From baby to adult: ontogenetic series of nine species of Ophiuroidea from Atlantic Southwestern

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Abstract. The post-metamorphic stage is essential in the life history of marine invertebrates. During this period, animals are more vulnerable and suffer high mortality, which influences the distribution and abundance of adult populations. It is also during this period that major morphological changes happen in the individuals, complicating their taxonomic identification. The juvenile ophiuroids dominate the meiofauna in certain times of the year and at some places. However, they are ignored by most ecological studies due to identification difficulties. Here we describe the ontogeny of nine deep-sea species from the Southeast and South regions of Brazil, with the first record of morphological modifications for eight of them. Most organisms were collected 60 to 800 m deep, between December 1997, January, 1998 and March, 1998, during the REVIZEE-Score South / Benthos program. We also included additional material from the Zoology Museum of Unicamp (ZUEC). For descriptions and identifications of the different stages, the specimens were dried and photographed. The juveniles were identified by "backwards" process through the growth series of adults to smaller individuals, a backwards method that was successful in previous studies. Some individuals were mounted on aluminum stubs for scanning electron microscopy. The species were: *Ophiacantha pentacrinus* (Ophiacanthidae), *Ophiomastus satelitae*, *Ophiomusium acuferum*, *Ophiomusium eburneum, Ophiomisidium tommasii*, *Ophiura ljungmani*, *Ophiura clemens* (Ophiuridae), *Amphiura complanata* (Amphiuridae) and *Ophiothrix rathbuni* (Ophiotrichidae). Many species could be identified since their most juvenile stage. Some structures remain almost unaltered during the whole life. Rev. Biol. Trop. 63 (Suppl. 2): 361-381. Epub 2015 June 01.

Key words: brittle stars, growth series, benthic fauna, taxonomy, ecology, distribution.

The first ontogenetic studies on post-metamorphic ophiuroid date back to more than one century ago and the progress in this area still slow (Stöhr, 2005). Due to difficulty in identifying juvenile stages, the first studies focused on knowingly brooding species, particularly *Amphipholis squamata* (Delle Chiaje, 1828), which has circumtropical distribution and incubates juveniles almost the whole year (Fell, 1946; Stöhr, 2005). Regarding non-brooding species, more than 30 had their post-larval stages described, most of them from the North Atlantic (Schoener, 1967; Schoener, 1969; Hendler, 1978; Bartsch, 1985; Turner & Miller, 1988; Sumida, Tyler, Gage & Nørrevang, 1998; Stöhr, 2005).

The morphological structures in the juveniles of many ophiuroids species differ from those in adults (Tommasi, 1970). Studies about ophiuroid post-larval development and growth series showed several structures that enable the identification of some species, even in early life stages (Schoener 1967, 1969; Turner & Miller, 1988; Monteiro, Reis & Pardo, 1992; Sumida et al., 1998; Stöhr, 2005). The external morphological features have few or no taxonomic value if the growth stage of the animal in particular is not mentioned (Stöhr, 2012).

The juvenile stages of ophiuroids dominate the composition of the meiofauna in certain times of the year (Stöhr, 2005). However, they are often ignored in ecological studies due

to difficulties in identifying these animals. For this reason, the description of juvenile stages shows itself essential to studies concerning about population dynamics, faunal composition and reproductive biology.

Additionally, the study of post-larval stages in different groups has been considered of great relevance in the resolution of phylogenetic problems (Schoener, 1967; Sumida et al., 1998). Hendler (1988) mentioned that the ontogenesis of homologous structures in post-larval ophiuroids may be useful to define phylogenetic and systematic relations between taxonomic groups, especially those which are more related.

Usually, the dorsal disc coverage is constituted entirely of primary plates at young individuals and small plates grow among these, increasing in number and size, complicating the identification of the primary plates in adults. Nevertheless, in some species, the primary plates remain evident during the individual's entire life, and they may even present different types of coloration (Tommasi, 1970; Monteiro, 1987; Stöhr, 2005).

The purpose of this study is to provide accurate descriptions of the juvenile stages of species traditionally known and identified from adults through external morphological character. Adults and juveniles of different sizes belonging to nine subtidal species from the Southeast and South from Brazil were analyzed, whereas eight of them are the first record of ontogenetic development in literature. Such isn't the case of *Ophiura ljungmani*, which has already been previously described (Schoener, 1967, 1969; Sumida et al., 1998) however it is analyzed here due to the large amount of sampled material.

MATERIAL AND METHODS

Most of the juveniles and adults of Ophiuroidea were collected by the REVIZEE-Score Sul/Bentos Programme, at depths between 60 and 800 m, during December 1997, January 1998 (Rio de Janeiro and São Paulo) and March 1998 (Paraná, Santa Catarina and Rio Grande do Sul). Samples were initially preserved in 6 % formalin and transferred to 70 % ethanol.

The species were chosen based on the relative abundance of different growth stages and individuals. Additional material from the Zoology Museum of UNICAMP (ZUEC) was also included in this study. Nine different juveniles ophiuroids are described in the present work: *Ophiacantha pentacrinus* (Ophiacanthidae), *Ophiomastus satelitae*, *Ophiomusium acuferum*, *Ophiomusium eburneum, Ophiomisidium tommasii*, *Ophiura ljungmani*, *Ophiura clemens* (Ophiuridae), *Amphiura complanata* (Amphiuridae) and *Ophiothrix rathbuni* (Ophiotrichidae).

Juveniles were identified by tracing characters backwards through growth series from adults to smallest individuals (Schoener, 1967, 1969; Sumida et al., 1998; Stöhr, 2005). All species were air-dried and then identified. We analyzed 4217 individuals, which four individuals (of different sizes) were selected for description of the growth series. Some entire specimens were set on aluminum stubs for scanning electron microscopy model (SEM) model JEOL JSM5800LV. We are showing images of adult individuals of each species, as well all the specimens used to analyze the growth series.

The term juvenile is here used for young animals after completion of metamorphosis until the development of adult characters. Some studies use the term "postlarvae" for specimens with disc diameter less than 2 mm (Webb & Tyler, 1985). However, few specimens of this size were analyzed, so for that reason, we prefer to use the term "juveniles". Disc diameter (dd) has been measured from the edge of an inter-radius across the dorsal disc surface to the edge of the opposite radius (distal edge of the radial shields). The number of arm segments was counted from the first "true" segment (containing a regular vertebrae and lateral plates), to the distal most segment before the terminal plate. The term primary rosette refers to the central primary plate and the five radial primary plates on the dorsal disc.

The terminology and abbreviations used follow Sumida et al. (1998) and Stöhr (2005).

RESULTS

Growth Series

OPHIACANTHIDAE
Ophiacantha pentacrinus Lütken, 1869
(Figs. 1 - 5)

Adult - Fig. 1

Material examined: 153 ex.

Specimens selected for description: 7.14 mm (ZUEC OPH 834); 4.95 mm (ZUEC OPH 835); 3.55 mm, 2.36 mm (ZUEC OPH 833).

In the two largest specimens (7.14 mm and 4.95 mm dd) the radial shields are completely separated (Fig. 2 A, B); while in the two smallest individuals these shields are joint posteriorly (Fig. 2 C, D). Spinelets are more numerous and robust in the three largest specimens (Fig. 3 A - C) than in the smallest (Fig. 3 D). Ventral interradius is covered with scales and few spinelets tapering in the two largest specimens, while in the two smallest specimens this section is fully covered by bifid or trifids spinelets. The arrangement of the oral papillae is similar in individuals of different sizes, except for the presence of four oral papillae in some jaws of the largest specimens (Fig. 4). In largest individuals (with 7.14 and 4.95 mm dd), dorsal arm plates fan-shaped and some diamond-shaped; smallest specimens with dorsal arm plates diamond. Ventral arm plate sub-pentagonal in the two largest specimens (Fig. 5 A, B), in the smallest individuals this plate is rounded (Fig. 5 C, D). The two largest specimens has seven arm spines on basal and medial segments; 3.55 mm dd with five, and 2.36 mm dd, four.

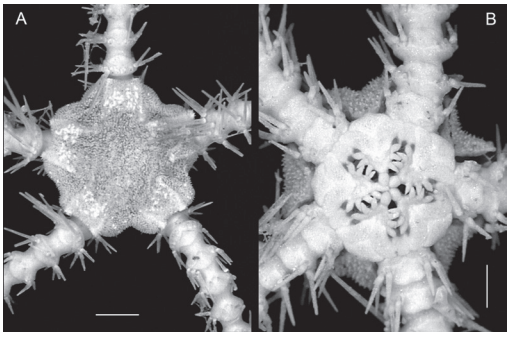

Fig. 1. *Ophiacantha pentacrinus*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

OPHIURIDAE
Ophiomastus satelitae
Tommasi & Abreu, 1974
(Figs. 6 - 8)

Adult - Fig. 6

Material examined: 15 ex.

Specimens selected for description: 5.12 mm, 4.65 mm (ZUEC OPH 864): 3.28 mm, 1.89 mm (ZUEC OPH 862).

Specimens with 5.12 mm and 4.65 mm dd have the disc flattened while the two smallest

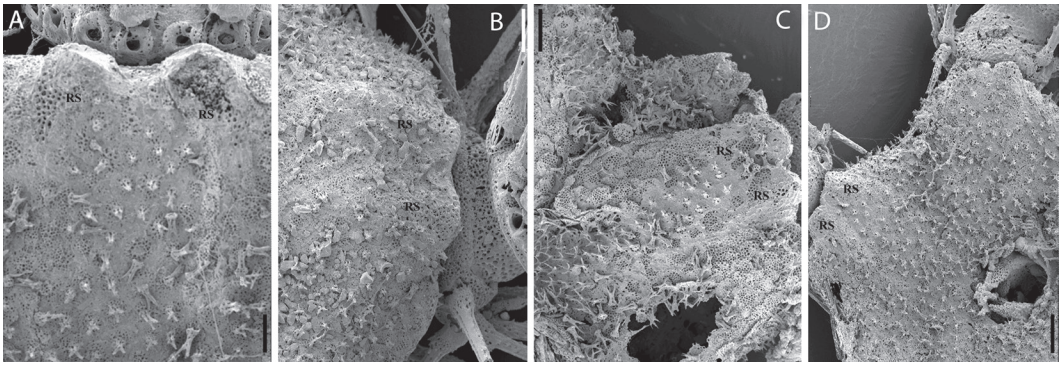

Fig. 2. *Ophiacantha pentacrinus*: partial view of dorsal disc, in detail radial shields **(A)** dd = 7.14 mm; **(B)** dd = 4.95 mm; **(C)** dd = 3.55 mm; **(D)** dd = 2.36 mm. **RS** – radial shield: (scale bar: 300 μm).

