

SYSTEMATICS OF THE OPHIDIASTERID SEA
STARS *COPIDASTER LYMANI* A. H. CLARK, AND
HACELIA SUPERBA H. L. CLARK
(ECHINODERMATA: ASTEROIDEA) WITH A
KEY TO SPECIES OF OPHIDIASTERIDAE FROM
THE WESTERN ATLANTIC

John E. Miller

Abstract.—*Copidaster lymani* A. H. Clark, 1948, is reported and redescribed from new material collected at Carrie Bow Cay (Belize), Portobelo (Panama), and Ascension Island. These are the first western Atlantic records of *C. lymani* since description of the holotype from Florida. Revisions by earlier authors, in which *Copidaster* is synonymized with the genera *Leiaster* or *Ophidiaster*, are rejected, and *Ophidiaster schismochilus* H. L. Clark, 1922, is referred to the genus *Copidaster*. A redescription of *Hacelia superba* H. L. Clark is presented. Previous accounts of this species from the western Atlantic have been limited to the type-locality, Barbados; new locality records from North and South Carolina, the east coast of Florida and the northern Gulf of Mexico are reported herein. Relationships between *H. capensis* Mortensen, 1925, from South Africa and *H. superba* are discussed. A key to the species of Ophidiasteridae from the western Atlantic is included.

In the tropical western Atlantic, Caribbean, and Gulf of Mexico, the asteroid family Ophidiasteridae is represented by 13 nominal species (Downey, unpublished; this study). For four species, *Copidaster lymani* A. H. Clark, 1948, *C. schismochilus* (H. L. Clark, 1922) new combination, *Hacelia superba* H. L. Clark, 1921, and *Ophidiaster bayeri* A. H. Clark, 1948, no new material has been reported from the western Atlantic since description of the holotypes.

At Carrie Bow Cay, Belize, Central America, four specimens of an unusual ophidiasterid sea star were found in shallow tide pools beneath heaps of coral rubble. They proved to be *Copidaster lymani*, a species previously known only from the type-specimen collected off Key Largo, Florida, and from material described by Nataf and Cherbonnier (1975) from the west coast of Africa. Subsequent examination of unidentified or misidentified material housed at the Smithsonian Institution revealed numerous additional specimens from Carrie Bow Cay and Ascension Island.

The generic position of *C. lymani* has been a matter for debate since Clark's (1948) description of this species. Downey (1973) referred *C. lymani* to the genus *Leiaster*, while Nataf and Cherbonnier (1975) preferred to drop the name *Copidaster* in favor of *Ophidiaster*. In the present study, important morphological characters of *Copidaster*, *Leiaster* and *Ophidiaster* are compared and the need to retain the generic name *Copidaster* is demonstrated. Additionally, *C. lymani* and *C. schismochilus* are shown to be congeneric.

During diving operations aboard Research Submersible *Johnson-Sea-Link I*,

several specimens of another ophidiasterid, *Hacelia superba*, were collected from a submerged oolitic reef off Sebastian, Florida. Although *H. superba* has been reported from the eastern Atlantic, off St. Helena (Mortensen 1933) and Angola (Nataf and Cherbonnier 1975, questionable record), its recorded distribution in the western Atlantic has been limited to Barbados, the type-locality. Catalogued material of *H. superba* at the Smithsonian Institution confirmed additional records from off the coasts of North and South Carolina and in the northwestern Gulf of Mexico. New information on distribution, variation, coloration, and habitat of *H. superba* is presented here. *Hacelia superba* and the South African species *H. capensis* Mortensen, may be conspecific; their similarities are discussed.

Voucher specimens have been deposited at the British Museum (Natural History) [BM(NH)], the Indian River Coastal Zone Museum, Harbor Branch Foundation, Inc. [IRCZM], the Museum of Comparative Zoology, Harvard University [MCZ] and the National Museum of Natural History, Smithsonian Institution [USNM].

Family Ophidiasteridae Verrill, 1867
Copidaster lymani A. H. Clark, 1948
Figs. 1, 2, 3A

Copidaster lymani A. H. Clark, 1948:55, figs. 1, 2.—1954:376 [listed].—Downey, 1979:80 [key].

Leiaster lymani.—Downey, 1973:62 [discussed].

Ophidiaster lymani.—Nataf and Cherbonnier, 1975:818, pl. I, fig. A, pl. II, figs. A, B, C, E, F.

Material examined.—Holotype (R = 85 mm, r = 9 mm, R/r = 9.4), USNM E7177, Key Largo, Florida, outer reefs, F. Lyman, Sep 1947.—1 specimen (R = 98 mm, r = 10 mm, R/r = 9.8), Paris Museum EC AS 1380, *Calypso*, Sta 50, Guinee, 1°24'04"S, 5°36'45"E, 7–10 m, 13 Jun 1956.—2 specimens (R = 100 mm, r = 10 mm, R/r = 10.0; R = 72 mm, r = 10 mm, R/r = 7.2), Paris Museum EC AS 1378, *Calypso*, Sta 103, Guinee, off Annobon Island, calcareous algae bottom, 4 Jul 1956.—1 specimen (R = 85 mm, r = 9 mm, R/r = 9.4), Paris Museum EC AS 1384, *Calypso*, Sta 42, Cape Verde, rock bottom, 15–30 m, 20 Nov 1959.—1 specimen (R = 21 mm, r = 4 mm, R/r = 5.3), USNM E19272, R/V *Pillsbury*, Sta P-926, West Indies, 73 m, 14 Jul 1969.—5 specimens (R = 57 mm, r = 7 mm, R/r = 8.1; R = 50 mm, r = 7 mm, R/r = 7.1; R = 46 mm, r = 5 mm, R/r = 9.2; R = 45 mm, r = 6 mm, R/r = 7.5; R = 42 mm, r = 5 mm, R/r = 8.4), USNM E18680, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, east side of cay in rubble field, intertidal, F. H. C. Hotchkiss (CBC-178), 3 May 1974.—1 specimen (R = 46 mm, r = 6 mm, R/r = 7.7), USNM E28829, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, inner edge of reef crest, intertidal, F. H. C. Hotchkiss (CBC-154), 4 May 1974.—1 specimen (R = 57 mm, r = 6 mm, R/r = 9.5), USNM E18679, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss (CBC-17), 5 May 1974.—1 specimen (R = 37 mm, r = 5 mm, R/r = 7.4), USNM E18689, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss, 6 May 1974.—1 specimen (R = 45 mm, r = 6 mm, R/r = 7.5) USNM E18678, Carrie Bow Cay, Belize, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss (CBC-97), 7

