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OPHIODERMA DEVANEYI AND *OPHIODERMA ENSIFERUM*, NEW BRITTLESTAR SPECIES FROM THE WESTERN ATLANTIC (ECHINODERMATA: OPHIUROIDEA)

Gordon Hendler and John E. Miller

Abstract.—Two new western Atlantic brittlestars are described and illustrated in color. *Ophioderma devaneyi* n. sp., is a large (up to 39.6 mm disc diameter), robust, red-spotted species collected from the outer continental shelf and upper slope between Cape Hatteras and central Florida, and observed in situ from the Research Submersible *Johnson-Sea-Link*. It has also been identified in seafloor photographs from the Gulf of Mexico, off southern Florida. *Ophioderma devaneyi* is distinguished from its congeners by a combination of characters including subdivided dorsal arm plates, radial and adoral shields bare of granules, and truncate ventralmost arm spines. *Ophioderma ensiferum* n. sp., is a moderate-sized (up to 22.0 mm disc diameter), fragile species with a splendid pink or reddish disc and yellow- or orange-colored arms, collected by divers on the reef slope of the Belize Barrier Reef, off Carrie Bow Cay, Belize. It differs from other *Ophioderma* species with unfragmented dorsal arm plates in having arm spines that cover the tentacle scale and reach the base of the ventralmost arm spine of the adjacent arm segment.

In his review of the genus *Ophioderma*, Ziesenhenne (1955) recognized 21 constituent species. A majority of them (11 species) occurs in the western Atlantic region and one species, *Ophioderma elaps*, is known from moderately deep waters of the Caribbean region and the Galapagos Islands. Of the remainder, one species is eastern Atlantic, four Panamic, two southern African, and two of uncertain systematic status and questionable provenance have been reported from the Pacific. Since Ziesenhenne's (1955) study, three additional species of *Ophioderma* have been described, *Ophioderma besnardi* Tommasi, 1970, and *Ophioderma divae* Tommasi, 1971, from Brazil, and *Ophioderma anitae* Hotchkiss, 1982, from Belize. In this paper we describe two new and quite distinctive species of *Ophioderma* that we collected from Florida and Belize. Thus, our increasing knowledge of the genus confirms that the greatest diversity of *Ophioderma* species occurs in the western Atlantic region.

The coasts of Florida and Belize, though comparatively well explored, have continued to yield novel species of echinoderms in recent years. To an extent, this growth in apparent echinoderm diversity may reflect the application of recently developed collecting techniques and an increasing accessibility of poorly explored collecting sites. For example, one species in this contribution was taken using a research submersible on the Florida shelf-slope break, and the other by using a diver-applied ichthyocide solution on the steep seaward wall of the Belize Barrier Reef.

Specimens from such unfamiliar biotopes might be sampled with conventional gear but taken so seldom that they would not be recognized as new taxa. Indeed,

the species studied from the shelf-slope break has been sampled previously with standard trawling equipment and deposited unidentified in the collections of the National Museum of Natural History and the University of Miami. Additionally, specimens and photographs were sent to us for identification from the Outer Continental Shelf Survey of Duke University sponsored by the United States Bureau of Land Management, and by Continental Shelf Associates Southwest Florida Shelf Ecosystems Study.

We expect that the diversity of the relatively well-known western Atlantic echinoderm fauna will continue to grow as a function of increasing attention from biologists employing conventional as well as state-of-the-art oceanographic gear especially in difficult-to-sample habitats. Therefore, although we are preparing a more detailed treatment of the genus *Ophioderma,* we offer this preliminary contribution to facilitate and encourage the identification of brittlestars in old and new collections of echinoderms from the western Atlantic region.

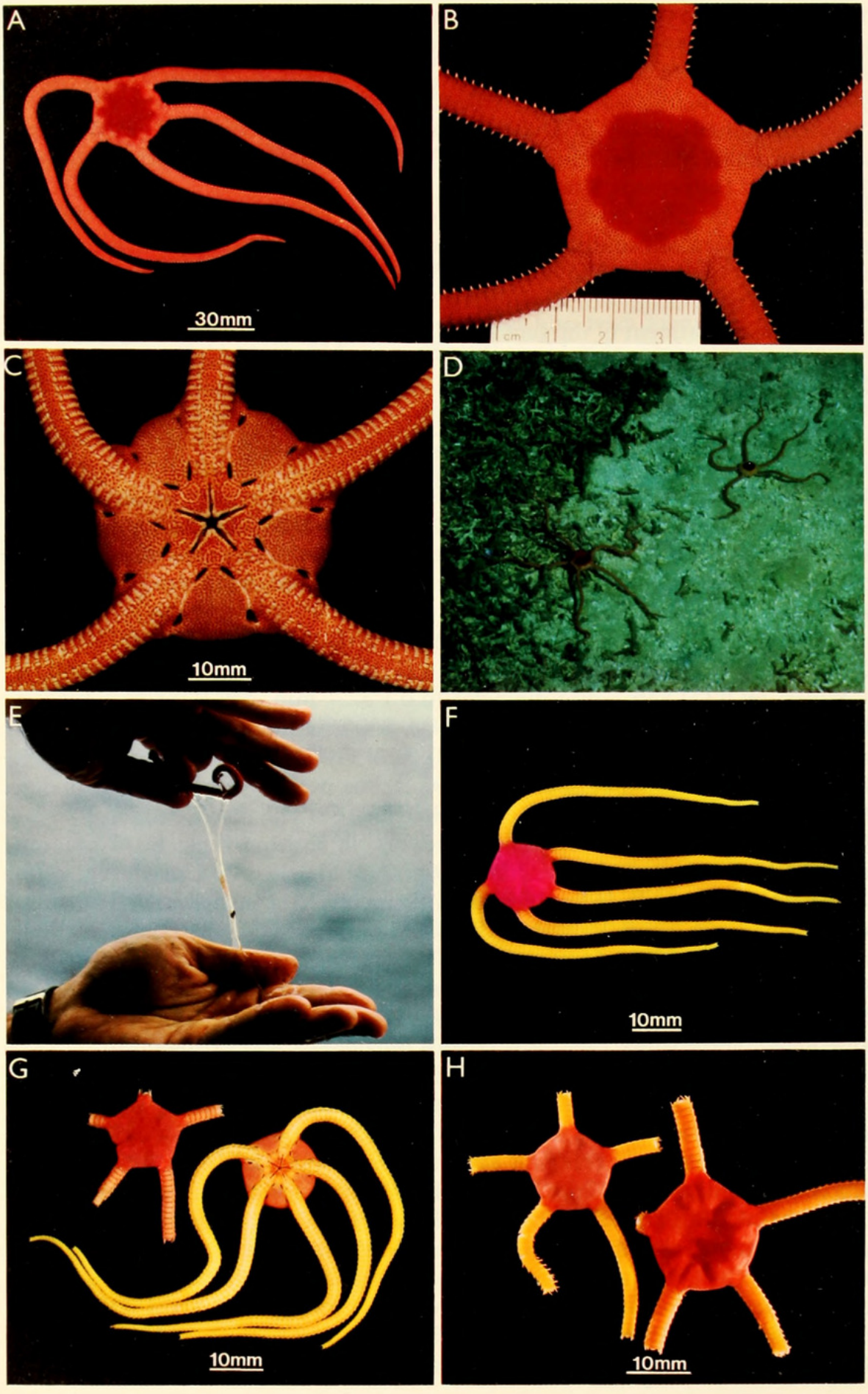
Ophioderma devaneyi, new species
Figs. 1–3.

Etymology.—This handsome species is named for the late Dr. Dennis M. Devaney, in recognition of his outstanding contributions to echinoderm biology.

Material examined.—All specimens in this series other than the holotype are paratypes.

