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A new species of brooding Psolidae (Echinodermata: Holothuroidea) from deep-sea off Argentina, Southwestern Atlantic Ocean

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ABSTRACT

This paper describes a new species of *Psolus* (Holothuroidea, Echinodermata), *P. lawrencei* sp. nov., (19 specimens) found in the deep sea (308–1398 m) in the Southwestern Atlantic Ocean (SWAO) (around 38°S–54°W) with brooders (up to 3.15 mm) in the tentacles of females and a penis-like genital papilla on males. The presence of dorsal scales, the concave shape of the ossicles with a bridge, the distribution of podia on the dorsal side and the absence of large and conspicuous oral and anal valves are unique for this species. Furthermore, this is the first species of this genus found outside Antarctica that broods between its tentacles. The paper also reviews the reproductive, brooding development and morphological characteristics of *P. lawrencei* sp. nov. and compares them with those of several members of the family Psolidae. Finally, a possible connectivity between the deep-sea populations in the SWAO and in Antarctica is considered based on the appearance of a similar reproductive pattern in populations found in both areas, which suggests a past or present connection between these regions.

1. Introduction

Brooding has been reported within multiple invertebrates, including sea cucumbers (e.g. Bohn and Heß, 2014). Indeed, about 130 species of echinoderms in southern waters have been reported to be brooders (Gutt, 1991; Pearse and Bosch, 1994; Brogger et al., 2013; Bohn and Heß, 2014). In shallow waters, the holothuroid family Psolidae includes seven species of brooders (McEuen and Chia, 1991; Bohn and Heß, 2014); however, there have been no reports of brooding species in the deep sea for this family (Théel, 1886; McEuen and Chia, 1991; O'Loughlin et al., 2009). Also, although there have been a great number of reports of brooding in echinoderms, in many of these, their reproductive mechanisms are not yet known (Gillespie and McClintock, 2007), especially for those species found in the Southwestern Atlantic Ocean (SWAO) area (Brogger et al., 2013).

Brooding behavior is one feature of these species, and has thus been studied by many authors (e.g. Thorson, 1950; Pearse, 1994). Thorson (1950) proposed that non-pelagic larval development is the rule in deep oceans, in the Antarctic and in the Arctic, due to their similar environmental conditions (e.g. low temperature, poor food conditions). Mileikovsky (1971) formalised this into the Thorson's Rule hypothesis, which argued that invertebrate species living in the Arctic, Antarctic and in the deep sea have non-pelagic larval development. This was

discussed by some authors relating to echinoderms, who generally concluded that several exceptions to this rule must be taken into account, especially for the class Asterozoa (Pearse, 1994; Poulin and Féral, 1998; Gillespie and McClintock, 2007). In particular, living in the deep sea, and participating in thousands of metres of vertical migration along the water column at post-embryonic and larval stages, followed by the return to the benthos to settle and metamorphose are quite challenging. Besides, predation and be swept away from suitable settling sites, tend to favour non-pelagic lecithotrophic developments, over deep-sea echinoderms (Young, 1994; Pearse, 1994; Gillespie and McClintock, 2007; Pearse et al., 2009).

The class Holothuroidea (Echinodermata), commonly known as sea cucumbers, has three species accepted as being brooders living in the southern part of the SWAO (around 23–54°S): *Cladodactyla crocea* (Lesson, 1830), *Psolus patagonicus* Ekman (1925) and *Pseudrotasfer microincubator* Bohn, 2007. The brooding strategies are different between species, i.e. *P. patagonicus*, brood beneath the sole, while, *Cladodactyla crocea* broods on a dorsal groove and *Pseudrotasfer microincubator* is an intraovarian brooder (Bohn, 2007; O'Loughlin et al., 2009; McEuen and Chia, 1991; Giménez and Penchaszadeh, 2010; Martinez et al., 2011; Martinez 2016). Offspring are even present in interradial pouches and between retracted tentacles, like with the Antarctic genus *Echinopsolus* Gutt (1990) and the species *Psolus dubiosus*

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Ludwig and Heding (1935), also from Antarctica (Gutt, 1991; Bohn and Heß, 2014). Moreover, for the genus *Echinopsolus*, O'Loughlin et al. (2009) and Bohn and Heß (2014) indicated the presence of a long genital papilla on the males. After the liberation of the oocytes by females, inside five interradial brood pouches, a long genital papilla of males could facilitate the fertilisation, by injection of spermatozeugmata via the male genital papilla into these brood pouches (Bohn and Heß, 2014).

