

New species of the genus *Ophiolepis* Müller & Troschel, 1840 (Echinodermata: Ophiuroidea: Ophiolepididae)

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The aim of the present work is to report and describe three new species of the tropical brittle-star genus Ophiolepis. The new species are described herein as Ophiolepis aemulata sp. nov., Ophiolepis buitronae sp. nov. and Ophiolepis crebra sp. nov. As these species were previously misidentified, morphological traits and similarities between them and other species are extensively discussed. Ophiolepis buitronae sp. nov. is widespread in tropical and warm waters of the western Atlantic from intertidal to 36 m. It has consistently been misidentified as Ophiolepis impressa as these two species share a similar distribution and are found together. Ophiolepis aemulata sp. nov. is found in western Australia, as are its congeners Ophiolepis superba and Ophiolepis unicolor, while Ophiolepis crebra sp. nov. is found in Australia and Indonesia. There are 25 extant species, including the three new species, which are currently referred to the genus Ophiolepis.

Keywords: *Ophiolepis crebra*, *Ophiolepis aemulata*, *Ophiolepis impressa*, *Ophiolepis buitronae*, morphology, Ophiolepididae

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INTRODUCTION

Much research in recent years has been focused on obtaining accurate species inventories from different ecosystems. Even in the deep-sea (Woolley *et al.*, 2016), brittle-stars are abundant in all marine habitats. *Ophiolepis* Müller & Troschel, 1840 is a worldwide genus, mostly found in tropical oceans at shelf depths (<200 m) (Stöhr *et al.*, 2012). Species from the western Atlantic were thought to be well-known and have been extensively documented (Hendler, 1975, 1988; Hendler & Turner, 1987; Hendler *et al.*, 1995; Pomory, 2007), whereas many Indo-west Pacific species have been recorded only a few times.

The taxonomy of the genus *Ophiolepis* has undergone several revisions. The genus was first described by Müller & Troschel (1840), with *Ophiura annulosa* Blainville, 1834 (= *Ophiolepis superba* H.L. Clark, 1915) as the type species (see Clark & Melville, 1976 for designation of type species). Then, Lyman proposed the new genus *Ophiozonia* Lyman, 1865, closely related to *Ophiolepis*. The main difference between these genera was the absence of the accessory dorsal arm plates in *Ophiozonia*. Therefore, *Ophiolepis impressa* Lütken, 1859 and *Ophiolepis pacifica* Lütken, 1856 were transferred to this genus as well as several other species. However, Matsumoto (1917) redefined and restricted the genus *Ophiozonia* only to

Ophiolepis impressa and *Ophiolepis pacifica*. Subsequently, Devaney (1974) synonymized *Ophiozonia* with *Ophiolepis*, transferring these two species back to the genus *Ophiolepis*.

The recent descriptions of new species (Hendler, 1988; McKnight, 2003) have led to a reconsideration of the taxonomy of the genus as subgroups have been identified based on diagnostic external morphological characters. Hendler (1988) suggested that there are three clearly distinct groups of species restricted to the Western Atlantic. The first group includes *Ophiolepis ailsae* Hendler & Turner, 1987, *O. gemma* Hendler & Turner, 1987, *O. impressa*, *O. kieri* Hendler, 1979 and *O. paucispina* Hendler, 1988, which have a convex and narrow disc with several columns of dorsal interradial scales and arms that are rounded and tapering. The second group is composed of *Ophiolepis elegans* Lütken, 1859, *O. crassa* Nielsen, 1932 and *O. variegata* Lütken, 1856 and is characterized by flat, short and basally broad arms. The last group includes only *O. pawsoni* Hendler, 1988, in which the disc scales are irregularly arranged. Recent research on higher taxonomy of ophiuroids, based on morphological characters, have shown that many families (i.e. Ophiolepididae Ljungman, 1867, Ophiomyxidae Ljungman, 1867 and Ophiocomidae Ljungman, 1867) represent paraphyletic groups (Thuy & Stöhr, 2016). Similar results have been reported from genetic data (O'Hara *et al.*, 2017), highlighting the need to solve phylogenetic relationships at lower taxonomic levels.

As a result of the inconsistencies at higher taxonomic classification of brittle-stars and genetic data suggesting the

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existence of undescribed species in well-sampled regions (Bribiesca-Contreras *et al.*, 2013) a complete revision of the genus is being carried out by TPE. The aim of the present paper is to report and describe the new species discovered in the course of examining specimens as part of that extensive systematic revision. We describe three new species, *Ophiolepis aemulata* sp. nov., *O. buitronae* sp. nov. and *O. crebra* sp. nov., and provide modified diagnoses of *O. impressa* and *O. superba*, that separate them from their congeners *O. buitronae* sp. nov. and *O. crebra* sp. nov., respectively. We also include the designation of the neotype for *O. superba*, the type species of the genus.

MATERIALS AND METHODS

A total of 695 specimens from eight different species of the genus *Ophiolepis* were examined (see Appendix Table 1). See Pomory (2007), Hendler *et al.* (1995) and Stöhr *et al.* (2012) for a detailed description of main characters considered for brittle-star taxonomy; see Pineda-Enriquez *et al.* (2014) for relevant morphological characters of the genus.

The type material of each new species was photographed using a multifocal microscope (Olympus SZX12-MDU). Some specimens from the type series were exposed to undiluted bleach until ossicles separated, except for specimens of *Ophiolepis crebra* sp. nov., where due to the low number of specimens or their small size no internal structures were taken. All the different structures were mounted on aluminium stubs, gold coated and examined in a Hitachi S-2460N (Laboratorio de Microscopia, Instituto de Biología, Universidad Nacional Autónoma de México) or a Leica 440 (SEM Lab, National Museum of Natural History, Smithsonian Institution) scanning electron microscope (SEM).

List of institutional abbreviations:

AMNH: American Museum of Natural History, New York.

CAS: California Academy of Sciences, San Francisco, California.

FLMNH: Florida Museum of Natural History, University of Florida, Gainesville, Florida.

ICML-UNAM: Colección Nacional de Equinodermos Dra. María Elena Caso Muñoz, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, México.

LACM: Los Angeles County Museum, Los Angeles, California.

MCZ: Museum of Comparative Zoology, Harvard University, Boston, Massachusetts.

MNHM: National Museum of Natural History, Paris.

MV: Museums Victoria, Melbourne, Australia.

NSMT: National Museum of Nature and Science, Tokyo, Japan.

SMNH: Swedish Museum of Natural History, Stockholm, Sweden.

USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

YPM: Yale Peabody Museum of Natural History, Connecticut.

ZMUC: Zoological Museum, Natural History Museum of Denmark, Copenhagen.

ZMB: Zoological Museum of Hamburg, Germany.

RESULTS

SYSTEMATICS

Order OPHIURIDA Müller & Troschel, 1840

Family OPHIOLEPIDIDAE Ljungman, 1867

Genus *Ophiolepis* Müller & Troschel, 1840

TYPE SPECIES

Ophiolepis superba H.L. Clark, 1915 (a replacement name for *Ophiolepis annulosa* Blainville, 1834).

SPECIES INCLUDED

Ophiolepis affinis Studer, 1882; *Ophiolepis ailsae* Hendler & Turner, 1987; *Ophiolepis biscalata* McKnight, 2003; *Ophiolepis cardioplax* Murakami, 1943; *Ophiolepis cincta* Müller & Troschel, 1842; *Ophiolepis crassa* Nielsen, 1932; *Ophiolepis elegans* Lütken, 1859; *Ophiolepis fulva* H.L. Clark, 1940; *Ophiolepis gemma* Hendler & Turner, 1987; *Ophiolepis grisea* H.L. Clark, 1940; *Ophiolepis impressa* Lütken, 1859; *Ophiolepis irregularis* Brock, 1888; *Ophiolepis kieri* Hendler, 1979; *Ophiolepis nodosa* Duncan, 1887; *Ophiolepis pacifica* Lütken, 1859; *Ophiolepis paucispina* (Say, 1825); *Ophiolepis pawsoni* Hendler, 1988; *Ophiolepis plateia* Ziesenhenné, 1940; *Ophiolepis rugosa* Koehler, 1898; *Ophiolepis superba* H.L. Clark, 1915; *Ophiolepis unicolor* H.L. Clark, 1938; *Ophiolepis variegata* Lütken, 1856.

Ophiolepis aemulata sp. nov.

(Figures 1–3; Table 1)

TYPE MATERIAL

Holotype: One adult specimen preserved in ethanol. (East Arm Boat Ramp, off Port Darwin, Northern Territory, Australia; coordinates: 12°20'30.8"S 130°53'39.1"E; intertidal) (USNM 1224609); coll. 12 March 1986.

Paratypes: Three adult specimens preserved in ethanol. (East Arm Boat Ramp, off Port Darwin, Northern Territory, Australia; coordinates: 12°20'30.8"S 130°53'39.1"E; intertidal) (USNM 40093); coll. 12 March 1986, one of the specimens has been disarticulated for SEM images and ossicles are preserved on a SEM stub.

ETYMOLOGY

The specific epithet derives from the Latin word *aemulatus*, to copy or equal something, referring to the strong resemblance with the species *Ophiolepis superba*.

COMPARATIVE MATERIAL EXAMINED

Ophiolepis superba one adult specimen in 70% ethanol. (Zanzibar, Tanzania, Western Indian Ocean; coordinates: -6.028749° 39.473784°) (Neotype MCZ 143456); coll. G.A. Cheney and Caleb Cook, 1860–1865. Six adult specimens in 70% ethanol. (Zanzibar, Tanzania, Western Indian Ocean; coordinates: -6.028749° 39.473784°) (MCZ 803); coll. G.A. Cheney and Caleb Cook, 1860–1865. One adult specimen in 70% ethanol. (SOL4934 31BS18, Australia, Joseph Bonaparte Gulf; coordinates: 11°38.123'S, 129°49.288'E; water depth: 26 m) (MV F171194); coll. 12 September 2009. *Ophiolepis aemulata* sp. nov. one adult specimen in 70% ethanol. (East Arm Boat Ramp, Darwin Harbor, Northern Territory, Timor Sea, Australia; intertidal) (NMST 2026);

