Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Post-larval development and growth intraspecific variations in *Ophiocoma echinata* and *Ophiocoma trindadensis* from Brazil (Echinodermata: Ophiuroidea)

Cecília J. S. Damiano[1], Helena Serrano[1], Renata A. S. Alitto[1], Joel B. Mendonça[2], Marcos Tavares[2] and Michela Borges[1]

[1]Museum of Biological Diversity – MDBio – Zoology Area (ZUEC), State University of Campinas (UNICAMP), Institute of Biology, Campinas, São Paulo, Brazil and [2]Zoology Museum, University of São Paulo, São Paulo, São Paulo, Brazil

Research Article

Cite this article: Damiano CJS, Serrano H, Alitto RAS, Mendonça JB, Tavares M, Borges M (2025). Post-larval development and growth intraspecific variations in *Ophiocoma echinata* and *Ophiocoma trindadensis* from Brazil (Echinodermata: Ophiuroidea). *Journal of the Marine Biological Association of the United Kingdom* **105**, e12, 1–15. https://doi.org/10.1017/S0025315424001164

Received: 10 May 2024
Revised: 11 November 2024
Accepted: 18 November 2024

Keywords:
brittle stars; growth series; morphometry; SEM; taxonomy

Corresponding author:
Cecília J. S. Damiano;
Email: damiano.cecilia14@gmail.com

Abstract

Identifying cryptic species and juveniles in the Ophiuroidea has always been a challenge. However, post-larval developmental studies have the potential to uncover the identity of these cryptic species and juveniles, as they offer valuable information that is not often found in adults. Although the importance of studying growth series is well-known in ophiuroids, it is difficult to obtain and identify the juvenile stages. For this reason, most studies are restricted to brooding species and information is lacking for many species, including those of the genus *Ophiocoma*. In this study, a growth series was developed to show the main differences during the development of two similar species of *Ophiocoma*: *Ophiocoma echinata* and *Ophiocoma trindadensis*. Using morphometry and scanning electron microscopy, we describe in detail the juveniles, intermediate stage, and adults of *O. echinata* and *O. trindadensis*. Differences in the shape of the ventral arm plate and dorsalmost arm spines, the number of tentacle scales, and the presence of granules ventrally were highlighted in the separation and identification of juveniles of both species.

Introduction

Studies of post-larval stages and growth series of ophiuroid species have been considered of great relevance for species identification, particularly for cryptic species and those in early life stages, in addition to contributing to the resolution of phylogenetic relationships and taxonomic uncertainties (Schoener, 1967; Monteiro *et al.*, 1992; Sumida *et al.*, 1998; Stöhr, 2005; Borges *et al.*, 2015; Martynov *et al.*, 2015; Humara-Gil *et al.*, 2022). Due to the difficulties associated with the identification of juvenile stages, these studies are mostly restricted to brooding species, whose assignment to the species level is unambiguous (Clark, 1914; Hendler, 1988; Stöhr, 2005; Falkner and Byrne, 2006; Borges *et al.*, 2015). Nevertheless, as only a small number of ophiuroid species are brooders (Clark, 1914; Schoener, 1967; Stöhr, 2005; Borges *et al.*, 2015), most identification keys do not routinely include juvenile characters, and images and detailed descriptions of early life stages are lacking in the literature (Sumida *et al.*, 1998; Stöhr, 2005).

Despite the importance of studying and describing juvenile specimens, this field is still underexplored. Of the approximately 2000 living ophiuroid species, early growth stages have been described for only 76 (3.5%) species so far (Ludwig, 1898, 1899; Clark, 1914; Mortensen, 1936; Schoener, 1967, 1969; Hendler, 1978, 1988; Webb and Tyler, 1985; Turner and Miller, 1988; Vadon, 1990; Monteiro *et al.*, 1992; Tyler *et al.*, 1995; Sumida *et al.*, 1998; Borges *et al.*, 2002, 2015; Stöhr, 2005; Falkner and Byrne, 2006; Olbers and Samyn, 2012; Martynov *et al.*, 2015; Alitto *et al.*, 2018; Humara-Gil *et al.*, 2022; da Silva *et al.*, 2023). Among the species with unstudied juvenile stages are those belonging to the genus *Ophiocoma* L. Agassiz, 1836. Species of *Ophiocoma* are known to be challenging to identify, especially juveniles, since their main diagnostic characteristics, such as the number of arm spines, change throughout growth and may overlap with other species at different stages of development. This problem is intensified by the lack of structures to distinguish the species and the fact that some of them can change their body colour from day to night (Hendler, 1984; Benavides-Serrato and O'Hara, 2008; Stöhr *et al.*, 2008). Although morphological information on post-larval developmental transformations could contribute to circumventing the existing limitations, the knowledge on growth changes in *Ophiocoma* is very limited. Grave (1898) provided information on the embryo stages of *Ophiocoma echinata* (Lamarck, 1816), but not on post-larval development. Devaney (1968) showed that the number of spines and tentacle scales change with growth in *Ophiocoma erinaceus* Müller & Troschel, 1842, *Ophiocoma aethiops*, and *Ophiocoma anaglyptica* Ely, 1944. Devaney (1970) detected that a particular disc size was correlated with the first occurrence of granules in *O. aethiops*, *O. anaglyptica*, *O. echinata*, *O. erinaceus*, and *Ophiocoma scolopendrina* (Lamarck, 1816) and discussed how this could help to identify these species within *Ophiocoma*. The correlation between the disc size and granule development was also studied by Price and

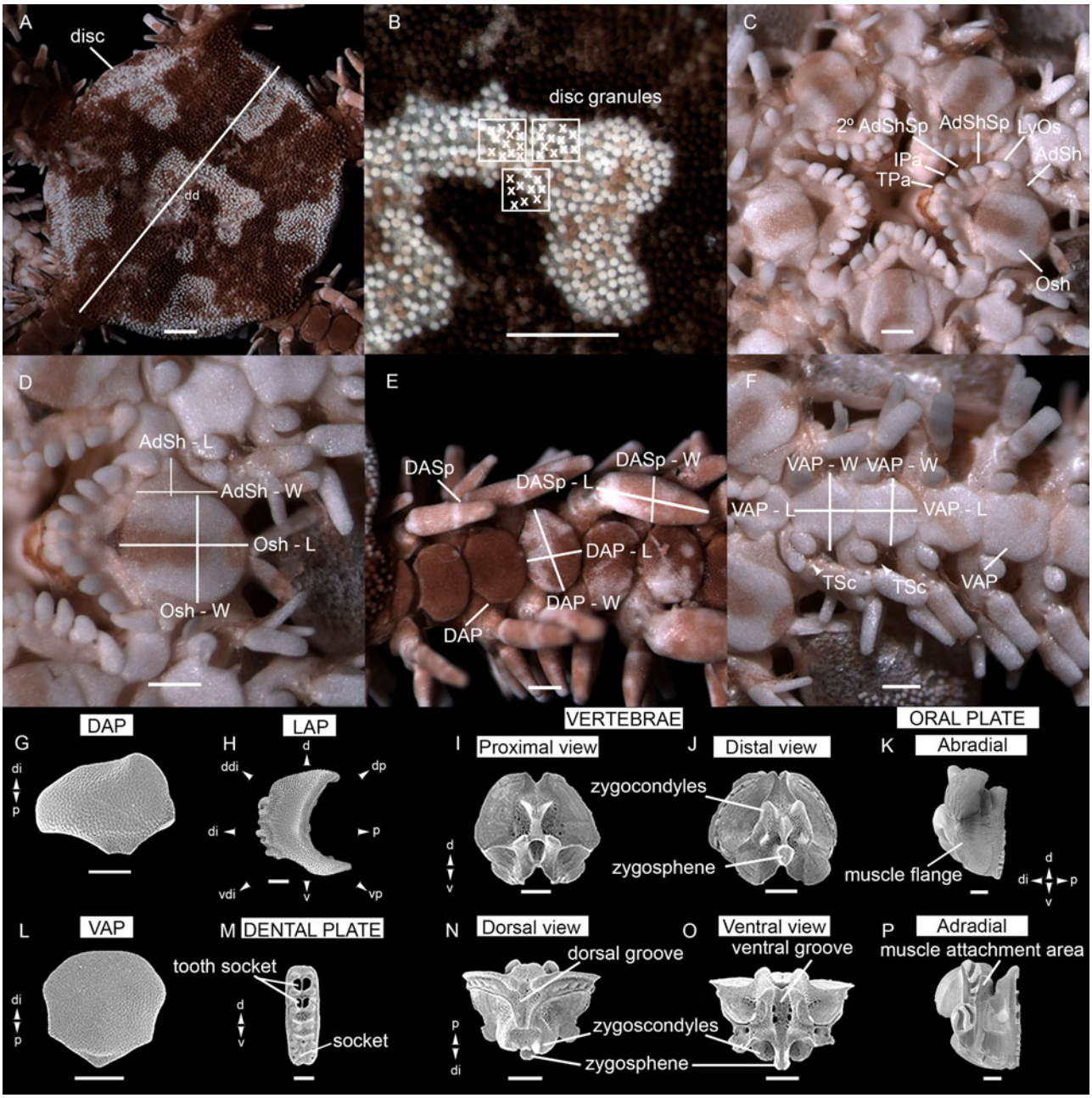

Figure 1. Schematic image with the structures measured and analysed: (A) dorsal view; (B) disc granules; (C) ventral view – detail of the papillae; (D) ventral view – detail of the oral and adoral shields; (E) detail of dorsal view of the arm; (F) detail of ventral view of the arm; (G) dorsal arm plate; (H) lateral arm plate – outer view; (I) vertebra – proximal view; (J) vertebra – distal view; (K) oral plate – abradial; (L) ventral arm plate; (M) dental plate; (N) vertebra – dorsal view; (O) vertebra – ventral view; (P) oral plate – adradial. 2° AdShSp, secondary adoral shield spine; AdSh, adoral shield; AdShSp, adoral shield spine; AdSh – L, length of adoral shield; AdSh – W, width of adoral shield; d, dorsal; DAP, dorsal arm plate; DAP – L, length of dorsal arm plate; DAP – W, width of dorsal arm plate; DASp, dorsalmost arm spine; DASp – L, length of arm spine; DASp – W, width of arm spine; dd, disc diameter; ddi, dorso-distal; di, distal; dp, dorso-proximal; IPa, infradental papilla; LyOs, Lyman's ossicle; Osh, oral shield; Osh – L, length of oral shield; Osh – W, width of oral shield; p, proximal; TPa, tooth papilla; TSc, tentacle scale; v, ventral; VAP, ventral arm plate; VAP – L, length of ventral arm plate; VAP – W, width of ventral arm plate; vdi, ventro-distal; vp, ventro-proximal. Scale bars: (A and B) 1 mm; (C–F) 0.5 mm; (G) and (I–P) 500 μm; (H) 200 μm.

Rowe (1996), but only for *O. erinaceus*. H.L. Clark (1933) and A.H. Clark (1939) analysed a juvenile of *O. echinata* (3 and 4.5 mm of disc diameter, respectively), but both only reported that the specimens had already developed disc granules, two tentacle scales in the first arm segments, and swollen dorsalmost arm spines.