In addition, there are some reports that demonstrate the close relationship between species in sub-Antarctic and Antarctic waters (O'Loughlin et al., 2011). This biological feature could be supported by the presence of Antarctic currents in the SWAO deep-sea area (Stramma and England, 1999).

The present paper describes a new species of *Psolus* found in the deep sea (308–1398 m) in the SWAO (around 38°S–54°W) with brooders in the tentacles and a penis-like genital papilla. The paper also presents a discussion on the reproductive behavior of Psolidae and the distribution of this family in the deep-sea SWAO and Antarctic waters.

2. Materials and methods

Samples were collected using dredge trawlers and fishing nets on board the B/O *Puerto Deseado* near the Mar del Plata Canyon area (see examined material) (Fig. 1). All the specimens were preserved in ethanol 96%. Holotype, paratypes and permanent slides of the ossicles were deposited in the Invertebrate Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-In), Buenos Aires, Argentina. Digital photos of the specimens were taken on board using a Canon PowerShot SX110. The ossicles were digitalised using a Zeiss Axio Imager Z1 microscope with an AxioCam HRc digital camera and Axiovision software. For the scanning electron microscope (SEM) examinations of the ossicles, small pieces of the body wall were

macerated in sodium hypochlorite solution, rinsed several times in distilled water and ethanol 96%, and then air dried. Finally, the ossicles were transferred to aluminium stubs, metal sputter-coated and observed under SEM (Philips XL 30).

3. Results

Psolus Jaeger (1833)

Diagnosis (from Mackenzie and Whitfield (2011)): Psolidae with large imbricating or contiguous dorsal and lateral scales; ventro-lateral scales at the margin clearly demarcated from a thin sole that lacks conspicuous scales; tube feet absent dorsally and laterally, except sometimes present orally and anally; 10 dendritic tentacles with eight large and two small ventrally.

Psolus lawrencei sp. nov

Diagnosis

Psolus with 30–35 dorsal scales between the mouth and anus. The scales near the mouth and anus encircle them in a crown formation without covering them. Tube feet on the dorsal side near the mouth and anus reduced in size. The sole is thick and hard, with 2 rows on the middle ambulacra and on the edges, from zigzags to a pair of rows. Males with extended genital papillae, which are absent in the females. Ossicles from the sole and dorsal side, with plates with 3–5 holes, a concave shape and sometimes with a bridge connecting one edge with a central spire; also buttons with multiple perforations. The podia and tentacles have slightly curved plates.

Etymology

The specific name *lawrencei* is used after Professor Emeritus John M. Lawrence from the University of South Florida, USA, in recognition for his studies and continuous support to young echinodermologists. It is a noun in apposition.

Description

Semicircular shape, up to 39.20 mm of total length, between the mouth and anus up to 36 mm length with 30–35 dorsal scales. Body colour light brown. Wide sizes up to 18.65 mm, height up to 16.40 mm. Dorsal scales up to 2.20 mm diameter for the centre, up to 3.18 mm for the lateral scales (Fig. 2a).

The scales near the mouth do not completely cover the tentacles and mouth; there is a crown disposition of oral and anal valves; 10 tentacles with two most ventral ones reduced to less than half size, in all the individuals. Females have pouches at the base of the tentacles; in the brooding period, the embryos are protected by these pouches between the tentacles and the oral scales (Fig. 3) one female have embryos between tentacles. The males have extended genital papillae, up to 4.26 mm (Fig. 4).

The tube feet on the dorsal side are reduced in size near the mouth and anus, up to 10 for the mouth in two to three circles, from the centre of the mouth to the oral papillae up 1.60 mm (Fig. 3a), and from the centre of the anus to the anal papillae up 3.84 mm. The sole is thick and hard, with 2 rows of middle ambulacra and for the lateral ambulacra, from zigzags to pair of rows (Fig. 2b). There is a terminal disc for the ventral middle and lateral tube feet up to 1.43 mm, with less than 0.5 mm difference between the middle and lateral tube feet. Marginal podia are present on the inner side of the valves up to 1 mm. arrange in one row, also one row for edge, middle ambulacra mainly in zigzag. Internal anatomy has one polian vesicle with drop shape, and one madreporite coral-like. Calcareous ring is simple with radial and interradial pieces with no differences (Fig. 2c).

