TWO NEW SPECIES OF *OPHIOLEPIS* (ECHINODERMATA: OPHIUROIDEA) FROM THE CARIBBEAN SEA AND GULF OF MEXICO: WITH NOTES ON ECOLOGY, REPRODUCTION, AND MORPHOLOGY

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ABSTRACT. Two new western Atlantic brittlestar species are described: *Ophiolepis gemma* from deep-reef habitats and *O. ailsae* from bathyal depths. *Ophiolepis gemma* has thin, polygonal major disc scales with light-reflective edges. Its distalmost arm segments are longer than wide. *Ophiolepis ailsae* has tumid major disc scales, smoothly joined to nearly continuous rows of intercalary scales. Its ventral arm surface is strongly furrowed by rows of depressed tentacle pores alongside the tumid ventral arm plates. Its distalmost arm segments are wider than long. *Ophiolepis gemma* broods its embryos; the mode of reproduction of *O. ailsae* is unknown. There are abnormally enlarged skeletal plates in 35% of the *O. gemma* examined. Specialized hooked distal arm spines are described in both new species and for the first time in their congeners. The probable development and function of the small, dorsally directed hooks are discussed, and it is suggested that they are used in feeding.

INTRODUCTION

Ophiolepis ailsae new species and *Ophiolepis gemma* new species, described in this paper, bring to six the number of *Ophiolepis* species reported from the western Atlantic. These new species were first taken by the U.S. Coast Survey steamer BLAKE in 1878–1879 and by the U.S. Fish Commission steamer ALBATROSS in 1884 and deposited in the U.S. National Museum of Natural History and the Museum of Comparative Zoology, Harvard University. Additional individuals of both species were collected between 1980 and 1986 by dredge and trawl in the Gulf of Mexico, by research submersibles in the Bahama Islands, and by SCUBA on the Belize Barrier Reef.

Lyman (1883) misidentified specimens of the new species in the BLAKE and ALBATROSS collections as *Ophiozona impressa* Lyman, 1865. The authorship was corrected to *O. impressa* (Lütken, 1859) in later references to Lyman's material, but the misidentification went undetected. Devaney (1974) reduced the genus *Ophiozona* Lyman, 1865, to the synonymy of *Ophiolepis* Müller and Troschel, 1840. Therefore, publications cited in the synonymies (below) presumably deal with mixed samples of *Ophiolepis impressa*, *O. gemma*, and *O. ailsae* as "*Ophiozona impressa*."

Contributions in Science, Number 395, pp. 1-14 Natural History Museum of Los Angeles County, 1987 The recognition of *O. gemma* and *O. ailsae* reinforces previous suggestions (Hendler and Miller, 1984) that echinoderm populations on seaward forereef slopes represent the shallow extension of a yet poorly sampled deep-reef fauna, and that further exploration of deep-reef habitats will increase the known diversity of Caribbean ophiuroids. In addition, study of these new species illuminates aspects of the brooding mode of reproduction and functional morphology of hooked arm spines in *Ophiolepis*. These points and details of the ecology, diversity, and distribution of the genus are discussed below.

The following abbreviations are used in this paper. Institutions and agencies: BLM-United States Bureau of Land Management; BMNH-British Museum (Natural History); IRCZM-Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution; LACM-Natural History Museum of Los Angeles County; MCZ-Museum of Comparative Zoology, Harvard University; USNM-National Museum of Natural History, Smithsonian Institution. Morphology: dd-disc diameter; spec-specimen.

SYSTEMATIC ACCOUNT

Family Ophiuridae

Subfamily Ophiolepidinae

Genus Ophiolepis Müller and Troschel, 1840

Ophiolepis gemma new species

Figures 1-3, 5A-E, H, 8

Ophiozona impressa: Lyman, 1883:225, as Ophiozona impressa Lyman, 1865 (incorrect author designation), in part; not Lütken, 1859.

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Figure 1. Ophiolepis gemma new species, paratype LACM 83-130.1: A, disc, dorsal view; B, portion of disc, ventral view; C, arm base, lateral view. Scale = 1 mm.

Ophiozona impressa: Verrill, 1899:8, as *Ophiozona impressa* Lyman, 1865 (incorrect author designation), in part?; not Lütken, 1859.

Ophiozona impressa: Clark, 1915:337, in part; not *O. impressa* Lütken, 1859. [See Introduction regarding misidentification of the species.]

ETYMOLOGY. *Gemma*, a noun in apposition from the Latin *gemma* meaning "bud (as on a plant)" and meta-phorically "gem, jewel"; applied in reference to the faceted, reflective scales adorning the dorsal surface of the disc.

MATERIAL EXAMINED. Unless otherwise stated, all specimens are preserved in alcohol, and all specimens from Belize were collected ESE of Carrie Bow Cay on the seaward slope of the Belize Barrier Reef, at 16°48.14′N, 88°04.50′W, by G. Hendler, with the assistance of divers cited in Acknowledgments.

Type material. BELIZE: (LACM 86-34.1), holotype, Sta. CBC-86-3, 3 Apr. 1986, 80 ft., poison station, SCUBA;

(LACM 83-130.1), 1 dry paratype, and (LACM 83-130.2), 4 alcoholic paratypes, Sta. Belize-83 No. 2, 2 Apr. 1983, 80 ft., poison station, SCUBA; (LACM 83-131.1), 1 dry paratype, Sta. Belize-83 No. 9, 6 Nov. 1983, 80 ft., poison station, SCUBA; (BMNH 1987.5.1.2), 4 paratypes, Sta. Belize-83 No. 9, 6 Nov. 1983, 80 ft., poison station, SCUBA; (LACM 80-86.1), 1 paratype, Sta. Belize-80 No. 20, 28 March 1980, 70-80 ft., in Halimeda, SCUBA; (LACM 83-132.1), 7 paratypes, Sta. Belize-83 No. 3, 3 Apr. 1983, 80 ft., poison station, SCUBA; (USNM E34357), 3 paratypes, Sta. Belize-83 No. 11, 8 Nov. 1983, 80 ft., poison station, SCUBA; (USNM E34358), 10 paratypes, Sta. CBC-85-6, 15 Jun. 1985, 75 ft., poison station, SCUBA; (IRCZM 74:503), 2 paratypes, Sta. CBC-86-31, 8 Apr. 1986, E of Curlew Cay on the seaward forereef slope of the Belize Barrier Reef, 16°47.38'N, 88°04.54'W, 70 ft., poison station, SCUBA.