Considering the importance of information on post-larval developmental transformations to further taxonomic and life history research, the present study aims to describe and illustrate the main morphological modifications during the growth of two species of *Ophiocoma*, *O. echinata and Ophiocoma trindadensis* Serrano *et al.*, 2023, selected due to their close morphological similarity. The study of numerous juvenile and adult specimens with the aid of morphometrical analysis and scanning electron microscopy (SEM) imagery revealed some structures that could be useful in distinguishing *O. echinata* and *O. trindadensis* from each other from the early stages of growth.

Materials and methods

Study sites and data collection

The studied specimens come from the collections of the Museum of Biological Diversity – MDBio, Zoology Area of the State University of Campinas (ZUEC – UNICAMP), Museum of Zoology, University of São Paulo (MZUSP – USP), and Paulo

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

Young Invertebrate Collection of the Department of Systematics and Ecology, Federal University of Paraíba (CIPY/DSE – UFPB). *Ophiocoma echinata* has been recorded from different locations at the Brazilian coast, especially the northeastern region, whereas *Ophiocoma trindadensis* is endemic to the remote oceanic archipelago Trindade and Martin Vaz (Serrano *et al.*, 2023 and references therein) (see Supplementary Tables S1 and S2).

Morphological analysis

The studies of the growth series were conducted using 189 specimens (94 of *O. echinata* and 95 of *O. trindadensis*), from the smallest juveniles to the largest adults of both species. After observations and analyses of external morphological characters, specimens of each species were classified according to morphological variations of the structures into young early stage (juveniles), intermediate stage, and adult stage (da Silva *et al.*, 2023) (see Supplementary Tables S3 and S4). The separation was based mostly on the shape of dorsal arm plates, the number of tentacle scales, the shape and number of arm spines, and the presence of granules ventrally.

Ophiocoma echinata

2.9–4.1 mm disc diameter (dd): young early stage;
4.2–9.5 mm dd: intermediate stage;
9.6–22.7 mm dd: adult stage.

Ophiocoma trindadensis

1.7–3.9 mm dd: young early stage;
4.0–9.5 mm dd: intermediate stage;
9.6–19.4 mm dd: adult stage.

Juveniles were defined as individuals lacking fully developed adult characters, differing, for example, in the number of tentacle scales or the shape of microstructures. Specimens in intermediate stages were considered those that presented some structures similar to juveniles and others similar to adults. The adult morphological characters of *O. echinata* and *O. trindadensis* were traced back to the smallest individuals available and compared with the original descriptions of both species. Species identification was aided by taxonomical keys and descriptions (Lamarck, 1816; Tommasi, 1970; Albuquerque, 1986; Hendler, 2018; Borges and Alitto, 2021; Serrano *et al.*, 2023).

Structures such as the disc, dorsal arm plates, ventral arm plates, and arm spines were measured following Serrano *et al.* (2023) (Figure 1, Table 1). All the samples were measured using a camera attached to a stereomicroscope ZEISS Discovery V.8 and the program AxioVision VS. 40.4.8.20 (Carl Zeiss Microscopy, Oberkochen, Germany) for specimens and structures smaller than 10 mm dd and/or with a digital caliper for specimens larger than 10 mm dd.

The data with continuous variables were analysed in a linear discriminant analysis (LDA), which was useful for determining morphological differences between the established groups (species and life stages). The LDA analysis was conducted in R version 4.0.4 using the software packages MASS (Venables and Ripley, 2002; R Development Core Team, 2018), ggord (Beck, 2022), vegan (Oksanen *et al.*, 2019), and tidyverse (Wickham *et al.*, 2019).

One individual of each stage of *O. echinata* and *O. trindadensis* was examined using a JEOL JSM5800LV scanning electron microscope at the Electron Microscopy Laboratory of the Institute of Biology at the State University of Campinas – UNICAMP. The internal and external microstructures present in the arm were taken for examination from the fifth to the tenth segments

Table 1. Definition of the external features measured and analysed

Character	Definition
Disc diameter (dd)	Distance from the distal edge of the radial shield to the opposite interradial edge of the disc (Alitto *et al.*, 2019; Humara-Gil *et al.*, 2022; Serrano *et al.*, 2023). See Figure 1A.
Disc granules	Photos were taken from the central region of the disc using a camera attached to a stereomicroscope ZEISS Discovery V.8. Using the program AxioVision VS. 40.4.8.20 the granules were counted from three frames measuring 0.2 mm^2. The average of these three frames was multiplied by five, estimating the number of granules in 1 mm^2 (Serrano *et al.*, 2023). See Figure 1B.
Length of oral shield (Osh – L)	Obtained from the distal to the proximal edge of one oral shield (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1D.
Width of oral shield (Osh – W)	Obtained from the right lateral edge to the left of one oral shield (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1D.
Length of adoral shield (Ash – L)	Obtained from the lateral edge of the oral shield to the distal edge of one adoral shield (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1D.
Width of the adoral shield (Ash – W)	Obtained from the right lateral edge to the left of one adoral shield (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1D.
Length of dorsal arm plate (DAP – L)	Obtained from the distal to the proximal edge of the third complete dorsal arm plate (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1E.
Width of dorsal arm plate (DAP – W)	Obtained from the right to the left lateral edge of the third complete dorsal arm plate (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1E.
Arm spines	Counted from the first, second, third, and tenth arm segments.
Length of dorsalmost arm spine (DASp – L)	Obtained from the proximal to the distal edge of the dorsalmost arm spine (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1E.
Width of dorsalmost arm spine (DASp – W)	Obtained from the right lateral edge to the left of the dorsalmost arm spine (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1E.
Length of ventral arm plate (VAP – L)	Obtained from the distal to the proximal edge of the second and third ventral arm plates (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1F.
With of ventral arm plate (VAP – L)	Obtained from the right lateral edge to the left of the second and third ventral arm plates (Alitto *et al.*, 2019; Serrano *et al.*, 2023). See Figure 1F.
Tentacle scales (TSc)	Counted in each pore from the first to fourth arm segments.

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

Table 2. Characters that differ between the two studied species of *Ophiocoma*

Characters	*Ophiocoma echinata*			*Ophiocoma trindadensis*		
	Young early (5 specimens: 2.9–4.1 mm dd)	Intermediate (41 specimens: 4.2–9.5 mm dd)	Adult (48 specimens: 9.6–22.7 mm dd)	Young early (10 specimens: 1.7–3.9 mm dd)	Intermediate (32 specimens: 4.0–9.5 mm dd)	Adult (53 specimens: 9.6–19.4 mm dd)
Dorsal arm plate	Fan-shaped (Figures 3J; 5A). As long as wide.	Fan-shaped with rounded distal and lateral edges (Figures 3K; 5B). Wider than long.	Fan-shaped with rounded distal and lateral edges (Figures 3L; 5C). Wider than long.	Fan-shaped (Figures 7J; 9A). As long as wide.	Fan-shaped to oval (Figures 7K; 9B). Wider than long. Dissociated plate with one elongated lateral edge (Figure 9B).	Fan-shaped to oval with one elongated lateral edge, straight proximal edge in adult stage, wider than long (Figures 7L; 9C).
Ventral arm plate	Weakly concave lateral and a rounded distal edge (Figure 5D).	Strongly concave lateral edge and rounded distal edge (Figure 5E).	Strongly concave lateral edge and rounded to straight distal edge (Figure 5F).	Strongly concave lateral edge (Figure 9D), and rounded distal edge.	Weakly concave lateral edge and rounded distal edge (Figure 9E).	Weakly concave lateral edge (Figure 9F).
Arm spines	Three to four. Cylindrical (Figure 5G).	Three to four. Cylindrical (Figure 5H).	Four to five. Cylindrical (Figure 5I).	Three to four. Conical and beginning to thicken (Figure 9G).	Three to four. Robust (Figure 9H).	Three to four. Robust and rounded (Figure 9I).
Tentacle scales	One or two in the entire arm (Figure 3M).	Two in the entire arm (Figure 3N).	Two or three in the first arm segment and two in the rest (Figure 3O).	One in the entire arm (Figure 7M).	One or two on the first arm segment (Figure 7E, N).	Two on the first arm segment (Serrano *et al.*, 2023) (Figure 7F, O).
Ventral granules	Without granules ventrally, only some granules next to Osh (Figure 3D, M).	Granules up to the median portion of the ventral interradial area and some next to Osh (Figure 3H).	Granules up to the median portion of the ventral interradial area and some next to Osh (Figure 3I, O).	Absent (Figure 7D, M).	Granules begin to descend into the ventral portion of the disc or granules present up to the median portion (Figure 7N).	Granules up to the median portion of the ventral interradial area (Figure 7O).

Osh, oral shields.
Ventral arm plates were described considering only dissociated plates.

(Figure 1). For internal microstructures of the buccal armature, the entire disc or a fragment was used (Figure 1). The fragments of the arms and the disc were immersed in regular household bleach (NaClO) until the tissues were removed and the ossicles were released (Stöhr *et al.*, 2008). The ossicles were then washed in distilled water, air-dried, arranged on aluminium stubs, gold coated, examined by SEM, and photographed.

The terminology and abbreviations used in all descriptions followed Thuy and Stöhr (2011, 2016), Stöhr *et al.* (2012), Alitto *et al.* (2018), Hendler (2018), O'Hara *et al.* (2018), and Goharimanesh *et al.* (2021).

Abbreviations

Morphological structures

2° AdShSp – secondary adoral shield spine;
AdSh – adoral shield;
AdShSp – adoral shield spine;
DAP – dorsal arm plate;
DASp – dorsalmost arm spine;
IPa – infradental papilla;
LAP – lateral arm plate;
LyOs – Lyman's ossicle;
Osh – oral shield;
TPa – tooth papilla;
TSc – tentacle scale;
VAP – ventral arm plate.

Results

Our study demonstrates that *Ophiocoma echinata* and *Ophiocoma trindadensis* can be distinguished during their growth, especially, due to differences in the shape of the VAP and DASp, the number of TSc, and the presence of granules ventrally. The main differences observed during the growth of the species and between them are highlighted in Table 2; the morphometrical analysis and the descriptions of the species are presented below.

Morphometry

A total of 94 specimens of *O. echinata* and 87 specimens of *O. trindadensis* were measured and separated into young early, intermediate, and adult stages. Damaged specimens of *O. trindadensis* were excluded from this analysis. The LDA using 14 morphological characters (see Supplementary Tables S3 and S4) was effective in separating the species, and partially separating the stages of development (Figure 2).

The width of the second VAP and the width of the DASp (VAP2.W and DASp.W) were the morphological characters with the highest positive coefficients, and the width of the first VAP and length of the Osh (VAP1.W and Osh.L) presented the highest negative coefficients in the first discriminant axis (LD1 – 67.53%) indicating a contribution of these characters in separating *O. echinata* from *O. trindadensis* (specimens in all stages). The second discriminant axis (LD2 – 27.5%) separated the adult and intermediate stages of both species from the young early stages with a high positive value in the width of the DASp (DASp.W), width of DAP (DAP.W), and width of the second VAP (VAP2.W), and, as negative coefficients, the width of Ash (Ash.W) and length of DASp (DASp.L) (Figure 2).

