Ocean

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Received: 17 August 2017 / Revised: 31 January 2018 / Accepted: 2 February 2018 / Published online: 15 February 2018

Abstract

Holothuroids of family Cucumariidae are known to brood their young, and several species from Southern Oceans present different brooding mechanisms, indicating the heterogeneity of this family in this regard. Since few reports analyze the brooding in this family, we studied the reproduction and development of brooders, in the cucumariid *Cladodactyla crocea* (Lesson, 1830), based on samples taken on several cruises between 38° and 55° up to 1738 m depth, from September 2009 to October 2016. Brooder specimens develop a dorsal marsupium where uncleaved eggs of about 0.94 mm are released in the fall and brooded, until juveniles are released in the following spring. Unreleased eggs of about 0.93 mm were also found in the fall, in the gonads. In addition, in the spring samples, we found ten specimens with 15 cleaved eggs of about 1.1 mm and 34 specimens with 2–35 brooded juveniles, in adults of 14.0–20.0 mm of length. Several adults had up to three different developmental stages at the same time: young pentactula (about 1.6 mm), pentactula (about 1.8 mm), and early juveniles (about 2.2 mm). The external brooding behavior of *C. crocea* is consistent with the observations made for other species of Cucumariidae in South America and Antarctica. Brooding is a common feature in species of Cucumariidae from the Southern Hemisphere. External brooding is common in South America and Antarctica specimens, while internal brooding has multiple examples in Australia and New Zealand. These different brooding strategies are discussed after the observations made in *C. crocea*.

Keywords Marsupium · Argentina · Dendrochirotida · Echinodermata · Holothuroidea · Reproduction

Introduction

There is a high number of benthic marine invertebrate species in the Southern Ocean with non-pelagic development (Pearse 1994; Gillespie and McClintock 2007; Pearse et al. 2009). McEuen and Chia (1991), O´Loughlin (1994), Alcock and O´Loughlin (2001), and O´Loughlin et al. (2009) analyzed the different brooding strategies in holothuroids, including Southern Ocean species for which most of the reproductive mechanisms are unknown (Gillespie and McClintock 2007; Brogger et al. 2013; Martinez and Penchaszadeh 2017). Moreover, many new species have been discovered in the past decade, indicating that there is still much to learn about the biology and diversity of holothuroids in the southwestern Atlantic Ocean (SWAO) (Martinez and Brogger 2012; Martinez et al. 2013, 2014; Martinez and Penchaszadeh 2017).

The Cucumariidae (Ludwig 1898) is one of the most diversified brooding families of holothuroids (Alcock and O´Loughlin 2001). Another well-known dendrochirotid family is Psolidae Burmeister 1837, in which brooding beneath the sole is almost the only known protected behavior (McEuen and Chia 1991). In contrast to psolids, in cucumariids there are many different sites of brooding (e.g., internal coelomic sacs, interradial pouches, dorsal marsupium) (Vaney 1925; O´Loughlin and O´Hara 1992; Alcock and O´Loughlin 2001; O´Loughlin et al. 2009; Bohn and Heß 2014).

There are around 40 brood-protecting cucumariids worldwide (Bohn and Heß 2014) and only three of them are from the SWAO, *Cladodactyla crocea* (Lesson 1830), *Trachythyone parva* (Ludwig 1875), and *Pseudrotasfer microincubator* Bohn 2007 (Bohn 2007; O´Loughlin et al. 2009). The

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last one is an internal brooder (intraovarian), a particular behavior known for only a few species around the world (Alcock and O´Loughlin 2001; Bohn 2007; O´Loughlin et al. 2009).

Thomson (1876) was the first in presuming brooding by *C. crocea*, after observing young on the dorsal side of adult specimens. Studer (1880), Ludwig (1898, 1904), and Ekman (1925) examined the anatomy of adults and juveniles of *C. crocea* from different collections. Recently, O´Loughlin et al. (2009, 2014) reported the presence of a marsupium in the dorsal side of *C. crocea* specimens, collected in the Malvinas/Falkland Islands.

The main goal of this work is to study the developmental stages, from egg to juvenile, of *C. crocea* and to increase knowledge about its brooding season, mechanism of brooding, and reproductive biology. Besides, we compare the ossicles and diagnostic features of the developmental stages with those of adults to help in the identification of free juveniles. In addition, *C. crocea* is compared with other brooding cucumariids with a restricted distribution. Finally, the brooding strategies and distribution of Cucumariidae are analyzed to establish connections between reproductive modes and its relationship with different geographical patterns.