Non-type material. BELIZE: (LACM 83-131.2), 1 spec, Sta. Belize-83 No. 9, 6 Nov. 1983, 80 ft., poison station, SCUBA; (LACM 83-132.2), 1 spec, Sta. Belize-83 No. 3, 3

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Figure 2. Ophiolepis gemma new species, holotype LACM 86-34.1: disc, dorsal view. Scale = 1 mm.

Apr. 1983, 80 ft., poison station, SCUBA; (LACM 83-133.1), 1 spec, 6 Nov. 1983, sand bores between Carrie Bow Cay and Wee Wee Cay, Belize Barrier Reef Lagoon, 16°46.40'N, 88°06.80'W, 10-20 ft., under rubble, SCUBA; (LACM 83-134.1), 2 spec, Sta. Belize-83 No. 10, 7 Nov. 1983, 80 ft., poison station, SCUBA; (LACM 85-164.1), 5 spec, Sta. CBC-85-5, 14 Jun. 1985, E of Southwater Cay on the seaward forereef slope of the Belize Barrier Reef, 16°49.07'N, 88°04.55'W, 70 ft., poison station, SCUBA; (LACM 86-34.2), 1 spec, Sta. CBC 86-3, 3 Apr. 1986, 80 ft., poison station, SCUBA; (USNM E34359), 3 spec, Sta. CBC-86-20, 6 Apr. 1986, 80 ft., poison station, SCUBA; (LACM 86-43.1), 3 spec, Sta. CBC-86-20, 6 Apr. 1986, 80 ft., poison station, SCUBA; (USNM E34360), 4 spec, Sta. CBC-86-31, 8 Apr. 1986, E of Curlew Cay on the seaward forereef slope of the Belize Barrier Reef, 16°47.38'N, 88°04.54'W, 70 ft., poison station, SCUBA; (LACM 86-59.1), 1 spec, Sta. CBC-86-42, 10 Apr. 1986, E of Southwater Cay on the seaward forereef slope of the Belize Barrier Reef, 16°49.07'N, 88°04.55'W, 70 ft., poison station, SCUBA. SOUTHWEST FLORIDA, GULF OF MEXICO: (USNM E34361), 1 dry spec, BLM Southwest Florida Shelf Ecosystems Study, Year 2, Cruise II (BLM 321-II), Sta. 23a, 1 Aug. 1981, 25°16.89'N, 83°37.79'W, 70-73 m, triangle dredge; (USNM E34362), 1 spec, BLM 321-II, Sta. 29b, 4 Aug. 1981, 24°47.51'N, 83°41.19'W, 60-65 m, triangle dredge; (USNM E34363), 1 dry spec, BLM Southwest Florida Shelf Ecosystems Study, Year 1, Cruise IV (BLM 210-IV), Sta. 29, 24 Apr. 1981,

Figure 3. Ophiolepis gemma new species, paratype LACM 83-131.1: disc and one arm, dorsal view. Scale = 1 mm.





Figure 4. Distribution of the number of arm spines on the arm segments of the holotypes of *O. gemma* new species (A) and *Ophiolepis ailsae* new species (B). Consecutive arm segments numbered from arm base to arm-tip. The range for number of arm spines on each segment reflects variation among different arms of the specimen.

24°47.51′N, 83°41.19′W, 61 m, triangle dredge. BARBA-DOS: (MCZ 331), 2 dry spec, BLAKE Sta. 278, 6 Mar. 1879, 13°04′50″N, 59°47′40″W, 69 fm, coral/broken shell and BLAKE Sta. 280, 6 Mar. 1879, 12°57′40″N, 59°36′50″W, 221 fm, sand (MCZ lot consists of specimens from two BLAKE stations combined); (MCZ 7429), 1 spec, BLAKE Sta. 272, 5 Mar. 1879, 13°04′12″N, 59°26′45″W, 76 fm, coral/broken shell, BLAKE Sta. 278, 6 Mar. 1879, 13°04′50″N, 59°47′40″W, 69 fm, coral/broken shell or BLAKE Sta. 298, 10 Mar. 1879, 13°03′28″N, 59°37′40″W, 120 fm, rock (specimen separated from MCZ 819, consisting of three specimens from three BLAKE stations combined as one lot; all three specimens originally identified as *Ophiozona impressa*).

DIAGNOSIS. Dorsal surface of disc convex; interradial dorsal field with three columns of major scales. Major disc scales polygonal, with straight edges reflecting light (especially evident in small wet specimens). Major scales thin; margins slightly tumid, raised above intercalary scales. Small, flat intercalary scales forming single continuous rows separating large scales only in large specimens. Radial primary plates separated by several wedge-shaped scales. Radial shields thin, smooth. Oral shields about as wide as long. Proximal one-third of each arm segment constricted; segments at arm-tip longer than wide. Dorsal arm plates separated by lateral

arm plates beginning at segments 3–19. Accessory dorsal arm plates only on proximal few arm segments. Three arm spines on most segments. Proximal ventral arm spine about onehalf length of arm segment; longer than dorsal arm spine. Adradial tentacle scales below disc generally smaller than abradial scales.

DESCRIPTION OF HOLOTYPE. Disc diameter 6.2 mm; arm length exceeds 26 mm; longest arm broken. Disc nearly circular; dorsal surface convex, with mid-dorsal region flattened; interradial region sloping ventrad; ventral surface flat. Arms slender, gradually tapering; dorsal surface rounded; ventral surface with slight convexity along midline. Segments at arm-tip longer than wide.

Most major disc scales about as long as wide, raised above small intercalary scales; margins thickened, angular, with straight edges joined at obtuse angles. Central plate nearly circular; diameter 0.58 mm. Radial plates with maximum width 0.60 mm. Intercalary scales flat, irregularly shaped, in single row, forming continuous border at distal edge of all but peripheral major dorsal disc scales.

One to three wedge-shaped scales between adjacent radial primary plates. Radial dorsal field of disc with three major scales distal to each radial primary plate; distalmost scale largest, inserted between radial shields. Radial shields nearly triangular, with slight adradial lobe; surface smooth. Two accessory radial shields distal to radial shields linked by small scale with three rounded edges. Interradial dorsal field of disc with three columns of major scales; central column with five scales equal to or larger than five scales of each lateral column. Several interradii with subdivided major scale in central column.

