



New species and occurrences of deep-sea Asteroidea (Forcipulatacea, Valvatida, Paxillosida) from the Pacific continental margin of Costa Rica

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Abstract

Deep-sea settings in the Eastern Tropical Pacific remain a poorly understood region with many further species awaiting discovery. Herein, four new species from Costa Rica are described from deep-sea habitats. New occurrences with *in situ* or living observations are made for eight species. New observations of hippasterine corallivory on deep-sea octocorals are included. A brief summary of Costa Rican species is presented.

Key words: Deep-sea, corallivory, Goniasteridae, Radiasteridae, Solasteridae, Pterasteridae, *in situ* observations, taxonomy, Central America

Introduction

Eastern Tropical Pacific echinoderms are a significant and diverse fauna (Maluf 1988), which are poorly understood, especially in the deep-sea. Costa Rica, located on the Central American Isthmus, displays coastlines along the Pacific Ocean and the Caribbean Sea and has an extensive ocean coastline. Costa Rica's Pacific marine territory, including the exclusive economic zone) is extensive, covering 544,813 km² and is home to diverse deep-sea habitats, depths below 200 m represent over 90% of the total area (Cortés, 2019; Rojas Jiménez *et al.*, 2020; Azofeifa-Solano and Cortés, 2021). It has been estimated that over 60% of Costa Rica's territory is below 2000 m with over one third of the country submerged below 3000 m. Shallow-water asteroids from the Pacific coast of Costa Rica are consistent with other faunas encountered in the Eastern Tropical Pacific (summarized in Alvarado 2010).

A literature- and museum-collections-based checklist of the deep-sea echinoderms from Costa Rica was recently summarized by Alvarado *et al.* (2022) in addition to a broader checklist of Costa Rican echinoderms (Alvarado 2010). Historical accounts of deep-sea Pacific Asteroidea begin with Ludwig's (1905) account of Eastern Pacific Asteroidea, including multiple species from Costa Rica with relatively few reports of Pacific Costa Rican asteroids since then. Checklist accounts of Caribbean echinoderms have been compiled by Alvarado (2011) and Cambronero-Solano *et al.* (2019).

Alvarado *et al.* (2022) summarized deep-sea (>900 m depth) Asteroidea from Costa Rica, including a total of 25 species, including caymanostellids described by Shen *et al.* (2024) and approximately three goniasterid species which are described herein. The listing of Pacific echinoderms for Costa Rica was begun by Alvarado *et al.* (2010) and Alvarado (2010), expanded by Solís-Marín *et al.* (2013), and updated by Alvarado *et al.* (2017).

Several notable deep-sea, > 1000 m depth, asteroids from this area have been recently described, including three wood-associated species, *Caymanostella scrippscognaticausa* Shen *et al.* 2024 and *C. davidalani* Shen *et al.* 2024 and the discoid asteroid *Xyloplax princealberti* Payne *et al.* 2023. Seid *et al.* (2025) presented a faunal inventory of taxa from the methane seeps on the Pacific margin of Costa Rica, including several asteroids which are treated in greater detail herein. Follow up investigation of asteroids presented by Seid *et al.* (2025) during a visit to the Scripps Benthic Invertebrate Collection in December 2024 motivated this report.

Materials and Methods

Materials herein were collected primarily from the vicinity of methane seeps and seamounts by the R/V *Falkor* with the Remotely Operated Vehicle (ROV) *SuBastian* during expedition FK190106 (2019) and by the R/V *Atlantis* with Human Occupied Vehicle (HOV) *Alvin* during expeditions AT37-13 (2017) and AT42-03 (2018). More complete collection details are summarized in Seid *et al.* (2025).

New species material and newly collected material referenced herein are housed at the Benthic Invertebrate Collection at Scripps Institute of Oceanography (SIO-BIC) with further historical comparative material housed at the Department of Invertebrate Zoology at the National Museum of Natural History (USNM). Where noted, some specimens possess dual catalog numbers at SIO-BIC and are housed in Costa Rica at the Museo de Zoología, Universidad de Costa Rica (MZUCR), San José, Costa Rica.

Not all specimens documented here were available to the author. Three specimens, E7330 (*H. phrygiana*), E7370 (*Ampheraster?*), and E7265 (*P. diaphanus?*) were lost following collection during their transport from the ship to Costa Rica. This material was sampled immediately on the R/V *Falkor* following collection. Although the subsamples were retained and sequenced by SIO-BIC, further examination and documentation of those specimens was obviously not possible. Otherwise, all other material described here was deposited at SIO and is compliant with appropriate documentation. Absent specimens are noted under each taxon heading.

For the sake of brevity, only diagnoses are provided for known species. Complete taxonomic descriptions were not included with any noteworthy variation mentioned under Comments.

GenBank accession numbers are provided for DNA sequences of mitochondrial cytochrome c oxidase subunit I (COI) or the mitochondrial ribosomal RNA 16S subunit (16S), generated as in Seid *et al.* (2025).

Systematics

FORCIPULATACEA Blake, 1987

“PEDICELLASTERIDAE” Perrier 1884 (paraphyletic assemblage)

Diagnosis. Modified from Clark & Downey (1992). Disk small, arms 5 to 6, abactinal skeleton irregularly reticulate, carinal series barely distinguishable, abactinal spines small, single, acute. Superomarginal plates irregularly 3 to 4 lobed, two interbrachial superomarginal plates enlarged, overlapping the 2 corresponding inferomarginals. Inferomarginal spines conspicuously larger than those of superomarginals, without accessory spinelets, Adambulacral spines monacanthid. First postoral pair narrowly separated or touching only at adoral corners. Straight pedicellariae large, felipedal, gonopores dorsal-facing.

Comments. A molecular phylogeny of the Forcipulatacea (Foltz & Mah, 2011) showed that the forcipulate group Pedicellasteridae, as outlined by Fisher (1928) and Clark & Downey (1992) is paraphyletic, composed of multiple separate lineages. This group had been characterized as possessing characters of plesiomorphic or stemward asteriids (e.g. Blake 1987, Fisher 1928), which appears to be assessed as more akin to a morphological “grade” rather than a monophyletic group. Some, such as the deep-sea/high-latitude Paulasteridae (Mah *et al.* 2015) have been further identified and described but further work is needed for this poorly understood group. They are referred to herein collectively out of convenience.

Alvarado (2010) lists two species of “pedicellasterids” from Costa Rica, *Hydrasterias improvisus* (Ludwig 1905) (2149 m), and *Tarsaster cocosanus* (Ludwig, 1905) (245 m).

Ampheraster? Fisher 1923

FIGURE 1A–B

cf. *Patiria* Alvarado *et al.* 2022: 3, Table 1, 3.

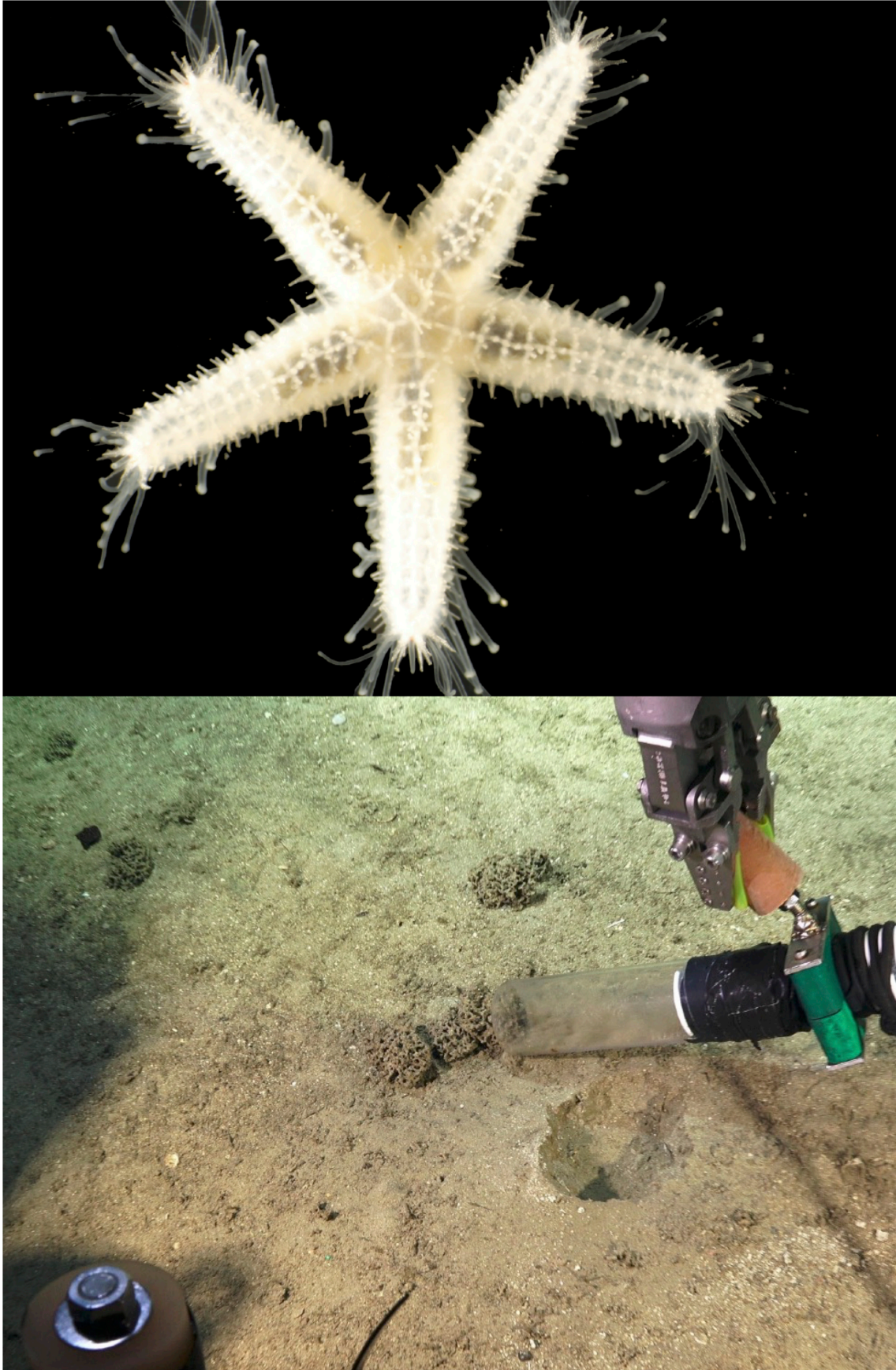


FIGURE 1. *Ampheraster*? A. Abactinal surface. B. Xenophyophore, collection substrate.

Comment on Specimen SIO-BIC E7370. This specimen was among the material lost following collection. This taxon was included in Table 1 of Alvarado *et al.* (2022), which shows this specimen identified as “cf. *Patiria*” from 950 m depth cataloged as SIO-BIC E7370. Examination of an image of this specimen as well as a COI (barcode) sequence alignment shows this published identification to be in error.

The specimen is an undetermined pedicellasterid, possibly in the genus *Ampheraster*. Figure 1 shows only the top surface, an image of the actinal surface was unavailable. A large series of spines which appeared to be those on the inferomarginal series was present. The skeleton was reticulate. A positive identification was uncertain, but these characters suggested *Ampheraster*.

This specimen was collected from the surface of a xenophyophore (Fig. 1B), a giant agglutinated foraminifera, but there was no *in situ* imagery of this specimen on the xenophyophore.

Occurrence/Distribution. Cocos Canyon, on the flanks of the emergent seamount Isla del Coco off Costa Rica, 950 m.

Material Examined. SIO-BIC E7370, Cocos Canyon, Costa Rica, 5.5845°N, 87.0676°W, 950 m. Coll. Greg Rouse & Avery Hiley, ROV *SuBastian* dive S0223, R/V *Falkor*, 18 Jan 2019. 1 wet spec. R=7.5 r=1.3 mm. GenBank. PX400634

TABLE 1. Stars of Costa Rica.

Species	Depth in m	Other occurrence	Reference	family
<i>Acanthaster ellisi</i>	shallow	Eastern tropical Pacific	Maluf (1988)	Acanthasteridae
<i>Ampheraster?</i> (SIO-BIC E7370)	950	CR only	Mah herein and “ <i>Patiria</i> ” in Alvarado <i>et al.</i> (2022) and Seid <i>et al.</i> 2025	Pedicellasteridae
<i>Asteropsis carinifera</i>	shallow	Indo-West Pacific	Alvarado <i>et al.</i> (2017)	Asteropseidae
<i>Astrolirus panamensis</i>	2149	west coast to Alaska		Brisingida
<i>Astropecten benthophilus</i>	1408	Eastern tropical Pacific	Alvarado (2010), Alvarado <i>et al.</i> (2022), Ludwig 1905	Astropectinidae
<i>Astropecten sulcatus</i>	121	Eastern tropical Pacific	Alvarado (2010), Alvarado <i>et al.</i> (2022), Ludwig 1905	Astropectinidae
<i>Bathyceramaster elegans</i>	1790–3335	Eastern tropical and North Pacific	Alvarado <i>et al.</i> (2022), Mah 2016	Goniasteridae
<i>Benthopecten spinuliger</i>	1789–1847	CR only	Alvarado (2010), Alvarado <i>et al.</i> (2022),	Benthopectinidae
<i>Caymanostella davidalani</i>	1002–1887	CR only	Shen <i>et al.</i> 2024	Caymanostellidae
<i>Caymanostella scrippsognaticausa</i>	990–1010	CR only	Shen <i>et al.</i> 2024	Caymanostellidae
<i>Ceramaster patagonicus</i>	18–1125	widely occurring	Mah 2011, Maluf 1988	Goniasteridae
<i>Coronaster marchenus</i>	shallow	Eastern tropical Pacific	Alvarado (2010)	Asteriidae
<i>Eremicaster pacificus</i>	2149	North Pacific	Alvarado (2010)	Porcellanasteridae
<i>Freyella?</i>	1895–1908	widely occurring	Seid <i>et al.</i> (2025)	Freyellidae
<i>Henricia sp.</i>	1071	widely occurring	Alvarado <i>et al.</i> (2022)	Echinasteridae
<i>Hippasteria glyphanos sp. nov.</i>	1052	CR only	Mah herein	Goniasteridae (Hippasterinae)
<i>Hippasteria phrygiana</i>	910 (10–1221)	widely occurring	Alvarado <i>et al.</i> (2022), Mah herein	Goniasteridae (Hippasterinae)
<i>Hippasteria turgida sp. nov.</i>	1412	CR only	Mah herein	Goniasteridae (Hippasterinae)
<i>Hydrasterias improvisa</i>	1618–2418	CR only	Alvarado (2010), Ludwig 1905	Pedicellasteridae
<i>Hymenaster purpureus ?</i>	2690	Hawaiian Islands	Mah herein, Fisher (1906)	Pterasteridae
<i>Leiaster teres?</i>	shallow	Eastern tropical Pacific	iNaturalist	Ophidiasteridae

.....continued on the next page

TABLE 1. (Continued)

Species	Depth in m	Other occurrence	Reference	family
<i>Leptychaster inermis</i>	1271–1408	Eastern tropical Pacific	Alvarado (2010), Alvarado <i>et al.</i> (2022), Ludwig 1905	Astropectinidae
<i>Linckia columbiae</i>	shallow	Eastern tropical Pacific	Alvarado (2010)	Ophidiasteridae
<i>Linckia multifora</i>	shallow	Indo-West Pacific	iNaturalist	Ophidiasteridae
<i>Luidia armata</i>	95	Eastern tropical Pacific	Maluf (1988)	Luidiidae
<i>Luidia sp.</i>	shallow	widely occurring	iNaturalist	Luidiidae
<i>Mediaster tenellus</i>	380–1829 m (997 m in CR)	widely occurring	Mah 2016	Goniasteridae
<i>Mithrodia bradleyi</i>	shallow	Eastern tropical Pacific	Alvarado (2010), Chacón-Monge <i>et al.</i> , 2021	Mithrodiidae
<i>Narcissia gracilis</i>	shallow	Eastern tropical Pacific	Alvarado (2010)	Goniasteridae
<i>Nidorellia armata</i>	shallow	Eastern tropical Pacific	Alvarado (2010), Chacón-Monge <i>et al.</i> , 2021	Oreasteridae
<i>Nymphaster diomedae</i>	702–1618	Eastern tropical Pacific	here; Mah 2016	Goniasteridae
<i>Pauliastra aenigma</i>	shallow/ mesophotic	CR only	Mah 2021	Asterodiscididae
<i>Pectinaster agassizi</i>	1789–1951	CR only	Alvarado (2010), Ludwig 1905	Benthopectinidae
<i>Pentaceraster cumingi</i>	shallow	Eastern tropical Pacific, Hawaiian Islands	Alvarado (2010), Chacón-Monge <i>et al.</i> , 2021	Oreasteridae
<i>Persephonaster armiger</i>	1951	CR only	Alvarado (2010), Ludwig 1905	Astropectinidae
<i>Pharia pyramidata</i>	shallow	Eastern tropical Pacific	iNaturalist, Alvarado (2010), Chacón-Monge <i>et al.</i> , 2021	Ophidiasteridae
<i>Phataria unifascialis</i>	shallow	Eastern tropical Pacific	iNaturalist, Alvarado (2010), Chacón-Monge <i>et al.</i> , 2021	Ophidiasteridae
<i>Pillsburiaster ernesti</i>	2149	Costa Rica, Cocos Island	Mah 2016	Goniasteridae
<i>Porcellanaster ceruleus</i>	1408–2149	widely occurring	Alvarado (2010), Alvarado <i>et al.</i> (2022),	Porcellanasteridae
<i>Pseudarchaster sp.</i>	1119–1281	widely occurring	Alvarado <i>et al.</i> (2022)	Pseudarchasteridae
<i>Pteraster diaphanus</i>	1246–1408	CR only	Alvarado (2010), Ludwig 1905	Pterasteridae
<i>Radiaster brocha sp. nov.</i>	1878	CR only	Mah herein	Radiasteridae
<i>Sclerasterias heteropaes</i>	80–88	Eastern tropical and North Pacific	Alvarado (2010)	Asteriidae
<i>Solaster arx sp. nov.</i>	1000	CR only	Mah herein	Solasteridae
<i>Tamaria obstipa</i>	shallow	Eastern tropical Pacific	Alvarado (2010), Ziesenhenné 1942	Ophidiasteridae
<i>Thrissacanthias penicillatus</i>	55–1503	Eastern tropical and North Pacific	Alvarado <i>et al.</i> (2022)	Astropectinidae
<i>Xyloplax princealberti</i>	1800–2000	CR, central Pacific	Payne <i>et al.</i> 2024	Xyloplacidae

PAXILLOSIDA Perrier, 1884

ASTROPECTINIDAE Gray 1840

Diagnosis. Modified from Clark & Downey (1992). Arms five with arms of varying length, shape, interradial arcs acute to more blunt-angled. Abactinal plates strongly paxillate, small and crowded. Apical or epiproctal cone present in some taxa. Papulae completely present over paxillar area in most, but in some, absent centrally and mid radially. Marginal plates blocky in shape, expressed variably among taxa, some displaying prominent dorsal and/or ventral facing versus others displaying plate surfaces more laterally, these armed with variable continuous spinelets

or granules, many with large spines, especially on the inferomarginal plates. Superomarginal and inferomarginal plate series with well-developed fascioles, lined by regularly arranged fine spineless on the opposing faces. Actinal plates variable, some showing very few plates limited to the disk (e.g. *Astropecten*) whereas others larger areas with a single series extending along the arm. Adambulacral plates broad, the furrow margin short and angular or convex in most, but others are straight, armed with large furrow and subambulacral spines. Oral plates large, modified triangular in shape but constricted and bar-like in some. Odontophore concealed, pedicellariae, if present fairly simple, spongiform, fasciculate. Tube feet tapering to a narrow tip or knob. Superambulacral plates well-developed.

