



Phylogenetic revision of the Hippasterinae (Goniasteridae; Asteroidea): systematics of deep sea corallivores, including one new genus and three new species

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The Hippasterinae is a subfamily within the Goniasteridae, consisting of five genera and 26 species, which occur in cold-water settings ranging from subtidal to abyssal depths. All known genera were included in a cladistic analysis resulting in two most parsimonious trees, supporting the Hippasterinae as monophyletic. Our review supports *Sthenaster emmae* gen. et sp. nov. as a new genus and species from the tropical Atlantic and two new *Evoplosoma* species, *Evoplosoma claguei* sp. nov. and *Evoplosoma voratus* sp. nov. from seamounts in the North Pacific. *Hippasteria caribaea* is reassigned to the genus *Gilbertaster*, which previously contained a single Pacific species. Our analysis supports *Evoplosoma* as a derived deep water lineage relative to its continental-shelf, shallow water sister taxa. The genus *Hippasteria* contains approximately 15 widely distributed, but similar-looking species, which occur in the northern and southern hemispheres. Except for *Gilbertaster*, at least one species in each genus has been observed or is inferred to prey on deep-sea corals, suggesting that this lineage is important to the conservation of deep-sea coral habitats. The Hippasterinae shares several morphological similarities with *Circeaster* and *Calliaster*, suggesting that they may be related.

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INTRODUCTION

Deep-sea or cold-water coral ecosystems have received worldwide attention (e.g. Roberts & Hirshfield, 2004). Exploration of these unique, productive regions has increased recently, leading to an improved understanding of and appreciation for these structure-forming habitats along continental slopes and other deep-sea settings (Hourigan *et al.*, 2007).

For example, the slope region off the south-eastern US may have one of the most extensive deep coral areas in US waters (Hain & Corcoran, 2004).

Amongst the most prominent members of deep-sea coral reefs are echinoderms (e.g. Chave & Malahoff, 1998; Krieger & Wing, 2002), especially members of the Asteroidea, also known as sea stars or starfish. Ecological interactions between asteroids and colonial cnidarians, such as corals have been heavily studied (e.g. Birkeland & Lucas, 1990) and available data suggest that asteroids are ecologically important in these settings (e.g. Birkeland, 1974). Conservation of coral habitats begins with an understanding of

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community structure and function of associated fauna, including identification and inventory of the taxa that compose that fauna.

Surveys of deep-sea coral habitats in the Atlantic and Pacific have led to the collection and observation of several asteroids, especially those in the Goniasteridae, which have been observed in association with deep-sea corals. These asteroids belong primarily to the Hippasterinae, a small but discrete subfamily known primarily from cold-water settings. New data, presented herein, demonstrate predation by nearly all members of this group on multiple species of deep-sea coral.

In the Atlantic, recent collections (S. W. Ross and M. Nizinski, unpubl. data) at multiple sites off the south-eastern coast of the US have revealed, to date, many specimens of asteroids, representing 12 families, 18 genera, and 18 species (M. Nizinski, unpubl. data), associated with deep-sea coral habitats. This includes two forms of hippasterines from the south-eastern US, including one species that was consistent with prior descriptions of '*Hippasteria*' *caribaea* as summarized by Verrill (1899) and a second species from the Georgia coast that did not fit into any known goniasterid genera.

In the North Pacific, surveys by the Monterey Bay Aquarium Research Institute (MBARI) from seamounts (Lundsten *et al.*, 2009) have also resulted in collections of several hippasterine asteroids, from deep-sea coral assemblages. Numerous collected specimens included *Hippasteria* and the rarely encountered *Cryptopeltaster*, and *Evoplosoma*. Collected *Evoplosoma* specimens were unknown from this region of the North Pacific and could not be reconciled with any known species.

Motivated by discovery of this new material in addition to new *in situ* observations of hippasterines preying on deep-sea corals, we present (1) descriptions of one new genus and three new species of previously undescribed hippasterine sea stars; (2) a review and phylogenetic revision of the Hippasterinae; and (3) discussion of corallivorous behaviour in the Goniasteridae. Because of the complex nature of relationships amongst species in *Hippasteria*, a comprehensive assessment of species in this genus was beyond the scope of the current study. However, a full summary of all known hippasterine species is provided as a starting point to encourage future studies.

TAXONOMIC BACKGROUND

Hippasteria Gray, 1840 and related taxa are amongst the first described asteroids (with pre-Linnean designation *Pentaceros planus* Linck, 1733). The subfamily Hippasterinae was designated by Verrill (1899) to

include *Hippasteria* and *Cladaster*. Fisher (1905, 1906) subsequently described two new genera, *Cryptopeltaster* and *Evoplosoma*, respectively, which he included in the Hippasterinae (Fisher, 1911). Fisher (1906) described *Gilbertaster* and suggested it was an 'aberrant member' of the Hippasterinae but never included *Gilbertaster* in this subfamily with *Cryptopeltaster* and *Evoplosoma*. Fisher (1911, 1940) later removed *Cladaster* from the Hippasterinae. Mah (2006) determined that *Cladaster* had closer affinities with *Circeaster* based on morphology, thus providing support for removal of *Cladaster* from the Hippasterinae. The Hippasterinae has not been widely recognized in recent monographs and classifications (e.g. Clark & Downey, 1992; Clark & McKnight, 2001). Fisher (1940) described the subfamily Hippasterinae as 'superfluous', based on perceived phylogenetic confluence (*Cladaster*) with the Goniasteridae. However, Spencer & Wright (1966) retained usage of the Hippasterinae and the grouping has persisted within the Goniasteridae (e.g. Clark & Downey, 1992). Dons (1937) recognized two subgenera, *Hippasteria* (*Euhippasteria*), with large, subquadrate or rectangular marginal plates and *Hippasteria* (*Nehippasteria*), which had more oval-shaped plates. These concepts, however, have never been tested. Although revisions of local faunas have been performed (Clark & Downey, 1992; Clark & McKnight, 2001; McKnight, 2006), a full evaluation of this group and its members has not been attempted.

Hippasteria, the type genus for the group, includes approximately 18 nominal living species distributed largely in cold-water settings, including high-latitude and deep-water habitats (Clark, 1993). Several of the species and subspecies, especially those associated with *Hippasteria phrygiana* and *Hippasteria spinosa*, are questionable and often show weakly defined species boundaries. Many of these species are widely distributed but may be morphologically indistinguishable. For example, the South Pacific–New Zealand *Hippasteria trojana* has been synonymized with the Atlantic *H. phrygiana* (Clark in H.E.S. Clark & McKnight, 2001). Surprising amounts of cryptic species diversity have been encountered in widespread species with highly similar to identical external morphology (e.g. Vogler *et al.*, 2008), suggesting that several of the species boundaries in *Hippasteria*, are unlikely to be resolved solely on morphological data.

Cryptopeltaster includes two nominal species, occurring in moderately deep-water (~200–700 m) along the west coast of North and South America. *Evoplosoma* includes four nominal species and occurs in deeper water (700–2000 m) in the Indian, Pacific, and Atlantic ocean basins (Clark, 1993). *Gilbertaster* occurs only in deep-water in the central and south Pacific (Clark & McKnight, 2001).

MATERIAL AND METHODS

In addition to new material provided by M. Nizinski and L. Lundsten (see map in Fig. 1 for collection localities), additional specimens from the Smithsonian Institution (USNM) and the Museum of Comparative Zoology (MCZ) were examined. External features and variation in accessory structures were primary sources of character data observed mostly from dried specimens, although wet specimens were also examined.

Mediaster aequalis (Stimpson, 1857) and *Peltaster placenta* (Müller & Troschel, 1842) were selected as outgroups based on preliminary morphological data supporting these taxa as stemward relative to *Hippasteria* (Mah, 2005a). *Cladaster* was also selected owing to its past classification history within the Hippasterinae.

Ingroup taxa were chosen based on their taxonomic inclusion in the Hippasterinae following Fisher (1911) and Spencer & Wright (1966). *Gilbertaster* was included based on the close morphological similarity mentioned by Fisher (1906) and partial support from preliminary morphological data (Mah, 2005b). *Hippasteria* includes a large number of morphologically

similar species, some of which occur across wide distances (e.g. northern vs. southern hemispheres) and a full revision was beyond the scope of the project. *Hippasteria* species chosen for inclusion were representative of the diversity of body plans observed within the genus. *Evoplosoma* was represented by two Atlantic species in addition to two undescribed Pacific species. Nearly every available species of *Evoplosoma* was studied from type or previously published specimen material. Type material for two of the known species (*Evoplosoma forcipifera* and *Evoplosoma augusti*) is missing.

METHODS

Phylogenetic analysis utilized morphological data from 46 characters scored from 12 ingroup taxa (see Appendices 1 and 2). Data were entered into MacClade, exported to PAUP*4.0b10 (Swofford, 2003) and analysed using the Branch-and-Bound search option. Characters were treated as unordered and with equal weight.

Branch support was calculated for Bremer and bootstrap values (Fig. 2). Both were calculated using

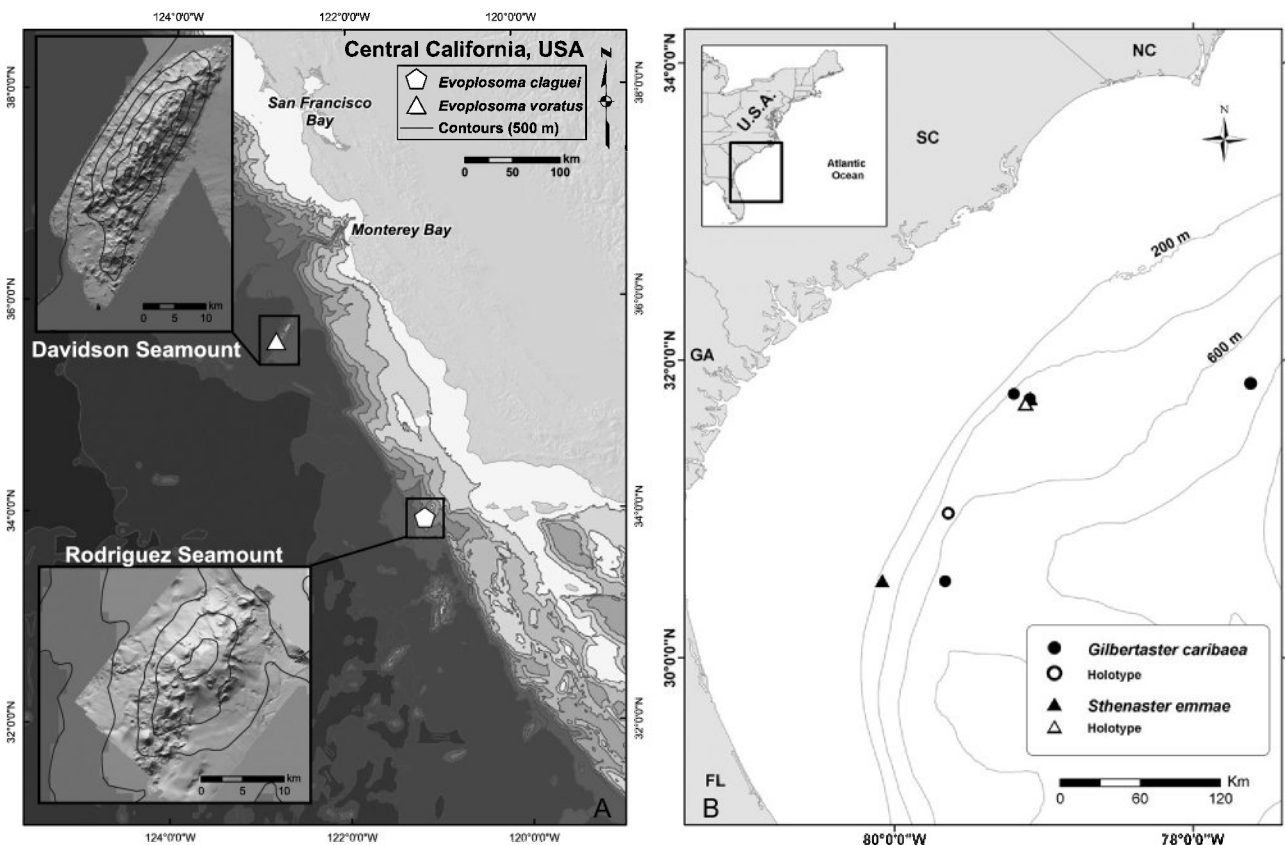


Figure 1. Collection locality maps. A, tropical Atlantic localities for *Sthenaster* and *Gilbertaster caribaea*; B, North-east Pacific localities for *Evoplosoma* spp. nov.

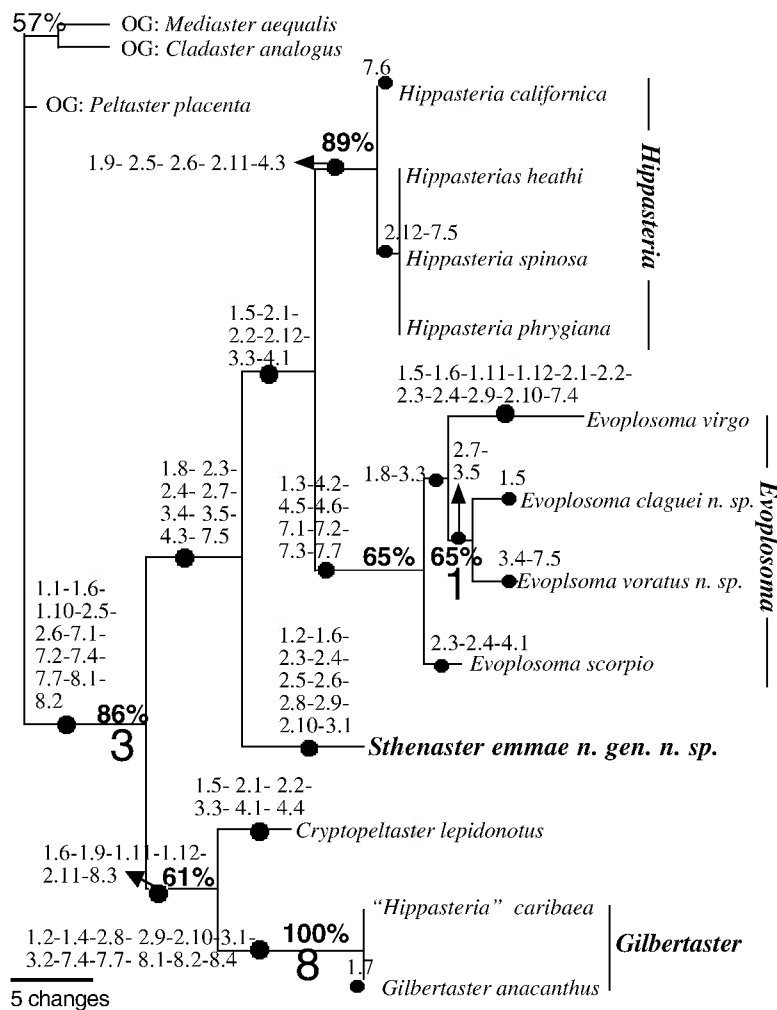


Figure 2. Tree results: topology and support values. In the other equally parsimonious tree topology the positions of *Evoplosoma virgo* and *Evoplosoma scorpio* are transposed. Otherwise the tree is identical. Bootstrap values are present as % in bold vs. Bremer values which are oversized numbers that sit below the bootstrap values. Decimal numbers represent apomorphies on each node for each member of ingroup taxa correspond to terms in Appendix 2. OG, outgroup.

PAUP. Bremer was calculated based on the addition of additional steps to the most parsimonious tree until branches collapsed into polytomies. Bootstrap values were calculated from 200 replicates using random stepwise addition.

RESULTS AND CLASSIFICATION

The analysis resulted in two most parsimonious trees each with 111 steps and a consistency index of 0.6036 and a homoplasy index of 0.3964. Each tree displayed essentially identical topologies (Fig. 2), differing only in the positions of *Evoplosoma virgo* and *Evoplosoma scorpio* (discussed further below).

The Hippasterinae (Fig. 2) are strongly supported (bootstrap = 99%) including a monophyletic *Hippasteria* (bootstrap = 85%), and *Gilbertaster* (boot-

strap = 100%), *Gilbertaster* + *Cryptopeltaster* (bootstrap = 62%), and *Evoplosoma* (bootstrap = 66%). The Hippasterinae was separated from the outgroup taxa, including *Cladaster*, which was previously included amongst the Hippasterinae. *Cryptopeltaster* and *Sthenaster* are both monotypic taxa and although some variation within the species is present, none warranted further testing within the context of the phylogeny. Bootstrap support was absent for the *Evoplosoma* plus *Hippasteria* branch as well as for *Hippasteria* itself.

Gilbertaster was relatively well supported within the Hippasterinae as the sister taxon to the monotypic *Cryptopeltaster* as part of the sister clade to the other hippasterines. This relationship loosely supports statements expressed by Fisher (1906: 1065) that '*Gilbertaster* appears to be allied to some of the

Hippasterine, particularly to *Cryptopeltaster* . . . as well as his general perception that *Gilbertaster* was 'intermediate between the Goniasterinae and Hippasterinae . . .' and 'might be considered . . . an aberrant member of the Hippasterinae'.

Hippasteria caribaea is strongly supported as sister taxon to the Pacific *Gilbertaster anacanthus* (bootstrap = 100%). Based on these results and the number of shared characters, *Hippasteria caribaea* is moved to the genus *Gilbertaster*. Two species are now included in *Gilbertaster*, which extends the range of this genus to include the western Atlantic.