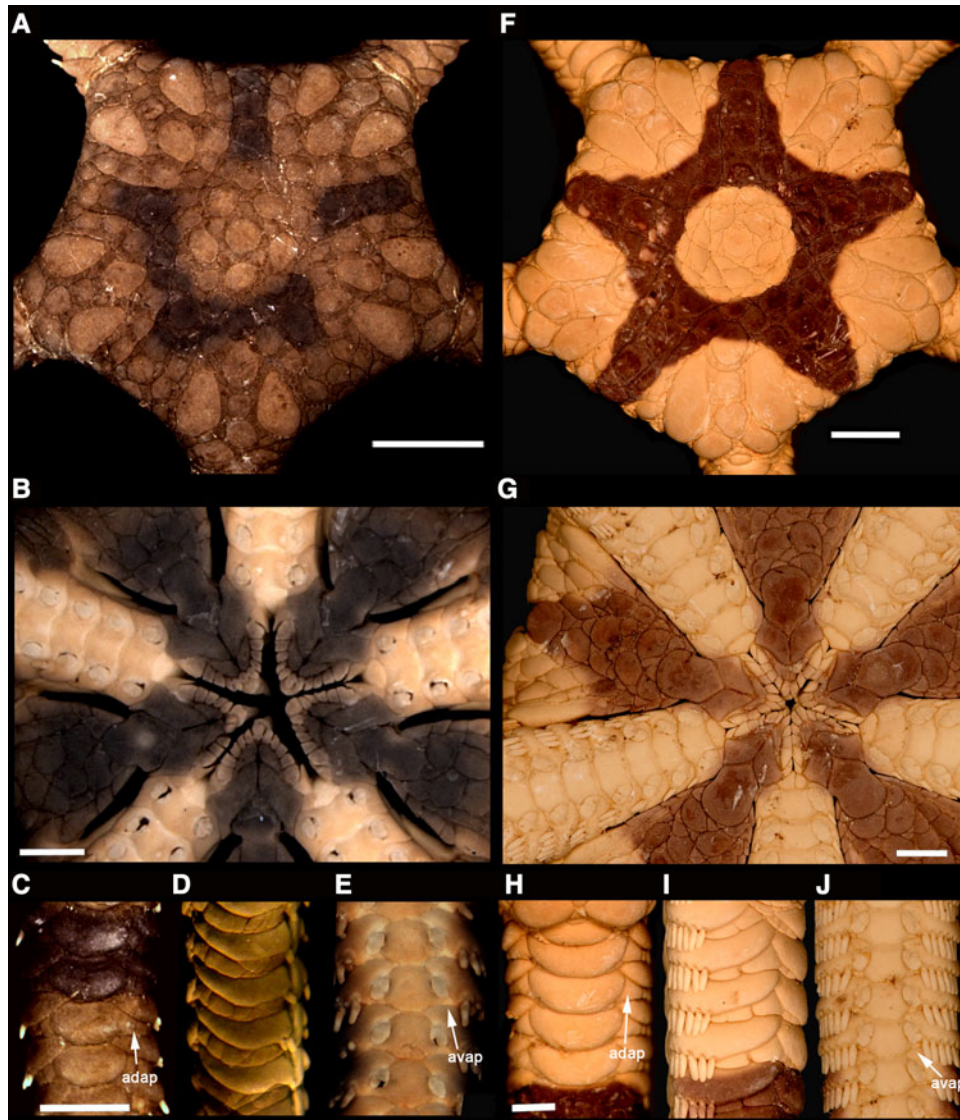


Fig. 1. Left: *Ophiolepis aemulata* sp. nov. Holotype USNM 1224609 (dd: 17 mm). Right: *Ophiolepis superba* Neotype MCZ 143456 (dd: 24 mm): dorsal disc surface (A, F); ventral disc surface (B, G); dorsal arm plates and ADAP (C, H); lateral arm plates (D, I) and ventral arm plates and AVAPs (E, J). Scale bars A, F, 5 mm; B–E, G–J, 2 mm.

coll. 12 March 1986. See Appendix for additional examined material.

DIAGNOSIS

Disc rounded-pentagonal, covered with numerous, flat, thin, larger scales slightly imbricated, with polygonal margins, surrounded by a continuous border of numerous smaller scales. Radial shields completely exposed, flat, irregularly triangular, almost twice as long as wide. Accessory dorsal arm plates fragmented in several pieces, extending from beneath the dorsal arm plates along the margin of the lateral arm plates and separating them. One small accessory ventral arm plate on each side between the lateral arm plate and the ventral arm plate, distal to the tentacle scales. Oral shields longer than wide, with concave lateral sides. Each jaw bears a single apical (ventralmost tooth) and five or six oral papillae. Lateral arm plates with two to four arm spines, rarely five, decreasing in size dorsally. Two tentacle scales, operculiform, attached to the lateral

arm plate; and two pairs of smaller tentacle scales around the rim of the pore, attached to the ventral arm plate.

HOLOTYPE DESCRIPTION

Disc diameter (dd) 17 mm; length of the longest arm (al) 46 mm (Figure 1). Disc rounded-pentagonal; dorsal surface flat, slightly elevated; ventral surface flat (Figure 1A). Interradius sloping ventrally from the lateral margin. Disc covers proximal eight arm segments. Arms stout, gradually tapering; dorsal surface rounded and ventral surface flat; arm tip finely tapered, dorso-ventrally flattened.

Disc covered with numerous flat, thin, large, irregular scales, completely separated from each other by a continuous row of slightly imbricated, irregular, smaller scales. Larger plates do not imbricate and are well separated by smaller scales. These scales are polygonal with irregular margins; central scales more rounded than the elongated scales at the interradius, which are ovoid and larger. Conspicuous central rosette; central plate the largest and rounded; radial plates

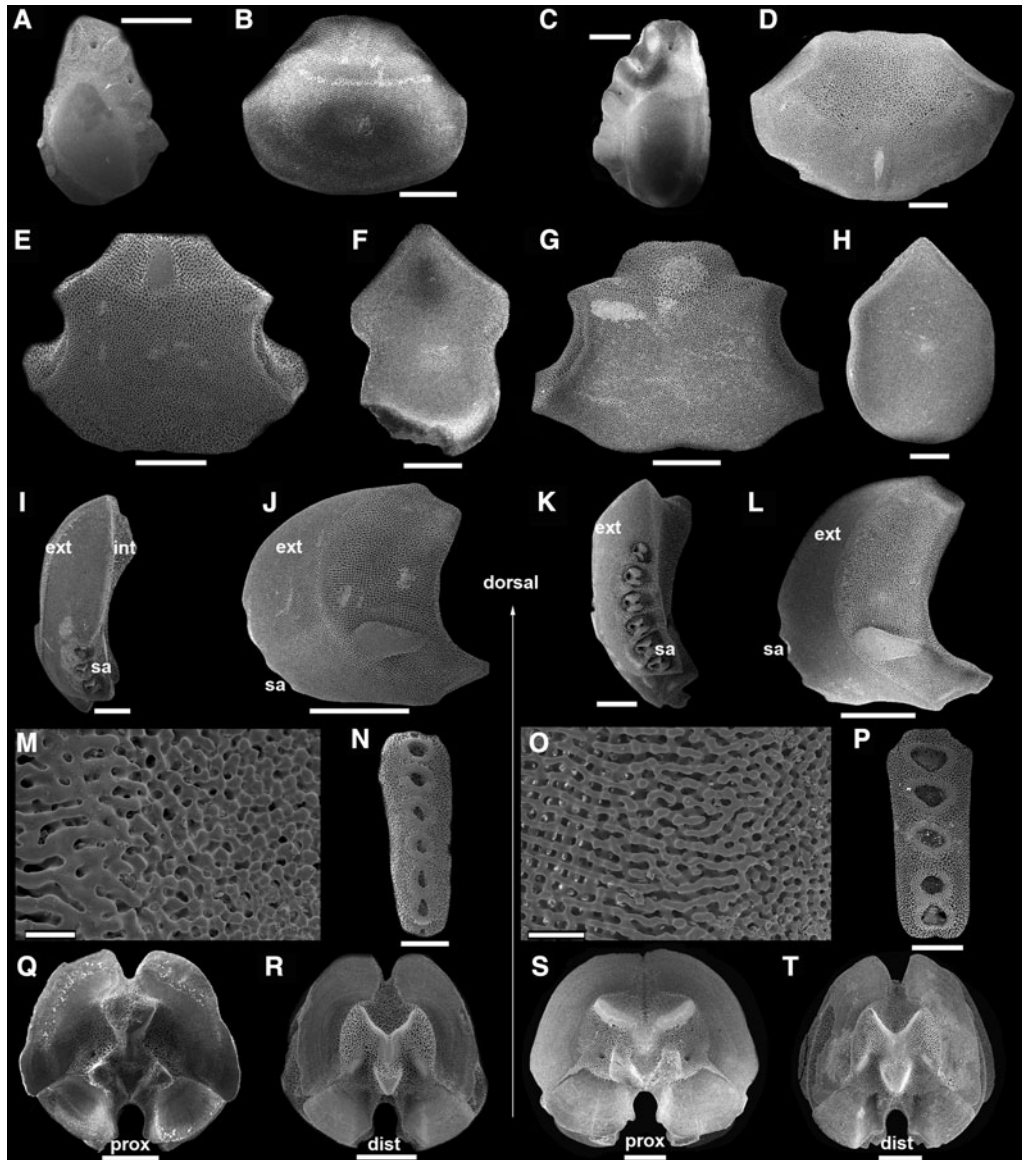


Fig. 2. Left: *Ophiolepis aemulata* sp. nov. Paratype USNM E40093 (dd: 17 mm), Right: *Ophiolepis superba* MCZ 803 (dd: 20 mm); radial shield, external aspect, proximal edge upwards (A, C); dorsal arm plate (B, D); ventral arm plate (E, G); oral shield (F, H); lateral arm plates, distal aspect with spine articulations (I, K) external aspect (J, L) and stereom structure (M, O); dental plate, external aspect, ventral downwards (N, P); arm vertebrae, dorsal upwards, proximal aspect (Q, S) and distal aspect (R, T). Scale bars A, C, 2 mm; B, D–L, N, P–T, 500 μ m; L, 100 μ m; and M, 50 μ m.

ovoid, five in number and surrounded by a continuous border of numerous smaller scales (which vary in shape and size). Dorsal interradii with three columns of larger scales; the central one radiates from each radial primary plate (Figure 1A). The central column has four large scales surrounded by smaller ones, which are darker than the rest of the scales creating a star-like pattern. Radial shields flat, at the same level of the disc scales, irregularly triangular, almost twice as long as wide, with convex abradial lobe, and widely separated by three large scales, the proximal one is the largest, the middle and distal scales are round, the latter is larger in size and has two adjacent scales at both sides, which are twice as wide as long and positioned diagonally outwards. There are nine larger scales surrounding each pair of radial shields, except at the distal edge.

Each jaw bears a single apical oral papilla (ventralmost tooth) and five oral papillae (Figure 1B). First and second

proximal papillae conical-shaped, third and fourth papillae quadrangular, as long as wide; distalmost the largest, elongated, attached to the adoral shield. Oral shields twice as long as wide, central region constricted; with an acute angle, rounded laterally; distal margin rounded and depressed. Madreporite with single, large hydropore. Adoral shields tumid; shaped almost like an isosceles triangle, twice as long as wide, with distal margin concave; lateral abradial margin somewhat convex; lateral adradial margin slightly concave; pairs contiguous interradially.

