

Mithrodia clavigera (Lamarck, 1816) (Echinodermata: Asteroidea: Mithrodiidae) from the central Atlantic Ocean and Gulf of Mexico

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Abstract.—New records of the Indo-Pacific seastar *Mithrodia clavigera* (Lamarck, 1816) include the north-central Gulf of Mexico, southeastern Florida, and Ascension Island. Material includes in-situ photographs, specimens from our own field collections, and museum specimens. This species was previously reported in the Atlantic basin in the 1880s off Brazil and in the western Caribbean Sea in the late 1960s and early 1970s. More recent findings are attributable to the advent of SCUBA, seafloor photography, and genetic analysis. The presence of *M. clavigera* in the Atlantic Ocean and adjacent waters probably represents a former connection with populations in the eastern Pacific Ocean before the rise of the Isthmus of Panama. Our observations here of specimens collected off Palm Beach and Fort Lauderdale, Florida, and the Gulf of Mexico add to our understanding of this species' behavior and ecology.

Keywords: Ascension Island, Florida, marine biogeography, seastar, Valvatida

The Mithrodiidae Viguer, 1878 is a small, poorly known family of large-bodied Indo-Pacific seastars (Blake 1980, Gosliner et al. 1996, Byrne et al. 2017). The family includes the genera *Mithrodia* Gray, 1840, with at least two species and perhaps up to four, and *Thromidia* Pope & Rowe, 1977, with four species. In addition to what is presently known of its biogeography, the external morphology has been fairly well studied, although the variably present, fasciculate pedicellariae (Downey 1975, Clark & Downey 1992) have rarely been reported (Fisher 1925) and are usually said not to occur [for *T. gigas* (Mortensen, 1935), cf. Cherbonnier 1975

and Clark & Courtman-Stock 1976]. Ossicle morphology has not been described at the level done by Blake (1980) on members of other families.

Internally, podial ampullae are doubled, i.e., constricted into two subchambers (Fisher 1911). Ludwig (1905) observed that the pyloric caeca of *Mithrodia clavigera* (Lamarck, 1816) largely filled the body cavity of the arms, that a female had small tufts of tubular ovaries arranged serially along the arms nearly to the tips; and that the ovaries contained mature eggs about 100 μm in diameter. Bipinnaria larvae, again known only for *M. clavigera*, are planktonic and presumably planktonic (Yamaguchi, unpublished, in Yamaguchi 1975, Galac et al. 2016, Collin,

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DOI: 10.2988/20-00009

Venera-Pontón, Driskell, Macdonald & Boyle 2020). Because of its sister relationship to the Ophidiasteridae and its echinasteroid body form (Sloan 1980, Jangoux 1982, Blake 1987, 1990; Mah & Blake 2012), the Mithrodiidae are assumed to be detritivores or microphagous extraoral feeders on encrusting animals. The few observations of presumed spongivory are rather anecdotal (Pope & Rowe 1977, Clark & Downey 1992, Reyes Bonilla et al. 2005).

Mithrodia clavigera has been known to occur throughout the tropical Indo-West Pacific Ocean and, arguably, the tropical Eastern Pacific Ocean for more than two centuries. The status of type material is uncertain, and the type locality is unknown (Engel et al. 1948, Clark & Downey 1992). Although two specimens were found off Brazil in the late 1800s (Bell 1882), it was not until much more recently (Clark & Downey 1992) that its occurrence in the Atlantic Ocean was confirmed. Over those 110 yr, the Brazilian record seems to have been largely ignored (e.g., Clark 1921, Steinbeck & Ricketts 2009 [1941]). Its large size, robust granule-coated spines, and gaudy coloration would seem to make it a conspicuous component of shallow reefs where it occurs. But the few Atlantic museum records so far are mostly for specimens collected at intermediate depths (24–157 m); the species is rarely found in shallow water (Humann 1992) and is nocturnal (Yamaguchi 1973, 1975; Jangoux 1986); and it lives in a microhabitat that historically has been difficult to sample (Fisher 1906, 1919; Clark & Downey 1992). In the Atlantic Ocean, *M. clavigera* is reported from Brazil (Bell 1882) and the western Caribbean Sea (Clark & Downey 1992, Humann 1992). Herein we add material from two locations from the east coast of Florida, U.S.A., from a site in the Gulf of Mexico, and from Ascension Island (Fig. 1, locations 5–7 and 9).

Materials and Methods

Twenty-five specimens of *Mithrodia clavigera* (Fig. 2A; HBOM 073:00388, 16 specimens, Harbor Branch Oceanographic Institute; LACM 1986-714.001, 4 specimens, Los Angeles County Museum; others not retained) were collected by John Miller (JEM) on a daytime drift SCUBA dive off Palm Beach, Florida, 3.5 km southeast of Lake Worth Inlet (26°45.0'N, 80°0.0'W) on 27 March 1986 aboard M/V *Hawksbill*. A strong (1.5-k) northward current allowed a bottom time of only 10 min at 30.5–32.0 m depth. The site had a hard limestone substratum that formed a flat plain occupied by large sponges (*Xestospongia*) and gorgonian corals.

A photographic record (Fig. 3A) from the Gulf of Mexico was taken during a towed camera survey conducted on 14 January 1986. Specimens of *Mithrodia clavigera* were observed and documented at the Rankin/28 Fathom Bank Complex (27°54.9'N, 93°26.8'W) during an environmental monitoring program sponsored by the oil and gas industry. The bank complex is located approximately 15 km east of East Flower Garden Bank. Rankin Bank is the northern topographic high feature of the complex with shallowest water depths around 50 m. Just south of Rankin Bank and separated by a 1000-m wide trench is 28 Fathom Bank with the shallowest water depth at approximately 60 m (Rezák & Gartner 1978). The biotic zones of the Rankin/28 Fathom Bank Complex have been well characterized, as based on sample collections and submersible observations (Rezák & Bright 1983), with a biotic assemblage at depths less than 92 m associated with an Algal Sponge Zone (Bright 1981, Rezák et al. 1985). This zone is generally defined as an area of active reef-building dominated by calcareous red algae that produce carbonate substratum.