Hippasteria has a fairly distinctive suite of diagnostic characters in addition to strong bootstrap support (Fig. 1). *Hippasteria californica* is supported as the sister group to a polytomy including *Hippasteria heathi*, *Hippasteria spinosa*, and *Hippasteria phrygiana*. *Hippasteria californica* shares at least one character, oval to rounded marginal plate shape, with *Hippasteria insignis* and *Hippasteria phrygiana strongylactis*, which are either synonymous or subspecies of *H. phrygiana*. *Hippasteria insignis* was included in a separate subgenus *Hippasteria* (*Nehippasteria*) (Dons, 1937) but has since been synonymized with *Hippasteria* (Clark & Downey, 1992). Some species, such as *Hippasteria falklandica* and *Hippasteria tasmanica* have been described as having more elongate marginals than those observed in *H. phrygiana* or *H. spinosa*, suggesting that further species may be considered for inclusion in *H. (Nehippasteria)*. Thus, further taxon and character sampling may provide the potential for discovering additional diversity within *Hippasteria*.

All four species of *Evoplosoma* included in this analysis were supported together on a single branch (Fig. 2) but taxonomic sampling remains incomplete. Information for almost all of the species of *Evoplosoma* was based on single specimens but all species seem to display a relatively consistent suite of morphological characters. The original description of the Indian Ocean species, *E. augusti* by Koehler (1909) (specimen could not be located for this study), suggests that this species may show greater divergence from the Atlantic and Pacific species and may actually demonstrate a morphology intermediate to other hippasterines.

SYSTEMATICS

Notes on terminology: Sections entitled *Diagnosis* are intended for summary descriptions for genera as opposed to sections entitled *Description*, which are intended for full species descriptions. Monotypic taxa did not warrant a diagnosis separate from specific description. A full summary of morphological terminology and an identification key is in Appendix 3.

Appendix 4 includes a full list of new genera and species as well as taxonomic changes included below.

FAMILY GONIASTERIDAE FORBES, 1841

SUBFAMILY

HIPPASTERINAE VERRILL, 1899

Verrill, 1899: 174; Fisher, 1906: 1165; 1910: 223; Spencer & Wright, 1966: U58

Notes: Our phylogenetic analysis supports the monophyly of the Hippasterinae as a discrete subgroup within the Goniasteridae. Several characters support hippasterines as members of the Goniasteridae, including a heavily calcified body wall, abactinal plates arranged into discrete primary-radial series and smaller inter-radial, secondary plates, papulae present radially but absent inter-radially, two series of clearly delineated and heavily calcified marginal plates, actinal plates arranged into distinct chevron-shaped rows as well as suckered tube feet in biserial rows.

Our assessment disagrees with Fisher's (1940) conclusion that the Hippasterinae is 'superfluous.' Fisher based his conclusion on the 'intermediate' morphological characters observed in *Cladaster*. Mah (2006) supported *Cladaster* as the sister group to the *Circeaster* lineage; however, it is possible that either the *Circeaster* and Hippasterine lineages are closely related or that Fisher (1940) referred to different *Cladaster* spp. than those utilized in Mah (2006). In either case, the data presented here support the Hippasterinae as a discrete group that is recognized herein.

Diagnosis: Pulpy tissue present. Abactinal plates with spiny-granular or angular accessory fringe. Abactinal plates tightly articulated. Superomarginal and inferomarginal plates, wide to quadrate with large, prominent spines in most taxa. Pedicellariae enlarged, abundant and often on raised base. Marginal plates facing laterally. Disk strongly swollen in most.

GILBERTASTER FISHER, 1906

Fisher, 1906: 1062; McKnight, 1973: 192; Mah, 1998: 66; H.E.S. Clark & McKnight, 2001: 49

Type species: *Gilbertaster anacanthus* Fisher, 1906.

Included species: *G. anacanthus* Fisher, 1906; *G. caribaea* (Verrill, 1899).

Diagnosis: Arms triangular, broad to tapering, narrow (Fig. 3A, E). Disk weakly swollen (Fig. 3A, E).

Tissue thick, pulpy covering abactinal, marginal, actinal plates. Abactinal plates low, polygonal covered by one to 12, closely articulated angular granules

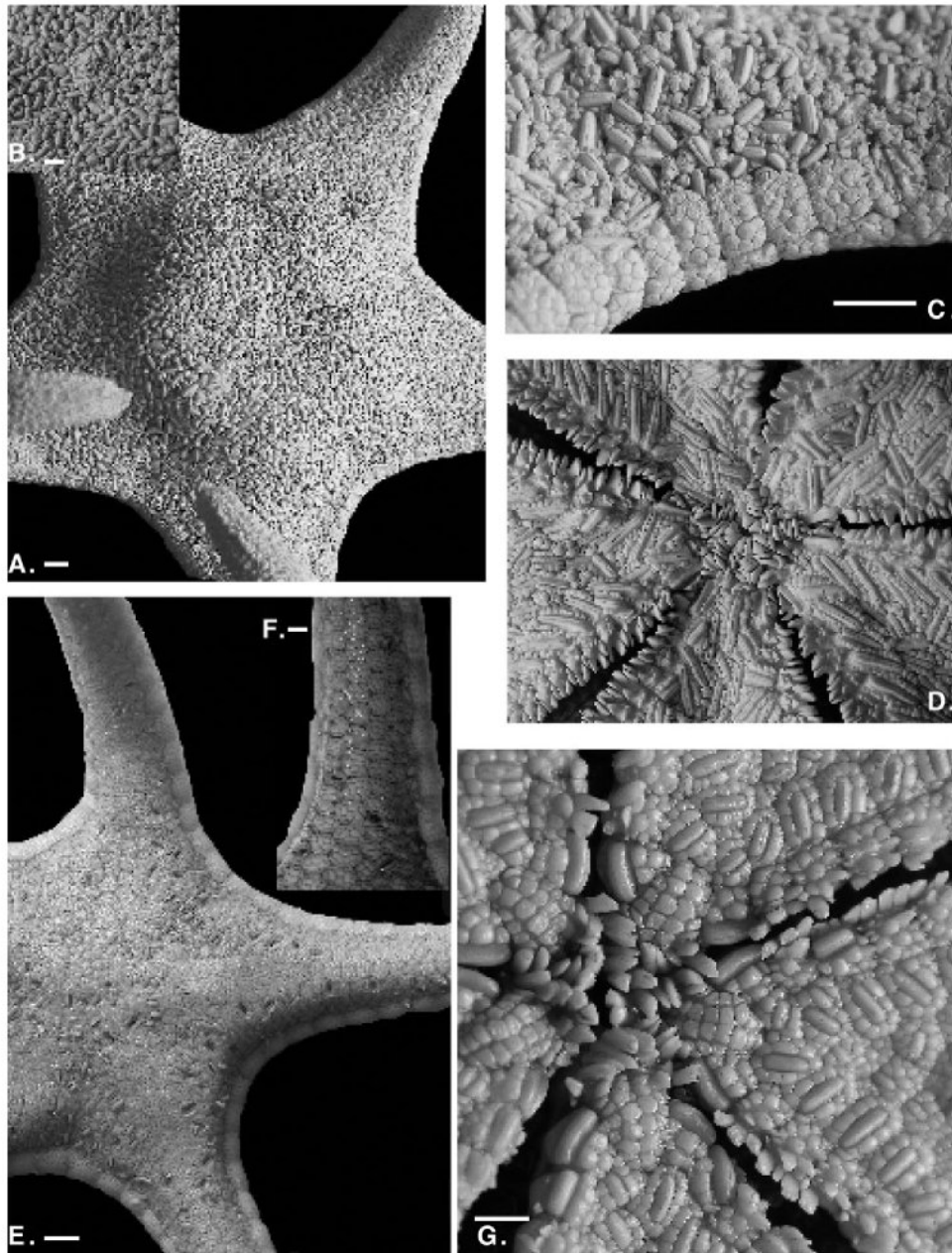


Figure 3. *Gilbertaster caribaea* comb. nov. USNM 1126236. A, abactinal surface; B, close-up abactinal surface; C, dorsolateral surface showing superomarginals; D, oral region. *Gilbertaster anacanthus* holotype USNM 021168; E, abactinal surface; F, close-up abactinal surface; G, oral region. Scale bars: A, C, E = 5 mm; B, F, G = 2 mm.

(Fig. 3A–C, E–G) elongate to round in length, flattened, forming smooth to rough surface texture. Fasciolar grooves shallow. Secondary plates present between abactinal plates (Fig. 3C). Abactinal plates with angular accessories (Fig. 3A–C). Pedicellariae large, bivalved with smooth valves, the length of one to two plates and abundant on abactinal surface (Fig. 3B, C).

Marginal plates, 50–70 per inter-radius (armtip to armtip), squarish in outline with rounded edges, com-

pletely covered by angular granules similar to those on abactinal surface. Variable surfaces smooth (on *G. anacanthus*) to roughened (on *G. caribaea*). Pedicellariae large, bivalve (Fig. 3C) similar to those on abactinal surface on marginal plate surface, often bisecting the width of the plate. Spines absent from superomarginal and inferomarginal plate series (Fig. 3A, C, E). Granules, densely arranged, covering superomarginal and inferomarginal plate series complete (Fig. 3A, B, C, E). Superomarginal and infero-

marginal plates quadrate at inter-radius (Fig. 3C, E). Fasciolar grooves on marginal and actinal surfaces absent. Fringe of accessories on marginal plates poorly differentiated. Superomarginal plates forming prominent dorsolateral fringe (Fig. 3A, E).

Actinal plates covered by one to 15 flattened, polygonal, angular granules. Large bivalve pedicellariae similar to those on abactinal, marginal plate surfaces abundant on actinal plates. Actinal plates with granules, but lacking large spines or spinelets (Fig. 3D, G). Pedicellariae, bivalved, present on plate series at perpendicular angle (Fig. 3A–G), adjacent to ambulacral furrow. Pedicellariae, flat-tong shaped with serrated blades present on actinal plates (Fig. 3D, F). Pedicellariae very abundant, present on raised bases (Fig. 3A–G).

Furrow spines two to four (usually three) blunt, thickened spines, horizontally flattened (*G. anacanthus*) to triangular/quadrate in cross-section (*G. caribaea*) (Fig. 3D, G). Subambulacral spines, one to four, blunt, flattened (Fig. 3D, G). Round to quadrate (*G. anacanthus*) to triangular in cross-section (*G. caribaea*). Pedicellariae, bivalved, enlarged on first ambulacral (similar to others) replacing subambulacral spination (Fig. 3D, G) and sometimes replacing furrow spination. Subambulacral spines smaller in size, more abundant (Fig. 3D, G). Furrow spines round in cross-section, not compressed.

Oral plates covered by ten to 20 flattened, angular, closely articulated granules (Fig. 3D, G), sometimes with enlarged bivalve pedicellariae. Oral plate furrow spines, typically five, flattened to oval in cross-section. Oral region concave (Fig. 3D, G).

GILBERTASTER ANACANTHUS FISHER, 1906

FIGURE 3E–G

Fisher, 1906: 1063; A.M. Clark, 1993: 223; H.E.S.

Clark & McKnight, 2001: 49 (as *Gilbertaster anacanthus*)

McKnight, 1973: 192; A.M. Clark, 1993: 223 (as *Gilbertaster brodiei*)

Occurrence: Hawaiian Islands, Palau to New Zealand. 277–868 m.

Material examined: HOLOTYPE: USNM 21168, Malae Point, Hawaii, 20°6'N, 155°59'W, 463–699 m, coll. USFC *Albatross*, 11.vii.1902 [1 wet spec. $R = 6.5$, $r = 2.2$]; CASIZ 159079, off Kona, 19°38'N, 156°2'W, 670.0 m, coll. Sandra Brooke & Michelle Wood on R/V *Pisces V*, 14.xii.2001 (1 wet spec. $R = 7.3$, $r = 2.2$); CASIZ 159080, Off Kona, 19°38'N, 156°2'W, 868.0 m, coll. Sandra Brooke & Michelle Wood on R/V *Pisces V*, 14.xii.2001 (1 wet spec. $R = 5.2$, $r = 2.2$); CRECH 129, Mutremdu, Palau, 7°16'N, 134°31'W, 277.3 m (910 ft),

coll. P. Colin aboard *Deep Worker* submersible, 6.iii.2001 (1 wet spec. $R = 9.9$, $r = 3.2$).

Description: Arms five. Disk broad, arms long, narrow ($R : r = 2.26–3.0$), distinct from disk.

Abactinal plates tightly abutted, covered by granules, one to six, round to irregularly polygonal to oblong to elongate in outline, forming angular fringe around each (Fig. 3E, F). Carinal series distinct (Fig. 3F). Granules slightly convex to rounded but low and close to disk surface (Fig. 3E, F). Periphery of plate surrounded by four to 12 elongate to rounded-polygonal granules that sit in low concavities on each plate. Plates larger proximally but becoming smaller distally at contact with superomarginal border. Madreporite pentagonal, with well-developed sulci. Secondary plates present but few. Pedicellariae bivalve large (~1.0–1.5 mm in length) and present in irregular cluster all across the abactinal disk surface. Apparently more common on disk but also present in less abundance on distal arm surface. Papulae present radially, absent inter-radially.

Marginal plates quadrate in shape, 18–22 in number (superomarginals and inferomarginals identical in number and appearance), largely flat but weakly convex and covered with granules, 20–70, flush, close-set, convex granules, forming a weakly expressed border around the disk periphery. Marginal plate surface more flattened inter-radially becoming more rounded and more convex distally. Granular covering angular, crowded but other major ornamentation (i.e. spines, etc.) absent from marginal plate surface. Granules form weakly differentiated periphery around marginal plate surface. Marginal fascioles absent (Fig. 3E, F). Superomarginal plate surface with dorsol facing (Fig. 3E), especially on distal arm segment. Pedicellariae, bivalved, uncommonly present on marginal plate surface.

Actinal plates, very tightly articulated, quadrate to rounded in shape, forming three distinct chevrons on actinal intermediate surface (Fig. 3G). Granules present, four to 16 in number, closely abutted and polygonal-oblong to irregular, rounded with low convex appearance in shape (Fig. 3G). Granular cover on actinals flush with those on adjacent inferomarginal plate series. Actinal plate series adjacent to adambulacral plate series each with one enlarged bivalved pedicellariae, decreasing in size proximally to distally, each one flanked by a granular ring, four to 12, enlarged, quadrate (Fig. 3G). Pedicellariae, bivalve, enlarged (~1.0 mm in length), present on several actinal plates, each surrounded by ring of enlarged quadrate granules.

Adambulacral plates quadrate. First adambulacral with giant pedicellariae, bivalved, smooth on each inter-radius, flush with furrow margin, extending

the whole length of the plate (Fig. 3G). Furrow spines, two or three, horizontally flattened, oval in cross-section, becoming reduced to a granule distally. Some adambulacral plates with spines, subequal and very small. These latter spines are observed in conjunction with subambulacral pedicellariae. Subambulacral armature varies. Plates covered by granules, four to six, prismatic to quadrate in cross-section in irregular rows (Fig. 3G). Small granular row present between adambulacrals and proximal actinal plate series. Other plates with large bivalve pedicellariae.

Oral plates slightly convex with furrow spines, five to six triangular in cross-section, largest proximally. Oral plate surface covered by granules similar to others, large, polygonal, flattened, five pairs on each plate.

Colour in life is dark orange to yellow. Fisher (1906) notes one specimen as 'Dull yellow on dorsal surface, brightest on marginal plates, central part of dorsal area with a brownish cast. Actinal surface a pale Naples yellow with a brownish suggestion'.

Habitat description: This species has been observed *in situ* by the Hawaiian Undersea Research Laboratory (HURL) as solitary individuals on soft substratum among round basaltic rocks (C. Kelley, HURL pers. comm., 2009).

GILBERTASTER CARIBAEA (VERRILL, 1899)

COMB. NOV.

FIGURE 3A–D

Verrill, 1899: 174, pl. 28; Halpern, 1970a: 190; Clark & Downey, 1992: 246 (as *Hippasteria caribaea*)

Occurrence: Known from Cumberland Island, Georgia, Savannah Banks, Stetson Banks, off Jacksonville, FL, and off the coast of West End, Grand Bahama. 500–805 m.

Material examined: HOLOTYPE: USNM 18425, Cumberland Island, Georgia, North Atlantic Ocean, 30°58'N, 79°38'W, 538 m, coll. USFC *Albatross*, st. 4041, 5.v.1886 (1 dry spec. $R = 1.8$, $r = 1.0$); USNM 1126236 Jacksonville Lithoherms, 30°31'N, 79°39'W, 553 m, coll. K.J. Sulak, JSL 4683, 10.vi.2004 (1 dry spec. $R = 7.7$, $r = 3.2$); USNM 1124498, Savannah Banks, 31°44'N, 79°05'W, 500 m, coll. S.W. Ross, JSL 4687 12.vi.2004 (1 wet spec. $R = 5.9$, $r = 2.8$); USNM 1126239 Savannah Banks, 31°46'N, 79°12'W, 509 m, coll. C. Morrison, JSL 4905, 30.x.2005 (1 wet spec. $R = 13.3$, $r = 5.1$); USNM 1126238 Stetson Banks, 31°50'N, 77°36'W, 694 m, coll. T. Casazza, JSL 4699, 18.vi.2004 (1 wet spec. $R = 4.3$, $r = 2.6$); MCZ 3806, Florida, off Jacksonville, 796–805 m (435–

440 fathoms), coll. *Atlantis* St. 3782 (1 dry spec. $R = 10.2$, $r = 3.4$). NSU no #. Off coast of West End, Grand Bahama. 27°04'N, 79°19'W, 604 m. JSL II 3698, coll. C. Messing. (1 wet spec. $R = 5.0$, $r = 2.3$).

Description: Arms five. Disk broad, arms short ($R : r = 2.1–2.4$) distinct from disk (Fig. 3A).