Growth series

Order OPHIACANTHIDA O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Family OPHIOCOMIDAE Ljungman, 1867

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

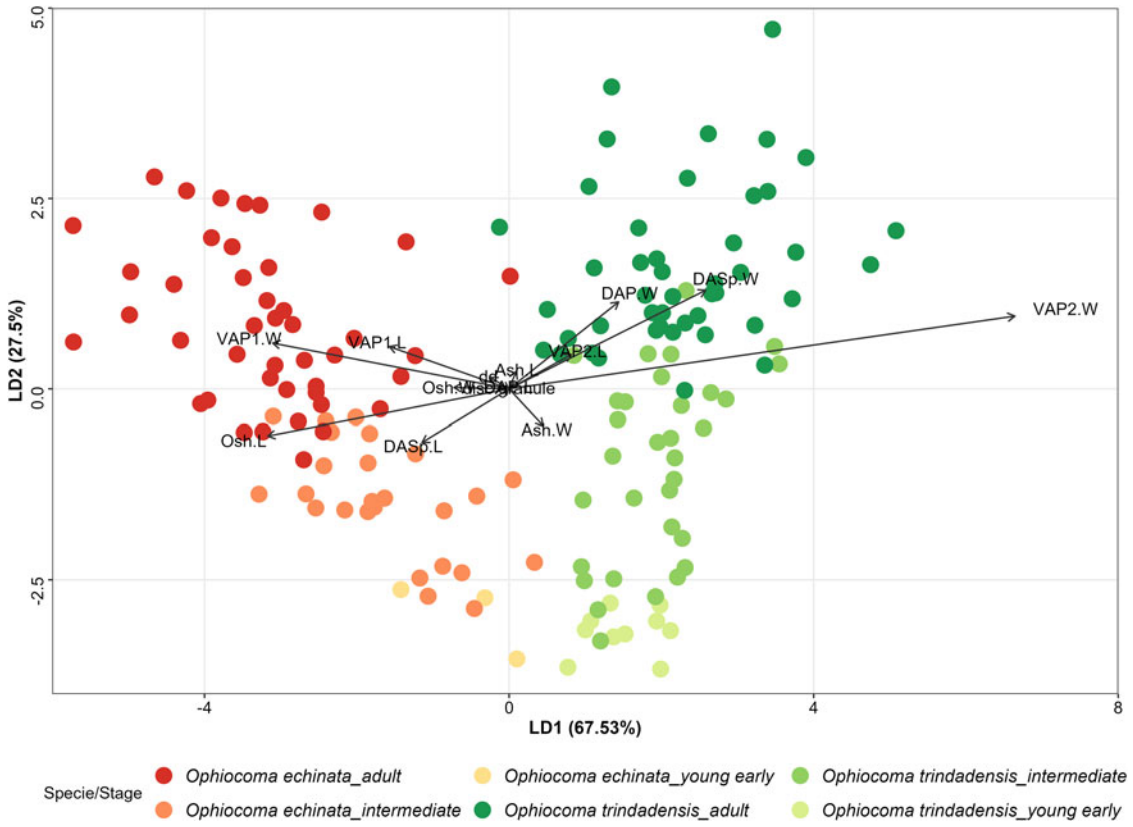

Figure 2. LDA analysis based on 14 morphological variables. Ash.L, length of adoral shield; Ash.W, width of adoral shield; DAP.L, length of dorsal arm plate; DAP.W, width of dorsal arm plate; DASp.L, length of dorsalmost arm spine; DASp.W, width of dorsalmost arm spine; dd, disc diameter; disc.granule, granules of disc; Osh.L, length of oral shield; Osh.W, width of oral shield; VAP1.L, length of first ventral arm plate; VAP1.W, width of first ventral arm plate; VAP2.L, length of second ventral arm plate; VAP2.W, width of second ventral arm plate.

Genus *Ophiocoma* L. Agassiz, 1836

Ophiocoma echinata (Lamarck, 1816)

Type locality. Antilles (Lamarck, 1816)

Distribution. Florida, Bermuda, Bahamas, Tortugas, St. Thomas, Antilles, Haiti, Puerto Rico, Antigua and Barbuda, Bonaire, Aruba, Curaçao, Grenada, Tobago, Panama, Venezuela (Cumana Bay), Liberia, and Brazil (Lyman, 1865; Rathbun, 1879; Verrill, 1899; Koehler, 1914; Clark, 1921; Clark *et al.*, 1921; Engel, 1939; Tommasi, 1970; Albuquerque, 1986). In Brazil, there are records in Ceará, Paraíba, Pernambuco, Alagoas, and Bahia (Rathbun, 1879; Verrill, 1899; Tommasi, 1970; Albuquerque, 1986; Manso, 1993; Manso *et al.*, 2008; Lima and Fernandes, 2009; Miranda *et al.*, 2012).

Material examined. 94 specimens (dd: 2.9–22.7 mm). See Specimen Information (Supplementary Table S1).

Disc. Pentagonal to rounded, covered by sparse, rounded granules (Figure 3A–C). Number of granules per mm^2 of disc varies and decreases as disc size increases.

Mouth. *At each half jaw*: TPa followed by IPa, 2° AdShSp, AdShSp, and LyOs (Figure 3D–I). Osh approximately rectangular with rounded edges (Figure 3D–I). AdSh triangular, wider than long (Figure 3D–I). Juveniles without granules ventrally, only some granules next to Osh (Figure 3G, M). Granules up to median portion of ventral interradial area and some next to Osh in intermediate and adult stages (Figure 3H, I, O).

Arms. DAP fan-shaped, as long as wide or almost as long as wide in juveniles (Figure 3J); DAP fan-shaped to oval in intermediate and adult stages (Figure 3K, L). VAP approximately square with rounded distal edge (Figure 3M–O). Three to four arm spines in juveniles and intermediate stage, three to five in adults up to 10th arm segment. DASp cylindrical, robust, and elongated (Figure 3J–L). One or two TSc on each pore in juvenile stage, two in intermediate stage, two to three in first arm segment, and two in remaining segments in adults (Figure 3M–O).

Morphological variations: One juvenile specimen (3.8 mm dd) presented some granules in two interradii, besides those next to the Osh. Three specimens in the intermediate and two in the adult stages showed the ventral granules extending up to the Osh as a fine line. In two specimens in the intermediate stage, three tentacle scales were observed in the first arm segment. In two specimens in the adult stage, three tentacle scales were observed in the third and fourth arm segments.

Microstructure of ossicles (Figures 4–6)

Specimens selected for description: 3.7 mm (ZUEC OPH 3220) – young early; 7.3 mm (ZUEC OPH 3219) – intermediate stage; 19.3 mm (ZUEC OPH 1538) – adult stage.

Dental plate. *Outer side*: Dorsalmost portion with two tooth sockets, only one with thin septum in young early stage; dorsalmost portion with three tooth sockets, all with thin septum in intermediate stage; dorsalmost portion with two tooth sockets, all with thin septum in adult stage (Figure 4A–C). Series of horizontal ridges in median portion and sockets for tooth papillae in ventralmost portion, tooth sockets surrounded by protruding knobs (Figure 4B, C). Protruding knobs, horizontal ridges, and sockets for tooth papillae still developing in young early stage (Figure 4A).

Oral plate. *Abradial*: Still-developing muscle flange with soft horizontal and diagonal striations in young early stage (Figure 4D), large and well-defined muscle flange with horizontal and diagonal striations in intermediate and adult stages (Figure 4E, F). *Adradial*: Muscle attachment area arranged vertically in middle region, long, tapering, spoon-shaped (Figure 4G–I).

Dorsal arm plates. *General outline*: Fan-shaped with rounded distal and lateral edges, straight proximal edge (Figure 5A–C).

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

Figure 3. External features of *Ophiocoma echinata* (Lamarck, 1816): (A, D, J, and M) young early specimen (3.7 mm dd – ZUEC OPH 3220); (G) young early specimen (3.8 mm dd – UFPB. ECH-2700); (B, E, H, K, and N) intermediate (7.3 mm dd – ZUEC OPH 3219); (C, F, I, L, and O) adult (19.5 mm – ZUEC OPH 3072). (A–C) Dorsal view; (D–F) ventral view; (G–I) detail of the jaw; (J–L) detail of dorsal arm; (M–O) detail of ventral arm. 2° AdShSp, secondary adoral shield spine; AdSh, adoral shield; AdShSp, adoral shield spine; DAP, dorsal arm plate; DASp, dorsalmost arm spine; IPa, infradental papilla; LyOs, Lyman's ossicle; Osh, oral shield; TPa, tooth papilla; TSc, tentacle scale; VAP, ventral arm plate; VG, ventral granules. Scale bars: (A, B, D, E, J, K, M, and N) 500 μm; (C) 2 mm; (F, L, and O) 1 mm; (G) 0.2 mm; (H and I) 0.5 mm.

DAP with asymmetrical lateral edges in intermediate stage (Figure 5B), and symmetrical in adult stage (Figure 5C).

Ventral arm plates. *General outline*: Pentagonal, distal portion wider than proximal, convex distal edge, proximal edge 'V' like (Figure 5D–F). Lateral edges with weak incisions in young early stage (Figure 5D), become strongly concave in larger specimens (Figure 5E, F).

Dorsal arm spines. Cylindrical, with approximately the same width in distal and proximal portions (Figure 5G–I).

Lateral arm plates. *General outline*: Arched shape. Ventral portion projecting ventro-proximally (Figure 5J–L). LAP decreases in width as disc size increases (Figure 5J–L). *Spine articulations*: Three to four, on elevated portion not bordered proximally by ridge (Figure 5J–L), restricted to central portion of distal edge and equidistant in young early and intermediate stages (Figure 5J, K), arranged over entire distal edge, and distance between spine articulation dorsalwards increasing in adult stage (Figure 5L).