Another specimen (Fig. 2B; FSBC I 139722, Florida Wildlife Research Insti-

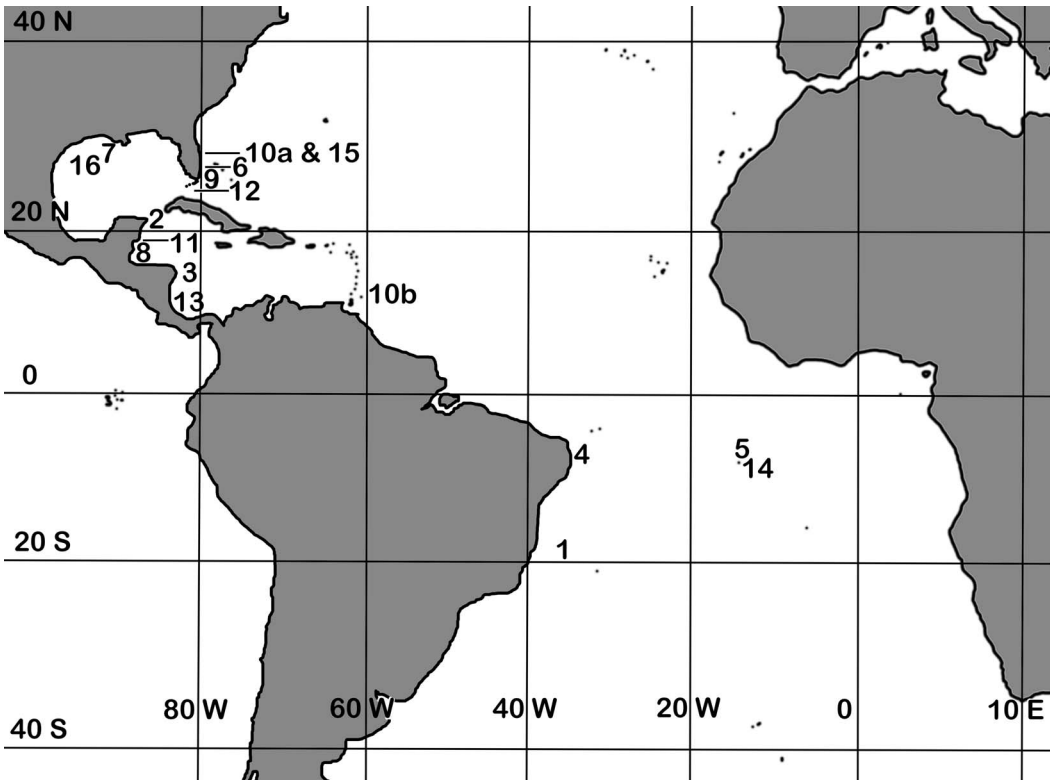


Fig. 1. Distribution of *Mithrodia clavigera* in the central Atlantic Ocean and adjacent waters. Locations are approximate; consult the text and original sources for location data. Locations: 1, Vitória Seamount, Brazil, 1879–1880 (Bell 1882); 2, Cancún, Mexico, 1967 (Clark & Downey 1992); 3, Puerto Cabezas, Nicaragua, 1971 (Voss 1971); 4, Pairabo State, Brazil, 1981 (Gondim et al. 2014); 5, Ascension Island, 1985 (present report); 6, Palm Beach, Florida, 1985–1987 (present report); 7, Rankin/28 Fathom Bank Complex, Gulf of Mexico, 1986 (present report); 8, Belize, ca. 1992 (Humann 1992); 9, Fort Lauderdale, Florida, 1998 (present report); 10a and 10b, Fort Pierce, Florida, and Barbados, ca. 2003 (larvae; Knott et al. 2003, Galac et al. 2016); 11, Cozumel Island, Mexico, 2011–2012 (Calderón-Gutiérrez et al. 2012); 12, Long Key, Florida (larvae; Galac et al. 2016); 13, Panama, 2013–2016 (larvae; Collin, Venera-Pontón, Driskell, Macdonald & Boyle 2020); 14, Ascension Island, 2016 (Brown et al. 2016); 15, Fort Pierce, Florida, 2017 (larva; USNM 1448413); 16, Flower Gardens National Marine Sanctuary, undated (Flower Gardens National Marine Sanctuary 2020).

tute) was collected by Bruce Graham (BDG) on 21 May 1998 using SCUBA at a depth of 4 m about 4.2 km north of Port Everglades Inlet, Fort Lauderdale, Florida (26°7.8'N, 80°5.6'W). The general location was a grounding site of a large vessel (146-m freight carrier) on the inshore hard bottom of a reef system composed of three, progressively deeper, terraced ridges that extend parallel to the north-south-oriented shoreline (Duane & Meisburger 1969). The geomorphology and ecology of this reef

system were described by Banks et al. (2008).

One specimen of *M. clavigera* (Fig. 2C; USNM E34135, alcohol) was examined from the United States National Museum of Natural History, Smithsonian Institution. It was collected on 26 November 1985 from Site 19 of Operation Origin, off North Point, east side of English Bay, Ascension Island, approximately 7°53'21"S, 14°22'42"W, at 20 m depth by SCUBA. Maureen E. Downey originally

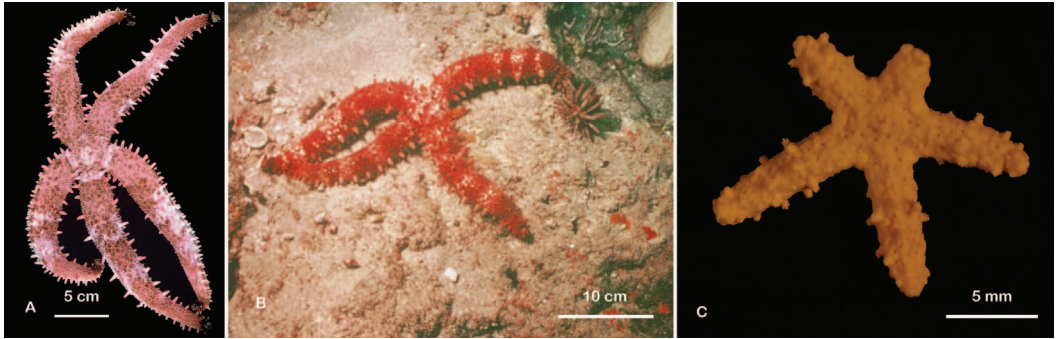


Fig. 2. *Mithrodia clavigera* from locations in (A) Palm Beach, Florida (HBOM 073:00388), (B) Fort Lauderdale, Florida (FSBC I 139722), and (C) Ascension Island (USNM E34135).

identified the specimen as *M. gigas* in March 1987. We compared this specimen to another (USNM E35532, dry) *M. clavigera* from Engebi Island, Eniwetok Atoll, Marshall Islands, collected intertidally in 1959.

Results

Palm Beach, Florida, location.—On 14 January 1986, one of us (Richard Turner) received a telephone call from Noreen Rouse of Noreen Rouse SCUBA, Inc., West Palm Beach, Florida, about the presence of large sponge-eating seastars off Palm Beach. JEM was contacted early in 1986 by Robert G. Ernest, Applied Biology, Inc., Jensen Beach, Florida, about a large “spinulosid” seastar and was referred to Rouse, who had found the seastars in depths of 34–40 m. The seastars had been seen by the dive boat personnel for about 1 yr (Gary Atkison, pers. comm.). The seastars were claimed to have locally eaten all sponges at 34 m depth. They were seen frequently on each dive, and around 21 March they were moving into deeper water and along the shore.

During a dive on 27 March 1986 off Lake Worth Inlet, JEM found *Mithrodia clavigera* (Fig. 2A) around the bases of *Xestospongia* sp., with a few seastars on the sides and in the oscula. One specimen

had its oral frame embedded in the body of the sponge. Rouse had observed in the past that some seastars were so deeply embedded in the sponge body wall that only the tips of the rays were exposed. The seastars appeared to be removing the accumulation of detritus on the surface of the sponges, changing the surface color from grey to white. Under natural light, *Mithrodia* were difficult to see against the sponges and sea floor, but the seastars were startlingly visible under a dive light. During the ascent of the dive, the seastars wrapped their rays around JEM’s arm until a depth of about 9 m, at which point they tended to release their grip, a phenomenon previously observed by Rouse. At the surface, animals began autotomizing the rays rapidly, with only one arm affected initially. Rays began softening at an autotomy plane at the base, and they broke free first at the oral surface. Iced sea water seemed to reduce the incidence of autotomy.