Abactinal surface covered by coarse granules, densely packed with no plate surface visible. Granules forming continuous cover, nearly contiguous with superomarginal plate series (Fig. 3A, B). Plates, each with one (exceptionally two or more) large round, tubercular granule(s), surrounded by three to six smaller rounded coarse granules (Fig. 3C). Abactinal plates closely abutting (Fig. 3B) in adult specimens, somewhat less so in smaller individuals (when $R = 4–5$ cm). Papulae single, distributed over most of abactinal surface but absent from narrow triangular area adjacent to contact with superomarginal plate series. Madreporite round with well-developed sulcae, surrounded by 12–15 plates. Pedicellariae large (0.8–2.0 mm in length), bivalve equivalent to three to six granules in relative length evenly distributed over abactinal surface (Fig. 3B, C).

Marginal plates elongate [length (L) > width (W)], largest inter-radially, becoming more equal in size and smaller distally. Marginal plates 40–50 per inter-radius (counted from armtip to armtip) covered by densely packed coarse granules (20–60 per plate) similar to those on abactinal surface. Granules more evenly spaced, less dense in smaller individuals ($R = 4–5$ cm). Plate surface not visible on inter-radial plates with smooth, bare patches present near arm terminus. Granule shape varies from round, hemispherical to polygonal to more oblong (Fig. 3C). Superomarginal granules prominent, strongly convex, not forming even surface with other granules (Fig. 3C). Granules on inferomarginal plates more polygonal, forming close pavement. Pedicellariae absent from marginals on paratype (smaller specimen) but present on holotype (larger specimen) where they bisect the entire width of superomarginal and inferomarginal plates. Distinct groove present around inferomarginal plate contact with actinal intermediate plate surface.

Actinal plates forming irregular chevron-like pattern. Actinal plates adjacent to adambulacral plates all with enlarged bivalved pedicellariae equal to length of plate on which it sits. Approximately six to seven granules flank each valve of these pedicellariae. Largest centrally becoming smallest near the ends of each pedicellariae. Other actinal intermediate plate chevron series more irregular with approximately 60% of plates bearing a large bivalve pedicellariae (Fig. 3D). Holotype with nearly all plates bearing a large bivalve pedicellariae. Remaining plates covered by four to 14 (mean of nine) granules.

One enlarged, convex granule, flanked by four to seven smaller polygonal granules, varying in size. Pedicellariae present closest to mouth and tube foot furrows becoming almost completely absent on plates adjacent to inferomarginal plate series.

Furrow spines, thick, triangular to round-oblong rectangle in cross-section, two to three per adambulacral plate with fewer spines on distal plates (Fig. 3D). One large thick (3–4 × thickness of furrow spines), angular, subambulacral spine, present immediately behind furrow spines. This large subambulacral spine flanked by one to two smaller spines, triangular in cross-section, roughly half the height of the large subambulacral (Fig. 3D). Several thickened, blunt granules, polygonal-triangular in cross-section, five to nine adjacent to the subambulacral spine, similar in size to those on actinal surface. Typically, one enlarged, round granule present adjacent to subambulacrals with other granules irregularly trailing off in size. Distinct groove between adambulacral plates and first adjacent actinal intermediate plate (which bears the large bivalve pedicellariae).

Enlarged triangular spines two, present on oral plate surface projecting into mouth, adjacent to four thick, polygonal spines on the side of each oral plate (Fig. 3D). Oral plate covered by two enlarged subambulacral spines, round to triangular in cross-section, three to four times as thick as the adjacent furrow spines. Smaller, lower polygonal granules, five to seven present on oral plate surface adjacent to enlarged pedicellariae adjacent to the mouth.

Colour in life is yellow-orange.

Biology: *Hippasteria* (= *Gilbertaster*) *caribaea* was measured for reflectance in a bioluminescence study presented by Johnson (2005).

Habitat description: Specimens provided by M. Nizinski were observed as solitary individuals collected on soft substrata. No other organisms were observed at the collection site.

STHENASTER GEN. NOV.

Description: As for species.

STHENASTER EMMAE SP. NOV.

FIGURE 4A–H

Occurrence: Known only from Savannah Banks and off the coast of Jacksonville, FL. 252–501 m.

Material examined: HOLOTYPE: USNM 1124468, Savannah Banks, 31°42'N, 79°07'W, 498 m, coll. T. Casazza, JSL 4902, 26.x.2005 (1 wet spec. $R = 9.6$, $r = 4.7$). PARATYPE-USNM E15539, off coast of Jacksonville, FL, North Atlantic Ocean. 30°31'N, 80°05'W,

252 m (1 dry spec. $R = 9.3$, $r = 4.4$); PARATYPE-USNM 1124469, Savannah Banks, 31°44'N, 79°05'W, 501 m, coll. C. Caddigan, JSL 4900, 22.x.2005 (1 dry spec. $R = \sim 9.2$, $r = 4.8$).

Etymology: Genus is derived from *sthenos*, Greek for 'strength' and *-aster* for 'star.' Specific epithet is named after Dr Emma Bullock in honour of her contributions to the geochemistry of meteorites and asteroids.

Description: Arms five, triangular in outline. Disk large, broad, swollen, especially in wet specimen. Body stout, thick (Fig. 4A, B).

Abactinal plates round to polygonal to oblong in outline with numerous interspersed secondary plates (Fig. 4F) embedded in a thick, pulpy tissue forming heavily thickened abactinal body wall (Fig. 4A). Plates with high-aspect; mound-like in shape, forming deep but open channels between plates (Fig. 4A, E). Abactinal plates are covered with two to ten blunt to conical spine-like granules, usually forming a periphery around plate edge with only one or two granules/spines centrally located. Some plates bear enlarged conical, spine-like granules, surrounded by smaller blunt spinelets. Large abactinal clam-shell like pedicellariae present, each with nine to 12 interlocking teeth per valve (Fig. 4E). Pedicellariae located centrally on plate surface varying in size from one-third to three-quarters of plate diameter, flanked by spine-like granules. Pedicellariae occurring unevenly over abactinal surface, becoming densely concentrated in some areas but absent from others. Madreporite sunken, bordered by seven to eight abactinal plates. Papulae, small, four to six, interspersed between plates.

Marginal plates wide ($W > L$), 42–45 per inter-radius (from armtip to armtip), which become smaller and with more equivocal dimensions distally adjacent to terminal. Large spines absent from marginal plates series. Fasciolar channels present between marginal plates, relatively deep (Fig. 4H). Supermarginals facing laterally, correspond 1:1 to inferomarginals along most of series with one to two plates irregularly offset, possibly because of sublethal predation. Supermarginal plate surface convex, bare except for 20–35 widely spaced, sharp, conical spinelets, which are most densely concentrated ventrally on plate at contact with inferomarginal plate (Fig. 4H). One to two relatively small clam-shell like pedicellariae with interlocking teeth present on nearly every marginal plate but regularly present, adjacent to inferomarginal contact, irregularly present closer to contact with abactinal surface. Periphery of each plate with 15–40 small evenly spaced conical spinelets, which occur more densely at contact with inferomarginals.

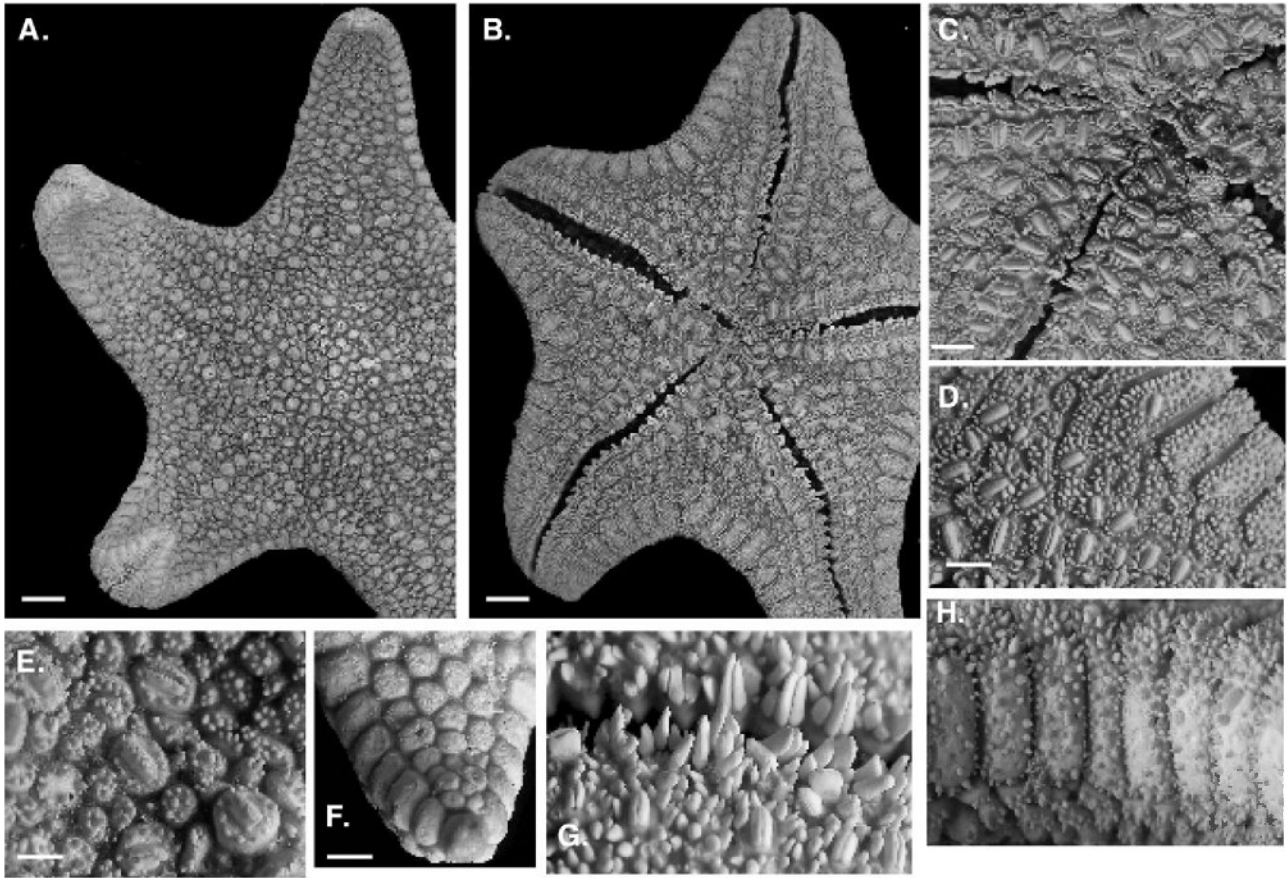


Figure 4. *Sthenaster emmae* gen. et sp. nov. USNM 1124468. A, abactinal surface; B, actinal surface; C, oral region; D, actinal-inferomarginal contact; E, close-up of abactinal surface showing pedicellariae; F, close-up of abactinal plates on arm tip; G, adambulacral furrow spines; H, marginal plates – lateral facing of superomarginal plates. Scale bars: A, B = 10 mm; C–H = 5 mm.

Inferomarginal plates with ventral facing and more densely covered by ten to 70 irregularly sized conical to blunt spinelets. Higher number of larger, conical, more pointed spinelets present closer to superomarginal contact. Higher numbers of spinelets present inter-radially decreasing distally corresponding with smaller inferomarginal plate size. Pedicellariae, one to four, typically two, identical to the type on superomarginals present on inferomarginals facing ventrally. Terminal plate round, bulbous.

Actinal intermediate plates, similar in size, shape to abactinal plates with well-developed fasciolar channels running between plates (Fig. 4C, D). Actinal plate series adjacent to adambulacral plate series with large pedicellariae nearly equal to size of plate on which it sits (Fig. 4C, D), teeth poorly developed to absent relative to those on abactinal plates. Pedicellariae on actinal series adjacent to adambulacral plates occur with less frequency distally along the arm with some smaller actinal plates adjacent to arm tip with pedicellariae absent, bearing only three

to six spinelets. Actinal pedicellariae occur most heavily adjacent to mouth, becoming less common to absent adjacent to inferomarginal plate contact. Pedicellariae on each actinal plate surrounded by 20–35 sharp spinelets, some round, some triangular to polygonal in cross-section (Fig. 4C, D). Actinal plates adjacent to inferomarginal plate series covered with four to 30 sharp, irregularly sized, conical granular spines. Some with polygonal to triangular in cross-section. Oral cavity sunken (Fig. 4B, C).

Adambulacral furrow spines blunt tipped, three to four per plate, triangular to oblong ovate in cross-section in weakly convex series (Fig. 4G). Distinct grooves between adambulacral plates. Central spines longest and thickest with spines shortest on ends. Subambulacral spines three in two series. Subambulacral spine series adjacent to furrow spines somewhat shorter than furrow spines but comparable in thickness, round to oval in cross-section (Fig. 4G). Subambulacral spine series farthest away from furrow spines shortest, with central

spines only slightly less thick than furrow spines with smallest spines located on ends of second subambulacral series. Distinct fasciolar channel separates adambulacral plates from actinal intermediate plates.

Oral plates with four to six furrow spines. Oral plate surface with three to four spines per plate (six to eight total on paired oral plates) with one to three spines projecting into oral opening (Fig. 4C). Spines triangular to flattened triangular in cross-section, most are comparable in length to furrow spines but sometimes with one or two that are similar to granular spines.

Colour in life is orange.

Habitat description: The holotype was collected on hard substrata covered by the gorgonian *Eunicella modesta* (Verrill, 1883). Other unidentified gorgonians, the scleractinian *Lophelia pertusa*, sponges, and coral rubble were observed at the collection site. The paratype was collected from Savannah Banks on hard substrata where various gorgonians, sponges, scleractinian corals, and coral rubble were also present.

CRYPTOPELTASTER FISHER, 1905

Fisher, 1905: 311; 1911: 237; Spencer & Wright, 1966: U58; A.M. Clark, 1993: 251.

Codoceo & Andrade, 1981: 379 (as *Criptopeltaster*)

Type specimen: NEOTYPE: USNM E 33356, south of Santa Cruz Island, Channel Islands, California, 33°55'30"N, 119°41'30"W, 486 m, coll. USFC *Albatross*, 7.ii.1889.

Included species: *Cryptopeltaster lepidonotus* Fisher, 1905 (*Cryptopeltaster philippii* is now a synonym of *C. lepidonotus*).

Diagnosis, distribution, and characters: As per species.

CRYPTOPELTASTER LEPIDONOTUS FISHER, 1905

FIGURE 5A–E

Ludwig, 1905: 138 (as *Hippasteria pacifica*)

Fisher, 1905: 311; 1911: 237; Lambert, 1978a: 9; Maluf, 1988: 34, 118; Clark, 1992: 251 (as *C. lepidonotus*)

Codoceo & Andrade, 1981: 379 (as *C. philippii*)

Pawson & Ahearn, 2001: 42 (as *Cryptopeltaster* cf. *lepidonotus*)

Occurrence: Chile to Aleutian Islands (Alaska), including records from Rodriguez Seamount, Santa Cruz, California and British Columbia 188–1244 m.

Material examined: CASIZ 108628, Monterey, CA off Point Sur, 914.0 m (500 fms), coll. M. Eric Anderson, 7.vi.1977 (1 wet spec. $R = 4.4$, $r = 1.7$); CASIZ 11828, Oregon, off the coast, 47°15'N, 124°53'W, 188–216 m, coll. Roger N. Clark aboard R/V *Miller Freeman*, 22.x.1996 (1 dry spec. $R = 13.1$, $r = 5.2$); USNM 1129943, Rodriguez Seamount, 34°2'N, 121°4'W, 667.3 m, coll. D. Clague, on board ROV *Tiburón*, 29.iv.2004 (1 wet spec. $R = 9.6$, $r = 6.1$); USNM E47396, Washington, north-west of Grays Harbor, 47°10'N, 124°57'W, 195–242 m, coll. R. N. Clark on board R/V *Miller Freeman*, 22.x.1996 (2 dry specs. $R = 9.8$, $r = 3.8$; $R = 10.8$, $r = 4.8$); USNM E51296, North of Seymour Island, Galapagos Islands, 00°21'S, 90°15'W, 599 m (1964 ft), coll. C. Baldwin & J. McCosker, *Johnson Sea Link II*, 26.vii.1998 (1 wet spec. $R = 8.1$, $r = 3.5$).

Description: $R : r = 2.3–2.6$, arms triangular, disk broad.

Abactinal surface covered by large, coarse, flat, angular granules, densely abutting around spines and pedicellariae. Abactinal plates largest proximally becoming smaller distally adjacent to contact with superomarginal plate series. Spines conical, present, large, numerous on abactinal surface with granules forming flattened, angular skirt around each spine base. Spines or pointed granules present on nearly every abactinal plate, especially those on radial regions, but are nearly absent distally on regions adjacent to superomarginal series. Pedicellariae large (length equivalent to about seven to nine granules), bivalved. Secondary plates present sometimes covered by granules, one or two, similar to others.

Marginal plates, 40–55 per inter-radius (from terminal to terminal), each covered with granules, densely arranged polygonal, quadrate to angular in shape. Number of marginal plates increases as adult size increases. Granules number 20–30 around each marginal plate periphery forming convex contact with abactinal and actinal surfaces. Granules on central marginal plate surfaces number 20–40. Granules, smooth, angular in outline, flattened to convex and often with a pointed tip, distributed evenly throughout surface. Spines, one to three (typically one), short, conical to tubercular present at lower end of each superomarginal plate adjacent to contact with inferomarginal plates. Spines present on inferomarginals inter-radially, becoming lower and more tubercular distally along arms. Granules becoming more flush with others distally on arms.