Ossicles from the sole and dorsal side consist of plates with 3–5 holes, in a concave shape, sometimes with a bridge connecting one edge with a central spire (60–150.54 µm) (Fig. 5a), and also with buttons

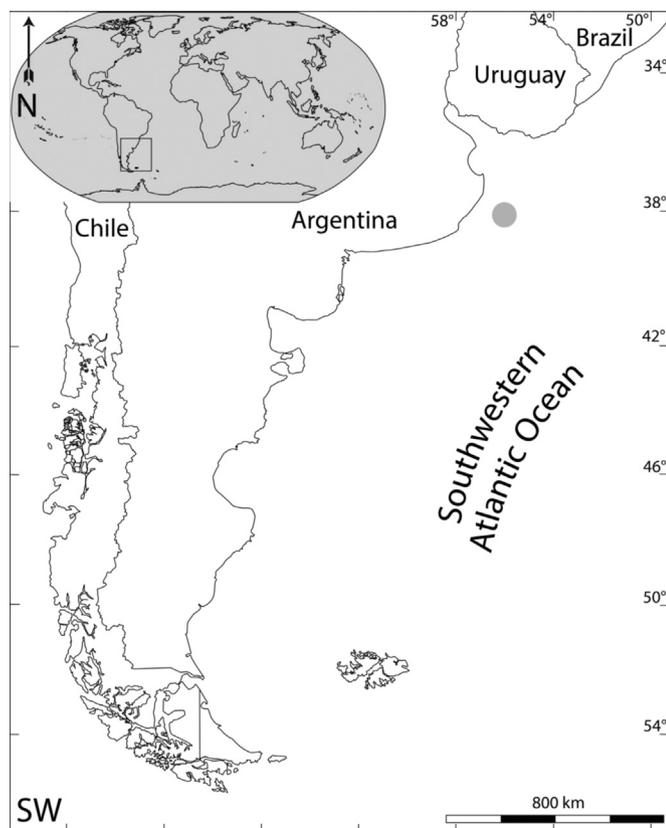


Fig. 1. Map showing the southern part of the Southwestern Atlantic Ocean; grey dot indicating the study area.

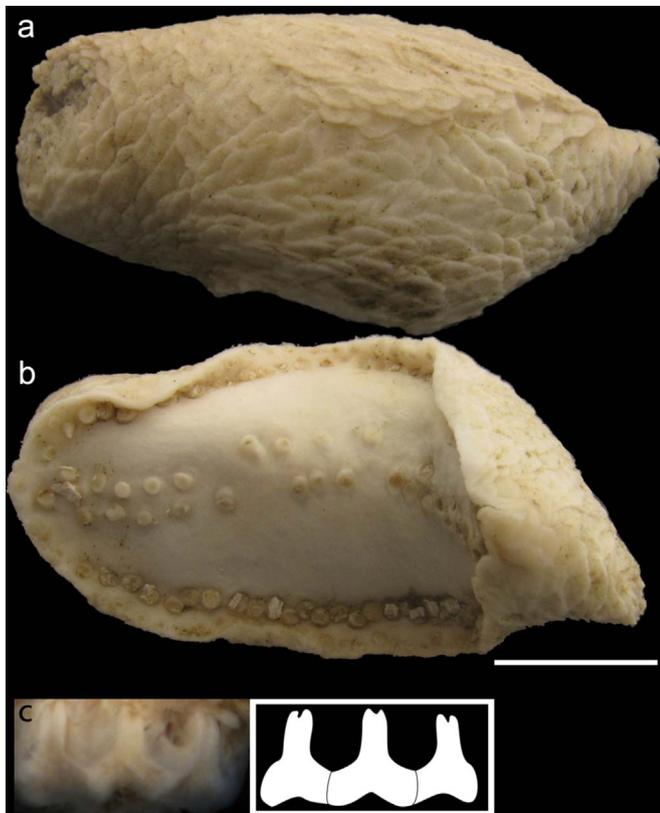


Fig. 2. Holotype *Psolus lawrencei* (MACN In 40713), (a) dorsal, (b) ventral, (c) calcareous ring, picture and shape. Scale: 1 cm. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

with multiple perforations up to 39 (380.84–505.13 μm large and 95.4–130.44 μm max. wide) (Fig. 5b). The podia and tentacles consist of slightly curved plates with 6–13 perforations (134.85–311.51 μm) (Fig. 5c, d).