Genital slit extending from oral shield to the end of the fourth ventral arm plate, not extending to the border of the disc; bordered by three short genital plates at the distal end and by the lateral arm plates and smaller scales on the proximal end (Figure 1B). The abradial genital plate only visible from the distal end of the genital slit, almost three times as long as wide, and as long as three arm segments; it is

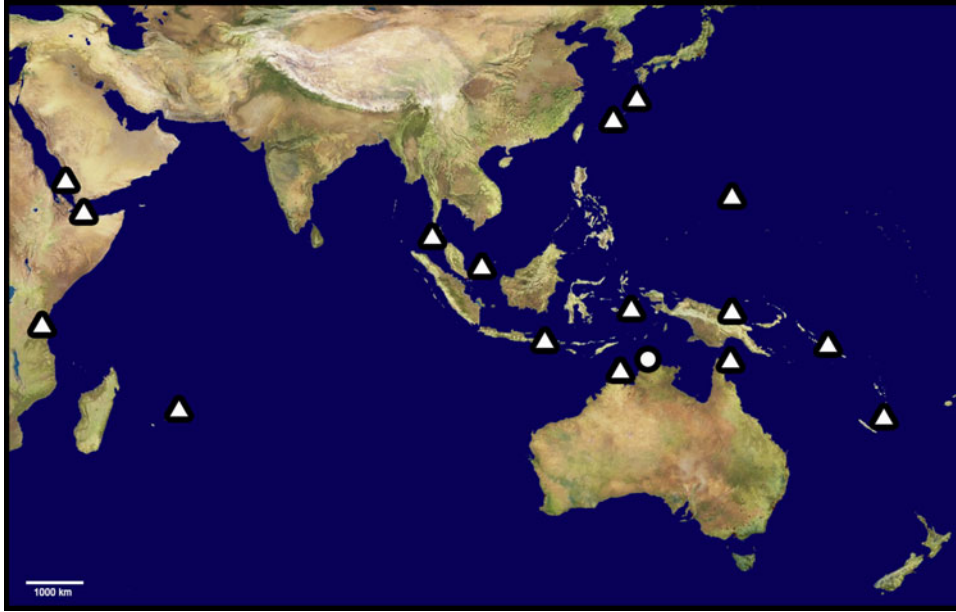


Fig. 3. Distribution map for *Ophiolepis aemulata* sp. nov. (○) and *O. superba* (Δ).

rounded on its proximal edge and pointed on its distal end, barely runs along the genital slit and it is separated from the arm by ventral disc scales. The adradial genital plate is only visible along the distal half length of the genital slit, it is narrow, shorter than two arm segments, and in contact with the arm and the distal genital plate. The abradial genital plate lies between the interradii disc scales and the scales at the base of the arm distally; it almost reaches the edge of the disc. Ventral interradius with some larger scales, partially surrounded by smaller ones.

Proximal dorsal arm plates (Figure 1C) are ovoid-shaped, thick, elevated distally; and separated from each other on the first few segments, the next arm plates overlapping,

concealing the proximal apex of the adjacent plate. The distal segments of the arm bear triangular dorsal arm plates, separated from each other by the lateral arm plates that are contiguous dorsally and ventrally. Accessory dorsal arm plates (ADAPs) large and fragmented into more than four small, irregular pieces which are arranged in a row that extends from beneath the dorsal arm plates, along the proximal and distal margins of the lateral arm plates, separating each arm segment laterally. Lateral arm plates (Figure 1D) are thick and elevated distally. Arm spines less than half of a segment in length, slightly tapering towards the tip; ventral-most spine largest and thickest, spines decreasing in size towards the dorsal surface. No arm spines on first and

Table 1. Comparison of morphological characters between *Ophiolepis aemulata* sp. nov., *O. unicolor* and *O. superba*.

	<i>O. aemulata</i> sp. nov.	<i>O. unicolor</i>	<i>O. superba</i>
Dorsal arm plates	Twice as wide as long, trapezoid-shaped, with distal border convex	Three times as wide as long, sub-rectangular to ovoid-shaped	Twice as wide as long, semilunar to ovoid-shaped, with distal border convex
Arm spines	3–4 (rarely 5)	5–7	6–7 (rarely eight)
Accessory dorsal arm plates	Fragmented into several pieces (>6), separating lateral arm plates along their entire margin, wide and thick, extending to ventral surface	Divided into 2–3 fragments, not separating lateral arm plates, not visible on ventral surface	Divided into 2–3 fragments, not separating lateral arm plates, not visible on ventral surface
Oral shields	Nearly as long as wide, arrowhead-shaped, laterally concave and convex distally	Nearly twice long as wide, pointed-shaped, laterally straight and convex distally	Nearly one quarter longer than wide; pointed-shaped, laterally straight and convex distally
Mouth papillae	Single apical papilla (ventralmost tooth), 5 pairs of oral papillae	Single apical papilla (ventralmost tooth), 4–5 pairs of oral papillae	4–5 pairs of oral papillae
Genital slit	3 segments of the arm	4 segments of the arm	6 segments of the arm
Colouration	Brown with dark brown patches in the interradius that sometimes connect to form a star-like pattern; arms with bandings	Dull uniform reddish brown; no arm banding	Deep buff with a well-defined deep purple star-like pattern; arms with bandings
Dorsal disc scales	With rounded to polygonal larger scales surrounded by polygonal-shaped (robust) smaller scales	With rounded larger scales surrounded by polygonal-shaped smaller scales	With rounded larger scales surrounded by rounded to polygonal-shaped smaller scales
Accessory ventral arm plate	Present	Present	Present

second segments, one spine on third to seventh segments, two spines on eighth segment, three spines on ninth and tenth segments, succeeding plates with three or four on each side, rarely five. Ventral arm plates (Figure 1E) overlapping; as long as wide on the first eight proximal arm segments; subsequent ventral arm plates slightly wider than long and somewhat hexagonal; distal ventral arm plates triangular and separated by lateral arm plates. Accessory ventral arm plates (AVAPs) are small, triangular, one on each distal edge of the ventral arm plates all across the length of the arm, which are inserted between the latter and the distal portion of the tentacle scales. Two tentacle scales forming ovoid operculum over each tentacle pore along the total arm length, attached to the lateral arm plates; first and second arm segments bearing a second pair of small tentacle scales around the rim of the pore, attached to the ventral arm plates; subsequent arm segments bear only one, but smaller scale on the inner part of each tentacle pore.

Paratype variation: The paratype series consists of three specimens (USNM E40093), with disc diameter: 17, 18 and 21 mm; and longest arm length: 36, 40, 47 mm, respectively. The morphology of the paratypes is nearly identical to that of the holotype. There are only slight variations in the extent of the dark brown patches on the dorsal surface of the disc. In some specimens the dark brown patches are connected to form a star-like pattern (specimens with dd: 17 and 18 mm), while in one of the other specimens, the patches are completely isolated from each other (specimen with dd: 21 mm). In the largest of the paratypes (dd: 21 mm) the oral shield is pointed proximally, with straight lateral edges and convex distal edge; with three tentacle scales on the first segment and two in all other segments; and no arm spines on the first six segments, one on the seventh to tenth segments, and variable on the rest of the segments (maximum of four spines). Additionally, one specimen (with dd: 17 mm), only has four oral papillae, instead of the five seen in the type and other paratypes (dd: 18 and 21 mm).

DISARTICULATED OSSICLES

Specimen analysed: one paratype USNM E40093 (dd: 17 mm). Radial shield (external view) irregularly triangular, with a raised smooth oval centre (visible part that is exposed, almost the entire radial shield) bordered by four pores in the proximo-abradial part (which is covered/overlapped by disc scales) (Figure 2A). Dorsal arm plate stout and somewhat oval-shaped, wider than long; distal and proximal edges rounded, but proximal half as long as distal, lacking spur on the proximal portion (Figure 2B). Ventral arm plate with proximal side truncated and with a spur, lateral side concave forming the border of the tentacle pore and with a conspicuous rim, distal side rounded (Figure 2C). Oral shield arrowhead-shaped, lateral borders slightly concave and distal side convex (Figure 2F). Lateral arm plate D-shaped, with three spine articulations along the distal aspect, each consisting of two parallel ridges (Figure 2I). The proximal edge of the outer lateral arm plate with a discernible band of different stereom structure, and one spur on the proximal edge (Figure 2J). The outer surface with equal and smooth stereom pores (Figure 2M). Dental plate thin and elongated, dorsal portion wider than ventral; with six ovoid to rounded tooth foramina, none of which perforates the plate (Figure 2N). Proximal vertebrae (Figure 2Q) almost quadrangular, with typical zygospondylous articulation, with

narrow muscle flanges and a V-shaped groove; distal view (Figure 2R).

COLOUR

Colour of specimen preserved in 70% ethanol (Figure 1); the dorsal side of the disc is brown with dark brown patches in the interradii, which sometimes connect to form a star-like pattern on the centre. The arms are banded with dark brown bands of two to three segments alternating with pale bands of four to six segments. The ventral side of the disc is dark brown all over. The ventral part of the arms is lighter in colour. Live colouration has not been recorded.

REMARKS

There are eight known species of the genus reported for the Indo-Pacific and Western Pacific regions, however this species is closely related to two of its congeners: *Ophiopsis superba* and *O. unicolor*. However, the distribution of *O. aemulata* sp. nov. is narrower and is not sympatric with any of these two species. Specimens of *O. aemulata* sp. nov. were first identified as *O. superba* due to its similarities, therefore differences between these are presented in Table 1. Records of juveniles or small size specimens of this species have not been found. *Ophiopsis aemulata* sp. nov. is easily recognized from its congeners by its colouration, the presence of two to four arm spines, five or more oral papillae and their distinct ADAPs that separate the lateral arm plates.

Ophiopsis superba H. L. Clark, 1915
(Figures 1–3; Table 1)

Ophiura annulosa. – Blainville, 1834: 244, pl. 24, figs 1–4.

Ophiopsis annulosa. – Müller & Troschel, 1840: 328; 1842: 89; Lütken, 1859: 100, 105, pl. II, fig. 5a, b; Lyman, 1865: 58; Studer 1882: 19; H.L. Clark, 1908: 289; Matsumoto, 1917: 300; A.M. Clark & Melville, 1976: 268.

Ophiopsis superba H.L. Clark, 1915: 89; 1921: 143; A.M. Clark & Rowe, 1971: 90, 128–129; Domantay & Domantay, 1966: 64–65; A.M. Clark & Melville, 1976: 269; Cherbonnier & Guille, 1978: 236–239; Stöhr et al., 2017.

TYPE MATERIAL

No type material or type locality has ever been designated for this species.

