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Redescription of *Hemieuryale pustulata* von Martens, 1867 (Echinodermata, Ophiuroidea) based on Brazilian specimens, with notes on systematics and habitat association

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Abstract

We redescribe *Hemieuryale pustulata* on the basis of 325 specimens obtained from the continental shelf off northeastern and southeastern Brazil. This is the first record of the species for Brazil. We illustrate for the first time details of the dental plate, oral plate, and vertebrae. Few morphological variations were observed in our extensive material. All specimens were associated with the gorgonian *Nicella guadalupensis*, suggesting an obligatory association in the Brazilian littoral. *H. pustulata* did not reveal a particular pattern of distribution on its host gorgonian, but larger gorgonians tend to support a larger number of ophiuroids. In addition to expanding the knowledge on morphology and ecology, we extend the known bathymetric distribution of the species, which is now known from 18 to 330 m.

Key words: Brittle-stars, Hemieuryalidae, morphology, taxonomy, ecology

Resumo

Este estudo apresenta uma redescrição para *Hemieuryale pustulata* a partir de 325 espécimes obtidos na plataforma continental do nordeste e sudeste brasileiro, sendo este o primeiro registro da espécie para o Brasil. São descritos e ilustrados pela primeira vez alguns caracteres internos para esta espécie, tais como placa dental, placa oral e vértebras. Poucas variações morfológicas foram observadas nos exemplares estudados. Todos os espécimes analisados estavam associados à gorgônia *Nicella guadalupensis*, sugerindo uma associação simbiótica obrigatória no litoral brasileiro. *H. pustulata* não apresentou um padrão claro de distribuição na gorgônia-habitat, porém, pode-se constatar que gorgônias maiores abrigam maior abundância de indivíduos. Além dos dados morfológicos e ecológicos apresentados, este estudo amplia o intervalo de faixa batimétrica desta espécie, agora conhecida de 18 a 330 m de profundidade.

Palavras-chave: Estrelas-serpentes, Hemieuryalidae, morfologia, taxonomia, ecologia

Introduction

Hemieuryalidae is probably one of the least known families of Ophiuroidea, regarding ecology and morphology, as well as phylogeny. Its species are rare and difficult to obtain (Murakami 1963). Probably for these reasons, knowledge of these animals is almost completely restricted to the original descriptions of the species.

The family Hemieuryalidae was erected by Verrill (1899a), initially to incorporate the genera *Ophioplus* Verrill, 1899a, *Hemieuryale* von Martens, 1867 and *Sigsbeia* Lyman, 1878. Over the next years, six new genera were established in this family, as follows: *Ophiochondrus* Lyman, 1869, *Ophiomoeris* Koehler, 1904,

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Ophioholcus H.L. Clark, 1915, *Amphigyptis* Nielsen, 1932, *Quironia* A.H. Clark, 1934, and *Ophioleila* A.H. Clark, 1949). The family has never been revised systematically since. Only recently, Martynov (2010) proposed to change the placement of the genera *Ophiochondrus* and *Ophiomoeris* from Hemieuryalidae to Ophiacanthidae Ljungman, 1867, based on his study of the morphology of the spine articulation and of the dental plate of all families of Ophiuroidea. The position of *Ophiomoeris* within Ophiacanthidae was recently confirmed by a molecular phylogeny reconstruction (O'Hara *et al.* 2014), but no hemieuryalid was included in that study. At present, Hemieuryalidae contains seven genera (all monotypic except for *Sigsbeia*) and 10 species (Stöhr *et al.* 2012).

Hemieuryale von Martens, 1867 is the type genus of the family. In the description of the genus, von Martens (1867) stressed its strong similarity with some Euryalida Gray, 1840. In his view, *Hemieuryale* represented an intermediate form between Euryalida and Ophiurida Müller & Troschel, 1840. However, this observation was not supported by a morphological cladistic analysis produced by Smith *et al.* (1995). Yet, the phylogenetic relationships of this genus/family with the remaining taxa of Ophiuroidea have still not been resolved. The only species known for the genus is *Hemieuryale pustulata* von Martens, 1867, originally described on the basis of two specimens from "Antilles". Although it represents one of the most common species of Hemieuryalidae, its morphology and ecology are practically unknown. The presence of a mosaic of small plates instead of dorsal arm plates is the main diagnostic character to separate *H. pustulata* from the remaining species in the family (e.g. Fell 1960). This character must be regarded as a specialization of *H. pustulata* (not as a family character) to allow the inclusion of species with regular dorsal arm plates in the same family.

Species of Hemieuryalidae usually live associated with octocorals of the genera *Nicella* Gray, 1870 (personal observation) and *Verrucella* Milne Edwards & Haime, 1857 (Verrill 1899a, b) and hydrocorals of the genus *Stylaster* Gray, 1831 (Hendler *et al.* 1995). Associations between ophiuroids and gorgonians are quite common, particularly at greater depths (below 100 m). In these environments, gorgonians (and other taxa such as antipatharians and sponges) may confer higher complexity to deep habitats, functioning as microhabitats for the macrofauna of these sites. Some of these relationships are obligate, the symbiont occurring only on one or a few host species, while others appear to be facultative (Buhl-Mortensen & Mortensen 2004; Moscher & Watling 2009). According to Buhl-Mortensen & Mortensen (2005), approximately 32% of the symbiotic associations between deep-water corals and other animals are obligatory. In a conservation context, it becomes important to know and understand these relations, particularly when poorly known species are involved, as is the case with *H. pustulata*.

In the present paper we redescribe *H. pustulata* on the basis of abundant material obtained from representative parts of the Brazilian littoral. We provide an extended diagnosis for the genus, the description of juvenile individuals and illustrations of internal characters, such as the dental and oral plates. None of these features were previously known for the species or family. We further present data on the abundance and distribution of *H. pustulata* on its host gorgonians and discuss the association of *H. pustulata* with its particular habitat.

Material and methods

The present study was based on 325 specimens of *Hemieuryale pustulata* associated with the gorgonian *Nicella guadalupensis* (Duchassaing & Michelotti, 1860). Of these, 150 were captured by a fisherman using a hook and line. They came from the continental shelf at about 40 km offshore of Macau City, along the northern coast of the State of Rio Grande do Norte, northeastern Brazil (4º42'09.9"S 36º28'08.2"W) from a depth of approximately 100 m. These specimens were preserved as dry samples and were deposited in the echinoderm collection of the Paulo Young Invertebrate Collection of the Federal University of Paraiba (UFPB.ECH). Three other specimens were obtained from dredgings during the Program REVIZEE Central Score (Programa de Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva), between 240 and 500 m depth in Rio de Janeiro (22°12'56"S 37º35'15"W), and they were preserved in alcohol at 70%, and deposited in the echinoderm collection (EQMN) of the in Museu Nacional, Rio de Janeiro (MNRJ). The remaining 172 specimens (preserved in alcohol at 70%) belong to the Laboratory of Biodiversity of the Federal University of Pernambuco (UFPE), being collected in the Potiguar Basin (05°05'19"S 36°31'18"W), State of Rio Grande do Norte, at a mean depth of 200 m. Unfortunately we do not have further details on methods of collecting of the material deposited in MNRJ and UFPE.

Taxonomic identification was based on the descriptions by von Martens (1867), and Verrill (1899b), and

achieved by using a key (Fell 1960), as well as by comparison with reliably identified museum material, including syntypes. The disc diameter was measured using a digital EDC 6" caliper, and the specimens were photographed using a Canon A640 10MP digital camera coupled to a Nikon SMZ800 stereomicroscope. For the SEM photographs, the jaw and fragments of the first 10 arm segments were submerged in commercial bleach (NaOCl) 2,5%, until all soft tissue was dissolved. The skeletal elements were washed in tap water, air-dried and mounted on aluminum stubs with carbon ribbons and metalized with gold.

In order to analyze *H. pustulata in situ*, the density and the distribution of individuals was calculated from gorgonians collected by chance with fishing line and hook. For each gorgonian, the following data were obtained: width and height of gorgonian (in mm), number of individuals of *H. pustulata* on each gorgonian and disc diameter (dd, in mm) of each specimen. To analyze the distribution of the gorgonians, they were subdivided into four quadrants (Fig. 1). For each quadrant, we obtained the number of individuals and the disc diameter for each specimen of ophiuroid.

To analyze the patterns in abundance and distribution of brittle star individuals among the studied gorgonians, we applied the PERMANOVA test. The same analysis was also used to compare the mean size of individuals in each quadrant. To measure the degree of dependence between the area of each gorgonian (width x height) and the abundance and size of the ophiuroids we used the Pearson correlation. The tests were run with the programs Primer 6.0 & Permanova+ and Bioestat 5.0. For all statistical analyses only ophiuroids that were attached to the gorgonian were considered. Those ophiuroids that had become detached from their gorgonian host were only used in the taxonomic study.

Abbreviations. dd = disc diameter; spm(s) = specimen(s).

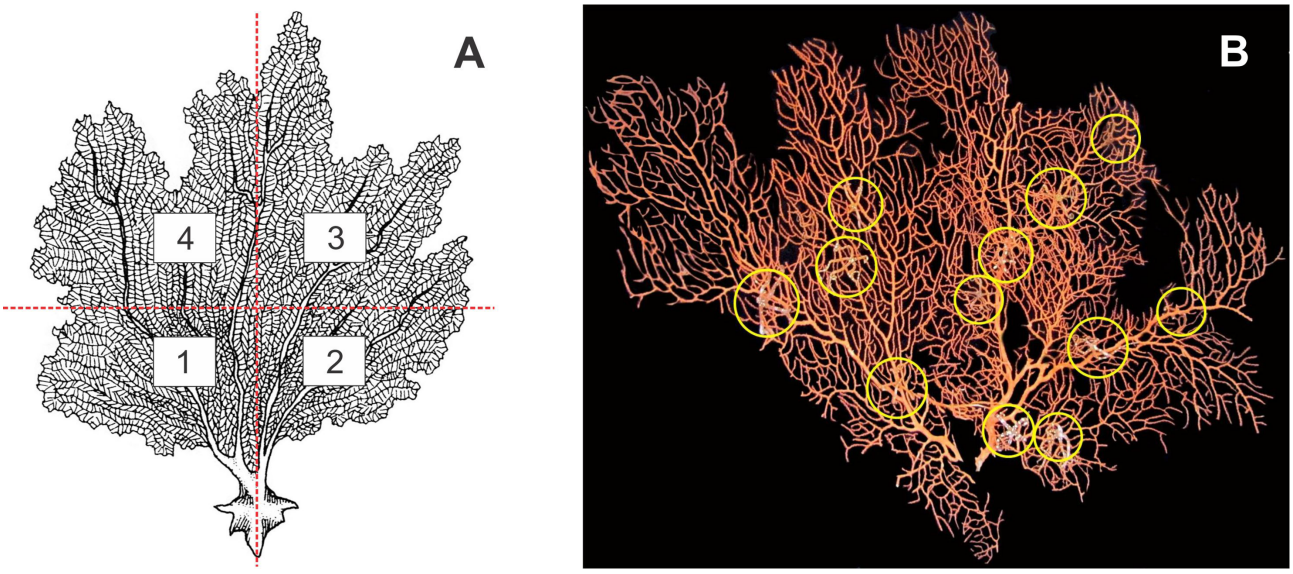

FIGURE 1. (A) Schematic drawing of a gorgonian colony, illustrating the subdivision into quadrants from which we obtained data on abundance and distribution of *Hemieuryale pustulata*; **(B)** Gorgonian *Nicella guadalupensis* with several juvenile and adult specimens of *H. pustulata* (UFPB.ECH.2169) distributed across the colony without an apparent pattern.