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

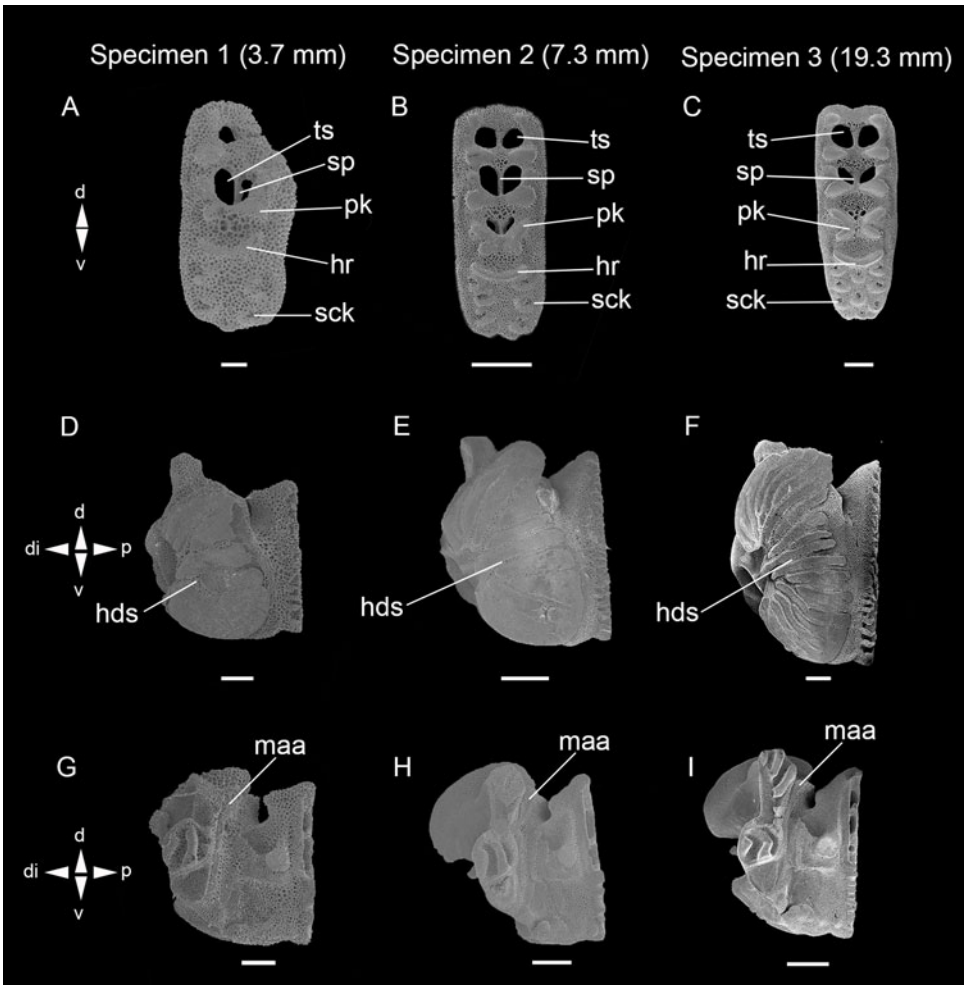

Figure 4. Oral ossicles of *O. echinata* (Lamarck, 1816): (A, D, and G) young early specimen (3.7 mm dd – ZUEC OPH 3220); (B, E, and H) intermediate (7.3 mm dd – ZUEC OPH 3219); (C, F, and I) adult (19.3 mm dd – ZUEC OPH 1538). (A–C) Dental plate – outer side; (D–F) oral plate – abradial; (G–I) oral plate – adradial. d, dorsal; di, distal; hds, horizontal and diagonal striations; hr, horizontal ridge; maa, muscle attachment area; p, proximal; pk, protruding knobs; sck, sockets; sp, septum; ts, tooth sockets; v, ventral. Scale bars: (A) 100 µm; (D and G) 200 µm; (B, C, E, F, H, and I) 500 µm.

Vertebrae. Zygospondylous articulation. *Proximal side*: Groove dorsally (Figure 6A–C). *Distal side*: Zygosphene fused with pair of parallel zygocondyles (Figure 6D–F). Well-developed muscle attachment area with knobs around dorsalmost lateral edges in adult stage (Figure 6I). *Dorsal side*: Dorsal groove not projecting beyond zygocondyles (Figure 6G–I). *Ventral side*: All specimens with 'V' cavities in proximal–ventral edge, zygosphene projecting beyond ventral edge of zygocondyles with projecting part shorter than zygocondyles (Figure 6J–L).

Ophiocoma trindadensis Serrano, Damiano, Alitto and Borges, 2023

Type locality. Trindade and Martin Vaz Oceanic Archipelago, Espírito Santo, Brazil (Serrano *et al*., 2023).

Distribution: Only known from its type locality (Serrano *et al*., 2023).

Material examined: 95 specimens (dd: 1.7–19.4 mm). See Specimen Information (Supplementary Table S2).

Disc. Rounded, covered by sparse, rounded granules (Figure 7A–C). Number of granules per mm^2 of disc decreases as disc size increases.

Mouth. *At each half jaw*: TPa followed by IPa, 2° AdShSp, AdShSp, and LyOs (Figure 7D–I), papillae still developing in the smallest juvenile (1.7 mm dd) (Figure 7G). Osh approximately rectangular with rounded edges (Figure 7D–I). AdSh triangular, wider than long (Figure 7D–I). Young early stage without granules ventrally (Figure 7D, M). Granules begin descending into ventral portion of disc or granules present up to median portion of ventral interradial area in intermediate stage (Figure 7N). Granules up to median portion of ventral interradial area in adult specimens (Figure 7O).

Arms. DAP fan-shaped, as long as wide or almost as long as wide in young early stage (Figure 7J), DAP fan-shaped to oval, wider than long in intermediate stage (Figure 7K), DAP oval in adult stage, wider than long (Figure 7L). VAP approximately square with rounded distal edge (Figure 7M–O). Three to four arm spines up to 10th arm segment. DASp conical and begins to thicken in young early stage (Figure 7J), robust and rounded in intermediate and adult stages (Figure 7K, L). Number of TSc in first segment varies: one in young early stage (Figure 7M), one or two in intermediate stage (Figure 7E, N), two in adult stage (Figure 7F, O), and one in remaining arm segments.

Morphological variations. The highest number of granules per mm^2 of disc (78–98) was observed at 1.7 and 4.5 mm dd, while the lowest (4) was observed at 19.4 mm dd. One specimen in the young early stage (3.4 mm dd) presented two TSc at most of the tentacle pores of the first arm segment. In one adult specimen (17.9 mm dd) a single arm segment with five arm spines was observed.

Microstructure of ossicles (Figures 8–10)

Specimens selected for description: 1.7 mm (ZUEC OPH 3092) – young early; 8 mm (MZUSP 2772) – intermediate stage; 14 mm (ZUEC OPH 3097) – adult stage.

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

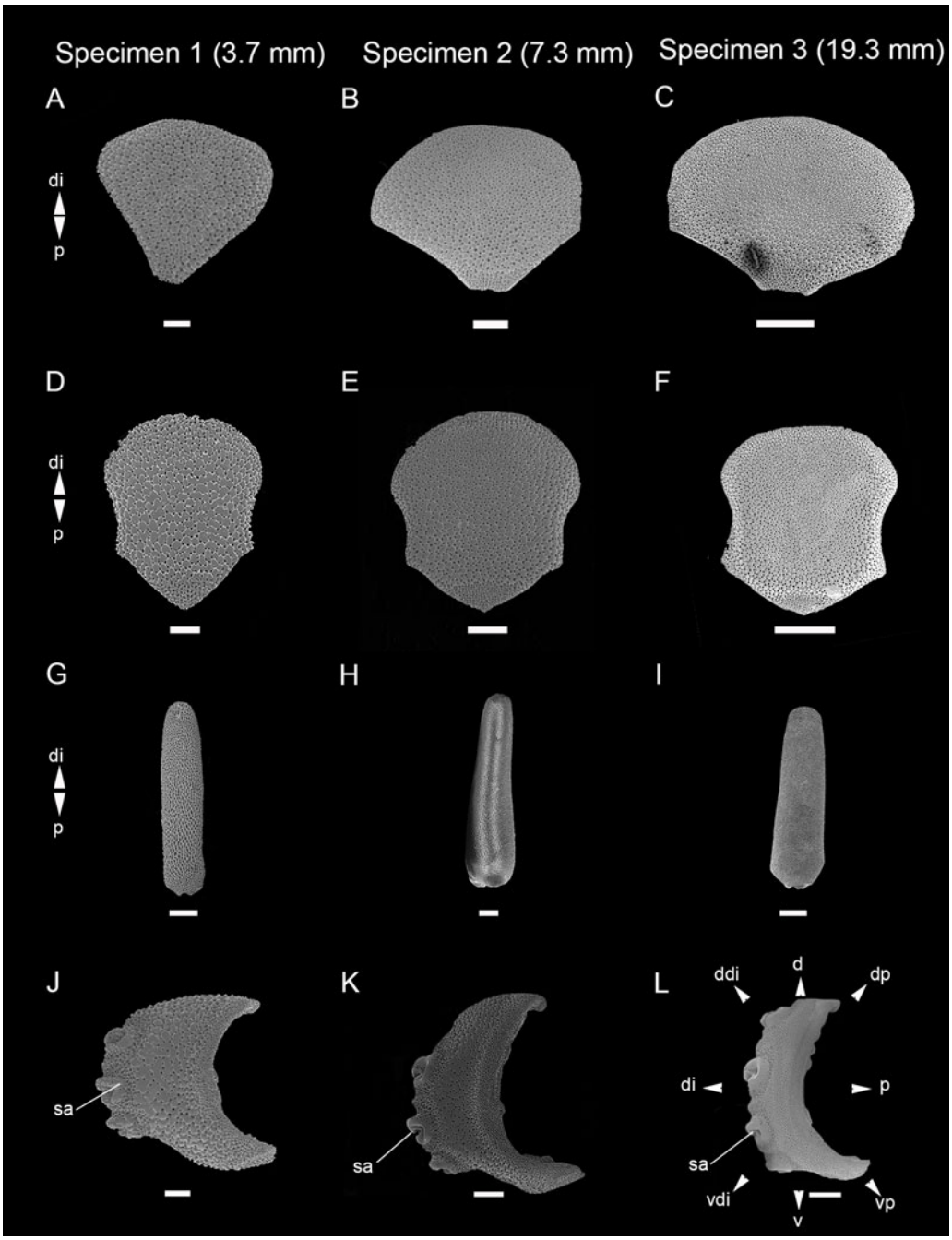

Figure 5. Arm plates and arm spines of *O. echinata* (Lamarck, 1816): (A, D, G, and J) young early specimen (3.7 mm dd – ZUEC OPH 3220); (B, E, H, and K) intermediate (7.3 mm dd – ZUEC OPH 3219); (C, F, I, and L) adult (19.3 mm – ZUEC OPH 1538). (A–C) Dorsal arm plate – outer side; (D–F) ventral arm plate – outer side; (G–I) dorsalmost arm spine; (J–L) lateral arm plate – outer side. d: dorsal; ddi: dorso-distal; di: distal; dp: dorso-proximal; p: proximal; sa, spine articulation; v: ventral; vdi: ventro-distal; vp: ventro-proximal. Scale bars: (A, D, and J) 100 μm; (B, C, E–H, and K) 200 μm; (I and L) 500 μm.

Dental plate. *Outer side*: Dorsalmost portion with tooth socket without septum, median portion with small tooth socket with septum in young early stage (Figure 8A). Dorsalmost portion with two tooth sockets with thin septum in intermediate and adult stages (Figure 8B, C). Series of horizontal ridges in median portion and sockets for tooth papillae in ventralmost portion, tooth sockets surrounded by protruding knobs (Figure 8B, C). Horizontal ridges, sockets for tooth papillae, and protruding knobs weakly developed in young early stage (Figure 8A).

Oral plate. *Abradial*: Developing muscle flange without horizontal and diagonal striations in young early stage (Figure 8D), large and well-defined muscle flange with horizontal and diagonal striations in intermediate and adult stages (Figure 8E, F). *Adradial*: Muscle attachment areas arranged vertically in middle region, long, tapering, spoon-shaped (Figure 8G–I).

Dorsal arm plates. *General outline*: Fan-shaped. DAP with rounded distal and lateral edges, proximal edge 'V' like in young early stage (Figure 9A). DAP with rounded distal and lateral edges, with one elongated lateral edge, straight proximal edge in intermediate stage (Figure 9B), fan-shaped to oval with one elongated lateral edge, straight proximal edge in adult stage (Figure 9C).