Each jaw bearing a single apical oral papilla, and five pairs of lateral oral papillae. Distad to apical papilla, first and second papillae pointed, quadrilateral (second sometimes divided into two smaller papillae); third papilla quadrilateral; fourth papilla largest with broadly rounded lateral margin; fifth papilla (=buccal tentacle scale) elongate, attached to adoral shield, free end extending dorsad to fourth papilla.

Oral shield with edges tumid, central region depressed; approximately as wide as long; proximal margins concave, meeting at acute point; distal margin nearly semicircular. Madreporite with single, large hydropore. Adoral shields tumid; pairs appear contiguous, but separated by microscopic gap.

Genital slit extending from oral shield to third ventral arm plate; bordered by long distal genital scale and 2–3 small scales proximad. Ventral interbrachial field of disc with about 20 large scales and several smaller scales.

Proximal dorsal arm plates appear quadrilateral; two proximal sides meeting at acute point; two distal sides forming

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Figure 5. SEM micrographs of: *Ophiolepis gemma* new species – A, B, lateral view of arm showing region with hooked dorsal arm spines (A) 6–9 segments from tip and (B) 1–4 segments from tip and terminal plate; C–E, segments near arm-tip of three individuals at higher magnification showing hooked and straight arm spines; H, detail showing hooked arm spine. *Ophiolepis ailsae* new species – F, hooked and straight arm spines on segment near arm-tip; G, dorsal view of arm near tip showing orientation of hooked dorsal arm spines; I, detail showing hooked arm spine. Scale = 100 μ m (A, B, F, G); 50 μ m (C, E); 25 μ m (D, H, I).



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Figure 6. Size-frequency distributions of *Ophiolepis gemma* new species and *Ophiolepis ailsae* new species, based on disc diameter.

obtuse angle. Plates of first 38 segments overlap, concealing proximal apex of plate. Distal plates nearly triangular; distal margin with small medial lobe. Accessory dorsal arm plates minute, occurring only on first 2–4 arm segments.

Lateral arm plates in dorsal view narrowed proximally, flared distally. Proximal one-third of each arm segment abruptly constricted, distal portion broad.

Arm spines minute; base and middle of spine thick, gradually narrowing to blunt point. Ventralmost spine near disc thicker than dorsal spines, having broad rounded tip, somewhat compressed shaft. Dorsalmost spine usually smallest, much less than one-half segment length; ventralmost spine longest, nearly one-half segment length. Spines usually three on each side of arm segment; 0–1 on first segment, one on second segment, 1–2 on third segment, generally three on subsequent distal segments, rarely four spines (Fig. 4A). Dorsalmost spine beginning with segment 44 bearing glassy terminal hook, often with secondary barb (Fig. 5A–E, H).

Ventral arm plates overlapping until segment 49, then separated by lateral arm plates. Plates beneath disc appear broader than long, flattened; plates beyond disc longer than broad, with slight medial ridge.

Two semicircular tentacle scales forming ovoid operculum over each tentacle pore; long axis of operculum approximately one-half length of ventral arm plate. Single miniscule tentacle scale on ventral arm plate concealed by operculum. Adradial tentacle scale conspicuously smaller than abradial scale even below disc. Both scales diminishing in size towards arm-tip.

Color of dried holotype. Most disc scales white, some orange, all stippled with microscopic, reddish-orange specks. Specks most numerous along margins of scales. Some disc scales with conspicuous reddish spots; radial shields with large reddish spot at distal corner. Arms banded; groups of 1–3 white dorsal and lateral arm plates alternating with orange or brown plates. Specks stipple dorsal arm plates, fewer on lateral arm plates; spots on ventral arm plates rare. Pigmentation of lateral arm plates continues to ventral surface of arm. Scattered red or brown specks on ventral arm plates. Arm spines with one to several orange or brown specks near base. Interradial scales at disc edge speckled; proximal scales gray. Oral frame white.

VARIATIONS. Size. Disc diameters of 59 specimens measured range from 1.9 to 6.2 mm (Fig. 6). The arms are long and slender (Fig. 3), length ranging from 8 mm for a specimen of 2.2 mm dd to 19 mm for a specimen of 3.5 mm dd and exceeding 26 mm for a specimen of 6.2 mm dd. The ratios of dd/arm length range from 3.4 to 5.6 ($\bar{x} = 4.8$).

Disc. Scales thin, polygonal with some straight, sharp edges. Sharp edges of scales of wet specimens, especially small individuals, reflect light, appearing bright under microscope illumination. Small specimens have a relatively irregular and incomplete row of intercalary scales bordering the major disc scales (Fig. 3), but specimens exceeding 3.6 mm dd tend to have a more uniform, continuous row around most of the major scales (Figs. 1A, 2). Arrangement of the large dorsal disc scales differs little from the holotype (Fig. 2) except in very small individuals. The central primary plate ranges from 0.38 mm diameter in a specimen of 2.3 mm dd to 0.64 mm in a specimen of 4.3 mm dd. Adoral shields may be contiguous or separated by a microscopic gap.

Arms. The arm segments are characterized by an abrupt proximal constriction, a feature that is most pronounced in small specimens (Fig. 3). However, even in larger individuals (3.8-6.2 mm dd) constrictions are evident within a few segments beyond the disc and are most pronounced at the distal end of the arm (Fig. 5A, B). Accessory dorsal arm plates characteristically appear only on the most proximal portion of the arm (e.g., Figs. 1A, 3: on the first arm segment beyond the disc). In many cases accessory plates are not present on all arms of an individual. There are 14 specimens without visible accessory plates on any arm, 30 with accessory plates only on the first arm segment beyond the disc, and 13 with accessory plates on segments 2-4 beyond the disc. The dorsal arm plates are in contact for the proximal 0-38 arm segments; in 91% of the individuals the dorsal arm plates are separated by lateral arm plates beginning at segments 3-19. Ventral arm plates are in contact on the proximal 2-49 arm segments, but in 90% of the individuals they are separated by lateral arm plates beginning at segments 3-12. There is 0-1 spine on each side of the first arm segment, 1-2 spines (rarely three) on the second, 2-3 (rarely one) on the third, three (rarely four) on the fourth (Fig. 4A). Except for the very large holotype, 48 specimens lack arm segments with four arm spines. and eight specimens have four arm spines on one or two arms. The segments bearing four arm spines are generally on the proximal portion of the arm, on segments 3-42, with 55% occurring on segments four and five, and 78% on segments 4-7. Arm segments with two spines are restricted to six or fewer of the terminal arm segments except for very small specimens.