Results

Systematics

Class Ophiuroidea Gray, 1840

Order Ophiurida Müller & Troschel, 1840

Family Hemieuryalidae Verrill, 1899

Hemieuryalidae Verrill 1899a: 70; 1899b: 363.—H.L. Clark 1915: 190.—Matsumoto 1915: 62, 65–66; 1917: 138–140.—A.H.

Clark 1921: 52.—Hyman 1955: 647.—Fell 1960: 12 (key).—Murakami 1963: 11–12, 40.—Tommasi 1970: 15.—Bernasconi & D'Agostino 1971: 455; 1977: 73.—Abreu-Pérez 1990: 3.—Hendler *et al.* 1995: 142.—Kutscher & Villier 2003: 189.—O'Hara & Stöhr 2006: 119.—Laguarda-Figueras *et al.* 2009: 172, fig. 68a–d.—Martynov 2010: 30, 44, 125.—Barboza & Borges 2012: 5.

Type genus. *Hemieuryale* von Martens, 1867.

Diagnosis (modified from Verrill 1899a and Martynov 2010). Disc pentagonal, covered by thick plates. Radial shields large. Dorsal arm plates entire or replaced by a mosaic of small plates, accompanied by accessory dorsal arm plate. Lateral arm plates separated by accessory plates. A row of oral papillae. Bursal slits small, placed near margins of oral shields. Arm spines short and few. Spine articulation composed of two parallel ridges placed at an angle to each other.

Remarks. According to Verrill (1899a) this family has strongly calcified jaw plates and its species are very similar, in shape and habitus, to species of Euryalida Lamarck, 1816 with simple arms. Its representatives live associated with calcareous hydrocorals and octocorals. Species are distributed from Hawaii and California (USA) to the Caribbean Sea. The present study expands this distribution range to the Brazilian coast (up to 18ºS). Species occur between depths of 4 and 500 m (Koehler 1914; Hendler *et al.* 1995).

The first fossil record of a member of the Hemieuryalidae dates from the Early Jurassic (Smith *et al.* 1995). Presently only one fossil species is known from the family, which belongs to the genus *Hemieuryale* (*H. parva* Kutscher & Jagt, 2000 †—from Lower Maastrichtian, Late Cretaceous). Thuy (2013) recently transferred the fossil species *Sigsbeia lunaris* (Hess, 1962) † (from Late Pliensbachian, Early Jurassic) to the extinct genus *Inexpectacantha* Thuy 2011† (Ophiacanthidae).

Genus *Hemieuryale* von Martens, 1867

Hemieuryale von Martens 1867: 484.—Lütken 1869: 47.—Lyman 1882: 249.—Verrill 1899b: 363–364.—H.L. Clark 1915: 192.
Sigsbeia (not *Sigsbeia* Lyman, 1878).—Barboza & Borges 2012: 5.

Type-species. *Hemieuryale pustulata* von Martens 1867.

Diagnosis. Swollen radial primary plates, numerous flat overlapping scales in center of dorsal disc. A mosaic of small plates on dorsal arm. Accessory dorsal arm plate swollen and rounded, much enlarged on first free arm segment. Lateral arm plate large with tuberculous stereom. Small triangular extraoral plate, present on all or only some jaws. Short bursal slits lateral to oral shields. Two short arm spines, about half the length of an arm segment, with a crown of thorns at tip.

Remarks. In the original description of the genus, von Martens (1867) provides the following diagnostic characters, some of which need to be modified according to the new findings (in parentheses): arms simple, sides of arms provided with a series of large bumps (= swollen accessory plates), without differentiated madreporic plate (in SEM identifiable by hydropore), bursal slit located on inferior and lateral parts of oral shields, a row of oral papillae, teeth absent (clearly present). According to Lyman (1878), *Hemieuryale* and *Sigsbeia* form a peculiar group, in which both genera are differentiated from each other by the shape of the dorsal arm plate, forming a mosaic of small pieces in the first genus, and being an entire plate in the second. A detailed study of *Sigsbeia* is needed to decide if they indeed are a monophyletic taxon.

Hemieuryale pustulata von Martens, 1867

Figures 2A–F; 3A–G; 4A–J; 5A–E

Hemieuryale pustulata von Martens 1867: 179, 484–486, fig. 2a–c.—Lyman 1869: 313; 1883: 277.—Verrill 1899b: 363–364.—H.L. Clark 1915: 192.—Matsumoto 1917: 140. —A.H. Clark 1921: 52.—Fell 1960: 12.—Emson & Woodley 1987: 33.—Martynov 2010: 48, fig. 36a.—Alvarado 2011: 270.—Alvarado & Solís-Marín 2013: 624.

Type material. Museum of Natural History of Berlin (Museum für Naturkunde). Two syntypes, MZB 1739. (Examined on photographs, provided by C. Lüter).

Type locality. 18° N; 70° W, Antilles, Caribbean Sea.

Material examined. Continental shelf in front of Municipality off Macau, of Rio Grande do Norte, 100 m: 1 spm, 17 Oct 2010 [UFPB.ECH.2159], 9 spms, 14 Sep 2012 [UFPB.ECH.2171], 13 spms, 06 Nov 2010 [UFPB.ECH.2169], 16 spms, 16 Feb 2011 [UFPB.ECH.2172], 23 spms, 17 Oct 2010 [UFPB.ECH.2173], 7 spms 04 Jul 2010 [UFPB.ECH.2175], 120 m: 25 spms, 24 Sep 2011 [UFPB.ECH.2170], continental shelf in front of Diogo Lopes, Macau, Rio Grande do Norte, 4º40'31,05"S 36º28'30,01"W, 130 m: 17 spms, 04 Jun 2012 [UFPB.ECH.2167], 5 spms, 15 Mar 2012 [UFPB.ECH.2168], 10 spms, 08 Dec 2012 [UFPB.ECH.2174], 4º42'09,9"S 36º28'08,22"W, 100 m: 7 spms, 23 Sep 2010 [UFPB.ECH.2163], 3 spms, 16 Aug 2012 [UFPB.ECH.2164], 4 spms, 09 Mar 2010 [UFPB.ECH.2166], 4º47'56,47"S 36º27'33,59"W, 130 m: 2 spms, 12 Dec 2011 [UFPB.ECH.2162], 8 spms, 18 Aug 2011 [UFPB.ECH.2165], 1 spm., 8 July 2010, [UFPB.ECH.212176], 2 spms., 04º44,8945'S, 36º25,4571, Potiguar Basin, 23 May 2011 [UFPB.ECH.2177], REVIZEE Central, col. N. Oc. Almirante Saldanha, 22º12'56"S, 250–500 m, calcareous bottom: 1 spm, 12 Jun 2002 [EQMN 2955], REVIZEE Central, 22º22'56"S 37º35'15"W, 240–300 m, bottom of rhodoliths: 2 spms, 12 Jun 2002 [EQMN 2953], Potiguar Basin, Rio Grande do Norte: 172 spms, Universidade Federal de Pernambuco, without registration number.

Diagnosis. Same as for genus.

Redescription (UFPB.ECH.2175). Disc pentagonal (dd = 5.62 mm), covered by strongly calcified, imbricated scales, of variable size and shape (Fig. 2A, C, 3A, D). Radial shields large, approximately half length of dd, triangular, with tuberculous stereom, separated along their full length by a row of small plates that extend to arm (Fig. 2C, E, 3A, E). Interradius covered by strongly calcified imbricated scales, slightly larger than those in center of disc. Central primary plate circular, flat and bulging (Fig. 2A, C, 3A, B). Scales of variable size and shape, some strongly swollen, others flattened, are found surrounding the central primary plate (Fig. 2A, C, 3A, B). Radial primary plates oval, strongly swollen on distal half (Fig. 2A, C, 3A, B), almost forming a tubercle between each radial shield pair. Ventral interradius short, with scales similar to dorsal ones in shapes and sizes (Fig. 2D), but more flattened and less imbricated. Bursal slits short and broad (Fig. 2D, E, 3D, F), located on lateral margins of oral shields. Oral shields large and flabelliform (Fig. 2D, 3D, F), stereom weakly tuberculous, occupying most of the ventral disc. Madreporic oral shield with large pore offset near lateral edge, stereom not tuberculous (Fig. 2D, 3D, F). Adoral shields slightly smaller than oral shields, swollen with tuberculous stereom (Fig. 2D, 3D, F). Small triangular extraoral plate, present on all or only some jaws (Fig. 2D, 3D, F). Three to five lateral oral papillae (Fig. 2D, 3D, F), the distal one largest and operculous, proximalmost papillae pointed and slightly infradental, middle papillae intermediate in size, rounded. One triangular pointed apical papilla (Fig. 2D, 3D, F).