Materials and methods

Specimens of *Cladodactyla crocea* were collected off Argentina in the SWAO. Specimens from multiple expeditions were collected from 38° to 55°S between 0 and 1738 m depth from September 2009 to April 2016 (Table 1). Samples in shallow waters were taken manually, using a dredge trawl or fishing nets on board of the vessel B/O *Puerto Deseado*. A total of 1044 specimens of *C. crocea* (adults

Table 1 Specimens of *Cladodactyla crocea* studied

Station code	Lat (S)	Long (W)	Depth (m)	# Specimens	Date (yyyy-mm-dd)	MACN In
TF E6	54°54′	68º08′	Intertidal	1	2012-03-12	41447
TF E8	54°52′	68°13′	25	4	2012-03-14	41448
CAV IV E1	54°29′	64°57′	111	1	2011-03-15	41449
CAV IV E2-L1	54°00′	65°11′	138	3	2011-03-15	41450
CAV IV E3-L1	51°32′	65°11′	138	3	2011-03-16	41451
CAV IV E2-L2	53°8′	65°11′	138	14	2011-03-16	41452
CAV IV E5-L1	47°48′	65°35′	46	1	2011-03-17	41453
CAV IV E22	39°53′	56°39′	96	1	2011-03-27	41454
BB E26-L24	54°24′	58°29′	135	2 (1 with uncleaved eggs in marsupium)	2016-03-29	41455
BB E26-L27	54°26′	58°30′	138	34	2016-03-29	41456
CAV E21-L107	54°18′	65°50′	72	2	2014-04-02	41457
CAV L27-L88	53°34′	66°32′	84	18	2014-04-02	41458
CAV E10-L122	54°59′	65°19′	128	4	2014-04-03	41459
BB E17-L282	54°38′	61°4′	195	75 (6 with early marsupium development)	2016-04-15	41460
BB E28-L287	54°3′	61°6′	140	1 with cleaved eggs in marsupium	2017-05-08	41461
BB E29-L283	53°49′	61°19′	197	15 (9 adults with cleaved eggs in marsupium)	2017-05-08	41462
TCI L2	39º57′	55°11′	291	30	2012-08-10	41463
TCI L3	38°00′	55°13′	250	102 (11 adults with broods, young pentactula, pentactula and early juvenile, in marsupium)	2012-08-10	41464
TCI L5	37°59′	55°9′	528	3	2012-08-10	41465
TCI L8	37°°58′	54º57′	647	12 (2 adults with broods, pentactula and early juvenile, in marsupium)	2012-08-10	41466
TCI L26	37°52′	53°57′	1738	1	2012-08-15	41467
TCI L32	37°56′	55°12′	319	25	2012-08-17	41468
TCI L33	37°59′	55°12′	308	436 (21 adults with broods young pentactula, pentactula and early juvenile, in marsupium)	2012-08-17	41469
MII E8	38°51′	55°39′	115	150 (38 juveniles)	2009-09-11	41470
MII E9	38°51′	55°35′	140	100 (15 juveniles)	2009-09-11	41471
MII E10-L1	39°05′	58°02′	74	1	2009-09-12	41472
GSJ E56	43°52′	64°14′	74	5	2016-10-25	41473

with and without broods) were identified. Specimens were analyzed, dissected under a stereomicroscope, and deposited at the Museo Argentino de Ciencias Naturales (MACN In) (Table 1). Digital photos of the specimens were taken using a Nikon D800 SLR digital camera. For scanning electron microscope (SEM) examination of the ossicles, small pieces of the body wall (from adults and brooded juveniles) were macerated in sodium hypochlorite solution (55 g Cl/l), rinsed several times in distilled water and ethanol 96%, and then air dried. Finally, the ossicles were transferred to aluminum stubs, metal sputter-coated, and observed under SEM (Philips XL 30).