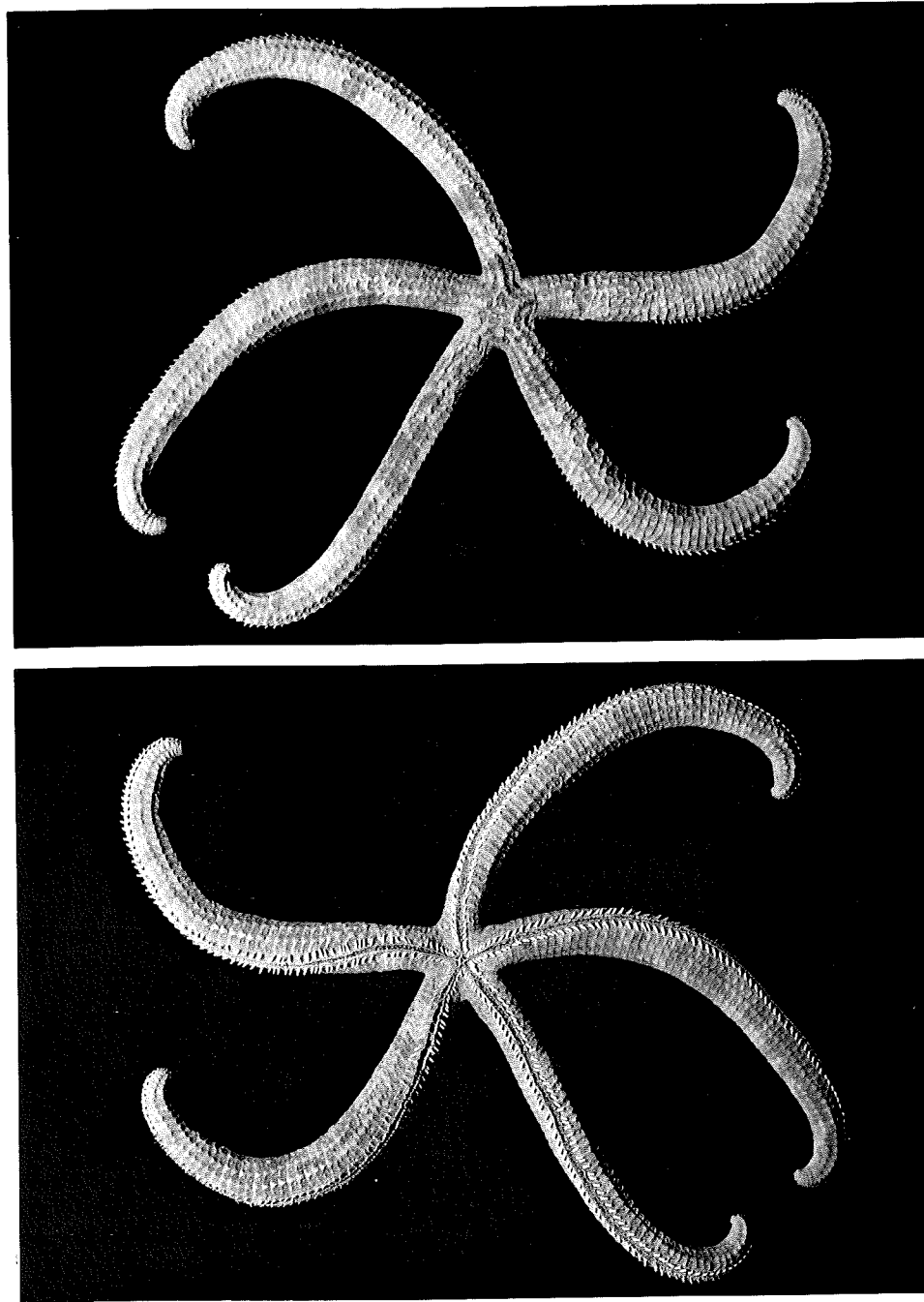


Fig. 1. *Copidaster lymani*, USNM E28831, R/r = 155 mm/13 mm. Upper, abactinal view; lower, actinal view.