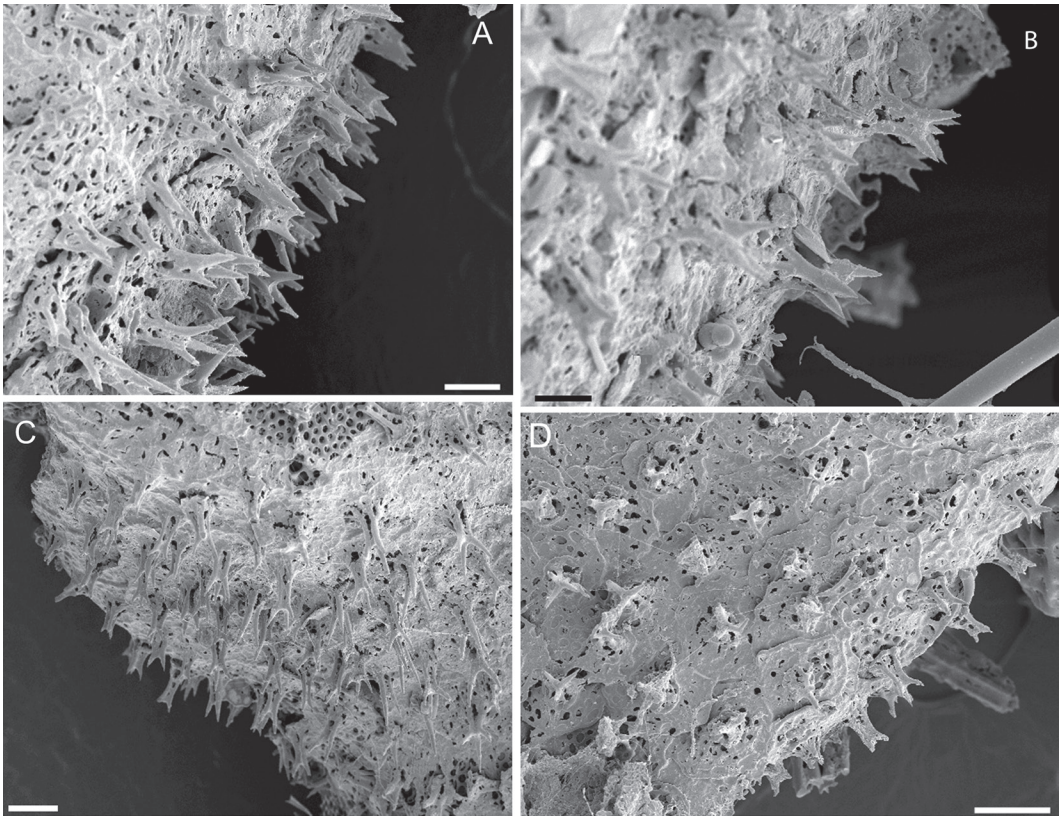

Fig. 3. *Ophiacantha pentacrinus*: partial view of dorsal disc, in detail spines: **(A)** dd = 7.14 mm; **(B)** dd = 4.95 mm; **(C)** dd = 3.55 mm; **(D)** dd = 2.36 mm (scale bar: 300 μm).

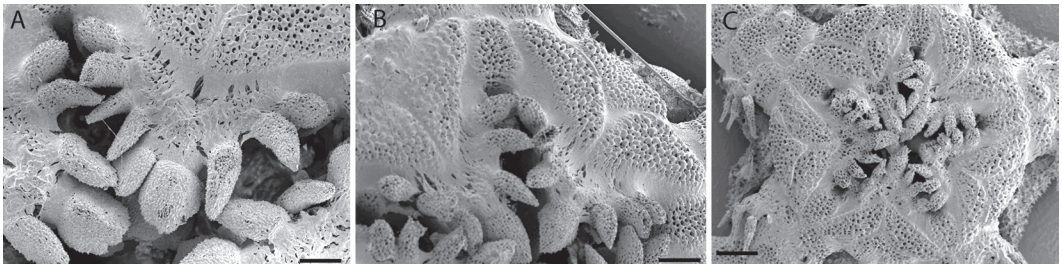

Fig. 4. *Ophiacantha pentacrinus*: partial view of ventral disc, in detail oral papillae: **(A)** dd = 7.14 mm; **(B)** dd = 4.95 mm; **(C)** dd = 2.36 mm (scale bar: 300 μm).

individuals have thicker disc. The three largest specimens have the disc covered with larger scales alternating with smaller ones, the primary and centrodorsal scales are evident (Fig. 7 A - C). In the smallest specimen (1.89 mm dd), the only evident plates are those form the primary rosette and the "primary" radial shields (Fig. 7 D). The ventral interradius portions of the largest specimen (5.12 mm dd) are covered by five disc plates and well developed genital plates, whereas the specimen with 4.65 mm dd has only three or four disc plates (Fig. 8 B), the 3.28 mm specimen, with a single plate (Fig. 8 C) and the smallest specimen this whole

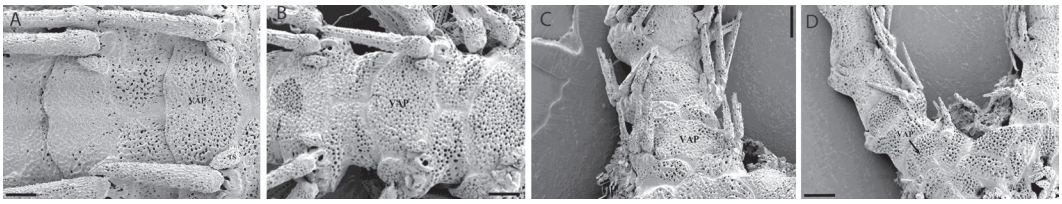

Fig. 5. *Ophiacantha pentacrinus*: partial view of ventral arm, in detail ventral arm plates **(A)** dd = 7.14 mm; **(B)** dd = 4.95 mm; **(C)** dd = 3.55 mm; **(D)** dd = 2.36 mm. **VAP** - ventral arm plate; **TS** - tentacular scale (scale bar: 300 µm).

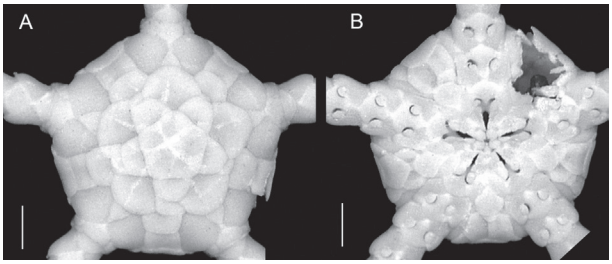

Fig. 6. *Ophiomastus satelitae*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

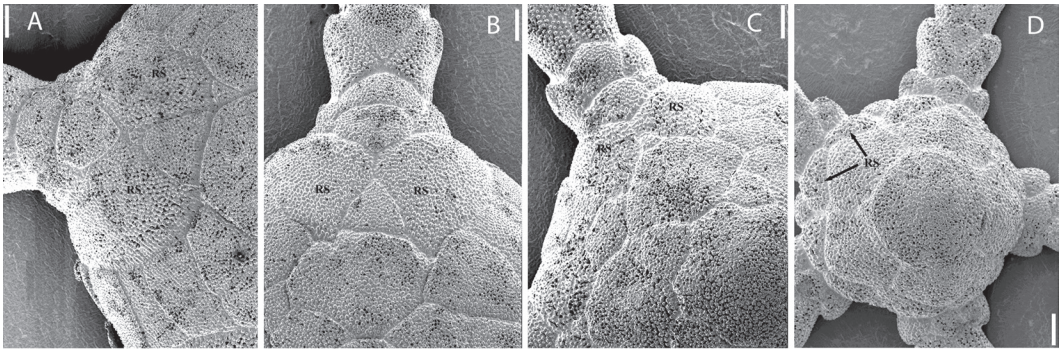

Fig. 7. *Ophiomastus satelitae*: partial view of dorsal disc, in detail plates and radial shields **(A)** dd = 5.12 mm; **(B)** dd = 4.65 mm; **(C)** dd = 3.28 mm; **(D)** dd = 1.89 mm. **RS** - radial shield: (scale bar: 300 µm).

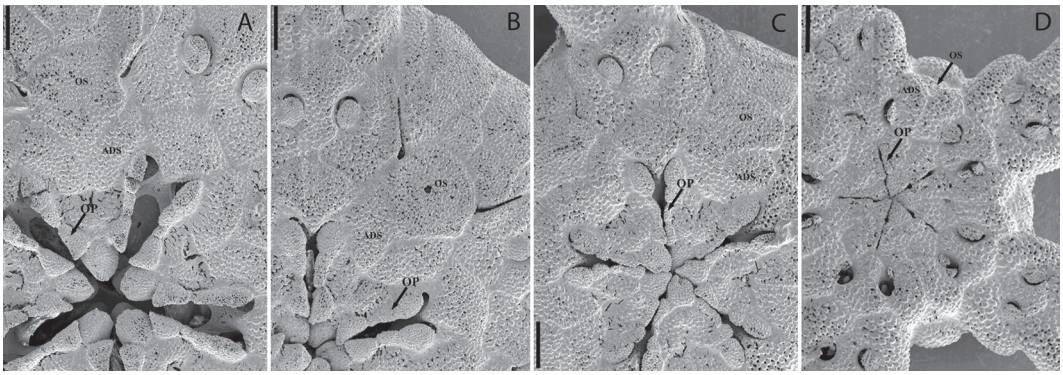

Fig. 8. *Ophiomastus satelitae*: partial view of ventral disc, in detail plates, oral and adoral shields and oral papillae: **(A)** dd = 5.12 mm; **(B)** dd = 4.65 mm; **(C)** dd = 3.28 mm; **(D)** dd = 1.89 mm. **OS** - oral shield, **ADS** - adoral shield, **OP** - oral papillae (scale bar: 300 µm).

portion is only covered by the oral and adoral shields (Fig. 8 D). In the largest specimen, with 5.12 mm dd, the oral shields have mild lateral recesses (Fig. 8 A), which are not observed in the smallest (Fig. 8 B - D). The three largest specimens have three oral papillae (Fig. 8 A - C) while the smallest only has two (Fig. 8 D). The dorsal arm plates are present until the 12th arm segment in the largest individuals (5.12 mm and 4.65 mm dd), while in the 3.28 mm dd until the eight-arm segment and until the third in the smallest specimen.

Ophiomisidium tommasii
Borges, Monteiro & Amaral, 2006
(Figs. 9 - 12)

Adult - Fig. 9

Material examined: 2232 ex.

Specimens selected for description: 4.32 mm, 3.23 mm, 2.46 mm (ZUEC OPH 681); 1.25 mm (ZUEC OPH 679).