Ventral arm plates. *General outline*: Pentagonal, distal portion wider than proximal, convex distal edge, proximal edge 'V' like (Figure 9D–F). Lateral edges strongly concave in young early stage (Figure 9D), becoming shallower incisions with growth (Figure 9E, F).

Dorsal arm spines. Conical and serrated in young early stage (Figure 9G). Becomes robust and cylindrical or rounded in intermediate stage (Figures 7K and 9H) and robust and rounded (almost circular) in adult stage (Figure 9I).

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

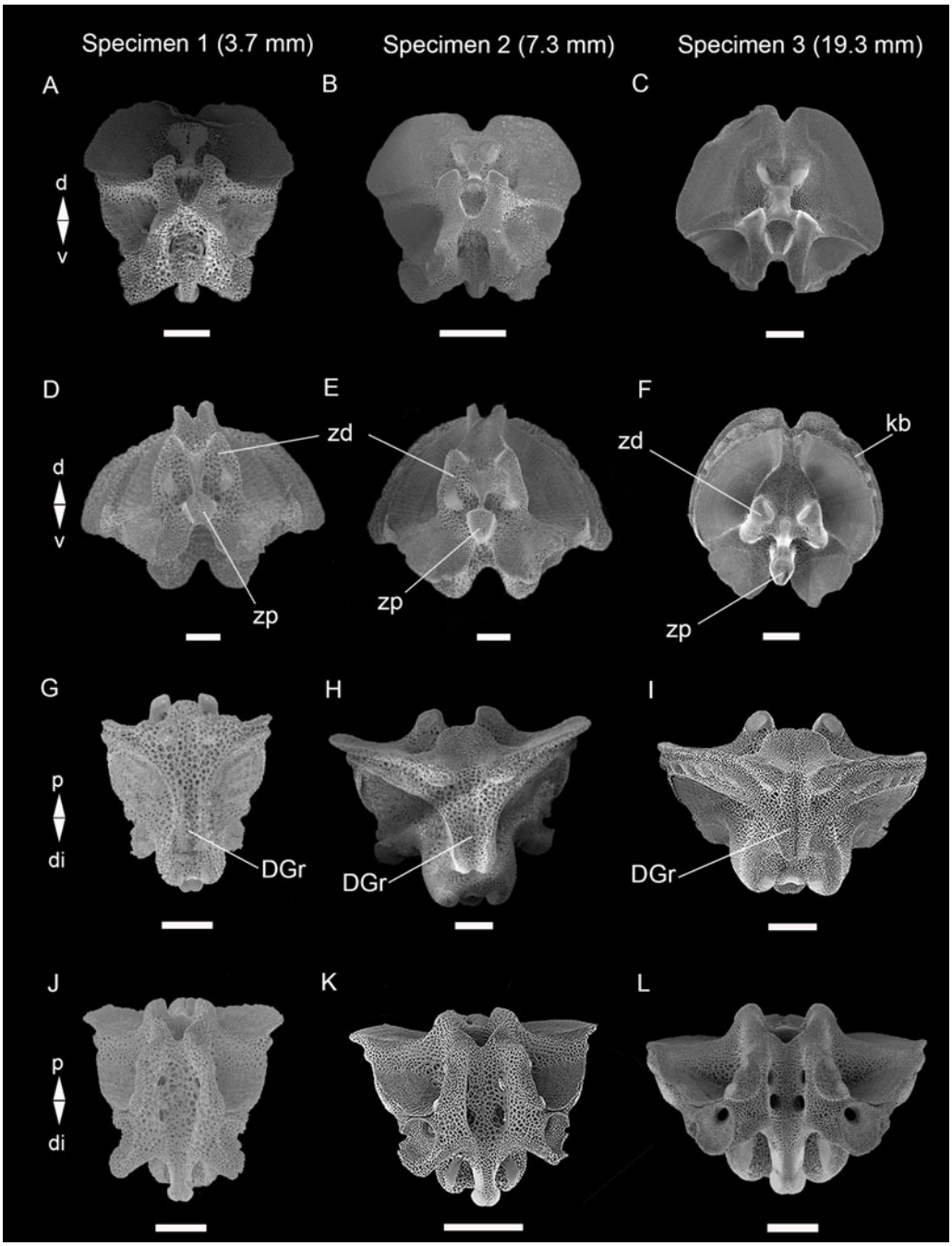

Figure 6. Vertebrae of *O. echinata* (Lamarck, 1816): (A, D, G, and J) young early specimen (3.7 mm dd – ZUEC OPH 3220); (B, E, H, and K) intermediate (7.3 mm dd – ZUEC OPH 3219); (C, F, I, and L) adult (19.3 mm dd – ZUEC OPH 1538). (A–C) Vertebrae ossicle – proximal surface; (D–F) vertebrae ossicle – distal surface; (G–I) vertebrae ossicle – dorsal surface; (J–L) vertebrae ossicle – ventral surface. d, dorsal; di, distal; DGr, dorsal groove; kb, knobs; p, proximal; v, ventral; zd, zygocondyles; zp, zygosphene. Scale bars: (D) 100 μm; (A, E, G, H, J, and K) 200 μm; (B, C, F, I, and L) 500 μm.

Lateral arm plates. *General outline*: Arched shape. Approximately rectangular in young early stage (Figure 9J). Ventral portion projecting ventro-proximal in intermediate and adult stages (Figure 9K, L). LAP decreases in width as disc size increases. *Spine articulations*: Three to four, on elevated portion not bordered proximally by ridge (Figure 9J–L), restricted to central portion of distal edge and equidistant in young early stage and intermediate stages (Figure 9J, K), arranged over entire distal edge and distance between spine articulation dorsalwards increasing in adult stage (Figure 9L).

Vertebrae. Zygospondylous articulation. *Proximal side*: groove dorsally (Figure 10A–C). *Distal side*: Zygosphene fused with pair of parallel zygocondyles (Figure 10D–F). Well-developed muscle attachment area with knobs around dorsalmost lateral edges in intermediate and adult stages (Figure 10E, F). *Dorsal side*: Dorsal groove not projecting beyond zygocondyles (Figure 10G–I). *Ventral side*: All specimens with 'V' cavities in proximal–ventral edge, zygosphene projecting beyond ventral edge of zygocondyles with projecting part shorter than zygocondyles (Figure 10J–L).

Discussion

Young early stage of *Ophiocoma echinata* and *O. trindadensis* have never been described previously, although adults of both species are common in shallow waters from northeastern Brazil and the remote oceanic archipelago Trindade and Martin Vaz, respectively (Rathbun, 1879; Tommasi, 1970; Albuquerque, 1986; Manso,

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

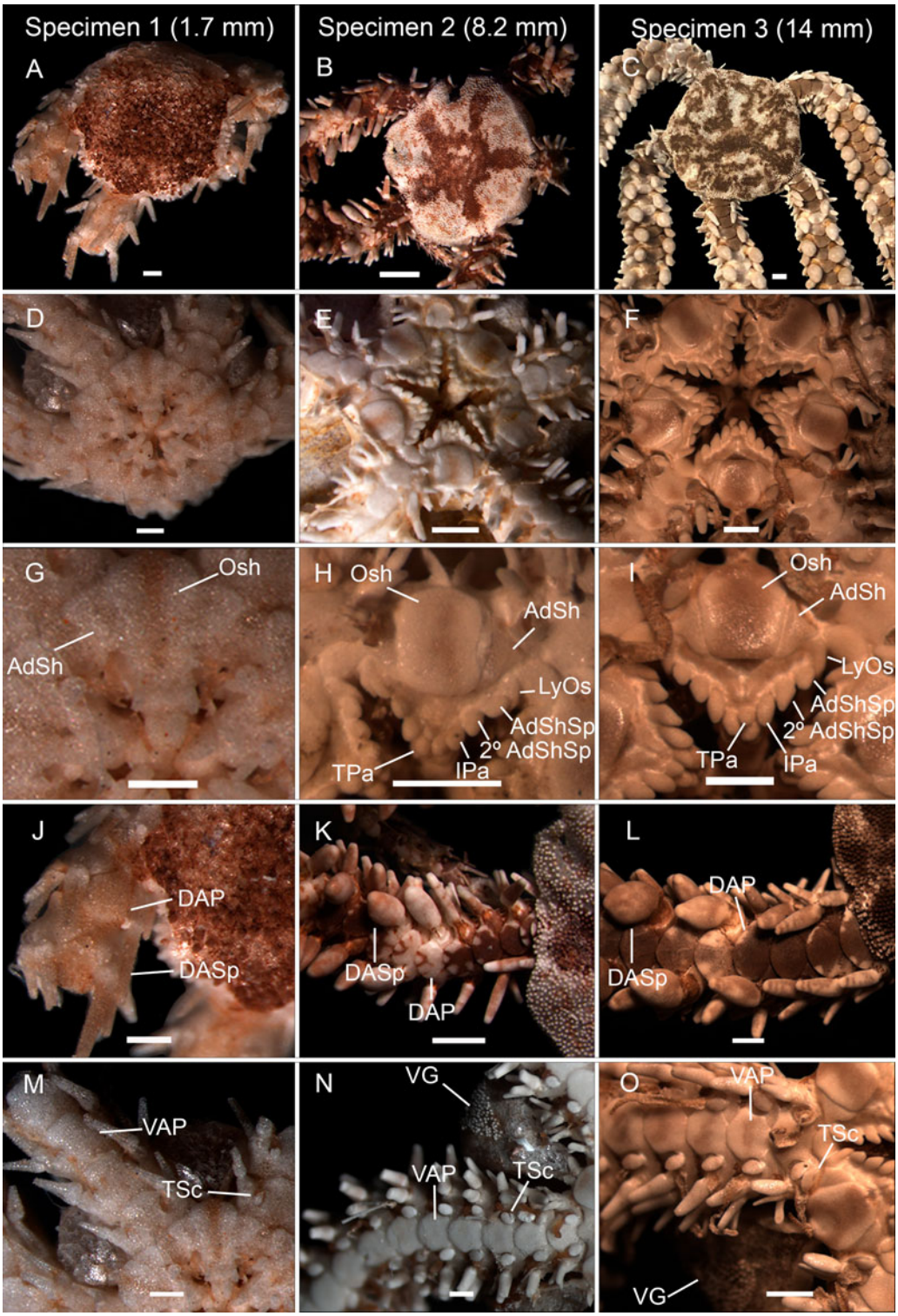

Figure 7. External features of *Ophiocoma trindadensis* Serrano *et al.*, 2023: (A, D, G, J, and M) young early specimen (1.7 mm dd – ZUEC OPH 3092); (B, E, H, K, and N) intermediate (8.2 mm dd – MZUSP 2784); (C, F, I, L, and O) adult (14 mm dd – ZUEC OPH 3097). (A–C) Dorsal view; (D–F) ventral view; (G–I) detail of the jaw; (J–L) detail of dorsal arm; (M–O) detail of ventral arm. 2° AdShSp, secondary adoral shield spine; AdSh, adoral shield; AdShSp, adoral shield spine; DAP, dorsal arm plate; DASp, dorsalmost arm spine; IPa, infradental papilla; LyOs, Lyman's ossicle; Osh, oral shield; TPa, tooth papilla; TSc, tentacle scale; VAP, ventral arm plate; VG, ventral granules. Scale bars: (D, G, J, and M) 0.2 mm; (E, F, H, I, L, and O) 1 mm; (B and K) 2 mm; (C) 10 mm; (A and N) 0.5 mm.

