



# Aboral brooding in the deep water sea star *Ctenodiscus australis* Lütken, 1871 (Asteroidea) from the Southwestern Atlantic

Pamela R. Rivadeneira<sup>a,\*</sup>, Martín I. Brogger<sup>b</sup>, Pablo E. Penchaszadeh<sup>a</sup>

<sup>a</sup> Laboratorio de Ecosistemas Costeros, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (CONICET), Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina

<sup>b</sup> Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos, Instituto de Biología de Organismos Marinos (CONICET), Bvd. Brown 2915, U9120ACD Puerto Madryn, Argentina

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## ABSTRACT

Different stages of development and growth were found in the dorsal surface under the paxillae of *Ctenodiscus australis*. The maximum number of broods found per specimen was 73 and in some cases different stages were observed on the same female. Oocytes were present in females of all months sampled and were diverse in size (120–850 μm in diameter). Continuous presence and variation in size and stage were also observed in the broods. The typical developmental stage resembles a modified brachiolaria. All these observations suggest continuous reproduction in this deep water species and it also provides new information about reproduction in the Ctenodiscidae family.

## 1. Introduction

Sea stars exhibit different reproductive strategies for sexual reproduction ranging from free larval stages to direct development. Some species incubate and brood their embryos. The location of the broods vary as well, including internal brooding, inside the gonads as in the genera *Patiriella* and *Cryptasterina* (Chia, 1976; Komatsu et al., 1990; Byrne and Cerra, 1996; Dartnall et al., 2003; Byrne, 2005) or in the stomach, like *Smilasterias multipara* and *Leptasterias groenlandica* (Fisher, 1930; O’Loughlin and O’Hara, 1990). In most brooding sea stars the incubation takes place externally to the mothers. In the family Pterasteridae, incubation and brood occurs in nidamental chambers formed by covering the abactinal spines with a supradorsal membrane (Fisher, 1940; Hyman, 1955; McClary and Mladenov, 1988, 1989). In other species the chamber is formed by arching the arms as in *Leptasterias ochotensis*, *L. hexactis* and *Henricia sanguinolenta* (Masterman, 1902; Osterud, 1918; Kubo, 1951), or within the oral region as in the genus *Anasterias* (Chia and Walker, 1991; Gil et al., 2011; Pérez et al., 2015). Less frequent is brooding on the dorsal surface, underneath the paxillae, as has been reported in members of the genera *Trophodiscus*, *Ctenodiscus* and *Leptychaster* (Fisher, 1917; Lieberkind, 1926; Kogure, 2002).

The class Asteroidea have two characteristics kind of larvae: bipinnaria and brachiolaria, within those categories, there are varia-

tions. Free larvae can occur through pelagic or benthic development with feeding or not feeding stages. For most brooding species, the benthic nonfeeding type is the most common developmental pathway (McEdward and Janies, 1993). The stages that occur in these organisms are not easy to classify and establishing similarities between different species is difficult as a consequence of modifications and/or the lack of some larval structures.

There have been prior works about deep sea asteroids but few of studies focus on reproduction (e.g.: Giese and Pearse, 1974; Mercier and Hamel, 2009) and even fewer are about the brooding condition. Studies are limited to some species of the families Pterasteridae (Chia, 1966; Janies, 1995), Porcellanasteridae (Benítez-Villalobos and Díaz-Martínez, 2010) and Astropectinidae (e.g.: Tyler et al., 1982a, b), as well as to the genus *Henricia* (Benítez-Villalobos et al., 2007; Mercier and Hamel, 2008) and some Concentricycloidea (Rowe, 1988; Mah, 2006).

In marine species the timing of reproduction occurs at a longer scale resulting of the initiation and progression of gametogenesis, and at a shorter scale, associated with spawning (Giese and Pearse, 1974; Mercier and Hamel, 2009). Particularly in deep sea environment, aseasonal or continuous reproduction is the most reported mechanism (Young, 2003), and continuous production of gametes is rare in an individual (Giese and Pearse, 1974).

*Ctenodiscus australis* is a small sea star from the Southwestern

\* Corresponding author at: Laboratorio de Ecosistemas Costeros, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (CONICET), Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina.