Arms. Five arms, approximately 4 to 7 times disc diameter long, and thick (Fig. 2A, B). A mosaic of small plates on dorsal arm, variable in size and shape (Fig. 2A, E, 3C). Accessory dorsal arm plate swollen and rounded (Fig. 2A, C, E, 3A, C, E). The first accessory dorsal arm plate is the largest and most swollen (Fig. 2E, 3A, E). Dorsal and accessory plates with simple stereom. Lateral arm plate visible dorsally and ventrally, with tuberculous stereom (Fig. 4A, C), pairs dorsally and ventrally widely separated. Isolated plate from proximal arm about as high as long, outer surface on distal two thirds strongly tuberculous, flatter, proximal band with simple stereom. Inner side of lateral plate with vertical ridge, almost for entire plate height, slightly slanting proximalwards, with round flat "knob" on lower proximal part; a single perforation almost in center of inner surface. Arm spine articulations two parallel ridges, of equal length, separated at both ends, nerve opening perforating, muscle opening shallow depression (Fig. 4C). Ventral arm plate axe-shaped, widest distally, with slightly convex distal edge, strongly concave lateral edges, obtuse proximal angle (Fig. 2F, 3G), tuberculous stereom. Consecutive plates just touching on proximalmost arm, further out separated. One oval, operculiform tentacle scale (Fig. 2F, 3G), longer than wide. Two thick round arm spines (Fig. 2F, 3G), slightly longer than half an arm segment, ventral spine shorter than dorsal, both with a crown of thorns at tip (Fig. 4E). Arm spines visible only on ventral side, absent on first two arm segments, two arm spines from third segment. Vertebrae streptospondylous (Fig. 4F, J).

Dental plate. Entire, non–perforated, with five shallow tooth sockets, three times longer than wide, widest ventrally with largest socket (Fig. 5C).

Oral plate. Approximately 1.5 times as long as high (Fig. 5A, B). Abradial muscular area small (approximately 300 μm in diameter), elliptical, positioned transversally (Fig. 5B). Adradial articular area slightly comma-shaped (Fig. 5A).

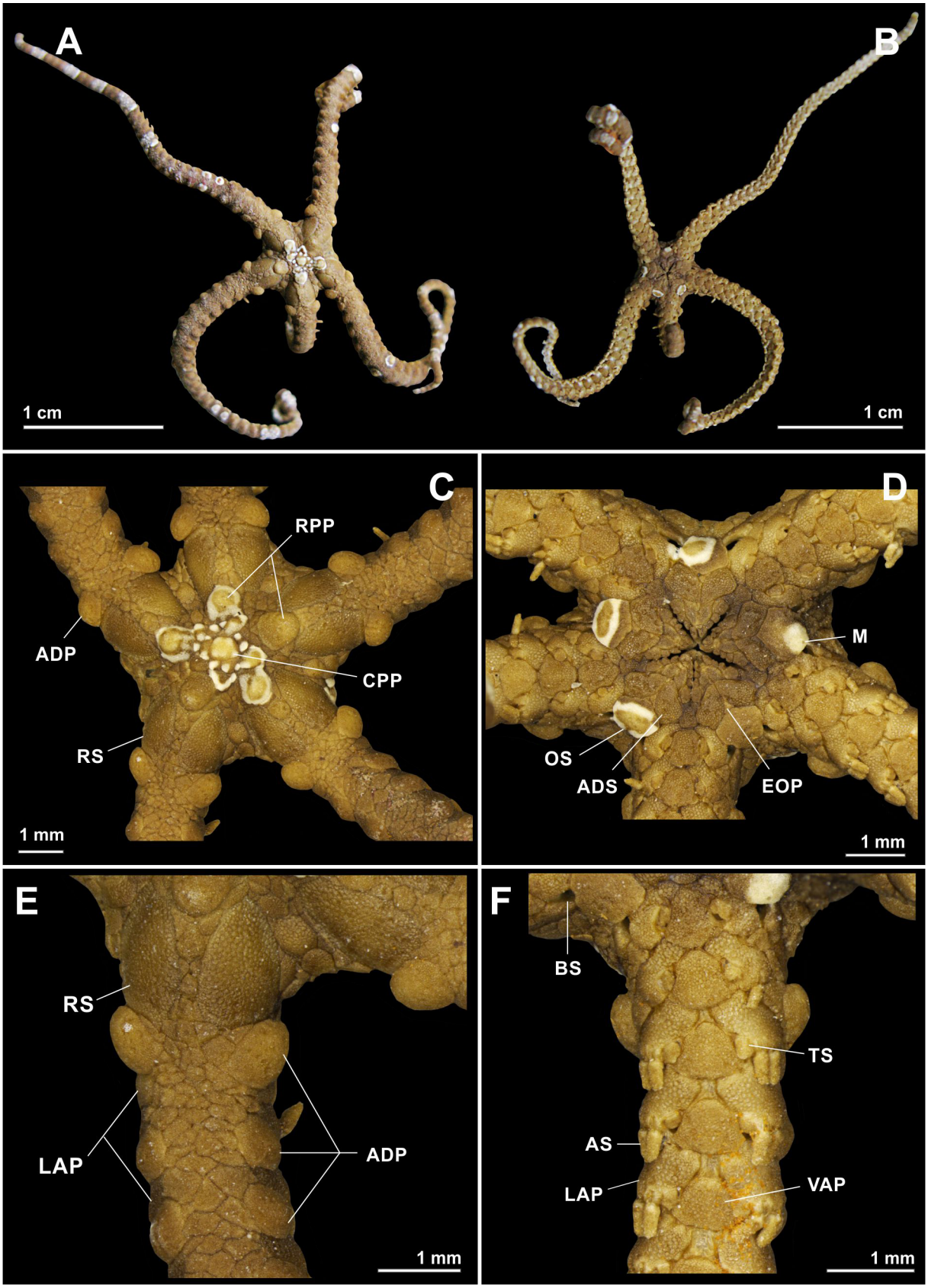

FIGURE 2. Morphological characters of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** Dorsal view; **(B)** Ventral view; **(C)** Dorsal view of disc; **(D)** Ventral view of disc; **(E)** Dorsal view of arm; **(F)** Ventral view of arm. ADP: accessory dorsal arm plate; ADS: adoral shield; AS: arm spine; BS: bursal slit; CPP: central primary plate; EOP: extraoral plate; LAP: lateral arm plate; M: madreporite; OS: oral shield; RPP: radial primary plates; RS: radial shield; TS: tentacle scale; VAP: ventral arm plate.

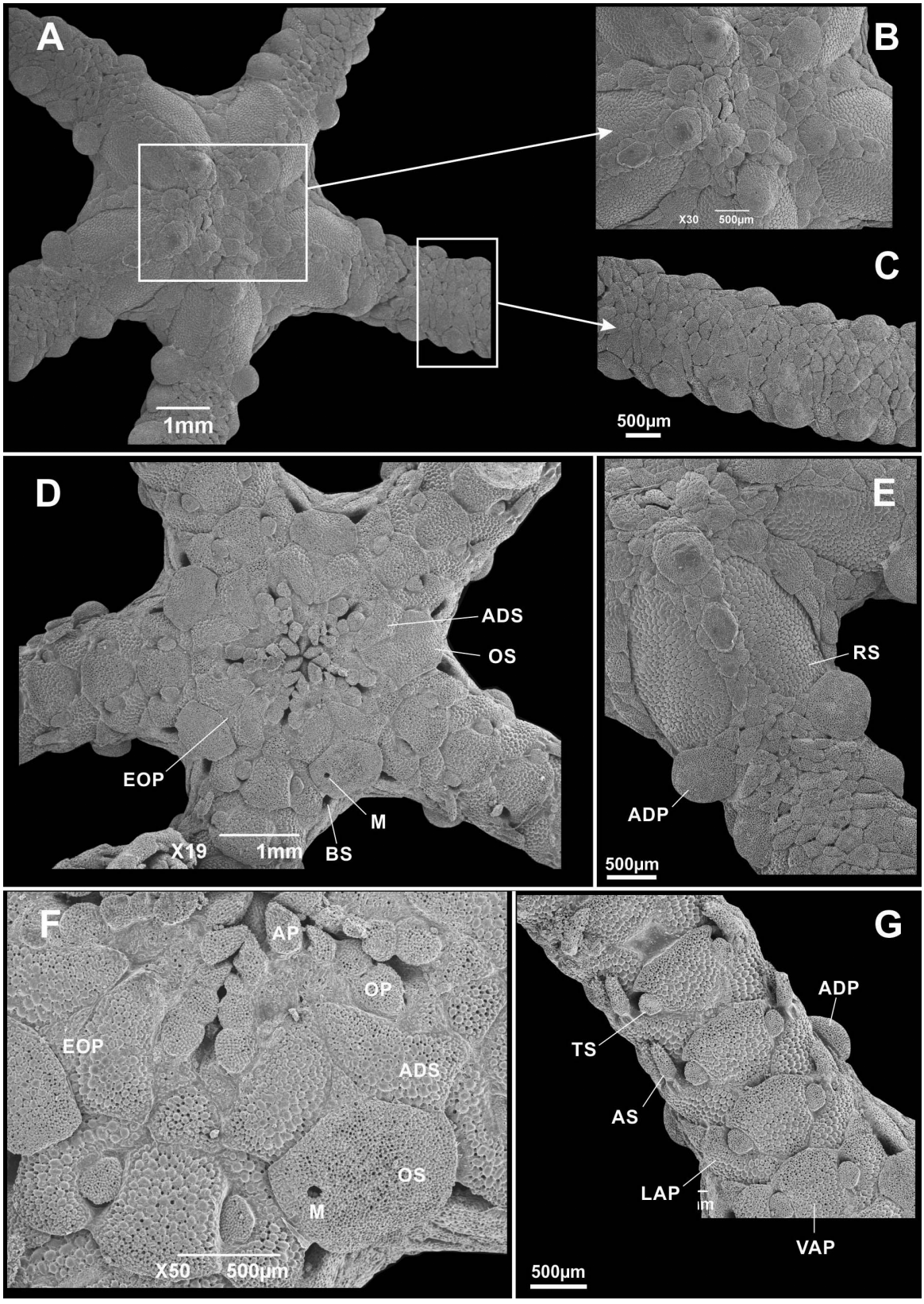

FIGURE 3. SEM photographs of external morphological characters of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** Dorsal view of disc; **(B)** Detail of central region of disc; **(C)** Dorsal view of arm; **(D)** Ventral view of disc; **(E)** Detail of the peripheral region of the disc; **(F)** Detail of jaws; **(G)** Ventral view of arm. ADP: accessory dorsal arm plate; ADS: adoral shield; AS: arm spine; AP: apical papillae; BS: bursal slit; EOP: extraoral plate; LAP: lateral arm plate; M: madreporite; OP: oral papillae; OS: oral shield; RS: radial shield; TS: tentacle scale; VAP: ventral arm plate.