FLORIDA: East of Sebastian Inlet: R/V JOHNSON Cr. 147, Sta. JSL-I-1267, 23 Sep 1982, 27°46.30′N, 79°58.52′W, 56 m, submersible manipulator, coll. J. E. Miller; HOLOTYPE—disc diameter (d.d.) 32.4 mm, dry (USNM E30565); Paratypes—d.d. 36.7 mm, alcohol (USNM E30566) [dissected], and d.d. 32.6 mm, alcohol (USNM E30567) [dissected]. R/V GOSNOLD, Cr. 248, Sta. 734, 18 Sep 1974, 27°49.7′N, 79°57.4′W, 76–80 m, box dredge, coll. L. E. Scotto; d.d. 13.0 mm, dry (USNM E30568). R/V GOSNOLD, Cr. 250, Sta. 759, 18 Feb 1975, 27°49.6′N, 79°58.9′W, 75–85 m, box dredge, coll. R. M. Avent; d.d. 27.1 mm, dry (USNM E30569). R/V JOHNSON, Cr. 062, Sta. JSL-I-583, 31 Aug 1978, 27°45.78′N, 79°56.79′W, 61 m, lock-out dive, coll. M. Mitchell; d.d. 38.9 mm, dry (USNM E30570). R/V JOHNSON, Cr. 147, Sta. JSL-I-1266, 22 Sep 1982, 27°46.30′N, 79°58.52′W, 56 m, submersible manipulator, coll. G. Hendler; d.d. 39.7 mm, 39.2 mm, 36.7 mm, 36.6 mm, and 35.5 mm, alcohol (USNM E30571), d.d. 34.9 mm, and 31.6 mm, dry (USNM E30572), and d.d. 34.6 mm, dry (British Museum Natural History 1984.2.16.1). R/V JOHNSON, Cr. 153, Sta. JSL-I-1323, 14 Mar 1983, 27°46.07′N, 79°58.52′W, 54 m, submersible manipulator, coll. J. E. Miller; d.d. 39.5 mm, dry (Indian River Coastal Zone Museum 074:00467), and d.d. 35.7 mm [damaged], dry (USNM E30573). FLORIDA: East of Key Largo (Straits of Florida): R/V COMBAT Sta. 457, 26 Jul 1957, 25°16′N, 80°07′W, 117 m; d.d. 29.7 mm, dry (USNM E30574). FLORIDA: Northeast of Cape Canaveral: R/V COMBAT Sta. 90, 3 Sep 1956, 28°52′N, 80°05′W, 117 m, from H. R. Bullis; d.d. 25.6 mm, alcohol (University of Miami Marine Laboratory 41.245). R/V JOHNSON, Cr. 141, Sta. JSL-I-1209, 17 Jun 1982, 28°46.7′N, 80°04.7′W, 76 m, submersible manipulator, coll. W. Japp; d.d. 39.6 mm, dry (USNM E30575).

SOUTH CAROLINA: R/V SILVER BAY Sta. 1393, 26 Oct 1959, 32°32′N, 78°40′W, 72–80 m, from H. R. Bullis; d.d. 33.3 mm, alcohol (UMML 41.246).


A
30mm
B
C
10mm
D
E
F
10mm
G
10mm
H
10mm

NORTH CAROLINA: Off Cape Fear: R/V EASTWARD Sta. OS05, sample no. 818055, 3 Mar 1981, 33°48.1'N, 76°34.7'W, 77 m, trawl, Dr. W. Kerby-Smith—Bureau of Land Management Outer Continental Shelf Survey (BLM); d.d. 32.5 mm, dry (USNM E30576). R/V DAN MOORE Sta. OS05, sample no. 818101, 14 May 1981, 33°48.3'N, 76°33.9'W, 104 m, Cerame-Vivas dredge, BLM; d.d. 27.1 mm, alcohol (USNM E30577). R/V CAPE HATTERAS Sta. OS05, sample no. 818318, 11 Nov 1981 33°48.3'N, 76°34.3'W, 100 m, Cerame-Vivas dredge, BLM; d.d. 29.9 mm and 25.6 mm, alcohol (USNM E30578).

PUERTO RICO TRENCH [Station data doubtful; sample label likely incorrect]: R/V PILLSBURY Sta. 1384, 6 Jul 1971, 19°09'N, 66°57.5'W, 7956 m, 41' otter trawl; d.d. 28.0 mm, alcohol (UMML 41.247).

Additional locality data (based on examination of photographs made from Continental Shelf Associates Southwest Florida Shelf Ecosystems Study).—FLORIDA: Gulf Coast shelf-break between Naples, Florida and Dry Tortugas Islands: Jul 1981—Transect C, Sta. +694, 25°45'30"N, 83°48'08"W, 106 m; Transect D, Sta. +841, 25°16'48"N, 83°57'01"W, 126 m; Sta. +839, 25°16'48"N, 83°56'50"W, 126 m; Sta. +769, 25°16'52"N, 83°50'35"W, 115 m; Sta. +843, 25°16'49"N, 83°57'12"W, 126.5 m; Transect F, Sta. +1013, 25°58'55"N, 83°44'43"W, 92 m; Sta. +130, 24°56'42"N, 83°47'05"W, 95 m; Sta. +675, 25°34'38"N, 83°47'59"W, 106 m; Sta. +670, 25°34'14"N, 83°47'50"W, 105 m; Sta. 36, 25°16'50"N, 83°57'21"W, 126 m. Nov 1981—Transect L, Sta. 21, 24°49'58"N, 83°56'27"W, 119.5 m; Sta. 27, 24°50'52"N, 83°57'21"W, 126 m; Sta. 28, 24°50'59"N, 83°57'33"W, 126.5 m; Sta. 30, 24°51'13"N, 83°57'51"W, 126.5 m; Sta. 31, 24°51'22"N, 83°58'02"W, 128 m; Sta. 48, 24°53'47"N, 84°00'40"W, 135.5 m; Sta. 62, 24°55'08"N, 84°01'57"W, 138 m; Sta. 76, 24°56'19"N, 84°03'31"W, 139 m; Sta. 88, 24°57'59"N, 84°05'25"W, 137 m.

Description of holotype.—Disc diameter 32.4 mm, longest arm 133.0 mm, broken just before tip.

Disc circular, periphery scalloped; inflated area at base of each arm. Rounded granules covering disc, not densely aggregated, extending to arm base; some granules between proximal-most dorsal arm plates. Radial shields bare, about 2.7 mm long × 1.6 mm wide; distance between paired shields about 1.6 times length of shield. Granules on aboral surface at center of disc approximately 54/mm^2, 85 ± 7 μm diameter ($\bar{x}$ ± s.d., n = 31); size increasing towards periphery of disc, largest at base of arms. Granules between paired radial shields approximately 45/mm^2, 122 ± 14 μm diameter (n = 31); those in ventral interbrachial area approximately 44/mm^2, 99 ± 9 μm diameter (n = 31).