In November 1986, Thomas F. Stewart of Palm Bay, Florida, informed JEM that “your red starfish” were at 21 m depth off Palm Beach. On 6 January 1987, Rouse reported to JEM that *M. clavigera* had returned to her dive sites at 34–40 m eating an orange sponge (*Agelas* sp.) at the bases and detaching them from the substratum. Most of the large *Xestospongia* sp. were gone from the site. Rouse recalled at that

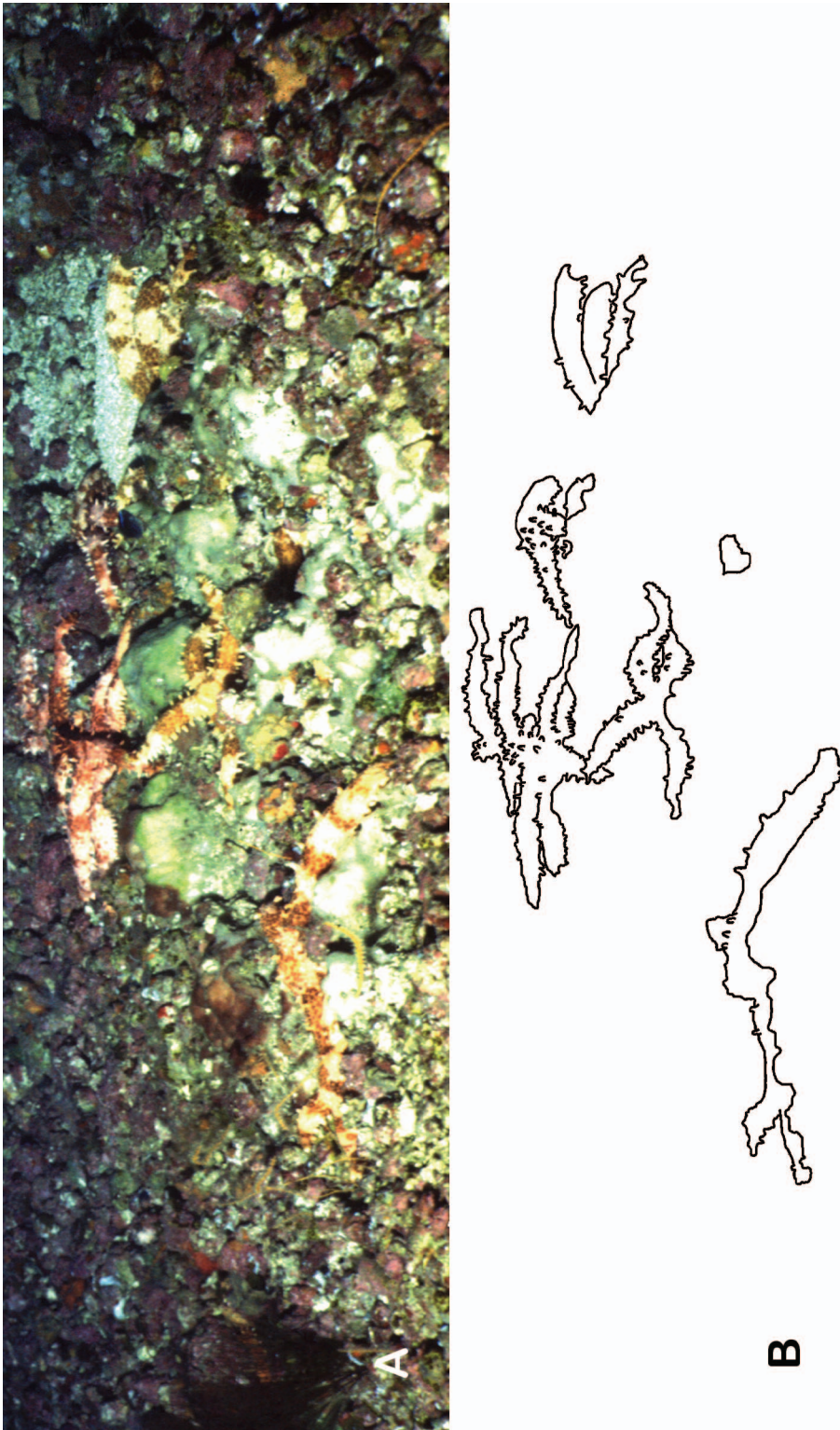


Fig. 3. *Mithrodia clavigera* on the Rankin/28 Fathom Bank Complex, Gulf of Mexico. A, in situ photograph; B, outlines of seven specimens illustrated in Fig. 3A to indicate their positions more clearly.

time that she and her personnel had encountered many *Agelas* sp. detached and rolling around the sea floor at depths < 40 m before having seen their first *M. clavigera*. Rouse concluded that *M. clavigera* had fed on and detached *Agelas* sp. in deeper water and that the detached sponges were then carried into diving depths by water currents. Upon localized depletion of sponges in deeper water, the seastars moved into shallower waters in search of more sponges. Rouse noted that some *Xestospongia* sp. that were lighter colored than others crumbled when touched. In undated notes to JEM from John and Lori Elsner, Gold Coast Charters, Inc., West Palm Beach, the seastars were found at 24 m at the bases of large irregular sponges and under rock ledges in five dive locations between Lake Worth and Jupiter inlets: Pastureland, Zimmerman's, Frank Snapper Reef, in rubble leading to South Juno Ball Ledge, McArthur's Park Ledge (mostly local or proprietary names for uncharted dive locations). Based on these observations from personal communications and directly by JEM, *M. clavigera* was seen off Palm Beach for at least 2 yr, from early 1985 to early 1987.

Size, autotomy, and regeneration: Our morphological notes here are based on the 16 dry specimens in HBOM 073:00388; the four specimens in LACM 1986-714.001 were not examined before shipment to the museum. The range in maximal arm length (R, major radius) is 180–270 mm and in disc radius (r, minor radius) 16–25 mm. The range of ratios R:r is 9.5–14.4, indicating the small disc and long arms typical of this species. Ten of these five-armed animals have freshly autotomized arms at 15 positions: six specimens having lost one arm; three specimens having lost two arms; one specimen having lost three arms between collection and preservation. Because the lot includes 22 loose arms, some of the arms belong to animals that are not represented in the lot. Animals with autotomized arms have autotomy

planes at the base of the arms at junctions as close as between the 6th and 7th adambulacral ossicle from the mouth frame but not farther than between the 8th and 9th. None of the 22 loose arms shows signs of prior autotomy or regeneration. Two specimens have one or two arms regenerating basally, presumably from prior events of autotomy. Three specimens have one or two arms with tips regenerating from thick stubs that are about the length of other arms; this condition might indicate prior events of sublethal predation.