Actinal intermediate areas covered with similar flattened, closely abutting, angular granules, almost all with spines or tubercles. Spines, conical single and prominent, on each actinal intermediate plate number highest proximal to mouth. Spines, smaller

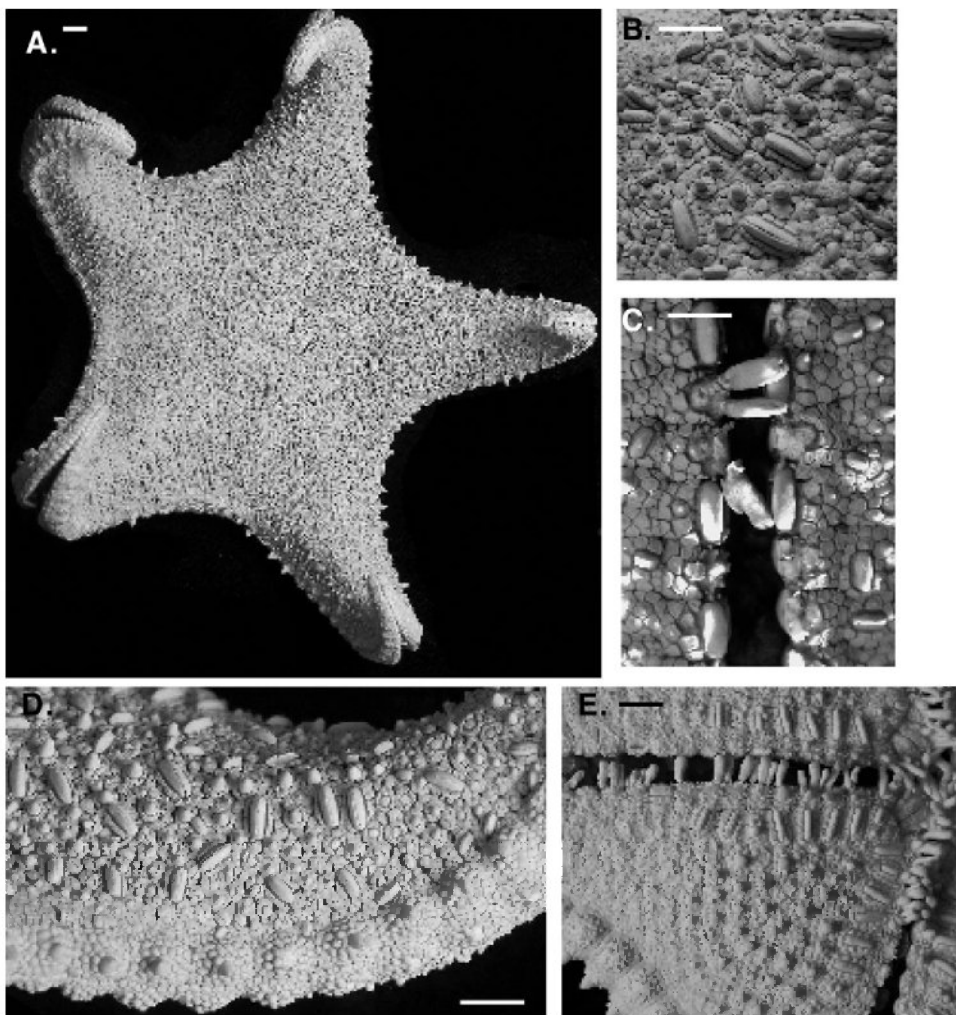


Figure 5. *Cryptopeltaster lepidonotus* neotype USNM 33356. A, abactinal surface; B, close-up of pedicellariae and large angular granules; C, adambulacral furrow spines and bivalve pedicellariae. USNM E47396; D, lateral view showing superomarginal plate series; E, actinal surface showing furrow spines, pedicellariae, and actinal spines and granules. Scale bars: A, D, E = 5 mm; B = 4 mm; C = 3 mm.

and disappearing distally (adjacent to inferomarginal plate contact). Large bivalve pedicellariae (length about 3.0 mm each) in a distinct linear series adjacent to adambulacral plate series, each surrounded by 11–15 angular granules. Approximately five to seven chevrons of actinal plates per inter-radius.

Adambulacral plates primarily occupied by two to three (primarily three) furrow spines per plate, but a large bivalve or trivalve pedicellariae will replace these spines on the first postoral adambulacral plate and irregularly if infrequently on the furrow spines. Furrow spines thick, club-shaped and round in cross-section. Each paired oral plate with six to eight angular granules along median axis but with four to six granules covering remaining oral plate surface. Furrow spines, three to four on each oral

plate. Spine, thickened, oblong in cross-section on the surface of each oral plate facing into the mouth.

Holotype: The original holotype for this species has been lost (C. G. Ahearn, pers. comm., 2007). A neotype (USNM 33356) from part of Fisher's original voucher series, collected near to the original type locality is herein designated as its replacement. Codoceo & Andrade (1981) were the last authors to refer to the holotype of *C. lepidonotus*.

Synonymy of C. philippii: A new Chilean species, *Cryptopeltaster philippii* was described by Codoceo & Andrade (1981) who distinguished *C. philippii* from *C. lepidonotus* on the basis of fewer pedicellariae on

the body surface, an undivided madreporite, and fewer supero- and inferomarginal plates per inter-radius. *Cryptopeltaster* from the Galapagos (USNM E51296) corresponds to this description (Pawson & Ahearn, 2001).

These characters fail to differentiate between these two species and strongly support the synonymy of *C. philippii* into *C. lepidonotus*. Based on the greater number of specimens available, it is determined that the characters vary across the range of the genus and amongst differently sized individuals. Pedicellariae number is variable across different individuals and does little to differentiate between any two specimens. The madreporite was atypically divided by a seam in the holotype (Fisher, 1911: pl. 47, fig. 1). Other specimens clearly show this to be unique to that specimen making this character individually variable and unhelpful as a diagnostic character. Finally, the number of marginal plates in *Cryptopeltaster* increases in larger specimens. The Galapagos specimen (USNM E51296) has approximately 42 marginal plates but is smaller ($R = 8.1$ cm) than specimens collected farther north. A small ($R = 4.4$ cm) specimen from off Point Sur, California, which otherwise corresponds to the description of *C. lepidonotus*, also had 42 marginal plates. *Hippasteria pacifica* Ludwig, 1905 from Mexico was synonymized with *C. lepidonotus* by Fisher (1911) and was represented by a smaller specimen ($R = 4.8$ cm) with approximately 40 marginal plates. Codoceo & Andrade (1981) did not include the size of the holotype, which is now apparently lost or unavailable (requests for material from the Museo Nacional de Historia Natural in Santiago, Chile have gone unanswered).

'*Cryptopeltaster lepidonotus*' is misidentified in Imaoka *et al.* (1991). The species pictured in their monograph features the oval marginal plates characteristic of *H. californica* and other '*Nehippasteria*' type hippasterines but absent in *Cryptopeltaster*. The polygonal granules, enlarged pedicellariae, and furrow spine replacement by pedicellariae are also absent from the specimen figured in their monograph.

EVOPLOSOMA FISHER, 1906

Fisher, 1906: 1065; Koehler, 1909: 96; Spencer & Wright, 1966: U58; A.M. Clark, 1993: 253.

Type species: Evoplosoma forcipifera Fisher, 1906

Diagnosis: Body strongly swollen, arm narrow.

Tissue with pulpy texture covers abactinal plates (seen more clearly in wet specimens). Abactinal fasciolar grooves shallow. Secondary plates present. Abactinal plates, flat and platform-like. Carinal series poorly distinguished. Abactinal plates tightly articu-

lated. Large spines or spinelets on abactinal, superomarginal, inferomarginal plate, and actinal series. Accessories on superomarginal and inferomarginal surface widely spaced.

Superomarginal plate series with lateral facing. Superomarginal and inferomarginal plates at inter-radius quadrate in shape. Spinelets present on both marginal plate series. Fasciolar grooves between marginal plate series shallow. Accessories around superomarginal and inferomarginal plate edge poorly differentiated. Actinal fasciolar grooves shallow. Actinal spinelets present. Furrow spines compressed, angular in cross-section, pedicellariae with serrated valves.

Included species: *E. augusti* Koehler, 1909; *Evoplosoma claguei* sp. nov.; *E. forcipifera* Fisher, 1906; *E. scorpio* Downey, 1982; *Evoplosoma timorensis* Aziz & Jangoux, 1985a; *E. virgo* Downey, 1982; *Evoplosoma voratus* sp. nov.

EVOPLOSOMA CLAGUEI SP. NOV.

FIGURE 7A–F

Occurrence: Known from CoAxial Cone and Rodriguez Seamount and off Islas Tres Marias in the North Pacific. 730–2405.6 m.

Material examined: HOLOTYPE: USNM 1124507. Rodriguez Seamount 33°57'N, 121°8'W, 1842.8 m, coll. ROV *Tiburón*, Sta. T-629, A8, 14.x.2003 (1 wet spec. $R = 9.9$, $r = 2.6$ cm). PARATYPES: SIO E2440, Islas Tres Marias, Mexico. 21°52'N, 106°12'W, 730 m, coll. R. Wisner, 18.v.1959 (1 wet spec. $R = 8.3$, $r = 2.6$).

USNM 1136366 CoAxial Cone Seamount, 46°30'N, -129°35', 2405.6 m. Coll. ROV Doc Ricketts, Sta. D77-A3. 30 Aug 2009 (1 wet spec. $R = 11.1$, $r = 2.7$ cm).

Etymology: This species is named after Dr David Clague, MBARI geologist and primary investigator of the cruise on which this species was collected.

Description: Disk pentagonal, with wide inter-radial almost straight lateral sides between arms. Arms elongate and triangular in outline, distinctly set off from the disk appearing to be attached at the disk corners. Abactinal surface inflated, swollen in life.

Abactinal plates rounded polygonal to completely round surrounded by 15–28 small blunt angular accessory granules forming plate periphery. Each plate with one prominent accessory that varies in shape from spherical tubercle to short, pointed granule to large conical (bullet-shaped) spine. Smaller specimens ($R = 8.3$) lack well-developed spines but have several pointed, bullet-shaped tubercles. Largest spines are about 2.0 mm in length and appear con-

sistent in size across the abactinal surface. Plates bearing large spines, especially those on the arms, are typically bare aside from accessory granules, but smaller plates may be completely covered by smaller accessory granules. Pulpy membrane present over surface, obscuring granulation and plate surface near periphery of disk at contact with marginal plates. Madreporite convex, swollen with shallow sulci present on surface. Abactinal surface on arms is sharply distinct from plates on disk (Fig. 7C). Abactinal plates larger, approximately six plates across from superomarginal to superomarginal, narrowing to one to two plates at distal end of arm. Each plate with a large, pointed conical spine per plate. Spine-bearing plates are bare except for periphery of 20–30 pointed granules on each plate (Fig. 7C). Spaces between abactinal arm plates covered by flattened, quadrate granules. Pulpy membrane present but not as strongly expressed and difficult to ascertain on dry specimens.

Marginal plate series face laterally, 58–60 plates per inter-radius (armtip to armtip) in the larger specimen ($R = 9.9$) and 50–54 plates in the smaller specimen ($R = 8.3$). Quadrate with rounded edges, plates wider distally ($W > L$) becoming more equivocal [$L = W$] inter-radially. Plates slightly convex, bare except for spines, and one to four tubercular granules present infrequently. Superomarginals slightly offset relative to inferomarginals. One to four large, conical to chisel-shaped spines per plate. Spines (three to four) and tubercles (one to five) present with higher numbers inter-radially. Spine number decreasing distally to one to two spines distally. More weakly developed spines on smaller specimen, with one to five bullet-shaped granules/tubercles present on plate surface. Single spines on inferomarginal plates form a distinct linear fringe. Pointed granules, 55–65 total, form periphery on marginal plates with approximately ten per side in contact with other marginal plates, approximately 15–18 per contact with abactinal surface. Terminal plate smooth but with three conical spines, two on distalmost tip, one on abactinal surface.

Actinal plate, chevron-like pattern is irregular with actinal plate series adjacent to adambulacral series very elongate, approximately three to four times the length of those in the centre of the actinal intermediate areas and angular in shape. Periphery of these plates covered by 13–40 quadrate granules, approximately 20 per side. Approximately 24 per inter-radius with 12 per side. Actinal plates restricted to disk, do not extend onto arms. Remaining actinal plates on disk approximately 25 per inter-radius, circular to irregular in shape, and size but becoming smaller adjacent to contact with inferomarginal plate series. Actinal plates with one to four large, conical spines and/or short, tubercular granules one each plate.

Accessory number varies with plate size. Actinals plates elongate with up to four spines and/or granules whereas smaller, circular plates with single spine.

Adambulacral plates elongate. Furrow spines four to six. Six proximally and decreasing in number distally. Nine to ten furrow spines on first adambulacral plate. Furrow spines flattened, paddle like to triangular in cross-section many with roughened, worn down ragged tips. Degree of wear varies from spine to spine but seems more pronounced on proximal spines. Subambulacral ornament composed of a single large clam-shell to paddle-shaped pedicellariae proximal on the adambulacral and an extremely thickened, large spine, many with pronounced club-like to almost lobate head with worn tip sometimes with pronounced striations. Ambulacral and subambulacral series flanked by ten to 15 round, hemispherical granules varying in size. Largest adjacent to subambulacral, becoming smaller and flatter adjacent to actinal inter-radial regions. Oral plates with four thick oral spines (quadrate in cross-section) projecting into mouth (two per plate) and four to five on surface of oral plate at apex of inter-radius. These latter spines are thick and round to quadrate in cross-section. Spines have worn tips with striations. Region between the oral plates and remainder of the actinal intermediate plates is covered by flattened, round granules, densely packed, similar to those adjacent to the subambulacral plates.

Colour in life was orange-reddish.

EVOPLOSOMA VORATUS SP. NOV.

FIGURE 8A–E

Occurrence: Known from Davidson Seamount, 2669.9 m.

Material examined: HOLOTYPE: USNM 1124506, Davidson Seamount, 35°37'N, 122°49'W, 2669.9 m, coll. J. Barry, L. Lundsten, Sta. T-947-A10, 2.ii.2006 (1 wet spec. $R = 8.4$, $r = 2.7$).

Etymology: The epithet for this species refers to the Latin *voratus* which means to 'greedily devour' in reference to its observed feeding habits on deep-sea coral.

Description: Arms tapering, slender but gradually extending from disk. Disk, swollen more pentagonal with relatively lateral to curved inter-radial arcs.

Abactinal surface with weakly developed pulpy surface with abactinal surface on arms appearing more pulpy. Abactinal plates round to polygonal becoming smaller and less round distally near contact with superomarginal plate series but larger distally, especially on arms. One to four plates across distance

of arm between superomarginal plate series. Abactinal plate surfaces mostly bare with short, stubby conical tubercles. Plates with tubercles not very abundant, only about four to six per arm base on disk. Each plate with ten to 30 peripheral rounded granules that are small and rounded to quadrate in cross-section. Region adjacent to madreporite (about 0.75×1.0 cm area) covered with densely packed, large, round granules about twice the size of granules on the abactinal surface and embedded in the pulpy tissue present on the body wall. Madreporite is oval-shaped with deeply etched sulci. Peripheral granules surround madreporite with some granules two to three times as large as others. One plate with two to four large granules on one end of madreporite. Paddle-shaped pedicellariae uncommonly scattered over surface, approximately one or two for every five to seven plates.

Marginal plates, bare with a single large, conical spine on most plates, arranged in linear series becoming smaller to absent on distalmost six or nine superomarginal plates. Several spines, especially along the arms, with four to six short, spiny granules at the base of each spine that are absent distally. Spines continue along all inferomarginal plates up to practically the terminal plate. Both marginal plate series covered by skin, which is difficult to observe in dry specimens. Pedicellariae small, tong-like present irregularly on superomarginals and inferomarginals, especially inter-radially. Peripheral granules rounded, 40–60 per plate, including ~ten per side adjacent to other marginal plate and ~25 per side adjacent to abactinal and actinal surface. Superomarginal and inferomarginal offset from one another and each series with different overall dimensions. Superomarginals number 44–45 from armtip to armtip, more elongate ($L > W$), becoming almost ovalate. Inferomarginals number 54–55 from armtip to armtip, more quadrate ($L = W$) overall. Superomarginal plate contact with abactinal surface, strongly convex, oval-like especially along the base and along the arm. Inferomarginal with more gently curved contact with actinal intermediate plates.

Actinal intermediate plates in approximately three to four chevron-like patterns but in very jumbled, irregular, unclear series present only on disk, ending at arm base. Plates quadrate to irregular in shape and bare with no spination or surface accessories with eight to 25 peripheral granules save for irregularly occurring paddle-like pedicellariae. Pedicellariae, one to six, present in actinal intermediate region.

Adambulacral plates elongate, with typically one (exceptionally two) large paddle-like to rectangular pedicellariae sitting on plate always closest to mouth adjacent to enlarged, thickened subambulacral spine that sits distal to mouth. Approximately six to eight

large granules on periphery of adambulacral plates in contact with actinal intermediate plates. Subambulacral spines up to two to three times the thickness of furrow spines with blunt to conical tips. Pedicellariae begin to occur on first adambulacral, becoming less regular on distal adambulacral plates. Furrow spines, compressed, quadrate to oval in cross-section, four to six in number, five on average, with middle spines tallest, shortest spines on the ends. Furrow spine tips darkened brown sometimes roughened and jagged. First adambulacral with six to seven furrow spines, significantly thicker with more jagged tips than other furrow spines.

Oral region concave with approximately 13–15 compressed furrow spines on each oral plate. Furrow spines, flattened and blade-like, one to two present at plate apex, the largest of which pairs off with its twin on the other oral plate and forms a closely articulated array of spines over the mouth. Oral plate surfaces appear bare save for soft, pulpy tissue covering approximately eight to 12 plates through which two to four short granules emerge.