Jaws bearing 16 to 20 oral papillae: outer papillae broadest, subtriangular; 1 to

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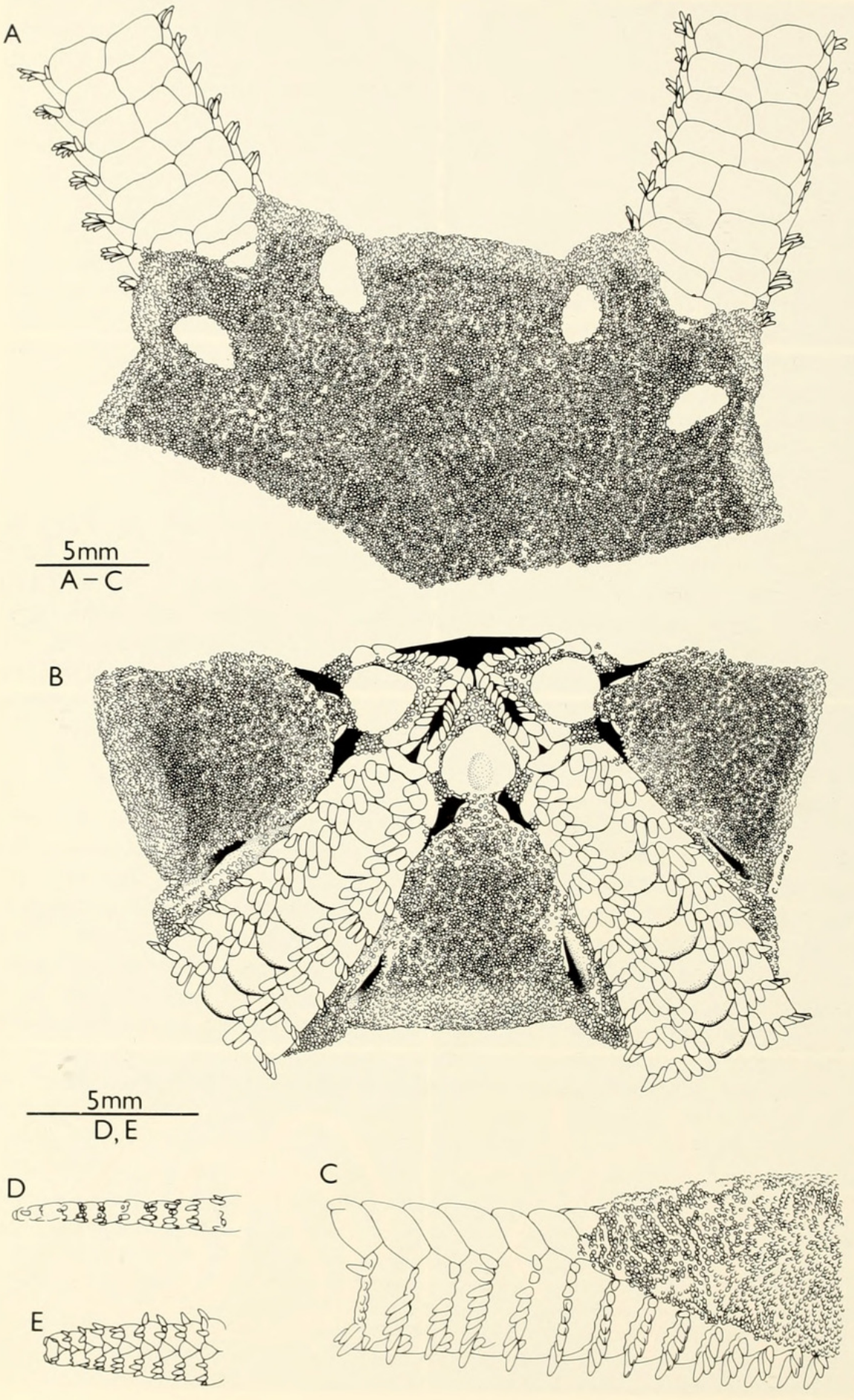
Fig. 1. A, *Ophioderma devaneyi* n. sp., holotype, USNM E30565, disc diameter 34.6 mm; B, *O. devaneyi* n. sp., holotype, dorsal view; C, *O. devaneyi,* n. sp., paratype, IRCZM 074:00467, disc diameter 39.5 mm, ventral view; D, *O. devaneyi* n. sp., in situ, *Oculina varicosa* coral bank, East of Sebastian Inlet, Florida, 56 m; E, *O. devaneyi* n. sp., mucous secretion flowing from broken arm fragment; F, *Ophioderma ensiferum* n. sp., holotype, USNM E30579, disc diameter 14.0 mm; G, *O. ensiferum* n. sp., (right) holotype, ventral view, (left) paratype USNM E30580, disc diameter 13.6 mm, dorsal view; H, *O. ensiferum* n. sp., paratypes, dorsal view, (right) USNM 30582, disc diameter 18.0 mm, (left) BMNH 1984.2.16.2, disc diameter 13.0 mm.


A
5mm
A – C
B
5mm
D, E
D
E
C

2 papillae at jaw apex irregularly spade-shaped, bluntly pointed, broad surface parallel with major plane of disc; lateral series of oral papillae irregularly shaped, their broad surfaces overlapping at an angle to plane of disc. Ventral buccal tentacle scale at jaw angle originating from adoral shield, extending into oral slit below oral papillae.

Oral shield about as wide as long; distal edge slightly concave; lateral edges nearly parallel; proximal, convex edges forming broadly rounded point. Granules border periphery of oral shields except for small gap along each genital slit. Madreporite slightly larger than oral shields, with median distal excavation.

Two pairs of genital slits per arm. Proximal slits extending from base of adoral shield to second arm-segment; shorter than distal pair. Indentation at disc margin running between end of distal genital slit and corresponding radial shield.

Granule cover extending from jaw apex, around oral shield to first lateral arm plate, into spaces between proximal lateral arm plates, across ventral interbrachial surface, around distal genital slits, over scales between edge of arm and distal slit. Thickened lateral area of adoral shield free of granules.

Arms ovoid in cross section near disc, tapering gradually, dorso-ventrally flattened near tip.

Dorsal arm plates with thickened distal edge; subdivided except near arm tip; fissures completely dissect subdivisions of dorsal arm plates: larger component pieces lateral, smaller pieces near central axis of the arm. Composite dorsal arm plates near disc arched, much wider than long (3.54:1 = length : width); distal medial edge slightly concave. Viewed laterally, dorsal arm plates occupying one-half height of arm; dorsal edge of lateral arm plate only reaching middle of arm.

Distal edge of lateral arm plate thickened, bearing up to 9 spines and 2 tentacle scales (Table 1), plate scalloped at base of each spine. Triangular ends of lateral arm plate inserting between successive dorsal and ventral arm plates.

Proximal, ventral arm plates somewhat wider than long (1.33:1 at ventral arm plate 10); most about as wide as long; proximal edges and lateral edges slightly indented; distal edges convex to semicircular. Paired pore-like gaps between distal edges of first proximal 2 to 3 ventral arm plates. Distal ventral arm plates longer than wide. Near arm tip, dorsal and ventral arm plates triangular; lateral arm plates massive, nearly hemispherical.

Tentacle scales near base of arm of nearly equal length; paired; inner scale subtriangular, slightly longer than outer scale. Beyond disc, inner scale becoming slender, ovoid, exceeding length of outer scale by up to one-third. At distal tip of arm, number of scales reduced to one; this remaining scale spine-like.

Dorsal arm spines thick, wedge-shaped in lateral aspect, with broad base and blunt tip. Ventral spines broader, with truncate tip. Most spines extending half way across adjacent lateral arm plate, length increasing slightly dorsad to ventrad. Ventral-most arm spine noticeably broadest and longest especially on proximal segments, partly overlapping tentacle scale of adjacent arm segment.

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Fig. 2. *Ophioderma devaneyi* n. sp., holotype, USNM E30565: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view; C, arm base, lateral view; D, arm tip, lateral view; E, arm tip, ventral view.