Hooked dorsal arm spines (Fig. 5A–E, H) occur on the outer one-third to one-half of the arm, hooks beginning on segments 11–44 depending on the size of the animal (Fig. 7). In rare cases, the middle spine is slightly hooked (noted only in three specimens with 2.3, 3.4, and 3.5 mm dd) (compare Fig. 5D–E). The ventral arm spine is usually longer than the dorsal and middle spines, and the middle spine is frequently longer than the dorsalmost (Fig. 5A–E). The ventral spine is equal to or slightly less than half the length of the arm segment except in one small individual (2.2 mm dd) with all arm spines conspicuously less than half the length of the arm segment.

There are abnormally enlarged skeletal plates (Fig. 8) in 35% of the specimens, including individuals from Florida and Belize. Usually a few of the lateral arm plates of the specimen are affected, but in several cases plates of the oral frame and dorsal surface of the disc are swollen. In small specimens, the enlarged plates are thin and expanded, forming a cavity in the plate. In large specimens the swelling is composed of solid skeletal material. Histological examination is needed to determine the cause of this disfigurement, as dissection of several specimens under a stereomicroscope did not reveal parasitic invasion of the abnormal plates.

Color of preserved specimens. Intensity of pigmentation varies directly with specimen size. Some small alcoholic specimens completely lack pigment. Disc scales gray-white, darker gray near center of disc. Reddish or brownish microscopic specks on dorsal and ventro-lateral disc scales, dorsal and some lateral arm plates, particularly pronounced at scale/plate margin. Number of specks on a dorsal arm plate ranging from about eight in small specimens to over 20 in large specimens. Radial shields often with conspicuous spots at distal corners. Arms often faintly banded. Specimens white ventrally, rarely with dark specks on ventral arm plates.

Color of living specimens. Disc pale reddish overall, gray at center. Some primary plates and large disc scales yellow, orange or pale tan. Large dorsal disc scales thin, transmitting



Figure 7. Scatter plot for *Ophiolepis gemma* new species, showing most proximal arm segment with hooked arm spines as a function of disc diameter. As specimens grow larger, the most proximal hooked spine occurs increasingly nearer the arm-tip.

dark color of underlying viscera. Arms banded with reddish and white, darkest proximad. Some dorsal arm plates brownish-orange and adjacent lateral arm plates orange-tan or pale brown with darker edge; dark lateral arm plate pigmentation



Figure 8. SEM preparations of *Ophiolepis gemma* new species, with abnormally enlarged skeletal plates: (A) arm segment on left with enlarged dorsal arm plate (paired arrows), segment on right with abnormal lateral arm plate (single arrow); (B) arm segment on left with enlarged lateral arm plate (single arrow), segment on right is normal. Scale = $100 \ \mu m$.



Figure 9. Geographical distribution of Ophiolepis gemma new species and Ophiolepis ailsae new species.

extends to ventral surface. Many disc scales and dorsal arm plates speckled with orange or reddish-brown. Radial shields often with orange-brown spots at distal corners. Some disc and arm plates have dark rust-brown spots. Spines usually white. Overall color of ventral surface white; ventral arm plates may be very pale brown. Proximal ventral arm plates and interradial plates of disc often gray at center. Small specimens relatively pale, with gray disc and whitish arms; relatively few red flecks. Dorsal and lateral arm plates pale tan for 1–3 segments, alternating with 1–3 lighter segments.

COMPARISONS. The disc scales of *O. gemma* are thin and flat; the terminal arm segments are longer than wide. In *O. ailsae* the major disc scales are tumid and the terminal arm segments are wider than long. Contrasts with other congeners are discussed after the description of *O. ailsae*.

DISTRIBUTION. Southern Gulf of Mexico, Belize, Barbados (Fig. 9); generally from 21 to 139 m (one exceptional Belizean specimen from approximately 5 m depth; BLAKE specimens from off Barbados possibly as deep as 404 m as indicated in Material Examined).

ECOLOGY. Most *O. gemma* from Belize were collected between 21 and 24 m on the seaward forereef wall of the Belize Barrier Reef. The wall is rough and steep (usually 50– 70° angle) with scattered concentrations of sponges, gorgonians, large platelike corals, and smaller corals (Hendler and Miller, 1984:459). Many individuals were collected as they emerged following the release of ichthyocide ("Noxfish") near large mounds of the coral, *Montastrea annularis* (Ellis and Solander), in habitats with other corals, sponges, and algae. The species seems to live primarily in pockets of *Halimeda* sand and in the calcareous alga *Halimeda* sp., and was sometimes collected by hand from *Halimeda* or from sediment and broken corals. The most abundant motile macrofauna collected with *O. gemma* were other ophiuroids, particularly *Ophioderma rubicundum* Lütken, *Ophiocoma paucigranulata* Devaney, and *Ophiurochaeta* spp.

One specimen of *O. gemma* was collected at a site in shallow water in the barrier reef lagoon from a sand bore at 3– 6 m. Bottom cover at the site was composed chiefly of the corals *Acropora palmata* Lamarck and *A. cervicornis* Lamarck, brain corals, coral rubble, sponges, and gorgonians (with colonies of *Montastrea* sp. occurring below 4.6 m). The area was heavily silted, and *Halimeda* flakes were a major component of the sediment. It is not clear if this record is anomalous or affinities of the lagoonal sand-bore habitat with the deep reef (low energy habitat with pockets of silt and *Halimeda* sand) could provide suitable conditions for populations of the species in shallow water. However, in numerous shallow-water collections made off Belize during the last five years (by G.H. and colleagues) this is the only instance of *O. gemma* occurring at less than 21 m depth.