Colour in life of the holotype was deep-brick red, which remained almost two weeks following preservation in 75% ethanol.

Observed *in situ* apparently feeding on *Trissopathes pseudotristicha* (Cladopathidae, Antipatharia).

EVOPLOSOMA AUGUSTI KOEHLER, 1909

Koehler, 1909: 96; Clark, 1993: 253

Occurrence: Indian Ocean-Laccadive Sea ($6^{\circ}31'N$, $79^{\circ}38'E$). 733 m (401 fms).

Comments: The type specimen of this species could not be located at the Museum national d'Historie naturelle, Paris, France and inquiries to the Calcutta Museum went unanswered. It is presumed lost.

EVOPLOSOMA FORCIPIFERA FISHER, 1906

Fisher, 1906: 1065; Clark, 1993: 253

Occurrence: Hawaiian Islands, east of Kauai Island, $48^{\circ}S$ $15^{\circ}W$. 929–1247 m (682–508 fms).

Comments: The specimen image of *E. forcipifera* from Trego (2008) lacks abactinal spination and shows quadrate marginals abutting along the midradius, a character absent from *Evoplosoma*, indicating that the specimen described in this paper is misidentified, invalidating Trego's (2008) range extension for this

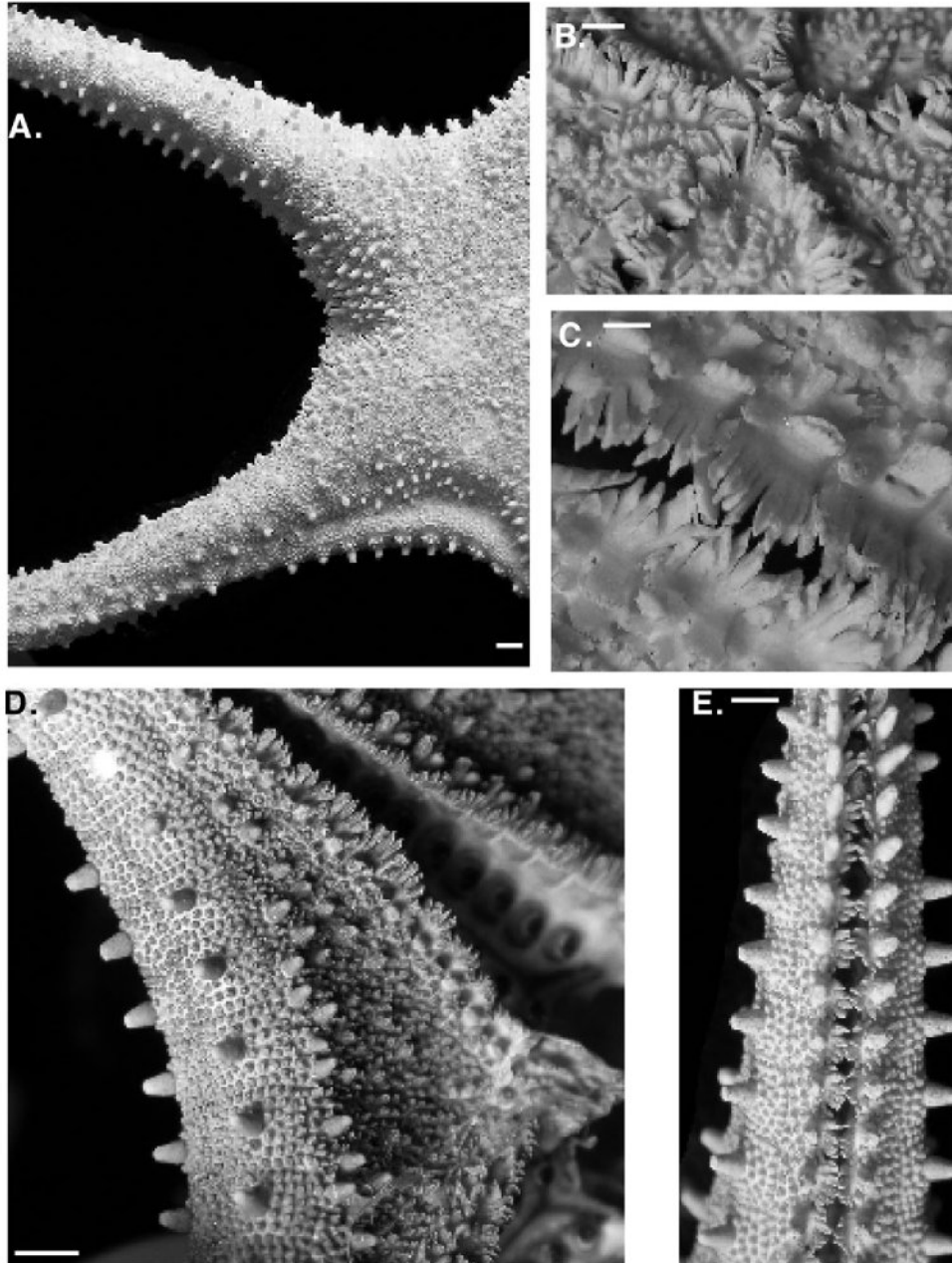


Figure 6. *Evoplosoma scorpio* USNM E23623. A, abactinal surface of disk and arms; B, actinal surface proximal to mouth; C, furrow spines and pedicellariae. USNM E50539; D, actinal intermediate surface region, showing adambulacral and furrow spination; E, adambulacral and furrow spination along actinal arm surface. Scale bars: A = 3 mm; B–E = 2 mm.

species. The holotype for this species is missing from the USNM collections (Ahearn, 1995).

EVOPLOSOMA SCORPIO DOWNEY, 1981

FIGURE 6A–E

Downey, 1981: 561; Gage *et al.*, 1983: 280; Clark & Downey, 1992: 242; Clark, 1993: 253.

Occurrence: South-west Rockall Trough to north-eastern European Basin (48.5°N, 10°W) extended

herein to off Delaware 38°45'N, 72°40'W. 1600–2105 m.

Material examined: USNM E50539, off Delaware, North Atlantic Ocean, 38°45'N, 72°40'W, 2105 m, coll. Lamont-Doherty Geological Observatory, DSRV *Alvin*, 15.vii.1981 (1 dry spec. $R = 5.5$, $r = 1.8$); USNM E23623, off Ireland, North Atlantic, 55°12'N, 15°50'W, 1900 m, coll. J. Gage, R/V *Challenger* (1 dry spec. $R = 8.2$, $r = 2.4$).

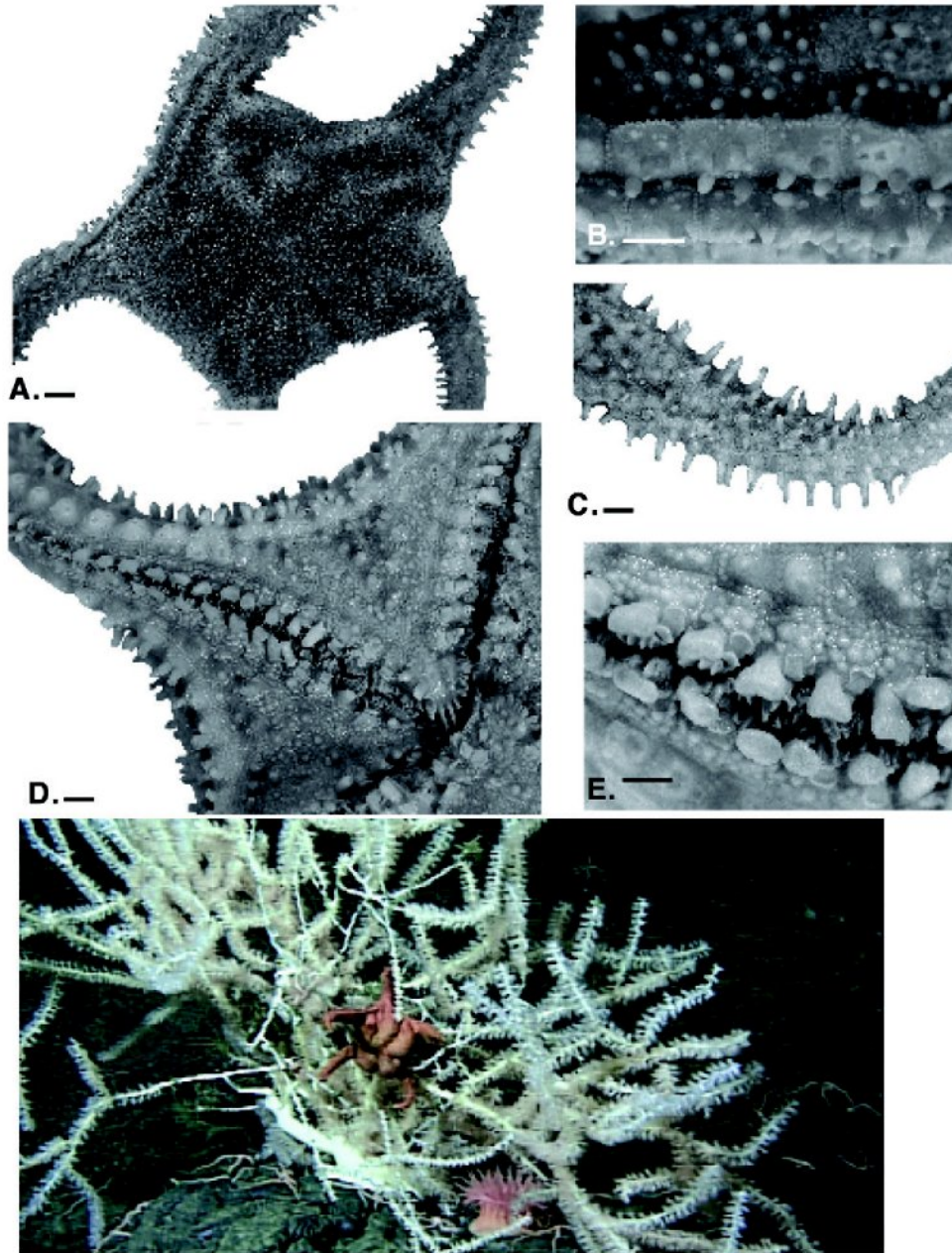


Figure 7. *Evoplosoma claguei* sp. nov. USNM 1124507. Holotype. A, abactinal surface; B, close-up showing abactinal plates, spines, and marginal series; C, abactinal plates on arm surface; D, actinal surface; E, close-up of furrow spines and adambulacral armature; F, *In situ* observation of *Evoplosoma* (cf. *E. claguei*) feeding on *Keratoisis* from Rodriguez seamount (dive 662-02, at 1842 m). Scale bars: A, D = 5mm; B, C, E = 3 mm; F = 5 cm.

EVOPLOSOMA TIMORENSIS AZIZ & JANGOUX, 1985
Aziz & Jangoux, 1985a: 263; Clark, 1993: 253

Occurrence: East Timor Region, Malaysia, 8°50.2'S, 127°2'E. 883 m.

Material examined: None.

EVOPLOSOMA VIRGO DOWNEY, 1982
FIGURE 9A–D

Downey, 1982: 772; Clark, 1993: 253

Occurrence: Gulf of Mexico, 2056 m.

Material examined: HOLOTYPE: USNM E24285, Gulf of Mexico, North Atlantic Ocean, 26°08'N,

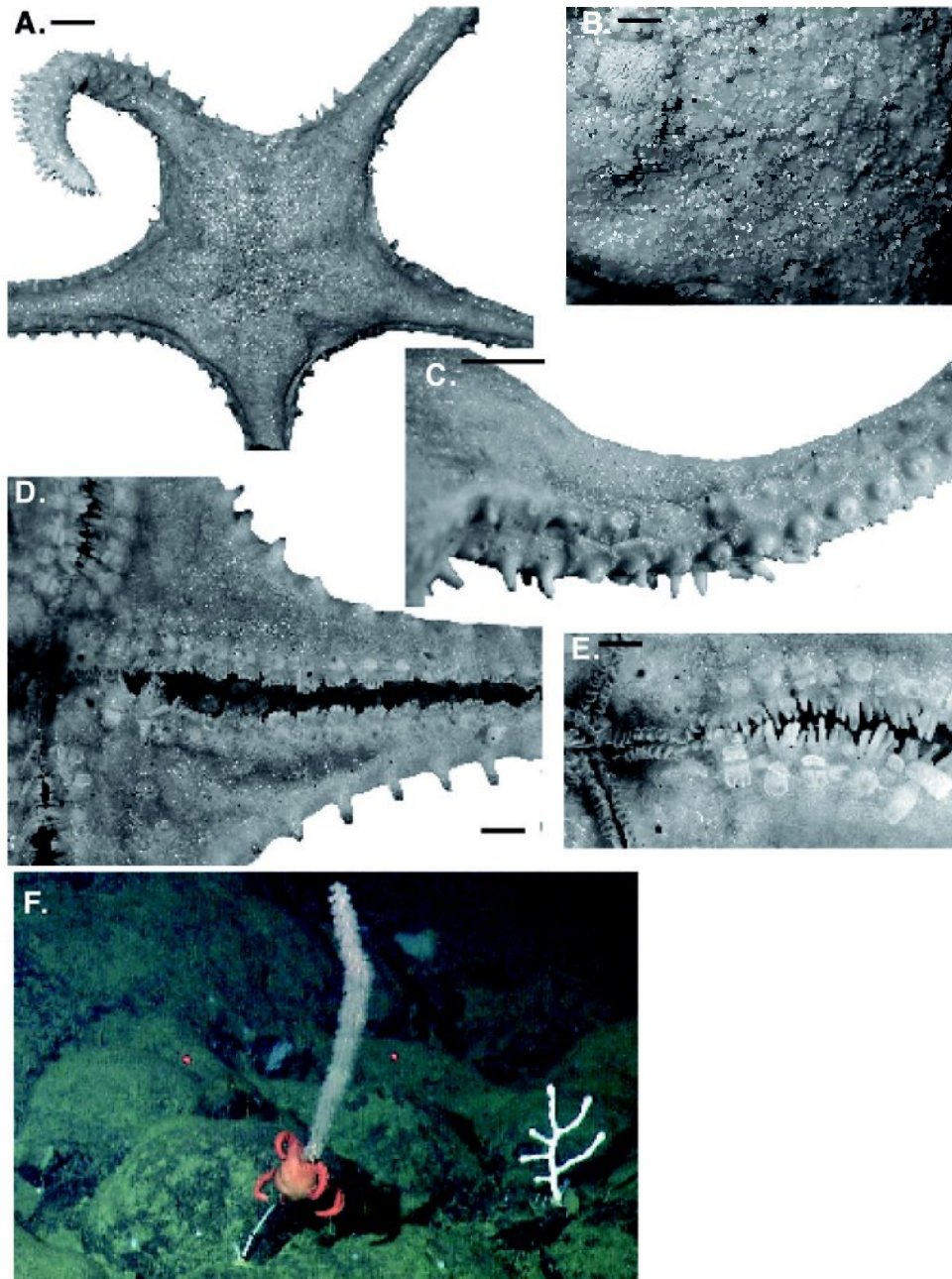


Figure 8. *Evoplosoma voratus* sp. nov. USNM 1124506. A, abactinal surface; B, close-up of abactinal plates and madreporite; C, lateral view of marginal plates; D, oral surface; E, close-up of furrow spines and adambulacral armature; F, *in situ* video of *E. voratus* feeding on *Trissopathes pseudotristicha* on Davidson Seamount. Two circular dots (lights) are 29 cm. Scale bars: A, B, D, E = 3 mm; C = 6 mm.

92°43'W, 2056 m (1124 fms), coll. W. Pequegnat, 30.vii.1971 (1 dry spec. $R = 11.5$ cm, $r = 3.3$ cm).

EVOPLOSOMA SP. 1

Fujikura, Okutani & Maruyama, 2008: 272 (as *Goniasteridae* gen. et sp. fig. 22.19)

Occurrence: Off Java (Indonesia). 2186 m.

Comments: This species was unidentified in Fujikura *et al.* (2008) but can be placed within the genus *Evoplosoma* based on its arm and disk shape as well as apparent surface spination.

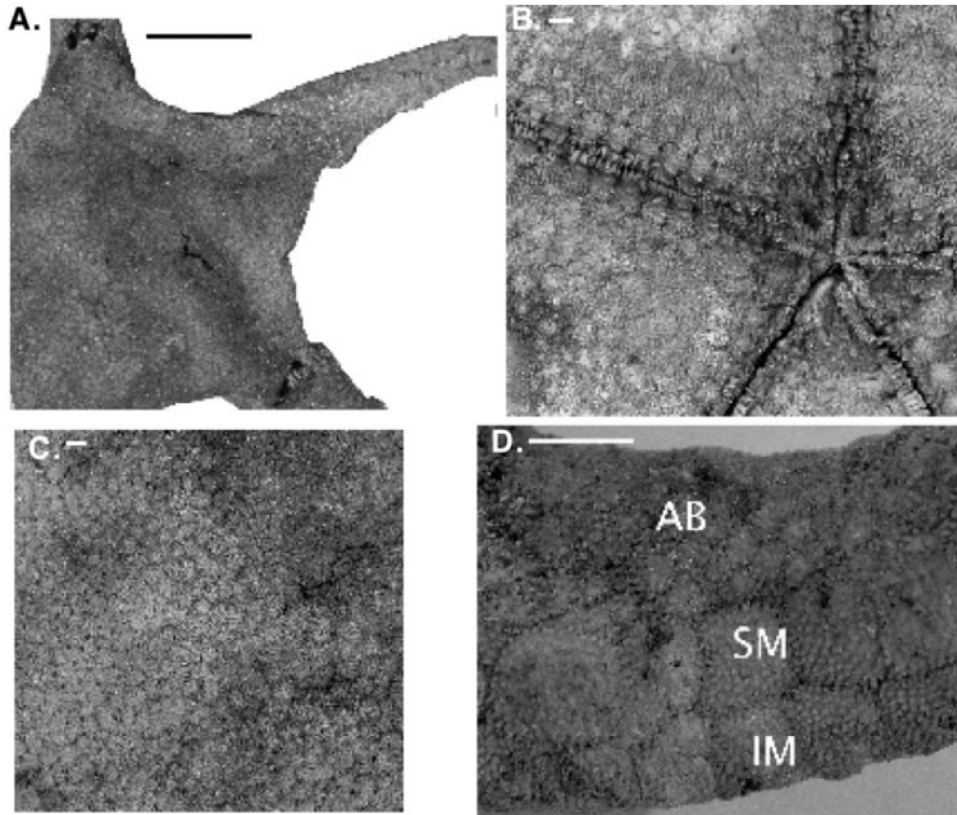


Figure 9. *Evoplosoma virgo* USNM E24285 HOLOTYPE. A, abactinal surface; B, oral surface showing furrow and adambulacral armature; C, close-up of abactinal granules; D, dorsolateral view showing abactinal plates (AB), superomarginal (SM), and inferomarginal (IM) plate series. Scale bars: A = 20 cm; B, C = 2 mm; D = 5 mm.