Results

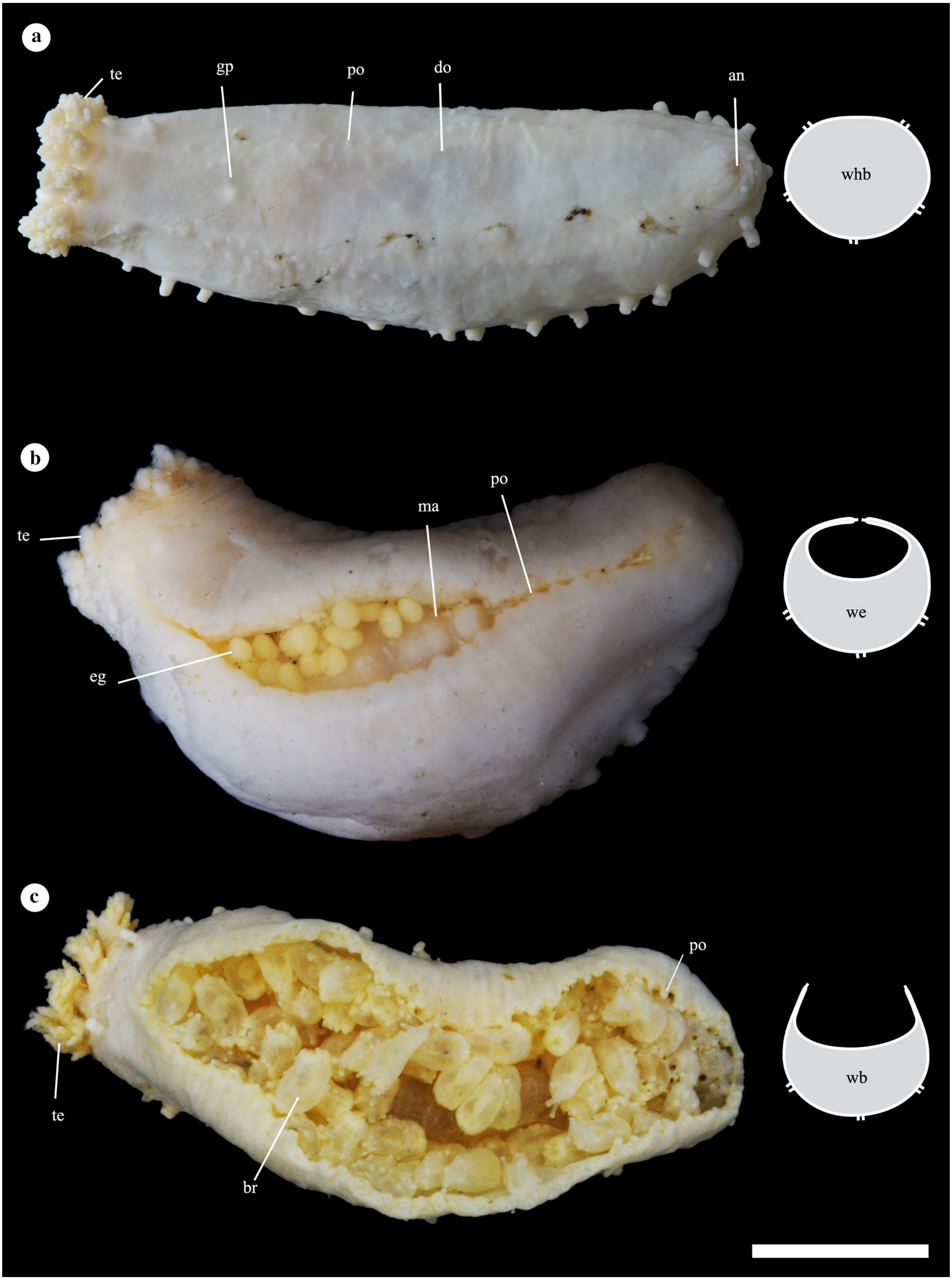
Anatomical differences were visible in the dorsal side of *Cladodactyla crocea* in samples from March and April (autumn) (Fig. 1). In adults with broods, the dorsal ambulacral rows were well developed, connected, and formed a tube. This tube, or marsupium, contained the broods, from uncleaved eggs to brooded juveniles, up to their release (Fig. 1b, c). In some specimens a papilla was observed in the anterior section of the body, and uncleaved eggs were found near the papilla, inside of the marsupium. In specimens without brooded pentactulae or early juveniles, podia were not raised up, or were not visible (Fig. 1a).