On the southwest Florida shelf, individuals were collected

at three stations between 60 and 73 m, from a pavement of coralline-algal nodules with some sand and rocky outcrops. Epibiotic cover varied seasonally from 25.9 to 68.0% at one site to 64.5 to 89.7% at a second site. Over 316 taxa were recorded from each of two sites, chiefly sponges, crustaceans, cnidarians, fishes, and echinoderms (K. Spring, pers. comm.). Specimens from Barbados, collected with shipboard gear, were taken at greater depths, extending the species' bathymetric range to a depth of at least 139 m.

It appears that many individuals are attacked by predators. Single regenerating arms were noted in 12 specimens, two regenerating arms in five specimens, and three regenerating arms in one specimen. Thus, at least 18 (31%) of the 59 specimens examined for repair have regenerating arms.

Ophiolepis gemma was almost invariably collected with its congener, *O. impressa.* The species co-occurred at 11 of 13 stations off Belize and were present in one suite of stations made by the BLAKE off Barbados.

REPRODUCTION. At least two of the specimens from Carrie Bow Cay, Belize, held embryos in their bursae. A brooding specimen 3.3 mm dd was collected 8 Nov. 1983; another 3.6 mm dd was collected 3 Apr. 1983. The larger specimen was partially dissected, revealing five embryos in one interradius, all at a developmental stage with only terminal arm plates. Since brooding was detected only by external observations, it is likely that some brooding individuals were overlooked and that other (possibly smaller and larger) individuals could have been sexually mature. Data are too few to infer the seasonality of reproductive activity. However, the occurrence of embryos at the same stage of development in one specimen is suggestive of synchronous brooding in that individual.

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Figures 5F, G, I, 10

- *Ophiozona impressa:* Lyman, 1883:225, as *Ophiozona impressa* Lyman, 1865 (incorrect author designation), in part; not Lütken, 1859.
- *Ophiozona impressa:* Verrill, 1899:8, as *Ophiozona impressa* Lyman, 1865 (incorrect author designation), in part?; not Lütken, 1859.
- *Ophiozona impressa:* Koehler, 1914:150, in part; not Lütken, 1859. Clark, 1915:337, in part; not Lütken, 1859. [See Introduction regarding misidentifications of the species.]

ETYMOLOGY. *Ailsae*, a noun in the genitive case to honor Miss Ailsa McGown Clark; in recognition of a highly esteemed student of the Echinodermata on her retirement from the British Museum (Natural History).

MATERIAL EXAMINED. All specimens are preserved dry unless stated otherwise.

Type material. ELEUTHERA, BAHAMA ISLANDS: (LACM 84-167.1), holotype, R/V JOHNSON Cruise 161, JOHNSON SEA-LINK II Dive 810, 10 Apr. 1984, 25°35.57'N, 76°44.27'W, off Riley Pt., Eleuthera, 270 m, Temp. = 17.50°C, coll. G. Hendler, P. Kier, T. Askew, C. Chulamanis. SOUTHWEST FLORIDA, GULF OF MEX- ICO: (LACM 81-84.1), 1 paratype, BLM Southwest Florida Shelf Ecosystems Study, Year 2, Cruise II (BLM 321-II) Sta. 38a, 2 Aug. 1981, 25°16.50'N, 84°14.77'W, 156-161 m, otter trawl; (LACM 81-85.1), 1 paratype, BLM 321-II Sta. 38c, 2 Aug. 1981, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge; (USNM E34364), 1 paratype, BLM 321-III Sta. 38b, 10 Feb. 1982, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge; (IRCZM 74:504), 1 paratype, BLM 321-III Sta. 38c, 8 Feb. 1982, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge; (BMNH 1987.5.1.1), 1 paratype, BLM 321-III Sta. 38c, 8 Feb. 1982, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge. CUBA: (USNM 12441), 4 paratypes, ALBA-TROSS Sta. 2327, 17 Jan. 1885, 23°11'45"N, 82°17'54"W, 182 fm, tangles bar; (USNM E31661), 1 paratype, ALBA-TROSS Sta. 2163, 30 Apr. 1884, 23°10'31"N, 82°20'29"W, 133 fm, tangles bar.

Non-type material. SOUTHWEST FLORIDA, GULF OF MEXICO: (USNM E34365), 1 spec, BLM 321-II Sta. 38a, 2 Aug. 1981, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge; (USNM E34366), 1 spec, BLM 321-III Sta. 35c, 7 Feb. 1982, 25°44.84'N, 84°21.03'W, 158-164 m, triangle dredge; (USNM E34367), 2 spec, BLM 321-III Sta. 38c, 8 Feb. 1982, 25°16.50'N, 84°14.77'W, 156-161 m, triangle dredge. CUBA: (USNM 12395), 1 spec, ALBATROSS Sta. 2166, 1 May 1884, 23°10'36"N, 82°20'30"W, 196 fm, tangles bar; (USNM 15288), 3 spec, ALBATROSS Sta. 2322, 17 Jan. 1885, 23°10'54"N, 82°17'45"W, 115 fm, tangles bar; (USNM 15304), 5 spec, ALBATROSS Sta. 2345, 20 Jan. 1885, 23°10'40"N, 82°20'15"W, 184 fm, tangles bar; (USNM 15365), 6 spec, ALBATROSS Sta. 2336, 19 Jan. 1885, 23°10'48"N, 82°18'52"W, 157 fm, tangles bar; (USNM 15366), 2 spec, ALBATROSS Sta. 2326, 17 Jan. 1885, 23°11'45"N, 82°18'54"W, 194 fm, tangles bar; (MCZ 326), 1 spec, BLAKE Cruise-Bartlett Sta. 29, 1880, 21°23'19"N, 82°54'42"W, 300 fm. ST. CROIX: (MCZ 329), 2 spec, BLAKE Sta. 132, 5 Jan. 1878, 17°37'55"N, 64°54'20"W, 117 fm, rock/shell. BARBADOS: (MCZ 7430), 1 alcoholic spec, BLAKE Sta. 272, 5 Mar. 1879, 13°04'12"N, 59°26'45"W, 76 fm, coral/broken shell, BLAKE Sta. 278, 6 Mar. 1879, 13°04'50"N, 59°47'40"W, 69 fm, coral/broken shell or BLAKE Sta. 298, 10 Mar. 1879, 13°03'28"N, 59°37'40"W, 120 fm, rock (specimen separated from MCZ 819, consisting of three specimens from three BLAKE stations combined as one lot; all three specimens originally identified as Ophiozona impressa).