This species broods its young in the bursae and often the juveniles arms could be seen through the oral opening. The smallest embryo

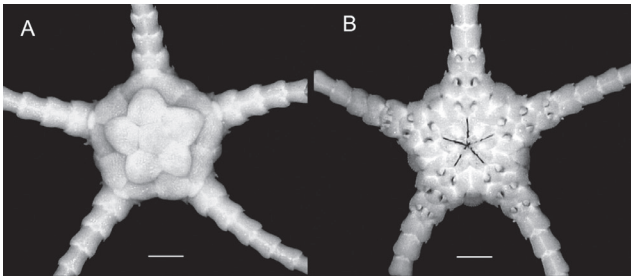

Fig. 9. *Ophiomisidium tommasii*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

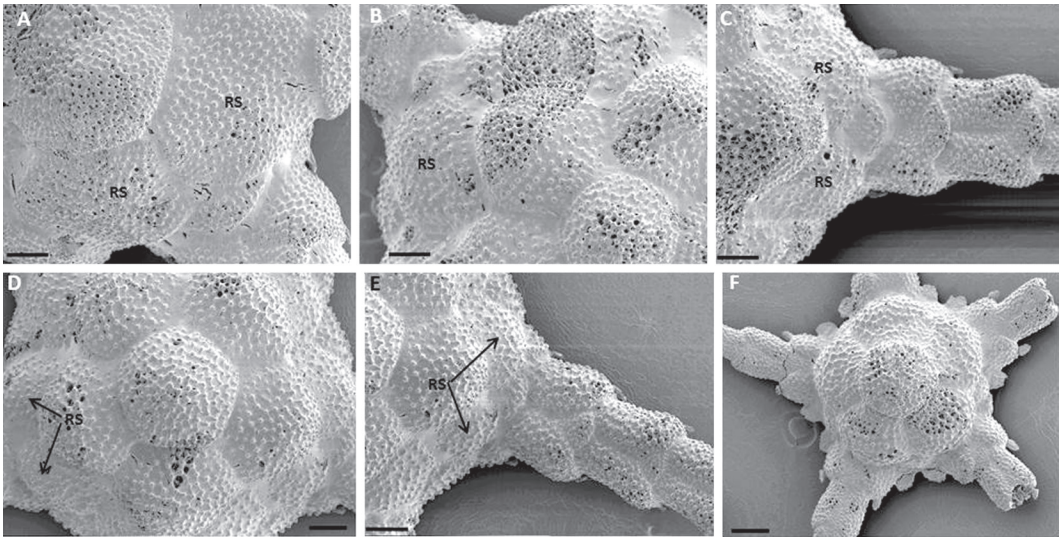

Fig. 10. *Ophiomisidium tommasii*: partial view of dorsal disc and arm, in detail radial shields **(A)** dd = 4.32 mm; **(B, C)** dd = 3.23 mm; **(D, E)** dd = 2.46 mm; **(F)** dd = 1.25mm. **RS** - radial shield (scale bar: 300 µm).

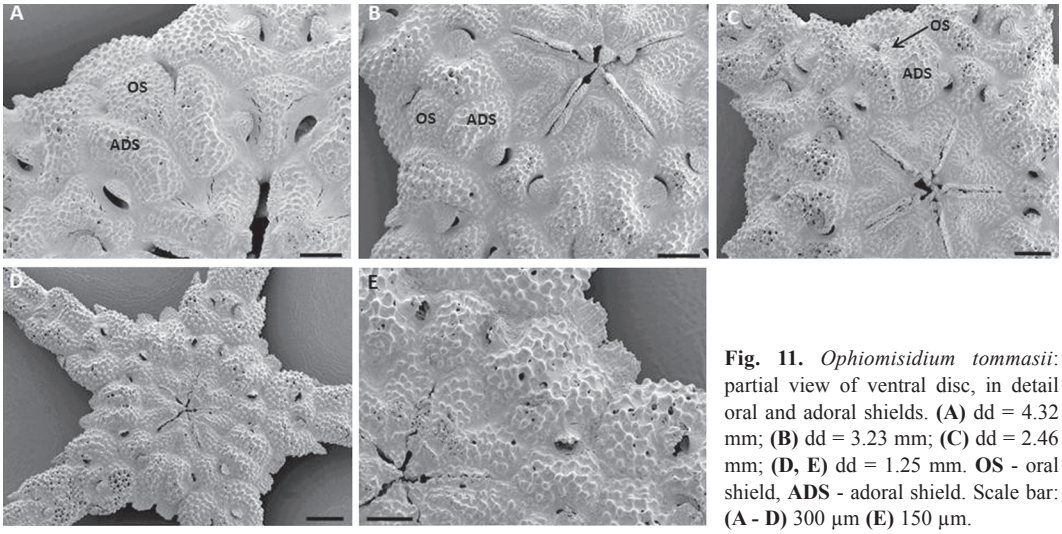

Fig. 11. *Ophiomisidium tommasii*: partial view of ventral disc, in detail oral and adoral shields. **(A)** dd = 4.32 mm; **(B)** dd = 3.23 mm; **(C)** dd = 2.46 mm; **(D, E)** dd = 1.25 mm. **OS** - oral shield, **ADS** - adoral shield. Scale bar: **(A - D)** 300 μm **(E)** 150 μm.

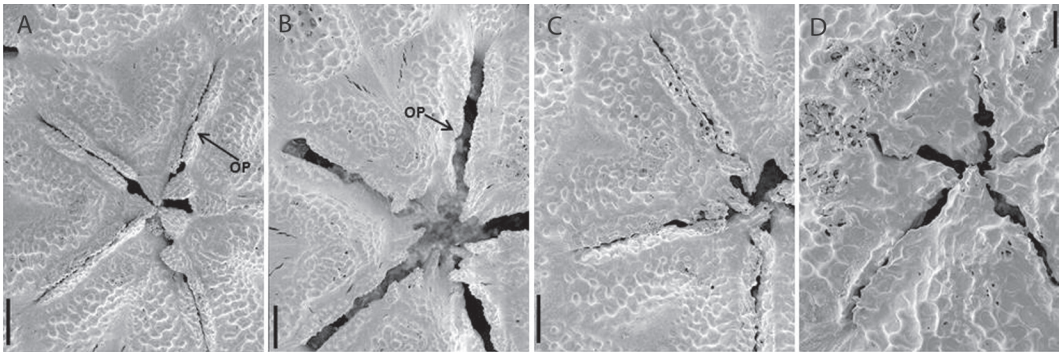

Fig. 12. *Ophiomisidium tommasii*: partial view of ventral disc, in detail oral papillae. **(A)** dd = 4.32 mm; **(B)** dd = 3.23 mm; **(C)** dd = 2.46 mm; **(D)** dd = 1.25 mm. **OP** - oral papillae. Scale bar: **(D)** 50 μm; **(C)** 150 μm; **(A, B)** 200 μm.

found inside in an adult was already quite well developed with 0.8mm dd and with three arm segments.

The three largest individuals have dorsal disc covered by primary rosette with swollen plates and radial shields (Fig. 9A, Fig. 10 A - E). The smallest individual has its disc covered only by the primary rosette (Fig. 10 F) and the radial shields not yet formed. With the development, the plate that separates different pairs of radial shields becomes more evident on the dorsal surface. The three largest specimens show the ventral interradius covered by one plate which extends to the dorsal surface of the disc, the side plates of the first arm segment and the oral and adoral shields (Fig. 11 A - C); the specimen that has 1.25 mm dd presents only two elongated and rectangular plates in ventral interradius, while the oral and adoral shields are not yet formed (Fig. 11 D, E). The specimen with 2.46 mm dd, the oral shield is quite reduced. The three largest specimens with three oral papillae on each side of the jaw (Fig. 12 A - C); at the specimen 1.25 mm dd, the papillae are undeveloped, and cannot be delimited from each other (Fig. 12 D). In addition the later specimens presents the dorsal arm plate until the ninth or tenth segment and the ventral arm plate until the fifth or sixth. The specimen with 1.25 mm dd has the dorsal arm plate until

the sixth segment and the ventral arm plate are present until the third segment. The largest specimens with one small arm spine in the three basal segments and two in the posterior; at 1.25 mm dd has only one spine across all segments.

Ophiomusium acuferum Lyman, 1875
(Figs. 13 - 15)

Adult - Fig. 13

Material examined: 874 ex.

Specimens selected for description: 8.19 mm, 6.01 mm (ZUEC OPH 630); 3.88 mm, 2.90 mm (ZUEC OPH 626).

In the largest specimen, the radial shields completely separated by three plates (Fig. 13 A, Fig. 14 A), the distal plate is larger and higher; each pair of radial shields is also separated from the other pair by two or three plates. While the three smallest individuals has the radial shields joined in a distal median point and separated previously by one or two triangular plates (Fig. 14 B - D). The specimen with 2.90 mm dd has some radial shields touching on the dorsal interradius (Fig. 14 D). The specimen with 8.19 mm dd, the ventral interradius is covered by well-developed genital plate and a large plate and oral shield, further four small plates interspersed. The three smallest specimens lacks the small plates inserted. Four or five oral papillae in the largest specimens (Fig. 15 A - C); and three in the smallest specimens (Fig. 15 D, E). The ventral arm plates are present until the fourth or fifth segment in the two largest individuals, and until the second segment in the two smallest individuals. The three largest specimens have three or four arm spines on basal segment and two in the posterior segments, at 2.90 mm dd, there is two arm spines.

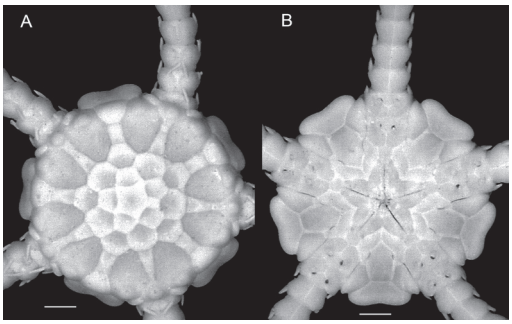

Fig. 13. *Ophiomusium acuferum*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

Ophiomusium eburneum Lyman, 1869
(Figs. 16 - 19)

Adult - Fig. 16

Material examined: 39 ex.

Specimens selected for description: 11.21 mm, 6.63 mm, 4.31 mm, 2.73 mm (ZUEC OPH 847).