Comments. Alvarado (2010), and Alvarado *et al.*, (2022) lists six astropectinid species from Costa Rica, which occur primarily 1000 and 1500 m depth, including *Astropecten benthophilus* Ludwig, 1905, *Astropecten sulcatus* Ludwig, 1905, *Leptychaster inermis* (Ludwig, 1905), *Persephonaster armiger* Ludwig, 1905, *Tethyaster canaliculatus* (A.H. Clark 1916), and *Thrissacanthias penicillatus* (Fisher 1905).

***Thrissacanthias* Fisher 1910**

Diagnosis and Comments

Monotypic. As for genus.

***Thrissacanthias penicillatus* (Fisher, 1905)**

FIGURE 2A–F

Persephonaster penicillatus Fisher 1905: 297

Thrissacanthias penicillatus Fisher 1910: 171; 1911: 79; Ziesenhenné 1937: 212; Blake 1973: 45; Alvarado *et al.* 2022: 3, Table 1; Seid *et al.* 2025: 159, Fig. 60G, H; Alvarado *et al.* 2022: 3, Table 1.

Thrissacanthias bispinosus Djakonov 1950 (1968): 24

Thrissacanthias sp. Alvarado *et al.* 2022: 3, Table 1.

Diagnosis. Modified from Fisher (1911). Body stellate to strongly stellate (Fig. 2A, D), R/r= 4.0–5.0.

Disk medium size, depressed, rays long, interradial areas acute. Abactinal surface paxillate, but arranged in oblique transverse rows with no enlarged radial series. Papulae present all over abactinal surface but lacking at arm tip. Madreporite large, not hidden. Marginal plates with large conspicuous spines (Fig. 2B), spongiform fasciate pedicellariae. Actinal intermediate plates extending far along ray. Gonads not confined to the interradial but extend for a short distance along ray as a number of separate tufts from the genital rachis. Adambulacral plates with actinal spines, 1 or 2 (Fig. 2E, F).

Comments. *Thrissacanthias penicillatus* is a monotypic taxon derived from the astropectinid *Persephonaster* by Fisher (1905) who differentiated the genus from other members of *Persephonaster* based on the distribution of gonads which were observed by Fisher to extend a short distance along a ray as a number of separate tufts along the arm. Internal anatomical characters, such as gonads have historically not found widespread use as taxonomic characters within the Asterozoa, except in very specific instances, such as in the Brisingida (e.g. Downey, 1986) and their usefulness as characters is largely untested, especially as function of these characters may cause them to vary. Further testing of *Thrissacanthias* with *Persephonaster* and other Astropectinidae is desirable.

Gut contents and associated sediment collected from trawls suggests this species is present in subsurface sediments, feeding on mollusks and other metazoans (Alton 1966, Mah unpublished observations).

Synonymy of *Thrissacanthias bispinosus* Djakonov 1950. Review of the English translation of Djakonov (1950/1968) in comparison with Fisher (1905, 1910) and further specimens of *Thrissacanthias penicillatus* from Monterey and Costa Rica does little to show *Thrissacanthias bispinosus* as a distinct species. Review of the description of *Thrissacanthias bispinosus* does not outline what characters serve to distinguish it from *T. penicillatus*. Abactinal paxillae spinelet number, superomarginal and inferomarginal plates, furrow spine number and nearly all characters used to distinguish *T. bispinosus* were identical to *T. penicillatus* and variation within the species was largely minimal even in specimens from Costa Rica.

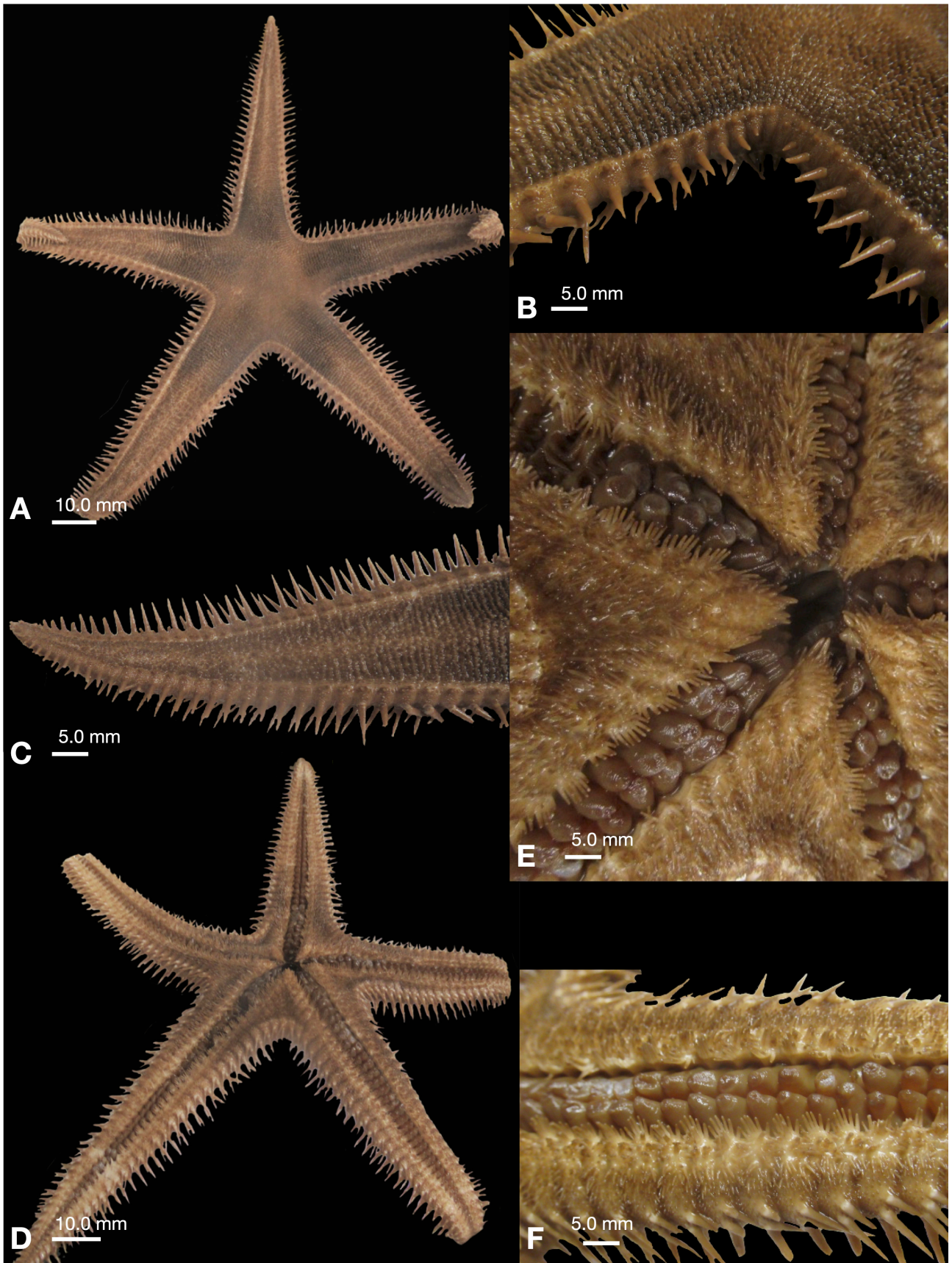


FIGURE 2. *Thrissacanthias penicillatus* SIO-BIC E7246. A. Abactinal. B. Abactinal-lateral. C. Armtip. D. Actinal. E. Oral-actinal. F. Adambulacral furrow.

Occurrence/Distribution. Outside of Costa Rica. Japan, Washington state, California, west from Monterey to Peru. 55–1503 m. Costa Rica, 1000–1281 m

Material Examined. SIO-BIC E7246 Mound 12 methane seep, Costa Rica, 8.9332°N, 84.3075°W, 1000 m. Coll. Greg Rouse & Amanda Glazier, HOV *Alvin* dive 4975, R/V *Atlantis*, 21 Oct 2018. 1 wet spec. R=13.7 r=3.7 cm. GenBank PQ304658

USNM 1418220, West of Monterey Bay, California, North Pacific Ocean, 36.77°N, 122.3°W, 1024 m. Coll. R/V *Point Sur*, 28 Feb 2010. 1 dry spec. R=23.3 r=4.0 cm.

RADIASTERIDAE Fisher 1916

Radiaster Perrier, 1881

Radiaster Perrier 1881: 17; Sladen 1882: 583; Perrier 1884: 163, 213; 1894: 173; Fisher 1911: 251, 2253; 1916: 4; 1919: 216–217; Mortensen 1927: 96; H.L. Clark 1946: 80; Spencer & Wright 1966: U65; McKnight 1973: 2; Blake 1987: 522.

Mimaster Sladen 1882: 702; 1882b: 579–580; 1889: 331–332; Perrier 1894: 249, 252; Ludwig 1903: 9; Fisher 1911: 160–161, 169, 175; Verrill 1914: 282; H.L. Clark 1916: 33–34 (Type species *M. tizardi* Sladen 1882 by monotypy).

Diagnosis. Modified from Clark & Downey (1992). Body form stellate, broad proximally, tapering to narrow tips, but circular in cross-section. Abactinal plates paxilliform, arranged in series parallel to the mid radial line. Individual paxillae with basal lobes numbering 4 to 6, columns tall and cylindrical, crowned with numerous slender spinelets. Papulae extending over abactinal area, 1 to 5 distributed between plates. Marginal plates similar closely aligned, each crowned with a tuft of spinelets. Actinal intermediate areas large, actinal plates numerous, separated by shallow fasciolar grooves associated with adambulacral plates. Furrow/adambulacral spines with larger, coarser spines graduating to finer ones. Tube feet biserial, with flattened, unsuckered tips.

Comments. *Radiaster*, including 2 Atlantic and 4 Pacific species, is the only genus within the Radiasteridae, which has enjoyed a long and storied taxonomic history (summary in Clark & Downey, 1992). One species has been recorded from the Philippines/central Pacific, with the remaining 3 from Australia and New Zealand. An undescribed *Radiaster* species was mentioned by Hendrickx (2011) but there have otherwise been no records of this taxon from the central American/ Eastern Tropical Pacific.

Radiaster brocha sp. nov.

FIGURE 3A–F

Tethyaster canaliculatus Alvarado *et al.* 2022: 3, Table 1.; Seid *et al.* 2025: 157–158, Fig. 60E, F.

Etymology. The species epithet *brocha* is derived from the Spanish word for “brush” alluding to the brush-like paxillae shape.

Diagnosis. Body stellate, R/r=2.75, arms triangular, strap-like in shape, armtips pointed. Interradial arcs acute. Abactinal paxillae with narrow acicular spinelets, 8 to 20, mostly 10 to 15 with fine pointed tips, directed upwards occupying approximately 40% of total shaft length. Marginal plates paxillate, 48–50 along each arm, 96–100 per interradius, arm tip to arm tip, widely spaced from one another becoming more widely spaced distally. Superomarginal plates with a distinct cluster of pointed spinelets, approximately 10–50 decreasing distally. Inferomarginal plates with spinelets, similar in size and shape, approximately 10–50 decreasing in size distally but larger than superomarginals, especially along arm length. Actinal surface in transverse, linear series with plates tracking from inferomarginal plates to adambulacral series, forming distinct fasciolar channels between actinal plates. Individual actinal plates paxillate, similar to abactinal plates, approximately 50% shaft height and 50% topped by spinelets with slender pointed tips, 10–20, approximately 12–15. Furrow spines (enlarged proximalmost spines on adambulacral plate), 2–3, remaining subambulacral spines, 4–10, mostly 7–9. Adambulacral spine clusters widely spaced from one another along series. Proximalmost adambulacral plate with 4 enlarged spines projecting into tube foot groove, with 7–9 remaining spines, smaller and thinner, comparable to those on adambulacral plates.

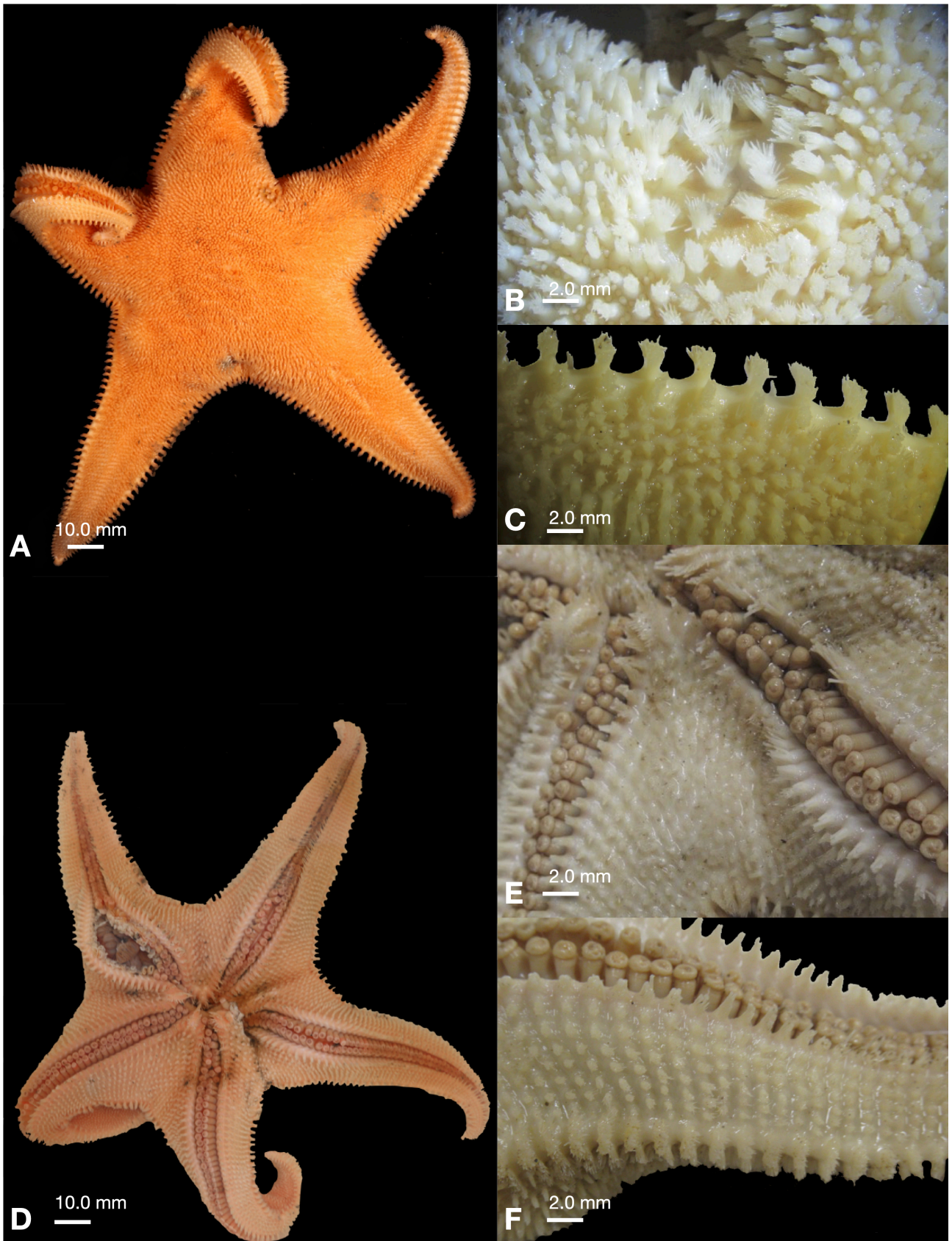


FIGURE 3. *Radiaster brocha* sp. nov. SIO-BIC E7036. A. Abactinal. B. Abactinal paxillae. C. Abactinal-marginals. D. Actinal. E. Actinal-oral view. F. Actinal-adambulacral.

Comments. *Radiaster brocha* sp. nov. is characterized by the 15–20 pointed, short brush-like paxillar spinelets each sitting on an elongate shaft with 10–50 spinelets on marginal plates (Fig. 3B). Its overall appearance is comparable to the tropical Pacific *Radiaster notabilis*, which has a flexible abactinal body surface which are round in cross-section. This is the first species of *Radiaster* recorded from Costa Rican waters.