Mature gonads with large oocytes of 0.93 ± 0.17 mm ($n = 35$; $N = 7$) in diameter, were found in specimens from April (beginning of autumn). In the same period (beginning of autumn), uncleaved eggs of 0.94 ± 0.14 mm ($n = 11$; $N = 1$) in diameter were observed in the marsupia (Table 2). After this stage (May, autumn–winter) cleaved eggs of 1.07 ± 0.04 mm ($n = 15$; $N = 10$) were found in the marsupia of several specimens (Table 2). Ovaries in August (winter) contained much smaller oocytes 0.07 ± 0.02 mm ($n = 30$; $N = 10$) in diameter, and in late October (spring), oocytes start growing, with a mean diameter size of 0.42 ± 0.05 mm ($n = 5$; $N = 11$). In this season, 34 specimens with 2 to 35 developing broods were found (Fig. 1c) in adults with a size range of 14.0–20.0 mm in length. Broods were found in different stages (Fig. 2, Table 2). The youngest pentactula stage found had undeveloped tentacles and a crown of podia near the anus with a size of 1.55 ± 0.08 mm ($n = 8$) (Fig. 2a, Table 2). The next pentactula stage observed had three developing podia per ambulacrum and a size of 1.82 ± 0.06 mm ($n = 13$) (Fig. 2b, Table 2). Internally, these stages had one non-calcified madreporite, one Polian vesicle, and no signs of a calcareous ring. We found a later stage (early juvenile) in which specimens of 2.17 ± 0.16 mm ($n = 10$) (Table 2) were morphologically similar to the adult, with no podia on the dorsal side and 3 podia in each ambulacrum on the ventral side. Tentacles in these specimens were slightly extended (Fig. 2c, d). Internally, the calcareous ring was delicate and thin. There was one non-calcified madreporite and one Polian vesicle. Respiratory trees in all brooding stages were not developed and the digestive system did not contain food. The ossicles of the pentactula had rods and plates without holes instead of well-developed plates with multiple holes and rods with two holes that are quite common in adults (Fig. 3). After this stage several free juveniles were found, outside the marsupium, in September (spring) with minimum size of 3.20 mm (Table 1).

Discussion

The present study is the first report on the development of *Cladodactyla crocea*. We found eggs in the marsupium (0.94 ± 0.14 mm) and several more inside the gonads (0.93 ± 0.17 mm) indicating that spawning was occurring during autumn. Moreover, also during fall, the specimens carried cleaved eggs in the marsupium (1.07 ± 0.04 mm) and then brooded pentactula or early juveniles. The smallest brooded pentactula we observed had a length of 1.55 ± 0.08 mm and brooded juveniles were of 2.17 ± 0.16 mm in length before release in spring. Thomson (1876), Ludwig (1898), and Ekman (1925) reported brooding in *C. crocea* because they found juveniles in dorsal surface of adults. In particular, Ludwig (1898) and Ekman (1925) suggested more than one brooding period, although in both cases no mention of a marsupia was made. The presence, in this work, of eggs and brooded young inside the marsupia in only one season of the year, suggests one period of reproduction. Besides in late October, we did not find adults with marsupia or any indicative of oocytes release, and the oocytes found were much smaller than the uncleaved eggs found in the marsupia during April and May (0.42 vs. 0.94 mm). O´Loughlin et al. (2009, 2014) found one egg in the marsupia of a single specimen from Malvinas/Falkland Islands (NMV F106967) collected in May. This and our findings suggest a brooding season from May to August (winter). Since youngs are released during spring, we suggest a coupling between the brooding period and the winter season, and youngs are released during the spring, with better conditions during their first free stage (see Andreo et al. 2016).

Previous authors have observed juveniles on the dorsal surface but no reference about the marsupium or brooded stages was made. In *C. crocea* these authors reported juvenile sizes of 1.8 mm (Ekman 1925), 2.0 mm (Ludwig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◂**Fig. 1** Specimens of *Cladodactyla crocea*, dorsal view and transversal draw. **a** adult without brooders (whb), **b** with eggs (we) and **c** with broods (wb). *te* tentacles, *gp* genital papilla, *po* podia, *do* dorsal side, *an* anus, *eg*, eggs, *ma* marsupium, *br* broods. Scale bar 5 mm

1898), and 5.0 mm (Thomson 1876). We found the previous stage, in which brooded young were inside the marsupium (1.55 ± 0.08 mm). Ossicles and external shape of individuals, in pentactula, and early juvenile stages from this study, do not differ from juveniles of 3.7 and 5.0 mm in length showed by Ekman (1925).