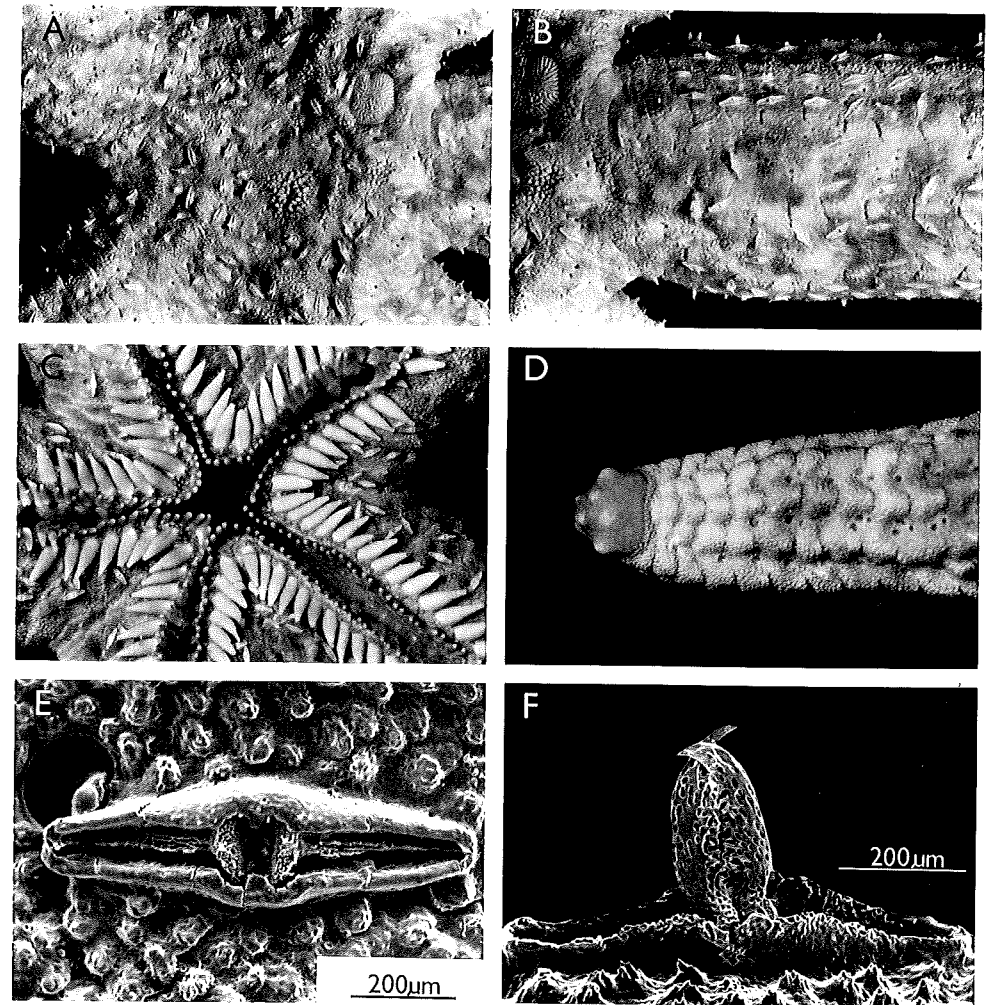


Fig. 2. *Copidaster lymani*, IRCZM 73:247. A, B (R/r = 55 mm/6 mm); A, Disk; B, Basal part of ray; C, D (R/r = 45 mm/5 mm); C, Mouth and basal part of rays; D, Distal tip of ray showing ocular plate; E, F, SEM micrographs of pedicellariae; E, Open valves laying in aveolus; F, Lateral view, valves closed, skin partly removed with bleach.

May 1974.—1 specimen (R = 45 mm, r = 5 mm, R/r = 9.0), USNM E29504, Iron Castle Point, Portobelo, Panama, under coral rubble, 1.5–3.0 m, G. Hendler, 8 Sep 1974.—1 specimen (R = 44 mm, r = 5 mm, R/r = 8.8), USNM E29505, Iron Castle Point, Portobelo, Panama, under rock, 0–1.5 m, G. Hendler, 27 Oct 1974.—2 specimens (R = 160 mm, r = 13 mm, R/r = 12.3; R = 155 mm, r = 13 mm, R/r = 11.9), USNM E28831, Ascension Island, offshore from Comfortless Cove, sandy and coarse sand, 33.5 m, B. S. McDowell, Apr 1981.—1 specimen (R = 125 mm, r = 10 mm, R/r = 12.5), USNM E28830, Ascension Island, 18 m off pierhead at Georgetown, common on rock and sand bottom, M. McDowell, May 1981.—1 specimen (R = 130 mm, r = 10 mm, R/r = 13.0) USNM E24787,

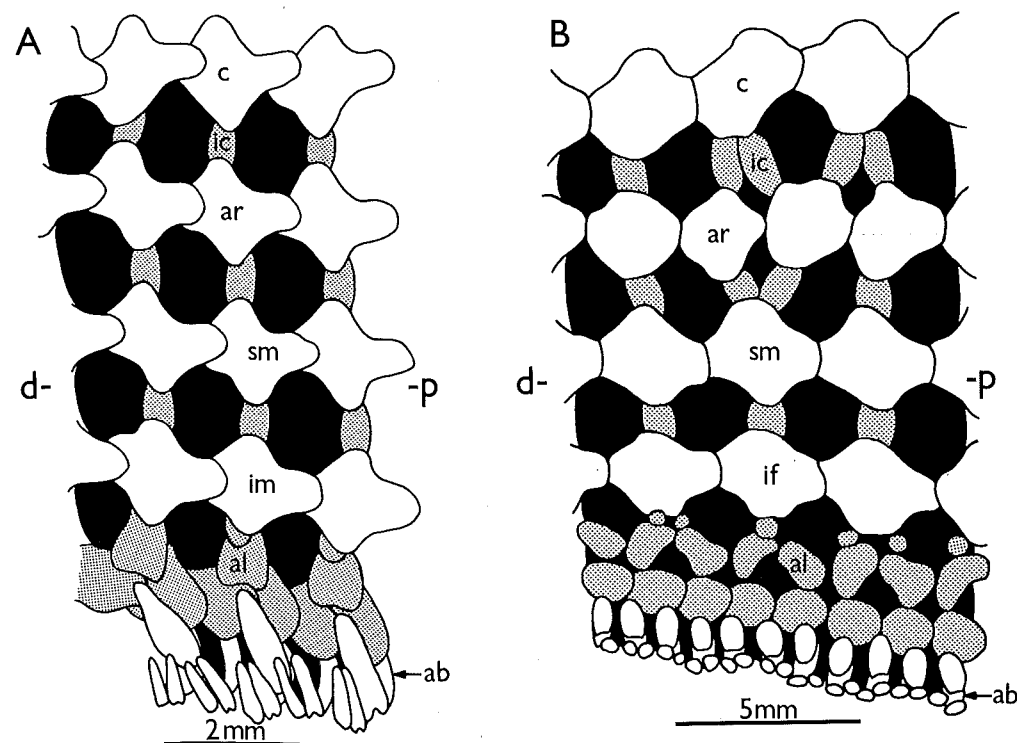


Fig. 3. Planar views of skeletal plates near mid-portion of ray. A, *Copidaster lymani*, IRCZM 73:247, R/r = 55 mm/6 mm; B, *Hacia superba*, IRCZM 73:227, R/r = 68 mm/14 mm. Abbreviations: d, distal; p, proximal; c, carinal; ic, internal connecting ossicle; ar, adradial; sm, superomarginal; im, inferomarginal; al, actinolateral; ab, adambulacral.