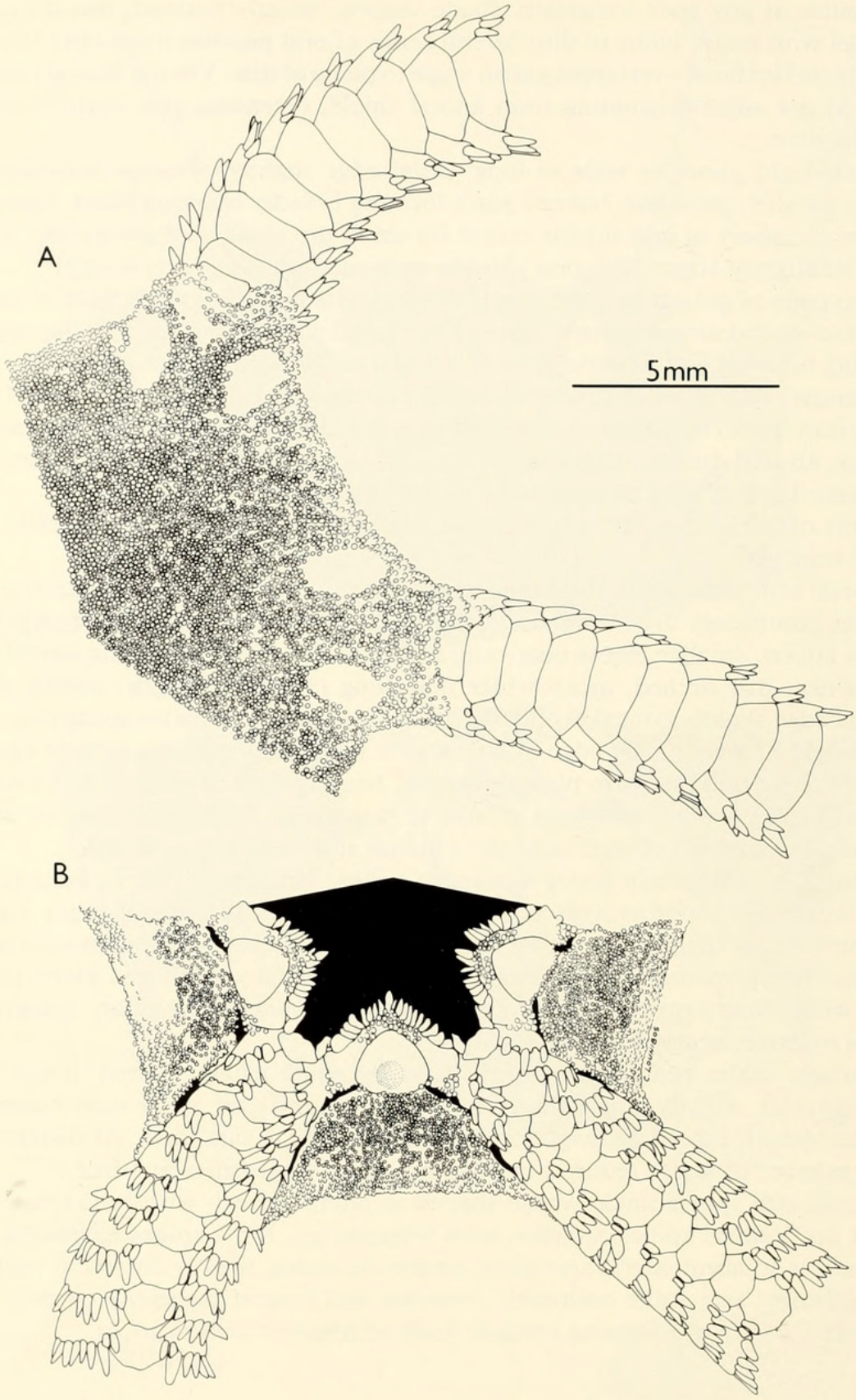

Fig. 3. *Ophioderma devaneyi* n. sp., paratype, USNM E30568: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view.

Color: Ground color of living specimen reddish-pink, covered by regularly-spaced deep-reddish spots. Ground color on dorsal surface, especially arms and radial shields, darker red and more intense than color on ventral surface. On ventral surface, jaws and arms more intensely pigmented than disc. Towards center of dorsal surface of disc, spots merge, forming a reticulate pattern, and then an irregular, stellate reddish-brown patch that covers middle of disc. Spots on disc have a more diffuse border than those on arms and radial shields. Spots cover remainder of animal except for distal portions of tentacle scales, oral papillae and arm spines. The white tips of these elements are strongly accentuated by the darker overall coloration of the animal. After preservation in alcohol, dried holotype shows same pattern of pigmentation, but pink and red coloration is replaced by pale tan and brown.

Variations in the Type-Series

Dimensions.—Disc diameters of the type-series range from 13.0 to 39.6 mm and maximum arm length from 47.0 to 193.0 mm. Ratios of arm length/d.d. range from 4.3 to 5.4 for specimens with intact arms.

Disc.—Number of granules/mm^2 at the center of the disc ranges from 43 to 88 ($\bar{x} \pm$ s.d. = 67.5 $\pm$ 14.3, n = 22). The granules range from 83 to 107 μm diameter ($\bar{x}$ = 92 μm), based on measurements of 31 mid-disc granules from each of 23 paratypes. In several of the paratypes, the granules between the first few dorsal arm plates are very few or missing entirely from all but one arm.

Radial shields.—Dimensions generally correlated with disc diameter. For the smallest specimen (13.0 mm d.d.) shield length is 0.88 mm and for the largest (39.7 mm d.d.), shield length is 1.16 mm, however the longest radial shields (1.96 mm) were measured on a 38.9 mm d.d. specimen.

Jaw.—There are 20 to 23 oral papillae on a jaw, exclusive of the buccal tentacle scale. Usually, there are 2 apical oral papillae, more rarely 1 or 3.

Oral shields.—Length/width ratio of the oral shield ranges between 0.88 and 1.13 ($\bar{x}$ = 0.99 $\pm$ 0.08, n = 23). In two specimens a genital scale adjacent to the oral shield is enlarged, resembling an accessory oral shield.

Adoral shields.—Only 2 of 23 paratypic specimens have any adoral shields completely covered by granules. One of these specimens has 1 of 10 shields covered, and the other has 2 of 10 shields covered and several that are partially concealed by granules.

Genital slits.—Proximal slits generally shorter, length rarely equal to or greater than, that of distal slits.

Dorsal arm plates.—All specimens with d.d. greater than 25 mm have numerous subdivided dorsal arm plates. A single specimen of 13.0 mm d.d. has only a few subdivided dorsal arm plates, but its arms are otherwise similar to those of larger specimens. Three of the arms (with 46, 49, and 52 segments) lack subdivided dorsal arm plates. A 31-segment arm has one subdivided plate and a 54-segment arm has 2 subdivided plates.

Arm spines.—The maximum number of arm spines of individuals in the type-series ranges from 7 to 10 (mode = 9, n = 23). The first arm segment with the maximum number is between segments 6 and 22 (mode = 10, n = 23) (Table 1).

Ventral arm plates.—Most paratypes have pairs of pore-like gaps between the

Table 1.—Numbers of arm spines per lateral arm plate presented for both sides of each arm segment of the holotype and for one side of the longest arm of a representative size-series of paratypes of *Ophioderma devaneyi* and *Ophioderma ensiferum*.