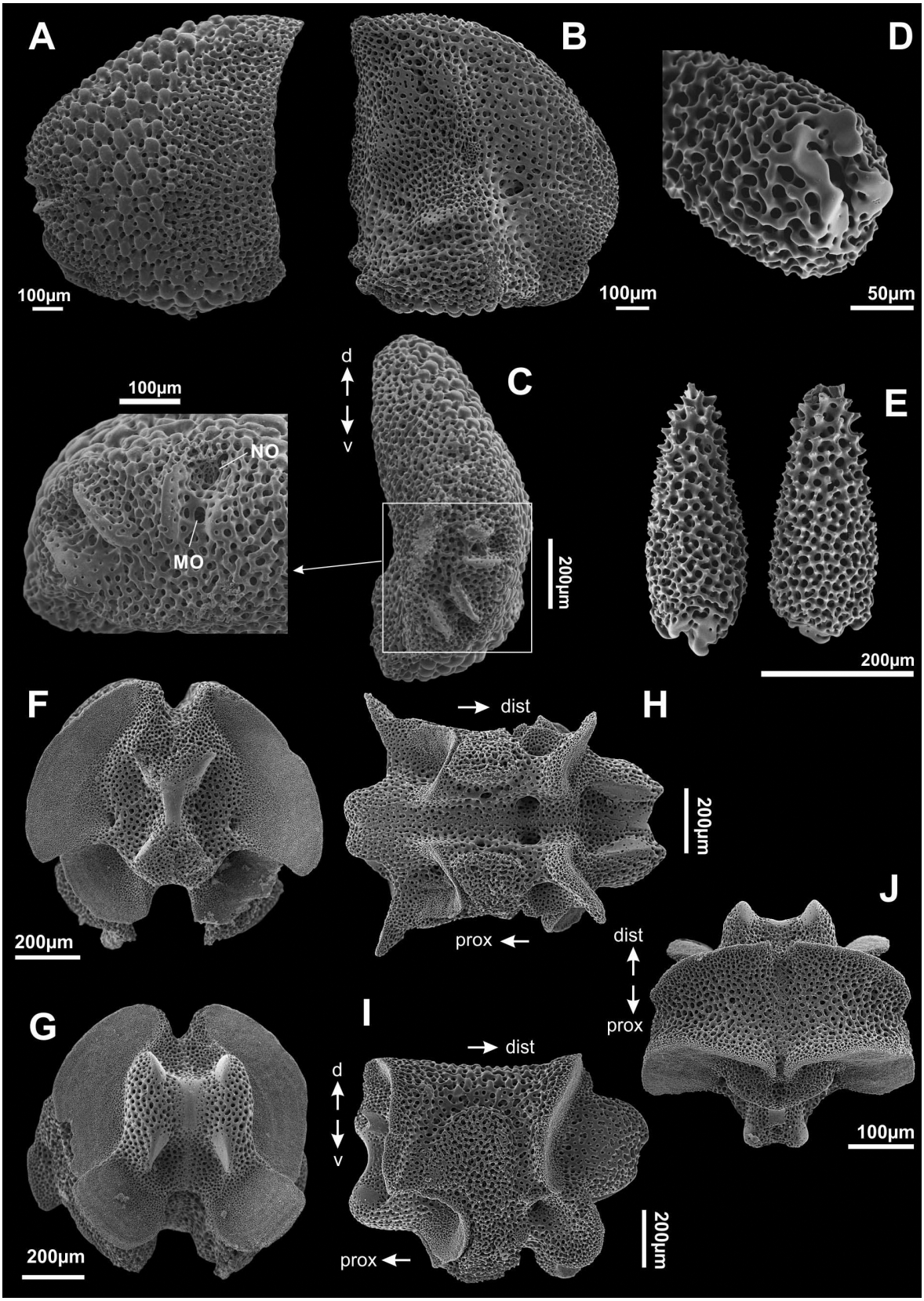

FIGURE 4. SEM photographs of internal skeletal characters of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** External view of lateral arm plate; **(B)** Internal view of lateral arm plate; **(C)** Distal view of lateral arm plate, detail of spine articulation; **(D)** Detail of surface of arm spine articulation; **(E)** Arm spines; **(F)** Distal view of vertebrae; **(G)** Proximal view of vertebrae; **(H)** Ventral view of vertebrae; **(I)** Lateral view of vertebrae; **(J)** Dorsal view of vertebrae. MO: muscle opening; NO: nerve opening. (Photo 4B courtesy of Ben Thuy).

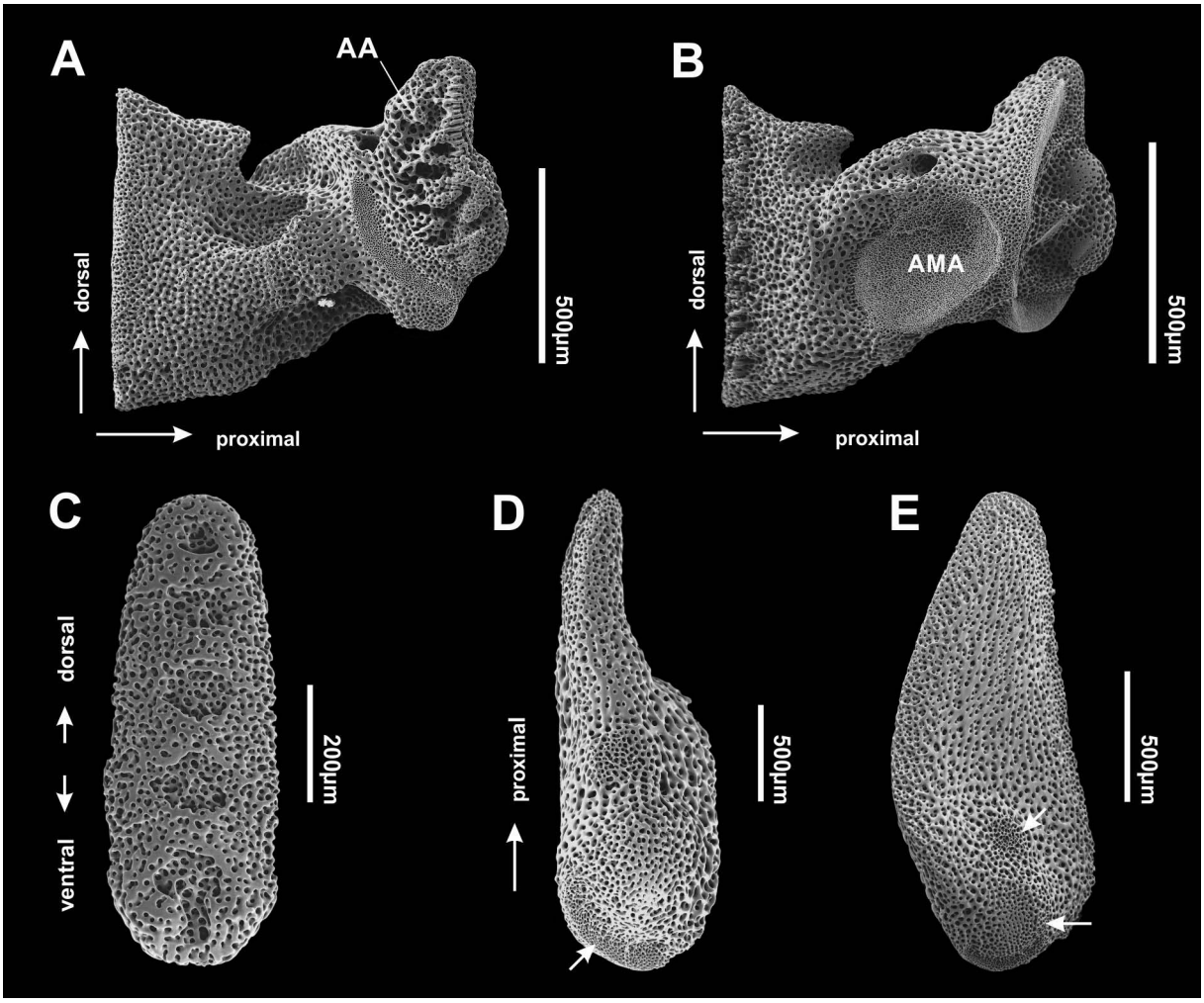

FIGURE 5. SEM photographs of internal skeletal characters of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** Abradial view of oral plate; **(B)** Adradial view of oral plate; **(C)** Dental plate; **(D)** Genital plate in dorsal view, long groove of the articulation surface (arrow); **(E)** Inner view of radial shield, articulation surface of radial (arrows). AA: adradial articular area; AMA: abradial muscular area.

Genital plates and radial shields. Adradial genital plate small (approximately as long as 3 arm segments) (Fig. 5D), positioned laterally from second to fourth vertebrae. Abradial genital plate may be absent or is extremely reduced and possibly similar to a disc scale that we were unable to identify. Articulation surface of adradial genital plate is a long curved distal band (Fig. 5D). Articulation surface of radial shield formed by two circular depressions, the distal one larger and deeper, and a narrow band corresponding to the band on the genital plate (Fig. 5E). Radial shield slightly comma-shaped, convex abradial edge, almost straight adradial edge, distal end twice as wide as proximal end.

Variations. The observed variation with respect to general morphology was small in the studied specimens. A small extraoral triangular plate (Fig. 2F, 3D, F) is present in most specimens. However, in some specimens, this plate was found absent on one or several jaws, or was even completely absent. This variation was observed both in juvenile and adult individuals. The extraoral plates are sometimes large, corresponding to about 1/3 of the length of the oral shield. The jaw plates (oral and adoral shields) are flattened in some specimens, differing from the typical pattern for this species (swollen plates). One specimen had one of the pairs of adoral shields fused, forming a single, slightly pentagonal plate, approximately of the same size as the oral shield. The ventral arm plate is be fragmented into two in few specimens. The primary plates are sometimes flattened and well developed or not evident, in which case the center of the disc is occupied by small scales of variable size and shape. In only one individual we observed the presence of one or two swollen scales (almost circular) between the radial shields. We observed five individuals with four- and two with six-fold symmetry (Fig. 9A–H) in the 325 studied specimens.