Ascension Island, 18 m off pierhead at Georgetown, under rocks, M. McDowell, Aug 1981.—4 specimens (R = 55 mm, r = 6 mm, R/r = 9.2; R = 50 mm, r = 5 mm, R/r = 10.0; R = 45 mm, r = 5 mm, R/r = 9.0; R = 42 mm, r = 5 mm, R/r = 8.4), IRCZM 73:247, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, tide pools among storm rubble of reef crest, intertidal, J. E. Miller, 23 Mar 1981.—2 specimens (R = 39 mm, r = 5.5 mm, R/r = 7.1; R = 41 mm, r = 5 mm, R/r = 8.2), MCZ 4672, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, among storm rubble of reef crest, 0–1 m, G. Hendler, B. Littman, 11 Jan 1983.—3 specimens (R = 47 mm, r = 5 mm, R/r = 9.4; R = 45 mm, r = 6 mm, R/r = 7.5; R = 39 mm, r = 5 mm, R/r = 7.8), BM(NH) 1983.8.18.2–4, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, reef crest and shallow spur and groove zone, 0–5 m, G. Hendler, B. Littman, 12 Jan 1983.—2 specimens (R = 58 mm, r = 5 mm, R/r = 11.6; R = 46 mm, r = 5 mm, R/r = 9.2), IRCZM 73:248, Carrie Bow Cay, Belize, 16°48'N, 88°05'W, among storm rubble of reef crest, 0–1 m, G. Hendler, B. Littmann, 20 Jan 1983.—1 specimen (R = 43 mm, r = 5 mm, R/r = 8.6), USNM E29502, Carrie Bow Cay, Belize, 16°48.1'N, 88°04.8'W, reef crest, under rubble, 0–2 m, G. Hendler, 23 Mar 1983.—2 specimens (R = 38 mm, r = 5 mm, R/r = 7.6; R = 35 mm, r = 5 mm, R/r = 7.0), USNM E29503, Carrie Bow Cay, Belize, 16°48.1'N, 88°04.8'W, reef crest, under rubble, 0–2 m, G. Hendler, 5 Apr 1983.

Diagnosis.—Skeleton concealed by thin, squamulose skin; scales or granules present in skin covering actinal interradial area; longitudinal series of abactinal plates connected by single internal plates; width of adambulacral plates alternating broad and narrow; proximal adambulacrals connected to inferomarginals by 3 series of actinolateral plates; 8 series of papular areas; excavate pedicellariae numerous.

Description.—Disk flat, small (R/r = 7.2–13.0); rays, 5, long, cylindrical, often unequal in length. Rays constricted at their bases, inflated medially, gently tapering to a blunt tip. Oculars conspicuous, swollen, subcircular, carrying 6–12 large tubercles. Actinal surface of oculars with prominent groove. One (occasionally 2 or more) short, conical spine arises from either side of groove, frequently meeting over middle of groove. Single, large, circular to oval madreporite with smooth, fine gyri. Anus near center of disk, surrounded by 20–40 enlarged granules.

Entire skeleton concealed by thin skin, embedded with numerous, imbricating scales actinally and abactinally. Scales noticeably larger on summits of primary abactinal plates, conspicuously marking regular transverse and longitudinal series. Viewed laterally, a transverse series of plates consists of carinal, adradial, superomarginal, inferomarginal, actinolateral (3 rows proximally), adambulacral ossicles. Primary abactinals quadrilobate; distal plates overlap proximal plates. In larger specimens, adradial plates often reniform beyond basal portion of ray; quadrilobate shape reappearing near distal tip. In smaller specimens, adradial series usually consisting of double row of plates near medial or distal portion of ray. Beneath and between adjacent longitudinal rows of primary abactinals lie a series of internal ossicles. Adambulacral ossicles alternately broad and narrow. Larger adambulacrals connected to inferomarginals by series of 3 (2 in smaller specimens) actinolateral plates. Proximal adambulacral plates carry one large, flattened subambulacral spine. Further out on ray, subambulacral spines shorter, more cylindrical and confined to wider adambulacral plates only. Marginal face of each adambulacral plate bears two subequal, cylindrical furrow spines. Each half jaw bears a single, cylindrical, bluntly rounded preoral spine, 4 similar though shorter, marginal spines and one large, flattened suboral spine.

Eight longitudinal rows of papular areas with 7–15 papulae per area (large specimens R ≥ 150 mm with up to 30). Largest papular areas found on inflated abactinal portion of rays.

Excavate pedicellariae numerous on all surfaces, especially disk, basal part of rays and actinal-interradial area. Conspicuous presence of pedicellariae gives specimens a spinous appearance when examined with naked eye. Pedicellaria consists of 2 sickle-shape valves lying in narrow, elongate alveolus, 600–800 μm in length. Distal tips of valves tapering to acute terminal tooth, crossing when valves close.

In life, abactinal surface pigmented reddish tan or orange, with darker red mottling or irregular banding. Distal portion of rays usually uniformly red. Oculars red or orange. Actinal surface orange; subambulacral spines and furrow spines white proximally and distally, orange medially. Tube feet transparent orange, distinctly tipped with white suckers. Lighter specimens with pink to tan ground color and orange mottling. Very dark specimens almost uniformly blood red. Pedicellariae and madreporite white, conspicuously contrasted by darker surrounding skin. Color fades rapidly in ethanol.

Type.—National Museum of Natural History, Smithsonian Institution, USNM E7177.

Type-locality.—Key Largo, Florida, outer reefs, depth not recorded.

Distribution.—In the western Atlantic, presently known from Carrie Bow Cay (Belize), Protobelo (Panama) and the type-locality, intertidal to 5 m. Also verified from Ascension Island, down to 33.5 m (present study). Reported from the west coast of Africa off Cape Verde, Guinea and Annobon Island, 10–30 m, (Nataf and Cherbonnier 1975).

Habitat.—The majority of specimens from Carrie Bow Cay was collected intertidally (0–1 m), among thick layers of coral rubble on the reef crest and the leeward base of the crest. A few specimens were found beneath rubble in the shallow (3–5 m) spur and groove zone of the reef. At Portobelo, specimens were taken in shallow water beneath rock and rubble. Specimens from Ascension Island were found on rock and sand bottoms. At Annobon Island (Gulf of Guinea), two specimens were taken from a calcareous algal bottom (Nataf and Cherbonnier 1975).

Discussion.—At present, considerable confusion exists over the generic status of *Copidaster*. Noting obvious similarities between *Copidaster* and *Leiaster* (skin concealing skeleton, alternately broad and narrow adambulacral plates, presence of excavate pedicellariae), Downey (1973:62) stated that *Copidaster* should be considered as a synonym of *Leiaster*. Later, Nataf and Cherbonnier (1975) placed *Copidaster lymani* in the genus *Ophidiaster* because they failed to distinguish the alternately broad and narrow adambulacral plates in their specimens from West Africa. I have examined their specimens, and they indeed possess adambulacral plates alternating in width. Table 1 lists several important taxonomic characters in the genera *Copidaster*, *Leiaster* and *Ophidiaster*. Through comparison of these characters, it can be noted that the distinctions between the genera are clear. The presence of a thin but conspicuous skin, and alternately broad and narrow adambulacral plates in *Copidaster* serves to separate that genus from *Ophidiaster*, which lacks a conspicuous skin and has adambulacral plates of equal width. Furthermore, *Leiaster*, with two rows of actinolaterals proximally and a thick, fibrous skin lacking granules, is distinct from *Copidaster*, with three rows of actinolaterals proximally and a thin, squamulose skin. Clearly, *Copidaster*, as envisioned by A. H. Clark (1948), merits full generic rank.