Occurrence/Distribution. Costa Rica, 1878 m.

Description. Body stellate, $R/r=2.75$, arms triangular, strap-like in shape, armtips pointed. Interradial arcs acute (Fig. 3A).

Abactinal surface fibrous in texture, composed of numerous slender paxillate abactinal plates, composed of a stout shaft, topped by slender, short pointed spinelets, pointed 10–40, mostly 20–30, each approximately comprising 50% of total length. Spinelets crowded. Paxillae cover abactinal surface completely, widely spaced from one another (Fig. 3B). Papulae, each single pores, on all of abactinal surface including disk and arms. Each present on surface individually or with one or two other papulae immediately adjacent. Madreporite moderate in size, approximately 1.0 cm in diameter, convex with well developed sulci. Surface with short paxillae, 7 present approximately central on plate. Madreporite itself surrounded by approximately 20–22 paxillae. Pedicellariae absent.

Marginal plates paxillate, 48–50 along each arm, 96–100 per interradius, arm tip to arm tip, widely spaced from one another becoming more widely spaced distally (Fig. 3A, C). Overall shape rectangular with proximalmost marginal plates larger, more equal in size and shape but with superomarginal and inferomarginal plates becoming more heteromorphic further along the arm. Superomarginal plates significantly smaller, approximately <50% of the size of the inferomarginal plates distally along the arm and are weakly offset, whereas those proximally are associated 1:1 forming zigzag contact. Superomarginal plates with a distinct cluster of pointed spinelets, approximately 10–50, decreasing distally. Inferomarginal plates with spinelets, similar in size, shape, approximately 10–50 decreasing in size distally but larger than superomarginals, especially along arm length. Terminal plates, smooth surface, tooth shaped with prongs in contact with superomarginal plate.

Actinal surface in transverse, linear series with plates tracking from inferomarginal plates to adambulacral series, forming distinct fasciolar channels between actinal plates (Fig. 3F). Individual actinal plates paxillate, similar to abactinal plates, approximately 50% shaft height and 50% topped by spinelets with slender pointed tips, 10–20, approximately 12–15. A distinct dermal tissue present over base of actinal surface. Furrow spines (enlarged proximalmost spines on adambulacral plate), 2–3, remaining subambulacral spines, 4–10, mostly 7–9. Adambulacral spine clusters widely spaced from one another along series. Proximalmost adambulacral plate with 4 enlarged spines projecting into tube foot groove, with 7–9 remaining spines, smaller and thinner, comparable to those on adambulacral plates. Distinct series of approximately 20–30 elongate spines along edge of either side of central oral plate diastema with proximalmost 1–2 spines enlarged and projecting into mouth (Fig. 3E). Distinct gaps between oral plates and adjacent adambulacral plates.

Biserial tube foot rows, widely spaced with blunt suckers (Fig. 3E, F).

Material Examined. Holotype. SIO-BIC E7036 Jaco Scar methane seep, Costa Rica, 9.1154°N, 84.8397°W, 1878 m. Coll. Greg Rouse & Jorge Cortés, HOV *Alvin* dive 4913, R/V *Atlantis*, 28 May 2017. 1 wet spec. $R=12.4$ $r=4.5$ cm.

VALVATIDA Perrier, 1884

GONIASTERIDAE Forbes, 1841

Diagnosis. Based on Mah (2026). Body shape pentagonal to strongly stellate ($R/r=1.0$ to 4.0), body variably soft to stout, thickness ranging from strongly arched to relatively flat, interradial arcs variably angular to straight. Surface covering ranges from bare and smooth to thick dermis embedded with granulation. Abactinal surface with widely variable range of plate morphologies ranging from discrete polygonal abutted plates, to shaft-like tabulae or paxillae to imbricate or irregularly arranged plates embedded in thick dermis. Plate surface ranges from smooth and bare to a highly variable range of primary ornamentation, such as large spines as well as smaller accessory structures as primarily granules, but also including spinelets, surficial plates and pedicellariae. Pedicellariae present or absent, ranging from bivalve, paddle-like to forceps-shaped. When large pedicellariae are present, these tend to be more consistent in location and presence.

Marginal plates, generally blocky, but variably forming well-defined periphery with either lateral or abactinal-facing in two distinct series, supermarginals and inferomarginals, present from terminal to interradius. Marginal plates with variable accessories, such as granules, spineless, or pedicellariae. Some groups with large primary structures such as spines. Marginal plate surface variably covered by dermis or bare. Several genera with abutted supermarginals over midline on arm, variably along whole length or near armtip.

Actinal plates, abutted, quadrate to polygonal or irregular in shape in chevron-like formation with full series adjacent to the adambulacral plate series becoming more irregular distally adjacent to the contact with the inferomarginal plate series. Actinal plate surface with variable cover of granules, spinelets or pedicellariae. Primary structures such as spines or large pedicellariae present in some taxa. Adambulacral plates with furrow spines, variably narrow to thick, with blunt or pointed tips. Further spination on adambulacrals variably granular to more spine or spinelet-like.

Comments. The Goniasteridae is the most diverse family within the Asteroidea, occupying many habitats and across a wide depth range, from 0 to 3000 m (Mah & Blake, 2012). Alvarado (2022) recorded six species, three from historical records, including *Bathyceramaster elegans* (Ludwig, 1905), *Nymphaster diomedea* Ludwig, 1905, and *Pillsburiaster ernesti* (Ludwig, 1905) and in addition, three further species which are described herein.

The subfamily Hippasterinae is represented by two species in the genus *Hippasteria*. Nearly all members of the Hippasterinae have been observed preying on cold-water or deep-sea cnidarians (e.g., Mah 2015, 2022), notably colonial octocorals. Although hippasterines are well documented in the North Pacific (e.g. Fisher 1911, Mah *et al.* 2010), only a single species, *Hippasteria lepidonotus* has been documented from the tropical Eastern Tropical Pacific.

***Ceramaster* Verrill, 1899**

Tosia (*Ceramaster*) Verrill, 1899: 161

Ceramaster Fisher, 1906: 1054; 1911: 162, 204; Verrill, 1914: 289; Koehler, 1924: 173; Mortensen 1927: 80; Djakonov, 1950: 38; Tortonese and A.M. Clark, 1956: 347; Halpern 1970: 212; Downey, 1973: 49; McKnight, 1973: 178; Downey, 1973: 49; A.M. Clark and Courtman-Stock, 1976: 61; Clark and Downey, 1992: 231; Mah, 2011: 5, 2016: 112.

Philonaster Koehler, 1909: 78 [type species *Pentagonaster* (*Philonaster*) *mortenseni* Koehler, 1909].

Tosiaster Verrill, 1914: 1054.

Diagnosis. Derived from Mah (2024). Body outline pentagonal in most (i.e., $R/r=1.1-1.5$) with some becoming more stellate. Abactinal plates tabulate, granules present on abactinal plates, marginals and actinal plates. Fasciolar grooves present among abactinal and marginal plates. Bare “patch” present or absent on dorsal facing of superomarginal plates on most species

***Ceramaster patagonicus* (Sladen 1889)**

FIGURE 4A–C

Pentagonaster patagonicus Sladen, 1889: 269, pl. 46, figs 3–4, pl. 44, figs 3–4.

Pentagonaster austrogranularis Perrier, 1891: K127, pl. 12, figs 3a–b.

Mediaster patagonicus Verrill, 1899: 195.

Pseudarchaster patagonicus Verrill, 1899: 195

Ceramaster patagonicus Fisher, 1911: 214, pl. 37, fig. 4., pl. 38, figs 1–2, pl. 40, fig. 3; 1940: 118; Djakonov, 1950: 48, figs. 27, 48; Bernasconi, 1963: 8, pl. 1, figs. 1–2, pl.2, fig. 3 ; Baranova & Belyaev 1968: pl. 17, fig. 2; Tommasi, 1970: 12, fig. 36;

Lambert, 1978: 62; Anderson *et al.*, 1993: 502; Branch *et al.*, 1993: 44 (illustr.); A.M. Clark, 1993: 249; Rowe & Gates, 1995: 65; O’Hara, 1998: 179, pl. 1d.; H.E.S. Clark in Clark & McKnight, 2001: 33; Stampanato & Jangoux, 2004: 4, 6.

Ceramaster lennoxkingi McKnight, 1973: 178, fig. 4; 1984:142; A.M. Clark, 1993: 249.

Ceramaster grenadensis patagonicus Clark & Downey, 1992: 236.

cf. *Ceramaster* sp. Alvarado *et al.* 2022: 3, Table 1, fig. 5C.

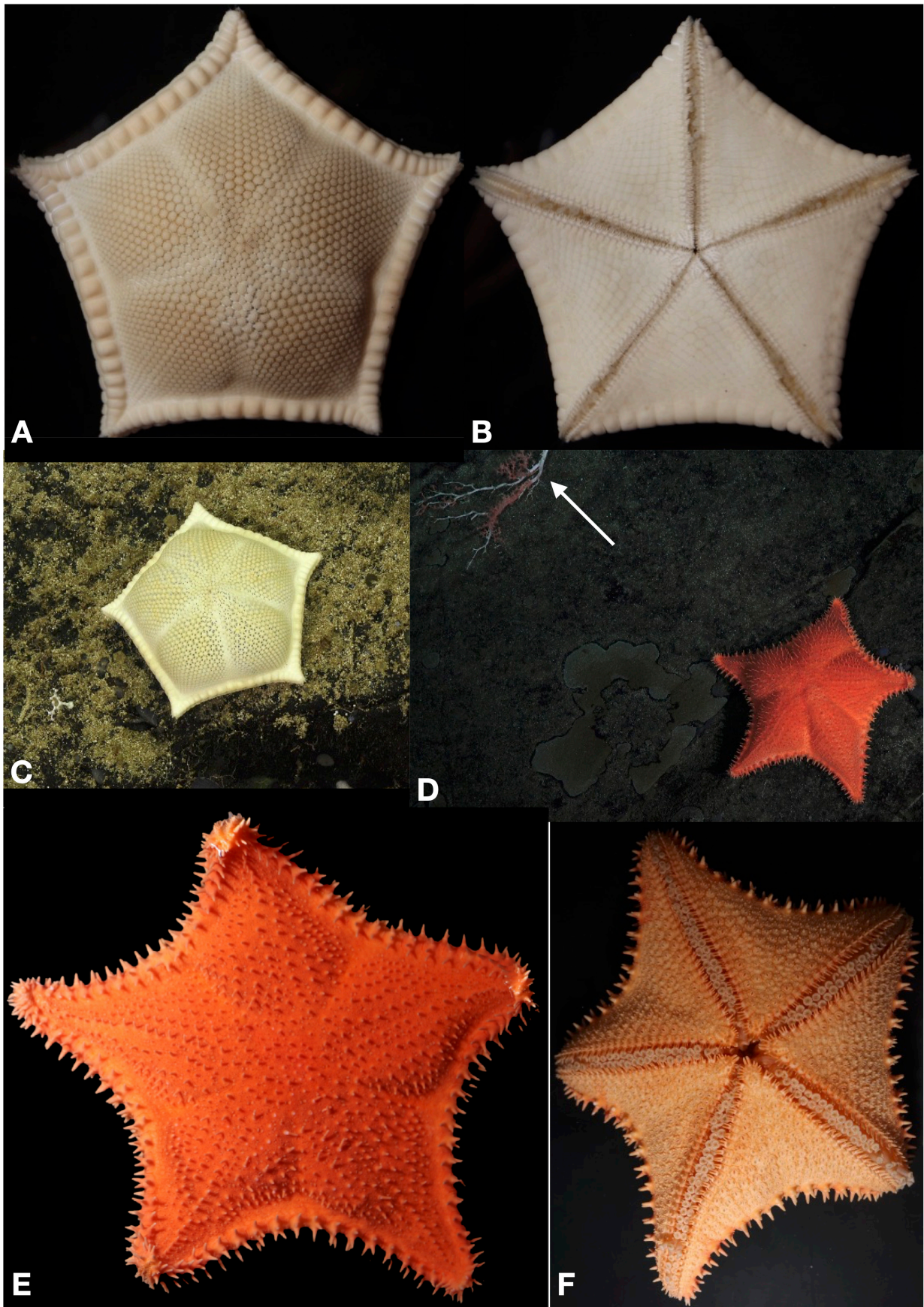


FIGURE 4. Goniasteridae living. A. *Ceramaster patagonicus*, SIO-BIC E7329, Abactinal. B. Actinal. C. *In situ*. D. *Hippasteria phrygiana*, SIO-BIC E7330 *in situ* with denuded coral indicated by the arrow. E. Abactinal. F. Actinal.

Diagnosis. Modified from Fisher (1911). Body pentagonal ($R/r=1.46$) Abactinal plates tabulate, rhomboid to hexagonal in outline each flat-topped covered with crowded polygonal granules, a minority of these plates with a bare spot, variably flat to tumid. Marginal plate series prominent dorsal facing, surface tumid, covered by crowded polygonal granules, save for a bare spot occupying the whole abactinal face of the plate. Actinal surface covered by rhombic to squarish plates in chevron-like series, each plate covered by polygonal granules. Furrow spinelets 4–5, robust but compressed. Subambulacral accessories 2–3, variably granular to stubby spinelets, subquarate with broadened tips. Pedicellariae, when present with two narrow spatulate valves present on each tabula or actinal plates.

Comments. As outlined in Mah (2025) and other references, it is argued that the status of *C. patagonicus* as a subspecies of *Ceramaster grenadensis* as per Clark and Downey (1992) is incorrect and that most species in *Ceramaster* should follow those taxa more consistent with the typological definitions as outlined by *Ceramaster granularis* and the more widespread *C. patagonicus*.

This species is known primarily from high-latitude, polar and sub-polar regions. This occurrence is the first from Costa Rica, although occurrence has been previously documented from the Gulf of California.

Distribution/Occurrence. Widely distributed. Bering Sea, Aleutian Islands, Alaska to British Columbia, Gulf of California, Costa Rica, to southern Australia (North of Macquarie Island), New Zealand and outlying areas (Bounty Islands and Macquarie Island). South Atlantic from near Cape Horn, Straits of Magellan, Falkland Islands, Falkland Plateau, Burdwood Bank. South Indian Ocean: Crozet Island, Kerguelen, Marion and Prince Edwards. 18–1125 m.

Material Examined. SIO-BIC E7329 (=MZUCR-ECH 2475) Seamount 7, Costa Rica. 6.9173°N 85.8833°W, 955 m. Coll. Greg Rouse & Avery Hiley, ROV *SuBastian* dive S0222, R/V *Falkor*, 16 Jan 2019. Tissue sample only, voucher lost.

GenBank accession: PX400632.

Hippasteria Gray 1840

Hippasteria Gray, 1840: 270; See Mah (2010) *et al.* for a full synonymy.

Diagnosis. Based on Mah *et al.* (2010, 2014). Body weakly pentagonal to stellate, $R/r=1.5–2.3$. Disk and arms thick. Arms relatively broad and short. Tissue with pulpy texture covers abactinal plates. Shallow fasciolar grooves present. Secondary plates present. Abactinal plates, tightly articulated, polygonal to irregular in outline, flat and elevated over surface. Carinal series are poorly distinguished. Abactinal spinelets (sometimes granular) forming fringe around abactinal plates. Spines, large, conical; granules common on abactinal plates. Large spines present on superomarginal and inferomarginal plates of most species. Superomarginal and inferomarginal plates bare, quadrate to rounded in outline at interradii with no other accessories other than large spines. Spinelets variably present on marginal plates in some taxa. Shallow fasciolar grooves present between marginal plates. Marginal accessories (granules, spinelets, etc.) differentiated into a fringe on superomarginal and inferomarginal plates. Superomarginal plates dorsal-facing in most species, Actinal fasciolar grooves shallow, large actinal spines and spinelets present. Subambulacral spines large (and thus few in number). **Furrow spines large, blunt, and round, usually few.** Enlarged bivalved pedicellariae on raised bases on body surface. Modified from Mah *et al.* (2010; 2014).

Comments. A genus including 12 living species which occur in the Atlantic, Pacific and Indian Oceans. One species, *Hippasteria phrygiana* (Parelius, 1768) was shown to be widely occurring throughout all three ocean basins (Foltz *et al.* 2013). Most species of *Hippasteria* occur in deep-sea settings (>200 m). Most if not all species have been observed as predators on various types of cnidarians, especially colonial octocorals (e.g. Mah 2015, 2022).

Only one hippasterine, *Hippasteria lepidonotus* (as *Hippasteria pacifica* Ludwig, 1905) was known from farther south in the Eastern Pacific. Other than the listing of *Hippasteria* cf. *phrygiana* (Alvarado *et al.* 2022: Table 1), the 3 species herein are the first known from Costa Rica and are the first hippasterines from this part of the eastern tropical Pacific.

***Hippasteria glyphanos* sp. nov.**

FIGURE 5A–G, 7A

Evoplosoma claguei Alvarado *et al.* 2022: 3, Table 1 (as *E. claguei*?); Seid *et al.* 2025: 159, Fig. 61C, D.

Etymology. The species epithet *glyphanos* is Greek for chisel, referring to the chisel shaped furrow spines that are distinctive for this species.

Diagnosis. Body stellate, $R/r=2.47$, arms triangular. Each plate covered by uniform pointed abactinal and actinal spines. Surface of abactinal, marginal, actinal plates covered by flat-topped polygonal to quadrate granules. **Abactinal, actinal and furrow spines pointed with distinctive dark tips which are also present on papulae. Furrow spines 2–3 with chisel-shaped tips. Large flattened paddle-like pedicellariae present adjacent to furrow spines.**

Comments. *Hippasteria glyphanos* sp. nov. is supported as *Hippasteria* based on the numerous abactinal and marginal spines as well as the prominent pedicellariae and especially the relatively low number of large furrow spines. It is distinguished by the distinctive furrow spines with flattened chisel-shaped tips, the high abundance of abactinal, actinal, and especially marginal spines and the presence of dark tips on the abactinal, actinal and furrow spines and papulae, which are observed on preserved specimens.