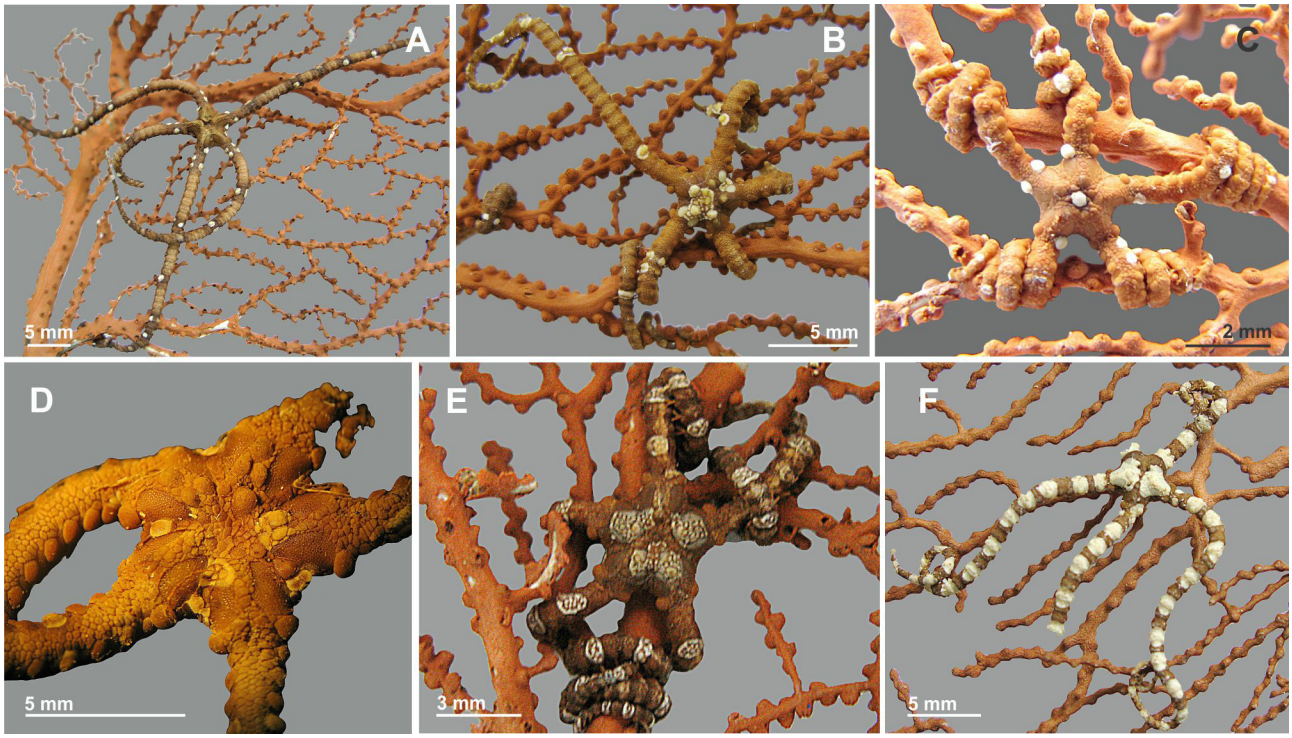

FIGURE 6. Some coloration patterns observed in specimens of *Hemieuryale pustulata*. **(A)** UFPB.ECH.2164; **(B)** UFPB.ECH.2170; **(C)** UFPB.ECH.2163; **(D)** UFPB.ECH.2162; **(E)** UFPB.ECH.2174; **(F)** UFPB.ECH.2172.

Color. *Hemieuryale pustulata* has a color similar to that of its host *Nicella guadalupensis* (Duchassaing & Michelotti, 1860), being reddish-brown (Fig. 6). The color pattern may vary from uniformly reddish-brown, reddish brown with white spots, to almost completely white with reddish-brown areas (Fig. 6A–F). This spotted pattern is extremely variable. Von Martens (1867) observed this same color pattern in the type specimens (Fig. 6C, D, E). Individuals of *H. pustulata* found associated with the octocoral *Verrucella* Milne Edwards & Haime, 1857 are reddish-brown or yellowish with white spots of variable shape and distribution (Verrill 1899b). Frequently some of the plates of the oral region are white.

Description of the juveniles (up to 3 mm dd). (UFPB.ECH.2175) Disc pentagonal (Fig. 10A, C) (dd = 1.5 mm), inflated, covered with strongly calcified and juxtaposed scales (Fig. 9A, C). Radial shields large (approximately half length of dd), triangular (Fig. 10A, C), largely separated by a row of scales which extend to the arm. Primary plates well developed, central and radials circular (Fig. 10A, C). These are the largest plates found on the disc. Interradius occupied by 3 or 4 scales (Fig. 10C). Bursal slits short and broad. One triangular apical papilla on tip of jaw. Four lateral oral papillae. Oral shield fan-shaped. Adoral shield large, slightly smaller than oral shields. Extraoral plate absent. Dorsal arm plate replaced by a mosaic of small plates (Fig. 10D). Dorsal plate on distal arm small, triangular. Lateral arm plate large, and tuberculous. Ventral arm plate pentagonal, distal margin wider. One arm spine with a crown of thorns at tip. Arm spines absent on two first arms segments. One large and rectangular tentacle scale.

Main differences between juveniles and adults. In general, juveniles are very similar to adults. The difference is that juvenile specimens (≤ 3 mm dd) have flattened scales on the disc and the accessory dorsal arm plate has not differentiated (Fig. 10). Usually juveniles are completely reddish-brown (as their octocoral host), the characteristic white spots observed in most adults being rare. Specimens larger than 2 mm dd already have accessory dorsal arm plates, but these are still not swollen. In these individuals only the first accessory dorsal arm plate becomes slightly hemispherical. Unfortunately, no postlarval stages were observed in this study.

Differentiation of the dorsal and accessory dorsal arm plates. In the beginning the dorsal and ventral surfaces of the arm are almost completely covered by the lateral arm plate (Fig. 11A). The lateral arm plate is large (corresponding to the full length of the arm segment) and they touch each other both dorsally and ventrally. Only in the distalmost portion do the two lateral arm plates become separate, forming a triangular opening in which the dorsal arm plate is inserted, forming a small triangular plate (Fig. 11A).Subsequently the dorsal arm plate

fragments into three plates (pc, pl I, and pl II) (Fig. 11B). Plates I and II (pl I-II) will differentiate into the accessory dorsal arm plate. After the first fragmentation, the central plate (pc) divides into four plates (pc^1, pc^2, pc^3, and pc^4) (Fig. 11C). Subsequently the plates formed from the first divisions continue to subdivide, giving rise to several plates of irregular shape and size (Fig. 11D). As the central plate divides into several other plates, the accessory dorsal arm plate is displaced to more lateral areas, becoming swollen posteriorly. At the end of the process of plate fragmentation the dorsal arm plate is replaced by a mosaic of small plates (Fig. 2E, 11E). In the adult arm segments it becomes impossible (without further experimental manipulation and more sophisticated topological marking techniques) to determine the central plate from which the final plates originated.

Distribution. Caribbean Sea (The Bahama Islands, Cuba, Jamaica, Dominican Republic, Martinique, Saint Lucia, Barbados, Grenada, Belize, Saba Bank – Netherlands Antilles, and Panama), Colombia (Emson & Woodley 1987; Alvarado 2011; Alvarado & Solís-Marín 2012), and Brazil (Fig. 7). In Brazil from Pará, Ceará, Rio Grande do Norte, Bahia, and Rio de Janeiro (Fig. 7). This study provides the first records for the Brazilian littoral.

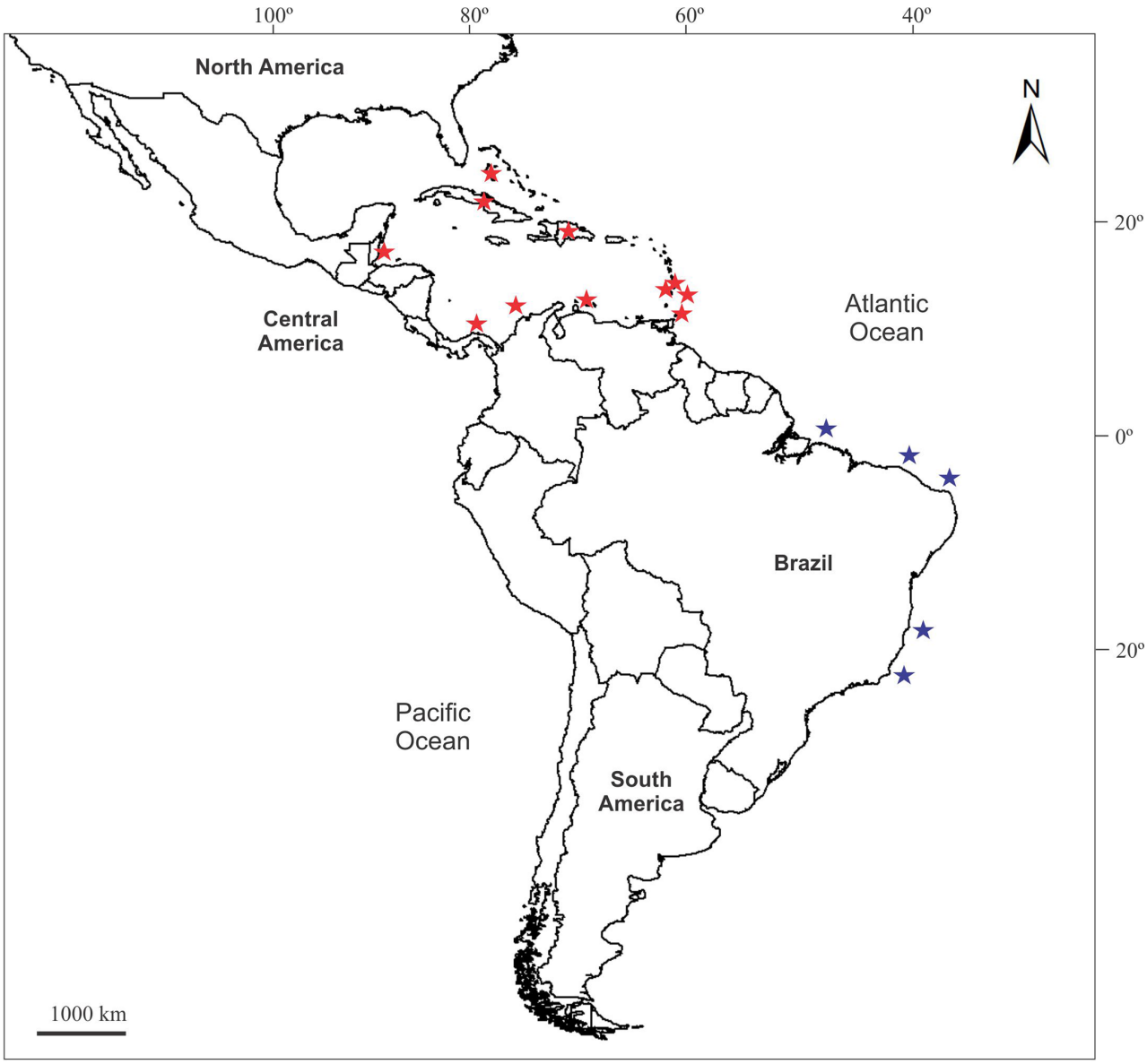

FIGURE 7. Geographical distribution of *Hemieuryale pustulata*. Red stars represent known records and blue stars represent new records.