NEOTYPE

Based on the IZCN 2000, article 72.4.2 the type specimen should be the one illustrated by Blainville (1834) and misidentified as *Ophiura annulosa* Lamarck, 1816. This specimen was recognized by Müller & Troschel (1840) as a distinct taxon and placed in their new genus *Ophiopsis* as the new combination *Ophiopsis annulosa*. Two years later Müller & Troschel (1842) published a description of *Ophiopsis annulosa*, presumably based on specimens from the Red Sea deposited in collections in Germany and the Netherlands. Lyman (1865) designated *Ophiopsis annulosa* as the type species for the genus and listed two lots of specimens from Zanzibar. Subsequently, *Ophiopsis annulosa* was renamed as *O. superba* by H. L. Clark (1905a), and that combination was officially established as the type for the genus (H. L. Clark, 1915; A. M. Clark & Melville, 1976; International Commission on Zoological Nomenclature, 1981). Unfortunately, the whereabouts of the specimen illustrated by Blainville (1834) and those described by Müller & Troschel (1842) are unknown

or could not be located. The only specimens that were located were those described by Lyman (1865), which are deposited in the Museum of Comparative Zoology, Harvard University, Boston, MA, USA. Although Müller & Troschel (1842) and Lütken (1859) have made brief descriptions of the species as *Ophiolepis annulosa*, a proper diagnosis is still missing. Both descriptions emphasized the distinctive colour pattern of thick black to dark-purple bands on the arms and a star-like pattern or star-shaped ring on the disc, while the rest of the body varies from deep buff to dark brown (Müller & Troschel, 1842; Lütken, 1859). Despite this, a specimen not showing this pattern was described briefly by H. L. Clark (1915). Therefore, neotypification provides the only solution for the latter problem and will help clarify the identity of the species. Herein we designate a neotype from MCZ 803; seven specimens; Zanzibar, Tanzania, belonging to the specimens studied by Lyman (1865: 58) and which conform to the colour pattern of the species as described by Blainville (1834: pl. 24), Müller & Troschel (1842: 89–90), and Lütken (1859: pl. II, fig. 5a, b). Following the ICZN 2000, Article 75.3, the specimen MCZ 143456, one adult specimen preserved in ethanol, is designated as the neotype.

COMPARATIVE MATERIAL EXAMINED

Ophiolepis superba six adult specimens in 70% ethanol. (Zanzibar, Tanzania, Western Indian Ocean; coordinates: -6.028749° 39.473784° ; intertidal) (MCZ 803); coll. G.A. Cheney and Caleb Cook, 1860–1865. *Ophiolepis superba* one adult specimen in 70% ethanol. (SOL4934 31BS18, Australia, Joseph Bonaparte Gulf; coordinates: $11^{\circ}38.123'S$, $129^{\circ}49.288'E$; water depth: 26 m) (MV F171194); coll. 12 September 2009. See Appendix for additional examined material.

DIAGNOSIS

Disc rounded-pentagonal, covered with numerous, flat, thin, larger scales slightly imbricated, with rounded margins, surrounded by a continuous border of numerous smaller scales. Radial shields completely exposed, flat, irregularly triangular, almost twice as long as wide. Accessory dorsal arm plates fragmented in two or three pieces. Each jaw bears four or five oral papillae. Lateral arm plates with seven arm spines, rarely eight, decreasing in size dorsally. Two tentacle scales, operculiform, attached to the lateral arm plates, plus two smaller scales attached to the rim on the ventral arm plate.

NEOTYPE DESCRIPTION

Disc diameter 24 mm; length of the longest arm 57 mm (Figure 1). Disc rounded-pentagonal; dorsal surface flat, slightly sunken in the centre; ventral surface flat (Figure 1F). Disc covers proximal eight arm segments. Arms stout, gradually tapering; dorsal surface rounded and ventral surface flat; arm tip finely tapered, dorso-ventrally flattened.

Disc covered with numerous flat, thin, large, rounded scales, completely separated from each other by a continuous row of slightly smaller scales (Figure 1F). Larger scales do not imbricate and are well separated by smaller scales. These scales are rounded-shaped with regular margins; central scales more polygonal-shaped than the elongated and rounded scales at the interradii, which are ovoid and larger. Inconspicuous central rosette; central plate rounded; radial plates not distinguishable, the centre of the disc is delimited by a dark star-like pattern. Dorsal interradii with three columns of larger scales.

The central column has four large scales surrounded by smaller ones, varying in size and shape; which are darker than the rest of the scales (pale-yellow) creating a star-like pattern. Radial shields flat, at the same level of the disc scales, irregularly triangular, almost twice as long as wide, with convex abradial lobe, and widely separated by three large scales, the proximal one is the largest, the middle and distal scales are round, the latter is larger in size and has two adjacent scales at both sides (distally), which are twice as wide as long and positioned diagonally outwards.

Each jaw bears four (rarely five) oral papillae (Figure 1G). First and second proximal papillae papiliform-shaped, third and fourth papillae quadrangular, as long as wide. The distal-most is the largest, elongated, attached to the adoral shield. Oral shields twice as long as wide, central region constricted; with an acute angle and straight laterally; lateral margins straight; distal margin convex. Madreporite with single, large hydropore, larger than the rest of the oral shields. Adoral shields tumid, twice as long as wide, with distal margin straight; lateral abradial margin somewhat convex; lateral adradial margin slightly straight; pairs contiguous interradially.

Genital slit extending from oral shield to the end of the sixth ventral arm plate, not extending to the border of the disc (Figure 1G). The abradial genital plate only visible from the distal end of the genital slit, almost three times as long as wide, and as long as three arm segments; it is rounded on its proximal and distal edges, runs along the genital slit. Ventral interradii with numerous larger rounded scales, partially surrounded by smaller ones.

Proximal dorsal arm plates are ovoid to semi-circular; the next arm plates overlapping, concealing the proximal apex of the adjacent plate (Figure 1H). The distal segments of the arm bear triangular dorsal arm plates. ADAPs large and fragmented into two or three small, irregular pieces which are arranged along the proximal margin of the lateral arm plates. Lateral arm plates are thick and smooth (Figure 1I). Arm spines almost half the length of the arm segment, rounded; increasing in size ventrally (Figure 1J). No arm spines on first and second segments, one spine on third to seventh segments, two spines on eighth segment, three spines on ninth and tenth segments, succeeding plates with three or four on each side, rarely five. Ventral arm plates overlapping; as long as wide on the first eight proximal arm segments; subsequent ventral arm plates slightly wider than long and somewhat hexagonal; distal ventral arm plates triangular and separated by lateral arm plates (Figure 1J). AVAPs are small, triangular, one on each distal edge of the ventral arm plates all across the length of the arm, which are inserted between the latter and the distal portion of the tentacle scales (Figure 1J). Two tentacle scales forming an ovoid operculum over each tentacle pore along the total arm length, attached to the lateral arm plates; first and second arm segments bearing a second pair of small tentacle scales around the rim of the pore, attached to the ventral arm plate; subsequent arm segments bear only one, but smaller scale on the inner part of each tentacle pore.

DISARTICULATED OSSICLES

Adult specimen: MCZ 803 (dd: 20 mm, al: 54 mm); not the neotype MCZ 143456 in order to preserve the latter in the best condition; both specimens belonged to the same lot. Radial shield (external view) irregularly triangular, with a raised smooth oval centre (visible part that is exposed,

almost the entire radial shield) bordered by three pores in the proximo-abradial part (which is covered/overlapped by disc scales) (Figure 1C). Dorsal arm plate thick and oval-shaped, almost twice as wide as long; distal edge rounded; proximal and lateral edges straight; lacking spur on the proximal portion (Figure 1D). Ventral arm plate with proximal side elevated in the midline, nearly straight sides, lacking spur, lateral sides concave forming the border of the tentacle pore and with a conspicuous rim, distal side sinuous-shaped, with a slight midline depression (Figure 1G). Oral shield pointed proximally, lateral borders straight and rounded distally (Figure 1H). Lateral arm plate D-shaped, with six noticeable spine articulations along the distal aspect, each consisting of two parallel ridges (Figure 1K). The proximal edge of the lateral arm plate with a discernible band of different stereom structure, and one spur towards the ventral surface. The outer surface with equal and smooth stereom pores (Figure 1O). Dental plate thin and elongated and somewhat quadrangular in shape, dorsal portion slightly wider than ventral portion; with five ovoid to rounded tooth foramina, none of which perforates the plate (Figure 1P). Proximal vertebra slightly longer than wide (Figure 1S), with typical zygospondylous articulation, narrow muscle flanges and a V-shaped groove; distal view (Figure 1T).

COLOUR

Colour of specimen preserved in 70% ethanol (Figure 1F); the dorsal side of the disc is deep buff with a deep-purple star-like pattern on the centre and interradial. The arms are banded with deep-purple bands of seven to eight segments alternating with pale bands of seven to eight deep buff (same colours as the disc); these bands are only present on the dorsal and lateral surface of the arms, not ventrally. The ventral side of the disc is deep-purple all over the jaws and interradial, with a star-like pattern. The ventral part of the arms is deep buff.

DISTRIBUTION

Specimens of this species have been found Zanzibar, Tanzania, Africa (Lyman, 1865); Ceylon, Sri Lanka (H.L. Clark, 1915); Saudi Arabia, Red Sea; Djibouti; Ambon Island and Gili Island, Indonesia; Pulau Tioman, Malaysia; east of Phuket, Thailand; Solomon Island; Gulf of Carpentaria and Gulf of Joseph Bonaparte Australia; Okinawa Island, Japan; Papua New Guinea; Mariana Island, Guam and Lifou, New Caledonia up to 50 m depth (Figure 3). The distribution that we present here is based on the specimens we revised and that certainly belongs to this species.

REMARKS

Ophiolepis superba is a well-known species from the Indo-Pacific region, its relatively large size and distinct colouration pattern make it relatively easy to recognize both in the field and in collections. Specimens with a dd of 7 mm or less tend to have five arm spines that are relatively small and seem to lack the AVAP. In specimens larger than 10 mm dd, this plate is either rudimentary or absent. This species is closely related to two of its congeners from the Indo-Pacific: *O. unicolor* and *O. aemulata* sp. nov. Differences between these species are presented in Table 1.

Ophiolepis buitronae sp. nov.
(Figures 4–6, Table 2)

TYPE MATERIAL

Holotype: One adult specimen in 70% ethanol (Isla Sacrificios, Veracruz, Veracruz, Mexico; 19°18.4'N 96°09.242'W; 7–10 m depth, scuba); (ICML-UNAM 3.122.56) coll. F.A. Solís-Marín, 8 March 2005.

Paratypes: One adult specimen in 70% ethanol (Isla Lobos, Tamiagua, Veracruz; 21°28.362'N 97°13.876'W; 12 m depth, scuba) (ICML-UNAM 3.122.73); 17 March 2011. One adult specimen, dried (Bajo Grande, San Bernardo Archipelago, Bolívar, Colombia; 09°44.522'N 75°41.98'W; 5.4 m depth) (ICML-UNAM 3.122.55); coll. 14 July 2004. Six adult specimens dried (Bizoton, Haiti) (MCZ 6259); coll. 1927. One adult specimen in 75% ethanol (Tennessee Reef, Florida Keys, Monroe County; 6 m depth) (UF 10269); coll. F. Michonneau, G. Paulay, S. McPherson, M. Bemis, H. Lin, J. Moore and N. Evans, 3 May 2010. One adult specimen in 80% ethanol (Rocroy sud, Guadeloupe Island, Lesser Antilles; 27 m depth) (UF 13765); coll. L. LeGall, Y. Buske and Y. Turpin, 10 May 2012. One adult specimen in 70% ethanol (SW side of Isla Uva, off Puerto Limon, Limon Province, Costa Rica; 6 m depth) (LACM E.1987-60.22); coll. G. Hendler, 1987. One adult specimen in 85% ethanol (SE Rendezvous Cay, Belize District, Belize; 4 m depth) (LACM E.1999-9.19); coll. G. Hendler, 1999. Six adult specimens in 70% ethanol (Looe Key National Marine Sanctuary, Inter-Mediate Deep Reef at Buoy #28, Florida Keys, Florida; 14 m depth) (USNM E37706); coll. G. Hendler; 7 May 1985.