HIPPASTERIA GRAY, 1840

Gray, 1840: 279; 1866: 9; Perrier, 1875: 271; (1876: 86); Sladen, 1889: 341; Fisher, 1911: 223; Verrill, 1914: 300; Koehler, 1924: 178; Mortensen, 1927: 88; Dons, 1937: 17; Mortensen, 1940: 125; Djakonov, 1950: 51 (1968: 42); Bernasconi, 1963: 15; Bernasconi, 1964: 253; Halpern, 1970a: 183; A.M. Clark & Courtman-Stock, 1976: 63; Clark & Downey, 1992: 246; Clark & McKnight, 2001: 54.

Type species: *Asterias phrygiana* Parelius, 1768 (with synonym *Hippasteria europaea* Gray, 1840 as well as all four nominal species included by Gray as synonyms with *H. phrygiana*).

Diagnosis: Disk strongly swollen, Arms relatively broad and short. Body often pentagonal to weakly stellate.

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 platform-like in shape. Carinal series are poorly distinguished. Abac-

tinal spinelets (sometimes granular) forming fringe around abactinal plates. Spines, large, conical, granules often present on abactinal plates.

Large spines present on superomarginal and inferomarginal plates of most taxa. Superomarginal and inferomarginal plates bare, quadrate to rounded in outline at inter-radii with no other accessories other than large spines. Spinelets present on marginal plates. 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 taxa,

Actinal fasciolar grooves shallow. Large actinal spines and spinelets present. Subambulacral spines large (and thus few in number). Furrow spines large, blunt, and round in cross-section, usually few in number. Enlarged bivalve pedicellariae on raised bases present on body surface.

Included species: *(asterisk denotes fossil taxon) *Hippasteria antiqua* Fell, 1956; *H. californica* Fisher, 1905; *Hippasteria colossa* Djakonov, 1950; *Hippasteria*

derjungini Djakonov, 1950; *H. falklandica* Fisher, 1940; *H. heathi* Fisher, 1905; *Hippasteria imperialis* Goto, 1914; *Hippasteria kurilensis* Fisher, 1911; *Hippasteria leiopelta* Fisher, 1910; *Hippasteria mamifera* Djakonov, 1950; *Hippasteria nozawai* Goto, 1914; *Hippasteria pedicellaris* Djakonov, 1950; *H. phrygiana phrygiana* (Parelius, 1768), *H. phrygiana argentinensis* Bernasconi, 1961; *H. phrygiana capensis* Mortensen, 1933; *H. spinosa* Verrill, 1909; *H. strongylactis* Clark, 1926; *H. tasmanica* McKnight, 2006.

Comments: *Hippasteria*, the best known genus of the hippasterines, is encountered on shallow, near-shore to deep-sea settings worldwide and includes approximately 19 nominal taxa, many of which are similar in appearance and have overlapping characteristics. Some taxa occur in a continuous distribution over a wide geographical range but show relatively conservative overall morphology. *Hippasteria phrygiana*, for example, occurs in the North Atlantic off Europe and North America, as well as off South America, South Africa, New Zealand, and in the Southern Ocean (Clark & Downey, 1992; Clark & McKnight, 2001). The morphologically similar *H. spinosa* was described by Lambert (2000) as having pelagic, lecithotrophic larvae. If it were to be found that other *Hippasteria* spp. had lecithotrophic larvae, then long distance dispersal could explain the observed broad geographical ranges. Some species, such as *H. imperialis* and/or *H. nozawai* may actually represent very distinct taxa from the *H. spinosa* and *H. phrygiana* complexes, but are poorly known and require further study. Further issues pertaining to *Hippasteria* species complexes are included below in the Discussion.

Biology: Other ecological observations have included interactions with hagfish, which exploit prey captured, but not consumed, by *H. phrygiana* (Auster & Barber, 2006) and associations with fish assemblages observed at human-made structures (Love & York, 2005). *Hippasteria* has been described as the host to a number of commensals and parasites, including polynoid polychaetes, in *H. californica* (Pettibone, 1969), the ascothoracid crustacean *Dendrogaster* in *H. phrygiana* (Hamel & Mercier 1994), and the parasitic chlorophyte *Coccomyxa astericola* in *H. phrygiana* (Mortensen & Rosenvinge, 1933).

Biochemical compounds have been extracted from *H. phrygiana* (Burnell, Apsimon & Gilgan, 1986; Levina *et al.*, 2005) and gonad ultrastructure has been studied by Walker (1979).

'HIPPIASTERIA' ANTIQUA FELL, 1956

Fell, 1956: 11.

Occurrence: Fossil taxon. From Senonian (upper Cretaceous) sediments in north Canterbury, New Zealand.

Comments: Based on Fell's (1956) description of this species, relatively few characters were readily observable from the available specimen. Characters used by Fell (1956) in the description of this specimen that placed it in *Hippasteria* include larger primary plates with a radial series that are circular in shape in addition to numerous smaller secondary plates scattered throughout and quadrangular marginal plates. These characters are plesiomorphic for the Hippasterinae and are present in stemward taxa, such as *Sthenaster*, and some *Hippasteria* spp. Further examination of the fossil and comparison with living taxa is required.

HIPPIASTERIA CALIFORNICA FISHER, 1905

FIGURE 6E–G

Fisher, 1905: 310; 1911: 233; HL Clark, 1913: 194; Alton, 1966: 1702; Lambert, 1978b: 62; Maluf, 1988: 34, 118 (as *H. californica*)

Imaoka *et al.*, 1991: 54 (as *Cryptopeltaster lepidonotus*)

Occurrence: California, Washington to British Columbia, and Hokkaido, Japan 110–1820 m.

Material examined: USNM 33354, San Miguel Island, Channel Islands, California. 34°15'N, 120°36'W, 519 m, coll. USFC Albatross, 5.i.1889. (1 dry spec. $R = 8.2$, $r = 4.3$); USNM E10413, south-west of mouth of Columbia River, Oregon. 45°52'N, 124° 52'W, 823 m. Coll. R/V *Commando*, 13.v.1963 (1 dry spec. $R = 6.3$, $r = 3.2$). USNM E 10414 south-west of mouth of Columbia River, Oregon. 45°54'N, 124°55'W. 823 m. Coll. R/V. *Commando*, 10.xii.1961. (1 dry spec. $R = 8.7$, $r = 3.3$). USNM E 10443, south-west of mouth of Columbia River, Oregon. 45°54'N, 124°55'W, 823 m. Coll. R/V *Commando* 10.xii.1961 (1 dry spec. $R = 4.2$, $r = 22$). USNM E 10441 south-west of Columbia River, Oregon. 46°2'N, 124°57'W, 915 m. Coll. R/V *Commando* 30.v.1964. (1 dry spec. $R = 1.9$, $r = 1.0$). USNM E10442 south-west of mouth of Columbia River, Oregon. 45°55'N, 124°54'W, 732 m. Coll. R/V *Commando* 5.ix.1964. (1 dry spec. $R = 2.9$, $r = 1.5$).

HIPPIASTERIA COLOSSA DJAKONOV, 1950

Djakonov, 1950: 55 (1968: 47); 1952: 411; Baranova, 1957: 162

Occurrence: Bering Sea, 238–250 m.

Comments: This is another of the possible synonyms that compose the *H. spinosa* complex in the Aleutian/North Pacific region. Characters that distinguish this species are either variable or plesiomorphic to *H. spinosa*.

Material examined: None.

HIPPASTERIA DERJUNGINI DJAKONOV, 1950

(*Hippasteria derjungini* Djakonov, 1949: 22 is a *nomen nudum*, insufficiently characterized)

Djakonov, 1950: 55 (1968: 46); 1952: 412

Occurrence: Okhotsk Sea, off the northeast coast of Sakhalin. 192 m.

Material examined: None.

HIPPASTERIA FALKLANDICA FISHER, 1940

Fisher, 1940: 125; Bernasconi, 1973: 287; Clark & Downey, 1992: 247; Stampanato & Jangoux, 2004: 6; McKnight, 2006: 97

Occurrence: Falkland Islands (=Islas Malvinas), northern Argentina, Marion and Prince Edward Islands region to south of Tasmania, approx. 49°S, 150°E. 225–1148 m.

Material examined: None.

HIPPASTERIA HEATHI FISHER, 1905

Fisher, 1905: 319; 1911: 231; Krieger & Wing, 2002: 86.

Occurrence: Alaska, Gulf of Alaska. 377–454 m.

Material examined: HOLOTYPE: USNM 22338, Guard Island, Behm Canal, Alexander Archipelago, Alaska, 55°N, 131°W, 377–454 m, coll. USFC *Albatross*, 9.vii.1903 (1 dry spec. $R = 7.8$, $r = 3.9$).

HIPPASTERIA IMPERIALIS GOTO, 1914

Goto, 1914: 338; Hayashi, 1952: 338; 1973: 6, 15; Imaoka *et al.*, 1990: 50; Mah, 1998a: 67; Fujikura *et al.*, 2008: 272 (as *H. imperialis*)

Grigg *et al.*, 1987: 387 (as *Hippasteria spinosa*)

Occurrence: Sagami Bay/Tosa Bay region, Kii Strait, southern Japan, Hawaiian Islands. 245–600 m.

Material examined: None.

HIPPASTERIA KURILENSIS FISHER, 1911

Fisher, 1911: 226 (as *H. spinosa kurilensis*)

Gish, 2007: 39 (as *H. kurilensis*)

Occurrence: Okhotsk Sea, off the southernmost point of Kamchatka and in the vicinity of Simushir Island (Kuriles), Petrel Bank, Aleutian Islands. 165–600 m.

Comments: This species was distinguished from others in the genus based on long, conical abactinal and marginal spines by Djakonov (1950). This was originally a subspecies designated by Fisher (1911) and later raised to a species by Djakonov (1950). This is also a likely synonym within the *H. spinosa* complex.

Material examined: None.

HIPPASTERIA LEIOPELTA FISHER, 1910

(with formae *aculeata* and *longimana* Djakonov, 1950)

Fisher, 1910: 553; 1911: 227; Djakonov, 1950: 56 (1968: 47); 1952: 413.

Occurrence: Southern Bering Sea, Okhotsk Sea, Tartar Strait, and Aniva Bay off the south-east coast of Kamchatka. 35–418 m.

Material examined: None.

HIPPASTERIA MAMMIFERA DJAKONOV, 1950

Djakonov, 1950: 54 (1968: 45), 1952: 409.

Occurrence: Okhotsk Sea. 97 m.

Comments: This species was described by Djakonov (1950) as a separate species based on extremely swollen and hemispherical marginal and abactinal plates. This character is plesiomorphic to *H. spinosa* (and to a certain extent, *H. phrygiana*), which undermines the distinctiveness of this species and further lends support to its synonymy with *H. spinosa*.

Material examined: None.

HIPPASTERIA NOZAWAI GOTO, 1914

Goto, 1914: 344.

Occurrence: Hokkaido, northern Japan. (No depth information available.)

Material examined: None.

HIPPASTERIA PEDICELLARIS DJAKONOV, 1950

Djakonov, 1950: 1950: 54 (1968: 45); 1952: 410.

Occurrence: Okhotsk Sea. At 'inconsiderable depths and above-zero water temperatures' according to Djakonov (1968: 46).

Comments: Characteristics used to distinguish this species include two to three adambulacral spines, one subambulacral spine with a flattened pedicellariae, and close-set granules on the abactinal plates. However, these characters are also observed in *H. spinosa* suggesting that this species may also be a synonym or part of the *H. spinosa* species complex.

Material examined: None.

HIPPASTERIA PHRYGIANA (PARELIUS, 1768)

HIPPASTERIA PHRYGIANA PHRYGIANA

(PARELIUS, 1768)

FIGURE 6A–D

Linck, 1733: 21 (as *Pentaceros planus*)

Parelius, 1768: 425 [1770: 349] (as *Asterias phrygiana*)

Lamarck, 1816: 555 [non *A. equestris* Retzius, 1805] (as *Asterias equestris*)

Gray in Johnston, 1836: 146 (as *Asterias johnstoni*)

Gray, 1840: 279, 1866: 9 (as *Hippasteria europaea*, *H. johnstoni*, *H. cornuta*)

Gray, 1840: 279; 1866: 9; Perrier, 1875: 270 [1876: 65], Danielssen & Koren, 1881: 268; Sladen, 1883: 159; Perrier, 1888: 764; Sladen, 1889: 341; Koehler, 1909: 88, 1924: 179 (as *Hippasteria plana*)

Forbes, 1841: 125 (as *Goniaster equestris*)

Müller & Troschel, 1842: 52; Duben & Koren, 1846: 246 (as *Astrogonium phrygianum*)

Forbes, 1843: 280 (as *Goniaster abbensis*)

Barrett, 1857: 47 (as *Astrogonium aculeatum*)

Norman, 1865: 128 (as *Goniaster phrygiana*)

Dons, 1937: 17 (as *Hippasteria* [*Euhippasteria*] *phrygiana* and *Hippasteria* [*Nehippasteria*] *insignis*)

Perrier, 1891: K128; A.M. Koehler, 1926: 107; Clark, 1962: 22 (as *Hippasteria hyadesi*)

Verrill, 1874: 413; 1885: 542, Ganong, 1893: 56; Grieg, 1895: 6; Verrill, 1895: 137, 1899: 148; Döderlein, 1900: 218; Hartlaub, 1900: 191; Ludwig, 1900: 457; Whiteaves, 1901: 50; Grieg, 1902: 21; Pearcey, 1902: 308; Simpson, 1903: 40; H.L. Clark, 1905: 1; Grieg, 1905: 4; Nordgaard, 1905: 160, 235; Grieg, 1907: 28, 32; Sussbach & Breckner, 1911: 215; Grieg, 1912: 6; 1913: 115; 1917: 8; 1921: 6; H.L. Clark, 1923: 270; Mortensen, 1927: 88, 1933: 245; Haubold, 1933: 200; A.H. Clark, 1949: 373; Djakonov, 1950 (tr. in

1968): 53; Blacker, 1957: 18, 45; Buchanan, 1966: 25; Wolff, 1968: 82, Walker, 1978: 361; Codoceo & Andrade 1978: 156; Franz, Worley & Merrill, 1981: 406, 415; O'Connor & Tyndall, 1986: 96; Moore *et al.*, 2004: 246 (as *Hippasteria phrygiana*)

Fell, 1958: 11, pl. 1, figs A, G; 1959: 136, fig. 21; 1960: 61, pls. 2, 3; 1962: 33; McKnight, 1967: 300; H.E.S. Clark, 1970: 3; A.M. Clark, 1993: 259; Rowe & Gates, 1995: 65; Koslow & Gowlett-Holmes, 1998: 44 (as *Hippasteria trojana*)

Occurrence: Arctic, North Atlantic: South to Cape Cod in the west, including Bear Seamount. To the Kattegat, northern Scotland, and northernmost Ireland in the east. Norwegian coast south to the Kattegat, south-western part of the Barents Sea, Kola Bay. South Pacific: Chile to Magellan Strait to the Marion and Prince Edward Island region to Chatham Island, east of New Zealand, Campbell Plateau, seamounts off southern Tasmania. Southern Ocean: Lavoisier Island, Antarctic Peninsula.

Depth is highly variable: 20–1275 m and varies by region. Most records for New Zealand are over 500 m.

Comments: Southern hemisphere *Hippasteria* species have been scrutinized since the early 20th century (e.g. Koehler, 1926, Clark, 1962) because of their strong morphological similarities with the northern Atlantic *Hippasteria phrygiana*. The New Zealand–South Pacific *H. trojana* was synonymized with *H. phrygiana* by H.E.S. Clark in Clark & McKnight (2001).

The sub-Antarctic *Hippasteria hyadesi* was synonymized with *H. plana* (= *H. phrygiana*) by Koehler (1926) but was thought to have had an incorrectly identified type locality by Clark (1962). Stampanato & Jangoux (2004) and Branch *et al.* (1993) regarded *H. hyadesi* as a valid species. However, examination of the specimens in the USNM collections from the South Pacific and Antarctic Peninsula (near the type locality) shows few to no morphological distinctions, suggesting that the original conclusion made by Koehler (1926) was correct. Magellanic–Antarctic forms of *Hippasteria phrygiana* may eventually be supported as cryptic species distinct from those in the northern hemisphere but based on specimens available for study, external morphology has limited usefulness and other characters will need to be considered.