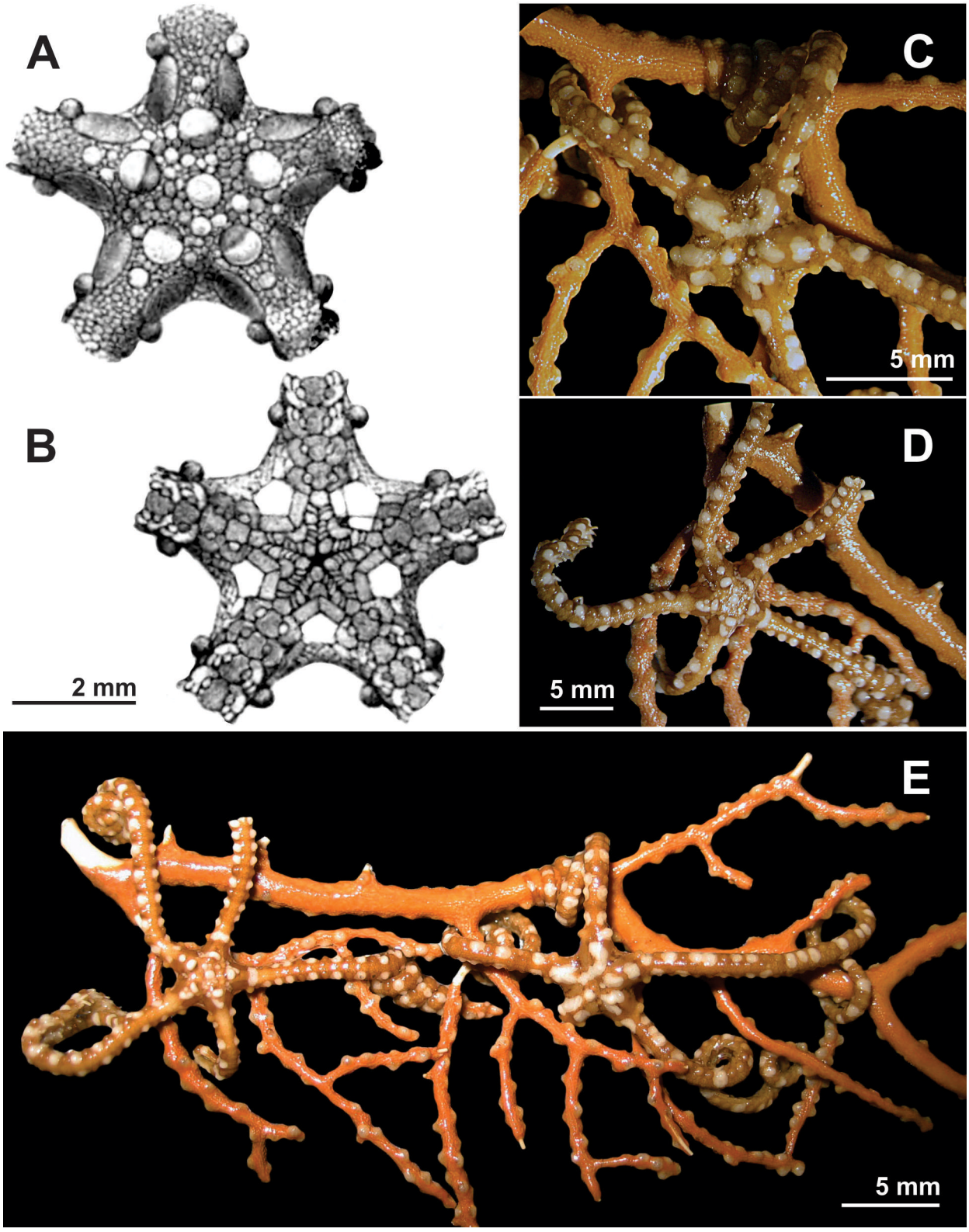

FIGURE 8. Images of type material of *Hemieuryale pustulata*. **(A–B)** Illustrations provided by von Martens (1867) in original description of species; **(C–E)** Photos of syntypes MZB 1739; **(C–D)** Detail of specimens; **(E)** Overview of specimens associated with octocoral. (Photos courtesy of C. Lüter)

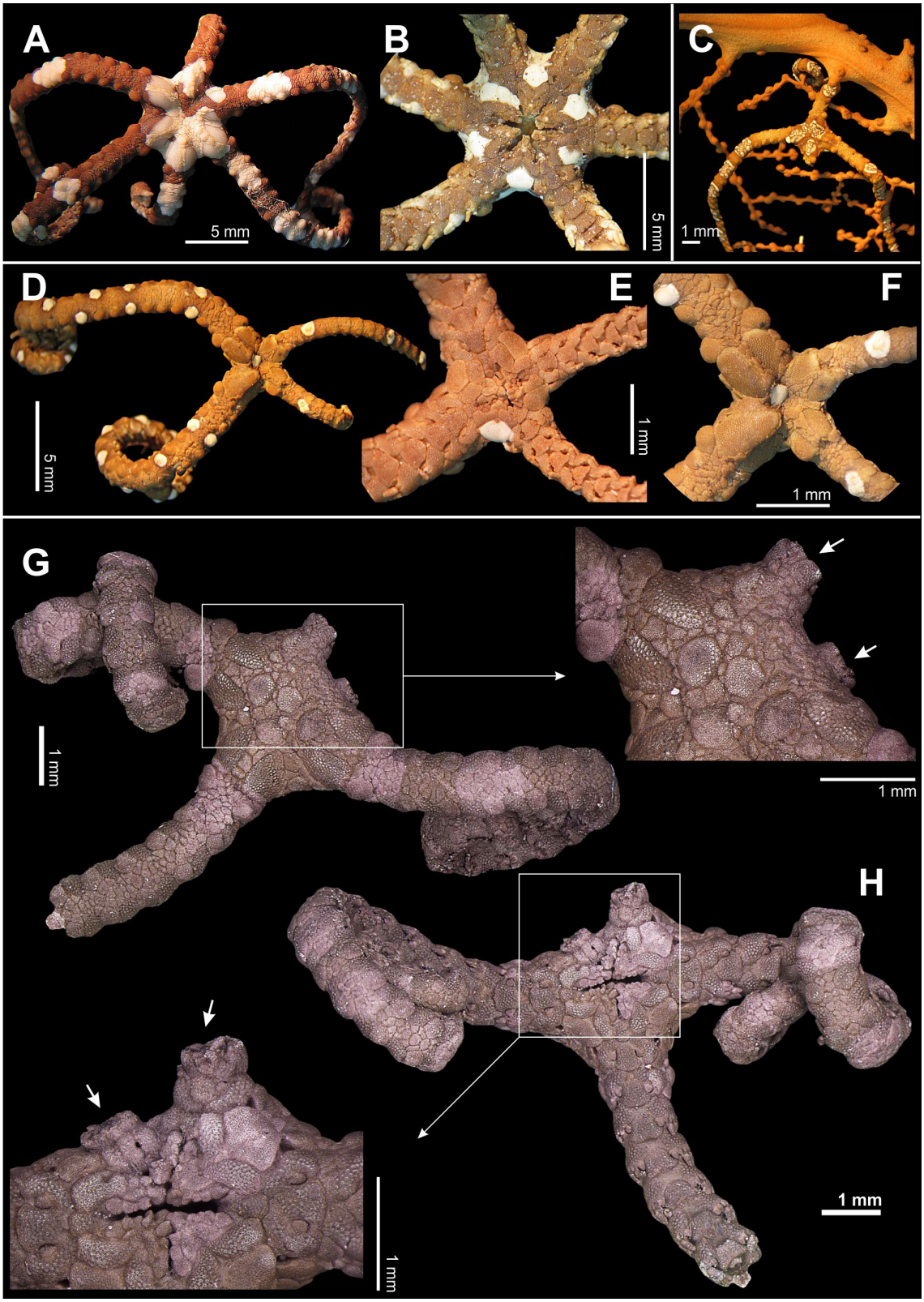

FIGURE 9. Tetramerous and hexamerous specimens of *Hemieuryale pustulata*. **(A)** Dorsal view of a specimen six-armed (UFPB.ECH.2175); **(B)** Ventral view of a hexamerous specimen; **(C)** Specimen with scars, suggesting predation attempts (UFPB.ECH.2174); **(D)** Dorsal view of tetramerous specimen (UFPB.ECH.2165); **(E)** Ventral view of tetramerous specimen; **(F)** Detail of disc of tetramerous specimen; **(F)** Dorsal view of the specimen with scars (arrows), suggesting predation attempts, detail of the disc (UFPB.ECH.2177); **(G)** Ventral view of the specimen with scars (arrows), suggesting predation attempts, detail of the disc.