		Ophioderma devaneyi																								
		Arm segment																								
d.d.	Arm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
32.4	1-A	2	3	5	5	5	6	7	8	9	9	9	8	8	9	8	8	8	8	7	8	7	7	7	7	7
	1-B	2	3	4	5	4	6	7	8	9	9	9	9	8	9	8	8	8	8	8	8	7	7	7	7	7
	2-A	3	3	4	5	5	5	6	8	8	9	8	8	8	8	8	8	8	8	8	8	7	8	8	7	8
	2-B	3	3	4	4	6	5	6	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	7
	3-A	2	3	4	5	5	6	7	8	9	8	9	8	8	8	8	8	8	8	8	8	7	7	8	7	7
	3-B	2	4	4	4	5	6	7	8	9	9	9	7	8	8	8	8	8	7	8	8	8	7	7	8	7
	4-A	2	3	4	5	6	6	7	8	9	9	9	8	9	8	9	8	8	8	8	8	8	7	6	6	6
	4-B	2	3	5	5	5	7	7	8	9	9	9	9	9	9	9	9	8	8	8	8	8	8	5	6	7
	5-A	3	3	4	4	5	6	7	8	9	9	9	8	7	9	9	8	8	7	8	8	8	8	8	8	7
	5-B	3	4	4	4	5	6	7	8	8	9	9	9	8	9	8	8	8	8	8	8	8	8	7	8	8
13.0		3	4	4	5	5	6	7	7	7	7	7	7	7	6	6	7	7	7	7	7	7	7	7	7	7
24.9		1	3	4	5	6	6	7	8	9	9	8	8	9	8	7	8	8	8	7	7	7	7	7	7	7
25.6		3	3	5	5	6	7	8	8	9	9	9	8	9	8	8	9	10	10	8	8	8	8	9	9	8
28.0		3	3	4	4	5	6	7	7	8	8	8	8	8	8	8	8	8	8	8	8	8	9	7	7	7
29.7		3	4	4	5	5	6	7	8	8	8	8	9	8	8	8	8	8	8	8	8	8	8	7	7	8
31.6		3	4	4	5	6	5	6	8	8	9	9	9	9	9	8	10	8	9	8	8	8	8	8	7	8
34.6		3	3	3	4	5	6	6	8	8	8	8	8	8	8	8	7	7	7	8	8	7	8	7	7	7
36.6		3	3	4	5	5	5	6	7	8	8	8	8	8	9	8	8	8	8	8	8	8	8	7	7	7
39.6		3	3	4	5	5	6	5	6	7	8	9	8	9	8	8	8	8	8	8	8	8	8	7	6	7

Table 1.—Continued.

		Ophioderma ensiferum																								
		Arm segment																								
d.d.	Arm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
14.0	1-A	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6
	1-B	1	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	6
	2-A	2	2	3	3	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	2-B	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6
	3-A	2	2	3	4	4	5	6	6	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5
	3-B	1	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6
	4-A	2	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	4-B	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5
	5-A	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	5	5	5
	5-B	3	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	6	5
13.0		2	3	3	4	5	6	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
13.6		2	3	3	4	5	5	6	6	6	6	6	6	6	6	6	6	6	6		B	R	O	K	E	N
18.0		3	2	3	4	4	5	5	6	7	7	7	7	6	6	6	6	6	6	6	7	6	7	6	6	6
19.5		2	3	3	3	4	5	5	6	6	7	7	7	6	7	7	5	5	6	7	7	7	7	6	6	6
22.0		3	4	4	4	4	5	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	7	6

first 4 ventral arm plates (a few specimens have pores between the first proximal 2 and 3 plates or between the first proximal 5 plates).

Tentacle scales.—Over half of the paratypes have 1 to 4 lateral arm plates with 3 (rather than 2) tentacle scales. The supernumerary scale is generally thinner than the flanking scales. Most extra scales are within 4 segments of the disc but some occur at least to segment 33.

Color.—The color pattern of the paratypes is similar to that of the holotype. Specimens briefly fixed in formaldehyde or in alcohol and dried retain much of their red pigmentation. Those preserved in alcohol for more extended periods are leached to varying degrees, and the pink and red coloration is replaced by pale tan and brown. In preserved material, the more intense ground coloration and the spots on the dorsal surface remain darker than the ventral color pattern. In faded specimens, the characteristic central patch remains evident on the dorsal surface of the disc, and even in severely faded specimens it is present as a pale gray area. This patch may cover from one-third to nearly the whole dorsal surface of the disc. The oocytes and ovaries have a reddish-pink color, similar to the pigmentation of the disc; the testes are white.

Relationships

In life, *Ophioderma devaneyi* is easily differentiated from all congeners by its distinctive red-spotted color pattern. In comparison with other western Atlantic congeners, preserved specimens even with leached pigmentation can be recognized as follows. Only four western Atlantic species have subdivided dorsal arm plates. Two of them, *Ophioderma guttatum* Lütken and *Ophioderma squamosissimum* Lütken, have flattened disc granules, while those of *Ophioderma devaneyi* and *Ophioderma cinereum* Müller and Troschel are round. Unlike *O. devaneyi, O. cinereum* has bare rather than granule-bearing scales bordering the dorsal base of the arm, tapered and pointed rather than truncate ventralmost arm spines, adoral shields generally covered with granules rather than with a bare spot, and oral shields markedly wider than long. *Ophioderma brevicaudum* Lütken and *Ophioderma elaps* Lütken, which rarely have subdivided dorsal arm plates, consistently have their radial shields covered by granules, while the radial shields of *O. devaneyi* are bare of granules. Care should be taken to differentiate faded, preserved specimens of *Ophioderma guttatum* and possibly *O. divae* from similarly stippled, preserved specimens of *O. devaneyi.*

Ecological Observations

Habitat.—The known range of *Ophioderma devaneyi* extends from North Carolina (East of Cape Fear) to the Straits of Florida (East of Key Largo), in depths between 54 and 117 m. The species has been identified from underwater photographs taken in the Gulf of Mexico at points west of Naples, Florida and the Dry Tortugas in depths between 92 and 139 m (see "Material examined" section).

All stations where *Ophioderma devaneyi* has been identified are on the edge of the continental shelf. At these depths, sunlight is considerably dimmer than at the surface. It is sufficient for visual navigation at close range, but for detailed observations artificial lighting is necessary. Light intensity may fluctuate drastically due to localized phytoplankton blooms and to turbidity from sediments

suspended by rough seas. Bottom currents also create sediment scour at the sampling sites (G.H. and J.E.M., pers. obs.).

Probably attributable to influence of the Gulf Stream, bottom temperatures from the northern end of the species' range are similar to those at the southern end and temperatures at both sites show definite seasonality. MacIntyre and Milliman (1970) reported mean monthly temperatures ranging from 17°–22.5°C off Cape Fear, North Carolina, and Reed et al. (1982) recorded a 7.5°–26.5°C annual range off Sebastian Inlet, Florida.

The shelf-break habitat of *Ophioderma devaneyi,* between North and South Carolina (the northern end of the species' range) has been characterized by MacIntyre and Milliman (1970) as a zone with variable development of terraces and ridges, and with rock surfaces protruding through a gravel-sand sediment. They noted an epifauna consisting of tube-building polychaetes, barnacles, bryozoans, and Foraminifera. A rich macrofauna including demosponges and crinoids is found there as well (W. Kerby-Smith, pers. comm.).

Further south, the habitat of *Ophioderma devaneyi* is markedly different. A dominant feature of the shelf-break of the East Coast of Florida is steeply sloping banks covered with thickets of the branching coral, *Oculina varicosa* Lesueur (Reed 1980). The substratum that is not occupied by coral in this region is covered with greenish silty sand and coral rubble. Numerous fish and dense invertebrate assemblages of hydrozoans, actinarians, and echinoderms inhabit the coral banks. South of the *Oculina* ridges, between Palm Beach and Fort Lauderdale, Florida, there is a narrow continental shelf and a shallow shelf-break supporting an "inactive" coral reef system (MacIntyre and Milliman 1970). *Ophioderma devaneyi* has not been sampled here, but it occurs at approximately the same latitude at the edge of the broad Gulf Coast shelf. There the bottom is sandy with chunks of rubble and occasional rock outcrops. Seafloor photographs of the area show fishes, numerous comatulid crinoids, gorgonian fans, antipatharian whips, some actinarians and tunicates, and an encrusting biota that appears to consist of calcareous algae, bryozoans and sponges.