DIAGNOSIS. Dorsal surface of disc convex; interradial dorsal field with three columns of major scales. Major disc scales tumid, appearing smoothly joined to surrounding intercalary scales. Radial shields smooth. Intercalary scales forming irregular to tessellate, nearly continuous single rows separating most large scales. Radial primary plates separated by several wedge-shaped scales. Oral shields longer than wide. Arm segments not markedly constricted, wider than long at arm-tip. Dorsal arm plates separated by lateral arm plates present on proximal 13–16 arm segments. Ventral surface of arms with tentacle pores in depressed furrows alongside tumid ventral arm plates. Three arm spines on most arm seg-



Figure 10. Ophiolepis ailsae new species, holotype LACM 84-167.1: A, disc, dorsal view; B, portion of disc, ventral view; C, arm base, lateral view. Scale = 1 mm.

ments. Ventral arm spines thicker, nearly twice length of dorsal arm spines near disc; length about one-half arm segment. Adradial and abradial tentacle scales equal in size on arm segments beneath disc.

DESCRIPTION OF HOLOTYPE. Disc diameter 7.5 mm; longest arm about 24.1 mm (tip broken). Disc nearly circular; dorsal surface convex, with mid-dorsal region flattened; interradial region sloping ventrad; ventral surface flat. Arms thick at base, distal half abruptly tapering, flattened near tip; segments at arm-tip wider than long. Arms with dorsal midline depressed; ventral surface ridged with lateral edge and midline raised, tentacle pores depressed. Lateral arm plates tumid.

Distinct central rosette with tumid primary plates. Central plate round; diameter = 0.64 mm; radial plates ovoid, maximum width = 0.86 mm. Major peripheral disc scales longer than wide; distal margin thickened. Small intercalary disc scales flat, irregular in outline; in single rows bordering primary plates and most major dorsal disc scales.

Two wedge-shaped scales between radial primary plates. Radial dorsal field of disc with two large scales distal to each radial primary plate; distal scale larger, inserted between radial shields. Radial shields nearly triangular, with smooth, tumid surface. Two accessory radial shields distal to radial shields and linked by small polygonal scale. Interradial dorsal field of disc with three columns of major scales; four scales in central column larger than five scales in lateral columns. Several interradii with one or two subdivided major scales in central column.

Each jaw bearing a single apical and five lateral pairs of oral papillae. Distad to apical papilla, first and third papillae quadrilateral; second papilla compressed, pointed; fourth papilla largest, margin broadly rounded; fifth papilla (=buccal tentacle scale) triangular, elongate, attached to adoral shield; free end extending dorsad to fourth papilla.

Oral shield pentagonal, longer than wide; length = 0.86 mm, width = 0.68 mm; proximal margins concave, forming acute point; lateral margins straight, diverging; distal margin

convex. Madreporite with small round depression near center; single hydropore. Adoral shields tumid; members of each pair appear contiguous, but separated by microscopic gap.

Genital slit extending from oral shield nearly to edge of disc; opening unobstructed to third arm segment; bordered by long distal genital scale, two small scales proximad. Ventral interbrachial field of disc with fewer than 12 large scales.

Dorsal arm plates trapezoidal. Near disc, lateral margins straight, divergent; distal margin convex. Near arm-tip, lateral margins concave, distal margin with small median projection. Proximal 23–27 plates in contact; remaining plates separated by lateral arm plates. Accessory dorsal arm plates minute, present on proximal 13–16 arm segments; only first pair larger than dorsal arm spine.

Lateral arm plates in dorsal view flat to slightly concave on proximal segments, convex on distal segments, imbricated, with distal spine-bearing ridge adpressed to succeeding arm segment; narrowing distally in lateral view, with rounded distal margin; ventral surface with inflated lateral margin.

Arm spines minute, abruptly tapering, bluntly pointed. Ventralmost spine nearly one-half length of segment. Near disc, ventralmost spine often twice length of dorsal spines; longer than dorsal spines except at arm-tip. Spines usually three on each side of arm segment; 0–1 on first segment, 1–2 on second and third segments, three on fourth and subsequent segments, and 1–2 spines at arm-tip (Fig. 4B). Dorsalmost spines from arm segments 30–35 to the arm-tip with glassy terminal hook, sometimes with proximal secondary barb (Fig. 5F, G, I).

Ventral arm plates beneath disc broader than long, flattened; beyond disc, surface of plate tumid, proximal and narrow, distal end flared with pointed corners, lateral margins deeply concave. Ventral arm plates in contact until segment 25–30, remainder separated by lateral arm plates.

Two rounded-triangular tentacle scales of lateral arm plate forming ovoid operculum over each tentacle pore; operculum approximately one-half length of ventral arm plate. One or two miniscule tentacle scales on ventral arm plate concealed by operculum. Operculum seated in conspicuous depression. Adradial and abradial tentacle scales beneath disc similar in size; scales diminish in size toward arm-tip; beyond segment 34–40 only abradial tentacle scale covers each pore.

Color of preserved holotype. Disc and arms pale gray. Major plates with one to several brown or dark gray spots. Dorsal arm plates irregularly mottled with brown and gray, often with light border. Series of darkly pigmented dorsal and lateral arm plates forming five to seven dark bands on each arm. Ventral surface grayish-white.

Color of living holotype. Dorsally, disc gray with small reddish-brown spots. Arms whitish with reddish-brown and brown spots and patches; banded every 4–5 segments. Several segments have blotches of pale brownish-red bordered with white every 4–5 segments, forming bands. Arms and disc mainly white ventrally. Interradial areas of disc grayish; scales with white center, gray border. Jaw plates tinged with beige. Tube feet and buccal tentacles with transparent shaft, whitish tip; with microscopic black flecks.

VARIATIONS. Size. Disc diameters of 33 specimens

measured range from 4.9 to 9.9 mm (Fig. 6). Arm lengths range from 23 mm for a specimen with 7.5 mm dd to 37 mm for a specimen with 8.3 mm dd. The ratios of dd/arm length range from 3.1 to 4.5 ($\bar{x} = 3.8$).

Disc. Disc scales and radial shields are generally tumid with a thickened margin and rarely bent or nodulose. The central primary plate ranges in diameter from 0.54 mm in a specimen with 4.9 mm dd to 1.00 mm in a specimen with 9.9 mm dd. Arrangement of the large dorsal disc scales differs little from the holotype except in very small individuals. The oral shield is longer than wide (mean L/W ratio = 1.4, n = 33). Adoral shields may be contiguous or separated by a microscopic gap.