Ophidiaster schismochilus H. L. Clark can be referred to the genus *Copidaster*. Although *Copidaster schismochilus* is presently known only from the type-specimen taken off Bermuda, the affinities between *C. schismochilus* and *C. lymani* are unmistakable, and *C. schismochilus* is therefore regarded herein as a new combination. It is possible that *C. schismochilus* and *C. lymani* are conspecific and that the differences noted are due to geographic and bathymetric variation. Some of the eastern Atlantic specimens of *C. lymani* superficially look like *C. schismochilus*. Lacking additional comparative material of *C. schismochilus*, a synonymy of the two species would seem unwise. If future material does suggest that *C. schismochilus* and *C. lymani* are conspecific, then *C. schismochilus* would have priority. Similarities between these species can be found in Table 1; important differences are noted in the Ophidiasteridae key (p. 206).

Remarks.—In reference to the pedicellariae of *C. lymani*, A. H. Clark (1948) states that in life the lateral borders of the alveoli can be brought together completely, concealing the valves of the pedicellariae. In examining Clark's type and all the new material examined herein, I have failed to find a single example of a

Table 1.—Comparative morphological characters of *Ophidiaster*, *Copidaster* and *Leiaster*.

Species examined	Skeletal covering	Number of pedicellariae	Jaw shape of pedicellariae	Arrangement of subambulacral spines beyond proximal 1/3 of ray	Number of longitudinal rows of actinolaterals proximally	Width of adjacent adambulacral plates
<i>Ophidiaster alexandri</i> Verrill	Fine layer of granules or scales, skin not evident	Variable, absent to numerous	Sugar-tongs, (sickle-shaped in <i>O. bullisi</i>)	Variable	2–5	Equal
<i>bayeri</i> A. H. Clark						
<i>bullisi</i> (Downey)						
<i>guidingi</i> Gray						
<i>ophidianus</i> (Lamarck)						
<i>reysi</i> Sibuet						
<i>Copidaster lymani</i> A. H. Clark	Thin skin containing numerous scales and granules	Numerous	Sickle-shaped	Present on alternating adambulacral plates	3	Alternating broad and narrow
<i>schismochilus</i> H. L. Clark						
<i>Leiaster analogus</i> Fisher	Thick, fibrous skin lacking visible scales and granules	Variable, absent to numerous	Sickle-shaped	Present on alternating adambulacral plates	2	Alternating broad and narrow
<i>callipeplus</i> Fisher						
<i>coriaceus</i> Peters						
<i>leachi</i> (Gray)						
<i>teres</i> (Verrill)						

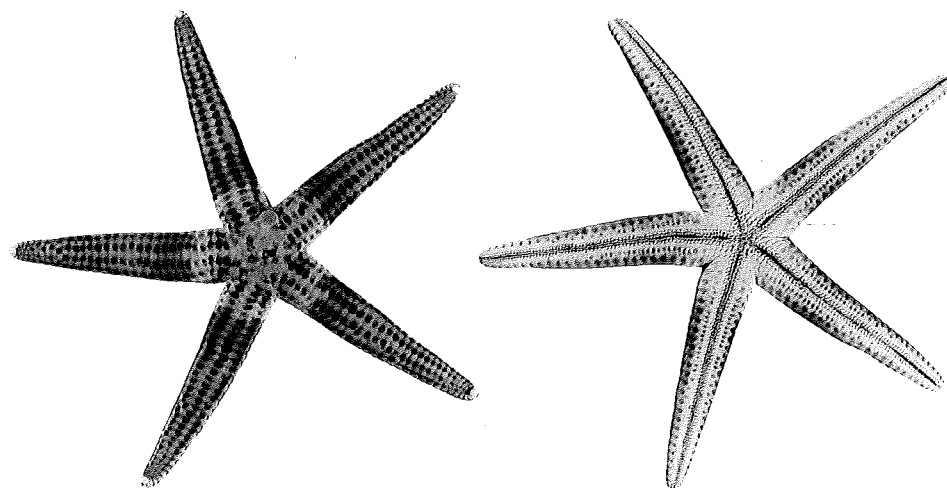


Fig. 4. *Hacelia superba*, IRCZM 73:227, R/r = 82 mm/15 mm, left, abactinal view; right, actinal view.

closed alveolus. This finding has been confirmed by G. Hendler (pers. comm.) who has observed live material at Carrie Bow Cay, Belize. Even direct mechanical stimulation of the pedicellariae failed to elicit a response in which the jaws of a pedicellaria were concealed by the alveolus.

At Carrie Bow Cay, *C. lymani* often occurs with *Ophidiaster guildingi* Gray which it frequently resembles in size, color and morphology. In the field, *C. lymani* can readily be distinguished from *O. guildingi* by the presence of conspicuous pedicellariae and a slimy skin in the former.

Hacelia superba H. L. Clark, 1921
Fig. 3B, 4, 5

Hacelia superba H. L. Clark, 1921:87, pl. 32, figs. 1, 2.—Mortensen, 1933:426, figs. 8, 9.—Downey, 1970:81 [key].—1973:61 [discussed].—A. M. Clark, 1974:436 [discussed].