Material examined: North Atlantic: USNM E 46610, Browns Bank, Nova Scotia, 42°34'N, 65°44'W, 93 m, coll. R/V *Albatross* IV, 15.x.1965 (1 dry spec. $R = 7.3$, $r = 3.5$); USNM E46606, south-east of Cape Elizabeth, Gulf of Maine, Maine, 43°31'N, 69°49'W, 97 m. Coll. R/V *Albatross* IV, 14.vii.1965 (1 dry spec. $R = 6.2$, $r = 3.7$). USNM 5236 off Eastern Point, Gloucester Harbor, Massachusetts. 42°30'N, 70°38'W, 78.6 m

(43 fms). Coll. R/V Speedwell (1 spec. $R = 9.2$, $r = 5.0$). USNM E 46611 Browns Bank, Nova Scotia, Canada. 42°45'N, 65°7'W. 97.0 m. Coll. R/V Albatross IV, 15.x.1965 (1 dry spec. $R = 1.7$, $r = 1.0$). USNM E46613 western part of Georges Bank, Massachusetts. 41°24'N, 68°25'W, 68 m. Coll. R/V Albatross IV, 28.x.1965 (1 dry spec. $R = 2.2$, $r = 1.7$). South Pacific: USNM E13586, north-west of Amundsen Sea, Southeast Pacific Basin. 54°49'S, 129°48'W, 549 m. Coll. R/V Eltanin. (3 dry specs. $R = 3.5$, $r = 2.0$; $R = 8.2$, $r = 4.6$; $R = 9.56$, $r = 5.1$). USNM 1121154. Magallanes y Antartica, Chile. 53°39'S, 70°55'W, 82 m. Coll. R/V Hero. (1 dry spec. $R = \sim 7.8$, $r = 4.6$). Southern Ocean. USNM E43921, Lavoisier Island, Bischof Islands, Antarctic Peninsula. 66°20'S, 67°47'W, 325 m. Coll. J. Tyler, 25.iii.1959. (1 dry spec. $R = 6.7$, $r = 3.1$). USNM 1082740. 67°23'S to 67°24'S, 180°00'W to 179°58'W, 595–516 m. Coll. R/V Eltanin. (2 dry specs. $R = 9.2$, $r = 4.0$; $R = \sim 11.0$, $r = 5.5$).

HIPPASTERIA PHRYGIANA ARGENTINENSIS
BERNASCONI, 1961

Bernasconi, 1961: 1; Clark & Downey, 1992: 248

Occurrence: Northern Argentina. 108–162 m.

Material examined: None.

HIPPASTERIA PHRYGIANA CAPENSIS
MORTENSEN, 1933

H.L. Clark, 1923: 270; 1926: 13 (as *Hippasteria phrygiana*)

Mortensen, 1933: 245; A.M. Clark, 1952: 170, 196 (as *Hippasteria phrygiana* var. *capensis*)

A.M. Clark & Courtman-Stock, 1976: 63; Clark & Downey, 1992: 249 (as *Hippasteria phrygiana capensis*)

Occurrence: South Africa, 310–980 m.

Material examined: None.

HIPPASTERIA PHRYGIANA STRONGYLACTIS H.L.
CLARK, 1926

H.L. Clark, 1926: 13; A.M. Clark, 1952: 196; A.M. Clark & Courtman-Stock, 1976: 63; Clark & Downey, 1992: 249

Occurrence: South Africa. 320–980 m.

Material examined: None.

HIPPASTERIA SPINOSA VERRILL, 1909

Verrill, 1909: 63; Fisher, 1911: 224; HL Clark, 1913: 194; Goto, 1914: 349; Verrill, 1914: 301; Djakonov, 1950: 53 (1968: 45); Baranova, 1957: 162; Alton, 1966: 1702; Carey, 1972: 38, 39; Lambert, 1978a: 4, 14; Maluf, 1988: 34, 118; Clark, 1993: 259; Lambert, 2000: 64.

Occurrence: Southern California, British Columbia, to Bering Sea. Okhotsk Sea off Cape Elizavety, and near the Kurile Islands. 49–1170 m.

Comments: This species forms an extensive species complex throughout the Aleutian and North Pacific sub-Arctic region similar in several ways to *Leptasterias* and other wide ranging high-latitude species. This extensive variation is likely to encompass all of the species described by Djakonov (1950 translated in Dyakonov, 1968) from the Okhotsk Sea and adjoining regions, including *H. mammifera*, *H. pedicellaris*, *H. colossa*, and *H. kurilensis*. These are mentioned here for future discussion but type specimens have not been examined.

Material examined: USNM 32470, west of San Nicolas Island, 33°13'N, 120°4'W, 825 m, coll. USFC Albatross, 26.iv.1911. (1 dry spec. $R = 0.9$, $r = 0.4$). USNM 33352 south-west of Cape Flattery, Washington. 48°17'N 124°52'W, 70 m. Coll. USFC Albatross 24.ix.1888 (1 dry spec. $R = 8.2$, $r = 4.3$); USNM 39833 Heceta Bank, Oregon, 43°58'N, 124°36'W, 170 m. Coll. USFC Albatross 1.ix.1889. (1 dry spec. $R = 9.2$, $r = 4.7$). USNM 47600 Umnak Island, Islands of Four Mountains, Aleutian Islands, Alaska. 53°3'N, 169°57'W, 146 m. Coll. R/V Harvester 11.viii.1980. (1 dry spec. $R = 7.1$, $r = 3.5$); USNM E10504. South-west of mouth of Columbia River, Oregon. 46°8'N 124°30'W, 137 m. Coll. R/V Cobb 14.i.1964. (1 dry spec. $R = 12.8$, $r = 7.1$).

HIPPASTERIA TASMANICA MCKNIGHT, 2006

McKnight, 2006: 97

Occurrence: South Tasman Rise, south of Tasmania, Australia. 935–1058 m.

Material examined: None.

OUTGROUP TAXA: *Cladaster analogous*. USNM E38569. Shag Rocks, Scotia Sea. 53°20'S, 42°42'W, 417–514 m. Coll. R/V Siedlecki, USARP. 29.xi.1986. (1 dry spec. $R = 3.2$, $r = 1.8$). *Mediaster aequalis*. USNM 33275. Dakins Cove, Santa Catalina Island, Channel

Islands, California. 33°17'N, 118°24'W, 86.0 m. Coll. USFC Albatross, 8.iv.1897. (1 dry spec. $R = 6.6$, $r = 3.3$). *Peltaster placenta*. USNM E12587 west of Barbuda, Antigua, Caribbean Sea. 17°38'N, 62°16'W, 329–338 m (180–185 fms). Coll. R/V *Oregon* 19.v.1967. (1 dry spec. $R = 7.2$, $r = 5.4$).

DISCUSSION

COMPARISONS WITH OTHER TAXA

A full summary of taxonomic changes is listed in Appendix 4. *Sthenaster*'s overall appearance is intermediate between *Evoplosoma* and *Hippasteria*, possessing the toothed pedicellariae and sharp spinelets of the former in conjunction with the pedicellariae, short arms, broad disk, and massive appearance of the latter. The presence of sharp spinelets and toothed pedicellariae is not observed in other goniasterid genera with the exception of *Lydiaster* and certain species in its sister genus, *Circeaster* (Mah, 2006). *Circeaster* has been observed sitting on coral skeletons, possibly feeding (Mah, 2006) suggesting that it may also share corallivorous habits with the Hippasterinae.

Also similar to hippasterines are *Calliaster* and those Goniasteridae related to *Calliaster*, such as *Mabahissaster* and *Milteliphaster* (Aziz & Jangoux, 1985b), which share the large conical spines, present on the abactinal, marginal, and actinal surface, bare marginal plates, and toothed pedicellariae. Chave & Malahoff (1998) observed *Calliaster pedicellaris* feeding on a deep sea gorgonian in the Hawaiian Islands region. Thus, three groups, the Hippasterinae, the *Circeaster* lineage, and the *Calliaster* 'group' share similar sets of morphological characters with preliminary evidence suggesting coral or cnidarian predation occurring nominally in each group. It is unclear if these characters are support for these different taxa as a single lineage, or are perhaps correlated with corallivory, occurring in parallel amongst different goniasterid lineages that have come to exploit an identical food source.

Cladaster was not supported as a member of the Hippasterinae (Fig. 2). However, its perceived similarity to hippasterines as suggested by Fisher (1911) and its sister group relationship to the *Circeaster* clade (Mah, 2006) suggest that it may occupy an intermediate or close phylogenetic position to these two taxa.

FOSSILS, BATHYMETRIC, AND BIOGEOGRAPHICAL PATTERNS

Bathymetric relationships mapped onto the tree (Fig. 11) support an 'onshore-offshore' hypothesis as outlined by Jablonski & Bottjer (1988, 1990). The more derived *Evoplosoma* is present in deep water

relative to hippasterines, such as *Gilbertaster* and *Cryptopeltaster*, which occur at relatively shallower depths. This pattern is observed in several other asteroid taxa including the Brisingida (Mah, 1998b), the Zoroasteridae (Mah, 2007a) as well as goniasterids in the Pentagonasterinae (Mah, 2007b).

The fossil '*Hippasteria antiqua*' Fell, 1956 supports the possibility that the hippasterines have occupied a wide geographical range in the past. Morphological characters, such as body shape, quadrate marginals, and the larger primary plates, are similar to more basal hippasterines such as *Cryptopeltaster* and/or *Sthenaster*, suggesting close relationships with these taxa. Given the geographical disparity between these taxa (west coast of North America, south-eastern United States) and *H. antiqua* (New Zealand), extinction of widely distributed hippasterines may provide one possible explanation for the distribution observed within the Hippasterinae.

In contrast, there is some suggestion that 'offshore-onshore' relationships may be present within the genus *Hippasteria*. All available proposed sister taxa to *Hippasteria* occur in relatively deep water (> 200 m) but several *Hippasteria* species occur at depths as shallow as 20 m (e.g. *H. phrygiana*, *H. spinosa*). This suggests that these shallow species may be more derived relative to those occurring at deeper depths, such as *H. californica*. Similar patterns have been observed in other goniasterids (e.g. Mah, 2005b).

Several species, such as *H. colossa*, *H. kurilensis*, and *H. derjungii*, from the North Pacific and Arctic regions probably represent a species complex with ties to the North Atlantic *H. phrygiana*. This relationship is consistent with relationships presented herein and with previous hypotheses (e.g. Nesis, 1961). Close affinities on the tree between *H. spinosa* and *H. phrygiana* may reflect a close biogeographical relationship reflecting glaciation-related, relatively recent diversification and gene flow via the Arctic, similar to that observed in other asteroids, such as *Leptasterias* (Foltz *et al.*, 2007) and *Asterias* (Wares, 2001). Franz *et al.* (1981) speculated on nominal relationships amongst several Atlantic-Arctic-Pacific taxa, including *Ceramaster*, *Leptychaster*, and *Pseudarchaster*.

More problematic is the assessment of Clark & McKnight (2001) that *H. phrygiana* occurs both in the North Atlantic and the South Pacific in and around New Zealand. This could possibly be a wide-ranging taxon with conserved morphology and genetic differentiation. It could alternatively be representative of cryptic species similar to what was observed amongst populations of the deep-sea *Zoroaster fulgens* (Howell *et al.*, 2004).

The sister group relationship (Figs 1, 11) between the tropical Atlantic *G. caribea* and the Pacific *G.*

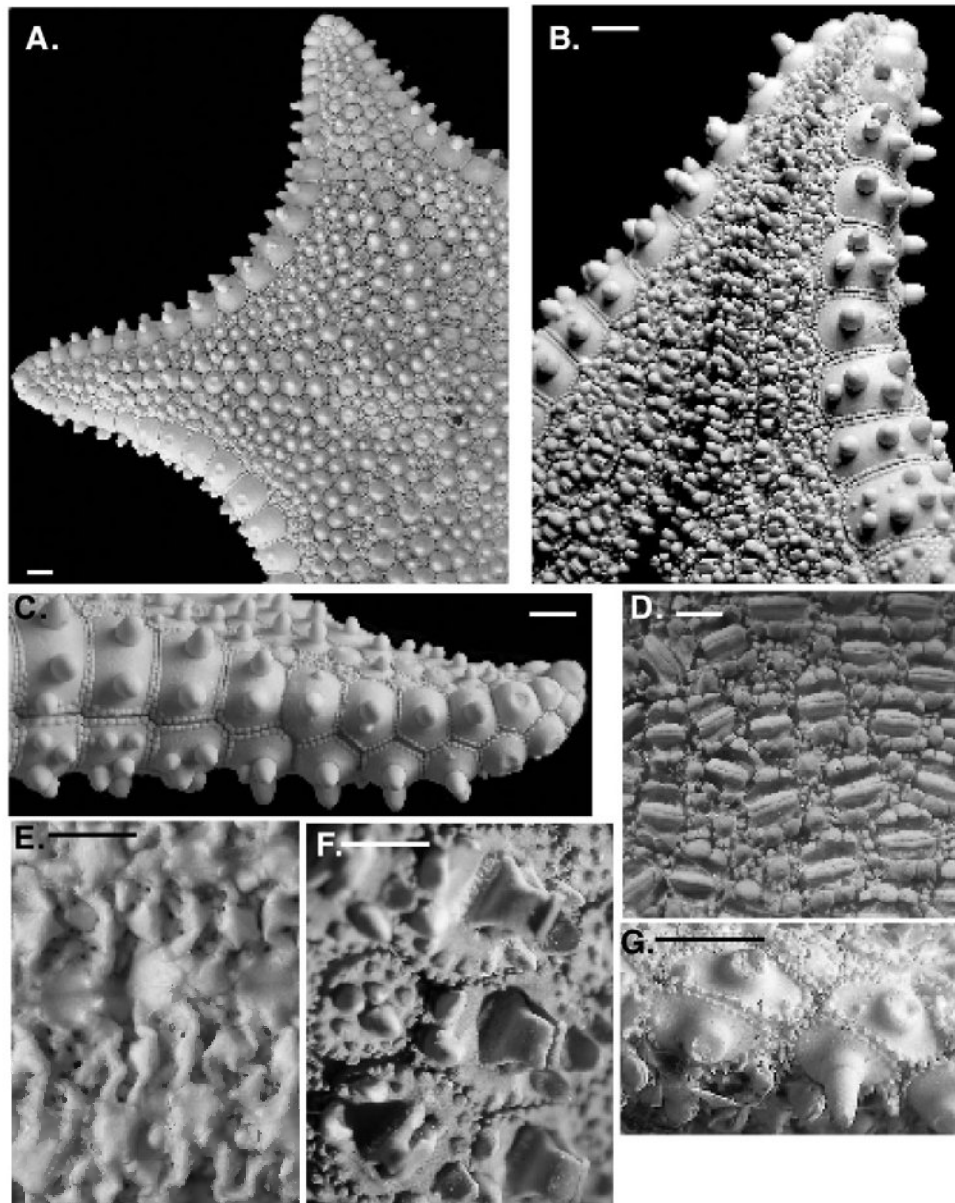


Figure 10. *Hippasteria phrygiana* USNM E46606. A, abactinal view; B, actinal view; C, lateral view; D, *H. phrygiana* USNM 5235. Actinal surface showing bivalve pedicellariae; E, *Hippasteria californica* USNM E10413. Abactinal plates internal view; F, *H. californica* USNM 33354 abactinal surface pedicellariae; G, USNM E10413. Lateral view showing marginal plate series. Scale bars: A–C, G = 5 mm; D, E = 2 mm; F = 1 mm.

anacanthus (Hawaii to New Zealand) suggests former continuity between the two *Gilbertaster* populations, perhaps before the closure of the Tethys Seaway (Smith, Smith & Funnell, 1994) by the formation of the Panamanian isthmus. This relationship has also been observed in the deep-sea goniasterid *Circeaster* between the tropical Atlantic *Circeaster americanus* and the Hawaiian *Circeaster pullus* (Mah, 2006). The sister group relationship between *Gilbertaster* and the Pacific *Cryptopeltaster* would suggest a Pacific ancestor for *Gilbertaster*.