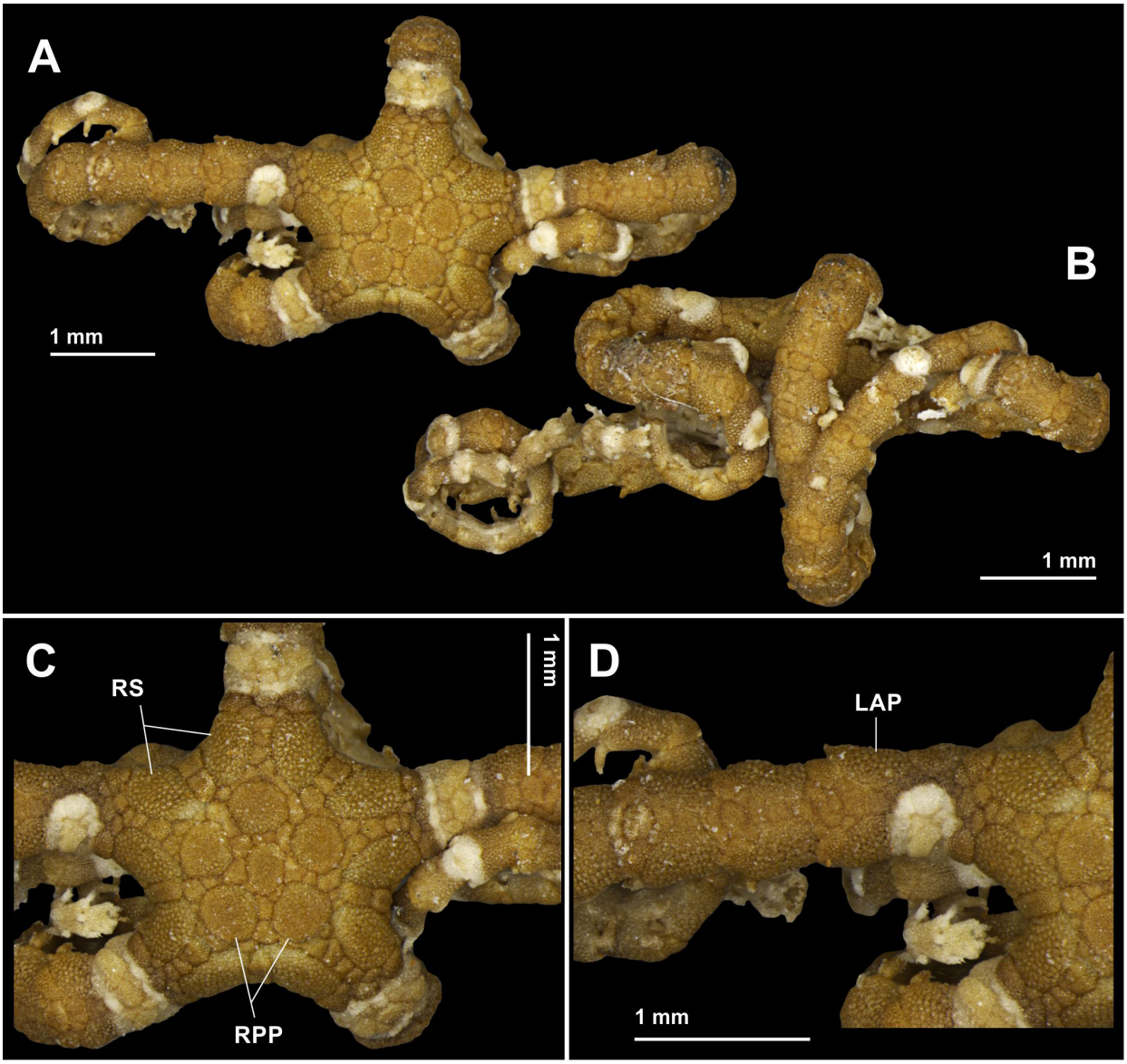

FIGURE 10. Morphological characters of a juvenile specimen of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** Dorsal view; **(B)** Ventral view; **(C)** Detail of disc in dorsal view; **(D)** Dorsal view of the arm. LAP: lateral arm plate; RPP: radial primary plates; RS: radial shield.

Depth range. From 18 to 330 m (Smithsonian Database; Verrill 1899b).

Remarks. Von Martens (1867) described this species on the basis of two specimens collected in the Antilles with a dd of 5 mm (Fig. 8). According to Verrill (1899b), *H. pustulata* is common in waters of moderate depth throughout the West Indies (Caribbean Sea), wherever *Verrucella* (as *Gorgonella* Nielsen) lives. Although this study represents the first record for Brazil, *H. pustulata* appears to be an abundant species across the littoral, at least in northeastern Brazil.

Insights on the ecology of *Hemieuryale pustulata*. Fifty-three gorgonians were observed, all belonging to the species *Nicella guadalupensis.* Their maximum length and width was 495 mm and 580 mm, respectively. Ophiuroids (Hemieuryalidae) were found on all collected gorgonians. A total of 251 specimens of *Hemieuryale pustulata* were recorded in association with these gorgonians, having a mean disc diameter of 2.91 mm (varying from 0.55 to 7.41 mm) (Table 1). Some individuals are clearly juveniles, strongly camouflaged and difficult to perceive on the gorgonian. Only 2.15% (n = 7) of the analyzed individuals had scars, suggesting predation attempts. The largest and smallest specimens with regenerated parts measured had 4.53 mm and 1.35 mm in dd, respectively.

TABLE 1. Data on the size (measured by disc diameter) and number of ophiuroid individuals found on each coral, collected on the continental shelf of Rio Grande do Norte State, northeastern Brazil. dd, disc diameter; H, height; No, running number; SD, standard deviation; Tsp, total number of specimens; W, width.

Gorgonian (*Nicella guadalupensis*)			Ophiuroid (*Hemieuryale pustulata*)		
No	H (mm)	W (mm)	dd (mm) of specimens	Mean (±SD)	Tsp
01	360	415	2.02–5.43	3.63 (±0.91)	14
02	360	360	1.59–4.45	2.78 (±1.09)	8
03	115	60	2.58–3.67	3.12 (±0.77)	2
04	155	130	1.35–4.49	2.92 (±2.22)	2
05	185	240	0.55–4.54	2.79 (±1.32)	8
06	290	230	2.31–4.68	3.81 (±0.72)	10
07	249	149	2.33–4.16	3.54 (±0.72)	5
08	290	240	2.12–4.47	3.20 (±0.68)	9
09	130	110	4.87	–	1
10	270	300	2.34–4.91	3.41 (±0.83)	12
11	130	110	1.80–3.97	2.65 (±1.15)	3
12	300	280	1.15–4.27	2.89 (±0.91)	13
13	270	280	3.46	–	1
14	260	200	2.75–4.28	3.46 (±0.77)	3
15	225	250	1.70–4.71	2.93 (±1.35)	4
16	120	85	1.27–4.90	3.08 (±2.56)	2
17	130	60	4.64	–	1
18	110	120	2.54–3.79	3.36 (±0.71)	3
19	97	110	2.63–3.53	3.08 (±0.63)	2
20	70	60	2.17	–	1
21	120	130	2.52–3.53	3.00 (±0.50)	3
22	95	65	2.92–3.40	3.16 (±0.33)	2
23	205	115	3.29	–	1
24	75	180	3.32–3.67	3.51 (±0.17)	3
25	107	580	1.68	–	1
26	150	160	0.96–5.74	3.35 (±3.37)	2
27	100	120	2.21–3.84	3.06 (±0.67)	5
28	160	260	1.88–4.77	3.40 (±0.88)	8
29	260	190	2.78–6.25	3.53 (±1.33)	6
30	260	180	3.53–4.44	3.98 (±0.64)	2
31	115	190	2.10–3.72	2.91 (±1.14)	2
32	300	325	1.14–4.34	2.91 (±1.22)	8
33	315	220	2.62–5.41	4.17 (±0.78)	9
34	190	185	3.55–4.36	4.04 (±0.43)	3
35	230	305	1.56–3.43	2.42 (±0.64)	10
36	310	110	3.21	–	1
37	160	95	2.51–4.15	3.31 (±0.82)	3
38	137	165	2.20–4.93	3.17 (±1.19)	5
39	190	180	2.59–3.85	3.20 (±0.53)	4
40	180	180	1.49–5.88	3.27 (±2.30)	3

.....continued on the next page

TABLE 1. (Continued)

Gorgonian (*Nicella guadalupensis*)			Ophiuroid (*Hemieuryale pustulata*)		
No	H (mm)	W (mm)	dd (mm) of specimens	Mean (±SD)	Tsp
41	315	430	4.31–5.63	5.14 (±0.72)	3
42	252	285	1.86–5.89	4.00 (±1.35)	9
43	385	370	1.08–3.62	2.41 (±1.27)	3
44	620	495	1.02–5.23	3.32 (±1.04)	30
45	130,2	130	4.22	–	1
46	480	560	1.85–4.90	3.71 (±1.12)	10
47	455	360	1.71–6.16	3.90 (±0.95)	26
48	325	225	5.32–7.41	6.16 (±0.98)	4
49	450	430	3.78–5.25	4.71 (±0.56)	5
50	610	275	3.06–5.69	4.36 (±0.77)	17
51	525	430	3.20–7.33	5.18 (±2.06)	3
52	590	420	1.53–5.47	3.58 (±1.45)	9
53	495	560	1.90–6.29	3.90 (±1.75)	15
Total number of specimens					251

Hemieuryale pustulata was present on 100% of the collected gorgonians, varying from one to 30 individuals on the same colony (mean of 5.9 individuals/gorgonian). Table 1 provides size data for the studied hemieuryalid individuals found on the analyzed gorgonians. In three colonies of *N. guadalupensis*, the presence of bivalves (family Pteriidae) and another species of ophiuroid (an unidentified Ophiacanthidae) were observed, in addition to *H. pustulata*. Comparing the studied gorgonians, we observed a significant difference in the abundance of *H. pustulata* among them (Pseudo-$F_{1\text{-}52}$ = 1.1614; p = 0.0016). Pearson's correlation showed a moderate relation between the number of individuals and the gorgonian area (p = 0.009; r = 0.351) (Fig. 10A). The majority of individuals were found on gorgonians with an area ranging from 0.004 and 0.2 m^2. However, there was no difference in the use of quadrants by individuals (Pseudo-$F_{1\text{-}52}$ = 1.8849; p = 0.3271), indicating no clear pattern of distribution regarding the place of occupation in the habitat (Fig. 1B).

Regarding size, individuals did not differ among the quadrants (Pseudo-$F_{1\text{-}52}$ = 1.088; p = 0.0327), suggesting the absence of distinct distribution patterns for juvenile and adult individuals across the host gorgonian. This result was similar to that found in another euryalid species, *Astrobrachion constrictum* (Farquhar, 1900) (Stewart & Mladenov, 1997). There was no correlation between the size of individuals and the area of the gorgonians (p = 0.09; r = 0.235) (Fig. 12B).

Discussion

A recent census counted 2065 species of ophiuroids known worldwide (Stöhr *et al.* 2012; Pineda–Enríquez *et al*. 2013). Many of these are only known from their original descriptions, not having been reported since, their current taxonomic status being unknown (Stöhr 2012). Under these circumstances, it becomes important to revise these taxa and to furnish new descriptions (including for example internal characters), more detailed illustrations and molecular data (genetic markers), in order to provide new data that may aid in phylogenetic reconstructions and in a more precise identification of species.