E-mail addresses: [rivadeneira@macn.gov.ar](mailto:rivadeneira@macn.gov.ar), [pamer28@gmail.com](mailto:pamer28@gmail.com) (P.R. Rivadeneira), [brogger@cenpat-conicet.gob.ar](mailto:brogger@cenpat-conicet.gob.ar) (M.I. Brogger), [pablopench@gmail.com](mailto:pablopench@gmail.com) (P.E. Penchaszadeh).

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Atlantic that is very common on soft bottoms from depths ranging from 70 to 700 m (one record from 4600 m seems to be doubtful according to Clark and Downey (1992), and with distribution from Southern Brazil (23°S) to Southern Argentina (55°S), including the Malvinas/Falkland Islands (Escolar et al., 2011; Brogger et al., 2013). The brooding condition of this species was first reported by Lieberkind (1926), who described two stages of development and observed that embryos were spread over the base of the arms, hidden within the paxillae towards the interradia, adopting unusual forms and forming a hold that he called “embryophor”. Bernasconi (1966) studied individuals collected off Peninsula Valdez and Golfo San Matías (Argentina) which presented broods at the same stage of development that has described previously by Lieberkind (1926), not providing new information about it.

In the congeneric *Ctenodiscus crispatus* different aspects of the reproduction were studied, without records to be a brooder species (Falk-Petersen, 1982; Falk-Petersen and Sargent, 1982; Jaramillo, 2001).

In this work, the aboral brooding of *C. australis* is documented, including descriptions of different development stages of the embryo and its simultaneous occurrence on a single mother. Also, observations of the reproductive condition of females were conducted, in order to contribute to the knowledge of reproduction in deep sea environments. Finally, differences in brooding stages and reproductive condition were analyzed between populations from different depths and from distant latitudinal extremes of distribution.

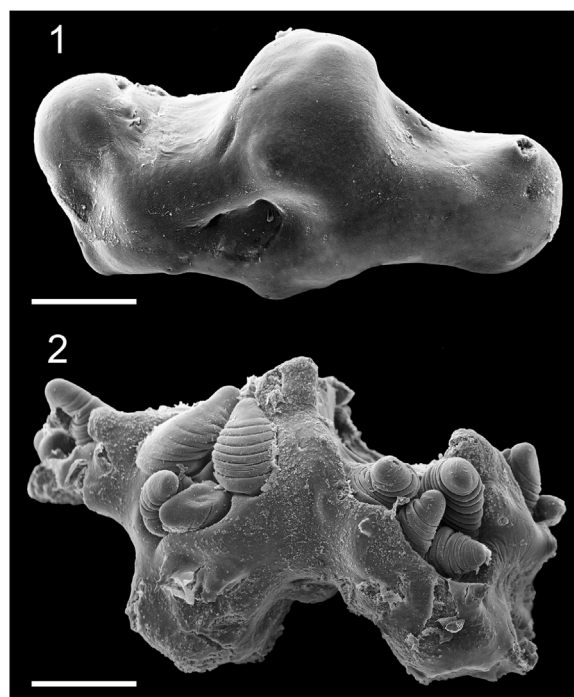
## 2. Materials and methods

During three years (2012, 2013 and 2016) a total of four cruises were conducted in the Southwestern Atlantic, including samples using fishing nets and dredges. Three sampling events were conducted in the Mar del Plata Submarine Canyon located in the Argentinean Continental Slope, an area about 250 km east of Mar del Plata, where most of the samples were collected at depths ranging from 200 to 2200 m. The samples of the fourth expedition were obtained from the Burdwood Bank (“Namuncurá” Marine Protected Area), at about 250 km south of Malvinas/Falkland Islands, at 147 m.

All specimens were preserved in 96% ethanol on board. In the laboratory, the samples of *Ctenodiscus* were studied and deposited in the invertebrate collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-In; Table 1). The specimens were observed in detail, looking for different stages of development