ETYMOLOGY

Named after an extraordinary echinoderm palaeontologist, Dra. Blanca Estela Buitrón Sánchez, researcher of the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM).

COMPARATIVE MATERIAL EXAMINED

Ophiolepis buitronae sp. nov. two adult specimens in 70% ethanol (SE of Key Largo, Florida Reefs, Unnamed Reef, Monroe Co, Florida, USA; coordinates: 25.011 N 80.36933 W; 12.1 m depth) (LACM E.2011-4.2); coll. G. Hendler, 31 March 2011. Two adult specimens in 75% ethanol (Port Louis, entrée grotte aux barracudas, Guadeloupe Island, Lesser Antilles; coordinates: 16.4557, -61.5345W) (UF 13764); coll. Buske, Yan; Vassard, Emmanuel, 15 May 2012. See Appendix for additional examined material.

DIAGNOSIS

Disc sub-pentagonal to rounded; dorsal surface rough; covered with thick, large, imbricated scales, arranged in three columns in each dorsal interradial. Radial shields depressed, with uneven surface, irregularly triangular, longer than wide. Accessory dorsal arm plates small (rudimentary), one on each distal edge of each dorsal arm plate, and inserted between the latter and the lateral arm plate. Oral shields longer than wide. Each jaw bears a single apical (ventralmost tooth) and four oral papillae. Arm spines usually four on each side of an arm segment, rarely five. Lacking accessory ventral arm plates.

HOLOTYPE DESCRIPTION

Disc diameter 13 mm; length of the longest arm 63 mm (Figure 4). Disc sub-pentagonal to rounded; dorsal surface rough, slightly convex with the central region slightly

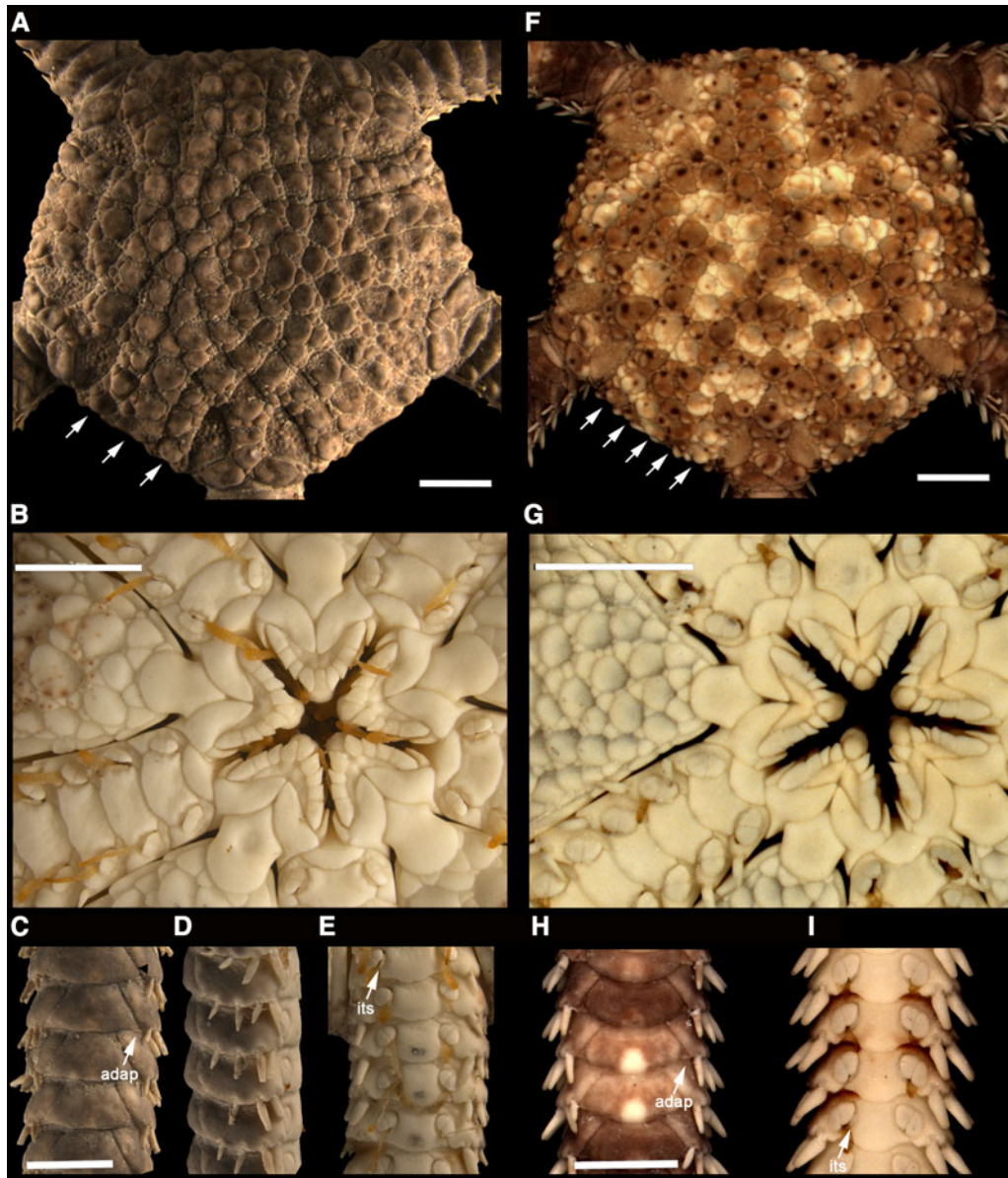


Fig. 4. Left: *Ophiolepis buitronae* sp. nov. Holotype ICML-UNAM 3,122.56 (dd: 13 mm); Right: *Ophiolepis impressa* Lectotype ZMUC NHMD 141838 (dd: 13 mm); dorsal disc surface (A, F); ventral disc surface (B, G); dorsal arm plates and ADAP (C, H); lateral arm plates (D); ventral arm plates and inner tentacle scales (its) (E, I). Scale bars A, B, F and G 5 mm, C–E and H–I, 2 mm.

sunken; ventral surface flat (Figure 4A). Disc covers proximal six arm segments. Arms slender, gradually tapering; dorsal surface rounded and ventral surface flat; arm tip finely tapered, dorso-ventrally flattened.

Disc covered with numerous thick, large, imbricated scales, with angular margins and straight edges joined at obtuse angles, elevated distally and sunken proximally (Figure 4A). Smaller irregular scales surrounding larger ones. Primary rosette barely distinguishable; central plate the smallest, surrounded by a continuous border of one row of numerous smaller scales (which vary in shape and size). Radial shields depressed, with uneven surface, irregularly triangular, longer than wide, with a slight abradial lobe, and widely separated by three larger scales, the proximal one is largest, the middle one is rectangular, wider than long, and the distal scale is rounded-triangular and has two adjacent scales at both sides, which are wider than long and positioned diagonally

outwards. Dorsal interradial with three columns of larger scales; central column with four scales equal to or larger than the four scales of each lateral column.

Each jaw bears a single apical oral papilla (ventralmost tooth) and four oral papillae (Figure 4B). First and second proximal papillae papilliform, third papillae quadrangular. The distalmost is the largest, with broadly rounded lateral margins, attached to the adoral shield. Oral shields longer than wide, central region depressed; proximal edge pointed and concave on both sides; lateral margins slightly concave; distal margin convex, nearly semicircular. Madreporite with single, large hydropore. Adoral shields with concave proximal side and convex distal side; distal edge pointed; lateral margin slightly concave; proximal margin pointed; pairs touching interradially. Genital slit extending from oral shield to fifth ventral arm plate; bordered by a long distal genital plate and two small scales proximally. Ventral interradial with few

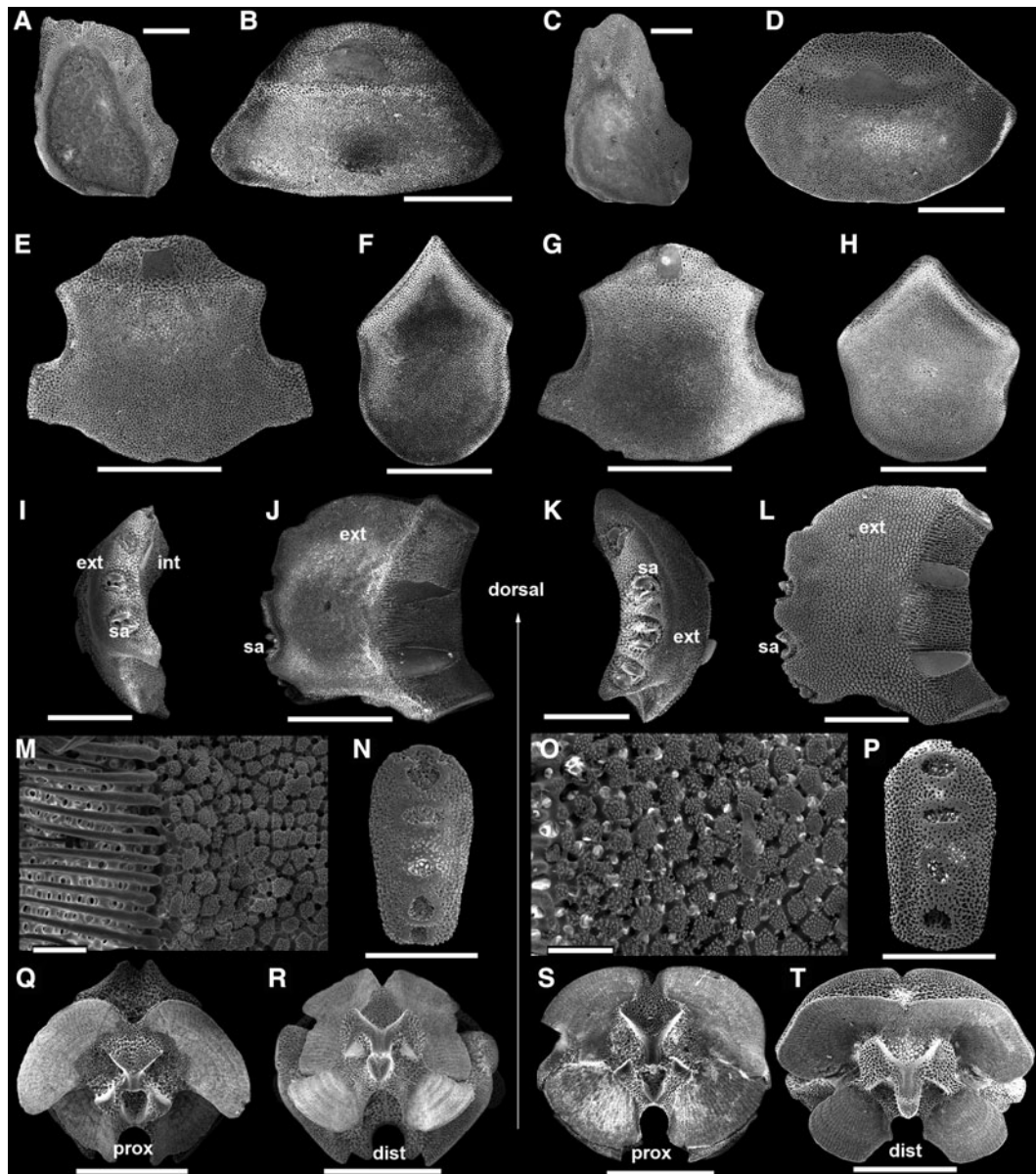


Fig. 5. Left: *Ophiolepis buitronae* sp. nov. Paratype USNM E37706 (dd: 8 mm), Right: *Ophiolepis impressa* USNM E37646 (dd: 9 mm); radial shield, external aspect, proximal edge upwards (A, C); dorsal arm plate (B, D); ventral arm plate (E, G); oral shield (F, H); lateral arm plates, distal aspect with spine articulations (I, K), external aspect (J, L) and outer surface ornamentation (M, O); dental plate, external aspect, ventral downwards (N, P); arm vertebrae, dorsal upwards, proximal aspect (Q, S) and distal aspect (R, T). Scale bars A, C, 1 mm; B, D–L, N, P–T, 500 μ m; M, O, 300 μ m.