The primary plates and centrodorsal plates are not very evident, except in the smallest specimens. The largest individual with 11.21 mm dd is covered by round, small and irregularly arranged scales on the dorsal disc. At 6.63 mm dd, the dorsal plates are smaller and more

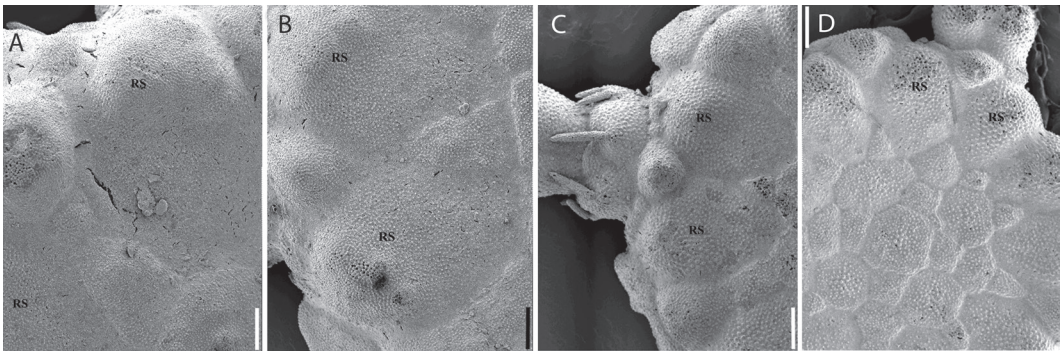

Fig. 14. *Ophiomusium acuferum*: partial view of dorsal disc, in detail radial shields **(A)** dd = 8.19 mm; **(B)** dd = 6.01 mm; **(C)** dd = 3.88 mm; **(D)** dd = 2.90 mm. **RS** - radial shield: (scale bar: 300 μm).

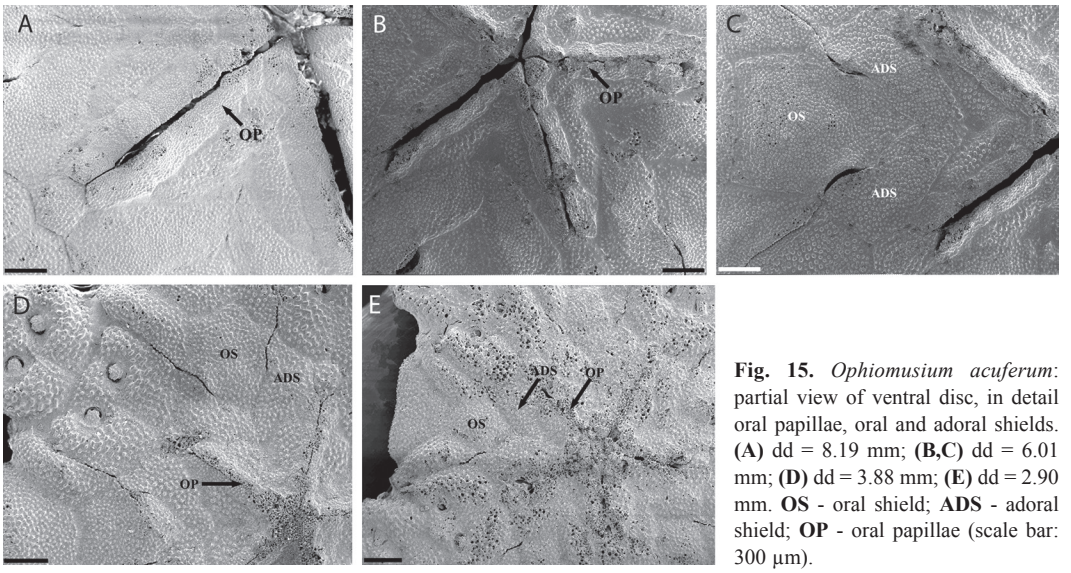

Fig. 15. *Ophiomusium acuferum*: partial view of ventral disc, in detail oral papillae, oral and adoral shields. **(A)** dd = 8.19 mm; **(B,C)** dd = 6.01 mm; **(D)** dd = 3.88 mm; **(E)** dd = 2.90 mm. **OS** - oral shield; **ADS** - adoral shield; **OP** - oral papillae (scale bar: 300 μm).

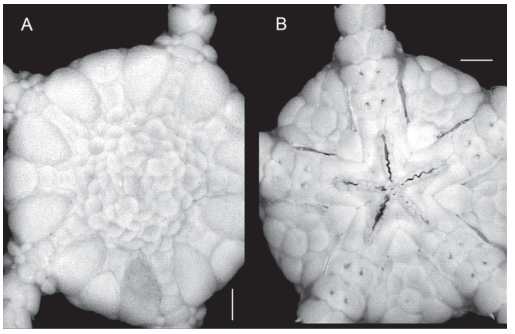

Fig. 16. *Ophiomusium eburneum*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

imbricated; primary plates and centrodorsal evident. At 4.31 mm dd, dorsal disc covered by the primary plates, very evident, interspersed with small plates; centrodorsal round. The specimen with 2.73 mm dd, primary plates occupy almost the whole disc, with a few small plates between them. The two largest individuals have radial shields longer than wide, fully separated by three to four small plates (Fig. 16 A, Fig. 17 A). At 4.31 mm dd, the radial shields are very close at one point in the middle portion, previously separated by a small triangular plate and posteriorly by a triangular plate that joins to first dorsal arm plate (Fig. 17 B); at 2.73 mm dd, the radial shields are united across the median-posterior area and previously separated by a triangular plate (Fig. 17 C). The largest specimen with 11.21 mm dd have ventral interradius with about ten circular plates, slightly elevated; at 6.63 mm dd, about five small elevated plates, at 4.31 mm dd, three and the smallest individual with only two plates. The three largest specimens have five contiguous oral papillae on each side of the jaw (Fig. 18 A - C); at 2.73 mm dd, four (Fig. 18 D). The largest individual with the first dorsal arm plate

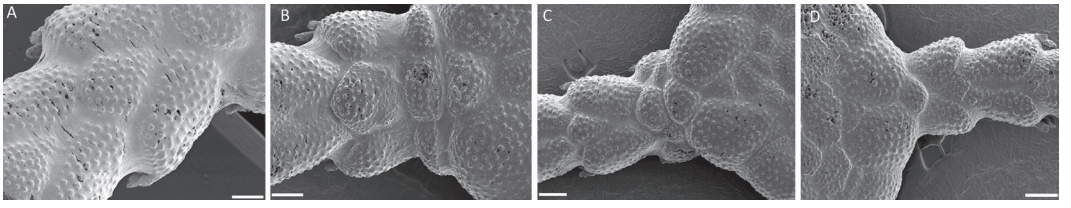

Fig. 17. *Ophiomusium eburneum*: partial view of dorsal disc and arm, in detail radial shields. **(A)** dd = 11.21 mm **(B)** dd = 6.63 mm; **(C)** dd = 4.31 mm; **(D)** dd = 2.73 mm. Scale bar: 300 μm.

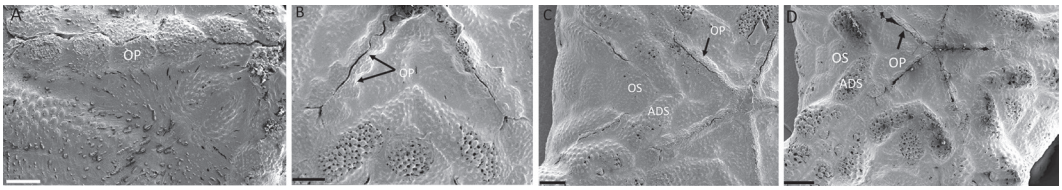

Fig. 18. *Ophiomusium eburneum*: partial view of ventral disc, in detail oral papillae. **(A)** dd = 11.21 mm; **(B, C)** dd = 6.63 mm; **(D)** dd = 4.31 mm; **(E)** dd = 2.73 mm (scale bar: 300 µm).

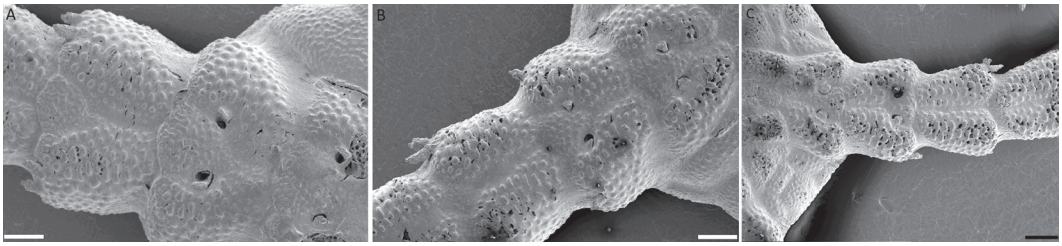

Fig. 19. *Ophiomusium eburneum*: first ventral arms segments. **(A)** dd = 6.63 mm; **(B)** dd = 4.31 mm; **(C)** dd = 2.73 mm (scale bar: 300 µm).

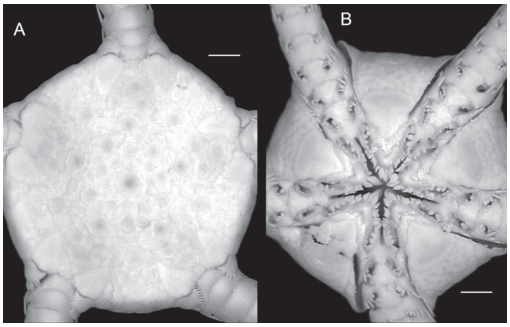

Fig. 20. *Ophiura ljungmani*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

pentagonal, posterior plates diamond-shaped and small (Fig. 17 A); at 6.63 mm dd, the first dorsal arm plate rectangular, second pentagonal and posterior plates diamond-shaped (Fig. 17 A); at 4.31 mm, the first semi-pentagonal and posterior plates diamond-shaped (Fig. 17 B); smallest specimen with all dorsal arm plates diamond-shaped, the first slightly larger (Fig. 17 C). Two largest specimens with lateral arm plates dorsally separated in the two basal arm segments; smallest individuals with lateral arm plates dorsally separated only at first arm segment. Two largest specimens with ventral arm plates present until the fifth or sixth segment (Fig. 19 A), decreasing in size until the end of the arm; at smallest until second or third (Fig. 19 B, C).

Ophiura ljungmani (Lyman, 1878)
(Figs. 20 - 23)

Adult - Fig. 20

Material examined: 164 ex.

Specimens selected for description: 9.48 mm, 6.83 mm (ZUEC OPH 791); 3.74 mm, 2.45 mm (ZUEC OPH 810).