Arms. Most specimens have accessory dorsal arm plates for up to half the length of the arm. The distalmost arm segment with accessory dorsal arm plates occurs between segments 7-31 (median = 19). The proximal dorsal arm plates overlap; distal plates are separated by the lateral arm plates beginning between segments 18-39 (median = 29). The proximal ventral arm plates overlap; distal plates are separated by the lateral arm plates beginning between segments 20-44 (median = 32). There is 0-1 spine on each side of the first arm segment, 1-2 spines on the second, 1-3 (usually two) on the third, three (rarely two) on the fourth. There are usually three arm spines on succeeding segments, but 28 of 31 specimens have four arm spines on at least one arm segment. One specimen has two arm segments with five arm spines. Arm segments with four spines are usually on the proximal portion of the arm. They occur between segments three and 16, but 50% are between segments five and seven and 85% are between segments four and nine. Hooked dorsal arm spines occur on the outer one-sixth to one-fifth of the arm's length for up to 22 of the small, distal segments. The most proximal segment with hooked spines ranges from 20 to $43 \pmod{3}$ (median = 31). Tentacle pores on most of the arm have double tentacle scales, but there are single scales near the tip of the arm. Transition from two to one tentacle scale occurs between segments 23 and 52 (median = 39).

COMPARISONS. Ophiolepis ailsae and O. gemma differ from congeners with: flattened discs and arms (O. affinis Studer, O. crassa Nielsen, O. elegans Lütken, O. plateia Ziesenhenne, and O. variegata Lütken), four or more arm spines (O. impressa, O. pacifica Lütken, O. superba H. L. Clark, and O. unicolor H. L. Clark), and tuberculate scales (O. nodosa Duncan and O. rugosa Koehler). The new species are readily distinguished from O. cincta Müller and Troschel, which has a continuous series of supplementary dorsal arm plates on each arm segment, and from O. irregularis Brock, which has markedly unsymmetrically arranged disc scales. They superficially resemble two other small Caribbean congeners, but O. paucispina (Say) has only two arm spines, and O. kieri Hendler has the central primary plate in contact with the proximal edge of the radial plates, and radial shields with a rough concave surface.

DISTRIBUTION. Southern Gulf of Mexico, Bahama Islands, Cuba, St. Croix, and Barbados (Fig. 9); from 156 to 549 m depth (BLAKE specimen off Barbados, possibly as shallow as 126 m, noted in Material Examined).

ECOLOGY. The habitat where the holotype of O. ailsae was collected appeared barren in comparison to other Bahamian sites explored with the JOHNSON-SEA-LINK II submersible. On dive JSL-II-810, the terrain between 200 and 300 m was a sloping bottom covered with very few boulders, Halimeda fragments, sand, and scattered debris including leaf fragments. No significant water current was noted during the dive, and the bottom temperature was 17.50°C. At 270 m one comatulid crinoid was collected on a piece of rubble. After the dive, a specimen of O. ailsae was found wedged in an irregularity in the rubble. The only other ophiuroids collected during the dive were the large, very common, epifaunal species Ophiomyxa tumida Lyman and Ophiothrix sp. Other macrofauna observed from the submersible included a hermit crab, a few stalked crinoids, widely spaced "herds" of up to 50 individuals of an epifaunal irregular echinoid (Paleopneustes tholoformis Chesher), and a number of sand-dwelling cerianthids or actinarians.

The two stations from the southwest Florida shelf yielding nine specimens of *O. ailsae* were located on sloping bottom, at 156–164 m. Substratum consisted of sand and some coarse rubble covering a hard surface with occasional rocky outcrops. The area is probably biologically richer than the Bahamas site, but thinly populated. The cover of epibiota was reported as 15.5–21.4% in summer and 6.3–10.7% in winter. Cnidarians and sponges were the dominant sessile epifauna. At one station there were 37 cnidarian and 30 echinoderm species, and at the other station there were 35 cnidarian, 33 sponge, 35 crustacean, and 31 echinoderm species (K. Spring, pers. comm.). Data for a specimen from Cuba (MCZ 326) collected with shipboard gear extend the bathymetric range of the species to 549 m.

The living holotype of *O. ailsae* was observed to have microscopic sand grains adhering to the dorsal surface of the disc and arms. The sediment was presumably entrained in mucus secreted by the ophiuroid. The function of the coating of mucus and sediment is unknown.

Despite the species' small size, cryptic habitat, and coating of sediment, 43% of the individuals had suffered damage presumably caused by non-lethal predation. Of 32 specimens examined, 10 individuals had one regenerated arm and four individuals had two regenerated arms.

REPRODUCTION. Examination of the bursae through the genital slits showed no indication of brooding. The reproductive mode of the species remains unknown.

DISCUSSION

During nineteenth-century marine explorations, three currently valid species of *Ophiolepis, O. paucispina, O. elegans,* and *O. impressa,* were reported from the western Atlantic. *Ophiolepis paucispina* is known from Bermuda to Brazil as well as in the Gulf of Guinea off Africa. *Ophiolepis elegans* is found from South Carolina to Florida and through the Antilles. *Ophiolepis impressa* is reported from Bermuda to Brazil and throughout the West Indian region (distribution data in Clark, 1933; Parslow and Clark, 1963; Madsen, 1970). *Ophiolepis kieri,* discovered relatively recently, is still known only from the type locality off Panama.

This report brings to six the number of *Ophiolepis* species in the western Atlantic. The new taxa have been sampled from only a few localities (Fig. 9), but they appear to be widespread in the Caribbean. *Ophiolepis gemma* occurs at 21–139 m (with an unusual occurrence at 5 m, and a doubtful record from 404 m), and *Ophiolepis ailsae* at 156–549 m (with a doubtful record from 126 m). On the basis of available information, the new species appear to be less widely distributed than *O. elegans* and *O. impressa*, more widely distributed than *O. kieri*, and generally to occur at greater depths than other western Atlantic congeners.