Characters in *Hippasteria glyphanos* sp. nov. suggest affinities with different *Hippasteria* groups (Mah *et al.* 2014). The oval to rounded marginal plates are shared with species associated with *Hippasteria californica* Fisher 1904, whereas the body shape, and abactinal-marginal spination are more reminiscent of *Hippasteria muscipula* Mah *et al.* 2014. The dark color on the spine tips are unusual for hippasterines and are not known from any other species.

Occurrence/Distribution. Known only from Costa Rica, 1052 m.

Description. Body stellate, $R/r=2.47$, arms elongate, triangular in shape, interradial arcs weakly curved. Abactinal surface arched, especially on radial regions.

Abactinal surface composed of round to polygonal plates, relatively small, approximately 1.0 mm diameter, homogeneous in size, shape extending to arm terminus. Plates on disk, arms each with a single conical spine with a pointed tip, dark brown in color (Fig. 5B–C), granules, 8 to 12, round to polygonal in shape, present around the periphery of each plate. Spines are uniformly present over the disk and arms, save for a narrow band of unspined plates in each interradius. Short tubercles present on the minority of plates where pointed spines are absent. Papulae single, each with a distinctive black to brown tip present over abactinal surface of disk and arms. Madreporite round to polygonal, convex, sulci shallow. Pedicellariae absent

Marginal plates 22–25 per arm, 44–50 in each interradius, weakly quadrate in shape, surface with a strongly raised convex surface, smooth, bearing spines, 1–9, conical with pointed tips, interradial plates with highest number of plates, 7–9 decreasing to distalmost plates with only 1–3 spines near terminus. Spines largest proximally becoming smallest distally. Marginal spines in two series, a cluster of 2–5 on upper superomarginal surface with a lower series of spines in a linear series, 2–3. Each spine with weakly convex, flattened granules present around the base of each spine. A smaller pedicellariae, paddle-like in shape present at base of each spine. Inferomarginal plates with pointed conical spines, 8–10 similar to those on superomarginal plates, widely spaced. Surface covered by flat-topped, round to polygonal granules, 7–10. Pedicellariae paddle-shaped, similar to those on superomarginals present at the base of each inferomarginal spine cluster.

Actinal regions large, approximately 5–7 full series with a single series extending completely to arm tip. Incomplete actinal plates irregularly arranged, smallest and most heterogeneous in shape present distally adjacent to inferomarginal plate contact. Each plate weakly quadrate in shape with rounded edges. Each plate with a single spine, conical with pointed, dark colored tip (Fig. 5B, C, E, G). Remainder of plate with 4 to 10 flat-topped granules around spine base and further rounded granules, 10 to 20 present around each plate periphery. A minority of actinal plates with a distinct pedicellariae, paddle-shaped present adjacent to the base of proximal actinal spines.

Furrow spines three, 2–3, each with wide, chisel-like tips with irregular tips (Fig. 5F, G) proximally becoming more irregularly blunt-tipped distally especially adjacent to the terminus. Furrow spine tips with dark tipped coloration similar to those on abactinal, actinal spination (Fig. 5E, G). Remainder of adambulacral accessories include a single subambulacral spine, approximately 2x to 3x the thickness of the adjacent furrow spines, with jagged to blunt tip. Pedicellariae, 1–2, composed of paddle like to paired rectangular plates (Fig. 5G), weakly curved, these present between the furrow and subambulacral spines. Adambulacral plate surface with flat-topped



FIGURE 5. *Hippasteria glyphanos* sp. nov. SIO-BIC E7081. A. Abactinal. B. Abactinal spination. C. Lateral view. D. Actinal. E. Actinal intermediate. F. Actinal oral region. G. Adambulacral furrow spines.

granules, 7–10, round to polygonal in shape. Oral plates with furrow spines, 6 with 2–3 enlarged projecting into oral opening, a total of up to 8 spines on each plate edge. Spines projecting into mouth enlarged with distinct angular, flattened edges (Fig. 5F). Oral plate surface covered by flat-topped polygonal to quadrate granules, 3 pairs, matched along central diastema with remainder of plate covered by irregularly sized flat-topped granules, 12–20, some 3x the size of the smaller ones.

Color in life, abactinally brick red to orange, more yellow-orange centrally on disk. Actinal surface lighter in color, similar to yellow-orange on abactinal surface.

Material Examined. Holotype. SIO-BIC E7081 Parrita Seep (also known as Mound Quepos) methane seep, Costa Rica, 8.96323°N 84.63622°W, 1052 m. Coll. Carlos Gómez & Odalisca Breedy, HOV *Alvin* dive 4923, R/V *Atlantis*, 6 June 2017. 1 wet spec. R=10.7 r=4.32 cm.

***Hippasteria phrygiana* (Parelius, 1758)**

FIGURE 4D–F

Hippasteria phrygiana Mah, Neill, Eleaume & Foltz, 2014: 441 for an extensive synonymy.

Alvarado *et al.* 2022: 3, Table 1.

cf. *Hippasteria* cf. *phrygiana* Alvarado *et al.* 2022: 3, Table 1.

Diagnosis. Based on Mah *et al.* 2014). Body stout, weakly stellate (R/r=1.69–2.0) arms short. Abactinal plates with a single, short to large conical spine or large, bivalve pedicellariae, which are surrounded by enlarged quadrate to polygonal granules, 6–20. Marginal plates 35–36 per interradius (arm tip to arm tip), each with short, conical spine 1–3, mostly one but those interradially with two. Marginal plates otherwise bare with smooth surface. Bivalve pedicellariae on many, if not most, proximal marginal plates extending to the arm base, but absent on distalmost plates. Actinal intermediate region large with numerous bivalve pedicellariae, especially large on actinal plates adjacent to the adambulacral plates. Furrow spines, 1–3, mostly 2, subambulacral spines, 1–3. All adambulacral spines robust, round in cross-section. Paddle-shaped pedicellariae large, 1–2 present immediately behind furrow spines.

Comments. This specimen was among the material lost following collection. *Hippasteria phrygiana* was found by Foltz *et al.* (2013) and Mah *et al.* (2014) to be a widely occurring single species with populations in the Atlantic, Pacific and Indian oceans, that led to a widespread synonymy of multiple *Hippasteria* species from these regions. Although a specimen was unavailable for examination, imagery for this specimen was sufficiently clear that diagnostic features, including the marginal plates, spination and abactinal and actinal features such as pedicellariae could be used to identify this species as the widely occurring *Hippasteria phrygiana*.

Distribution/Occurrence. Widely occurring, Atlantic, Pacific and Indian Ocean, 10–1221 m.

Material Examined. SIO-BIC E7330 Seamount 7, Costa Rica, 6.9168°N 85.8835°W, 910 m. Coll. Greg Rouse & Avery Hiley, ROV *SuBastian* dive S0222, R/V *Falkor*, 16 Jan 2019. Tissue sample only, voucher lost. GenBank Accession: PX400633.

***Hippasteria turgida* sp. nov.**

FIGURE 6A–F, 7B

Etymology. The species epithet *turgida* is based on the Latin for swollen, alluding to this species appearance *in situ* and the strongly arched abactinal surface observed in the holotype.

Diagnosis. Body strongly stellate, R/r=3.0. Abactinal plates embedded in pulpy body wall, surface plates with tubercle-like spines, rising only approximately 1–3 mm above the surface with variably pointed to blunt tips. Pedicellariae large, approximately 2.0 mm, up to 3 plates in length. Marginal plates approximately 16–18 per arm, 32–36 per interradius, superomarginal and inferomarginal plates variably quadrate to irregularly polygonal to hemispherical. Superomarginal plates with spines, 1 to 3, short, conical with pointed tips. Bivalve pedicellariae, 1–3, mostly single, also present on each superomarginal plate surface, bisecting or extending the length of the plate on which it sits. Inferomarginal plates also with spines, 4–7, short, conical pointed tips. Inferomarginal plates also with distinct bivalve pedicellariae, 1–3, present on surface of all, bisecting or along length of each plate. Actinal

plates each with a single, large bivalve pedicellariae present on nearly every plate, these nearly bisecting the length of the plate on which they sit. Large, coarse granules, flat-topped, polygonal in shape covering the surface of each plate, each evenly spaced in close arrangement. Furrow spines 2–3, blunt tipped, variable in height, but with central spines greatest in length, each thick and arranged in close palmate formation. Subambulacral spines two, but each single, each one behind the other, thick with a blunt tip. Large bivalve pedicellariae, 1–3, mostly 1–2, with flat, rectangular valves sitting adjacent or at an angle to the subambulacral spines.

Comments. Based on the abundance of large bivalve pedicellariae and the presence of low round and pointed tubercles, and few furrow spines this species is argued as a member of the *Hippasteria heathi* group as outlined by Mah *et al.* (2014). *Hippasteria turgida* **sp. nov.** shows characters similar to the New Zealand species, *Hippasteria mcknighti* Mah *et al.* 2014 including the low abactinal and marginal tubercles as well as the granular cover (Fig. 6B, C, E) but is distinguished by the absence of the coarse granular cover, especially on the marginals (Fig. 6C), the presence of pointed spines, and the difference in furrow spine morphology, which is more chisel-like in *H. mcknighti*. Pedicellariae are much larger and more abundant in *H. mcknighti*.

Figure 7B shows this species feeding *in situ*.

Occurrence/Distribution. Known only from Costa Rica, 1412 m.

Description. Body strongly stellate, $R/r=3.0$, body strongly arched, disk thick, arms triangular, elongate and tapering. Interradial arcs weakly curved to straight (Fig. 6A).

Abactinal plates round, closely abutted, homogeneous, embedded in thickened body wall. (Fig. 6B). Surface plates with tubercle-like spines, short-rising only approximately 1 to 3 mm above the surface, variable pointed to blunt, widely spaced from one another, approximately one per plate (Fig. 6C). Spines present widely over disk and arms, but especially around lateral abactinal surface (Fig. 6C). Papulae present widely as large single pores, but clustered in bunches of 1–4. Pedicellariae, bivalve, abundant, variably rectangular with rounded edges, smooth valves present in abundance over abactinal surface distributed between spines and papulae. Pedicellariae large, approximately 2.0 mm, up to 3 plates in length (Fig. 6B). Exceptionally pedicellariae trivalve, a third smaller valve present perpendicular to the paired valves (Fig. 5C). Madreporite round to polygonal, sulci shallow.

Marginal plates approximately 16–18 per arm, 32–36 per interradius, superomarginal and inferomarginal plates variably quadrate to irregularly polygonal to hemispherical (Fig. 6D, E). Plates larger proximally becoming smaller more irregular in shape distally. Superomarginal plates with spines, 1–3, short, conical with pointed tips. Bivalve pedicellariae, 1–3, mostly single, also present on each superomarginal plate surface, bisecting or extending the length of the plate on which it sits. The more prominent the pedicellariae, the smaller or fewer the spines present on each plate. Distalmost plates with a single trivalved pedicellariae in conjunction with a distinct, large conical pointed spine (Fig. 6C). Inferomarginal plates with spines similar to those on superomarginals, 4–7, short, conical pointed tips. Inferomarginal plates also with distinct bivalve pedicellariae, 1–3, present on surface of all, bisecting or along length of each plate. Spine number variable but distalmost spines with a single distinct conical spine (Fig. 6D, E, F). Terminal plate pentagonal, smooth.

Actinal surface composed of three weakly ordered actinal series with a more irregular arrangement of plates distally adjacent to the contact with the inferomarginal plates (Fig. 6D). Actinal plates round to polygonal in shape with weakly developed fasciolar grooves. A single, large bivalve pedicellariae present on nearly every plate, these nearly bisecting the length of the plate on which they sit (Fig. 6E). Large, coarse granules, flat-topped, polygonal in shape covering the surface of each plate, each evenly spaced in close arrangement. Granules becoming larger and more tubercular distally, adjacent to contact with inferomarginal contact.

Furrow spines 2–3, blunt tipped, variable in height, but with central spines greatest in length, each thick and arranged in close palmate formation. Subambulacral spines two, but each single, each one behind the other, thick with a blunt tip (Fig. 6F). Large bivalve pedicellariae, 1–3, mostly 1–2, with flat, rectangular valves sitting adjacent or at an angle to the subambulacral spines (Fig. 6E). Proximally pedicellariae, especially large and thick. Distally on some arms pedicellariae with crescents of granules forming spines around each pedicellariae. Adambulacral plates covered by small, polygonal evenly distributed granules, becoming smaller on more distal plates. Oral plates with blunt, thick rounded, blunt spines, either side with 6, totaling 7 with the 7th enlarged and paired with that of the other oral plate. Oral plate surface with approximately 8 cuboidal to irregularly polygonal, flat-topped granules on either side of the diastema between the oral plates. Remainder of oral plate surface covered with flat-topped granules, widely spaced.

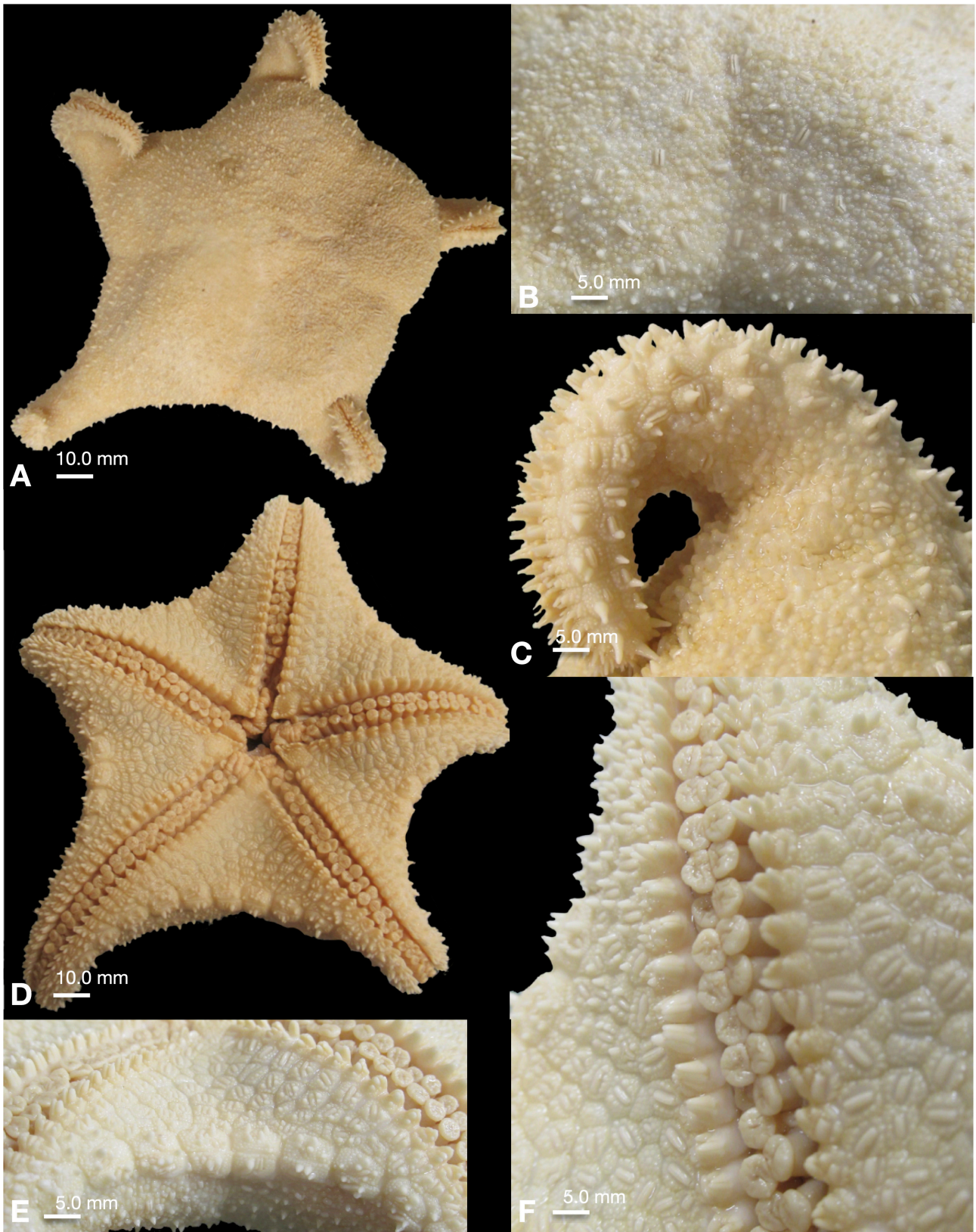


FIGURE 6. *Hippasteria turgida* sp. nov. SIO-BIC E7261. A. Abactinal. B. Abactinal surface. C. Lateral distal arm. D. Actinal. E. Actinal-marginals. F. Actinal-adambulacral.