larger imbricated scales, surrounded by smaller ones; the largest of them centred and near the margin.

Proximal dorsal arm plates trapezoid with straight margins except the distal one, which is rounded; neighbouring plates overlap, concealing proximal apex of the previous plate (Figure 4C). ADAPs small (rudimentary), one on each distal edge of each dorsal arm plate, and inserted between the latter and the lateral arm plate. Lateral arm plate stout, slightly thicker distally (Figure 4D). Arm spines stout; base and middle thick, gradually narrowing to blunt point; one on first three segments, two on fourth segment, three on fifth segment, and four (rarely five) on subsequent segments distally. Ventralmost spine the longest, more than half the length of the arm segment, and thicker than the dorsal most spine, spines decrease in size towards the dorsal surface; dorsal arm-spines are thinner and pointed, and as long as

one third of the segment length. Ventral arm plates overlapping; twice as wide as long on the first four proximal arm segments; subsequent ventral arm plates as wide as long; distal arm plates triangular and separated by lateral arm plates (Figure 4E). Two tentacle scales attached to lateral arm plates, forming an ovoid operculum over each tentacle pore along the total arm length; first and second arm segments bearing a second pair of tentacle scales attached to the ventral arm plate; subsequent arm segments bearing one smaller rim-like scale attached to the ventral arm plate.

DISCARTICULATED OSSICLES

Specimen analysed: one Paratype USNM E37706 (dd: 8 mm). Radial shield (external view) irregularly triangular, with a rough and sunken centre (visible part that is exposed, almost the entire radial shield) bordered by a groove all

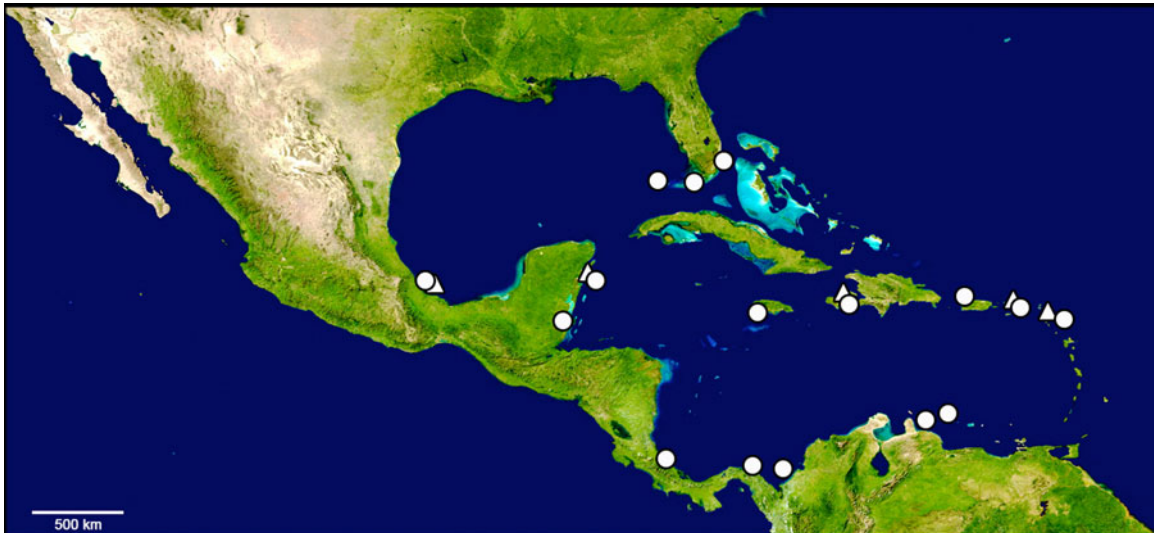


Fig. 6. Distribution map for *Ophiolepis buitronae* sp. nov. (Δ) and *O. impressa* (\circ).

around with three pores in the proximo-abradial part (which is covered/overlapped by disc scales) (Figure 5A). Dorsal arm plate trapezoidal, proximal margin slightly convex with a spur, distal and lateral margins straight (Figure 5B). Ventral arm plate wider than long; proximal edge is truncated and with a spur, slightly depressed at the centre, distal lateral edges are tumid at their distal portion, which forms the edge of the tentacle pore; distal edge is slightly rounded but with a small notch at the centre (Figure 5E). Oral shield almost twice as long as wide, pointed proximally, lateral sides slightly concave, distal side rounded (Figure 5F). Lateral arm plate D-shaped, with four spine articulations along the distal aspect, each consisting of two parallel ridges (Figure 5J). External view of lateral arm plate; proximal edge has a discernible band of different stereom structure, with horizontal striations and two spurs (Figure 5J). The outer surface with spiny stereom pores (Figure 5M). Dental plate sub-oval in outline, dorsal portion wider than the ventral portion, with five tooth foramina, none of which perforates the plate; the third and fourth foramina dorsal to ventral are ovoid while the rest are almost circular (Figure 5N). Proximal vertebra (Figure 5Q) with typical zygospondylous articulation, slightly elongated, with wing-like muscle flanges and U-shaped groove, distal view (Figure 5R).

COLOUR

Live colouration is either all dark brown or with a specific pattern; the disc being reddish light brown, with dark brown scales surrounding the primary disc plates and the radial shields. The arms are light brown with a banded dark brown pattern. Ventral surface is very light in colour, as well as the arm spines. Dried specimens are darker on the dorsal surface and the colouration pattern is less conspicuous but still evident. Specimens preserved in ethanol have the same colouration as live ones.

REMARKS

There are seven other ophiolepidid species in the Western Atlantic (*Ophiolepis ailsae*, *O. elegans*, *O. gemma*, *O. impressa*, *O. kieri*, *O. paucispina* and *O. pawsoni*). *Ophiolepis buitronae* sp. nov. possesses three rows of larger scales on each dorsal interradius, similar to *O. ailsae*, *O. gemma*, *O. kieri* and *O. paucispina*, but the larger scales on these species are not as thick as on *O. buitronae* sp. nov. Also, they are slightly convex in *O. ailsae*, *O. gemma*, *O. kieri* and *O. paucispina*. *Ophiolepis elegans* differs in having a single row of flat, larger scales. In comparison *O. pawsoni* has a different arrangement of dorsal disc scales, in which the thin intercalary scales are rare, thus the disc is mostly covered by large, thick,

Table 2. Comparison of morphological characters between *Ophiolepis buitronae* sp. nov. and *O. impressa*.

	<i>O. buitronae</i> sp. nov.	<i>O. impressa</i>
Dorsal disc scales (adults)	Thick, large and imbricated, elevated distally, sunken proximally	Numerous, large and imbricated scales
Dorsal interradius	With three columns of larger scales	With five columns of larger scales
Dorsal arm plates	Trapezoid-shaped, with straight distal edge	Trapezoid-shaped, sinuous to convex distal edge
Accessory dorsal arm plate	Rudimentary	Rudimentary
Ventral disc scales	Few imbricated scales	Numerous imbricated scales
Arm spines	4 (rarely 5)	4
Oral shields	Longer than wide, proximal edge pointed with concave borders, lateral edge concave and distal end convex (semicircular)	As long as wide, proximal edge pointed with concave borders, lateral edge straight and distal end semicircular
Tentacle scales	Two, equal size	Two, abradial longer than adradial
Accessory ventral arm plate	Absent	Absent

round to ovoid scales. *Ophiolepis buitronae* sp. nov. is clearly distinguished from its closest Western Atlantic congener not only by its unique colour pattern (which is darker than *O. impressa*, with more prominent arm-banding; Figure 4) but also by consistently thicker disc scales which are somewhat rounded, swollen, with thicker borders and uneven surface; by the presence of radial shields with an uneven surface and fewer scales in each ventral interradius. The most conspicuous difference is the presence of three columns of well-defined interradiial disc scales in *O. buitronae* sp. nov., rather than the five irregular columns of disc scales in each interradius present in *O. impressa*.

Specimens of this species can be distinguished from *O. impressa* even when the disc is as small as 5 mm in diameter. On smaller specimens, three rows of dorsal interradiial disc scales are present in both species. Nevertheless, disc scales of *O. buitronae* sp. nov. are thicker even at that size, and the dorsal surface of the disc on its congeners has more disc scales. Differences between *O. impressa* and *O. buitronae* sp. nov. are presented in Table 2.

Ophiolepis impressa Lütken, 1859

(Figures 4–6, Table 2)

Ophiolepis impressa Lütken, 1859: 101–102; Ljungman, 1866: 306; Devaney, 1974: 154–155; Lewis & Bray, 1983: 173; Hotchkiss, 1982: 405; Hendlér, 1988: 269; Alvarado & Solís-Marín, 2013: 633; Gondim *et al.*, 2013: 50, 54–55.

Ophiozona impressa. – Lyman, 1865: 64; Verrill, 1899: 8; H.L. Clark, 1901: 242; 1915: 337; 1919: 57, 72; 1933: 41, 73; Koehler, 1907: 289; 1914: 2, 11, 150; Matsumoto, 1915: 82; 1917: 298, 389; A.H. Clark, 1921: 57; 1922: 213; 1939: 452; 1954: 378; Fell, 1960: 33; Tommasi, 1970: 74.

TYPE MATERIAL

Lectotype: One specimen preserved dry. (Saint Thomas, U.S. Virgin Island; 1 m depth) (ZMUC NHMD 141838); coll. Riise.