Distribution.—Although the shallow, landward portions of the continental shelf have been sampled off North Carolina, and the Atlantic and Gulf Coasts of Florida, *Ophioderma devaneyi* has been collected only from a narrow zone spanning the continental slope break (J. Reed, W. Kerby-Smith, K. D. Spring, pers. comm.; G. H. and J. E. M., pers. obs.). In addition, the species was not observed during extensive series of submersible dives at depths where it might be expected to live off Grand Bahama and San Salvador Islands in the Bahama Islands. That *Ophioderma devaneyi* does not have a wider distribution is remarkable considering the broad temperature range, stressful conditions, and the variety of reef and hard bottom habitats occupied by the species.

Ophioderma devaneyi was consistently found on the upper 10 meters of the *Oculina* ridges off Sebastian Inlet, Florida, during a series of vertical transects run with the *Johnson-Sea-Link* submersible between 56 and 86 m depth. Extensive operations with the submersible on a number of the Florida slope-break ridges have shown that the distribution of *O. devaneyi* is not uniform. There are extensive areas where the brittlestar is not seen, but where it does occur, densities of 3 to 4 individuals per m^2 are common.

Typically, large individuals are observed in the open or less frequently, under

coral colonies or rubble with several arms completely exposed (Fig. 1D). Limited examinations of *Oculina* thickets and rubble revealed no small *Ophioderma devaneyi* or concealed adults. In photographs of the Gulf Coast population specimens were usually located near areas with rubble or rock outcrops. In photographs showing contiguous expanses of sand and of rubble, *O. devaneyi* was always near the rubble rather than on the comparatively featureless terrain nearby. They resembled deep-sea ophiuroids rather than their shallow-water congeners in that they remained in the open rather than concealed, even when shelter was available nearby. In New Zealand, *Pectinura maculata* (Verrill), a reddish species similar in size to *O. devaneyi* lives in the same way in some areas (D. L. Pawson, pers. comm.).

Most specimens had a disc diameter (d.d.) exceeding 25.0 mm, and specimens reached 39.6 mm d.d. and an arm length of 193.0 cm. The only small specimen examined (13.0 mm d.d., 47.0 mm arm length) was recovered from a box dredge sample that included a specimen of *Ophioderma elaps*. Since we found *O. elaps* under clumps of *Oculina*, the dredge observation suggests that small *O. devaneyi* may be more cryptic than large specimens.

Behavior.—Shallow-water reef-associated ophiuroids show a spectrum of behavioral and morphological types from extremely agile and delicate species such as *Ophioderma appressum* (Say) to sluggish, heavily calcified species such as *Ophioderma brevicaudum*. *Ophioderma devaneyi* is much larger but similar to the latter species in that it is heavily calcified and responds with slow movements to mechanical stimulation (e.g., prodding with a submersible manipulator). When the submersible manipulator suction tube was applied to *O. devaneyi*, specimens invariably extended and stiffened their arms.

Only one specimen was seen actively crawling without artificial provocation. This observation was made during the afternoon. At night, *Ophioderma devaneyi* occupied similar positions and showed similar postures as in the day. They usually were situated on the sediment with one or several arm tips slightly raised, and sometimes with their disc somewhat raised off the bottom (Fig. 1D).

The arms of some specimens were regenerated, indicating that *Ophioderma devaneyi* is subject to predation; arm damage from physical stress is unlikely in these resilient ophiuroids. How their vulnerability can be reconciled with their tendency to remain in the open is unclear. Although their red speckling and red disc stand out in artificial illumination, under natural light their pigmentation pattern and slow movement could provide camouflage, and their large size could deter some predators. The ability of *O. devaneyi* to produce mucus may also provide some defense. Injured animals, specimens that were roughly handled, and specimens subjected to fresh-water shock exuded copious quantities of mucus that was so viscous it could be cut with scissors (Fig. 1E). Since the mucus was tasteless (to G.H.) it is likely that its slipperyness acts as a mechanical defense rather than as an irritant to predators. Two shallow-water congeners, *Ophioderma guttatum* and *O. squamosissimum*, also produce mucus when injured, but tests for copious mucus production in other *Ophioderma* species (*O. appressum*, *O. brevicaudum*, *O. brevispinum*, *O. cinereum*, *O. phoenium* H. L. Clark, and *O. rubicundum* Lütken) gave negative results (G. H., pers. obs.).

Ophioderma devaneyi also differs from reef-associated congeners in its unresponsiveness to fresh bait. Specimens offered crushed sea urchins (*Centroste-*

phanus longispinus rubricingulus H. L. Clark) in situ showed no feeding response, even when in direct contact with echinoid tissue. Fishes were attracted to the area and fed on the urchins within 15 sec. The stomach contents of two *O. devaneyi* were examined. In addition to the largest item, a 2.3 mm long gastropod, the stomachs contained 2–3 gastropod postlarvae or veligers, remains of several copepods and an amphipod carrying eggs, a fecal pellet, a few unidentifiable crustacean parts, and some shell fragments. These items are not revealing of the feeding habits of the species. They not only resemble items ingested by the carnivorous, shallow-water *Ophioderma brevispinum,* but also the stomach contents of *Ophioderma longicaudum* (Retzius), a microphagous feeder (Deschuyteneer and Jangoux 1978; Hendler 1982). *Ophioderma devaneyi* more closely resembles the latter species in that its lack of response to bait is like the negative chemosensory response of *O. longicaudum* and completely unlike the ravenous feeding behavior and positive chemosensory reactions of *O. brevispinum* and reef-dwelling congeners (Reimer and Reimer 1975; G.H., pers. obs.). Although the stomachs examined were not filled with sediment, evidence of selective feeding suggested by the stomach contents of *O. devaneyi* cannot be reliably gauged on the basis of only two specimens.

Reproduction.—Shallow-water, reef-dwelling *Ophioderma* species (*O. appressum, O. brevicaudum,* and *O. rubicundum*) have oocytes about 0.3 mm in diameter (Hendler 1979). *Ophioderma devaneyi* of 36.0 mm d.d. and 32.6 mm d.d., collected 23 Sep 1982, had oocytes about the same size ($\bar{x} \pm$ s.d. = 0.32 ± 0.02 mm and 0.32 ± 0.03 mm, n = 30 for each). Other *Ophioderma* species that have been reared (*O. brevispinum, O. cinereum,* and *O. longicaudum*) have eggs of the same size and all produce rapidly-developing, lecithotrophic vitellaria larvae (Hendler 1979). Considering the agreement found between ophiuroid oocyte size and mode of reproduction (Hendler 1975), it seems likely that *O. devaneyi* has a vitellaria larval form.

Ophioderma ensiferum, new species
Figs. 1, 4.

Etymology.—The specific epithet is derived from the Latin words ensis, "sword" and fero, "to bear," referring to the long, pointed arm spines of the species.

Material examined.—BELIZE: ESE of Carrie Bow Cay on the seaward forereef slope of the Belize Barrier Reef. Sta. Belize-83 No. 02, 2 Apr 1983, 24 m, poison station, coll. G. Hendler, B. Littman, B. Spracklin; HOLOTYPE—disc diameter (d.d.) 14.0 mm, dry (USNM E30579) and paratype, d.d. 13.6 mm, alcohol (USNM E30580). Sta. Belize-83 No. 10, 7 Nov 1983, 24 m, poison station, coll. G. Hendler, B. Littman, B. Sullivan; paratypes, d.d. 22.0 mm, and 19.5 mm, alcohol (USNM E30581). Sta. Belize-83 No. 11, 8 Nov 1983, 24 m, poison station, coll. M. Byrne, M. Carpenter, G. Hendler, B. Littman, B. Sullivan; paratypes, d.d. 18.0 mm, dry (USNM E30582) and 13.0 mm, dry (British Museum Natural History 1984.2.16.2).