**Table 1**  
Data from brooding females.

Date	Depth (m)	Latitude	Longitude	Brooders	Broods per female	Maximum developmental stages per specimen	Stages found	MACN-In number
10-Aug 2012	250	38° 00' S	55° 13' W	6	1–6	2	8, 9	40952
	291	37° 57' S	55° 11' W	2	23	2	8, 9	40953
	647	37° 58' S	54° 57' W	4	1–32	1	7	40954
	652	37° 58' S	54° 56' W	2	3–4	2	7	40955
11-Aug 2012	852	38° 00' S	54° 42' W	4	6–15	2	5, 6	40956
13-Aug 2012	1508	37° 57' S	54° 11' W	2	15–42	1	8	40957
15-Aug 2012	1738	37° 52' S	53° 57' W	2	5	1	7	40958
26-May 2013	780	37° 54' S	54° 43' W	2	20–30	1	2, 10	40959
8-Sep 2013	1763	37° 53' S	53° 54' W	2	1–73	1	8, 9	40960
11-Sep 2013	1444	37° 59' S	54° 10' W	9	9–40	4	1, 2, 3, 4, 8, 9, 10	40961
11-Sep 2013	1404	37° 55' S	54° 14' W	4	4–14	2	7, 8, 10	40962
13-Apr 2016	174	54° 45' S	59° 51' W	2	5–71	2	9, 10	40963

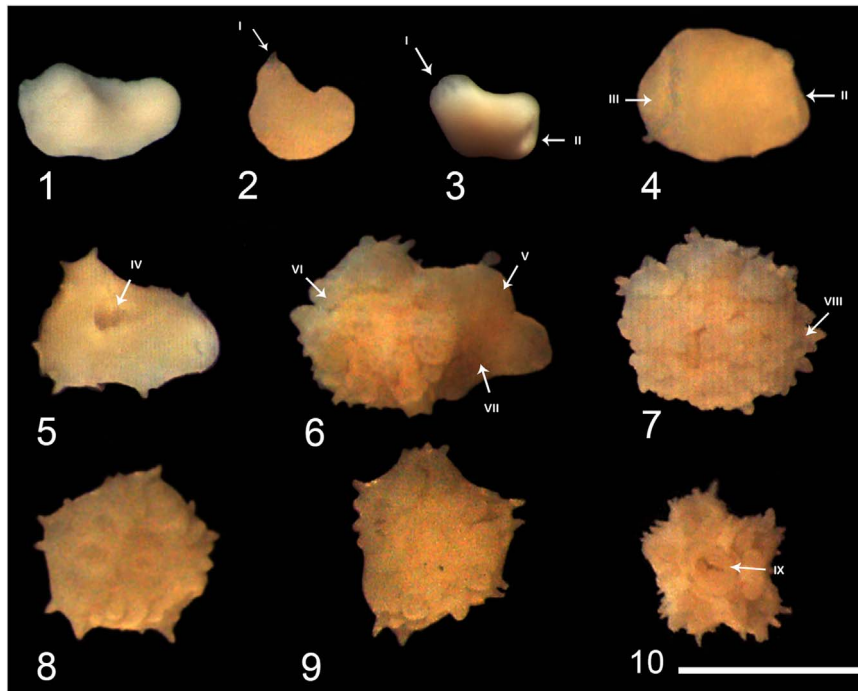


**Fig. 1.** Different stages of broods showing the body form according to the surrounding paxillae disposition: an early stage (1) and a late stage (2). Scale bars=200 μm.

under the paxillae of the aboral surface using a stereoscopic microscope. The offspring were measured and photographed. The brooding animals were defined as brooders, while the individuals that were being brooded were defined as broods. The images were taken with a Leica IC 80 HD and under a scanning electron microscope (SEM). All adult specimens were recorded, with or without broods and many of them were dissected to observe the state of the gonad. When oocytes were found, these were counted and measured inside the ovarian tubules under the stereoscopic microscope.

## 3. Results

Of the 72 adult specimens that were studied (from 296 collected in total), 41 were females with a total of 597 broods found hidden under the paxillae (Fig. 1). They were distributed across the aboral surface,



**Fig. 2.** Stages of development in *Ctenodiscus australis*. 1- Early amorphous stage. 2- Curved stage with a translucent mesh at one of the ends of the body (I). 3- Brood showing an invagination of the archenteron (II) and an evident mesh on the other side of the body (I). 4- Rounded shape body with two opposite invaginations (II, III) and without a mesh. 5- Stage with spines and hydopore in the middle of the body (IV). 6- Modified brachiolaria stage carrying the preoral lobe (V), water ring with radial canals (VI) and adhesive disk (VII). 7- Round shaped brood with the remaining preoral lobe (VIII). 8–10- Advanced stages with differentiated arms carrying two pairs of feet; the spines are located at the end of each arm and the main difference between these stages is the grade of development. Most developed brood with the mouth completely formed (IX) and elongated arms. Scale bar: 1–9=1 mm; 10=2 mm.

and were found on the whole disc area rather than in a specific place on it; they were found next to the superomarginal plates as well as in the center of the disc. However they were never located in the depressed line of the major radius. The number found per female varied in a wide range from 2 to 73 ( $X=13.4$ ,  $SD=15.9$ ) (Table 1). Different sizes and stages were observed.