? *Ophidiaster superbus*.—Nataf and Cherbonnier, 1975:820, pl. III, figs. A, B. [Non *Hacelia floridae*.—A. H. Clark, 1954:376, (footnote b)]

Material examined.—Holotype (R = 73 mm, r = 14 mm, R/r = 5.2), MCZ 764, Barbados, Hassler Expedition, 183 m.—1 specimen (R = 45 mm, r = 7 mm, R/r = 6.4), Paris Museum EC AS 662, J. Meulebergh coll., Angola, between Luanda and Novo Redondo, Jan 1966.—1 specimen (R = 26 mm, r = 6 mm, R/r = 4.3), IRCZM 73:022, R/V *Gosnold* Cruise 262, Sta 785, 27°50.0'N, 79°58.3'W to 27°51.0'N, 79°57.5'W, box dredge, 70–90 m, L. Becker, L. Scotto, 13 Aug 1975.—1 specimen (R = 60 mm, r = 13 mm, R/r = 4.6), USNM E18202, Texas A&M Cruise 78-69 III, Dive No. 115, Geyer Bank, northern Gulf of Mexico, 923–122 m, T. Bright, 10 Dec 1978.—1 specimen (R = 60 mm, r = 11 mm, R/r = 5.5), USNM E19196, Texas A&M *Black Seal* Cruise 79, Dive No. 5, West Flower Gardens, Gulf of Mexico, T. Bright, 23 Sep 1979.—1 specimen (R = 73 mm, r =

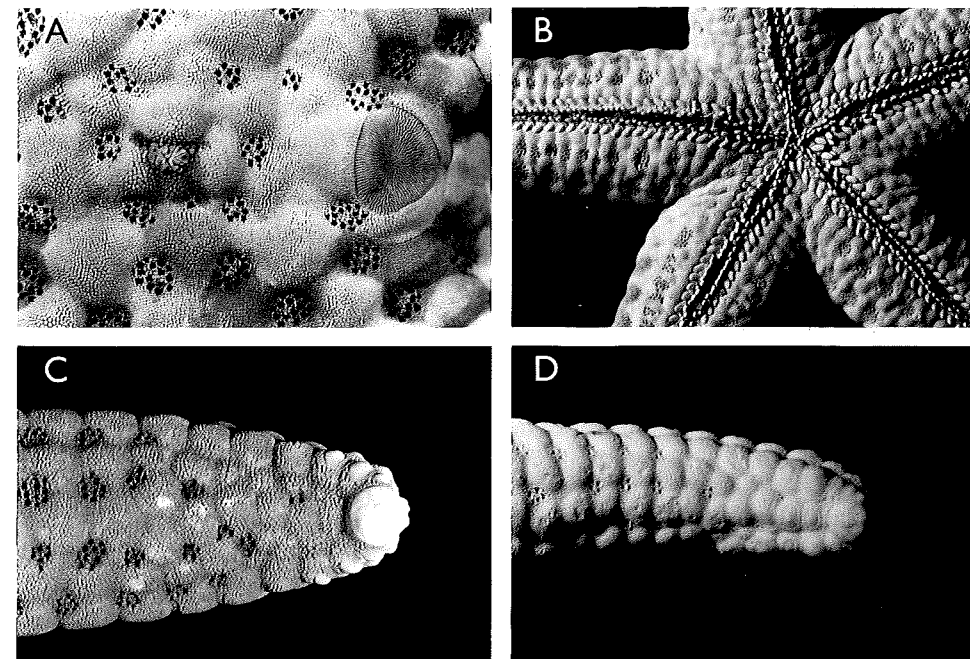


Fig. 5. *Hacelia superba*, A, B, MCZ 4670, R/r = 53 mm/11 mm; A, Disk; B, Mouth and basal part of rays; C, MCZ 4670, R/r = 58 mm/11 mm, distal tip of ray, adult specimen; D, IRCZM 73:022, R/r = 26 mm/6 mm, distal tip of ray, juvenile specimen, note central bare areas on distal carinal plates.

15 mm, R/r = 4.9), USNM E26486, R/V *Eastward* Sta 505, SE of Cape Lookout, North Carolina, 33°48'18"N, 77°34'06"W, 100 m, Wm. Kirby-Smith.—1 specimen (R = 47 mm, r = 12 mm, R/r = 3.9), USNM E26487, R/V *Eastward*, South Carolina Marine Resource Research Institute, SE of Cape Lookout, North Carolina, 33°48'18"N, 76°34'06"W, 100 m, Wm. Kirby-Smith, 14 May 1981.—1 specimen (R = 43 mm, r = 10 mm, R/r = 4.3) USNM E26488, R/V *Eastward*, SE of Cape Lookout, North Carolina, 33°48'42"N, 76°34'30"W, 99 m, Wm. Kirby-Smith, 14 May 1981.—3 specimens (R = 82 mm, r = 15 mm, R/r = 5.5; R = 70 mm, r = 13 mm, R/r = 5.4; R = 68 mm, r = 14 mm, R/r = 4.9), IRCZM 73:227, R/V *Johnson* Cruise J-147, *JSL-I* Dive No. 1266, off Sebastian, Florida, 27°46.2'N, 79°58.4'W, coral rubble, 68 m, G. Hendler, 22 Sep 1982.—1 specimen (R = 45 mm, r = 9 mm, R/r = 5.0), BM(NH) 1983.8.18.1, R/V *Johnson* Cruise J-147, *JSL-I* Dive No. 1267, off Sebastian, Florida, 27°46.2'N, 79°58.4'W, coral rubble, 65 m, J. E. Miller, 23 Sep 1982.—2 specimens (R = 58 mm, r = 11 mm, R/r = 5.3; R = 53 mm, r = 11 mm, R/r = 4.8), MCZ 4670, R/V *Johnson* Cruise J-153, *JSL-I* Dive No. 1323, off Sebastian, Florida, 27°46.1'N, 79°58.5'W, coral rubble, 65 m, J. E. Miller, 14 Mar 1983.

Diagnosis.—Actinal surface of rays distinctly flattened; distalmost marginal plates with central bare area; adambulacrals connected to inferomarginals by series of 3 actinolateral plates; 10 rows of large, conspicuous papular areas (8 in specimens with R < 55 mm), with up to 60 papulae per area.

Description.—Disk small, flat; 5 moderately long rays, tapering gently throughout their length, distal tips curved dorsally. Rays distinctly flattened actinally, somewhat triangular in cross section. Oculars prominent, swollen, circular, each carrying 4–5 distinct tubercles often worn smooth in larger specimens. Well-defined circular, square or triangular madreporite with fine, straight to undulating gyri, situated near margin of disk. Anus in contact with central plate, concealed by 10–15 enlarged scales, many with a distinct concavity.