At 9.48 mm dd, individual with characteristics of an adult, is evident only a centrodorsal scale. In smallest specimens with 2.45 mm dd, the primary scales are still distinguishable. Radial shields completely separated at two largest specimens (Fig. 21 A - C), with about ten scales between them in the individual with 9.48 mm dd and five at 6.83 mm dd. At 3.74 mm and 2.45 mm dd, these shields are united distally and separated at anterior portion by one to three scales, respectively (Fig. 21 D - F). The number of scales between each pair of radial shields increases with the size of the individual. Oral shields well developed in all specimens; in the two largest individuals this shields occupy almost half of the ventral interradius (Fig. 20

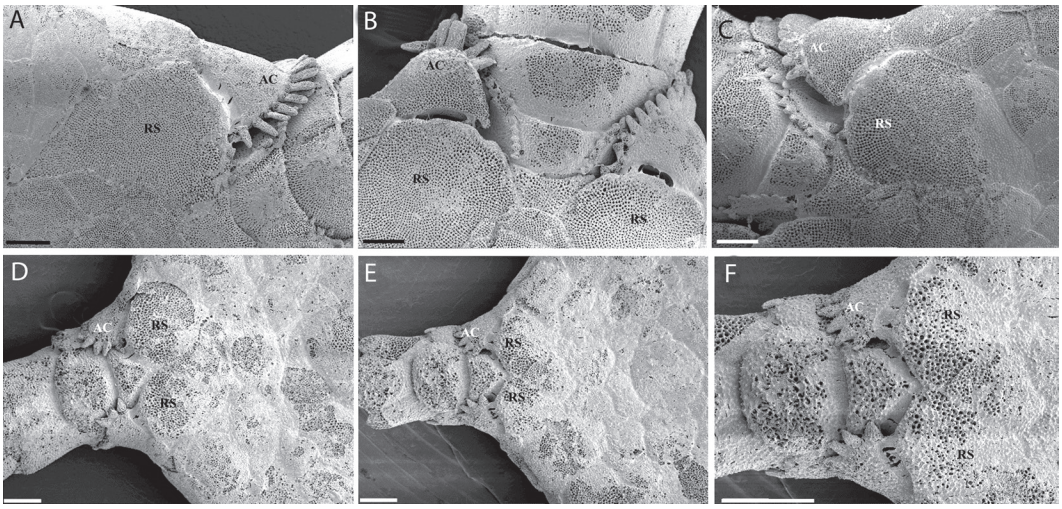

Fig. 21. *Ophiura ljungmani*: partial view of dorsal disc, in detail radial shields and arm comb: **(A)** dd = 9.48 mm; **(B,C)** dd = 6.83 mm; **(D)** dd = 3.74 mm; **(E,F)** dd = 2.45 mm. **AC** - arm comb; **RS** - radial shield (scale bar: 300 μm).

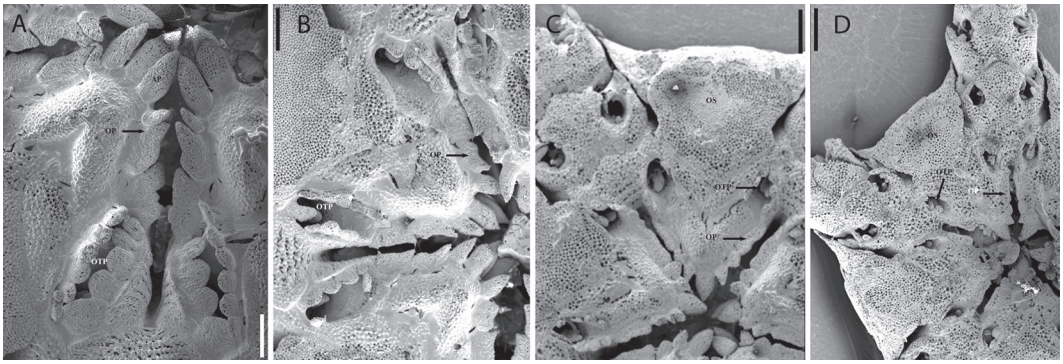

Fig. 22. *Ophiura ljungmani*: partial view of ventral disc, in detail oral papillae and oral tentacular pore: **(A)** dd = 9.48 mm; **(B)** dd = 6.83 mm; **(C)** dd = 3.74 mm; **(D)** dd = 2.45 mm. **AP** - apical papillae; **OP** - oral papillae; **OS** - oral shield; **OTP** - oral tentacular pore (scale bar: 300 μm).

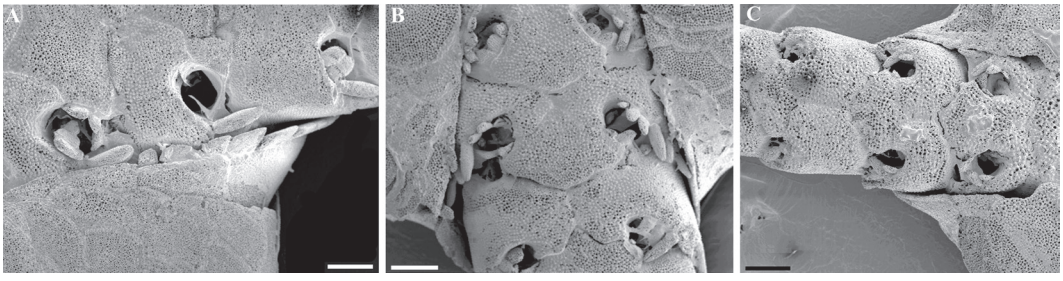

Fig. 23. *Ophiura ljungmani*: partial view of ventral arm, in detail tentacular pore and arm comb: **(A)** dd = 9.48 mm; **(B)** dd = 6.83 mm; **(C)** dd = 3.74 mm (scale bar: 300 μm).

B), at smallest specimens, they occupy the whole interradius (Fig. 22 C, D). The two largest individuals have four oral papillae on each side of the jaw; one or two apical papillae (Fig. 22 A, B); at two smallest specimens with four to five oral papillae and one apical (Fig. 22 C, D). At 9.48 mm dd, the oral tentacular pore has 10 - 12 scales (Fig. 22 A); at 6.83 mm dd about eight scales (Fig. 22 B); at 3.74 mm dd, about five (Fig. 22 C) and the smallest specimen, there are three to four (Fig. 22 D). The two largest individuals have broad tentacular arm pore at three basal arm segments (Fig. 23 A, B), first with seven scales, second with five and third with three, reducing to one scale in subsequent segments. At 3.74 mm dd has four to five scales at first tentacular arm pore, two at second and from the third, one scale (Fig. 23 C); at 2.45 mm dd with two scales on first arm pore and from the second one (Fig. 22 D).

Ophiura clemens (Koehler, 1904)
(Figs. 24 - 28)

Adult - Fig. 24

Material examined: 617 ex.

Specimens selected for description: 7.85 mm (ZUEC OPH 854); 5.76 mm, 4.83 mm, 3.27 mm (ZUEC OPH 866).

The largest specimen with radial shields united in the median portion and previously separated by a small triangular scale and a large sub-lozenge, at the posterior region by a triangular scale (Fig. 25 A, B); at three smallest individuals, these shields are separated in the proximal region only by diamond scale, and there is not the triangular scale separating them distally (Fig. 25 C - E). In the two largest individuals, there are about eight scales between each pair of radial shields (Fig. 26 A, B); at 4.83 mm dd there are three to four scales (Fig. 26 C) and at 3.27 mm dd, two (Fig. 25 E). Largest specimen with about ten scales covering the second oral tentacle pore (Fig. 27 A, B); at 5.76 mm and 4.83 mm dd, seven to eight scales (Fig. 27 C, D) and the smallest specimen with four (Fig. 27 E). In the two largest individuals, first arm segment with large pore covered for approximately six to eight tentacular scales,

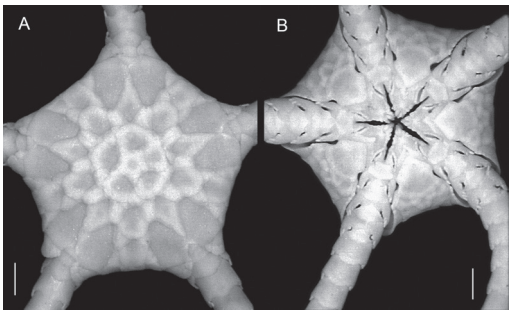

Fig. 24. *Ophiura clemens*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

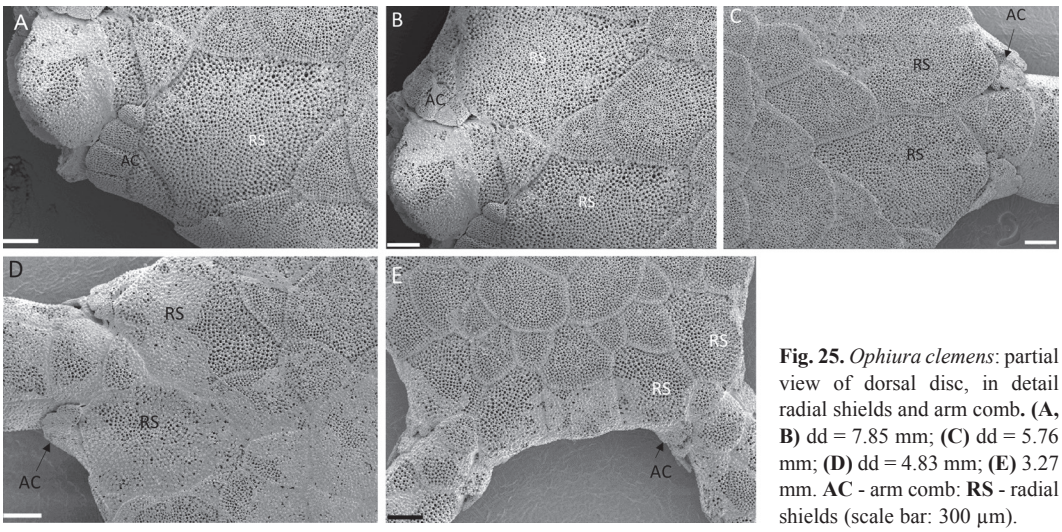

Fig. 25. *Ophiura clemens*: partial view of dorsal disc, in detail radial shields and arm comb**. (A, B)** dd = 7.85 mm; **(C)** dd = 5.76 mm; **(D)** dd = 4.83 mm; **(E)** 3.27 mm. **AC** - arm comb: **RS** - radial shields (scale bar: 300 μm).

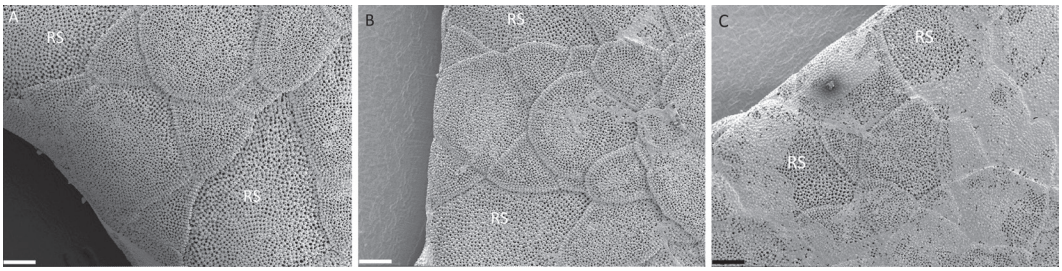

Fig. 26. *Ophiura clemens*: dorsal view of dorsal disc, in detail plates and radial shields. **(A)** dd = 7.85 mm; **(B)** dd = 5.7 6mm; **(C)** dd = 4.83 mm. **RS** - radial shield: (scale bar: 300 µm).