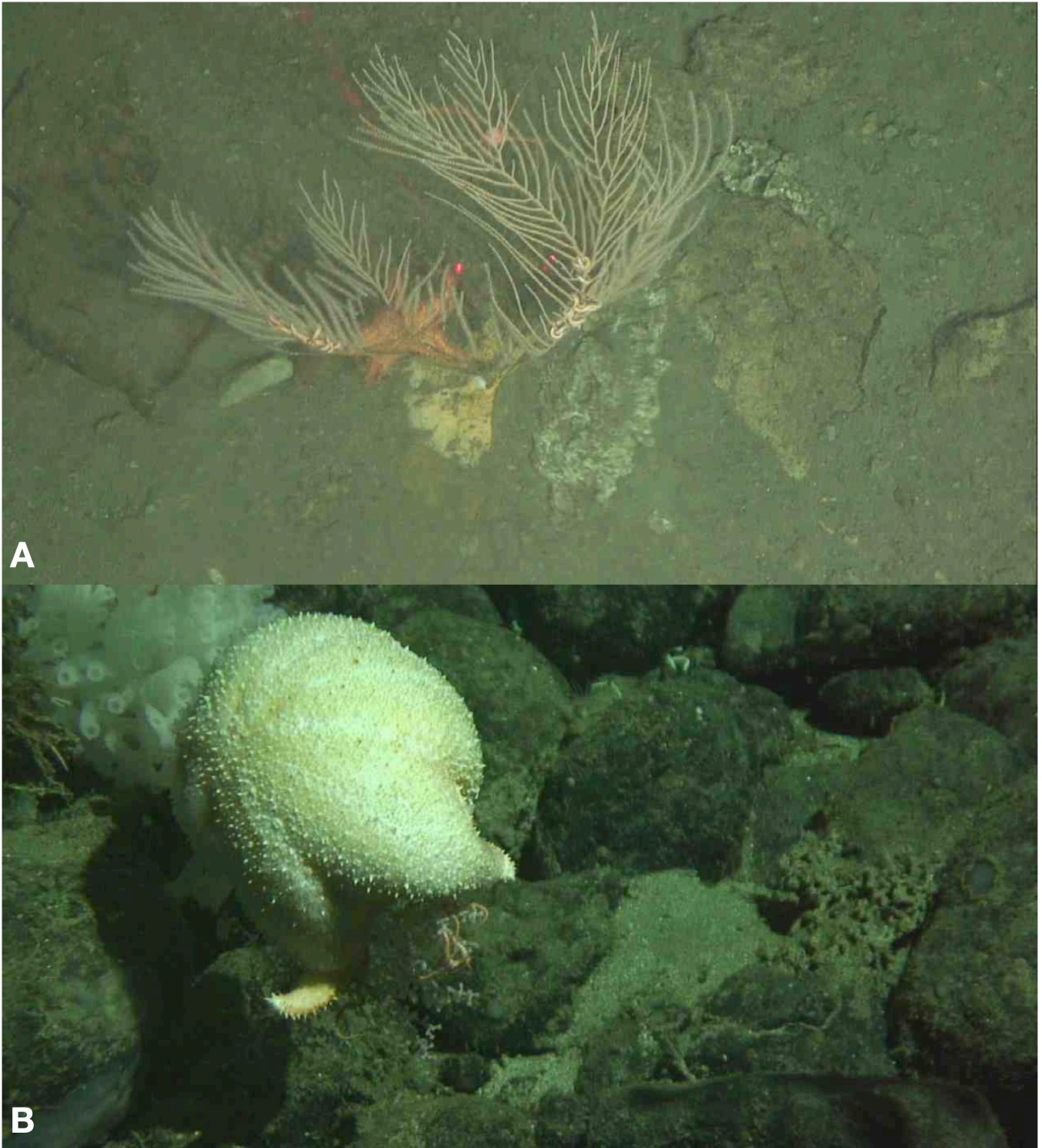


FIGURE 7. *Hippasteria* n. spp. *in situ*. A. *Hippasteria glyphanos* sp. nov. SIO-BIC E7081. B. *Hippasteria turgida* SIO-BIC E7261.

Color in life white with dark orange arm tips and interradial areas. Actinal intermediate areas yellow to light orange, adambulacral plate series dark orange.

Material Examined. Holotype. SIO-BIC E7261 Quepos Plateau Hills, Costa Rica, 8.5322°N, 84.7908°W, 1412 m. Coll. Juan José (Chepe) Alvarado & Charlotte Seid, HOV *Alvin* dive 4981, R/V *Atlantis*, 27 Oct 2018, 1 wet spec. R=11.4 r=3.8 cm. GenBank. PX400630.

***Mediaster* Stimpson, 1857**

Mediaster Stimpson 1857: 530; Perrier 1894: 377; Verrill 1899: 178; Fisher 1911: 196; Verrill 1914: 295; 1915: 108; Fisher 1919: 255; Macan 1938: 369; H. L. Clark 1946: 83; Bernasconi 1963: 11; Halpern 1970: 202; Clark & Downey 1992: 251.

Diagnosis. Based on Mah (2017). Body stellate, arms triangular. With tabulate abactinal plates displaying internally radiating ossicles from base of each plate. Abactinal tabulae plates with granules or spinelets. Abactinal plates in most, extending to arm tip, but exceptionally with distalmost superomarginals abutting. Abactinal, marginal, actinal surface covered by granules.

***Mediaster tenellus* Fisher 1905**

FIGURE 8A–E, 10B

Mediaster tenellus Fisher 1905: 307; 1911: 202; Alton 1966a (as *M. tenellus?*): 1680, 1688, 1702; Maluf 1988: 34, 118; A.M. Clark 1993: 263; Hendrickx *et al.* 2011: 808; Mah 2016: 120;

Mediaster transfuga Ludwig, 1905: 120; Mah 2016: 120–121.

Ceramaster gen. inconclusive. Seid *et al.* 2025: 159, Figs 61A–B.

Diagnosis. Based on Mah (2016). Body variably stellate, $R/r=1.9–3.1$, arms triangular, interradial regions weakly curved. Abactinal plates tabulate, topped with spinelets and granular accessories. Peripheral spinelets, 6–30, mostly 15–24, well-spaced, lobate. Central plate surface with 1–10 (mostly 4–7) round, low, blunt granules; distally short spinelets present adjacent to superomarginals. Marginal plates 30–60 (arm tip to arm tip), both marginal plate series covered with granules, 60–200 (most with about 150). No pedicellariae. Actinal plates round to polygonal in shape, in 3–4 full series arranged in chevron formation. Each plate covered by granules, 2–12, typically 6–8, polygonal, widely spaced granules. Furrow spines slender, 3–6, most commonly four or five, quadrate in cross section, blunt tipped, approximately 10–20% longer than subambulacral spines. Subambulacral spines two or three, each about twice as thick as a furrow spine and twice as long.

Comments. The specimen described herein represents the southernmost occurrence for this already widely distributed species and a significant extension to Central America. Individuals observed from farther north were white when alive, whereas individuals figured here are orange.

Fisher (1911) was the first to suggest that *Mediaster transfuga* Ludwig 1905 intergraded closely with *Mediaster tenellus*, possibly forming morphological extremes of a single species. Mah (2016) briefly summarized the possibility that these two species could be synonymous. Based on specimens herein, furrow spine number, abactinal tabular granules and number of marginal plates per interradius are all similar with that of *M. tenellus*, thus it is argued that *Mediaster transfuga* is synonymous with *Mediaster tenellus* Fisher 1904.

Ecological Comments. Mah (2016) made prior observations of this species from the North Pacific in the Axial seamount region (>1000 m depths) on soft sediment and basalt rock bottoms. Observations herein showed this species on soft sedimented bottoms from Costa Rica, consistent with these observations. Based on gut content analyses and *in situ* observation, this species appears to be a sediment feeder/detritivore (Mah 2016).

Occurrence/Distribution. Aleutian Islands & Gulf of Alaska. Pioneer Seamount and west to Axial Seamount, Co-Axial Seamount. North Pacific region, SW of mouth of Columbia River, Oregon, Mulberry Seamount, Catalina Island (Southern California). Acapulco. 380–1829 m.

Costa Rica, 997 m.

Material Examined. SIO-BIC E7048 Mound 12 methane seep, Costa Rica, 8.9304°N, 84.3126°W, 997 m. Coll. Greg Rouse & Ben Moran, HOV *Alvin* dive 4917, R/V *Atlantis*, 1 June 2017. 1 wet spec. $R=7.9$ $r=3.4$ cm. GenBank. PX400629

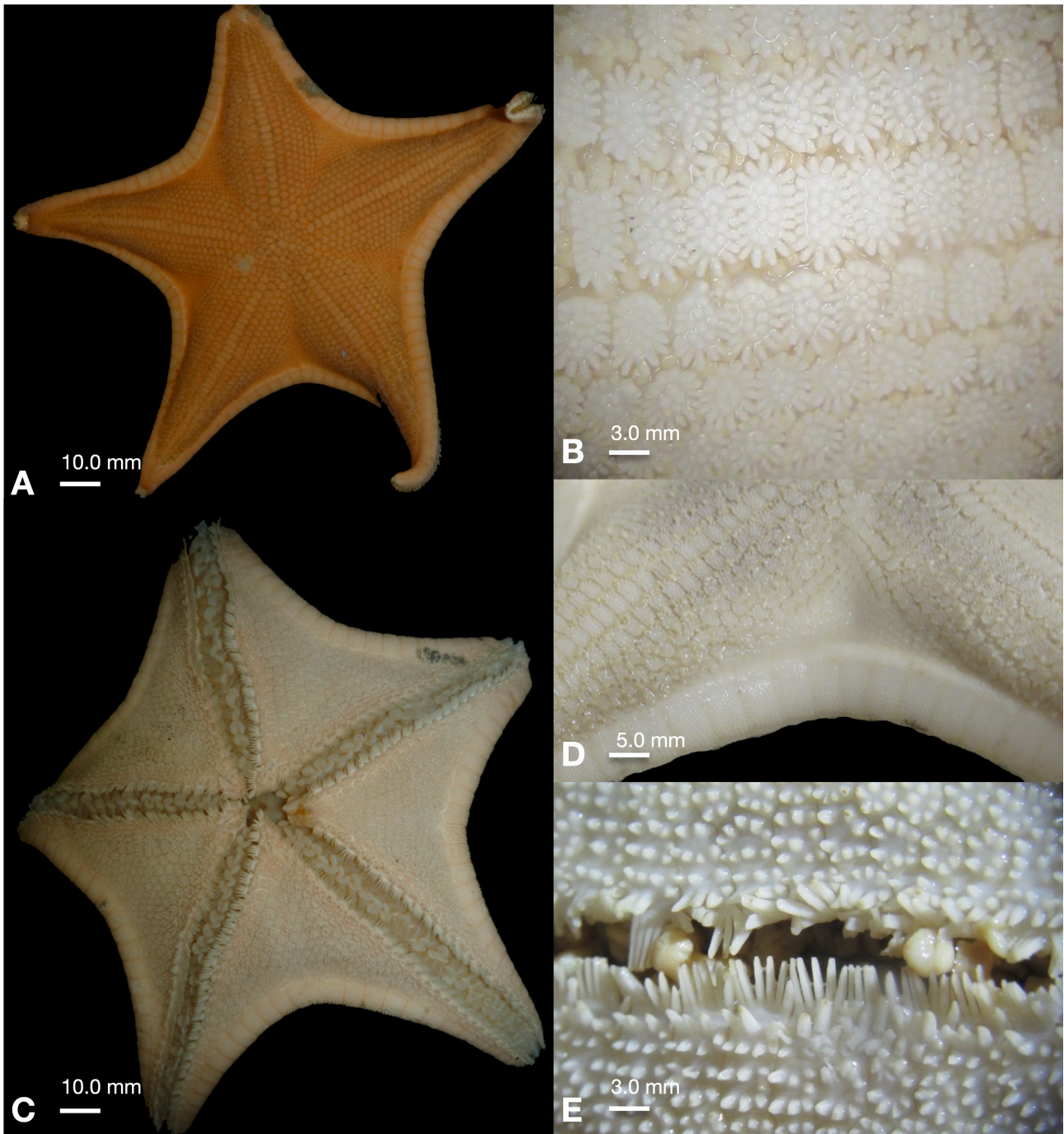


FIGURE 8. *Mediaster tenellus* SIO-BIC E7048. A. Abactinal. B. Abactinal paxillae. C. Actinal. D. Abactinal-marginals. E. Adambulacral furrow.

Nymphaster Sladen 1889

Nymphaster Sladen 1885: 612 (*nomen nudum*; diagnosed but no species named); 1889: 294; Fisher 1917: 167; 1919: 261; Spencer & Wright 1966: U62; Halpern 1970: 222; 1970: 88; Downey in Clark & Downey 1992: 253.
non-*Dorigona* Gray 1866 Perrier 1885: 39; 1894: 365; Koehler 1909: 54

Diagnosis. Based on Mah (2016, 2026). Strongly stellate body form, $R/r=3.6$ to 5.0 , triangular arms with rapidly tapering, pointed tips, quadrate in cross-section. **Abactinal surface showing weakly tabulate plates with granules covering surface. Supermarginals abutted over mid-radius along entire arm length, forming prominent frame around disk.**

Comments. *Nymphaster* is a complex genus that includes 16 species in the Atlantic, Pacific and Indian Oceans with approximately 12 fossil species represented primarily by ossicles from European Cretaceous chalks (e.g. Breton, 1988).

Current understanding of *Nymphaster* species diversity, especially between different oceans invites scrutiny, as Atlantic and Indian Ocean species, *N. arenatus* and *N. moebi*, have argued as widely occurring and variable single species (Clark & Downey, 1992; Macan, 1938, respectively) whereas in contrast, eight species of *Nymphaster* were described from the Indo-Pacific and summarized by Fisher (1913, 1919). This does not include the sole East tropical Pacific species, *Nymphaster diomedea*. It is unclear how a greater survey of phylogeography and/or specimens throughout *Nymphaster*'s distribution will play a role in understanding the boundary between species.

***Nymphaster diomedea* Ludwig, 1905**

FIGURE 9A–E, 10A

Ludwig, 1905: 128; Fisher 1928: 490; Macan, 1938: 374; Maluf, 1988: 34 (table), 118 (list); 1991: 349 (list); A.M. Clark, 1993: 265; Maluf & Brusca, 2005: 331 (list); Hendrickx *et al.*, 2011: 809; Mah 2016: 123; Alvarado *et al.* 2022: 3, Table 1; Seid *et al.* 2025: 159–160, Fig. 61D–F. Alvarado *et al.* 2022: 3, Table 1.

Diagnosis. Based on Mah (2016). Body strongly stellate, flattened. Disk broad with arms triangular in outline, tapering at arm tips, trapezoid in cross-section. Body strongly stellate, flattened. Disk broad with arms triangular in outline, tapering at arm tips (Fig. 9A, D).

Abactinal plates irregularly rounded to variably polygonal, largest along radial regions proximal on disk. Carinal plate series largest, widest with adjacent radial series smaller, with sides having similar length and width. Interradial abactinal plates smaller, more quadrate and irregular in shape. Interradial abactinal plates largest proximally on disk becoming smaller and more crowded distally adjacent to contact with superomarginal plates. Abactinal plates covered with granules, 4–12, roughly hemispherical in shape, evenly distributed on plate surface. More widely distributed on radial and proximal plates but becoming smaller and more crowded distally, adjacent to superomarginal plate contact. Papular pores present only on radial regions of disk, absent interradially with fewer pores present on primary circlet. Pores, four to six per plate, decreasing in number and absent adjacent to superomarginal arm plates. Madreporite, round to polygonal with deep sulci, flanked by five abactinal plates. Fasciolar well-developed along radial regions, but weak to absent interradially.

Superomarginal plates, 20–36 per arm, 40–72 per interradius (armtip to armtip). Superomarginals offset from inferomarginals. Superomarginals wide ($W > L$) becoming more equivocal distally. Distalmost 10–30 superomarginals abutted over midline. Inferomarginals, ~32–72 per interradius (armtip to armtip, but tips are broken). Marginal plates in cross-section with rounded edges with abactinal superomarginal surface and actinal inferomarginal surface weakly convex. Granules, evenly spaced, similar to those on abactinal, actinal surface completely cover marginal plate surface. Granules, 80–100 cover superomarginal and inferomarginal plate surface. Granules on inferomarginal surface, less crowded but more similar in distribution and shape with those granules on actinal plate surface.

Actinal plates in chevron formation, quadrate to irregularly polygonal; largest proximally, but becoming smaller, crowded and more irregular in shape adjacent to inferomarginal contact. Granules 6 to 15 cover each actinal plate; variably round to weakly pointed. Shallow fasciolar grooves present among actinal plates and between actinal and adambulacral plates.

Furrow spines, 2–6, mostly 4, blunt, slender but round to quadrate in cross-section (Fig. 9E). Longest furrow spines proximal becoming shorter distally. Furrow spines proximally 2–4 increasing in number distally. Subambulacrals separated by discrete space, spines short and granular but angular to round in cross-section, approximately twice as large as granules present on actinal surface. Adambulacral plates elongate longer distally. Oral plate with 4 to 6 furrow spines per side, similar in length and shape to furrow spines elsewhere. Oral plate surface covered by pointed granules, blunt, angular to round in cross-section becoming more spine like adjacent to mouth and furrow spines pointing into mouth. No pedicellariae observed on abactinal, marginal actinal, or adambulacral plate surfaces.

Color in life of this species is white to straw-like whitish-yellow.