Populations of O. ailsae are bathyal, occurring at depths in excess of hermatypic coral reef formations. Ophiolepis gemma, a deep-reef organism, also occurs well below depths accessible by SCUBA. However, its upper bathymetric limit is the relatively shallow crest of deep-reef walls. A similar deep-reef distribution seems to be typical of other newly described Caribbean ophiuroids (Hendler and Miller, 1984). It is interesting that most O. gemma collected from the seaward face of the Belize Barrier Reef are hardly half the size of the largest specimen (Fig. 6), whereas the few specimens dredged from deeper water (off Florida and Barbados) are larger than most individuals from Belize. In contrast to the size-frequency distribution for O. gemma, the distribution of O. ailsae is skewed to the right. The predominance of larger O. ailsae may be an artifact of selectivity of the sampling gear. It is possible that maximum body size of these species is related to depth or a correlated parameter, but data are too few for meaningful analysis.

At relatively shallow SCUBA stations (<25 m), Ophiolepis gemma was consistently collected with O. impressa, and occasionally with a yet undescribed congener (G.H., in prep.). This is noteworthy since O. impressa is also sympatric with O. kieri and O. paucispina in Panama (Hendler, 1979). Ophiolepis kieri was found under rubble fragments that sheltered congeners, but never with species of other ophiuroid genera. Thus it is possible that these Ophiolepis species have quite similar ecological requirements and are successful in analogous habitats over a range of depths. Ophiolepis impressa has been reported to occur from shallow water to 293 m, but its bathymetric range is probably much narrower since some deep-water specimens, previously referred to O. impressa, have been re-identified in this paper as O. ailsae. Ophiolepis impressa actually seems most abundant in shallow water, in sandy back-reef habitats (G.H., pers. obs.).

Ophiolepis gemma is the third small species in the genus reported to brood embryos. *Ophiolepis paucispina* is a simultaneous hermaphrodite, and individuals 3.2–5.4 mm dd are sexually mature (Hendler, 1979). *Ophiolepis kieri* is a protandrous hermaphrodite, sexually mature females ranging from 4.5 to 6.4 mm dd. *Ophiolepis gemma* reaches 6.2 mm dd, but individuals only 3.3 mm dd are capable of brooding. Its mode of sexuality is not known, but hermaphroditism is common for small brooding brittlestars (Hendler, 1975) and could be expected in *O. gemma*. If it is a synchronous brooder, as suggested above, it resembles *O. kieri* rather than *O.*

paucispina, which broods embryos of different ages (Hendler, 1979). The occurrence of brooding in *O. gemma* bears out an apparent tendency (Hendler, 1979) for *Ophiolepis* species to have modified embryos or larvae. Larger congeners, *O. elegans* and *O. cincta*, have yolky eggs, lecithotrophic larvae, and abbreviated development (Hendler, 1979).

The hooked arm spines observed in O. ailsae and O. gemma are a feature that previously has not been reported for the genus. Mortensen (1937) illustrated an ophiuroid fragment with hooked arm spines (possibly an ophiolepidine) from a Jurassic deposit in Germany. Hooked spines have been found in Ophiura species of the Ophiurinae (Paterson, 1985) and in species of Ophiomusium and Ophiosphalma in the Ophiolepidinae (Clark, 1941; Bartsch, 1983). They also occur in Ophiolepis species including O. paucispina, O. elegans, and O. impressa (G.H., pers. obs.). In comparison to the hooked spines of O. gemma, those of O. ailsae are more robust, have more pronounced subterminal barbs, and have a denser stereom (Fig. 5H, I).

It is clear from the detailed observations on O. gemma that the hooked spines arise on newly formed segments at the arm-tip, i.e., near the terminal plate. The location of the most proximal arm segment with hooked spines is directly related to the size of the individual. For example, in a specimen of 1.9 mm dd hooked spines are found on the eleventh arm segment, but in specimens greater than 3.6 mm dd hooks are found only between the twentieth segment and the end of the arm (Fig. 7). Therefore, hooked spines must be reshaped on the proximal arm segments while new hooked spines arise on young, distal segments. Since nearly all arm segments bear sets of three spines, it is obvious that the hooks are not shed and replaced by straight spines. In fact, a few transitional segments on each arm have spines with a shape intermediate between the hooked and the straight morphology. The abruptness of the change, over a span of a few arm segments, indicates that the terminal hook is not abraded, but rather is reshaped through the addition of new skeletal material. These observations strongly support Lyman's speculation that the hooked arm spines of Ophiura species originate as an "embryonic organ" (Lyman, 1869:320) at the tip of the arm and are "so overgrown as to form a stumpy spine" at the base of the arm.

Several functions might be attributed to the hooked arm spines, but direct observations on their function are lacking. Epifaunal ophiuroids such as Ophiothrix species use hooked spines for traction. However, their hooked spines are ventral and downward directed, while those of Ophiolepis species are directed upwards and project above the dorsal side of the arm (Fig. 5A, B, G). Juvenile Ophiothrix have relatively large, hooked arm spines with which they cling to appropriate substrata as they recruit to the benthos. In contrast, the Ophiolepis species that brood, and thus have benthic "crawl away" young, have hooked spines that probably are not needed for attachment to epibenthic substrata or for traction. Their role as "defensive" or "offensive" structures seems unlikely as well, the most compelling argument against such functions being the minute size of the spines. Moreover, Ophiolepis impressa does not compete successfully for space against sympatric ophiuroids (Sides, 1985), and western Atlantic *Ophiolepis* species are cryptic, avoiding contact with predators and sometimes even with other ophiuroids (Hendler, 1979). However, they exhibit a high incidence of non-lethal damage, as indicated by the substantial incidence of regeneration reported in this paper for *O. ailsae* and *O. gemma*. Thus, if the hooked spines are defensive or offensive in nature their effectiveness appears to be limited.

It is possible that the hooked spines function in feeding activities. Even relatively robust and seemingly rigid-bodied ophiuroids, such as *Ophioderma* species, can quickly coil the thin distal tip of the arm to capture prey (G.H., pers. obs.). When disturbed, *Ophiolepis paucispina* and *O. impressa* (especially the small specimens of the latter) can rapidly pull each of their arms into a tight coil atop the dorsal surface of the disc (G.H., pers. obs.). Although feeding behavior has not been reported for *Ophiolepis* species, the above observations on arm movement suggest that the hooked spines near the arm-tip might be used to retain small motile prey and other items for transfer to the mouth.

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