Cladodactyla crocea was found in this study along the Argentine coast (38º to 54ºS) up to 1738 meters. Bell (1908) described this species (as *Cucumaria crocea*) from Coulman Island (Antarctica). This is the only report of *C. crocea* for Antarctica (Pawson 1964). The presence of *C. crocea* south of the Beagle Channel has not been confirmed and is doubtful, particularly as O´Loughlin described a congeneric species *Cladodactyla sicinski* (O´Loughlin in O´Loughlin et al. 2013) in Antarctica (O´Loughlin et al. 2013, 2014). Examination of the external anatomy and shape of the ossicles in *C. crocea*, showed no differences between adult specimens along the Argentine coast 38°–54°S (Fig. 3) and adult specimens from Malvinas/Falkland (51°S) studied by O´Loughlin et al. (2014), supporting the wide distribution of this species. Morphological differences, along the distribution, was observed between brooding specimens (with marsupia) and those that were not brooding (without marsupia), as shown by O´Loughlin et al. (2009). Moreover, the presence of a genital papilla was reported previously by O´Loughlin et al. (2014): "genital papilla anterior mid-dorsal in marsupium." Here we confirm this observation. Furthermore, the presence of eggs near the genital papilla could indicate that this structure releases the eggs into the marsupia.

Compared with other cucumariids in the SWAO, the diagnostic ossicles in adults (i.e., rods from the body wall and spinous plates) allow the distinction from *Pentactella* species, *P. leonina* (Semper 1867), and *P. perrieri* (Ekman 1927) that have knobbed plates, and *Hemioedema spectabilis* (Ludwig 1883) that has spectacle-like rods.

There are at least 40 brooding species of Cucumariidae known (Bohn and Heß 2014). This family has an extraordinary number of different types of brooding mechanisms, indicating the heterogeneity and radiation of this aspect (e.g., internal, external, marsupia, brood pouches, and tentacles). Moreover, the concentration of brooding species in southern oceans is high (SWAO, Antarctica, Australia, and New Zealand). From all the kinds of brooding mechanisms, external brooding in all their varieties is common in South America and Antarctica (SAA). In contrast, internal brooding has multiple examples in Australia and New Zealand (ANZ). These different strategies could be related to different conditions between SAA and ANZ and similar physical forces; or similar conditions in each area, then the difference in internal and external brooding resulted from a common ancestor in each area. Both strategies (internal vs external brooding) appear in the Southern Hemisphere. This agrees with the conclusions of Thorson (1950) and Pearse et al. (2009), about the great amount of brooders in the Southern Ocean, but a new idea of thinking about these hypotheses instead of compare brooding vs not brooding is to analyze the different types of brooding. Each brooding mechanism could be affected by different factors. In particular for the cucumariids, the appearance of internal brooding, observed in ANZ species, could reflect different conditions from the presented in SAA. A proper taxonomical study of the whole family Cucumariidae needs to be made, considering the large distribution (worldwide) and brooding examples, in order to study the evolution of the different types of brooding mechanisms and its relationship with the different areas. Moreover a phylogenetic study using molecular, taxonomic, and reproductive characters should reveal how many times brooding arose in this family and if those different modes are the result of separate evolution, or one evolved into another.

Table 2 Developmental stages and broods size from uncleaved egg to early juvenile

Developmental stages	Season	Mean (SD) (mm)	*n*	*N*
Uncleaved eggs	Beginning of autumn	0.94 ± 0.14	11	1
Cleaved eggs	Autumn–winter	1.07 ± 0.04	15	10
Young pentactula	Winter	1.55 ± 0.08	8	34
Pentactula	Winter	1.82 ± 0.06	13	34
Early juvenile	Winter	2.17 ± 0.16	10	34

n number of brooded individuals measured, *N* number of brooding specimens examined