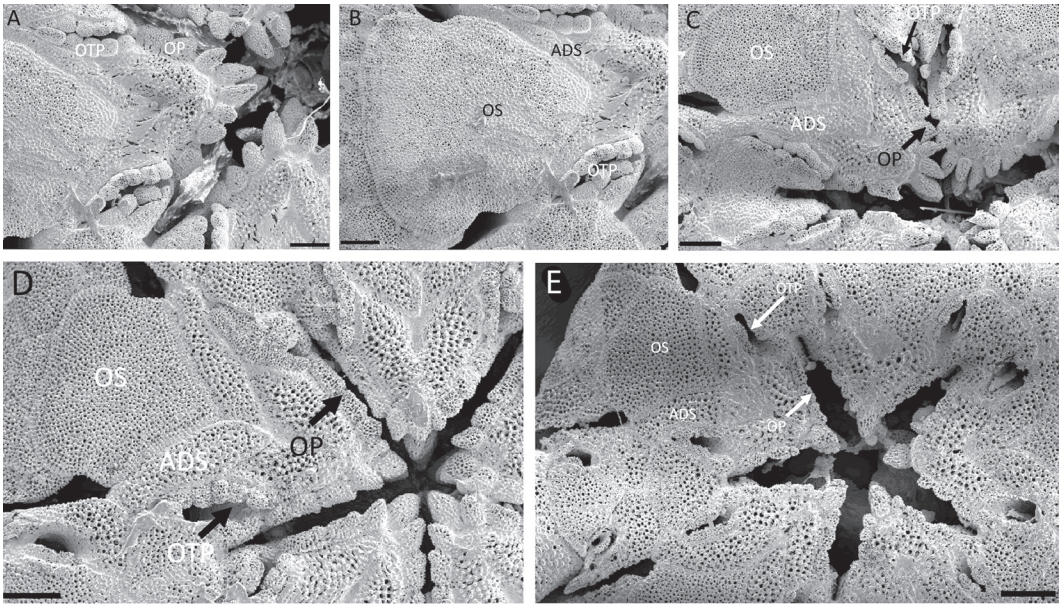

Fig. 27. *Ophiura clemens*: partial view of ventral disc, in detail oral tentacular pore: **(A, B)** dd = 7.85 mm; **(C)** dd = 5.76 mm; **(D)** dd = 4.83 mm; **(E)** dd = 3.27 mm. **ADS** - adoral shield; **OP** - oral papillae; **OS** - oral shield; **OTP** - oral tentacular pore (scale bar: 300 µm).

the second with five scales (Fig. 28 A, C) and third with three (Fig. 28 B, D); at 4.83 mm dd, the first tentacular arm pore with six scales, the second with three (Fig. 28 E, F) and the third with two (Fig. 28 G); at 3.27 mm dd there are two scales on first arm pore and from second, one (Fig. 28 H, I). The smallest individual with a very little arm comb (Fig. 25 E).

AMPHIURIDAE

Amphiura complanata Ljungman, 1867

(Figs. 29 - 32)

Adult - Fig. 29

Material examined: 19 ex.

Specimens selected for description: 11.57 mm (ZUEC OPH 785); 9 mm (ZUEC OPH

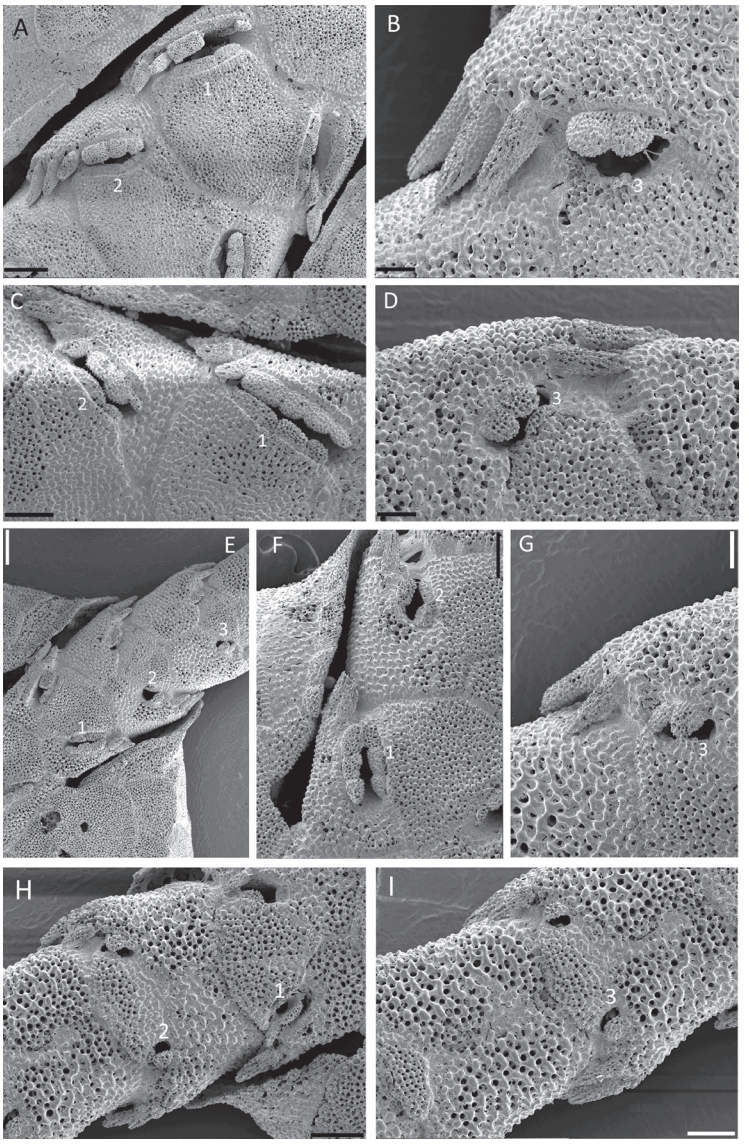

Fig. 28. *Ophiura clemens*: First ventral arm segments, in detail tentacular pores: **(A)** segments 1 and 2 (dd = 7.85 mm); **(B)** segment 3 (dd = 7.85 mm); **(C)** segments 1 and 2 (dd = 5.76 mm); **(D)** segment 3 (dd = 5.76 mm); **(E,F)** segments 1 and 2 (dd = 4.83 mm); **(G)** segment 3 (dd = 4.83 mm); **(H)** segments 1 and 2 (dd = 3.27 mm); **(I)** segment 3 (dd = 3.27 mm). Scale bar: **(B, G)** 100 µm; **(I)** 150 µm; **(C, F, H)** 200 µm; **(A, D, E)** 300 µm.

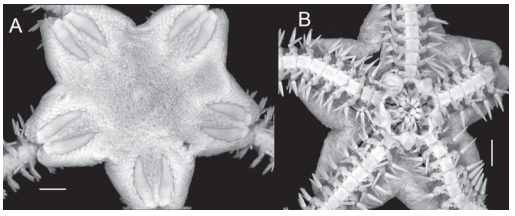

Fig. 29. *Amphiura complanata*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

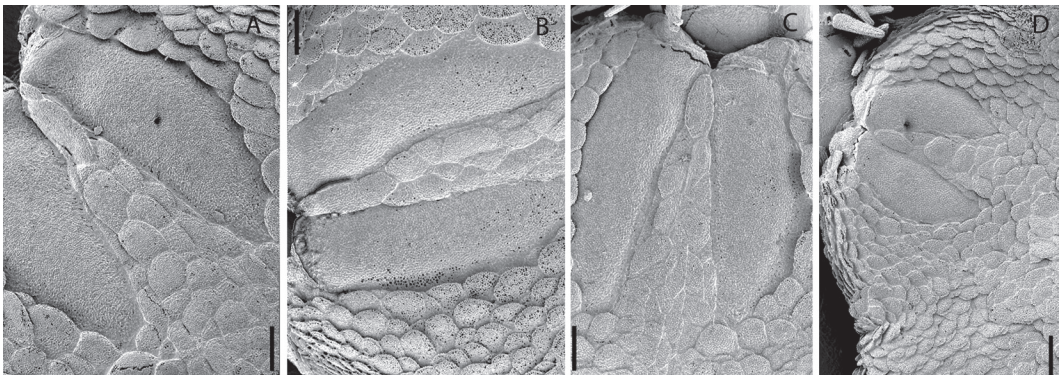

Fig. 30. *Amphiura complanata*: partial view of dorsal disc, in detail plates and radial shields: **(A)** dd = 11.57 mm; **(B)** dd = 9.0 mm; **(C)** dd = 6.78 mm; **(D)** dd = 4.23 mm (scale bar: 300 μm).

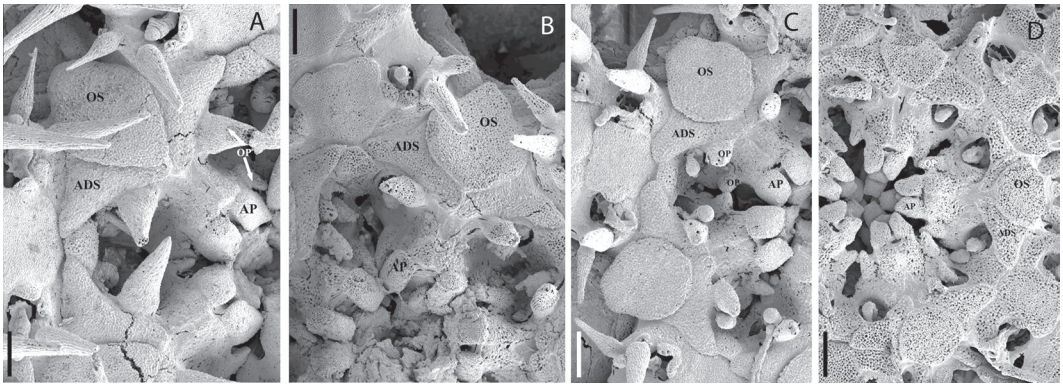

Fig. 31. *Amphiura complanata*: partial view of ventral disc, in detail oral and adoral shields: **(A)** dd = 11.57 mm; **(B)** dd = 9.0 mm; **(C)** dd = 6.78 mm; **(D)** dd = 4.23 mm. **ADS** - adoral shield; **AP** - apical papillae; **OP** - oral papillae; **OS** - oral shield (scale bar: 300 μm).