In some cases, traces of broods were observed despite the absence of the brood itself. These traces were expressed by a mark on the paxillae called “embryophors” as described by Lieberkind (1926). In these places paxillae were pushed aside or even absent.

Different developmental stages of *C. australis* could be differentiated (Fig. 2). Sizes were taken by measuring the length (l) and width (w) for each form:

Stage 1: correspond to the less developed stage found in which no structure, organ or appendix was observed. It has a large and slightly arched shape with a size of  $l=915\ \mu\text{m}$  and  $w=566\ \mu\text{m}$  ( $N=1$ ).

Stage 2: translucent mesh in one of the sides appear and the shape becomes more arched (I). Size  $l=608\ \mu\text{m}$  and  $w=549\ \mu\text{m}$  ( $N=2$ ).

Stage 3: the invagination of the archenteron was formed on the opposite side of mesh (II). Size  $l=646\ \mu\text{m}$  and  $w=402\ \mu\text{m}$  ( $N=1$ ).

Stage 4: the shape changed completely being more round and bigger. An additional invagination of archenteron appeared replacing the mesh (III). Size  $l=991\ \mu\text{m}$  and  $w=745\ \mu\text{m}$  ( $N=2$ ).

Stage 5: a big hole at the center of this stage could be observed and spines were well formed (IV). Size  $l=970\ \mu\text{m}$  and  $w=701\ \mu\text{m}$  ( $N=1$ ).

Stage 6: a big preoral lobe (V) with adhesive disk (VII) and water ring with radial channels (VI) were formed. Size  $l=1042\ \mu\text{m}$  and  $w=910\ \mu\text{m}$  ( $N=1$ ).

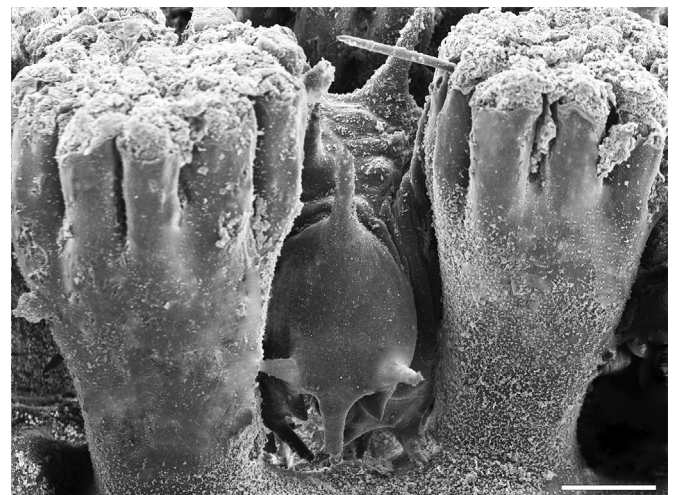
Stage 7: very round shape with remain preoral lobe (VIII) and with the future radial endings defined. Size  $l=1048\ \mu\text{m}$  and  $w=1048\ \mu\text{m}$  ( $N=29$ ).

Stages 8–10: in these stages different grades of development of the arms were observed carrying two pairs of tube feet in each one of

them. The spines were located in pairs at the end of the arms, and both surfaces and mouth were completely formed (IX). (Fig. 2 (8,9,10)). Size  $l_8=961\ \mu\text{m}$ ,  $w_8=922\ \mu\text{m}$ ;  $l_9=1000\ \mu\text{m}$ ,  $w_9=843\ \mu\text{m}$ ;  $l_{10}=1654\ \mu\text{m}$ ,  $w_{10}=1231\ \mu\text{m}$ . ( $N_{2,8}=194$ ,  $N_{2,9}=127$ ,  $N_{2,10}=239$ ).