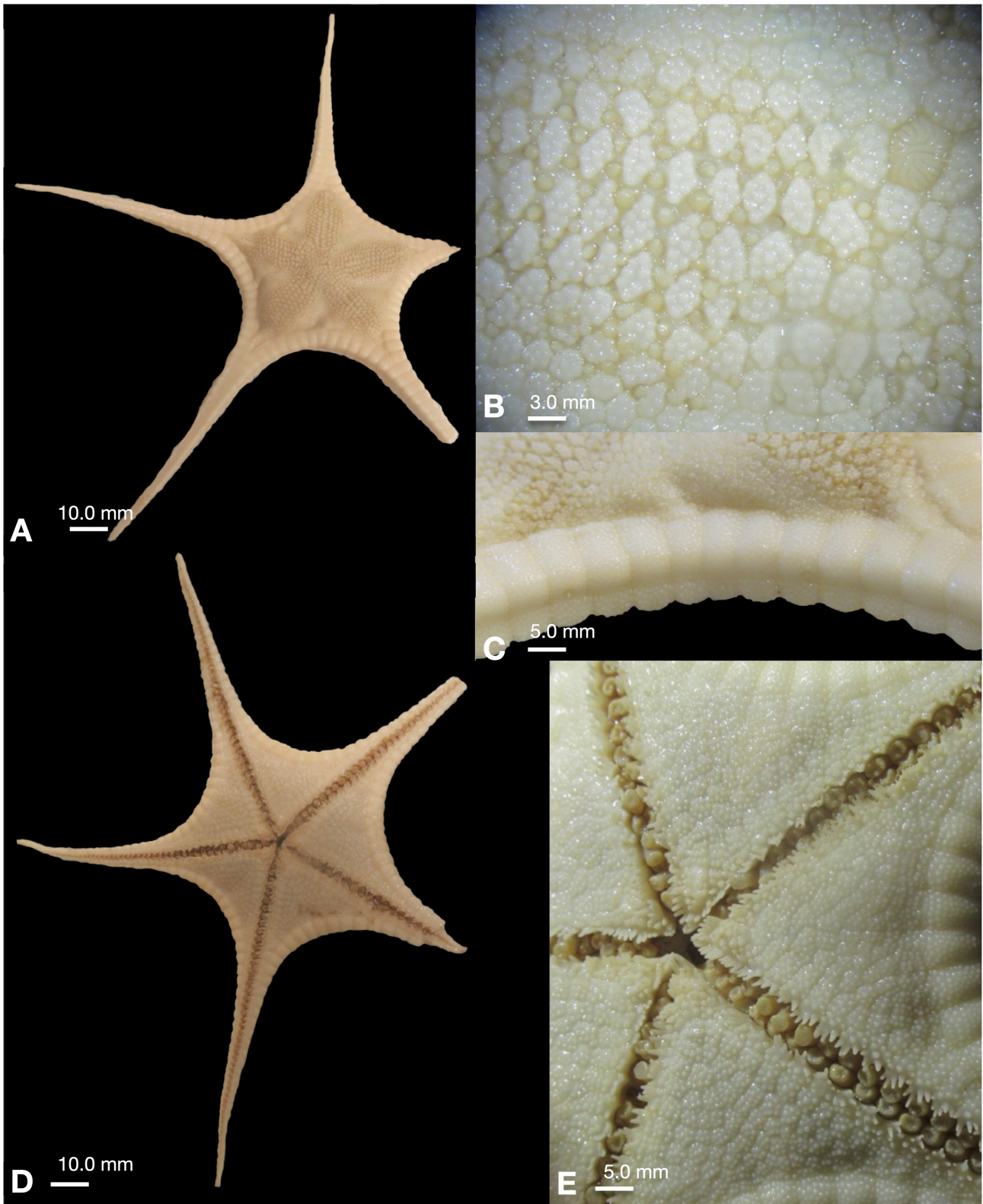


FIGURE 9. *Nymphaster diomedea* SIO-BIC E7067. A. Abactinal. B. Abactinal plates. C. Abactinal-lateral. D. Actinal E. Actinal-adambulacral.

Comments. The syntypes of *Nymphaster diomedea* were collected from Costa Rica, the Galapagos, and Panama and specimens described herein agree with the description of this material. Consideration of *N. diomedea* invites comparison with the widely occurring Atlantic *Nymphaster arenatus*, whose range of morphological variation/full

synonymy had not been established when *N. diomedea* was described (Ludwig 1905). Distinct morphological differences, including furrow spine number, 2–4 versus 4–9 (mostly 7), differing abactinal plate shape and fewer abactinal granules per plate are among characters that distinguish the two species.

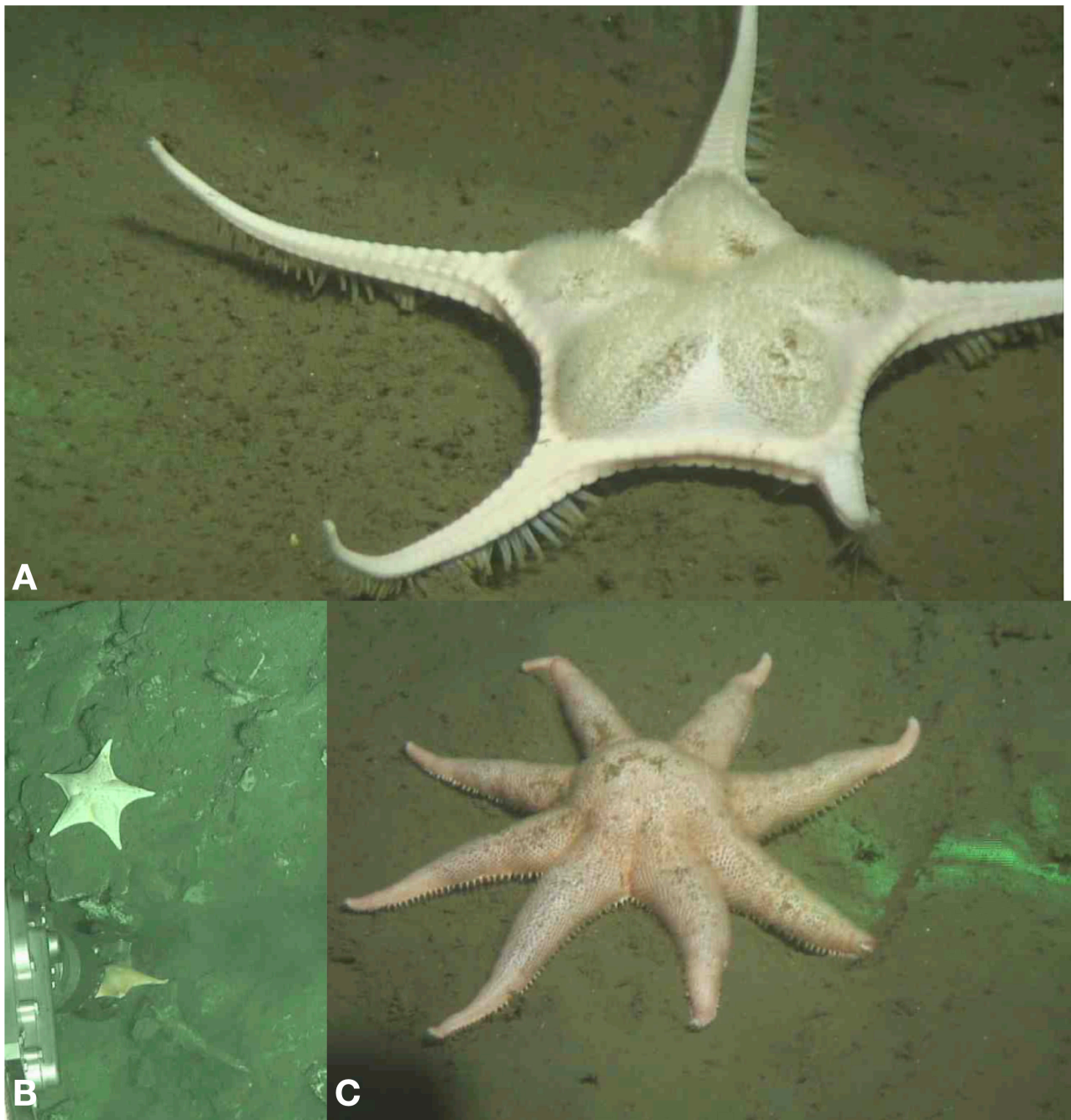


FIGURE 10. Asteroidea *in situ*. A. *Nymphaster diomedea*. B. *Mediaster tenellus* SIO-BIC E7048. C. *Solaster paxillatus costaricensis* sp. nov. SIO-BIC E7050.

Mah (2016) observed this species in association with a moribund squid, suggesting that it shows detritivorous habits. The Atlantic *Nymphaster arenatus* has been observed *in situ* on soft sediments, and displays likely scavenging and possibly opportunistic predatory habits (Mah 2020).

Occurrence/Distribution. Gulf of California, Mexico, Coiba Island (Panama), Cocos Island (Costa Rica), continental margin of Costa Rica, Galapagos Islands (Ecuador), 702–1810 m.

Material Examined. SIO-BIC E4386 (GenBank PQ449001) Mound 11 methane seep, Costa Rica, 8.919°N, 84.304°W, 1004–1011 m. Coll. Tony Rathburn & Helena Molina, HOV *Alvin* dive 4504, R/V *Atlantis*, 25 Feb 2009. 1 wet spec.

SIO-BIC E7028 Mound 12 methane seep, Costa Rica, 8.9294°N 84.3120°W, 994 m. Coll. Lisa Levin & Charlotte Seid, HOV *Alvin* dive 4907, R/V *Atlantis*, 22 May 2017. 1 wet spec. R=12.6 r=3.6 cm.

SIO-BIC E7051 Mound 12 methane seep, Costa Rica, 8.9336°N, 84.3077°W, 996 m. Coll. Greg Rouse & Ben Moran, HOV *Alvin* dive 4917, R/V *Atlantis*, 1 June 2017. 1 wet spec. R=8.0 r=2.8 cm.

SIO-BIC E7067 Parrita Seep methane seep, Costa Rica, 8.9740°N, 84.6280°W, 1097 m. Coll. Carlos Gómez & Odalisca Breedy, HOV *Alvin* dive 4923, R/V *Atlantis*, 6 June 2017. 1 wet spec. R=8.3 r=2.3 cm.

SIO-BIC E7069 (=MZUCR-ECH2476) Parrita Seep methane seep, Costa Rica, 8.9740°N, 84.6280°W, 1097 m. Coll. Carlos Gomez & Odalisca Breedy, HOV *Alvin* dive 4923, R/V *Atlantis*, 6 June 2017.

SIO-BIC E7235 Mound 12 methane seep, Costa Rica, 8.9292°N, 84.3058°W, 1001 m. Coll. Greg Rouse & Amanda Glazier, HOV *Alvin* dive 4975, R/V *Atlantis*, 21 Oct 2018. 1 wet spec. R= 11.1 r=2.8 cm.

SOLASTERIDAE Viguiet, 1878

Diagnosis. Modified from Clark & Downey (1992). Disk moderate in size to large, arms 5–15, rounded, tapering to acute tip, abactinal surface variably fenestrate to reticulate. Plates lobate, paxillate, variably short and low to elongate, capped with multiple spinelets. Papulae present between plate openings, single or in groups. Marginal series one or two consisting of enlarged tuft-like paxillae. Actinal plates mostly confined to disk, in a minority of taxa extending to arm terminus. Adambulacral plates with two combs of spines, furrow spines parallel to the groove and a transversely oriented subambulacral series

Comments. Solasterids are another group of cold-water/deep-sea asteroids that are relatively well known in the North Pacific but poorly understood from the Eastern Tropical and South Pacific regions. There are no prior records of the Solasteridae from Costa Rica. Observations of *Lophaster* have been recorded from deep-sea settings in the Galapagos (Maluf 1987), but *Solaster* has not been previously recorded from low-latitudes in the Eastern Pacific.

Most members of the Solasteridae have been observed as predators on a variety of prey, notably echinoderms including ophiuroids, crinoids, sea cucumbers, and other asteroids (Mauzey *et al.* 1968; Van Veldhuizen & Oakes 1981; Mah 2023).

Solaster Forbes, 1839

Forbes, 1839: 120; Gray 1840: 183; Danielssen & Koren 1882: 50; Sladen 1889: 452; Perrier 1894: 151; Acloque 1900: 256; Fisher 1911: 306; Hayashi 1939: 297; 1940: 174; Djakonov 1950: 65; Bernasconi 1964: 258, 1970: 249; Clark & Downey 1992: 301; Mah 2023: 71.

Diagnosis. Based on Mah (2023). Arms 7–17. Abactinal skeleton composed of close-set cruciform or rounded plates (paxillae also referred to as pseudopaxillae) with non-penicillate spinelets. Papular pores single. Marginal plates paxillate in some species, disproportionately sized small superomarginals similar in size to abactinal paxillae, inferomarginals, prominent, 3x–4x larger than abactinal paxillae, evenly spaced along arm length. Actinal plates spinose with multifid tips. Subambulacral spines forming distinct transverse fans. Furrow spines palmate, unwebbed.

Comments. *Solaster* includes 23 species with the majority of described species described from the cold to temperate North Pacific, especially around the Aleutians and adjacent Russia and Japan (Fisher 1911; Hayashi 1939, 1940; Djakonov 1968) and the North Atlantic (Clark & Downey 1992), with further species present between the intertidal to approximately 3000 m. Additional species occur throughout the Indian and at high-latitudes in the Antarctic (e.g. Mah 2023).

Solaster spp. have been reported as ecologically significant predators on multiple taxa, but primarily on echinoderms, especially asteroids and ophiuroids (e.g. Van Veldhuizen & Oaks 1981; Mah 2023). No *Solaster* species have been recorded from Costa Rica or from the Central American Pacific region.

Solaster paxillatus costaricensis n. subspecies.

FIGURE 11A–F, 10C

Crossaster borealis Seid *et al.* 2025: 161.

Etymology. The subspecies is named for its occurrence from Costa Rica.

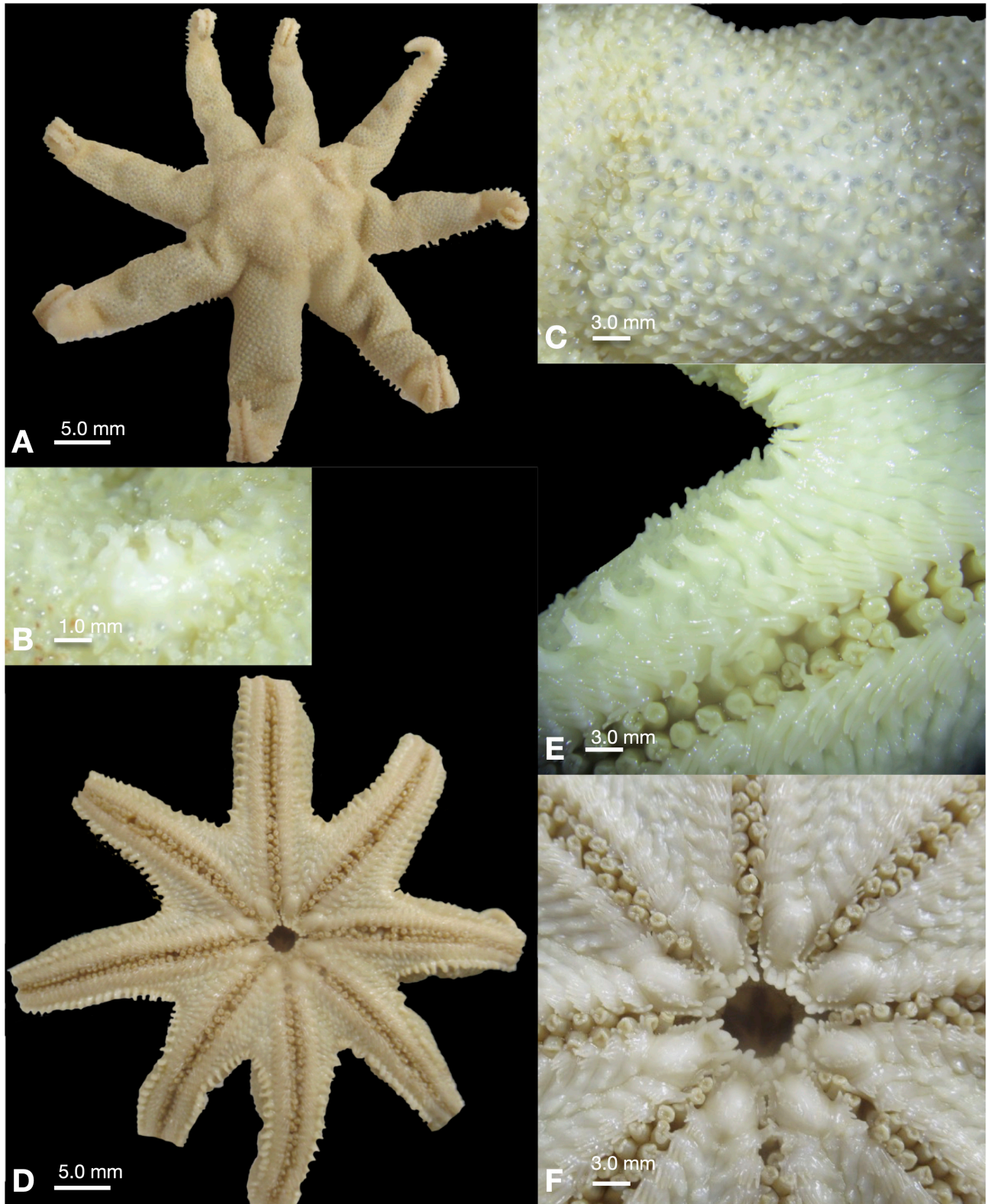


FIGURE 11. *Solaster paxillatus costaricensis* sp. nov. SIO-BIC E7050. A. Abactinal. B. Abactinal paxillae. C. Abactinal fenestrate arm pattern. D. Actinal. E. Actinal-lateral. F. Actinal oral.

Diagnosis. Body thick, stellate, $R/r=3.3$, arms 8, each tapering, elongate, round in cross-section. Interradial arcs acute. **Abactinal surface fenestrate with paxillate plates bearing very short pointed spinelets, 3 to 4, such that they barely extend over the plate surface.** Shaft of these plates is approximately 3X the distance of the tip of the plate with spinelets. Marginal plates a single series along the actinolateral margin, approximately 48 to 50 along each arm, approximately 96 to 100 per interradius. Each marginal plate paxillate, cylindrical in shape, eye-shaped in cross-section, topped with short spinelets, 20–30, pointed with webbed bases. **Actinal plates with short paxillae, 1 to 4, mostly 2 to 3 short spinelets similar to those on the abactinal surface. Furrow spines, 2 to 3, mostly 2, small, blunt free from one another. Adambulacral plates, each with 7 to 8 elongate spines, thick, with pointed tips cylindrical in cross-section in transverse series, 6 to 8 times the length of the furrow spines.**

Comments. This represents the first occurrence of *Solaster* from Costa Rica and from the Central American region.