Description of holotype.—Disc diameter 14.0 mm; longest arm 66.0 mm, all arms broken before tip.

Disc subpentagonal, covered with rounded granules; about 160 granules/mm^2, diameter 61 ± 4 μm ($\bar{x} \pm$ s.d., n = 31) at center of upper surface of disc. Granules slightly larger but less numerous around the dorsal periphery of the disc and on

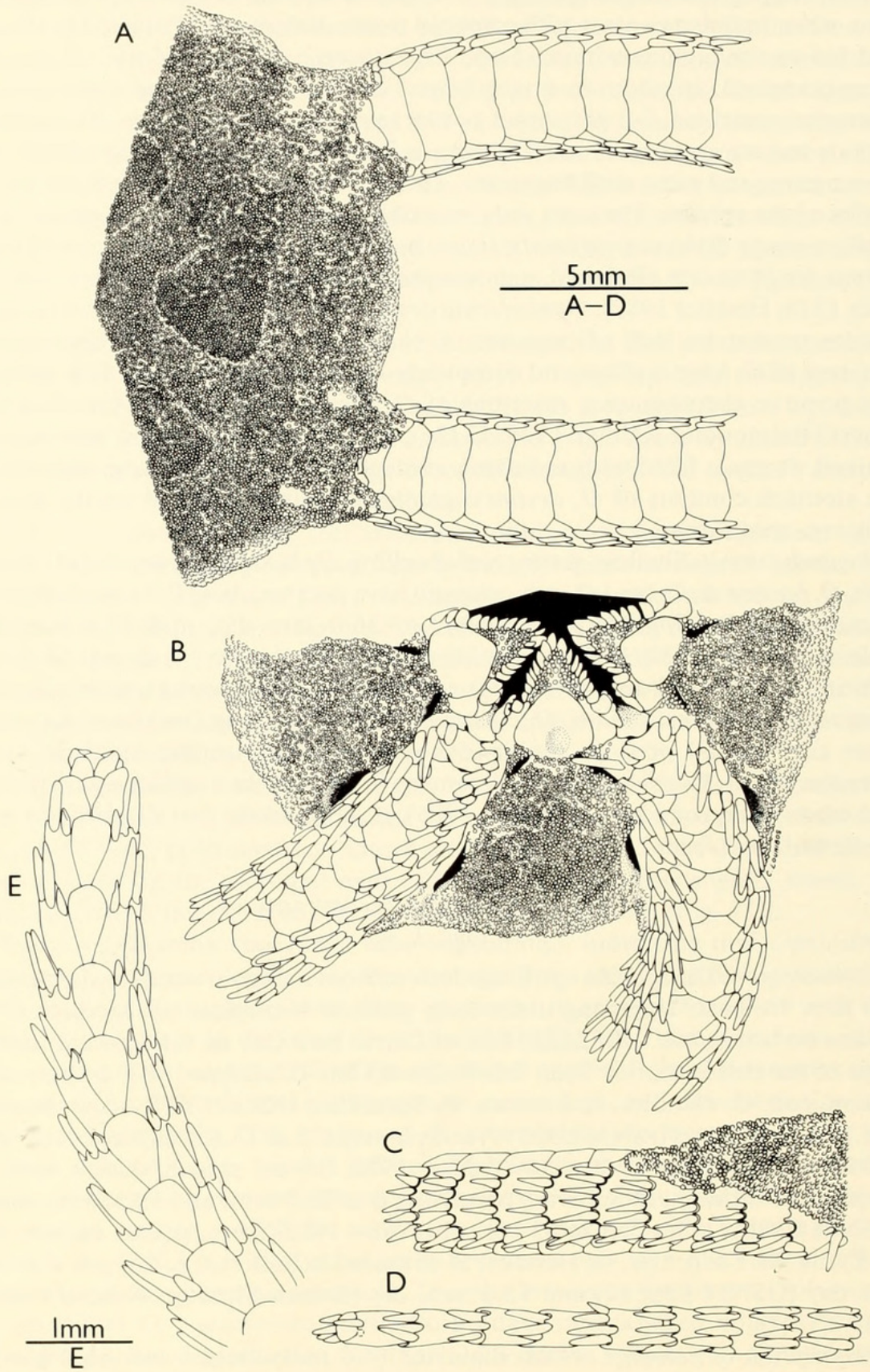

Fig. 4. *Ophioderma ensiferum* n. sp., holotype, USNM E30579: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view; C, arm base, lateral view; D, arm tip, lateral view; E, arm tip, ventral view.

scales at arm base. Approximiately 79 granules/mm^2, diameter 70 ± 6 μm (n = 31) between paired radial shields; approximately 110/mm^2, diameter 69 ± 7 μm (n = 31) in ventral interbrachial region. Radial shields small (mean length × width = 0.75 × 0.48 mm) and with very few attached granules. Paired radial shields separated by gap about 2.9 × shield length.

Jaws bearing 16 to 19 oral papillae. Two to 3 apical papillae and distalmost 2 to 3 papillae largest; broad surface of apical papillae and 3 to 4 distal papillae parallel to major plane of disc; plane of proximal papillae perpendicular to disc plane. Ventral buccal tentacle scales at jaw angle attached to adoral shields, projecting into oral slit below oral papillae.

Oral shields pentagonal, slightly wider than long (length : width = 1:1.26); broad base almost straight; short lateral edges nearly parallel; proximal edges convex; apex rounded. Madreporite slightly larger, more irregular in outline than oral shields; lateral ends of base convex; medial distal surface slightly depressed.

Two pairs of genital slits per arm; proximal slit extending from base of oral shield to first arm segment; distal slit longer than proximal, separated from arm by narrow portion of genital plate bare of scales and granules.

Most of surface of adoral shields free of granules. Widely spaced granules, taller than interbrachial granules, covering jaw from base of oral papillae just to proximal edge of oral shield; band of smaller granules along distal edge of oral shield and proximal end of genital slit to first lateral arm plate; granules covering ventral interbrachial surface.

Arms tapering gradually, proximal portion flattened-ovoid in cross section; dorsal surface slightly arched near disc, flattened near tip of arm.

Dorsal arm plates not fragmented; L:W ratio = 1:2.1 at base of arm; distal edge slightly concave and not thickened, often with small medial notch; lateral edges rounded, with curved postero-lateral corners and antero-lateral corners converging proximally to meet the preceding dorsal arm plate. Distal dorsal arm plates with long, convex antero-lateral edges; plates triangular near tip of arm.

Lateral arm plates covering nearly entire side of the arms; triangular ends of plate insert between dorsal and ventral arm plates; thickened distal edge, scalloped at base of arm spines, bearing maximum of 7 arm spines and 2 tentacle scales (Table 1).

Paired pore-like gaps between edges of first proximal 2 to 3 ventral arm plates. Beyond pores, proximal ventral arm plates octagonal, slightly wider than long (ratio 1:1.1), proximal and lateral edges slightly concave. Distal ventral arm plates longer than wide, hexagonal; posterior edge convex, lateral edges concave, slightly concave proximal edges converging towards preceding ventral arm plate.

Inner tentacle scales ovoid to spatulate, longer and thinner than polygonal outer tentacle scale, increasingly more slender towards tip of arm. At distal end of arm number of scales reduced to one; this remaining scale elongate, with sharp tip.

Arm spines thin, slightly flattened laterally, gradually tapering to blunt tip; length increasing from dorsal to ventral end of lateral arm plate: dorsal spine spanning one-half width of adjacent lateral arm plate, penultimate ventral spine touching edge of adjacent ventral arm plate. Ventralmost spine similar but thicker and longer than those dorsad, extending beyond tentacle scale of adjacent segment to base of ventralmost arm spine.