Spines and pedicellariae: The specimens show typical features of mithrodiids and *M. clavigera* specifically. The small disc gives rise to five long cylindrical arms that are constricted at the bases (Fig. 2). Spines, some up to 9 mm in length, are thick, cylindrical, tapering only gradually to an obtusely rounded tip. The major spines occur in nine rows along each arm (Fig. 4): a carinal row along the aboral radius; this row flanked on each side in succession around to the ambulacral groove by the superomarginal, inferomarginal, actinolateral, and subambulacral rows. The primary ossicles on which the major spines articulate also occur in single rows. The spines increase in length but decrease in number from the ambulacral grooves to the aboral surface. For every 30 subambulacral spines near the base of a ray, there are 8–17 actinolateral spines of somewhat greater length, 4–7 inferomarginal spines, 1–5 superomarginal spines, and 1–4 carinal spines. Spines of infero- and superomarginals and of carinals are approximately equal in length, although the carinal spines can be shorter. The frequency of carinal spines decreases distally, and the outer half of an arm is usually devoid of large carinal spines. Engel et al. (1948) also noted the decrease in number of large spines from ventrum to dorsum in the nine series and from proximal to distal regions in the carinal series in *M. clavigera*. In addition to the subambulacral spine, each adambu-

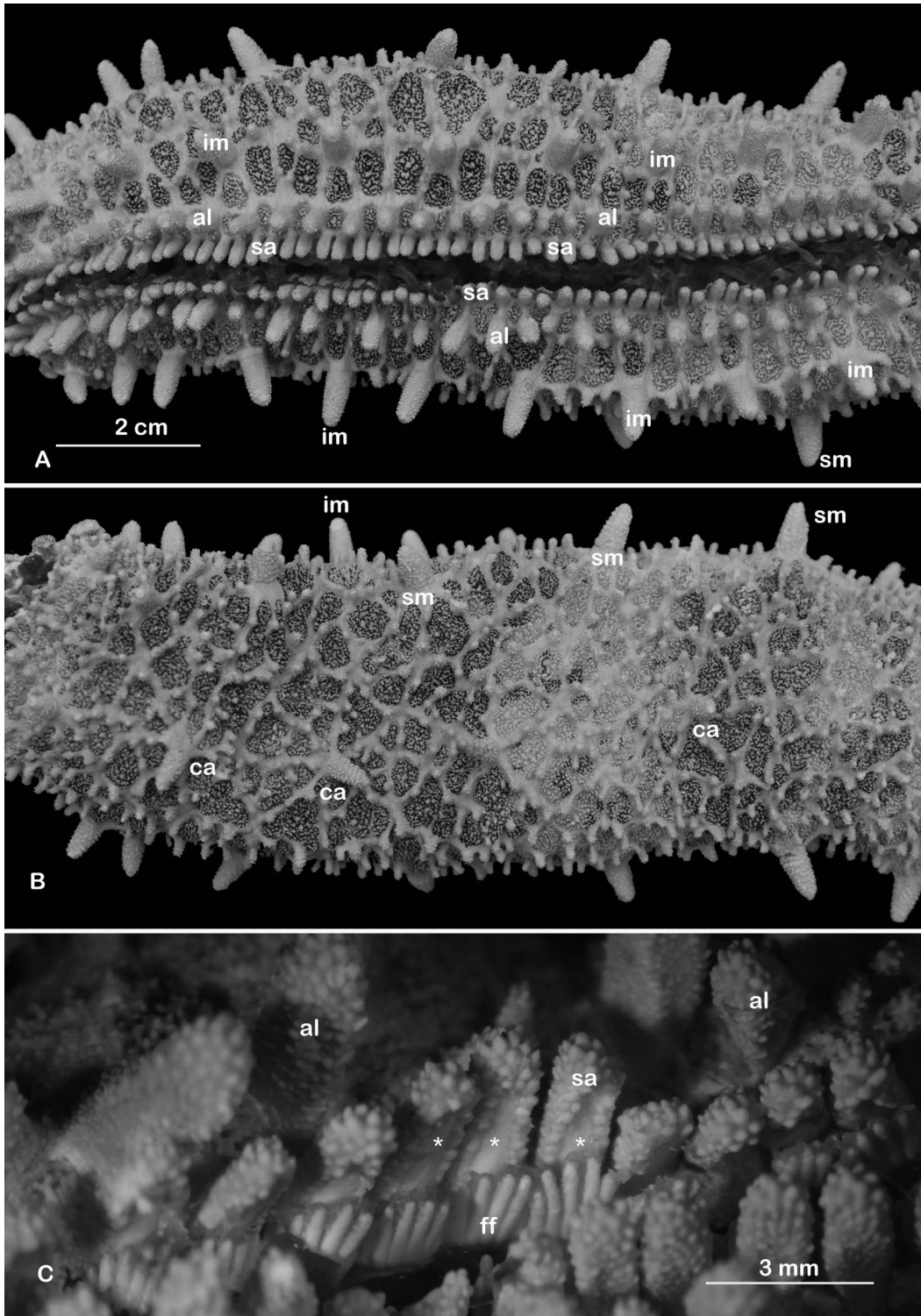


Fig. 4. Spine series of *Mithrodia clavigera* (HBOM 073:00388). A, adoral view; B, aboral view; C, detail of ambulacral furrow. al, actinolateral spine; ca, carinal spine; ff, furrow fan, 4–5 furrow spines visible per fan; im, inferomarginal spine; sa, subambulacral spine; sm, supermarginal spine; *, adradial surface of furrow spines without granules.

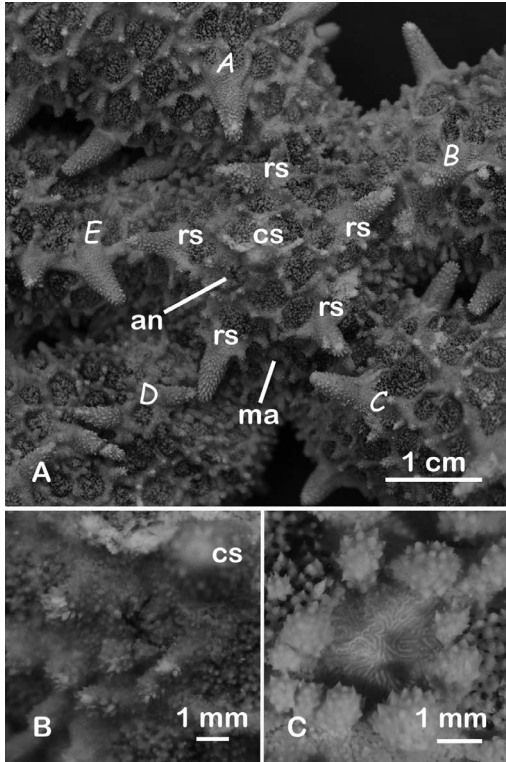


Fig. 5. Detail of the aboral disc (HBOM 073:00388). A, aboral view of the disc; the first carinal of each arm is labeled at its base by the italicized letter (*A–E*) that designates the position of the arm relative to the madreporite. an, anus; cs, central spine; ma, madreporite; rs, radial spine. B, anus, adjacent to the central spine (cs) and surrounded by several spinelets. C, madreporite with meandroid ridges and sulci, surrounded by several spinelets.

lacr al ossicle bears an arched fan of small furrow spines webbed together by skin (Fig. 4C). The webbed fan is usually hidden by the overarching subambulacral spines. Each fan has 4–5 longer spines along the furrow and 1–5 smaller spines of strongly diminishing length on each side (proximal and distal). The subambulacral spine, adjacent furrow fans, and podia make the smaller furrow spines hard to see and to count, giving the impression of fans having only 4 or 5 spines. The disc bears a large central spine with adjacent anus in interradius *DE* (Fig. 5B) and the nearby