Remarks

Holotypes and paratypes have the same characteristics for their external and internal morphology, including ossicles. Specimens up to 21.15 mm do not have dorsal papilla near the mouth or anus. Juveniles up to 10 mm do not have concave plates with a bridge.

Examined material

(Holotype) Off Mar del Plata, L8 37°58'S–54°57'W, 647 m, 10 Aug 2012, 39.50 mm (MACN In 40713); (Paratypes) 2 female specimens with broods, off Mar del Plata – same locality as holotype, 37.05 mm (flask a); 34.95 mm (flask b); 1 specimen, off Mar del Plata – same locality as holotype, 29.70 mm (flask c); 8 specimens – same locality as holotype: 37.90 mm, 28 mm, 19.60 mm, 13.56 mm, 12.83 mm, 12.36 mm, 11.47 mm, 11.01 mm (flask d); 1 male specimen, off Mar del Plata – same locality as holotype, 45.00 mm (flask e) (MACN In 40714); 1 female specimen with broods, off Mar del Plata L33, 37°59'S–55°12'W, 308 m, 17 Aug 2012, 35.40 mm (MACN In 40715); 3 specimens, L59, off Mar del Plata, 37°50'S–54°05'W 1398 m, 10 Sep 2013, 21 mm, 15 mm, 16.30 mm (MACN In 40716); 1 specimen, L15, off Mar del Plata, 38°01'S–54°25'W, 12 Aug 2012, 1200 m, 21.15 mm (MACN In 40717); 1 specimen, L36, off Mar del Plata, 37°57'S–54°24'W, 1289 m, 22.70 mm (MACN In 40718).

Distribution

Off Mar del Plata, near Mar del Plata Submarine Canyon (around 38°S–54°W).

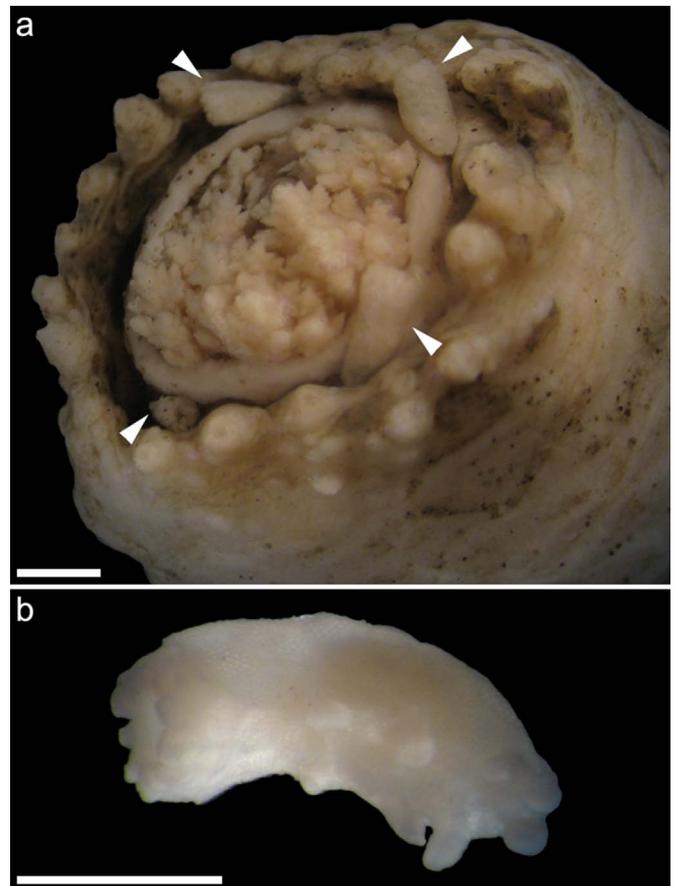


Fig. 3. *Psolus lawrencei*, (a) female (MACN In 40715) with broods, (b) brood from F1 (MACN In 40714; flask a). Scales (a): 2 mm, (b): 1 mm.

Bathymetrical distribution

308–1398 m.

Brooding

Three females with offspring were found with up to 28 brooders, in which the maximum length of the brooders was 3.15 mm (Table 1). All the brooders are between tentacles or on oral pouches and are contained by a crown of scales that surround the oral region. The individual specimens with brooders were only found in August.