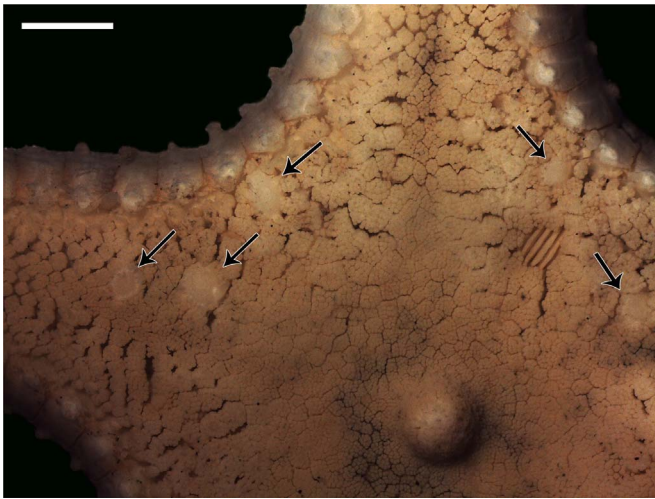
Broods in stages 2, 4, 8 and 9 were simultaneously found on the same brooder and those in stages 5 and 6 were found together on other brooder (Table 1). Less developed stages were completely covered by the paxillae (Fig. 3). The more advanced stages were easy to see at the abactinal surface, where broods were protruding out the paxillae (Fig. 4).

Among all samples collected, the smallest juvenile (free living specimens, not carried by the mother) measured from  $R=3\ \text{mm}$ ,



**Fig. 3.** Scanning electron microscope image of the position of an embryo, located between the paxillae. Scale bar=200  $\mu\text{m}$ .





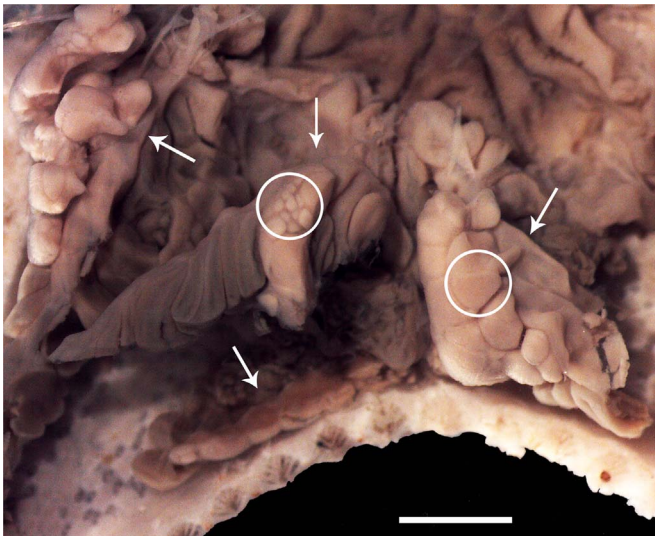
**Fig. 4.** View and distribution of the most advanced stage of incubation (arrows) on the aboral surface of the female. Scale bar=2 mm.

$r=2$  mm to  $R=29$  mm,  $r=10$  mm.

Oocytes were observed in gonads of many females, including those that were brooding. This is consistent with the observation that in most females, broods occur in different stages simultaneously. Some ovarian tubules contained up to fifteen oocytes, ranging from 120 to 850  $\mu$ m in diameter (Fig. 5).

#### 4. Discussion

Most species in the order Paxillosida develops through a bipinnaria larva that, in some species with lecithotrophic development, can be replaced with a ciliated yolk barrel-shaped larva (Byrne, 2013). Nevertheless a different larval stage was reported in *Ctenodiscus australis* and some authors proposed that would be a yolk non feeding larva or a direct developing mesogen (McEdward and Miner, 2001). In this work, one of the stages clearly resembles to a stage with characteristics pertaining to a modified type of brachiolaria which lacks the larval arms, as also observed in *Pteraster tessellatus* (Strathmann, 1992). This kind of larva often has an adhesive disk between the arms that allows it to adhere to the substrate. In *C. australis*, an adhesive



**Fig. 5.** Ovarian tubules (arrows) full of oocytes of different diameters. Both white circles represent a surface equal to one square millimeter, one containing more than 10 small different oocytes, while the other barely more than only one. This condition was observed in specimens from all months. Scale bar=2 mm.

disk is found at the center of the preoral lobe. The adhesive disk could allow attachment of the larva under the paxillae until the increase in size of the broods allows its retention there. This stage resembles the description of *Echinaster echinophorus* (Atwood, 1973).