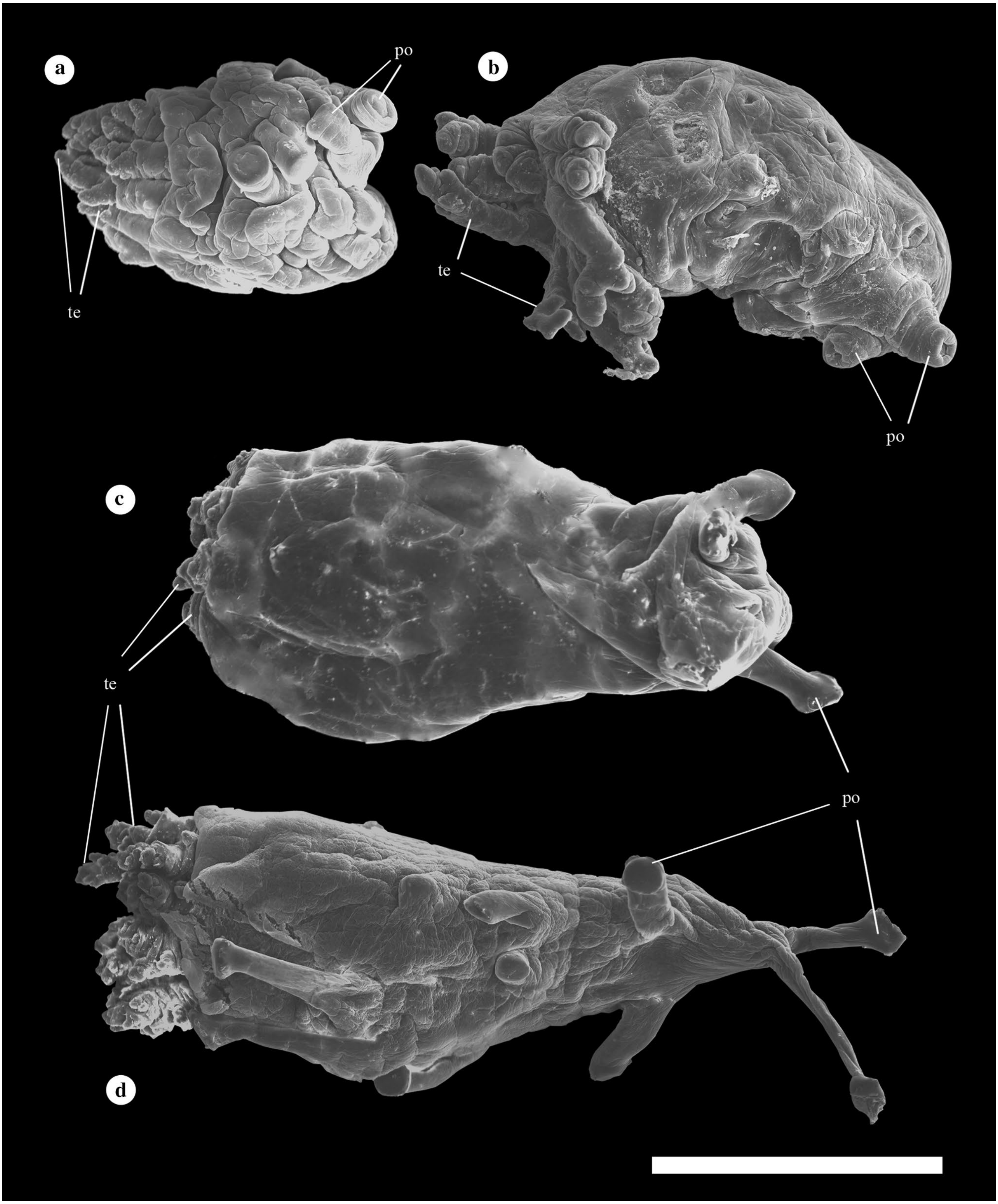

Fig. 2 Broods in three different stages from **a** young pentactula, **b** pentactula, and **c** almost juvenile in dorsal and **d** ventral views. *po* podia, *te* tentacles. Scale bar 1 mm