4. Discussion

After the taxonomical changes made by Bohn and Heß (2014), we conclude that this entity is a clear species member of the genus *Psolus*. The presence of dorsal scales and the ossicles' shape with the distribution of podia on the dorsal side show clear differences from *Echinopsolus*. In addition, *P. lawrencei* sp. nov. could be differentiated from other co-generic species by the absence of large and conspicuous oral and anal valves. For instance, oral and anal valves are present in *Psolus dubiosus* Ludwig and Heding (1935); *Psolus punctatus* Ekman (1925) and *Psolus figulus* Ekman (1925). In particular, for *P. punctatus*, the presence of few podia on the middle ambulacra differs distinctly from the two rows of podia observed on *P. lawrencei* sp. nov. (Fig. 2). Apart from these differences, the ossicles are quite dissimilar, e.g. the concave plates with the bridge of *P. lawrencei* sp. nov. are quite unique for this genus.

In different groups of invertebrates it is common to have different paths of brooding behavior for the same genus. Just for the genus *Psolus* there are several examples of species that have developed different strategies, like brooding cycles and free larvae. For instance, *Psolus fabricii* (Düben and Koren, 1846) have a pelagic phase during their

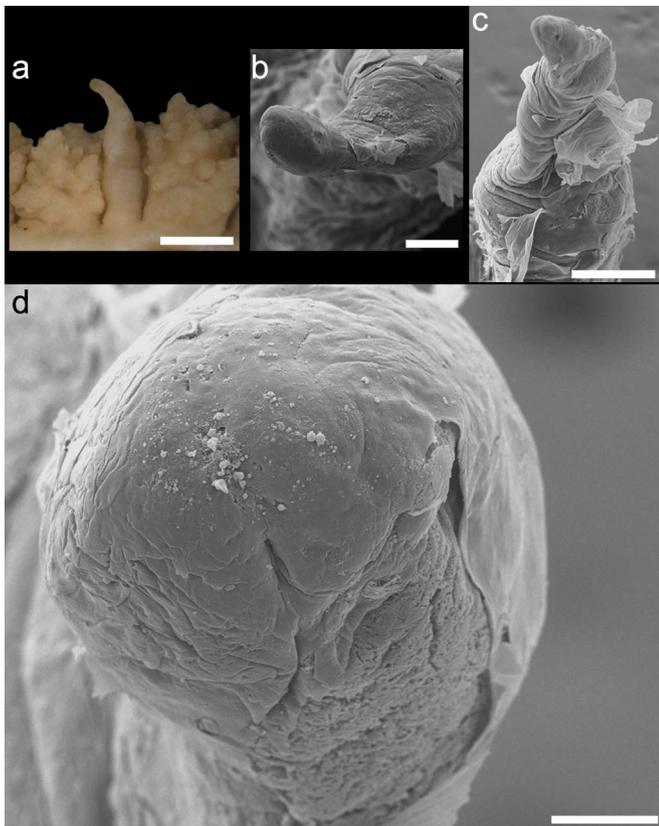


Fig. 4. Large papillae from a male (MACN In 40714 flask e), (a) relative position between the two most dorsal tentacles, (b), (c) and (d) different SEM images of the papillae. Scales (a) 2 mm, (b) 200 μ m, (c) 500 μ m, (d) 50 μ m.

brooding cycle, while *Psolus patagonicus* Ekman (1925) broods in the sole (Giménez and Penchaszadeh, 2010). However, *P. lawrencei* sp. nov. appears to be the first described species of this genus, outside Antarctica, that broods in oral pouches and between tentacles. Although all these species have different reproductive strategies, together they share the diagnostic features of the genus *Psolus*.

P. lawrencei sp. nov. also has large genital papillae, indicating that, after females transfer the oocytes to the tentacles, the males could inject sperm directly into the pouches of the females or to the tentacles, where the oocytes are located, as was described in Bohn and Heß (2014) for *Echinopsolus*. Ekman (1925) similarly described a large genital papilla in *P. punctatus*, in which brooding was reported under the sole. This indicates that the fertilisation could be assisted by the presence of a penis-like long genital papilla in different species of both *Echinopsolus* and *Psolus*. Also the fertilisation mechanism is not always related with tentacle brooding species, indicating that other species with under sole brooding could develop this behavior.