COI data extracted from this species was compared with other known *Solaster* species and shown to be 98.95–99.85% identical with *Solaster paxillatus* from British Columbia. However, morphology of this species, while similar to *S. paxillatus*, also showed several distinct character differences, notably among paxillae, furrow and other spine number differences from characters described for North Pacific *S. paxillatus*. It was also discovered that a subspecies, *S. paxillatus celebesensis* Aziz & Jangoux 1985 has been collected from Makassar Strait, in Indonesian waters, sharing closer resemblance to North Pacific individuals. Based on the morphological disparity in conjunction with the close genetic similarity it was determined that the best conclusion was to designate this individual as a further subspecies, *Solaster paxillatus costaricensis* n. ssp. a further morphotype to be tested within the context of intraspecific variation of what is conceivably a very widely distributed taxon.

Solaster paxillatus costaricensis **sp. nov.** invited comparison with the North Pacific *Solaster exiguus* Fisher, 1910 known primarily from Southern California with 7 arms, 2 furrow spines and 3 to 5 adambulacral spinelets. Although superficially similar, furrow and adambulacral spinelets are slender and elongate in *S. exiguus*. Furrow spines in *Solaster paxillatus costaricensis* **sp. nov.** are less than 50% of the length and are substantially thicker and more numerous than in *S. exiguus*. *Solaster paxillatus costaricensis* **sp. nov.** is also similar to *Solaster torulatus* Sladen 1889 from north of the Kermadec Islands in having a similar body shape and arm number ($n=8$), sharing paxillae with 2 to 5 spinelets but differing in having much fewer marginal plates per arm, 5 furrow spines and 3 to 4 subambulacral spines. Interestingly, this species and *S. torulatus* share some resemblance with the Atlantic *Solaster benedicti* Verrill 1894. Some deep-sea echinoderms, especially those at depth, occur widely. Further phylogeographic data may show these to be related or even synonymous taxa but testing the boundaries and associated hypotheses of this group are beyond the scope of this report.

Occurrence/Distribution. Known only from Costa Rica, 1000 m.

Description. Body thick, stellate, $R/r=3.3$, arms tapering, elongate, round in cross-section. Interradial arcs acute. Arms eight.

Abactinal surface fenestrate with paxillate plates bearing very short pointed spinelets, 3 to 4, such that they barely extend over the plate surface. Shaft of these plates is approximately 3X the distance of the tip of the plate with spinelets. Paxillae widely spaced from one another where the plates intersect. Papulae single, elongate emerging through numerous single pores present on the abactinal skeleton above the height of the paxillae. Papular pores forming transverse regular series along lateral surfaces on arm with plates in a more irregular arrangement on disk and along radial arm regions. Individual plates tumid, cruciform in shape. Distinct single carinal series present. Each interradius on disk forming appressed fold between arms. Madreporite difficult to distinguish, small, round, overlain by abactinal surface.

Marginal plates a single series along the actinolateral margin, approximately 48–50 along each arm, approximately 96–100 per interradius. Each plate paxillate, cylindrical in shape, eye-shaped in cross-section, topped with short spinelets, 20–30, pointed with webbed bases. If superomarginal plates are present they are smaller, paxillate and indistinguishable from adjacent abactinal plates. Small abactinal paxillae, consistent with those on the abactinal surface, are present between the widely spaced marginal plates, but they did not occur in direct series to the terminus and it is unclear if these are proper marginal plates.

Actinal intermediate region relatively small, composed of approximately 20 transverse series extending from inferomarginal to adambulacral plate series. Distinct dermis present along actinal surface covering fasciolar channels and the actinal intermediate surface between the actinal plates, which display small, short paxillae, 1–4, mostly 2–3 short spinelets similar to those on the abactinal surface.

Furrow spines, 2–3, mostly 2, small, blunt free from one another. Adambulacral plates, each with 7 to 8 elongate spines, thick, with pointed tips cylindrical in cross-section in transverse series, 6 to 8 times the length of the furrow spines. Oral plates with approximately 10 furrow spines, proximalmost 3 spines projecting into mouth, these spines 2–3 x the thickness of adjacent spines. Oral plate with strongly arched central convexity, each side with approximately 5–6 spines on either side of the central diastema.

Color in life white-orange with darker orange present in each interradius.

Material Examined. Holotype. SIO-BIC E7050 Mound 12 methane seep, Costa Rica, 8.9326°N, -84.3069°W, 1000 m. Coll. Greg Rouse & Ben Moran, HOV *Alvin* dive 4917, R/V *Atlantis*, 1 June 2017. 1 wet spec, 8 arms. R=7.6 r=2.3 cm.

VELATIDA Perrier, 1893

PTERASTERIDAE Perrier, 1875

Hymenaster Wyville Thomson 1873

Hymenaster sp.

FIGURE 12A–B

Diagnosis. Modified from Clark & Downey (1992). Body shape variably pentagonal to weakly stellate. Supradorsal membrane variably thin and transparent to parchment-like to fleshy and/or gelatinous with bands of muscle fibers and few to many spiraculae. Osculum large, paxillae restricted to radial areas, actinolateral spines embedded in and supporting actinal membrane. Adambulacral spines few, unwebbed, but may be ensacculate. Oral plates broad, keeled with oral, suboral spines, tube feet in 2 rows.

Comments. This specimen was among the material lost following collection. Based on available imagery, this species demonstrated a well-developed, gelatinous to thin supra dorsal membrane with a ruffled texture, actinal surface covered with well-developed membrane, two rows of well-developed elongate tube feet. The animal was a uniformly deep red-orange with lighter highlights on the actinal surface. Tube feet were dark orange.

This is the first *Hymenaster* documented for Costa Rican waters. H.L. Clark (1920) provided a useful, if now outdated summary key. Unfortunately, taxonomy for *Hymenaster* species is complex owing to relatively few characters, widespread distribution and variation in addition to damaged specimens from trawl collection. Images suggest similarity with *Hymenaster pentagonalis* Fisher 1906 from the Hawaiian Islands, but since the figured specimen could not be examined, definitive characters could not be examined for a conclusive identification. Undescribed *Hymenaster* species also remains a distinct likelihood.

Distribution/Occurrence. This species observed from Seamount 5.5, Costa Rica, 1354 m.

Material Examined. SIO-BIC E7328, Seamount 5.5, Costa Rica, 8.0530°N, 85.7616°W, 1354 m. Coll. Greg Rouse & Avery Hiley, ROV *SuBastian* dive S0221, R/V *Falkor*; 15 Jan 2019. Tissue sample only, voucher lost.

Pteraster diaphanus? Ludwig, 1905

FIGURE 12C–D

Diagnosis. Modified and translated from Ludwig (1905). Body pentagonal with R/r=1:3. “Dorsal” = abactinal side is strongly arched, thin and translucent. Numerous, very small and irregularly distributed spiracles present throughout the supra dorsal membrane. Paxillar crowns with one central and 6–8 peripheral rod-shaped blunt-ended spines. Paxillae each with a quadrilobate base, each in contact forming a diamond-shaped network each filled with multi-lobed papulae. Five anal plates surrounding the small osculum, each with 15–18 spines at their apex supporting the oscular opening. Furrow spines 4, each clear, in transverse series.

Comments. This specimen was among the material lost following collection. Although the voucher specimen of SIO-BIC E7265 could not be examined, details of the specimen images were compared with that of the description in Ludwig (1905) and the USNM holotype. Superficially it is similar with the “strongly arched” dorsal side (=abactinal

surface) and a pentagonal body shape with comparable R/r, approximately 1.0 to 1.1 versus 1.3 on the holotype. Furrow spines are arranged transversely and number 4 in series and small spiracles are present in the supra dorsal membrane of both specimens. However, the holotype, USNM 34411 is damaged and missing the abactinal surface. Characters strongly suggest *Pteraster diaphanus*, but voucher material is needed for a conclusive identification. If confirmed, this is the first occurrence of this species since its original description by Ludwig (1905).

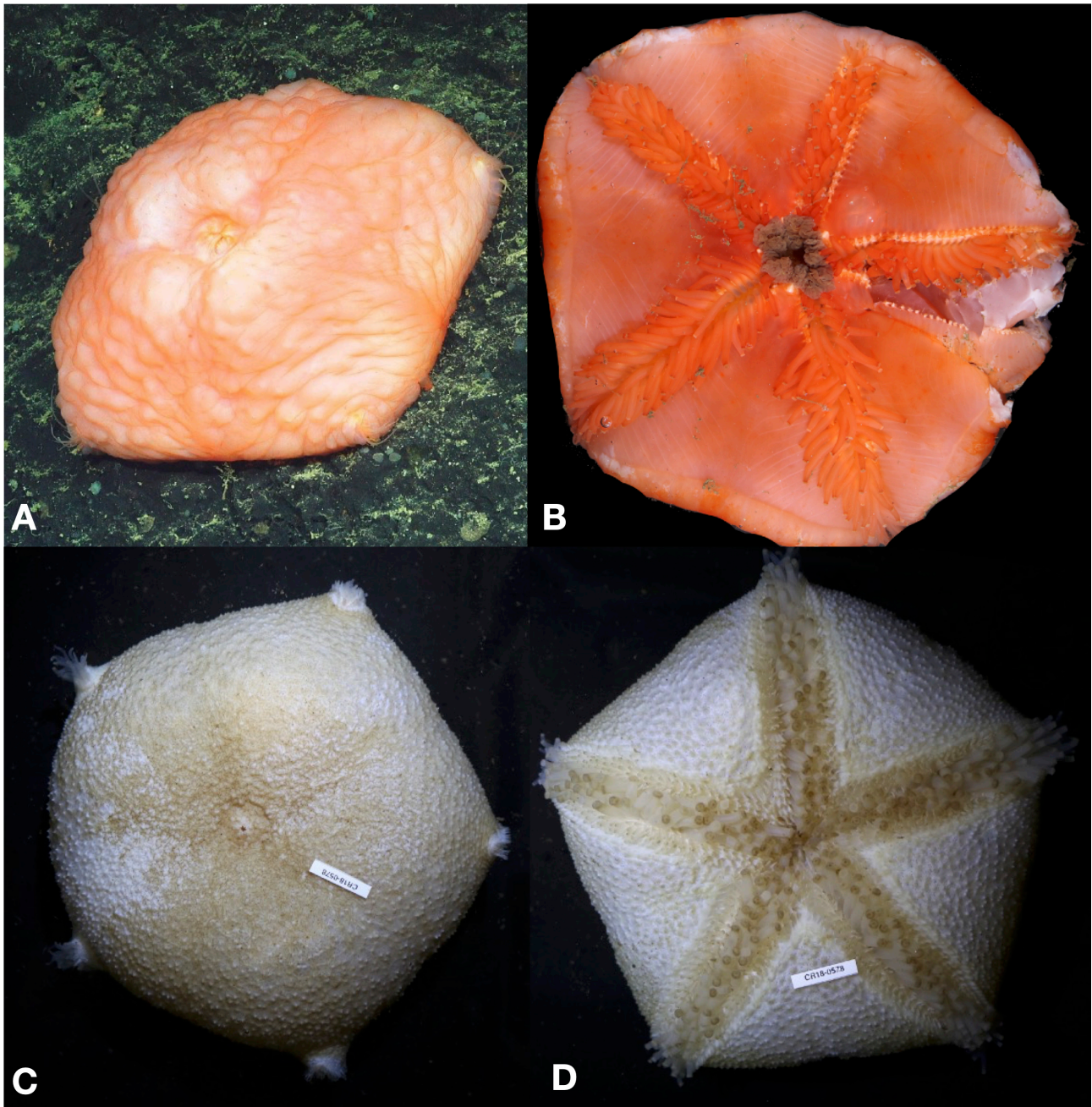


FIGURE 12. Pterasteridae. A. *Hymenaster* sp. SIO-BIC E7328 Abactinal. B. Actinal. C. *Pteraster diaphanus*? SIO-BIC E7265 Abactinal. D. Actinal.

Distribution/Occurrence. Known only from Costa Rica, 1246–1408 m.

Material Examined. SIO-BIC E7265, Seamount 3, Costa Rica, 8.5427°N, 85.1598°W, 1246–1390 m. Coll. Ekin Tilic & Chris Roman, HOV *Alvin* dive 4982, R/V *Atlantis*, 28 Oct 2018. Tissue sample only, voucher lost. GenBank. PX400631

USNM 34411 Cocos Island, Costa Rica, 5.4389°N, 86.9167°W, 1408 m. Coll. USFC Steamer *Albatross*, 1 March 1891. 1 wet spec. R=8.0 r=6.0 mm.

Discussion

Four new species are described herein from the Pacific coast of Costa Rica. A total of six species are new occurrences for Costa Rica. This includes 3 species of *Hippasteria*, which are the first accounts of this taxon from the Central American/Costa Rican region. Three of the new species described herein are based only on the holotype. The addition of *Ceramaster patagonicus* and *Hippasteria* spp. adds to the goniasterid diversity known from Costa Rica, which had included *Bathyceramaster elegans*, *Nymphaster diomedae*, and *Pillsburiaster ernesti*. Prior to description of the species herein, no members of the Solasteridae nor the Radiasteridae were known from Costa Rica.

Ecological Observations

In situ observations from the R/V *Falkor* and the R/V *Atlantis* show 2 of the 3 species of *Hippasteria* included predated on primnoid octocoral colonies, consistent with prior observations of other *Hippasteria*. *Hippasteria glyphanos* sp. nov. was observed feeding on a colonial octocoral *Callogorgia* sp. (tissue sample SIO-BIC Co2941; voucher MZUCR 3140, Museum of Zoology at the University of Costa Rica) in the family Primnoidae. When observed *in situ* (Fig. 6B) the abactinal surface of *Hippasteria turgida* n. sp. was strongly arched with papulae extended over the surface. This species was observed feeding on a colonial octocoral in the Primnoidae. *Hippasteria capstonei* has also been described feeding on primnoid octocorals (Mah 2022).

Hippasteria phrygiana was observed *in situ* (Fig. 3D) and although not seen feeding, there was a denuded octocoral branch, which is a possible prey item for this individual. This is consistent with previous reported feeding preferences (e.g. Mah 2015).

Other *in situ* observations (Fig. 10A–C) include those of *Nymphaster diomedae*, *Mediaster tenellus* and *Solaster paxillatus costaricensis* n. sp, occupying primarily soft sediment bottoms. For *Nymphaster* and *Mediaster*, these are consistent with prior observations (Mah 2016).

Widespread Distributions of Asteroidea

Solaster paxillatus costaricensis n. ssp. described herein was described as part of what is perceived as a more broadly distributed species complex throughout the deep-sea, including the North Pacific *Solaster paxillatus* which occurs from Japan to the Pacific coast of North America and the Indonesian subspecies *Solaster paxillatus celebesensis*. Other *Sollaster* species, such as the high-latitude southern hemisphere *Solaster regularis* are known from widespread distributions. This is not the first discussion of a solasterid with a widespread distribution shared between the northern and southern hemisphere. Mah (2023) summarized the history of *Crossaster japonicus* which was thought by Fell (1958) to be present in the North and South Pacific. No taxonomic consensus was met for these taxa.

However, molecular phylogeography by Foltz *et al.* (2013) and Mah *et al.* (2014) showed that several species of *Hippasteria* present in the Atlantic, Pacific, and Indian Oceans were a single widely distributed species, *Hippasteria phrygiana*, based on COI population genetics. It is possible that further widely occurring species complexes similar to this occur but have yet to be recognized. Many of the synonymized species of *Hippasteria phrygiana* were considered distinctly separate species prior to being sampled for population phylogeography.

Diversity of Asteroidea in Costa Rica

In addition to the four new species described herein, 4 novel occurrences are recorded adding 8 new records to Costa Rica, totaling 45 species (Table 1). Of the total number of species, 29 are known from relatively deep-sea settings (95–3335 m) whereas the remaining 15 are known from nearshore or shallow water habitats.

Affinities and composition of the fauna appear to be diverse and scattered. Many of the observed shallow-water species, such as *Asteropsis carinifera* (Lamarck, 1816) and *Linckia multifora* (Lamarck, 1816) are distributed widely across the Indo-Pacific in contrast to more localized Eastern Tropical Pacific species, such as *Nidorellia armata* (Gray, 1840), *Pharia pyramidata* (Gray, 1840), and *Phataria unifascialis* (Gray, 1840). In contrast, several deep-sea species, such as the Porcellanasteridae, *Porcellanaster ceruleus* Wyville Thomson, 1878 and *Eremicaster pacificus* (Ludwig, 1905) have wide-ranging distributions extending from the Pacific and to the Atlantic. *Hippasteria phrygiana* has recently been shown to demonstrate a widespread nearly cosmopolitan distribution (Foltz *et al.* 2013, Mah *et al.* 2014).

Many of the recorded deep-sea taxa show widespread distribution but are limited to the coastal region along the North Pacific, including the goniasterid *Bathyceramaster elegans* and the brisingid *Astrolirus panamensis* (Ludwig, 1905).

Taxonomic Conclusions

1. *Thrissacanthias bispinosus* Djakonov 1950 is a synonym of *Thrissacanthias penicillatus* Fisher, 1904.
2. *Mediaster transfuga* Ludwig 1905 is a synonym of *Mediaster tenellus* Fisher 1905.
3. A new species of *Radiaster* is described in addition to two new species of *Hippasteria* and a new subspecies of *Solaster*.

List of Included and Observed Species

PAXILLOSIDA

Astropectinidae

Thrissacanthias penicillatus Fisher, 1905

Radiasteridae

Radiaster brocha sp. nov.

VALVATIDA

Goniasteridae

Hippasterinae

Hippasteria glyphanos sp. nov.

Hippasteria phrygiana (Parelius, 1768)

Hippasteria turgida sp. nov.

Ceramaster patagonicus

Mediaster tenellus Fisher 1904

Nymphaster diomedeeae Ludwig, 1905

Solasteridae

Solaster paxillatus costaricensis sp. nov.

VELATIDA (images only)

Pterasteridae

Hymenaster sp.