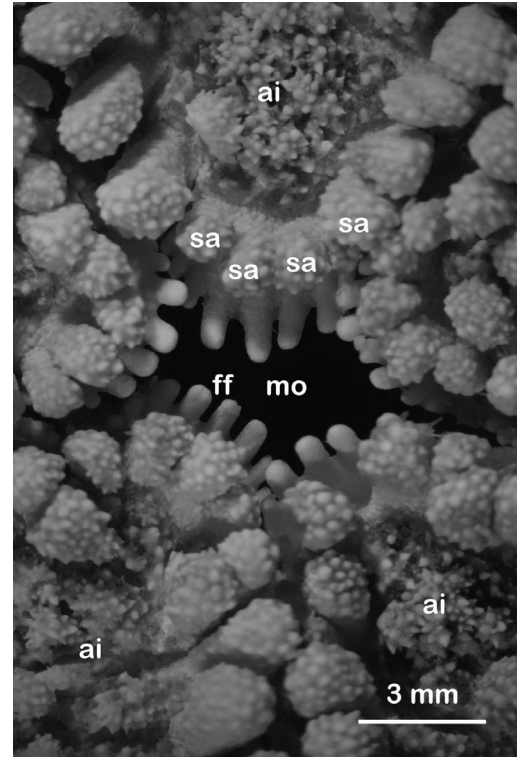


Fig. 6. Detail of the adoral disc (HBOM 073:00388). Five jaws project into the oral field, each jaw bearing four subambulacral spines and a fan of furrow spines. An actinal intermediate area lies distal to each jaw. ai, actinal intermediate area; ff, furrow fan; mo, mouth; sa, subambulacral spine.

madreporite (its presence defining interradius *CD*) (Fig. 5C). The disc bears five radial spines. One spine, the first carinal, occurs just distal to the junction of the disc and each arm in line with the rest of the carinal row (Fig. 5A). Each half jaw of the mouth frame bears one or two subambulacral spines and its own furrow fan (Fig. 6). The actinal intermediate skeleton is small, confined to the area immediately distal to the jaw, not extending beyond the disc; the ossicles only bear short tubercles (Fig. 6). Fasciculate pedicellariae (Fig. 7) have 4–9 (mostly 6) incurved spinelets on ring-shaped baseplates as described and illustrated by Engel et al. (1948). A few straight, outwardly directed spinelets at the periphery of the baseplate give the

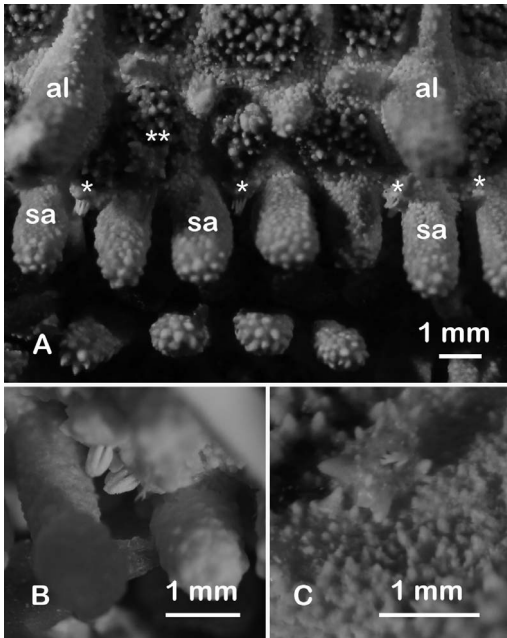


Fig. 7. Fasciculate pedicellariae of *Mithrodia clavigera* (HBOM 073:00388). A, pedicellariae in papularia at bases of subambulacral spines. One pedicellaria (**) is visible in plan view, showing four peripheral spinelets. al, actinolateral spine; sa, subambulacral spine; *, pedicellaria. B, two pedicellariae with clusters (fascicles) of valves, between bases of two subambulacral spines. C, a pedicellaria with central cluster of valves and several peripheral spinelets.

intact pedicellaria the appearance of a crown or tricorn hat, depending on their lengths and number (Fig. 7A, C). Pedicellariae are present at the adradial border of the small papularia between the adambulacral and actinolateral series of ossicles and appear to be adjacent to or between the subambulacral spines (Fig. 7A). They also occur in papularia between the other series of ossicles. Pedicellariae vary widely among specimens in frequency. Those near the subambulacral spines are numerous from base to arm tip on some specimens, are rare and only on the outer half of the arm in some, and are not found on other specimens, even those that seem to have been well preserved. Among other series of ossicles along the arm, pedicellariae are

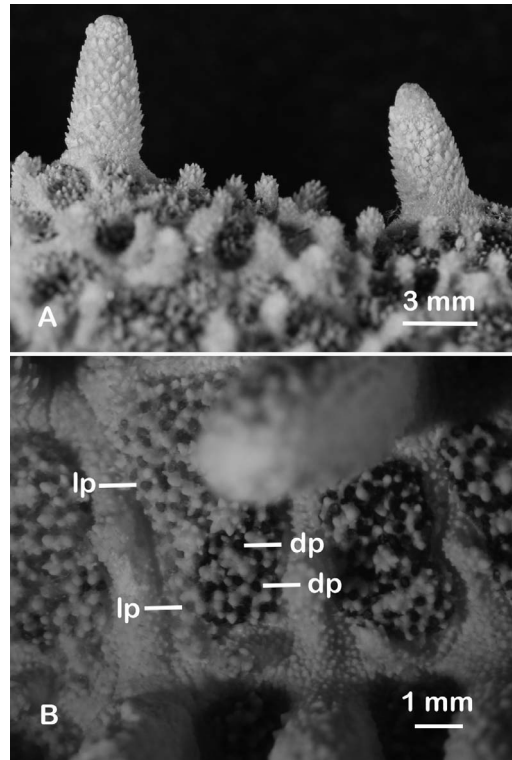


Fig. 8. Dermal features of the body wall (HBOM 073:00388). A, two superomarginal spines covered with granular skin. B, papularia among elements of the reticulated skeleton, with darkly and lightly pigmented papulae among granules and spinelets in skin. dp, darkly pigmented papula; lp, lightly pigmented papula.

rare or absent regardless of their frequency near the subambulacral spines.

Integument: Almost the entire body is covered with a thick skin invested with scale-like denticles and conical granules (Fig. 8), a feature of family Mithrodiidae. This rough skin covers the major spines (Fig. 8A), tubercles of the reticulated skeleton of the body wall, and the abradial surface of subambulacral spines. Shafts of spines are covered with closely overlapping scales with their points oriented apically; near the tips of spines, the granules are more conical (Fig. 8A). The rough skin is absent from the flat meandroid madreporite (Fig. 5C), terminal plate at the arm tip, within the ambulacral groove, furrow fan,

pedicellariae, and much of the adradial surface of subambulacral spines (Fig. 4C) where podia might contact them during extension. Large polygonal papular areas occur among primary, secondary, and tertiary elements of the reticulated body skeleton (Fig. 8B). The papularia are large dorsally, decrease in area on the sides of the arms, and are smallest between the actinolateral and adambulacral series of ossicles (cf. Fig. 4A, B). Variation in pigments of the papulae (Fig. 8B) gave the live animals a beige ground color with bands and blotches of orange to reddish-brown (Figs. 2A–B, 3A); the pattern of bands and blotches remains in the dried specimens only as differences in shades of tan. Skin overlying the ossicles is always beige.