The Antarctic species *Psolus dubiosus* carries brooders of up to 2.30 mm length in the tentacles (Gutt, 1991). This feature, which was seemingly exclusive for the Antarctic species of the genus, is here observed in *P. lawrencei* sp. nov. outside of Antarctica for the first time. *P. lawrencei* sp. nov. has bigger brooders, up to 3.15 mm, and a lower adult size (37.05 mm) in comparison with *P. dubiosus* (44.7 mm). The differences in the present study could have been associated with the different growth stage of the broods at the moment in which both species were analysed.

Trumbo (1996) support the idea that brooding behavior is categorised by a stable, structured environment; while a harsh environment is categorised by a scarce, specialised food resource or high predation pressure (Gillespie and McClintock, 2007). Deep-sea waters have a combination of all these features in addition to the challenge of needing to go up and down in the water column. This idea goes in concordance

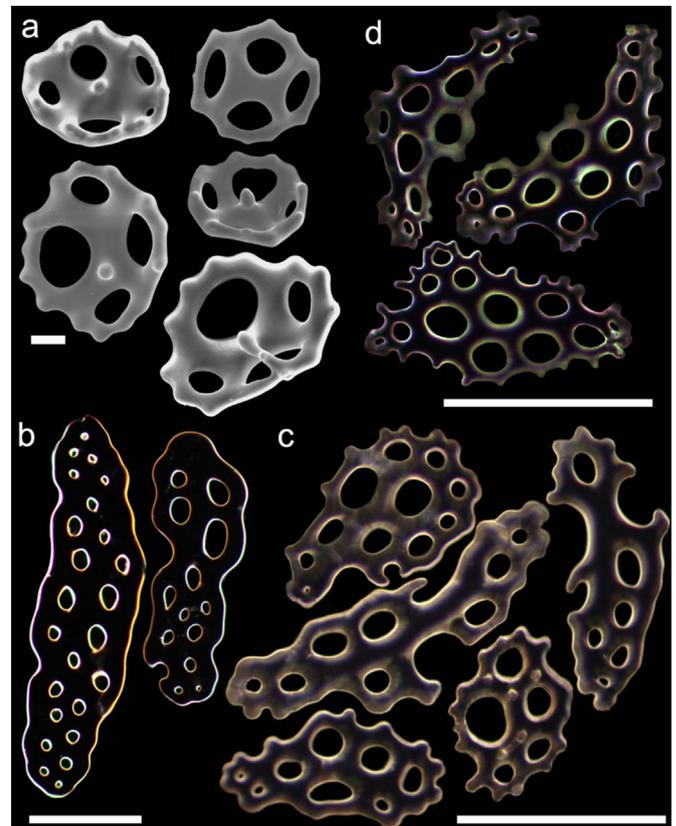


Fig. 5. Ossicles from the dorsal and ventral sides, (a) concave plates with bridge, (b) buttons from the ventral side, perforated bars from (c) the podia and (d) the tentacles. Scales (a) 20 μ m, (b) and (c), (d) 100 μ m.

Table 1

Females found with brooders, with their lot number. For each female, its size and number of broods with the maximum brood length is shown.

Females with museum number	Size of specimen (mm)	Number of brooders	Max. length of brooders
F1 (MACN In 40714, Flask a)	37.05	28	2.90
F2 (MACN In 40714, Flask a)	35.40	11	3.15
F3 (MACN In 40715)	34.95	8	2.60

with the brooding behavior observed in the present work for the deep-sea psolid, *P. lawrencei* sp. nov.. Nevertheless, given the different histories and ecologies of each particular species and the difficulties of finding a single driving agent for selection (Pearse, 1994; Trumbo, 1996; Gillespie and McClintock, 2007), it is clearly challenging to develop one single rule to understand the reproduction in species in deep-sea southern waters. Recent discussions started by O'Loughlin et al. (2009) and Bohn and Heß (2014), about similarities in the reproductive behaviours and their implications on phylogenetics, become the observations of the present study, more important in the identification of different species. More reproductive studies need to be done to determine whether there are other *Psolus* species with brooding development, especially in tentacles, and to assess the morphological differences among others with different brooding behaviours (e.g. under the sole). In addition few reports on deep-sea reproduction are known (Smiley et al., 1991), for this, revisions on southern deep-sea species distribution and reproduction could lead to a better understanding of the connectivity between deep-sea populations in the SWAO and Antarctica. Only a few references regarding this interaction are known (e.g. O'Loughlin et al., 2011). However, in the present paper, we

have discussed the appearance of a similar reproductive pattern in a genus quite diverse in Antarctic waters, which has led us to think that there may be a closer past or present connection between both areas.

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