1993; Manso *et al.*, 2008; Lima and Fernandes, 2009; Miranda *et al.*, 2012; Serrano *et al.*, 2023). *Ophiocoma echinata* and *O. trindadensis* are morphologically similar, particularly at smaller sizes. However, the study of their growth series proved to facilitate the identification of young early, intermediate stages, and adults.

Schoener (1967, 1969), Monteiro (1987), and da Silva *et al.* (2023) showed that some structures in brittle stars are not deeply affected during ontogeny, while others suffer important changes depending on the species. In *Ophiocoma echinata* and *O. trindadensis*, the number of granules per mm^2 and shape of DAP varied between young early stage and adults, whereas disc shape and type of dorsal coverage remained essentially unchanged during growth, as did the general shape of dental and oral plates. It has also been documented that the number of TSc is usually

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

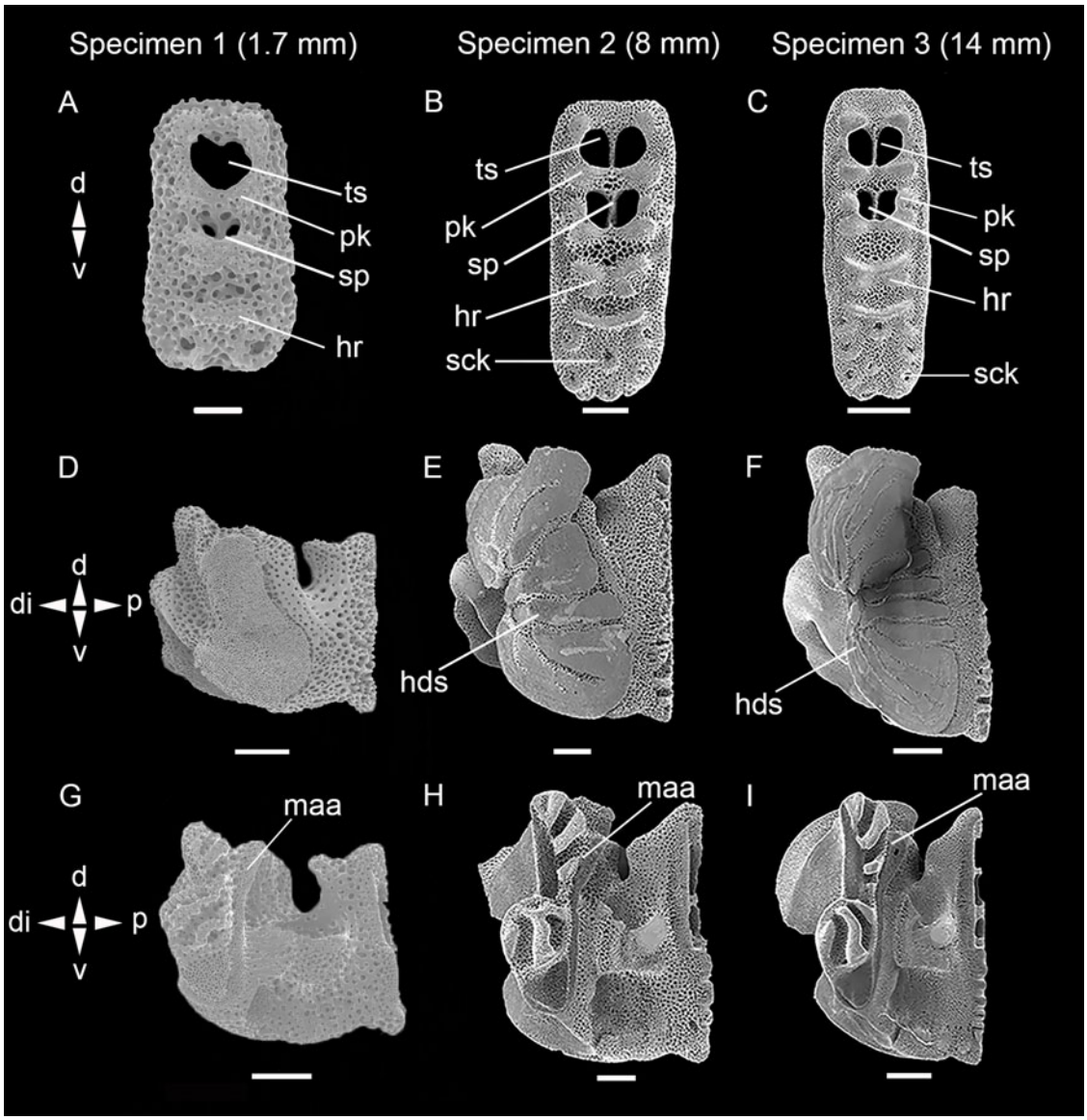

Figure 8. Oral ossicles of *O. trindadensis* Serrano *et al*., 2023: (A, D, and G) young early specimen (1.7 mm dd – ZUEC OPH 3092); (B, E, and H) intermediate (8 mm – MZUSP 2772); (C, F, and I) adult (14 mm dd – ZUEC OPH 3097). (A–C) Dental plate – outer side; (D–F) oral plate – abradial; (G–I) oral plate – adradial. d, dorsal; di, distal; hds, horizontal and diagonal striations; hr, horizontal ridge; maa, muscle attachment area; p, proximal; pk, protruding knobs; sck, sockets; sp, septum; ts, tooth sockets; v, ventral. Scale bars: (A) 50 μm; (C, F, and I) 500 μm; (D and G) 100 μm; (B, E, and H) 200 μm.

smaller or even absent in smaller specimens (Monteiro, 1987; Stöhr and Martynov, 2016; Humara-Gil *et al*., 2022) and the number of arm spines is lower in young early stage (Vadon, 1990; Sumida *et al*., 1998; Stöhr, 2005; Borges *et al*., 2015; Humara-Gil *et al*., 2022). Similarly, a small number of TSc and arm spines were observed in the young early stage of the species herein studied. The number and position of the mouth papillae can also change during development (Vadon, 1990; Sumida *et al*., 1998; Borges *et al*., 2002; Stöhr, 2005; Borges *et al*., 2015). In this study, a lower number of mouth papillae was observed only in the smallest young early specimen of *O. trindadensis* (1.7 mm dd), while the smallest specimen of *O. echinata* analysed (2.9 mm dd) already had a similar number of mouth papillae to the adult.

As summarized in Table 2, the main differences between the two species are related to the ventral arm plate, dorsalmost arm spines, the number of tentacle scales, and the presence of granules ventrally. The young early stage of *Ophiocoma echinata* has a shallow incision in the lateral edges of the ventral arm plate and a strong incision in the intermediate and adult stages, while *O. trindadensis* has a strong incision in young early stage and shallow in the intermediate and adult stages. The shape of dorsalmost arm spines also differentiated these species: in *O. echinata* it is cylindrical and always longer than wide. In *O. trindadensis* it is conical in young early specimens, cylindrical to robust in the intermediate stage, and robust and rounded in the adult stage, and it can be as long as wide or almost as long as wide. At first look, some dorsalmost arm spines of adults of *O. echinata* can seem similar in size to those of *O. trindadensis*, but the proportion between length and width is usually smaller in *O. trindadensis*. The young early specimens of *O. echinata* have one or two tentacle scales in the proximal arm segments, specimens in the intermediate stage have two in almost the entire arm, and adults have two or three in the first arm segment and two in the rest. In contrast, young early specimens of *O. trindadensis* have one tentacle scale in all arm segments, one and two in the first arm segment in the intermediate stage, two in the first arm segment and one in all other segments in the adult stage. In young early specimens of *O. echinata*, the ventral granules are absent, but there are some granules next to the oral shields, and in the intermediate and

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

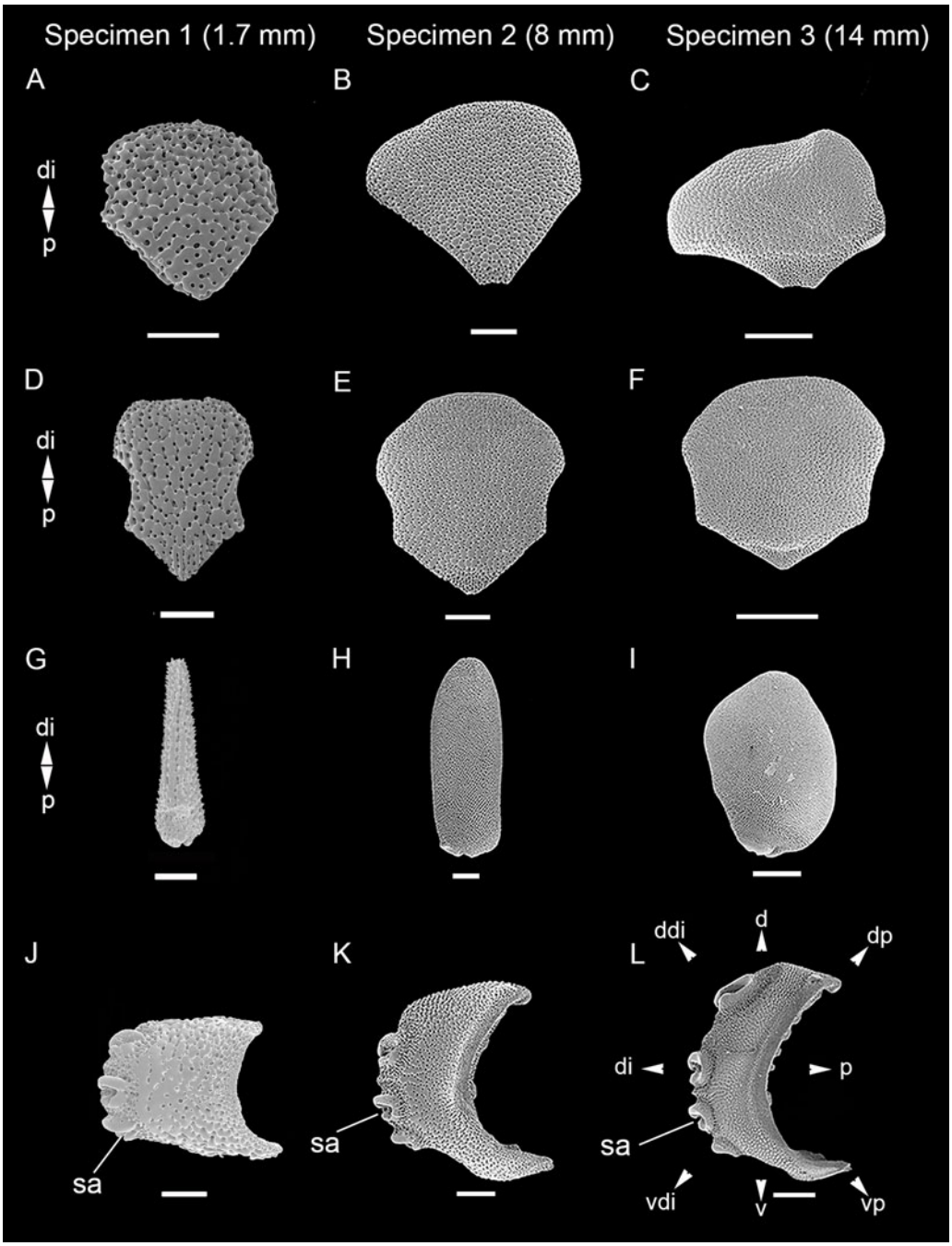

Figure 9. Arm plates and arm spines of *O. trindadensis* Serrano *et al*., 2023: (A, D, G, and J) young early specimen (1.7 mm dd – ZUEC OPH 3092); (B, E, H, and K) intermediate (8 mm dd – MZUSP 2772); (C, F, and I) adult (14 mm dd – ZUEC OPH 3097); (L) adult (19.3 mm dd – ZUEC OPH 3095). (A–C) Dorsal arm plate – outer side; (D–F) ventral arm plate – outer side; (G–I) dorsalmost arm spine; (J–L) lateral arm plate – outer side. d, dorsal; ddi, dorso-distal; di, distal; dp, dorso-proximal; p, proximal; as, spine articulation; v, ventral; vdi, ventro-distal; vp, ventro-proximal. Scale bars: (A, D, G, and J) 100 μm; (B, E, H, and K) 200 μm; (C, F, I, and L) 500 μm.