Paralectotype: Eleven specimens preserved dry. (Saint Thomas, U.S. Virgin Island; 1 m depth) (ZMUC NHMD 107681). Paralectotype: one specimen preserved dry. (Saint Thomas, U.S. Virgin Island; 1 m depth) (ZMB 865).

COMPARATIVE MATERIAL EXAMINED

Ophiolepis impressa two adult specimens in 70% ethanol (Reef Flat, Near Smithsonian Laboratory, Station Cbc 80–29, Carrie Bow Cay Belize; 2 m depth) (LACM E.1980-177.2); coll. G. Hendlér, 01 April 1980. Six adult specimens in 75% ethanol (Port Louis, Epave avion, Guadeloupe Island, Lesser Antilles; coordinates: 16.426833 N –61.54275 W) (UF 12774); coll. LeGall, Line, Buske, Yan, Turpin, Yannis, Vassard, Emmanuel, Moolenbeek, Robert and Netchy, Kris, 14 May 2012. See Appendix for additional examined material.

EMENDED DIAGNOSIS

Conspicuous central rosette and four or five radiating columns of larger scales in each interradius (Figure 4); disc covered with numerous thick, rounded, larger scales, surrounded by a continuous row of numerous smaller scales (Figure 4F). Ventral interradii covered by numerous large and thick scales (Figure 4G). Radial shields depressed, rugose, irregularly triangular, longer than wide. Oral shields about as long as wide. Each jaw with four oral papillae, plus an apical papilla (ventralmost tooth). Lateral arm plates with four or five arm spines, slightly decreasing in size

dorsally; two ventralmost spines are thicker and almost as long as one arm segment (Figure 4I, E). Accessory dorsal arm plates present on almost all arm segments, distally between the dorsal arm plates and the lateral arm plates (Figure 4H). Three thin genital plates along the genital slit, increasing in size distally (Figure 4G). Lacking accessory ventral arm plates.

DISARTICULATED OSSICLES

Specimen analysed: one specimen USNM E37646 (dd 9 mm). Radial shield (external view) irregularly triangular, with a swollen central region (exposed region) bordered by a groove with four pores in the proximo-abradial part (which is covered/overlapped by disc scales) (Figure 5C). Dorsal arm plate trapezoidal; proximal and lateral sides straight and distal side rounded with a wide proximal spur (Figure 5D). Ventral arm plates wider distally than proximally; proximal edge is convex and with a centred spur; lateral edges convex proximally where the tentacle pore opens and distal edge is slightly rounded (Figure 5G). Oral shield almost as wide as long, pointed proximally, with lateral sides nearly straight and rounded distally (Figure 5H). Lateral arm plate D-shaped, with four spine articulations along the distal aspect, each consisting of two parallel ridges (Figure 5J). External view of LAP; proximal edge with a discernible band of different stereom structure, with horizontal striations and two spurs (Figure 5L). The outer surface with spiny stereom structure (Figure 5O). Dental plate ovoid, dorsal portion slightly wider than the ventral portion, with four tooth foramina but none perforating the plate; the second foramen (from dorsal to ventral) is ovoid while the rest are almost circular (Figure 5P). Proximal vertebra (Figure 5S) with typical zygospondylous articulation, almost quadrangular, with narrow muscles flanges and V-shaped groove, distal view (Figure 5T).

REMARKS

Specimens from the type material include both *Ophiolepis impressa* and a previously undescribed species (see above) as specimens of these two species are often found together. From the 15 specimens of the original syntype material, there are 13 specimens that correspond to *O. impressa* (Figure 4); from which one was designated as the lectotype (ZMUC NHMD 141838), and the 12 remaining were designated as paralectotypes (ZMUC NHMD-107681) and (ZMB 865). It can be easily distinguished from its western Atlantic congeners by the presence of more than four columns of disc scales on each interradius, the smooth radial shields, a greater density of scales on the ventral interradii, the presence of four to five arm spines and by its lighter cream-brown colour with darker spots on the dorsal surface. The arms also show a banded pattern of cream and brown.

Ophiolepis crebra sp. nov.

(Figures 7 and 8; Table 3)

TYPE MATERIAL

Holotype: One adult specimen preserved in 75% ethanol. (North-western Australia, SS05/2007 Stn. 161; coordinates: 14°33.732'S 122°55.092'E; 95 m depth) (MV F162621); coll. 4 July 2007.

Paratype: One adult specimen preserved dried (Ambon Island, Indonesia; 70 m depth) (ZMUC OPH 5920); coll. Theodor Mortensen, February 1922.

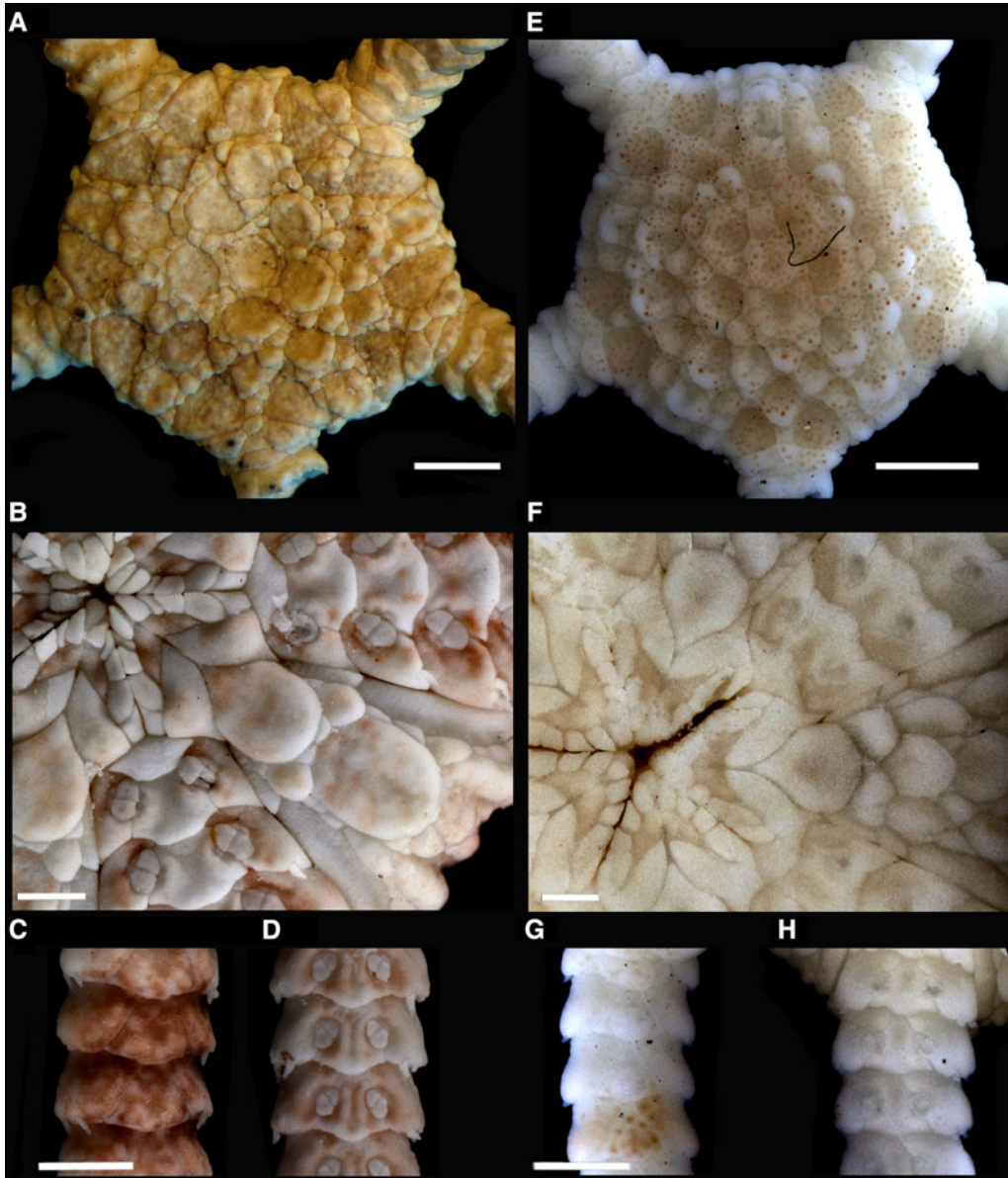


Fig. 7. Left: *Ophiolepis crebra* sp. nov. Holotype MV F162621 (dd: 7 mm), Right: *Ophiolepis rugosa* MV F122623 (dd: 4.2 mm); dorsal disc surface (A, E); ventral disc surface (B, F); dorsal arm plates (C, G); ventral arm plates (D, H) Scale bars A, C–E, G–H, 1 mm; and B, F, 0.5 mm.

ETYMOLOGY

The specific epithet derives from the Latin word *creber*, thick, which refers to the thickness of the disc scales.

COMPARATIVE MATERIAL EXAMINED

Ophiolepis rugosa one adult specimen in 75% ethanol. (Sso5/2007 125, Lacepede, North-western Australia; coordinates: 15.8112 S 121.0623 E; 85–100 m depth) (MV F122623); Dianne J. Bray; coll., 29 June 1905. One adult specimens in 75% ethanol. (Biolum 22, Lizard Island, Big Vicki, Australia; coordinates: 14.69 S 145.43667 E; 5–12 m depth) (MV F1109845). See Appendix for additional material.

DIAGNOSIS

Disc slightly pentagonal covered with imbricated, thick, large scales, which have a tuberculous dorsal surface and irregular swollen distal margins, each surrounded by a continuous

border of thick, smaller and irregular scales. A single row of two larger, sunken, ovoid scales in each interradius, the distal being the largest, longer than wide. Single large scale proximally on each ventral interradius, and two vertical irregular scales distally, these with elevated margins and with some smaller scales on the sides of the genital plates. Oral shields longer than wide, droplet-shaped. Lateral arm plates with three small, pointed arm spines, similar in size. Dorsal arm plates trapezoid, swollen on the distal margin. Accessory dorsal arm plates present only on basal segments. Two tentacle operculiform scales attached to the lateral arm plate, with only one small tentacle scale attached to the rim on the ventral arm plate. Lacking accessory ventral arm plates.