Gulf of Mexico location.—At least seven animals are identifiable in the photograph taken from the Rankin/28 Fathom Bank Complex in the central Gulf of Mexico (Fig. 3). The robust cylindrical spines and gaudy coloration distinguish this species as *M. clavigera*, for no other species of seastar in the Atlantic basin and adjacent waters has these features (Clark & Downey 1992). Indeed, the presence of its large spines serves as the basis for two common names: “studded sea star” (Humann 1992) and “nail sea star” (Flower Gardens National Marine Sanctuary 2020). Two or three large, globular sponges [cf., *Neofibularia nolitangere* (Duchassaing & Michelotti, 1864)] are in the middle of this group of seastars.

There is no basis for estimating size of the animals except very roughly from the large numbers of major spines in the longitudinal series of the arms. There are only a few carinal spines on each animal, several superomarginal spines, and, where visible, even more inferomarginal spines per section of arm. In areas of the bodies not overexposed by the photographic sled lights, spines and much of the body are beige. The clusters of polygonal papularia

can be seen where papulae are orange to red-brown.

Arms of the animals are contorted as they conform to the topography of the substratum (Fig. 3). At least two animals at the top of the photograph are so close to each other that it is difficult to distinguish them; but there are too many arms for one individual. The animal to the lower left of the group seems to be the largest one, although only one arm is fully in view. The animal to the far right might be as large or larger. The least visible animal is in the lower right, and only a small part of the body is exposed; it is, however, too far from other animals to belong to one of them.

Fort Lauderdale location.—Following the grounding and removal of the freighter from a relatively shallow-water hard-bottom ridge, displaced corals and limestone-substratum rubble were gathered for subsequent restoration activities (primarily for coral reattachment). The grounding location and where the *M. clavigera* specimen was observed was a relatively high-energy environment visually dominated by sponges, octocorals (including *Gorgonia ventalina* Linnaeus, 1758 and various plexaurids), and hard corals [including brain corals *Pseudodiploria clivosa* (Ellis & Solander, 1786) and *P. strigosa* (Dana, 1846), the great star coral *Montastraea cavernosa* (Linnaeus, 1767), and the smooth star coral *Solenastrea bournoni* Milne Edwards & Haime, 1849]. Individuals of these species of hard coral typically had a growth morphology that was low profile and sprawling. The proportions of these epifaunal components were spatially variable on the low-relief limestone substratum of the inner ridge where the specimen was found. When first sighted on 19 May 1998, the seastar was near some of the grounding-associated coral and substratum rubble and quite noticeable by its regionally anomalous appearance, in particular the large robust spines along the arms. BDG had never seen such a seastar in his

working for more than 15 yr as a marine scientist, with the majority of his work underwater off Broward and Palm Beach counties, Florida. The seastar was sedentary, loosely draped on some of the rubble material with no distinguishable ongoing behavioral activity such as feeding. The seastar was not collected on the date it was first seen. What seemed to be the same specimen of *M. clavigera* (Fig. 2B) was collected on 21 May 1998 from a location similar to where it was first observed within the grounding site. At the time of collection (Fig. 2B), the seastar and a sea urchin *Eucidaris tribuloides* (Lamarck, 1816) were in sedentary positions among the grounding-associated rubble. The rubble included fragments of limestone substratum and displaced coral. The now-exposed undersides of the coral were occupied by a relatively abundant assemblage of encrusting and coelobiontic (cavity-dwelling) organisms, including ophiuroids, polychaetes, crustaceans, sponges, ascidians, and mollusks. This assemblage was exposed and more vulnerable to predation, as evidenced by the presence of numerous fish such as the Spanish hogfish and yellowhead wrasse feeding on newly exposed coral and limestone surfaces within the rubble piles. Although *M. clavigera* was not observed feeding, some components of this newly exposed assemblage could also have been a targeted food source for the collected specimen, which remained near the rubble piles for an extended time period. Whereas the Palm Beach *M. clavigera* specimens were associated with and perhaps feeding on sponges, including *Xestospongia* sp., the Fort Lauderdale specimen was not associated with sponges. The large barrel sponge *Xestospongia muta* (Schmidt, 1870) was a common component of the inner-ridge hard-bottom biological assemblage. But where the seastar was collected, *X. muta* and other large sponges [*Aiolochoxia crassa* (Hyatt, 1875), *Aplysina* sp., *Niphates* sp.] were sparsely distributed.

In the field (Fig. 2B), this animal had the distinctive features of *M. clavigera*: cylindrical arms banded with deep orange and beset with prominent spines. One arm had up to ten robust superomarginal spines and about seven smaller carinal spines. Four of the arms were full size, and one was regenerating from a fairly recent event of autotomy.

The preserved specimen (alcohol) has lost all banding and dark pigment. The regenerating arm is 44 mm long and had autotomized between adambulacral ossicles 8 and 9. The other four arms are subequal with $R = 182\text{--}227$ mm, and the disc has $r = 20$ mm, giving a maximal $R:r$ of 11.4. As in the specimens from Palm Beach, the number of major spines on the primary series of ossicles decreases from adambulacrals to carinals: along one least-distorted arm from its base out to 30 adambulacral ossicles, there are 12 actinolateral, 7 inferomarginal, 4 superomarginal, and 4 carinal spines. Counts and morphology of furrow spines are as for the Palm Beach specimens. Unlike the dried Palm Beach specimens with flat or slightly raised papularia, the alcoholic specimen from Fort Lauderdale has inflated papularia that look like muffins within the network of interconnected body wall ossicles. No pedicellariae are visible on this specimen.

Ascension Island.—The specimen (Fig. 2C) from Ascension Island is small (R 10.2 mm, r 2.8 mm) and has relatively short arms ($R:r$ 3.6). Of 47 specimens examined from around the basins of the Pacific and Indian oceans, Engel et al. (1948) had none so small as the Ascension Island specimen; their range of $R:r$ was 5–15, with smaller values found in smaller specimens. They measured the two syntypes of *M. victoriae*, both much larger (R 32 and 29 mm) than the Ascension Island specimen and with somewhat longer arms ($R:r$ 4.6 and 7). The specimen (USNM E35532) we examined from Engebi Island, Eniwetok Atoll, Marshall Islands was only about twice the size

(R 19.3 mm, r 4.0 mm) of the Ascension Island specimen, and its arms were relatively short (R:r 4.8).

Cynthia Ahearn, museum curatorial staff who handled the loan, sent us a few pages of what seems to be a rare expedition report (Taylor & Irving 1985) that we have otherwise been unable to access. The dive log described the animal as a “small spiked starfish” taken “from within a *Strombus* shell. Arms brown with small ‘spikes’.” The few other pages sent by Ahearn, part of a long table of collected specimens, revealed only two other species taken at Site 19 based on handwritten entries by Ahearn and Stephen Cairns: the ophiuroid *Ophiactis lymani* Ljungman, 1872 and the hard coral *Rhizosmilia* cf. *gerdae* Cairns, 1978.