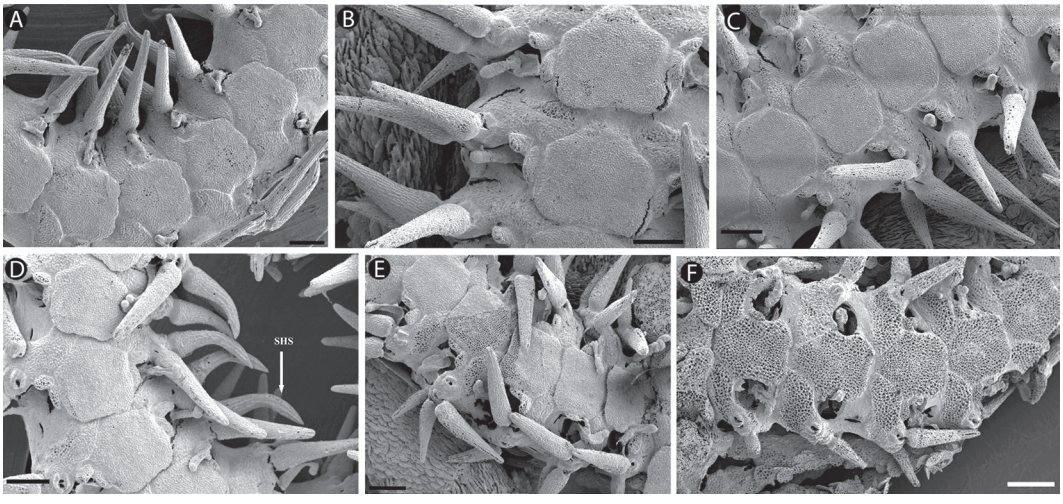

Fig. 32. *Amphiura complanata*: partial view of ventral arm, in detail spines: **(A)** and **(B)** dd = 11.57 mm; **(C)** dd = 9 mm; **(D)** and **(E)** dd = 6.78 mm; **(F)** dd = 4.23 mm. **SHS** - spine hook-shaped (scale bar: 300 μm).

815); 6.78 mm (ZUEC OPH 824); 4.23 mm (ZUEC OPH 827).

Primary scales evident only in the lower specimen. Centrodorsal scale evident in all individuals. Radial shields narrower and separated at two largest specimens (Fig. 30 A, B), two smaller specimens with these shields united later (Fig. 30 C, D). Two largest specimens with about 25 irregularly shaped small scales between the pair of radial shields (Fig. 30 A, B); at 6.78 mm dd, about 18 and at 4.23 mm dd (Fig. 30 C), about 12 scales (Fig. 30 D). In the three largest specimens with oval oral shields, longer than broad, and adoral shields contiguous along internal median line of jaw (Fig. 31 A - C); at 4.23 mm dd, oral shield more rounded, as wide as long, and adoral shields separate in the anterior portion (Fig. 31 D). At 11.57 mm dd, hyaline spine hook-shaped from 14th arm segment; at 9 mm dd from 13th, at 6.78 mm dd from 15th and at 4.23 mm dd, from tenth. In this specimen is more difficult to observe the hyaline spine. Two largest specimens with six arm spines in the basal segments and five in the end; at 6.78 mm dd, five spines at basal segments and four in the end and at 4.23 mm dd, four arm spines (Fig. 32).

OPHIOTRICHIDAE

Ophiothrix rathbuni Ludwig, 1882

(Figs. 33 - 35)

Adult - Fig. 33

Material examined: 104 ex.

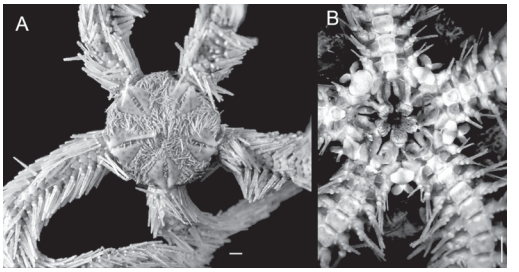

Fig. 33. *Ophiothrix rathbuni*: **(A)** dorsal view. **(B)** ventral view (scale bar: 1 mm).

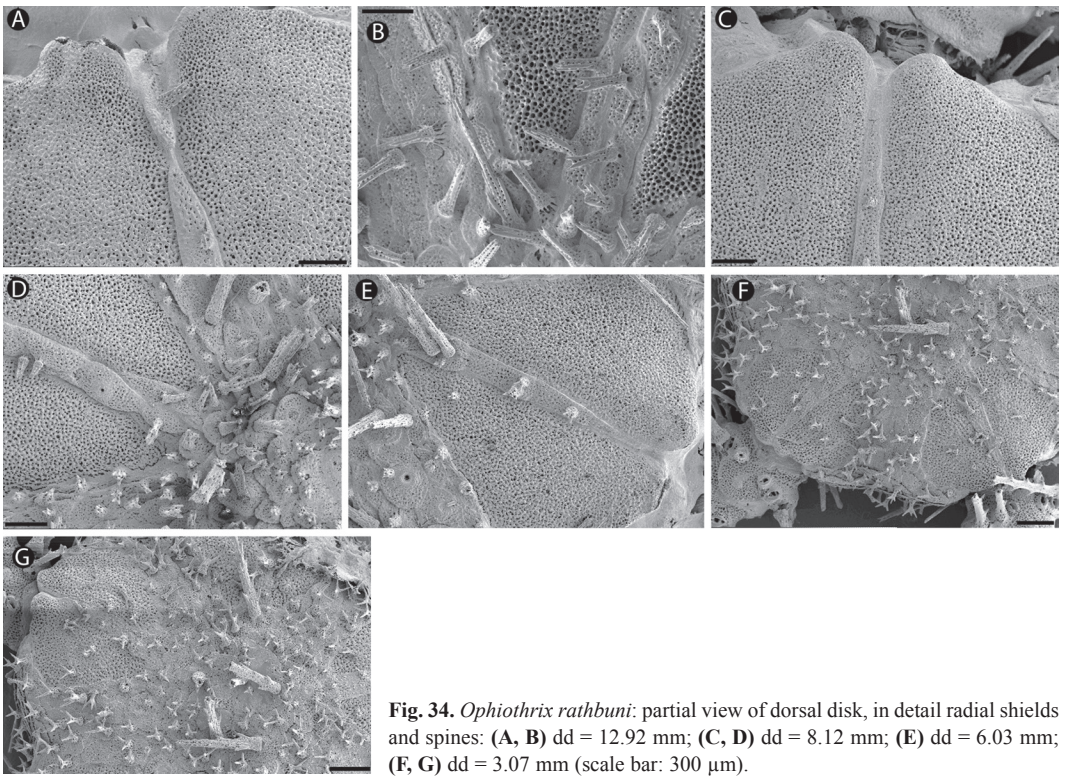

Fig. 34. *Ophiothrix rathbuni*: partial view of dorsal disk, in detail radial shields and spines: **(A, B)** dd = 12.92 mm; **(C, D)** dd = 8.12 mm; **(E)** dd = 6.03 mm; **(F, G)** dd = 3.07 mm (scale bar: 300 μm).

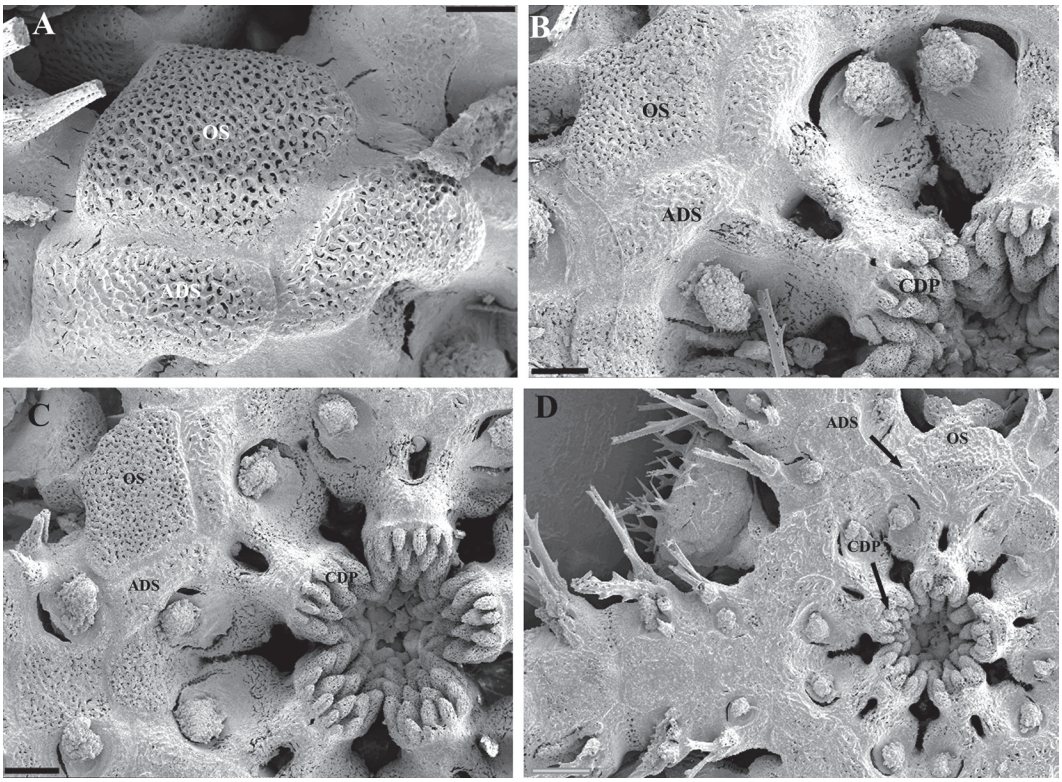

Fig. 35. *Ophiothrix rathbuni*: partial view of ventral disc, in detail oral and adoral shields and cluster of dental papillae: **(A)** dd = 12.92 mm; **(B)** dd = 8.12 mm; **(C)** dd = 6.03 mm; **(D)** dd = 3.07 mm. **ADS** - adoral shields; **CDP** - cluster of dental papillae; **OS** - oral shield (scale bar: 300 μm).

Specimens selected for description: 12.92 mm (ZUEC OPH 857); 8.12 mm, 6.03 mm, 3.07 mm (ZUEC OPH 858).

Specimen of 12.92 mm dd with dorsal disc covered with scales and elongated spines with marginal denticles, and short spines bifid and trifids; at 8.12 mm dd there are few elongated spines on the disc, this is mainly covered by small spines; at 6.03 mm dd only small spines on dorsal disc and smallest individual there are mainly short spines, but there are about six spines elongated (Fig. 34 F, G). Two largest specimens have radial shields completely separated (Fig. 34 A - D); two smallest individuals have this shields united later (Fig. 34 E - G). The two smallest specimens with few spines on ventral interradius, this region is mainly covered by scales. At 12.92 mm dd, the adoral shields extended in the posterior portion (Fig. 35 A); three smallest specimens with elongated adoral shields (Fig. 35 B - D). Three largest individuals have seven arm spines and ventral spine modified in hook from the eighth or ninth arm segment; at 3.07 mm dd, five and spine-hook from fourth or fifth.