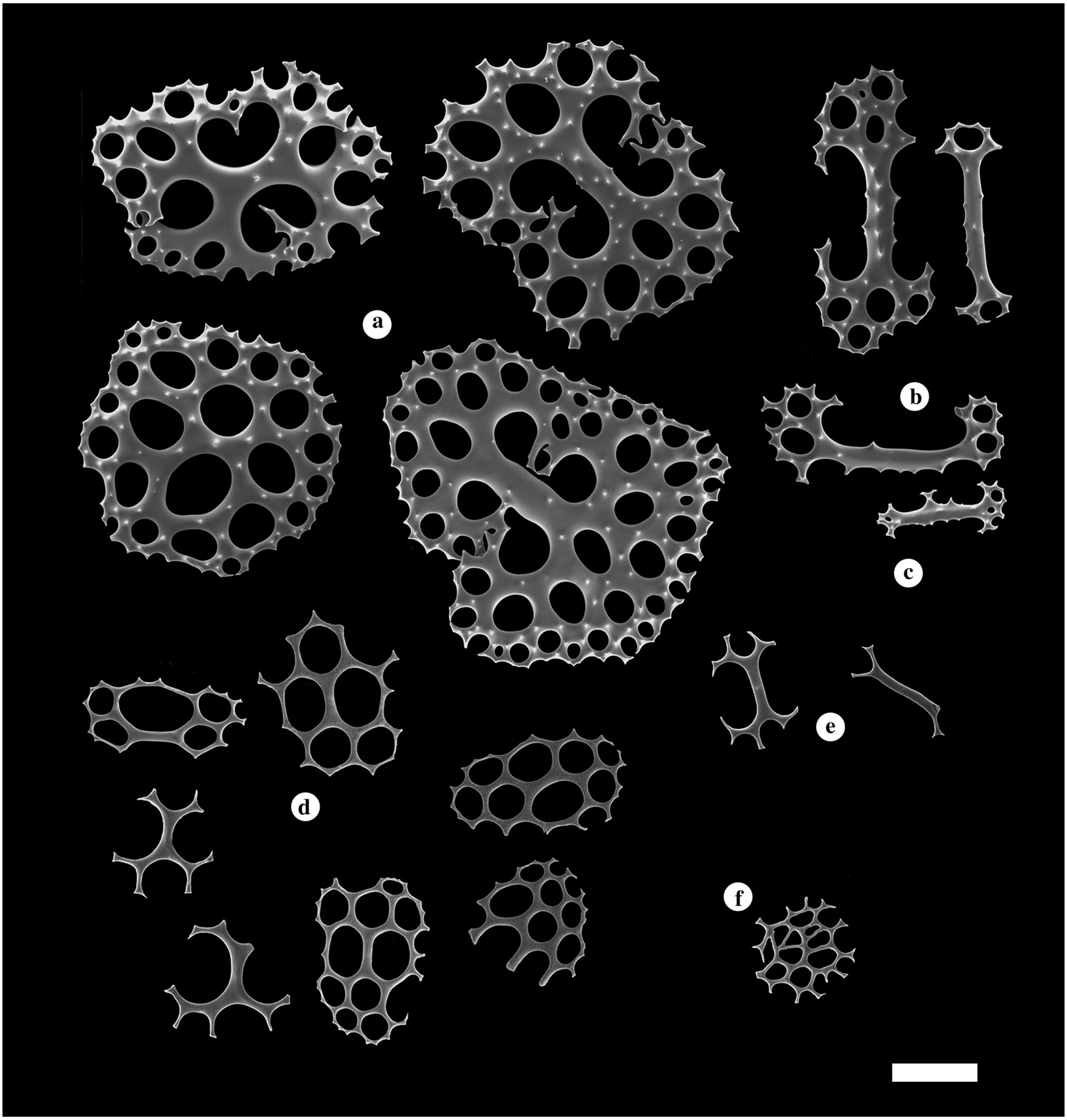

Fig. 3 Ossicles from adult (**a**–**c**) and pentactula (**d**, **f**, **e**). **a**, **d** plates from body wall. **b**, **e** rods from body wall, **c** rods from podia, and **f** terminal plate from podia. Scale bar 400 µm

Acknowledgements The authors would like to express their gratitude to the colleagues on board the B/O Puerto Deseado during different cruises along the Argentine coast; especially Carlos Sánchez Antelo, Juan José Berecoechea, Pamela Rivadeneira, Jonathan Flores, and Martín Brogger. We thank Fabian Tricarico for the assistance with the SEM. Also we would like to thank John Lawrence, Mike Reich, Dieter Piepenburg, and three anonymous reviewers, for valuable suggestions and commentaries that improved this manuscript. This work was partially founded by PICT 2013-2504, PICT 2015-0428, and PICT 2016-0271 from the Agencia Nacional de Promoción Científica y Tecnológica.

Compliance with ethical standards

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

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