The arms are cylindrical, barely tapering to the arm tip. Unlike *Thromidia* spp., the Ascension Island specimen lacks spines in the papular areas of the dorsum, and it already has nine rows of spines developing around the arms, of which the carinal, two superomarginal rows, and two inferomarginal rows are proportionately long and covered with spiny granules. Already at this size, there are two or three large spines in the carinal, superomarginal, and inferomarginal series (Fig. 2C). *Thromidia* has no carinal or superomarginal series of long spines. The actinal armature is still immature. Furrow spines are about four, not the 12 or more of mature *Mithrodia* and *Thromidia*; but if you look at the furrow spines of typical specimens, the central ones are very long, and the series tapers to very small ones to each side of the central ones, suggesting that the additional spines are added later in growth. Engel et al. (1948) also noted an increase in number of furrow spines with size of specimen. Additionally, Gondim et al. (2014) found only four furrow spines in their Brazilian comparably small specimen (R 9.8 mm). It makes sense that a small specimen would have only a few furrow spines and that more are added as the adambulacral plates

grow larger. Such a small specimen might not yet show the multiple actinal intermediate plates of *Thromidia* if it were a *Thromidia*; and it might not show the very broad, blunt-ended arms of *Thromidia*. In these features, one might expect a juvenile not to show these diagnostic characters of *Thromidia* and make it look like a *Mithrodia*. But the presence of the rows of large carinal, superomarginal, and inferomarginal spines and its similarity to the small Marshall Island specimen examined here assure its identity as *Mithrodia clavigera*. The morphology of these two juvenile *M. clavigera* also agrees with descriptions and illustrations of other small *M. clavigera*: Gondim et al. (2014) for a specimen from coastal Brazil; two syntypes of *M. victoriae* (Bell 1882, Engel et al. 1948, Clark & Downey 1992).

Discussion

The first record of *M. clavigera* in the Atlantic basin was from Vitória Seamount (Victoria Bank; 20°42'S, 37°27'W) 271 km off Espírito Santo State, Brazil, by H.M.S. *Alert* at a depth of 39 fm [24–71 m] from a bottom of dead coral in 1879–1880 (Bell 1882) (Fig. 1, location 1). The two small (R = 26.5 mm, 30 mm) syntypes formed the basis for a new species, *M. victoriae* Bell, 1882. Bell (1882) illustrated one of the specimens. H.M.S. *Alert* apparently took no other echinoderms from Vitória Seamount (Bell 1881); and the area has not been sampled for echinoderms since 1880. On the other hand, Ridley (1881) listed two species of demosponge and five of calcareous sponge from this location. Bell (1882) compared the morphology of his new species to that of *M. clavigera*, but he did not account for the small size of his specimens. Numerous authors have listed Bell's record of *Mithrodia* from Vitória Seamount over the last 140 yr, sometimes having questioned or ignored the geographic source (e.g., Steinbeck & Ricketts

2009 [1941], Pope & Rowe 1977) and rarely having re-examined the syntypes in the British Museum (Natural History). Engel et al. (1948) examined Bell's syntypes and included a photograph of one. They noted differences from *M. clavigera*, differences that were not "essential". The three authors disagreed on the taxonomic status of *M. victoriae* but decided it "safer to regard it as a separate species." Cherbonnier (1975) suspected that *M. victoriae* might be only a geographic variant of *M. clavigera*. Pope & Rowe (1977) and Clark & Downey (1992) synonymized *M. victoriae* with *M. clavigera* based on their examination of the syntypes; they dismissed differences noted by Bell (1882) and Engel et al. (1948). New specimens from coastal Brazil were not reported until 1981, when one small (R 9.8 mm) specimen of *M. clavigera* was collected off Paraibo State (Fig. 1, location 4) from 26 m on a rhodolith bank (Gondim et al. 2014; their Fig. 7F–I).

The second discovery of *Mithrodia clavigera* in the Atlantic basin (Fig. 1, location 2) was in the western Caribbean Sea where four *M. clavigera* were collected 32 km off Cancún, Yucatán Peninsula, Mexico, on 9 September 1967 (Clark & Downey 1992, Nancy Voss, pers. comm.). The specimens were taken from Station 887 (Arrowsmith Bank; 21°05'N, 87°28'W) on Cruise 6717 of the R/V *Gerda* by 10-ft otter trawl at a depth range of 37–157 m along with 15 crinoids (Nancy Voss, pers. comm.). Clark & Downey (1992) examined the four specimens, including USNM E30125 (one specimen); they reported R > 150 mm and included a photograph of the arm tip of one specimen (Clark and Downey's Plate 71C) and line drawings (their Fig. 46) of various body parts of a specimen with R = 170 mm. A few years later, a fifth specimen was taken in the western Caribbean Sea (Fig. 1, location 3) 125 km east of Puerto Cabezas, Nicaragua, on 29 January 1971 (Voss 1971). The specimen was collected at Station 1343

(13°58.3'N, 82°03.7'W) on Cruise P-7101 of the R/V *John Elliott Pillsbury* by 10-ft otter trawl at a depth range of 24–26 m on a hard bottom with sponges (*Xestospongia*, *Haliclona*, *Verongia*) and coral debris. In his journal, Voss (1971) wrote, "The most spectacular item was a large bright orange red *Linkia*-like [*sic*] starfish with swollen arms with numerous large blunt spines. We have seen nothing like it in any of our tows." The specimen (USNM E30124) was examined by Clark & Downey (1992), who reported it to have R = 205 mm and included photographs of aboral and oral views (their Plate 71A, B). Clark & Downey (1992) wrote that the Yucatán and Nicaragua specimens were "undoubtedly conspecific with the syntypes of *victoriae*, by comparison with growth changes in large and small Indo-Pacific specimens of *clavigera*." Most records of *M. clavigera* for the western Caribbean in the literature have referred to these specimens; unfortunately, some records from "Cuba" are attributable to the Yucatán material (Abreu-Pérez 1997, Abreu-Pérez et al. 2005, Alvarado 2011). Since the early reports of Caribbean *M. clavigera*, new records include Belize (coral rubble, 5–8 m depth; Humann 1992, Bryan J. Nichols, pers. comm.) (Fig. 1, location 8) and the Aerolito de Paraiso anchialine cave system on Cozumel Island, Mexico (2011/2012 on a clay/mud substratum at maximal depth of 27 m; Calderón-Gutiérrez et al. 2012, Bribiesca-Contreras et al. 2013) (Fig. 1, location 11). Most recently, Collin et al. (2020a, 2020b) identified larval *M. clavigera* by DNA barcoding from plankton tows taken in 2013–2016 from the Caribbean coast of Panama (Fig. 1, location 13).

Pawson (1978) found no *Mithrodia clavigera* in the two extensive collections of invertebrates made at Ascension Island in the central South Atlantic in the 1970s. The specimen described herein was collected in 1985 (Fig. 1, location 5), but it was apparently overlooked by Clark & Downey (1992) in their monograph of seastars of

the Atlantic Ocean despite its presence (as *M. gigas*) in the collections of the Smithsonian Institution. It might have been the exclusion of this specimen in their monograph that led Brown et al. (2016) to claim their discovery of a first *M. clavigera* at Ascension Island on 23 January 2016 (Fig. 1, location 14). Brown et al. (2016) included a color photograph *in situ* of *M. clavigera* on a rocky reef off Porpoise Point (7°53.9'S, 14°21.1'W) at a depth of 15 m. The authors did not deposit a voucher specimen in a museum, and they did not describe the substratum or associated fauna. The species has not been reported yet from the nearest island, St. Helena (1100 km distant), despite the moderate similarity of its echinoderm and other shallow-water marine fauna to that of Ascension Island (Pawson 1978).