The poorly known genus *Hemieuryale* and its only known recent species *H. pustulata* forms a uniquely defined taxon based on the presence of the following characters: accessory dorsal arm plate swollen and hemispherical, and dorsal arm plate replaced by a mosaic of small plates. This genus is similar to *Sigsbeia*, from which it differs by the aspect of the dorsal arm plate, accessory dorsal arm plate, and in the shape of the arm spines (see description and remarks).

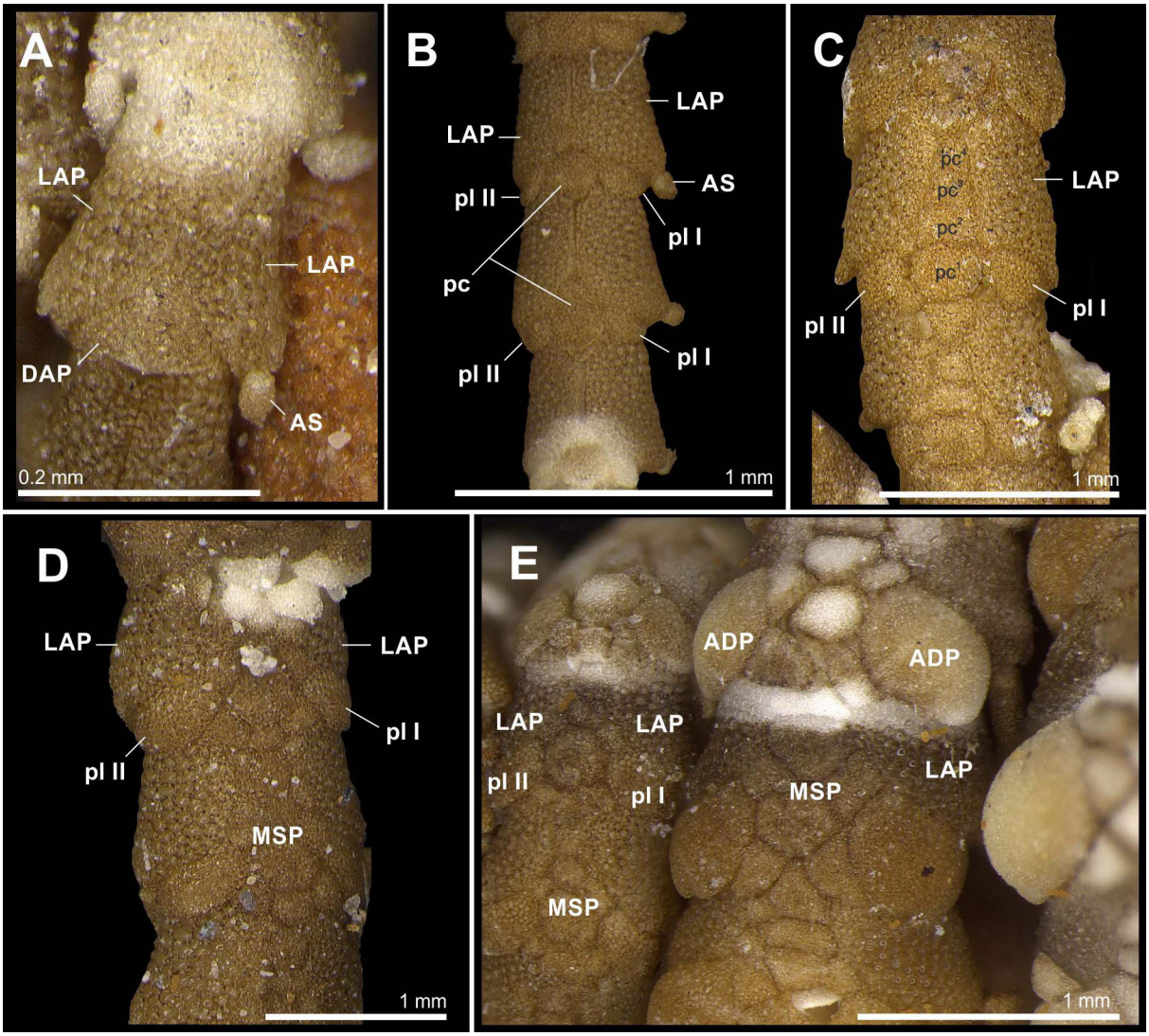

FIGURE 11. Dorsal view of the arms showing the process of differentiation of the dorsal and accessory dorsal arm plates in specimens of *Hemieuryale pustulata* (UFPB.ECH.2175). **(A)** First stage of dorsal arm plate; **(B)** Second stage of dorsal arm plate; **(C)** Beginning of formation of mosaic of plates; **(D)** Dorsal surface of the arm totally covered by a mosaic of plates; **(E)** Two distinct differentiation stages of arm plates (left: beginning of formation of mosaic of plates and accessory dorsal arm plate not swollen; right: mosaic of small plates totally formed and accessory dorsal arm plate swollen). AS: arm spine; DAP: dorsal arm plate; LAP: lateral arm plate; MSP: mosaic of small plates; pc: central plate; pl (I and II): lateral plates.

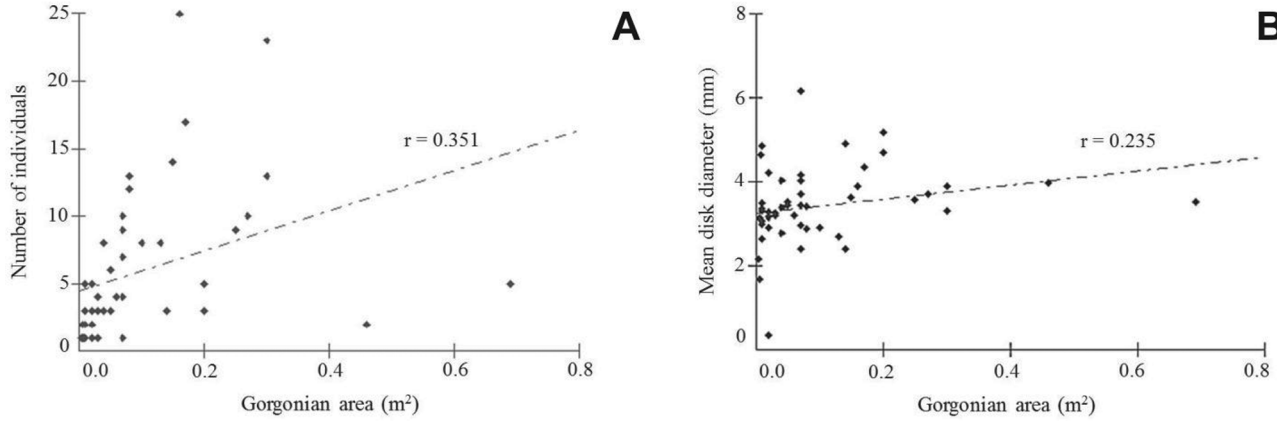

FIGURE 12. Pearson correlation between width **(A)** and height **(B)** of gorgonians and numbers of ophiuroids.

The dental plate of *Hemieuryale pustulata* (Fig. 5C) is very similar to the genus *Ophiolepis* Müller & Troschel, 1840 (compare to Murakami 1963: 13, pl. III, Fig. 28). The shape of the teeth and the dental plate sockets are characteristic for an apparently related group of genera and families (Martynov 2010). The phylogeny by O'Hara et al. (2014) suggests that the family Ophiolepididae as currently defined is a polyphyletic group from which at least the genera that are close to *Ophiomusium* Lyman, 1869 need to be removed. We thus regard Ophiolepididae in a restricted sense as the taxa close to *Ophiolepis*. It is plausible to consider a close relationship between Hemieuryalidae and Ophiolepididae Ljungman, 1867 (in particular *Ophiolepis*). According to Martynov (2010), ophiolepidid evolution towards massive disc and arm plates and streptospondylous vertebrae may have led to the appearance of the hemieuryalid taxa. Smith *et al.* (1995) suggested close affinities among Hemieuryalidae and some Ophiacanthidae, but their analysis included the genera *Ophiochondrus* and *Ophiomoeris* Koehler, 1904, which are now recognized as Ophiacanthidae (Stöhr et al. 2014; O'Hara et al. 2014). Considering our findings of morphological similarity of dental plates and arm spine articulation, strongly calcified endoskeletal plates, and extraoral plates with some species of *Ophiolepis* (Tania Pineda personal communications), we agree with the observation of Martynov (2010) that Hemieuryalidae is rather similar to the restricted Ophiolepididae. However, the phylogenetic relationships among several taxa of ophiurans still remain obscure. A taxonomic revision and phylogenetic analysis of Hemieuryalidae is under way in our lab.

Along the Brazilian littoral, *Hemieuryale pustulata* was found associated exclusively with the octocoral *Nicella guadalupensis*, suggesting the existence of an obligatory symbiotic association between these two species. In contrast to other species of brittle stars that live associated with octocorals, without permitting the colonization by any other organisms (e.g *Ophiocreas oedipos* Lyman, 1879), *H. pustulata* co-occurs with species of ophiuroids (Ophiacanthidae), bivalves, bryozoans, sponges and corals on the same colony. *Hemieuryale pustulata* was nevertheless the most abundant species, usually being distributed over the entire gorgonian. The color of *H. pustulata* is very similar to that of its host. Usually there are rows of white verruciform plates along the dorsal arms, resembling in size and color the verrucae of the coral, which has a brown ground-color, like that of *Hemieuryale* (Verrill 1899b). This color pattern makes *H. pustulata* almost imperceptible on the host colony, evidencing the strong mimicry of this species.

Hemieuryale pustulata reproduces sexually, as indicated by the presence of a large number of juvenile individuals in several colonies of *N. guadalupensis*. Nevertheless, our data are only visual. Studies of developmental biology are needed to confirm our observations. We also observed a small number of individuals (approximately 2.25% of specimens) clearly showing scars (Fig. 9C, G, H), evidencing an apparently low rate of predation on these individuals.

Similar to the observations of Mosher & Watling (2009) on *O. oedipus* and *Metallogorgia melanotrichos*, we also believe that the relationship between *H. pustulata* and *N. guadalupensis* is not mutualistic, since no benefit to the coral has been perceived. However, further studies are necessary to clarify this issue. Our data from the northeast coast of Brazil suggest that the occurrence of *H. pustulata* is strongly associated with the presence of the octocoral *N. guadalupensis*. Finally, we stress the high ecological relevance of octocorals as habitats on ocean bottoms, where they contribute directly to species richness and diversity in these environments.

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