Actinal and abactinal surfaces uniformly covered with dense layer of granules, commonly spherical, becoming polygonal to form mosaic platform on summits of abactinal plates on disk and proximal portion of rays. Distalmost 2–4 (up to 8) marginal plates swollen, with central bare area. Skeletal plates prominent, arranged in regular transverse and longitudinal series. Viewed laterally, transverse series consists of carinal, adradial, superomarginal, inferomarginal, actinolateral (3 rows proximally), adambulacral ossicles. Abactinal and marginal plates quadrilobate, proximal margin overlapping distal margin of adjoining plate. Longitudinal series from carinal to inferomarginal connected by internal ossicles. Three rows of actinolaterals between inferomarginals and adambulacrals. Lowest row with circular to square plates, extending total length of ray. Middle row with reniform plates, extending $\frac{2}{3}$ length of ray; these plates angled at 45° to lower row, thus forming arch for passage of papulae. Upper row with subcircular plates, extending $\frac{1}{2}$ length of ray. Each adambulacral plate carries 1 (2 often on proximalmost and distalmost plates) subambulacral spine and 2 furrow spines. Proximally, subambulacral spines short, swollen, truncate. More distally, spines conical, becoming granuliform near distal tip of ray. Furrow spines subequal, laterally compressed, triangular to oval in cross section. Each half jaw bears a single, heavy preoral spine, 3–4 truncate marginal spines and a large inflated, bluntly rounded suboral spine.

Ten rows of papular areas, 2 below inferomarginals. Lowest papular row on each side of ray often lacking or visible as isolated papulae in specimens with $R < 55$ mm. In larger individuals, lowest papular row ending $\frac{1}{2}$ to $\frac{2}{3}$ along length of ray. Abactinal and marginal papular areas large, lying in deep depressions formed by elevated surrounding skeletal plates. Number of papulae per area varies considerably with size: $R > 80$ mm, 40–60 papulae per area; $R = 45$ –60 mm, 15–1 papulae per area; $R = 26$ mm, 5–7 papulae per area. Papular areas on actinal face with fewer papulae. Individual papulae surrounded by 6–8 elongate granules.

Pedicellariae usually absent; when present, on actinal surface overlying actinolaterals in proximal part of ray. Valves spatulate, situated in deep, elongate alveoli, lying just below surface of surrounding granulation.

In life, disk and proximal part of rays pink to orange, remainder of rays dark red. Some specimens distinctly banded with reddish brown and pink. Madreporite dark orange. Actinal surface white to light tan with red or orange papular areas. Tube feet white. Color fades rapidly in ethanol. Dried, formalin-fixed specimens generally retain natural pigmentation.

Type.—Museum of Comparative Zoology, Harvard University, MCZ 764.

Type locality.—Barbados, Hassler Expedition, 183 m.

Distribution.—In the western Atlantic, presently known off North and South Carolina, the east coast of Florida, NW Gulf of Mexico and Barbados, 65–183

m. In the eastern Atlantic, reported from St. Helena (Mortensen 1933) and Angola (Nataf and Cherbonnier 1975, questionable record, see remarks), 40–100 m.

Habitat.—Specimens collected with the *Johnson-Sea-Link* submersible were taken from a deep-water, pinnacle reef found in 85 m off the east central coast of Florida, $27^\circ 46.2'N$, $79^\circ 58.5'W$. Covering the east, west and northern slopes of the reef was a thick layer or rubble, remains of the branching scleractinian coral *Oculina varicosa* Lesueur. Scattered about the southern slope were large intact mounds of dead *Oculina*. The reef supported a diverse fauna of fish and invertebrates, especially crustaceans, echinoderms, cnidarians and mollusks. *Hacelia*, although a relatively common component of this fauna, appeared to occur only at 65–70 m on the southern slope of the pinnacle. No specimens were observed near the crest (58 m) or the base (84 m) of the pinnacle nor on any other slope. Additional information on structure and faunal composition of the reef is given in Hendler and Miller (in press).

Discussion.—As in the holotype of *H. superba*, all but one specimen examined have carinal and adradial plates completely covered with granulation and several (up to 8) marginal plates with a central bare area. In the exceptional specimen, $R/r = 26$ mm/6 mm (smallest specimen examined), 2 distal carinal plates, as well as several marginal plates, have central bare areas (see Fig. 5D). This arrangement is reminiscent of *H. capensis*, from off Natal, originally described as a variety of *H. superba* by Mortensen (1925). Mortensen distinguished his variety of *H. superba* from the western Atlantic *H. superba* on the basis of central bare areas on several radial and lateral plates. The size of the holotype was not stated by Mortensen (1925), but Clark (1974, 1976) reported on a second specimen of *H. capensis* from Natal, $R/r = 15$ mm/3 mm in which several carinal plates had central bare areas. It is likely that the presence or absence of bare areas on distal carinal or adradial plates is simply a growth character related to age. As *H. superba* has been confirmed from the eastern Atlantic (Mortensen 1933), perhaps *H. capensis* represents nothing more than the young of *H. superba*. Even Mortensen (1933:427) in his description of several specimens of *H. superba* from St. Helena states, "Here and there a single one of the dorsal plates at the end of arm may show a small naked spot." Ironically, Mortensen felt that this finding added further evidence for the validity of his variety *capensis* (here Mortensen inadvertently substituted the name "africana" for "capensis" p. 427).

Considering the numerous pedicellariae found on the small specimen of *H. capensis* examined by Clark (1974), the presence or absence of pedicellariae appears to be an unreliable character in both *H. capensis* and *H. superba*. Mortensen (1925) made no mention of pedicellariae on his type of *H. capensis*, and with the exception of one specimen taken in the northern Gulf of Mexico, none of the western Atlantic specimens of *H. superba* described herein nor the St. Helena specimens described by Mortensen (1933) possess pedicellariae.

Although *H. superba* from the western Atlantic and St. Helena may be conspecific with *H. capensis* from South Africa, combining the species would seem a hasty approach with so little comparative material of *H. capensis* available.

Remarks.—In his species list of the echinoderms from the Gulf of Mexico, Clark (1954:376) included *Ophidiaster alexandri* Verrill, *O. pinguis* H. L. Clark and *Hacelia superba* H. L. Clark as synonyms of *Hacelia floridae* = [*Tamaria*

floridae (Perrier, 1881)]. Downey (1973:61) reversed Clark's assignment after examining the types of these species and finding them to represent valid species. Further investigation by Downey (in preparation) has shown that the holotype of *D. pinguis* represents a large specimen of *O. alexandri*. During the course of this study, I also had an opportunity to examine the types of *O. alexandri*, *O. pinguis*, *H. superba* and *T. floridae*, and I concur with Downey's findings.