Our observations of adult *M. clavigera* from Palm Beach (1985–1987) and Fort Lauderdale (1998) (Fig. 1, locations 6, 9) are the first from the east coast of Florida. They probably formed the basis for listing of *M. clavigera* by Camp et al. (1998) among the shallow-water echinoderms of Florida, a document to which we contributed unpublished records. Three later records are for larvae. Galac et al. (2016) collected several bipinnaria larvae in May 2012 from plankton tows taken in the Florida Current south of Long Key, Florida (Fig. 1, location 12). They described the larvae as “non-cloning bipinnarias with a red-brown colored gut”. They assigned the larvae to *M. clavigera* based on comparison of their genetic markers to those of adult *M. clavigera* from Cozumel Island, Mexico, and adult *M. bradleyi* from Baja California, Mexico. Galac et al. (2016) genetically identified the 12 cloning bipinnaria larvae of “ophidiasterid” group 4 studied by Knott et al. (2003) as *M. clavigera*; these larvae were collected off the east coast of Florida and Barbados (Fig. 1, locations 10a and 10b, respectively). Finally, a photographic image by Michael Boyle reported to be a

larval *M. clavigera* is deposited at the U.S. National Museum of Natural History (USNM 1448413). The larva was collected from the Gulf Stream off Fort Pierce, Florida, on 14 August 2017 from R/V *Sunburst* of the Smithsonian Marine Station at Fort Pierce (Fig. 1, location 15).

The photograph analyzed herein of *M. clavigera* from the Rankin/28 Fathom Bank Complex (Fig. 1, location 7) in 1986 is the first record of the species from the Gulf of Mexico despite numerous prior expeditions and surveys since the early 1800s (Galtsoff 1954). No *M. clavigera* were collected on the Project Hourglass cruises of 1965–1967 by the Marine Laboratory, Florida State Board of Conservation (now the Florida Fish and Wildlife Conservation Commission) in the eastern Gulf of Mexico. Depth, gear, and bottom type for Stations B, C, J, and K were appropriate for collection of *M. clavigera* if it were present during the 28 monthly collections (Joyce & Williams 1969). Hopkins et al. (1977) did not find the species among the benthos during their SCUBA transects in 1975–1976 over the coral and high-relief rocky substrata of the Florida Middle Grounds at depths of 23–36 m. The image library of the Flower Gardens National Marine Sanctuary (2020) does, however, include an *in situ* undated photograph of *M. clavigera* among its seastars of the coral cap region of the sanctuary at 0–40 m depth (Fig. 1, location 16).

The accumulation of only four records of *Mithrodia clavigera* in the tropical and subtropical Atlantic Ocean was slow over the first century (1880/1881 to 1985), the locations were far apart, and the specimens were few. One factor for this paucity of data was noted by Clark & Downey (1992), who pointed out the tendency of mithrodiids to wedge themselves into the rough substratum of their reef habitat (Fig. 3). Their echinasteroid body plan (Blake 1989) allows great flexibility of the arms to conform to the substratum, either

the reef foundation and rubble or sponges and other living habitats, thereby reducing the effectiveness of benthic collecting gear. Fisher (1906) reported that almost all his specimens of *M. fisheri* (as *M. bradleyi*) “were taken with hempen tangles from bottom too rough for dredging nets.” And Fisher (1919) reported no *M. clavigera* among the 190 species of asteroid collected by the U.S.S. *Albatross* over 3 yr of dredging at 224 stations in the Philippines. The great increase in records of *M. clavigera* in the Atlantic basin in the last five decades might be attributed in part to the advent of SCUBA (Taylor & Irving 1985, Calderón-Gutiérrez et al. 2012, Bribiesca-Contreras et al. 2013, Brown et al. 2016), seafloor photography, and genetic analysis (Galac et al. 2016, Collin, Venera-Pontón, Driskell, Macdonald & Boyle 2020, Collin, Venera-Pontón, Paulay, & Boyle 2020). Turner & Graham (2003) used a similar explanation when they added two echinoid species to the Gulf of Mexico fauna inhabiting high-relief live-bottom biotopes.

Clark (1921), in his report on the brittlestars of the Barbados-Antigua Expedition, wrote, “In view of the past intercommunication between the Caribbean Sea and the Pacific the similarity of certain elements of the Caribbean fauna and of that of the western coast of tropical America is not surprising; the latter, however, includes a very considerable number of genera which occur nowhere else, together with a few species of characteristic Indo-Malayan types, such as *Mithrodia*, *Acanthaster*, *Anthenea*, *Leiaster*, *Astropyga*, etc., which are not represented in the Caribbean Sea.” Verrill (1867) had noticed this pattern in general for echinoderms, but Perrier (1878) rejected existence of such a pattern for asteroids. Of 350 species of asteroid recorded by Clark & Downey (1992) from the Atlantic Ocean, four species are extra-Atlantic, either in the eastern tropical Pacific or in the Indo-West Pacific or

both: *Luidia ludwigi*, *Luidia sagamina*, *Linckia guildingi*, and *Mithrodia clavigera*. To these extant species can be added *Heliaster microbrachius*, which was recorded from Cenozoic deposits (“Tami-mi Formation?”) in Florida (Jones & Portell 1988) and is extant in the eastern Pacific Ocean. Maureen Downey might have identified the small Ascension Island specimen (recorded herein) as *Mithrodia gigas* (now *Thromidia gigas*) because of its proximity to South Africa, the type locality of Mortensen’s species. Rafting of adult echinoderms from South Africa on the kelp *Ecklonia maxima* has been postulated (Mortensen 1933) or reported (Arnaud et al. 1976) and explains the establishment of some echinoderms on St. Helena, 1100 km south of Ascension Island. Pawson (1978) and Barnes (2017) considered recruitment by long-lived planktonic larvae to be a better explanation for colonization of Ascension Island. Collin, Venera-Pontón, Paulay, & Boyle (2020) also proposed this mechanism for invasion of the Atlantic basin by *M. clavigera*. But the Cape Point phylogeographic barrier created by the divergence of the warm Agulhas Current and cold Benguela Current (David et al. 2016) probably would prevent adult rafting and larval drift into the South Atlantic by the more tropical *Thromidia gigas* of South Africa, let alone *M. clavigera* from higher latitudes in the Indian Ocean (Engel et al. 1948, Clark & Courtman-Stock 1976). The best explanation for the current, nearly pantropical distribution of *Mithrodia clavigera* is its presence in the middle Miocene Caribbean Province, with Pacific and Atlantic populations later separated by the Pliocene rise of the Isthmus of Panama (Jones & Portell 1988, Lessios 2008) and with eventual divergence of *M. bradleyi* (if it is a separate species; Clark & Downey 1992) from *M. clavigera* in the eastern tropical Pacific.

Acknowledgments

We thank the late Noreen Rouse of Noreen Rouse SCUBA, Inc., and others mentioned herein for alerting us to the presence of *Mithrodia clavigera* off Palm Beach, Florida, and for keeping us updated on later findings of this seastar. Rouse and two diving instructors Gary Atkison and Rodney Colson assisted JEM in collecting specimens during the dive off the vessel M/V *Hawksbill* piloted by Cpt. J. D. Duff. Museum specimens were provided by Paula Mikelsen (then of the Harbor Branch Oceanographic Museum) and the late Cynthia Ahearn (National Museum of Natural History). The specimens from Palm Beach were collected by JEM while employed by Harbor Branch Oceanographic Institution. The seafloor photo from Rankin Bank and specimen from Fort Lauderdale were taken while BDG was conducting projects under contract to CSA Ocean Sciences Inc. We also thank John M. Lawrence (University of South Florida) for providing translations of some French-language literature into English.

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Note added in proof: Additional Brazilian records for *Mithrodia clavigera* were reported by