adult stages granules occur up to the median portion of the ventral interradial area and there are some granules next to the oral shields. The ventral granules are also absent in the young early specimens of *O. trindadensis*, and in the intermediate and adult stages granules occur up to the median portion of the ventral interradial area and do not reach the oral shields.

Devaney (1970) reported that as the development of the granules on the disc can change species specifically according to disc size in *Ophiocoma*, it may help to identify the species. In his study, the author reports disc granules in specimens of *O. echinata* with 2.3 mm dd (Devaney, 1970), whereas the present study reports disc granules in a specimen with 1.7 mm dd of *O. trindadensis*.

The LDA analysis confirmed the separation of the species from each other. Serrano *et al.* (2023) indicated that the main morphological characters that separate the two species are the width of the second ventral arm plate, the length of the first ventral arm plate, the length of the oral shield, and the oral diameter. The present study carried out the LDA analysis with more specimens including different stages of development of both species, and confirmed that the width of the second ventral arm plate and length of the oral shield are important for distinguishing the species. Additionally, the width of the dorsalmost arm spines and the width of the first ventral were also important in their separation. The length of the first ventral arm plate, despite not having presented the highest positive coefficient on the

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

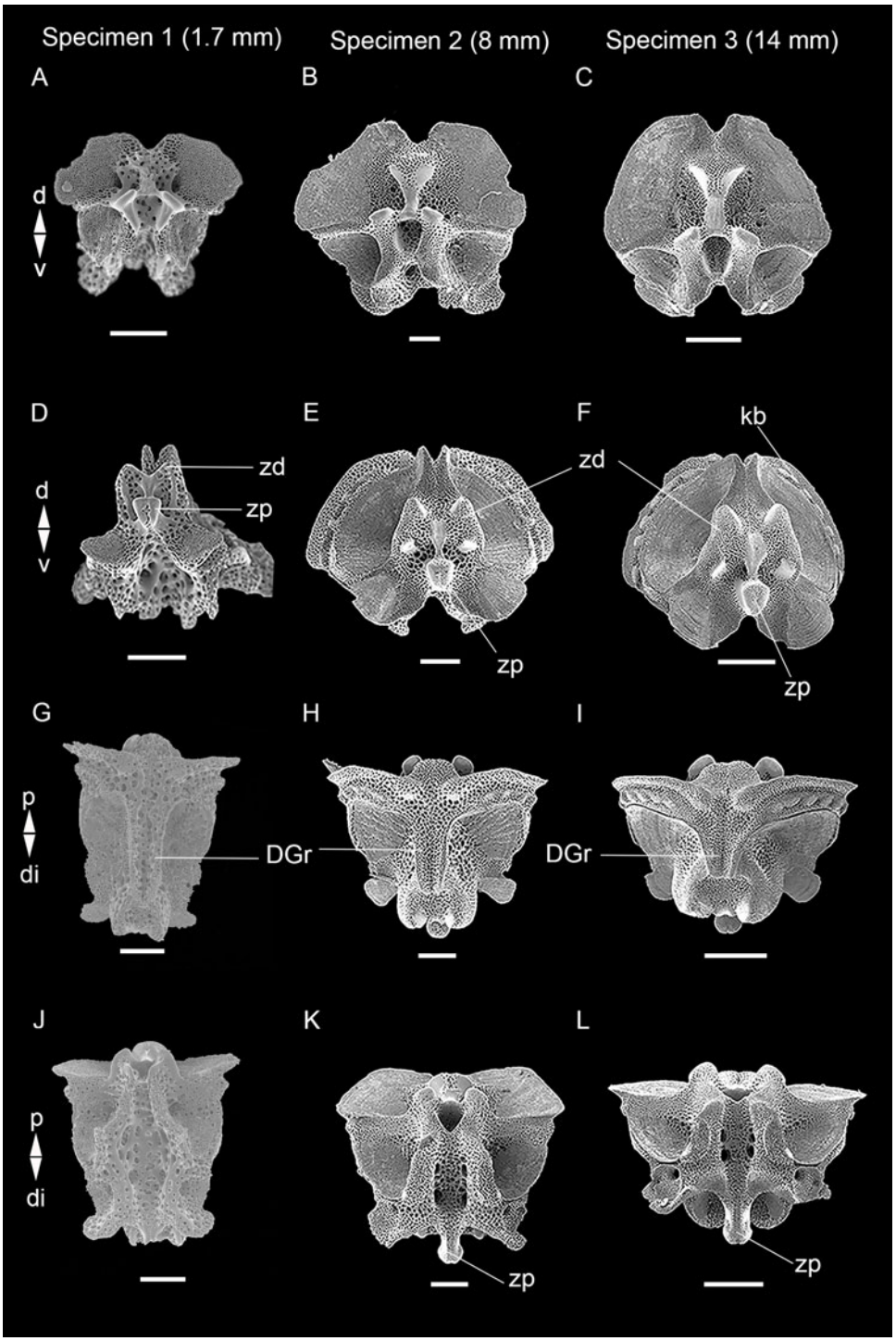

Figure 10. Vertebrae of *O. trindadensis* Serrano *et al*., 2023: (A, D, G, and J) young early specimen (1.7 mm dd – ZUEC OPH 3092); (B, E, H, and K) intermediate (8 mm dd – MZUSP 2772); (C, F, I, and L) adult (14 mm – ZUEC OPH 3097). (A–C) Vertebrae ossicle – proximal surface; (D–F) vertebrae ossicle – distal surface; (G–I) vertebrae ossicle – dorsal surface; (J–L) vertebrae ossicle – ventral surface. d, dorsal; di, distal; DGr, dorsal groove; kb, knobs; p, proximal; v, ventral; zd, zygocondyles; zp, zygosphene. Scale bars: (A, D, G, and J) 100 μm; (B, E, H, and K) 200 μm; (C, F, I, and L) 500 μm.

LD2 axis, was also shown in the analysis, especially to separate the adult and intermediate stages of the two species from the young early stage of development. The oral diameter was not analysed in this study. Adults and intermediate specimens are easily separated from young early specimens mainly by the width of the dorsalmost arm spines, the width of the dorsal arm plate, the width of the second ventral arm plate, the width of the adoral shield, and the length of dorsalmost arm spines. To better separate young early specimens between species, more specimens in this stage need to be analysed in further studies.

The results obtained here reinforced that morphometrical analysis and SEM imagery may help to morphologically distinguish species from the early stages of growth. In addition, they illustrate the importance of growth series studies in increasing our knowledge about *Ophiocoma*, and additional progress can be made in the taxonomy of the group with more studies on the morphological changes during ontogeny and the correlation of young early specimens and adults in other species of the genus.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424001164.

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

Data. All data generated or analysed during this study are included in this published article and its Supplementary materials.

Acknowledgements. We are grateful to the Paulo Young Invertebrate Collection of the Federal University of Paraíba, especially Jéssica Prata, for granting access and donation of specimens of *Ophiocoma echinata* for comparative studies. We also acknowledge the access to equipment and assistance provided by the Electron Microscope Laboratory (LME/UNICAMP). We are grateful to the researcher Dr Pablo D. B. Guilherme for the assistance with the statistical analysis.

Financial support. This study was funded by the São Paulo Research Foundation (FAPESP, Process no. 2019/01620-9; Process no. 2019/05997-0), and CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil) – Finance Code 001. This work was also supported by the BIOTA-Collections Project (Process no. 2018/10313-0), and the ProTrindade Project (Process no. 443278/2019-9). We thank the Brazilian Navy (1st District) and SECIRIM (Interministerial Secretariat for Marine Resources) for all the support provided in Trindade and Martin Vaz. This is the contribution number 18 of the ProTrindade Marine Invertebrates Project.

Competing interests. None.

Ethical standards. The study was registered at the National System for the Management of Genetic Heritage and Associated Traditional Knowledge – SisGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado), according to Brazilian legislation Law number 13.123/2015 and Decree 8772/2016. The approval ID for this study was A3014E0.

References

Albuquerque MN (1986) *Ophiuroidea Gray, 1840 (Echinodermata) da plataforma continental do norte e nordeste brasileiro*. PhD thesis, Universidade de São Paulo, São Paulo, Brasil.

Alitto RAS, Amaral ACZ, Oliveira LD, Serrano H, Seger KR, Guilherme PDB, Di Domenico M, Christensen AB, Lourenço LB, Tavares M and Borges M (2019) Atlantic West *Ophiothrix* spp. in the scope of integrative taxonomy: confirming the existence of *Ophiothrix trindadensis* Tommasi, 1970. *PLoS ONE* **14**, e0210331.

Alitto RAS, Bueno ML, Guilherme PDB, Di Domenico M, Christensen AB and Borges M (2018) Shallow-water brittle stars (Echinodermata: Ophiuroidea) from Araçá Bay (southeastern Brazil), with spatial distribution considerations. *Zootaxa* **4405**, 1–66.

Beck MW (2022) ggord: ordination plots with ggplot2. R package version 1.1.7. Available at https://zenodo.org/badge/latesdoi/35334615.

Benavides-Serrato M and O'Hara TD (2008) A new species in the *Ophiocoma erinaceus* complex from the south-west Pacific Ocean (Echinodermata: Ophiuroidea: Ophiocomidae). *Memoirs of Museum Victoria* **65**, 51–56.

Borges M and Alitto RAS (2021) Classe Ophiuroidea. In Steiner TM, Amaral ACZ and Borges M (eds), *Manual de identificação dos invertebrados marinhos da região sudeste-sul do Brasil*. São Paulo: Editora da Universidade de São Paulo, pp. 278–306.

Borges M, Alitto RAS and Amaral ACZ (2015) From baby to adult: ontogenetic series of nine species of Ophiuroidea from Atlantic Southwestern. *Revista de Biología Tropical* **63**, 361–381.