Color: In life, holotype brilliantly pigmented with deep-pink disc and yellow

arms. Under low-power magnification, disc granules pale pink, almost white; disc scales and radial shields pink with minute, deep pink flecks. Minute pink flecks along lateral and distal edges of bright yellow dorsal arm plates. Lateral arm plates yellow. Ventral arm plates pale yellow flecked with microscopic orange spots, border of plates golden-yellow. Near distal tip of arm microscopic flecks disappear, yellow color more intense. Ventral surface of disc slightly more pale than dorsal surface, especially near oral frame. Yellow color of arms less intense ventrally than dorsally. Arm spines banded with yellow and white at base and tip. Tube foot shaft pale reddish-orange, tip red. Oral and adoral shields pale orange, speckled with microscopic red spots; edge of oral shield pink. Jaws pink, flecked with red specks; oral papillae pink.

Holotype preserved in alcohol and dried: granulose portion of disc very pale tawny off-white color, arms and oral frame and radial shields white.

Variations in the Type-Series

Disc.—Disc diameters of paratypes range from 13.0 to 22.0 mm. Shape and granulation of paratype discs similar to holotype. On one large specimen, a few scales near the arm base lacked any granules. For paratypes, the density of mid-disc granules ranges from 104 to 165/mm^2, and the diameter of granules from 56 to 84 μm.

Radial shields.—The density of granules on the radial shields is lower than elsewhere on the disc. One paratype (19.5 mm d.d.) has radial shields that partly lack granules; about one-half of each shield is bare. Dimensions of the radial shield are proportional to the size of the specimen. The smallest specimen (13.0 mm d.d.) has radial shields 0.79 mm long; the largest (22.0 mm d.d.) has shields 1.17 mm in length.

Jaws.—All paratypes have 16 to 18 oral papillae (excluding the buccal tentacle scales) per jaw.

Oral shields.—Widths range from 1.15 to 1.37 times the length of the shield. In the larger specimens, the oral shield is more subpentagonal than subcordate, with the proximal edges nearly straight rather than convex.

Genital slits.—Relative length of the proximal and distal slits is variable, even within a single specimen. Proximal slits are more often smaller or equal in size rather than longer than distal slits. There are a few granules occupying the space between the distal genital slit and the arm in only 3 slits of the largest (22.0 mm d.d.) specimen. Other specimens consistently lack granules in this region.

Arms.—One paratype with arms broken just before the tip has 90.0 mm arms and a 19.5 mm disc, arms of other paratypes broken near disc. Ratio of arm length to disc diameter in the relatively undamaged specimen (4.6:1) is similar to that of the holotype.

Dorsal arm plates.—For paratypes, L:W ratio near disc ranges from 1:1.91 to 1:2.70 ($\bar{x}$ = 1:2.32).

Ventral arm plates.—Several paratype specimens have paired pore-like gaps between only one pair of proximal ventral arm plates rather than between several plates.

Arm spines.—Only one specimen has a maximum of more than 7 arm spines. It has 8 arm spines on only one lateral arm plate (Table 1).

Tentacle scales.—In a single case, 3 scales are found on one arm segment near the disc. All other proximal arm segments of the paratypes have paired tentacle scales.

Color.—In life, the color of the disc may vary according to the size of the specimen, and the color of the arms is more variable than that of the disc. Individuals 13.0 to 14.0 mm d.d. had a deep-pink disc, and the specimens 18.0 to 22.0 mm d.d. had dark reddish-pink discs. The arms of one small paratype were pale pink, but the other small specimens had bright yellow arms. One large specimen had orange arms, and the arms of another large paratype were reddish-orange. The colors on the ventral side of the discs and arms of all specimens were paler than those described for the dorsal surface. As in the holotype, the oral shields of other examples in the type series were tinted pale orange to pale red, and the jaws were pink.

The pigments of *Ophioderma ensiferum* are rapidly leached by ethanol. Alcoholic specimens and dry specimens initially preserved in alcohol have white arms and a gray disc. Two specimens held in formaldehyde overnight prior to drying lost some orange pigment during preservation, but they retained much the same color they had in life.

Relationships

The gaudy pigmentation of living *Ophioderma ensiferum* type specimens is unique in the genus, but it is a variable and labile characteristic. Only 6 other western Atlantic species of *Ophioderma* with unfragmented dorsal arm plates and bare radial shields have been described. None of these species: *O. anitae, O. besnardi, O. divae, O. pallidum, O. phoenium,* and *O. rubicundum* have ventral arm spines that cover the tentacle scale and reach the base of the ventral spine on the adjacent arm segment. *Ophioderma ensiferum* also is unique in lacking bare scales at the base of the arms and in lacking scales between the arm and distal genital slit (these characters were not discussed in the descriptions of *O. besnardi* and *O. divae*).

Ecological Observations

The six specimens of the type series were collected on the seaward face of the Belize Barrier Reef. The habitat, a section of the reef about 24 m deep on a 50° to 70° slope, was characterized by mounds of shelflike coral colonies of *Montastrea annularis* (Ellis and Solander), and by large plates of *Agaricia lamarcki* Milne Edwards and Haime, distributed every few meters. The living and dead coral structures were surrounded by a dense cover of algae (especially *Halimeda* and *Lobophora* spp.) and separated by patches of coarse calcareous sand. Also at this depth were numerous, scattered small colonies of platy, foliose and massive corals (e.g., *Mycetophyllia, Diploria, Agaricia,* and *Siderastrea* spp.), small branching gorgonians (e.g., *Pseudoplexaura* and *Pseudopterogorgia* spp.) and a variety of desmosponges. Invariably, we noted a slow current moving along the face of the reef slope and found that visibility varied on different days from about 10 to over 30 m. This biotope is further illustrated and described by Rützler and MacIntyre (1982:30–37).

Ophioderma ensiferum was collected at 3 of 6 poison stations in this area. The specimens were forced from interstices under coral colonies by applying a commercial ichthyocide ("Noxfish", Peneck Corp.). They were acutely affected by the ichthyocide, remaining inactive after capture. The predominant associated organisms driven from the reef were other brittlestars, mostly *Ophioderma rubicundum* and *Ophiurochaeta* spp., and modest numbers of small fish and crustaceans.

Acknowledgments

We dedicate this contribution to Mr. S. Dillon Ripley, Secretary of the Smithsonian Institution, in gratitude for his efforts to foster field research in systematic biology.

The basis for naming a new species *Ophioderma devaneyi,* briefly alluded to in the etymology, merits elaboration. The late Dennis Devaney served as Chairman of the Department of Zoology at the Bernice Pauahi Bishop Museum and was a major contributor to echinoderm biology, particularly the systematics of Ophiuroidea. Dennis Devaney disappeared while diving off the island of Hawaii, near Mahukona, on 13 August, 1983. We very deeply regret the loss of an invaluable and highly esteemed colleague.

The crews of the R/V JOHNSON and JOHNSON-SEA-LINK I of Harbor Branch Foundation, Inc. (HBF) offered indispensable assistance during our *Oculina* reef dives. Mr. John Reed (HBF) was of great help in providing specimens of *Ophioderma devaneyi* and advice based on his extensive work on the offshore coral pinnacles.

Dive buddies in Belize who assisted in the pursuit of *Ophioderma ensiferum,* included Dr. Maria Byrne, Messrs. Michael Carpenter, Barry Spracklin and Brian Sullivan. Special thanks are due to Ms. Barbara Littman who collected half the specimens herein described and helped ably in many other aspects of the field program.

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Mr. George Steyskal (U.S. Dept. Agriculture) generously shared his knowledge of the classical languages to clarify nomenclatorial questions arising from this study. Dr. David L. Pawson reviewed the manuscript. Mrs. Charissa B. Lounibos prepared the line drawings, and Mr. Tom Smoyer (HBS) helped produce the color plate.

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