A small specimen (R/r = 47 mm/7 mm) of ?*H. superba* from Angola was described by Nataf and Cherbonnier (1975) as possessing 8 rows of papular areas. My examination of this animal has revealed at least three isolated papulae occurring actinally below the row of papular areas adjacent to the inferomarginal series of plates. This condition is what one would expect in a specimen of this size and confirms the genus *Hacelia*. Whether or not this individual is a valid specimen of *H. superba* remains uncertain. The specimen is in poor condition (two rays incomplete, much of the granulation rubbed off, many ambulacral spines broken), but the broad-based rays steadily tapering to a fine tip and the distinctly unequal furrow spines are both characters reminiscent of *H. attenuata* (Gray). In any case, their reassignment (based on a single specimen) of *H. superba* to the genus *Ophidiaster*, a genus in which all species have eight rows of papular areas was unjustified.

Key to the species of Ophidiasteridae from the western Atlantic, Caribbean and Gulf of Mexico (modified in part from Downey, 1970, 1973)

- 1. Primary plates arranged in regular transverse and longitudinal series ... 2
 - Primary plates not arranged in regular transverse and longitudinal series ... 11
- 2. Papular areas at base of rays in 10 longitudinal series (8 in specimens with R < 55); actinal surface of rays distinctly flattened ...
 - *Hacelia superba* H. L. Clark
 - Papular areas at base of rays in 4-8 longitudinal series; actinal surface of rays not distinctly flattened ... 3
- 3. Papular areas present on actinal surface below inferomarginals ... 4
 - Papular areas absent from actinal surface below inferomarginals ... 9
- 4. Skeletal plates covered by distinct skin containing numerous scales or granules; adambulacral plates alternately broad and narrow ... 5
 - Skeletal plates covered by fine layer of naked granules, skin not evident; adambulacral plates equal in width ... 6
- 5. Carinal series of plates connected to adradial series by 2-3 dorsolateral plates in proximal half of ray; skin covering actinal interradial area lacking scales or granules ...
 - *Copidaster schismochilus* (H. L. Clark), new combination
 - Carinal series connected to adradial series by single internal plate in proximal half of ray; skin covering actinal interradial area containing scales or granules ... *Copidaster lymani* H. L. Clark
- 6. Pedicellariae present ... 7
 - Pedicellariae absent ... 8

- 7. Valves of pedicellariae sickle-shaped, most numerous on abactinal surface ... *Ophidiaster bullisi*¹ (Downey)
 - Valves of pedicellariae sugar-tong shaped, most numerous on actinal surface ... *Ophidiaster alexandri* Verrill
- 8. Adambulacral series armed with single row of subambulacral spines ...
 - *Ophidiaster guildingi* Gray
 - Adambulacral series armed with double row of subambulacral spines ... *Ophidiaster bayeri* A. H. Clark
- 9. Rays short (R/r < 3.0), subpetaloid ... *Tamaria passiflora* Downey
 - Rays long (R/r > 3.5), tapering ... 10
- 10. Papular areas with average of 3-4 papulae; oculars small, inconspicuous ...
 - *Tamaria floridae* (Perrier)
 - Papular areas with average of 7-8 papulae; oculars large, conspicuous ... *Tamaria halperni* Downey
- 11. Rays triangular in cross section; papulae isolated, scattered ...
 - *Narcissia trigonaria* Sladen
 - Rays circular in cross section, papulae grouped ... 12
- 12. Large, swollen plates scattered randomly on rays and disk; madreporite single ... *Linckia nodosa* Perrier
 - Large, swollen plates absent, frequently 2 madreporites present ...
 - *Linckia guildingi* Gray

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¹ In describing the genus *Drachmaster*, type-species *D. bullisi*, Downey (1970) characterized *Drachmaster* by the presence of internal connecting ossicles which were believed to be absent from other genera in the family Ophidiasteridae. Her further examination has shown that many ophidiasterid genera possess internal connecting ossicles. Accordingly Downey (in preparation) has referred *Drachmaster* to synonymy with *Ophidiaster* and her new combination *O. bullisi* is accepted herein.

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Literature Cited

- Clark, A. H. 1948. Two new starfishes and a brittle-star from Florida and Alabama.—Proceedings of the Biological Society of Washington 61:55–66, 1 pl.
- . 1954. Echinoderms (other than holothurians) of the Gulf of Mexico.—Bulletin of the United States Fish Commission 55:373–379.
- Clark, A. M. 1974. Notes on some echinoderms from southern Africa.—Bulletin of the British Museum (Natural History), Zoology 26(6):423–487, 16 figs., 3 pls.
- , and J. Courtman-Stock. 1976. The echinoderms of southern Africa. 277 pp., 276 figs. London: British Museum (Natural History).
- Clark, H. L. 1921. The echinoderm fauna of Torres Strait: its composition and its origin.—Department of Marine Biology, Carnegie Institute, Washington, 10: viii + 223 pp., 38 pls.
- . 1922. The echinoderms of the Challenger Bank, Bermuda.—Proceedings of the American Academy of Arts and Sciences 57 (13):353–361, 1 pl.
- Downey, M. E. 1970. *Drachmaster bullisi*, new genus and species of Ophidiasteridae (Echinodermata: Asteroidea), with a key to the Caribbean species of the family.—Proceedings of the Biological Society of Washington 83(6):77–82, 6 figs.
- . 1973. Starfishes of the Caribbean and the Gulf of Mexico.—Smithsonian Contributions to Zoology 126:vi + 158 pp., 48 pls.
- Hendler, G., and J. E. Miller. [In press]. Feeding behavior of *Asteroporpa annulata* a gorgonocephalid brittlestar with unbranched arms.—Bulletin of Marine Science.
- Mortensen, T. 1925. On some echinoderms from South Africa.—Annals and Magazine of Natural History 9(16):146–154, 5 figs, pl. VIII.
- . 1933. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. 66. The echinoderms of St. Helena (other than Crinoids).—Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn 93:401–472, 29 figs, pls. XX–XXII.
- Nataf, G., and G. Cherbonnier. 1975. Troisieme contribution à la connaissance des Asterides de la côte occidentale d'Afrique.—Bulletin du Muséum National D'Histoire Naturelle, Paris, 3(311), Zoologie 218:813–834, 3 pls.

Harbor Branch Foundation, Inc., RR 1, Box 196, Ft. Pierce, Florida 33450.