HOLOTYPE DESCRIPTION

Disc diameter 7 mm; length of the longest arm 20 mm (Figure 7). Disc slightly pentagonal; dorsal surface elevated;

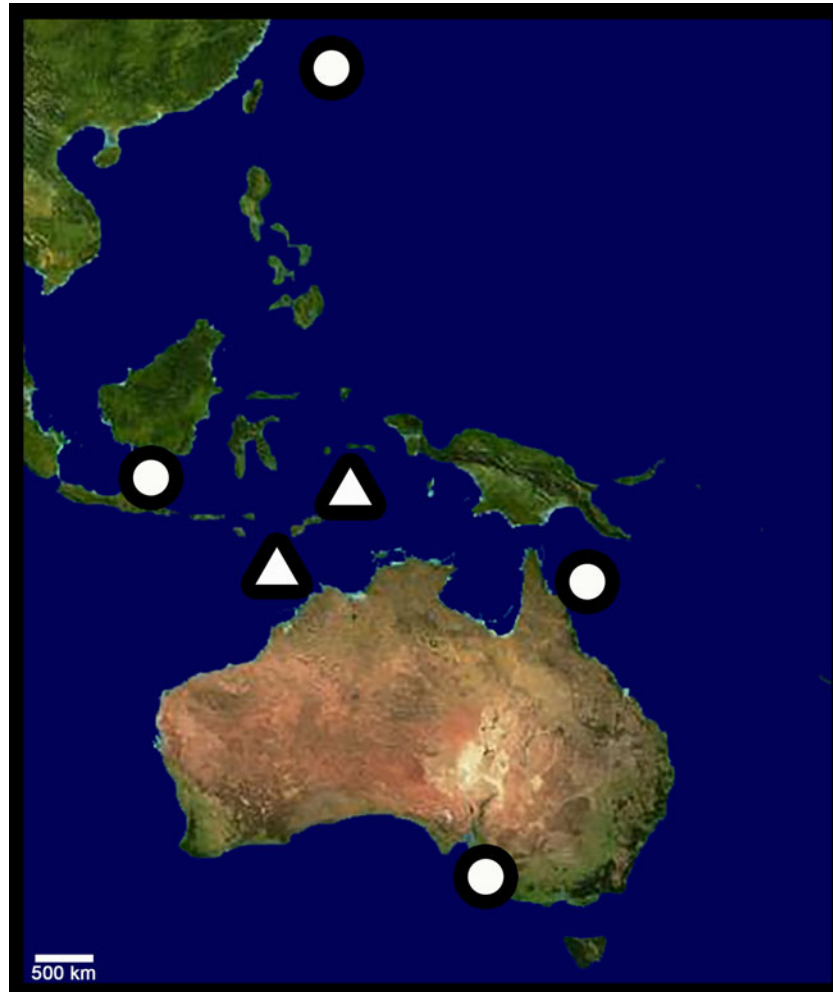


Fig. 8. Distribution map for *Ophiolepis crebra* sp. nov. (Δ) and *O. rugosa* (\circ).

ventral surface flat (Figure 7A). Interradii sloping ventrally from the lateral margin. Disc covers proximal five arm segments. Arms slender, dorso-ventrally flattened, gradually tapering; dorsal surface rounded and ventral surface flat.

Disc covered with numerous, conspicuous, thick, imbricated large scales (<0.5 mm), with swollen distal margins and uneven surface proximally; these scales are surrounded by smaller ones which are also tumid, irregular in shape and size (Figure 7A). Conspicuous central rosette; central plate rounded and the five radial plates slightly ovoid. Dorsal interradii with one column of two large ovoid scales, the distal one is longer than wide. Radial shields with uneven surface, sunken, irregularly triangular, wider than long, with convex abradial lobe and separated radially from each other by three larger scales; the proximal one is the largest, the middle one is the smallest and slightly rectangular, wider than long and the distal scale is irregularly shaped with two adjacent scales at both sides, which are broader than long and somewhat triangular, with rounded angles. Five larger scales bordering each pair of radial shields on their proximal side. Each jaw bears a single apical oral papilla (ventralmost tooth) and four oral papillae (Figure 7B). First and second proximal papilla very stout, third papillae quadrangular longer than wide. The distalmost is the largest, rectangular, wider than long, attached to the adoral shield. Oral shield

tumid, longer than wide; proximal edge pointed with concave margins; lateral and distal margins nearly semicircular. Madreporite with single, large hydropore. Adoral shields tumid; distal angle pointed, claw-shaped; lateral margin slightly straight; proximal edge pointed; pairs joined together. Genital slit extending from oral shield to fourth ventral arm plate at the border of the disc; bordered by two genital plates, the proximal is narrower and shorter than the distal one, which extends to almost the edge of the disc. Ventral interradii with one large oval scale, distally two vertical irregular scales with elevated margins and with some smaller scales on the sides of the genital plates surrounded by smaller ones.

Proximal dorsal arm plates are trapezoid-shaped, almost twice as long as wide, elevated distally; neighbouring arm plates overlapping, concealing the proximal apex of preceding plates (Figure 7C). Single ADAP at both distal edges of a few basal dorsal arm plates, irregular in shape. The distal segments of the arm bear triangular dorsal arm plates, separated from each other by the lateral arm plates that are touching dorsally and ventrally. Lateral arm plates thicker at distal margins. Arm spines slender, pointed and short, almost as long as one fourth of the length of an arm segment; none on first segment, one on second segment, two on third segment, and three on subsequent segments. Ventral arm plates overlapping and elevated, longer than wide and somewhat bell-shaped, with sharply

Table 3. Comparison of morphological characters between *Ophiolepis crebra* sp. nov. and *O. rugosa*.

	<i>O. crebra</i> sp. nov.	<i>O. rugosa</i>
Dorsal arm plates	Triangular outline, thicker dorsally, no tubercle	Triangular outline, one tubercle on proximal to middle segments
Dorsal disc scales (adults)	Larger and fewer scales, 1 column of large scales in each interradius	Larger and fewer scales, 3 columns of larger scales in each interradius
Ventral disc scales	Large scales proximally, multiple smaller scales interradially	Numerous smaller scales, all about the same size
Arm spines	3	3 (rarely 4)
Oral shields	Longer than wide, proximal edge pointed with concave borders, rounded distally	Droplet-shaped, longer than wide, proximal edge pointed with concave borders, rounded distally
Ventral arm plates	Longer than wide, bell-shaped (proximally) to triangular (distally), with a midline sulcus; not overlapping	Triangular (only the first one) to quadrangular (segment 2 to distal)
Accessory ventral arm plate	Absent	Absent

pointed distal lateral edges; distal ventral arm plates triangular and separated by lateral arm plates (Figure 7D). Two large tentacle scales attached to the lateral arm plate, forming ovoid operculum over each tentacle pore all along the length of the arm; adradial tentacle scale is shorter and more triangular in shape and abradial is larger and somewhat D-shaped. Second and third arm segments bear a second pair of extra tentacle scales attached to the ventral arm plates, smaller in size; subsequent arm segments bear only one smaller rim-like scale attached to the ventral arm plate.

DISTRIBUTION

The species is found off North-western Australia and Ambon Island, Indonesia (Figure 8).

REMARKS

Due to limited number of specimens of *O. crebra* sp. nov. and their designation as type material, no ossicles were isolated and only external morphology is described. *Ophiolepis crebra* sp. nov. possesses thick arm plates, which could be mistaken with the nodular arm plates present in *O. rugosa* and *O. nodosa*; however the nodular dorsal arm plates are well defined in the latter species (see Fujita, 2016 for a photograph of *O. nodosa*, and Pineda-Enriquez *et al.*, 2014, for a discussion on the systematic position of this species). The closest relative to *O. crebra* sp. nov., is *O. rugosa* and the morphological differences and similarities between these two species are summarized in Table 3 (Baker, 1979; Fujita, 2016; Pineda-Enriquez *et al.*, 2014).

DISCUSSION

As part of an extensive revision of the genus we identified three new species of *Ophiolepis* (*O. buitronae* sp. nov., *O. aemulata* sp. nov. and *O. crebra* sp. nov.), that mainly consists of misidentified specimens. Species of *Ophiolepis* are delimited in accordance to the pattern, distribution, size, and thickness of the disc scales, as well as the shape and size of the dorsal arm plates, and the presence of accessory dorsal and ventral arm plates (Pineda-Enriquez *et al.*, 2014). Based on these characteristics it was evident to us that, in some cases, specimens in museum lots corresponded to two different species.

Specimens of the new species *Ophiolepis buitronae* sp. nov. had been consistently misidentified as *Ophiolepis impressa* since 1856, when this species was described by Lütken, who

included specimens of both species as part of the type series of *O. impressa*. These 14 specimens were collected by A.H. Riisse on the small island Saint Thomas, in the Caribbean Sea (type locality of *O. impressa*). There are no previous reports on morphological variation within *O. impressa*, but the distinguishing taxonomic characters we suggest are conspicuous and consistent across all specimens. Furthermore, the existence of *Ophiolepis buitronae* sp. nov. is supported by molecular evidence (Bribiesca-Contreras *et al.*, 2013).

Initially, Bribiesca-Contreras *et al.* (2013) compared specimens of *O. impressa* from inside the anchialine cave Aerolito de Paraiso and from open waters and found that they formed two clades rather than one, and that these clades were not separated geographically. We examined these specimens and were able to separate each clade using the morphological characters outlined above. Thus, molecular and morphological evidence both suggest that *O. buitronae* is a new species. It has a sympatric distribution, and it has been collected together with specimens of *O. impressa* (as in the type material for the latter, designated by Lütken). Thus, they are easily misidentified due to the morphological similarities when observed in the field. The distribution of both species may be broader than reported here, as only the material we examined and reliable photographic records were considered. As many specimens had been misidentified, it will be necessary to review all previous reports not included in this study.

The species *Ophiolepis aemulata* sp. nov. had been misidentified as *O. superba*. A few specimens deposited in the scientific collection of the USNM and NSMT were found under this name, but they clearly belong to the new species. *Ophiolepis aemulata* sp. nov. has been recorded only from around Darwin, Australia. We suspect that the species has a wider distribution as it is likely that there are more misidentified specimens that were not found during this revision. This also applies for *Ophiolepis crebra* sp. nov., as we found specimens in scientific collections identified as other species (e.g. *O. irregularis*). Finally, this work prompted the designation of the neotype of *O. superba*, which will help clarify its identity.

According to our results and previous accepted species (Stöhr *et al.*, 2017), the genus *Ophiolepis* now comprises 25 species. Eight of these occur in the Western Atlantic: *O. ailsae*, *O. gemma*, *O. elegans*, *O. kieri*, *O. paucispina*, *O. pawsoni*, *O. impressa* and *O. buitronae* sp. nov. One species occurs in the Eastern Atlantic: *O. affinis*. Across the Indo-west Pacific, our findings have increased the species richness of the genus to nine species: *O. biscalata*, *O. cardioplax*, *O. cincta*, *O. irregularis*, *O. nodosa*, *O. rugosa*, *O. superba*, *O. unicolor*, *O. aemulata* sp.

nov. and *O. crebra* sp. nov. Lastly, there are six species that are found in the eastern Pacific Ocean: *O. crassa*, *O. fulva*, *O. grisea*, *O. pacifica*, *O. plateia* and *O. variegata*.

It is evident that a complete systematic revision of the Ophiolepididae and Hemieuryalidae is required at both genus and family-level. O'Hara *et al.* (2017), in a new robust molecular phylogeny of the Ophiuroidea, have shown that the traditional Ophiolepididae was not monophyletic. Instead it consists of four family-level clades, the Ophiolepididae (restricted), Hemieuryalidae, Ophiomusaidae and Ophiosphalmidae, the latter two placed in an order (Ophiurida), separate from the former two (Amphilepidida). The phylogeny also showed that several ophiolepidid genera (in particular *Ophiozonella* Matsumoto, 1915) are also not monophyletic.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315417001503>.

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