Borges M, Monteiro AMG and Amaral ACZ (2002) Taxonomy of Ophiuroidea (Echinodermata) from the continental shelf and slope of the southern and southeastern Brazilian coast. *Biota Neotropica* **2**, 1–69.

Clark HL (1914) Growth changes in brittle stars. *Carnegie Institution of Washington Publication* **5**, 93–126.

Clark HL (1921) The echinoderm fauna of Torres Strait: its composition and its origin. *Carnegie Institution of Washington Publication* **10**, 1–330.

Clark HL (1933) A handbook of the littoral echinoderms of Porto Rico and the other West Indian Islands. Scientific survey, Porto Rico and Virgin Islands. *New York Academy of Sciences* **16**, 1–147.

Clark AH (1939) Echinoderms of the Smithsonian-Hartford Expedition 137, with other West Indian records. *Proceedings of the United States National Museum* **86**, 441–456.

Clark AH, Rathbun MJ, Boone PL, Shoemakae CR and Clark HL (1921) Reports on the Crinoids, Ophiurans, Brachyura, Tanidacea and Isopoda, Amphipods and Echinoidea of the Barbados-Antigua expedition of 1918. *University of Iowa, Studies in Natural History* **9**, 1–63.

da Silva JF, Prata J and Christoffersen ML (2023) Intraspecific variations in species of Ophiuroidea (Echinodermata) from the Tropical Southwest Atlantic, northeast Brazil. *Organisms Diversity & Evolution* **23**, 577–602.

Devaney DM (1968) *The Systematics and Post-Larval Growth Changes in Ophiocomid Brittlestars*. PhD thesis, University of Hawaii, Honolulu, USA.

Devaney DM (1970) Studies on ophiocomid brittlestars. I. A new genus (*Clarkcoma*) of Ophiocominae with a reevaluation of the genus *Ophiocoma*. *Smithsonian Contributions to Zoology* **51**, 1–41.

Engel H (1939) Echinoderms from Aruba, Curaçao, Bonaire and northern Venezuela. *Martinus Nijhoff, The Hague, Netherlands* **8**, 1–12.

Falkner I and Byrne M (2006) Skeletal characters for identification of juvenile *Ophiactis resiliens* and *Amphiura constricta* (Echinodermata): cryptic ophiuroids in coralline turf habitat. *Journal of the Marine Biological Association of the United Kingdom* **86**, 1199–1207.

Goharimanesh M, Stöhr S, Mirshamsi O, Ghassemzadeh F and Adriaens D (2021) Interactive identification key to all brittle star families (Echinodermata; Ophiuroidea) leads to revised morphological descriptions. *European Journal of Taxonomy* **766**, 1–63.

Grave C (1898) Embryology of *Ophiocoma echinata*, Agassiz. (Preliminary Note). *Johns Hopkins University Circulars* **18**, 6–7.

Hendler G (1978) Development of *Amphioplus abditus* (Verrill) (Echinodermata: Ophiuroidea). II. Description and discussion of ophiuroid skeletal ontogeny and homologies. *Biological Bulletin* **154**, 79–95.

Hendler G (1984) Brittlestar color-change and phototaxis (Echinodermata: Ophiuroidea: Ophiocomidae). *Marine Ecology* **5**, 379–401.

Hendler G (1988) Ophiuroid skeleton ontogeny reveals homologies among skeletal plates of adults: a study of *Amphiura filiformis*, *Amphiura stimpsonii* and *Ophiophragmus filograneus* (Echinodermata). *Biological Bulletin* **174**, 20–29.

Hendler G (2018) Armed to the teeth: a new paradigm for the buccal skeleton of brittle stars (Echinodermata: Ophiuroidea). *Contributions in Science* **526**, 189–311.

Humara-Gil KJ, Granja-Fernández R, Montoya-Márquez JA and López-Pérez A (2022) A morphological and morphometric approach to study Ophiuroidea (Echinodermata): size changes of *Ophiocomella alexandri*. *Journal of Morphology* **283**, 35–50.

Koehler R (1914) A contribution to the study of ophiurans of the United States National Museum. *Bulletin of the United States National Museum* **84**, 1–173.

Lamarck JBPA (1816) Histoire naturelle des animaux sans vertèbres. *Verdière* **2**, 1–568.

Lima EJB and Fernandes MLB (2009) Diversidade de equinodermos (Echinodermata) no Estado de Pernambuco (Brasil). *Revista Brasileira de Zoociências* **11**, 55–63.

Ludwig H (1898) Die Ophiuren der Sammlung plate. *Zoologische Jahrbuecher Supplement* **4**, 750–786.

Ludwig H (1899) Jugendformen von Ophiuren. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften* **14**, 210–235.

Lyman T (1865) Ophiuridae and Astrophytidae. *Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College* **1**, 1–200.

Manso CLC (1993) Ofiuroides da plataforma brasileira. Parte II: norte do estado do Rio de Janeiro, estado do Espírito Santo, sul do estado da Bahia e bancos Royal Charlotte, Hostpur e Davis. (Echinodermata: Ophiuroidea). *Revista Brasileira de Biologia* **53**, 189–195.

Manso CLC, Alves OFS and Martins LR (2008) Echinodermata da Baía de Todos os Santos e da Baía de Aratu (Bahia, Brasil). *Biota Neotropica* **8**, 179–196.

Martynov A, Ishida Y, Irimura S, Tajiri R, O'Hara T and Fujita T (2015) When ontogeny matters: a new Japanese species of brittle star illustrates the importance of considering both adult and juvenile characters in taxonomic practice. *PLoS ONE* **10**, e0139463.

Miranda ALS, Lima MLF, Sovierzoski HH and Correia MD (2012) Inventory of the Echinodermata collection from the Universidade Federal de Alagoas. *Biota Neotropica* **12**, 135–146.

Monteiro AMG (1987) *Ophiuroidea (Echinodermata) da região de Ubatuba (SP) – aspectos morfológicos e ecológicos*. PhD thesis, Universidade de São Paulo, Instituto Oceanográfico, São Paulo, Brasil.

Monteiro AMG, Reis MO and Pardo EV (1992) Morfologia comparativa e distribuição batimétrica de duas espécies de Ophiuroidea, na região costeira de Ubatuba. *Boletim do Instituto Oceanográfico* **40**, 39–53.

Mortensen T (1936) Echinoidea and Ophiuroidea. *'Discovery' Reports* **12**, 199–348.

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press

O'Hara TD, Stöhr S, Hugall AF, Thuy B and Martynov A (2018) Morphological diagnoses of higher taxa in Ophiuroidea (Echinodermata) in support of a new classification. *European Journal of Taxonomy* **416**, 1–35.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E and Wagner H (2019) vegan: community ecology package. R package version, 2.5-6. R package version. Available at https://cran.rproject.org/web/packages/vegan/vegan.Pdf.

Olbers JM and Samyn Y (2012) The *Ophiocoma* species (Ophiurida: Ophiocomidae) of South Africa. *Western Indian Ocean Journal of Marine Science* **10**, 137–154.

Price ARG and Rowe FWE (1996) Indian Ocean echinoderms collected during the Sindbad Voyage (1980–81): 3. Ophiuroidea and Echinoidea. *Bulletin of the Natural History Museum London (Zoology)* **62**, 71–82.

Rathbun R (1879) A list of the Brazilian echinoderms, with notes on their distribution, etc. *Transactions of the Connecticut Academy of Arts and Sciences* **5**, 139–158.

R Development Core Team (2018) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/.

Schoener A (1967) Post-larval development of five deep-sea ophiuroids. *Deep-Sea Research* **14**, 645–660.

Schoener A (1969) Atlantic ophiuroids: some post-larval forms. *Deep-Sea Research* **16**, 127–140.

Serrano H, Damiano CJS, Alitto RAS, Guilherme PDB, Cerqueira WRP, Mendonça JB, Tavares M and Borges M (2023) A new species of *Ophiocoma* (Echinodermata: Ophiuroidea) from Archipelago Trindade and Martin Vaz, Southeastern Atlantic, and redescription of *Ophiocoma echinata*. *Journal of the Marine Biological Association of the United Kingdom* **103**, 1–16.

Stöhr S (2005) Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society* **143**, 543–576.

Stöhr S, Conand C and Boissin E (2008) Brittle stars (Echinodermata: Ophiuroidea) from La Réunion and the systematic position of *Ophiocanops* Koehler, 1922. *Zoological Journal of the Linnean Society* **153**, 545–560.

Stöhr S and Martynov A (2016) Paedomorphosis as an evolutionary driving force: insights from deep-sea brittle stars. *PLoS ONE* **11**, e0164562.

Stöhr S, O'Hara TD and Thuy B (2012) Global diversity of brittle stars (Echinodermata: Ophiuroidea). *PLoS ONE* **7**, e31940.

Sumida PY, Tyler PA, Gage JD and Nørrevang A (1998) Postlarval development in shallow and deep-sea ophiuroids (Echinodermata: Ophiuroidea) of the NE Atlantic Ocean. *Zoological Journal of the Linnean Society* **124**, 267–300.

Thuy B and Stöhr S (2011) Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. *Zootaxa* **3013**, 1–47.

Thuy B and Stöhr S (2016) A new morphological phylogeny of the Ophiuroidea (Echinodermata) accords with molecular evidence and renders microfossils accessible for cladistics. *PLoS ONE* **11**, e0156140.

Tommasi LR (1970) Os ofiuróides recentes do Brasil e de regiões vizinhas. *Contribuições Avulsas do Instituto Oceanográfico, Universidade de São Paulo, Série Oceanografia Biológica* **20**, 1–146.

Turner RL and Miller JE (1988) Post-metamorphic recruitment and morphology of two sympatric brittlestars. In Burke RD, Mladenov PV, Lambert P and Parsley RL (eds), *Echinoderm Biology: Proceedings of the Sixth International Echinoderm Conference, Victoria, 23–28 August 1987*. Rotterdam: A.A. Balkema, pp. 493–502.

Tyler PA, Patterson GJL, Sibuet M, Guille A, Murtons BJ and Segonzac M (1995) A new genus of ophiuroid (Echinodermata: Ophiuroidea) from hydrothermal mounds along the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom* **75**, 977–986.

Vadon C (1990) *Ophiozonella novaecaledoniae* n. sp. (Ophiuroidea, Echinodermata): description, ontogeny and phyletic position. *Journal of Natural History* **24**, 165–179.

Venables WN and Ripley BB (2002) Random and mixed effects. In Venables WN and Ripley BB (eds), *Modern Applied Statistics with S*. New York, NY: Springer, pp. 271–300.

Verrill AE (1899) Report on the Ophiuroidea collected by the Bahama expedition in 1893. *Bulletin from the Laboratories of Natural History of the State University of Iowa* **5**, 1–88.

Webb PM and Tyler PA (1985) Post-larval development of the common northwest European brittle stars *Ophiura ophiura*, *O. albida* and *Acrocnida brachiata* (Echinodermata: Ophiuroidea). *Marine Biology* **89**, 281–292.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD'A, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K and Yutani H (2019) Welcome to the tidyverse. *Journal of Open Source Software* **4**, 1686.

https://doi.org/10.1017/S0025315424001164 Published online by Cambridge University Press