Main differences between juvenile and adult individuals were listed for each specie (Table 1) to make clearer the most important changes between them, regarding characters of the dorsal disc, jaw and arms.

DISCUSSION

The description of the morphological characters from the largest individual and the growth series showed that some structures remain almost unaltered (number of apical papillae) during the entire life of the post-metamorphic

TABLE 1
Differences between young and adult individuals for each species

Species	Dorsal disc		Jaw		Arms	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Ophiacantha pentacrinus	Radial shields completely separated	Radial shields joint posteriorly	Four oral papillae in some jaws	Three oral papillae	Dorsal arm plates fan-shaped and some diamond-shaped Ventral arm plates sub-pentagonal	Dorsal arm plates diamond Ventral arm plates rounded
Ophiomastus satelitae	Larges scales alternating with smaller ones	The only evident scales are the primary rosette and radial shields	Three oral papillae	Two oral papillae	Dorsal arm plates present until the 12th arm segment	Dorsal arm plates present until the 3rd arm segment
Ophiomisidium tommasii	Covered by primary rosette with swollen plates and radial shields	Covered only by primary rosette and radial shields not yet formed	Three oral papillae	Oral papillae undeveloped	Dorsal arm plates until the 9th or 10th segment Ventral arm plates until 5th or 6th	Dorsal arm plates until the 6th segment Ventral arm plates until the 3rd
Ophiomusium acuferum	Radial shields completely separated	Radial shields joined in a distal median point	Four or five oral papillae	Three oral papillae	Ventral arm plates present until 4th or 5th segment	Ventral arm plates present until 2nd segment
Ophiomusium eburneum	Radial shields longer than wide, fully separated by three to four plates	Radial shields united across the median-posterior area and anteriorly separated by a triangular plate	Five oral papillae	Four oral papillae	The 1st dorsal arm plate pentagonal, posterior diamond-shaped and small Ventral arm plates until 5th or 6th segment	All dorsal arm plates diamond-shaped, the 1st slightly larger Ventral arm plates until 2nd or 3rd
Ophiura ljungmani	Radial shields completely separated by ten scales	Radial shields united posteriorly and separated at anterior portion by one or three scales	Four oral papillae and one or two apical papillae	Four to five oral papillae and one apical papillae	Oral tentacular pore has 10-12 scales	Oral tentacular pore has three-four scales
Ophiura clemens	Radial shields united in the median portion and anteriorly separated by a small triangular scale	Radial shields separated posteriorly by diamond scale	The 2nd oral tentacle pore covered by ten scales	The 2nd oral tentacle pore covered by for scales	The 1st arm segment with large pore covered by six-eight tentacular scales, 2nd with five and 3rd with three	The 1st arm segment with large pore covered by two scales and 2nd by one scale

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TABLE 1 (Continued)

Species	Dorsal disc		Jaw		Arms	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Amphiura complanata	Radial shields narrower and separated	Radial shields united posteriorly	Oral shields oval, longer than broad and adoral shields contiguous along internal median line of jaw	Oral shield more rounded, as wide as long and adoral shields separated anteriorly	Six arm spines in the basal segments and five in the end	Four arm spines
Ophiothrix rathbuni	Radial shields completely separated	Radial shields united posteriorly	Adoral shields extended posteriorly	Adoral shields elongated	Seven arm spines	Five arm spines

organism, while others (radial shields, oral papillae and arms) are subject to transformations. Thus, this work contributes to a broader knowledge of some ophiuroid species, concerning the characterization of their different development stages. Particularly, we described species from deeper regions of Brazil, from 60 m until 800 m, not commonly studied, due to inherent difficulties obtaining such sizes.

The study and the possibility of identifying specimens of Ophiuroidea in their different development stages are outmost relevance, for example, when it is considered that these organisms are subject to a high mortality rate, especially the juveniles (Gage, 1984; Tyler, Gage & Billett, 1991; Sumida et al., 1998). Besides, the ontogenesis of homologous structures in post-larval ophiuroids can be useful in defining systematic and phylogenetic relations between taxonomic groups (Hendler, 1988).

In the present work, the structures that suffered most change during development were: radial shields, oral papillae, dorsal and ventral arm plates and number of arm spines. The shape of the radial shields changes considerably during the growth of the individual, which has been pointed as an important morphological character to diagnose the species (Monteiro, 1987). The oral papillae change, especially in the number and/or position, which increase during development (Schoener, 1967, 1969; Monteiro, 1987 and Sumida et al., 1998). Arm characteristics, such as the size and shape of dorsal and ventral arm plates and the number of arm spines, which is lower in youngest, can also be very useful (Sumida et al. 1998; Stöhr, 2005).

In this work, the radial shields present different shapes: i) completely separated in the largest individuals and joint posteriorly in smallest individuals, such as *Ophiacantha pentacrinus*, *Ophiura ljungmani, Amphiura complanata* and *Ophiothrix rathbuni* (which is joint later); ii) completely separated in largest individuals and joint anteriorly in smallest individuals, such as *Ophiomusium acuferum*; iii) with one plate between the radial shields that becomes more evident throughout the individual's growth and unformed shields in the smallest individuals, as in *Ophiomisidium tommasii*; and iv) largest specimens with longer, rather than broader, radial shields, as in *Ophiomusium eburneum*.

Regarding to jaw, some species showed changes in the size and shape of the oral and adoral shields throughout their development, for example, *Ophiomastus satelitae*, *Ophiomisidium tommasii*, *Ophiura ljungmani*, *Amphiura complanata* and *Ophiothrix rathbuni*, which is similar to another studies (e.g. Schoener, 1967, 1969; Monteiro, 1987 and Sumida et al., 1998). Furthermore, *Ophiomastus satelitae*, *Ophiomusium acuferum*, *Ophiomusium eburneum* suffered changes in the number of oral papillae.

In some species, the oral structures remained almost unaltered in the different

growth stages, as it has been registered for *Ophiacantha pentacrinus*. According to Sumida et al. (1998), the oral structures of congeneric species, including post-larval stages, is very similar and conservative within the group, which suggests that they may compete for the same type of food. Alterations in a single individual may also be verified, such as the number of oral papillae in the different jaws of *Ophiacantha pentacrinus*, thus indicating individual variation, unrelated to size.

The shape of the arm plates may also vary according to the size of the individual's, but usually juveniles are similar to the tips of adults arms (Clark, 1914; Monteiro, 1987). The same pattern has been observed in the species *Ophiomusium eburneum*. The dorsal arm plates are diamond shaped, and are present along the entire arm in the smallest individuals while in the largest specimens are present at the tip of the arms.

The number of arm spines change accordingly to the size of the organism observed. In *Ophiacantha pentacrinus*, *Ophiomusium acuferum* and *Amphiura complanata* the number of arm spines is higher as the disc diameter increases. The same happens with the number of tentacle scales, which decreases in smaller specimens.

Regarding development time from young to adult, there are few published studies (Gage & Tyler, 1982; Sumida et al., 1998; Sumida, Tyler, Lampitt & Gage, 2000; Lampitt, Sumida & Pérez-Castillo, 2002). These studies show that this time may depend on the high predation rates to which these animals are exposed, which may accelerate growth causing them to achieve adulthood faster, as occurs with *Ophiocten gracilis* (Sumida et al., 2000).

Our work contributes considerably to the knowledge about development of some brittle stars, because actually, less than 50 juvenile forms are known and juvenile characters often differ considerably from adult ones and may potentially be valuable for phylogenetic considerations (Stöhr, 2012). We emphasized that studies about post-metamorphic development in ophiuroids show that changes resulting from growth, demand great caution in specific differentiation, and related species must always be compared to each other from similar size, as seen in previous studies (Sumida et al., 1998; Stöhr, 2012).

ACKNOWLEDGMENTS

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RESUMEN

De bebé a adulto: serie ontogenética de nueve especies de Ophiuroidea del Atlántico sudoccidental. La etapa post-metamórfica es esencial en la historia de vida de los invertebrados marinos. Durante este período, los animales son más vulnerables y sufren una elevada mortalidad, que influye en la distribución y abundancia de las poblaciones de los adultos. También es durante este período cuando grandes cambios morfológicos ocurren en los individuos, lo que complica su identificación taxonómica. Los ofiuroideos juveniles son el componente principal para la mayor parte de la composición de la meiofauna en ciertas épocas del año y en algunos lugares. Sin embargo, son ignorados por la mayoría de los estudios ecológicos debido a las dificultades de identificación. De esta manera, la descripción de las fases juveniles presenta mayor importancia, sobre todo en estudios relacionados con la dinámica poblacional y de composición de fauna. Este trabajo tiene como objetivo describir la ontogenia de nueve especies de aguas profundas de las regiones Sudeste y Sur de Brasil, siendo el primer registro en la literatura sobre cambios morfológicos –a partir del crecimiento– para ocho de ellos. La mayoría de los organismos se tomaron en el intervalo de 60 a 800 m de profundidad, entre diciembre de 1997, enero de 1998 y marzo de 1998, durante el programa REVIZEE Sur-Score / Bentos. También se incluyen en este estudio material adicional del Museo de Zoología de la Unicamp (ZUEC). Para las identificaciones y descripciones de las diferentes etapas, las muestras se secaron y fueron fotografiadas. Los juveniles fueron identificados por "al revés" el proceso de crecimiento a través de la serie desde adultos hasta los individuos de menores tallas, una metodología exitosa en estudios anteriores. Las especies seleccionadas para la descripción de la serie de crecimiento fueron escogidas de acuerdo a su abundancia relativa en diferentes etapas de desarrollo. Algunos individuos fueron montados en tacos de aluminio para la microscopía electrónica de barrido. Las especies se estudiadas fueron: *Ophiacantha pentacrinus* (Ophiacanthidae), *Ophiomastus satelitae*, *Ophiomusium acuferum*, *Ophiomusium eburneum*, *Ophiomisidium tommasii*, *Ophiura ljungmani*, *Ophiura clemens* (Ophiuridae),

Amphiura complanata (Amphiuridae) y *Ophiothrix rathbuni* (Ophiotrichidae). El análisis del desarrollo post-metamórfico de los individuos reveló que muchas especies podrían ser identificadas desde sus etapas más juveniles, sobre todo a partir de caracteres morfológicos externos. Este estudio nos permite sostener que algunas estructuras permanecen casi inalteradas durante toda la vida del organismo, mientras que otras están sujetas a transformaciones. De este modo, se contribuye al conocimiento más amplio de algunas especies de ofiuroideos, con relación a la caracterización de sus diferentes etapas de desarrollo.

Palabras clave: estrellas de mar, series de crecimiento, fauna bentónica, taxonomía, ecología, distribuición.

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