Pteraster diaphanus? (Ludwig, 1905)

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References

Acloque, A. (1900) *Faune de France contenant la description de toutes les espèces indigènes- avec un préface par E. Perrier* (1899). Baillièrre, Paris, 500 pp.

- Alton, M. (1966) Bathymetric distribution of sea stars (Asteroidea) off the Northern Oregon coast. *Journal of the Fisheries Research Board of Canada*, 23 (11), 1673–1714.
<https://doi.org/10.1139/f66-158>
- Alvarado, J.J. (2010) Isla del Coco (Costa Rica) Echinoderms: State of knowledge. In: Harris, L.G., Boetger, S.A., Walker, C.W. & Lesser, M.P. (Eds.), *Echinoderms: Durham: Proceedings of the 12th International Echinoderm Conference, 7–11 Aug 2006*. CRC Press, pp. 103–113.
- Alvarado, J.J. (2011) Echinoderm diversity in the Caribbean Sea. *Marine Biodiversity*, 41, 261–285.
<https://doi.org/10.1007/s12526-010-0053-0>
- Alvarado, J.J., Chacon-Monge, J.L., Azofeifa-Solano, J.C. & Cortés, J. (2022) Diversity of Deep-Sea Echinoderms from Costa Rica. *Frontiers in Marine Science*, 9, 918878.
<https://doi.org/10.3389/fmars.2022.918878>
- Aziz, A. & Jangoux, M. (1985) Four new species and one new subspecies of Asteroidea (Echinodermata) collected by the Siboga Expedition in the Indo-Malayan Region. *Bijdragen tot de Dierkunde*, 55 (2), 263–274.
<https://doi.org/10.1163/26660644-05502005>
- Bernasconi, I. (1963) Asteroideos argentinos. 4. Familia Goniasteridae. *Revista Museo Argentino de Ciencias Naturales Bernardino Rivadavia. Zoología*, 9 (1), 1–25, pls. 1–5.
- Bernasconi, I. (1964) Asteroideos argentinos. Claves para los órdenes, familias, subfamilias y géneros. *Physis Buenos Aires*, 24, 241–277.
- Blake, D.B. (1987) Classification and phylogeny of post-Paleozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History*, 21, 481–528.
<https://doi.org/10.1080/00222938700771141>
- Cambronero-Solano, S., Benavides, R., Solis-Marin, F.A. & Alvarado, J.J. (2019) New reports of echinoderms on the Caribbean continental slope of central America. *Zoosymposia*, 15, 5–12.
<https://doi.org/10.11646/Zoosymposia.15.1.3>
- Chacón-Monge, J-L., Azofeifa-Solano, J-C., Alvarado, J-J. & Cortés, J. (2021) Área de conservación Guanacaste Echinoderms, North Pacific of Costa Rica. *Revista de Biología Tropical*, 69, suppl. 1.
<http://dx.doi.org/10.15517/rbt.v69isuppl.1.46391>
- Clark, A.M. (1993) An index of names of recent Asteroidea – Part 2: Valvatida. *Echinoderm Studies*, 4, 187–366.
- Clark, A.M. (1997) An index of names of recent Asteroidea – Part 3: Velatida and Spinulosida. *Echinoderm Studies*, 5, 183–250.
- Clark, A.M. (1993) An index of names of recent Asteroidea – Part 2: Valvatida. *Echinoderm Studies*, 4, 187–366.
- Clark, A.M. (1997) An index of names of recent Asteroidea – Part 3: Velatida and Spinulosida. *Echinoderm Studies*, 5, 183–250.
- Clark, A.M. & Downey, M.E. (1992) *Starfishes of the Atlantic*. Chapman and Hall, London, 794 pp.
- Clark, A.M. & Courtman-Stock, J. (1976) *The Echinoderms of Southern Africa*. British Museum of Natural History, London, 277 pp.
- Clark, H.L. (1916) Report on the sea-lilies, starfishes, brittle-stars and sea-urchins obtained by the F.I.S. *Endeavour* on the coasts of Queensland, New South Wales, Tasmania, Victoria, South Australia, and Western Australia. *Biological Results of the Fishing experiments carried on by the F.I.S. Endeavour 1909–1914*, 4 (1), 1–123.
<https://doi.org/10.5962/bhl.title.13854>
- Clark, H.L. (1920) Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the US Fish commission Steamer *Albatross*, from October 1905 to March 1905, Lt. Cmdr. L.M. Garrett, USN, Commanding. XXXII. Asteroidea. *Memoirs of the Museum of Comparative Zoology*, 39 (3), 70–154.
<https://doi.org/10.2307/4073012>
- Clark, H.L. (1946) The Echinoderm fauna of Australia. Its composition and its origin. *Publications of the Carnegie Institution of Washington*, 566, 1–567.
- Danielssen, D.C. & Koren, J. (1882) Fra den norske Nordhavsexpedition, Echinodermer. *Nyt Magazin for Naturvidenskaberne*, 27, 267–299.
- Djakonov, A.M. (1950) Morskije Zvezdy Morei SSSR T U 34, 1–203. [Translated as Dyakonov, A.M. (1968) *Sea stars (Asteroidea) of the USSR Seas. Keys to the Fauna of the USSR* 34. Zoological Institute of the Academy of Sciences of the USSR, ed. By Strelkov, A.A., Israel Program for scientific translations Ltd. Jerusalem, 183 pp.]
- Downey, M.E. (1973) Starfishes from the Caribbean and the Gulf of Mexico. *Smithsonian Contributions to Zoology*, 126, 1–158.
<https://doi.org/10.5479/si.00810282.126>
- Fisher, W.K. (1905) New starfishes from deep water off California and Alaska. *Bulletin of the Bureau of Fisheries*, 24, 291–320.
- Fisher, W.K. (1906) The starfishes of the Hawaiian islands. *Bulletin of the United States Fish Commission*, 23, 987–1130.
- Fisher, W.K. (1911) Asteroidea of the North Pacific and adjacent waters. 1. Phanerozonia and Spinulosida. *Bulletin of the US National Museum*, 76, xiii, 1–420.
<https://doi.org/10.5479/si.03629236.76.i>
- Fisher, W.K. (1916) Notes on the systematic position of certain genera and higher groups of starfishes. *Proceedings of the*

Biological Society of Washington, 29, 1–6.

- Fisher, W.K. (1917) Notes on Asteroidea. *Annals of the Magazine of Natural History*, 20 (8), 166–172.
- Fisher, W.K. (1919) Starfishes of the Philippine seas and adjacent waters. *Bulletin of the United States National Museum*, 3 (100), 1–547. 156 pls.
- Foltz, D., Fatland, S., Eléaume, M., Markello, K., Howell, K., Neil, K. & Mah, C. (2013) Global population divergence of the sea star *Hippasteria phrygiana* corresponds to onset of the last glacial period of the Pleistocene. *Marine Biology*, 160 (5), 1285–1296.
<http://dx.doi.org/0.1007/s00227-013-2180-1>
- Forbes, E. (1839) On the Asteroidea of the Irish Sea. *Memoirs of the Wernerian Natural History Society of Edinburgh*, 8, 114–129.
- Halpern, J.A. (1970) Goniasteridae (Echinodermata: Asteroidea) of the Straits of Florida. *Bulletin of Marine Science*, 20 (1), 193–286.
- Hayashi, R. (1939) Solasterids in Japanese waters. *Journal of the Faculty of Imperial Science of Hokkaido University*, 6 (3), 297–311.
- Hayashi, R. (1940) Contributions to the Classification of the sea-stars of Japan. I. Spinulosa. *Journal of the Faculty of Imperial Science of Hokkaido University*, 6 (7), 107–204.
- Hendrickx, M., Mah, C. & Zarate, C-M. (2011) Deep-water Asteroidea (Echinodermata) collected during the slope cruises in the Gulf of California, Mexico. *Revista Mexicana de Biodiversidad*, 82, 798–824.
<https://doi.org/10.22201/ib.20078706e.2011.3.692>
- Koehler, R. (1909) An account of the deep-sea Asteroidea collected by the Royal Indian Marine Survey Ship *Investigator*. *Echinoderma of the Indian Museum*, 5, 1–143.
- Ludwig, H. (1903) Seesterne. Résultats du voyage du S.Y. *Belgica* en 1897–1898–1899. *Rapports scientifiques*, 1–72 and 7 plates.
- Ludwig, H. (1905) Asteroidea. *Memoirs of the Museum of Comparative Zoology at Harvard*, 32, vii–xii, 1–292+ plates.
- Macan, T.T. (1938) Asteroidea. *Scientific Reports, John Murray Expedition 1933–1934*, 4 (9), 323–435, pls. 1–6.
- Mah, C.L. (2015) A new Atlantic species of *Evoplosoma* with taxonomic summary and *in situ* observations of Atlantic deep-sea corallivorous Goniasteridae (Valvatida; Asteroidea). *Marine Biodiversity Records*, 8 (5), 1–8.
<https://doi.org/10.1017/S1755267214001407>
- Mah, C.L. (2016) Deep-sea (>1000 m) Goniasteridae (Valvatida; Asteroidea) from the North Pacific, including an overview of *Sibogaster*, *Bathyceramaster* n. gen. and three new species. *Zootaxa*, 4175 (2), 101–141.
<https://doi.org/10.11646/zootaxa.4175.2.1>
- Mah, C.L. (2020) New Species, Occurrence Records and Observations of Predation by Deep-sea Asteroidea (Echinodermata) from the North Atlantic by NOAA Ship *Okeanos Explorer*. *Zootaxa*, 4766 (2), 201–260.
<https://doi.org/10.11646/zootaxa.4766.2.1>
- Mah, C.L. (2021) The East Pacific/South Pacific Boundary: New Taxa and Occurrences from Rapa Nui (Easter Island), New Caledonia and adjacent regions. *Zootaxa*, 4980 (3), 401–450.
<https://doi.org/10.11646/zootaxa.4980.3.1>
- Mah, C.L. (2022) New Genera, Species and Occurrence of Deep-Sea Asteroidea (Valvatacea, Forcipulatacea, Echinodermata) collected from the Tropical Pacific Ocean by the CAPSTONE Expedition. *Zootaxa*, 5164 (1), 1–75.
<https://doi.org/10.11646/zootaxa.5164.1.1>
- Mah, C.L. (2023) New Genera, Species, and observations on the biology of Antarctic Valvatida (Asteroidea). *Zootaxa*, 5310 (1), 1–88.
<https://doi.org/10.11646/zootaxa.5310.1.1>
- Mah, C.L. (2025) New Australian Deep-Sea Goniasteridae (Asteroidea; Valvatacea). *Memoirs of the Museum Victoria*, 84, 49–88.
<https://doi.org/10.24199/j.mmv.2025.84.02>
- Mah, C.L. & Foltz, D.W. (2011a) Molecular Phylogeny of the Valvatacea (Asteroidea, Echinodermata). *Zoological Journal of the Linnean Society*, 161, 769–788.
<https://doi.org/10.1111/j.1096-3642.2010.00659.x>
- Mah, C. & Foltz, D.W. (2011b) Molecular Phylogeny of the Forcipulatacea (Asteroidea: Echinodermata): Systematics & Biogeography. *Zoological Journal of the Linnean Society*, 162, 646–660.
<https://doi.org/10.1111/j.1096-3642.2010.00688.x>
- Mah, C.L., Neill, K., Eleaume, M. & Foltz, D. (2014) New Species and global revision of *Hippasteria* (Hippasterinae: Goniasteridae; Asteroidea; Echinodermata). *Zoological Journal of the Linnean Society*, 171, 422–456.
<https://doi.org/10.1111/zoj.12131>
- Mah, C.L., Linse, K., Copley, J., Marsh, L., Rogers, A., Clague, D. & Foltz, D. (2015) Description of a New Family, New Genus and Two New Species of deep-sea Forcipulatacea (Asteroidea), including the first known sea star from Hydrothermal Vent Habitats. *Zoological Journal of the Linnean Society*, 174, 93–113.
<https://doi.org/10.1111/zoj.12229>
- Maluf, Y. (1988) *Composition and distribution of the central eastern Pacific echinoderms*. Natural History Museum of Los Angeles County, 242 pp.

- Maluf, L.I. & Brusca, R.C. (2005) Echinodermata. Chapter 18. In: Hendrickx, M.E., Brusca, R.C. & Findley, L.T. (Eds.), *A Distributional checklist of the macrofauna of the Gulf of California, Mexico. Part I. Invertebrates. [Listado y distribución de la macrofauna del Golfo de California, México, Parte I. Invertebrados]*. Arizona-Sonora Desert Museum, Tucson, Az. USA, pp. 327–343.
- Mauzey, K.P., Birkeland, C. & Dayton, P.K. (1968) Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology*, 49, 603–619.
<https://doi.org/10.2307/1935526>
- McKnight, D.G. (1973) Additions to the asteroid fauna of New Zealand: families Radiasteridae, Solasteridae, Pterasteridae, Asterinidae, Ganeriidae and Echinasteridae. *NZOI Records*, 2 (1), 1–15.
- Mortensen, T. (1927) *Handbook of the Echinoderms of the British Isles*. Oxford University Press, London.
- Parelius, J. (1768) Beskrivelse over Nogle Korstroid. *Kongelige Norske Videnskabers Selskab Skrifter*, 4, 423–428, pl. 14.
- Payne, C.Y., Tilic, E., Boschen-Rose, R.E., Gannon, A., Stiller, J., Hiley, A.S., Grupe, B.M., Mah, C.L. & Rouse, G.W. (2023) *Xyloplax princealberti* (Asteroidea, Echinodermata): A New Species That Is Not Always Associated with Wood Falls. *Diversity*, 15, 1212.
<https://doi.org/10.3390/d15121212>
- Perrier, E. (1881) Report on the Results of dredging in the Gulf of Mexico and in the Caribbean Sea, 1877–79, by the United States Coastal Survey Steamer Blake. 14. Description sommaire des espèces nouvelles d’Astéries. *Bulletin of the Museum of Comparative Zoology*, 9, 1–31.
- Perrier, E. (1884) Mémoire sur les étoiles de mer recueillis dans la mer des Antilles et le golfe du Mexique : durant les expéditions de dragage faites sous la direction de M. Alexandre Agassiz. *Archives (Muséum national d’histoire naturelle (France))*, 2 (6), 127–276.
<https://doi.org/10.5962/bhl.title.82184>
- Perrier, E. (1891) Echinoderma I. Stellérides. *Mission Scientifique du Cap Horn, 1882–83. Zoologie*, 6 (3), 1–198.
- Perrier, E. (1894) Stellérides. *Expéditions Scientifique Travailleur et du Talisman*, 3, 1–431, 26 pls.
- Seid, C.A., Hiley, A.S., McCowin, M.F., Carvajal, J.I., Cha, H., Ah Yong, S.T., Ashford, O.S., Breedy, O., Eernisse, D.J., Goffredi, S.K., Hendrickx, M.E., Kocot, K.M., Mah, C.L., Miller, A.K., Mongiardino Koch, N., Mooi, R., O’Hara, T.D., Pleijel, F., Stiller, J., Tilic, E., Valentich-Scott, P., Waren, A., Wicksten, M.K., Wilson, N.G., Cordes, E.E., Levin, L.A., Cortés, J. & Rouse, G.W. (2025) A faunal inventory of methane seeps on the Pacific margin of Costa Rica. *ZooKeys*, 1222, 1–250.
<https://doi.org/10.3897/zookeys.1222.134385>
- Shen, Z., Mongiardino Koch, N., Seid, C.A., Tilic, E. & Rouse, G.W. (2024) Three New Species of Deep-Sea Wood-Associated Sea Stars (Asteroidea: Caymanostellidae) from the Eastern Pacific. *Zootaxa*, 5536 (3), 351–388.
<https://doi.org/10.11646/Zootaxa.5536.3.1>
- Sladen, W.P. (1882) Asteroidea dredged during the cruise of the *Knight Errant* in July and August 1880. *Proceedings of the Royal Society of Edinburgh*, 11, 698–700.
- Sladen, W.P. (1882b) Description of *Mimaster*, a new genus of Asteroidea from the Faeroe Channel. *Transactions of the Royal Society of Edinburgh*, 11, 698–707.
- Sladen, W.P. (1889) Asteroidea. *Report of the Scientific Results of H. M. S. Challenger*, 30, 1–893.
- Spencer, W.K. & Wright, C.W. (1966) Asterozoans, Part U: Echinodermata. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology* 3, 1. University of Kansas Press, Lawrence, pp. U4–U107.
- Stampanato, S. & Jangoux, M. (2004) The asteroid fauna (Echinodermata) of Marion and Prince Edward Islands. *Annals of the South African Museum*, 112 (1), 1–16.
- VanVeldhuizen, H.D. & Oakes, V.J. (1981) Behavioral responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni* (responses of asteroids to the predator *Solaster dawsoni*). *Oecologia*, 48 (2), 214–220.
<https://doi.org/10.1007/BF00347967>
- Verrill, A.E. (1894) Descriptions of new species of starfishes and ophiurans, with a revision of certain species formerly described; mostly from the collections made by the United States Commission of Fish and Fisheries. *Proceedings of the United States National Museum*, 17 (1000), 245–297.
<https://doi.org/10.5479/si.00963801.1000.245>
- Verrill, A.E. (1899) Revision of certain genera and species of starfishes and ophiurans. *Proceedings of the US National Museum*, 17, 245–297.
- Verrill, A.E. (1914) Monograph of the shallow-water starfishes of the North Pacific coast from the Arctic Ocean to California. *Harriman Alaska series: US National Museum*, 14, 1–408.
<https://doi.org/10.5962/bhl.title.25926>
- Ziesenhene, F.C. (1937) The Templeton Crocker Expedition. X. Echinoderms from the West Coast of Lower California, the Gulf of California and Clarion Island. *Zoologica: Scientific Contributions New York Zoological Society*, 22 (3), 209–289.
<https://doi.org/10.5962/p.184686>