In some cases, such as in *Anasterias minuta*, it has been reported that a modification of the brachiolar complex serves as a connection cord to prevent (among other functions) the loss of different stages of development (Gil et al., 2011). This type of modification was not found in *C. australis* since it is not as necessary to maintain the offspring together, due the place where they are housed is more sheltered compared to the oral location.

The translucent mesh observed in some early stages, according to the proposed by Chia and Walker (1991), was formed during a mid-gastrula stage and localized around the archenteron. Later will be located in stomodeal region of the embryo (related to the formation of the larval mouth) as shown in the Fig. 2. The cavities observed, correspond to the invagination of the archenteron, one becoming the larval anus (II) and the second one the larval mouth (III). The big hole present in the stage with spines, possibly corresponds to the hydropore of the hydrocele that will originate the water ring canal, that is present on the oral side of the adult. According to previous works the larval mouth and the anus are closed during metamorphosis, and in the adult they are new openings (Chia and Walker, 1991).

The largest oocytes and the first brood stage found are slightly different in size and form. It is clear that there are missing stages between the forms with two invaginations (Fig. 2.4), the first that had spines (Fig. 2.5) and the stage with an evident preoral lobe (Fig. 2.6).

The oocyte diameters registered here for *C. australis* (120–850  $\mu$ m) correspond to those of asteroids with lecithotrophic development (300–1500  $\mu$ m) (Chia and Walker, 1991; Byrne, 2013). In a previous study of the congeneric sea star *Ctenodiscus crispatus* collected from 250 m depth in Conception Bay (Newfoundland, Canada), the reported oocytes range size was 250–982  $\mu$ m (Jaramillo, 2001), similar to our observations. Also for *C. crispatus*, Falk-Petersen (1982) observed from fresh gonads that the diameters of the largest oocytes were between 500–600  $\mu$ m. Nevertheless *C. crispatus* is not reported nor considered a brooding species. Asteroidea brooding species produce eggs ranging from 300  $\mu$ m to 3500  $\mu$ m diameter (Emlet et al., 1987).

The maximum number of broods found previously in *C. australis* on one specimen was 23 (Lieberkind, 1926), while we recorded a total of 73 on one single female. These broods were in the most advanced stages of development and the abactinal face was completely covered with them. Data obtained suggest that the size at which broods are released from their mother would not be much bigger than those recorded at the most developed stage ( $R=827$   $\mu$ m and  $r=615$   $\mu$ m). Smaller sizes found in stages 1–7 were scarce, while stages 8–10 were numerous. This could indicate that the first stages of development occur relatively quickly, while a long period is spent during the final phases of incubation.

The fact we found different brooding stages together with ovarian tubules full with oocytes of different sizes in the same specimens, could be indicative of aperiodic reproduction. Other result that support this idea is that samples with broods and oocytes were collected in different months of the year: April, May, August and September. Continuous reproduction has been reported for many deep sea species as an adaptation to the environment (Thistle, 2003; Robison et al., 2014). Nevertheless, this results are not conclusively of continuous reproduction in an individual because gametogenesis could takes more than one year and overlapping different generations of oocytes (Falk-Petersen, 1982). In this work, aperiodic reproduction is referring to the population of *C. australis*, in which gametogenesis may be staggered among different individuals during the year (Giese and Pearse, 1974). This type of reproduction that includes large egg size and lack of seasonality may be a consequence of the stable low temperature environment of the deep sea that allowed more efficiency in reproduction (Mercier and Hamel, 2009). Since in deep sea the environmental conditions are

relatively constant, the absence of a seasonal reproduction can be attributed to internal mechanism: accumulation of nutrients and interplay of hormones between the controlling centers and the gonads (Giese and Pearse, 1974). In *C. australis* aperiodic reproduction seems to be the strategy, since specimens from varied depths and months, and from different latitudes, were found brooding large number of broods of various developmental stages.

*Ctenodiscus australis* is the only species of the family Ctenodiscidae reported as a brooding species, and is the first for which aspects of its development are known.

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