THE HIPPASTERINAE AND CORALLIVOROUS GONIASTERIDAE

Deep-sea corals form habitats that are host to a variety of associated fauna, including fishes and invertebrates. The importance of these habitats to fishes has been investigated in a number of regions (Huesbo *et al.*, 2002; Costello *et al.*, 2005; Stone, 2006; Ross & Quattrini, 2007). However, habitat utilization by invertebrates is not fully understood. Several recent investigations conducted in both the eastern

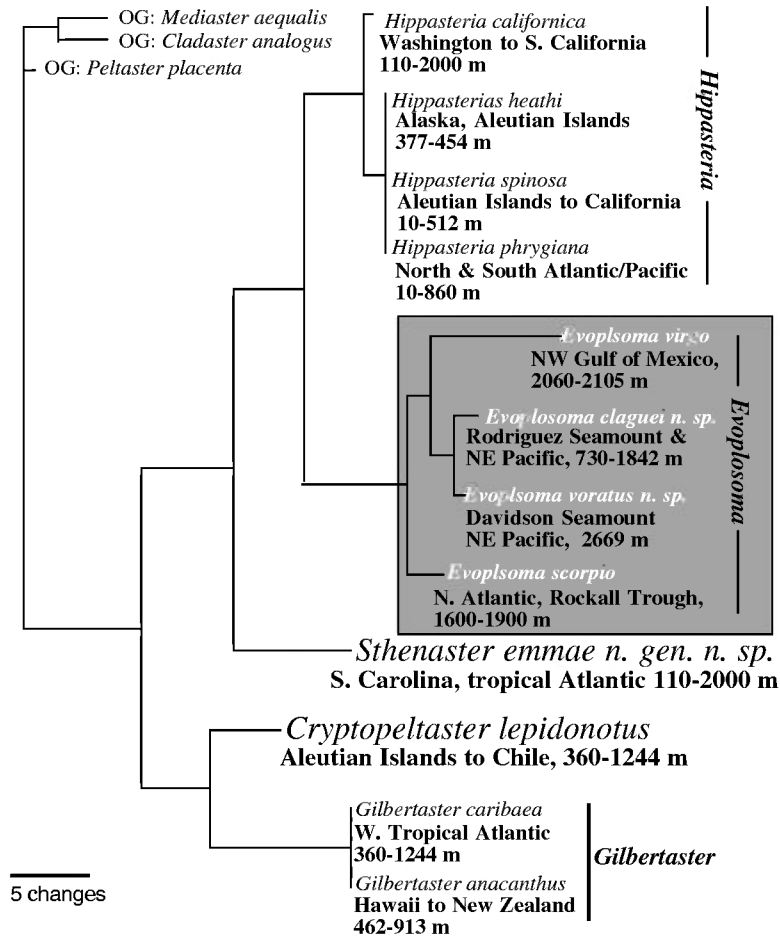


Figure 11. Biogeographical and bathymetric ranges mapped onto the phylogenetic tree. *Evoplosoma* occurs in a distinctly deeper depth range (indicated by the shaded box) than any of the other hippasterines. Sampled *Evoplosoma* spp. were Atlantic and Pacific (*Evoplosoma* includes additional species from the tropical Indian and Pacific Oceans) but all occur in this depth range. OG, outgroup.

and western North Atlantic involving quantitative surveys of mega- and macroinvertebrates report diversity to be extremely high (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Jonsson *et al.*, 2004; Reed *et al.*, 2005, 2006; Henry & Roberts, 2007; Roberts *et al.*, 2008). These recent surveys, however, often report only a fraction of the diversity associated with these habitats because sampling methods utilized target only a portion (either size- or taxon-specific) of the associated fauna, the interest of the investigators is limited to a few taxonomic groups, or the overall goals of the project are such that not all associated fauna are collected. As a result, many megafaunal taxa are often over-looked during collections or are under-sampled.

Asteroids are known from many deep-sea coral study sites but observations of these taxa have lacked taxonomic precision, precluding more precise ecological interpretations. Several papers provide vague

entries (unidentified asteroid, Mortensen *et al.*, 1995; Asteroidea, unid. sp., Reed, Weaver & Pomponi, 2006) or have identified individuals only to the generic level (Mortensen *et al.*, 1995; Jonsson *et al.*, 2004). Few report species-level identifications (e.g. Jensen & Frederiksen, 1992; Henry & Roberts, 2007).

Much remains to be learned about the megafauna associated with deep-sea coral habitats. Large, prominent animals such as the Asteroidea have been shown to have ecologically complex relationships with cnidarians from shallow marine habitats (e.g. Birkeland, 1974; Birkeland & Lucas, 1990) and seem to be important to those living in deep-sea habitats as well (e.g. Chave & Malahoff, 1998; Krieger & Wing, 2002).

The *in situ* observations of Krieger & Wing (2002) documented *Hippasteria* as a main predator of deep-sea coral. Subsequent observations have now shown that at least one species of every genus included in Hippasterinae (Goniasteridae), except for *Gilber-*

taster, has been reported to feed on deep-sea corals, mainly gorgonians, but also alcyonaceans, antipatharians, and other cnidarian species. Krieger & Wing (2002) reported *H. heathi*, in addition to other species, as the main predator on the gorgonian *Primnoa* sp. in the Gulf of Alaska. *Hippasteria imperialis* has been observed feeding on isidid corals in the Hawaiian Islands, off Kona (C. Mah, unpubl. observ.). Japanese researchers using submersibles have also observed an unidentified species of *Evoplosoma* feeding on deep-sea coral in Java (Fujikura *et al.*, 2008).

In the Pacific, submersibles from the Monterey Bay Aquarium Research Institute have documented several instances of hippasterines feeding on deep-sea cnidarians, including gorgonians (*Paragorgia*), bamboo corals (*Keratoisis* and *Lepidisis*) and sea whips (*Halipteris*) by *Cryptopeltaster*, *Evoplosoma*, and *Hippasteria* at Rodriguez and Davidson seamounts off the west coast of California.

Video observations of *Sthenaster* show the holotype hunched over colonies of the co-occurring gorgonian *Eunicella modesta* (Verrill 1883). Gut contents of the holotype of *Sthenaster* (USNM 1124468) included distinctive spicules belonging to the *E. modesta* (Verrill, 1883). These observations support the hypothesis of corallivory in *Sthenaster*, and suggests that dietary preferences would be similar to other known hippasterines. If *Sthenaster* is indeed a predator on gorgonians, this would be the first account of hippasterine predation on gorgonians in the Atlantic.

It is unclear how specific nutritional preferences are within the Hippasterinae. Feeding in the shallow-water *Hippasteria* suggests a feeding preference for many types of cnidarians but not to the exclusion of other food sources. The north-west Pacific species *Hippasteria spinosa* has been reported as a predator on the sea pen *Ptilosarcus* (Mauzey, Birkeland & Dayton, 1968; Birkeland, 1974), the white-plumed sea anemone *Metridium* sp., the zoanthid *Epizoanthus scotinus* (Wood, 1958), the tunicate *Metandrocarpa* sp., the polychaete *Nereis* sp., and eggs of the nudibranch *Armina* sp. (Lambert, 2000). Additionally, *H. spinosa* elicits an escape response in the sea anemone *Stomphia* sp. (Lambert, 2000). Similar to its north-west Pacific congener, *H. phrygiana* has been reported to incite swimming behaviour in the Atlantic sea anemone, *Stomphia coccinea* (Müller, 1776) (Robson, 1961). *Hippasteria phrygiana* preys upon *Metridium senile* (Linné, 1761) in Maine (Harris, 1991) and has been reported feeding on 'cnidarians' (Mercier & Hamel, 2008). Stomach contents from *H. phrygiana* have indicated that echinoderms, polychaetes, molluscs, and sediment are also incorporated in the diet of this species. In contrast, stomach contents from the deep-sea *H. californica* suggest that it is primarily a

sediment/detrital feeder (Carey, 1972). Sediments were also found in the gut of *H. spinosa* (Birkeland, 1974).

Other examples of presumed corallivory in non-hippasterine members of the Goniasteridae include the Hawaiian *Calliaster pedicellaris* (Fisher, 1906) (Chave & Malahoff, 1998) and *Circeaster pullus* (Mah, 2006), and the Atlantic *Plinthaster dentatus* (Perrier, 1884) (Halpern, 1970a, b) and *Tessellaster nobilis* (Clark, 1941).

This work represents a first step to further our understanding of the major taxonomic concepts within the neglected Hippasterinae. Future efforts would be best directed towards a complete investigation of *Hippasteria*, which occurs worldwide, is the most speciose of the Hippasterinae, and is one of the most frequently encountered asteroids observed feeding on deep-sea corals. Questions relating to dietary preferences/restrictions correlated to phylogeny could be important particularly with regard to management and conservation of these ecosystems.

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REFERENCES

- Ahearn CG. 1995.** Catalog of the type specimens of seastars (Echinodermata: Asteroidea) in the National Museum of Natural History, Smithsonian Institution. *Smithsonian Contributions to Zoology* **572**: 1–59.
- Alton M. 1966.** Bathymetric distribution of sea stars (Asteroidea) off the Northern Oregon coast. *Journal of the Fisheries Research Board of Canada* **23**: 1673–1714.
- Auster PJ, Barber K. 2006.** Atlantic hagfish exploit prey captured by other taxa. *Journal of Fish Biology* **68**: 618–628.
- Aziz A, Jangoux M. 1985a.** 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**: 263–274.
- Aziz A, Jangoux M. 1985b.** On the status and affinities of the goniasterid genus *Calliaster* G 1840. In: Keegan BF, O'Connor BDS, eds. *Proceedings of the 5th International Echinoderm Conference, Galway, 1984*. Balkema: Rotterdam, 585–586.
- Baranova ZI. 1957.** [Echinoderms of the Bering Sea]. *Issledovaniya Dalny-Vostok Morei USSR* **4**: 149–266. (In Russian).
- Barrett L. 1857.** Descriptions of four new species of Echinodermata. *Annals of the Magazine of Natural History* **20**: 46–48.
- Bernasconi I. 1961.** Una nueva especie de asteroideo. *Neotropica* **7**: 1–2.
- Bernasconi I. 1963.** Asteroideos Argentinos. IV. Familia Goniasteridae. *Revista del Museo Argentino de Ciencias Naturales (Zoología)* **9** (1): 1–25.
- Bernasconi I. 1973.** Los equinodermos colectados por el Walther Herwig en el Atlántico Sudoeste. *Revista del Museo Argentino de Ciencias Naturales* **3**: 287–334.
- Birkeland C. 1974.** Interactions between a sea pen and seven of its predators. *Ecological Monographs* **44**: 211–232.
- Birkeland CE, Lucas JS. 1990.** *Acanthaster planci*: major management problem of coral reefs. Boca Raton, FL: CRC Press.
- Branch ML, Jangoux M, Alva V, Massin CL, Stampanato S. 1993.** The Echinodermata of subantarctic Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **23**: 37–70.
- Burnell DJ, Apsimon JD, Gilgan MW. 1986.** Occurrence of saponins giving rise to asterone and asterogenol in various species of starfish. *Comparative Biochemistry and Physiology* **85B**(2): 389–391.
- Carey AG. 1972.** Food sources of sublittoral, bathyal and abyssal asteroids in the Northeast Pacific Ocean. *Ophelia* **10**: 35–47.
- Chave EH, Malahoff A. 1998.** *In deeper waters: photographic studies of Hawaiian deep-sea habitats and life forms*. University of Hawaii Press.
- Clark AM. 1962.** Asteroidea. *B.A.N.Z. Antarctic Research Expedition 1929–1931* **B9**: 68–70.
- Clark AM. 1993.** An index of names of recent Asteroidea – Part 2: Valvatida. *Echinoderm Studies* **4**: 187–366.
- Clark AM, Courtman-Stock J. 1976.** *The echinoderms of Southern Africa*. London: British Museum of Natural History.
- Clark AM, Downey ME. 1992.** *Starfishes of the Atlantic*. London: Chapman and Hall.
- Clark HES, McKnight DG. 2001.** The Marine Fauna of New Zealand: Echinodermata: Asteroidea (sea-stars), Order Valvatida. *NIWA Biodiversity Memoir* **117**: 1–270.
- Clark HL. 1913.** Scientific results of the expedition to the Gulf of California in charge of C.H. Townsend, by the U.S. Fisheries Steamship "Albatross" in 1911, Cmdr. G.H. Burrage, USN Commanding, VIII. Echinoderms from Lower California with descriptions of new species: supplementary report. *Bulletin of the American Museum of Natural History* **32**: 185–236.
- Clark HL. 1926.** Echinoderms from the South African Fisheries and Marine Biological Survey. 2. Sea-stars. *Reports of the Fisheries and Marine Biological Survey of the Union of South Africa* **4**, *Special Report* **7**: 1–33.
- Clark HL. 1941.** Reports on the scientific results of the Atlantis Expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. *Memorias de la Sociedad Cubana de Historia Natural*, **15** (1): 1–154.
- Codoceo MR, Andrade H. 1978.** Asterozoos arquibentonicos de Chile Central. *Anales del Museo de Historia Natural de Valparaiso* **11**: 153–174.
- Codoceo MRH, Andrade H. 1981.** Nuevo asteroideo para Chile: *Criptopeltaster philippii* n. sp. (Goniasteridae, Hippasteriinae). *Revista de Biología Marina y Oceanografía de Valparaiso* **17**: 379–387.
- Costello MJ, McCrea M, Freiwald A, Lundälv T, Jonsson L, Bett BJ, vanWeering TCE, deHaas H, Roberts JM, Allen D. 2005.** Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald A, Roberts JM, eds. *Cold-water corals and ecosystems*. Berlin-Heidelberg: Springer-Verlag, 771–805.
- Djakonov AM. 1950.** Sea stars (asteroids) of the USSR seas. *Izdatel'stvo Akademii Nauk SSSR Moskva-Leningrad* **34**: 1–203.
- Djakonov AM.** [Translated as Dyakonov] **1968.** Sea stars (asteroids) of the USSR seas. In: Strelkov AA, ed. *Keys to the fauna of the USSR* **34**. *Zoological Institute of the Academy of Sciences of the USSR*. Jerusalem: Israel Program for scientific translations Ltd. 183 pp.
- Dons C. 1937.** Zoologische Notizen XXXIV. *Hippasteria insignis* n. sp. *Det Kongelige Norske Videnskabers Selskab Forhandlinger* **10**: 16–19.
- Downey ME. 1981.** A new goniasterid seastar, *Evoplosoma scorpio* (Echinodermata: Asteroidea), from the northeastern Atlantic. *Proceedings of the Biological Society of Washington* **94**: 561–563.
- Downey ME. 1982.** *Evoplosoma virgo*, a new goniasterid starfish (Echinodermata: Asteroidea) from the Gulf of Mexico. *Proceedings of the Biological Society of Washington* **95**: 772–773.
- Düben MW, Koren J. 1846.** Ofversigt af Skandinaviens

- Echinodermer [in Swedish; under name of Loven] *Ofvers. K. VetenskAkad. Forh.* **1845**: 73–77.
- Fell HB. 1956.** New Zealand Fossil Asteroidea. 2. *Hippasteria antiqua* n. sp. from the Upper Cretaceous. *Records of the Canterbury Museum* **7**: 11–12.
- Fell HB. 1958.** Deep-sea echinoderms of New Zealand. *Zoology Publications from Victoria University of Wellington* **24**: 1–40.
- Fell HB. 1959.** Starfishes of New Zealand. *Tuatara* **7**: 127–142.
- Fell HB. 1960.** Biological results of the Chatham Islands 1954 Expedition. Part 2. Archibenthal and littoral echinoderms of the Chatham Islands. *Bulletin, New Zealand Department of Scientific and Industrial Research* **139**. New Zealand Oceanographic Institute **5**: 55–75.
- Fell HB. 1962.** *Native in New Zealand: Native Sea-Stars*. A.H. & A.W. Reed, Wellington, New Zealand. 64 pp.
- Fisher WK. 1905.** New starfishes from deep water off California and Alaska. *Bulletin of the Bureau of Fisheries* **24**: 291–320.
- Fisher WK. 1906.** The starfishes of the Hawaiian islands. *Bulletin of the United States Fish Commission* **23**: 987–1130.
- Fisher WK. 1910.** New genera of starfishes. *Annals of the Magazine of Natural History* **5**: 171–173.
- Fisher WK. 1911.** Asteroidea of the North Pacific and adjacent waters. 1. Phanerozonia and Spinulosida. *Bulletin of the US National Museum* **76**: xiii+420 pp. 122 pls.
- Fisher WK. 1940.** Asteroidea. *Discovery Reports* **20**: 69–306.
- Foltz DW, Nguyen AT, Kiger JR, Mah CL. 2007.** Pleistocene speciation of sister taxa in a North Pacific clade of brooding sea stars (*Leptasterias*). *Marine Biology* **154**: 593–602.
- Forbes E. 1841.** *A history of British starfishes and other animals of the class Echinodermata*. London: John Van Voorst.
- Franz DR, Worley EK, Merrill AS. 1981.** Distribution patterns of common seastars of the Middle Atlantic continental shelf of the Northwest Atlantic (Gulf of Maine to Cape Hatteras). *Biological Bulletin* **160**: 394–418.
- Fujikura K, Okutani T, Maruyama T. 2008.** [*Deep-sea life-biological observations using research submersibles*]. Kanagawa, Japan: Tokai University Press (in Japanese).
- Gage JD, Pearson M, Clark AM, Paterson GLJ, Tyler PA. 1983.** Echinoderms of the Rockall Trough and adjacent areas. 1. Crinoidea, Asteroidea and Ophiuroidea. *Bulletin of the British Museum of Natural History (Zoology)* **45** (5): 263–308.
- Gish RK. 2007.** The 2006 Petrel Bank Red King Crab Survey. *Fishery Management Report (Alaska)* **07-44**: 1–90.
- Goto H. 1914.** A descriptive monograph of Japanese Asteroidea. 1. *Journal of the College of Sciences, Imperial University of Tokyo* **29**: 1–808.
- Gray JE. 1840.** XXXII. A Synopsis of the genera and species of the Class Hypostoma (Asterias, Linnaeus). *Annals and Magazine of Natural History* **1**: 275–290.
- Grigg RW, Malahoff A, Chave EH, Landahl J. 1987.** Seamount benthic ecology and potential environmental impact from manganese crust mining in Hawaii. *Geophysical Monograph* **43**: 479–390.
- Hain S, Corcoran E. 2004.** The status of the cold-water coral reefs of the world. In: Wilkinson C, ed. *Status of coral reefs of the world: 2004*, 1st edn. Townsville, QLD: Australian Institute of Marine Science, 115–136.
- Halpern JA. 1970a.** A monographic revision of the goniasterid sea stars of the North Atlantic. Unpublished PhD thesis: University of Miami.
- Halpern JA. 1970b.** Goniasteridae (Echinodermata: Asteroidea) of the Straits of Florida. *Bulletin of Marine Science* **20**: 193–286.
- Hamel J-F, Mercier A. 1994.** New distribution and host record for the starfish parasite *Dendrogaster* (Crustacea: Ascothoracida). *Journal of the Marine Biological Association of the United Kingdom* **74**: 419–425.
- Harris LG. 1991.** Comparative ecology of subtidal actinarians from the coasts of California and the Gulf of Maine, USA. *Hydrobiologia* **216/217**: 271–278.
- Haubold S. 1933.** Über eine neue Form sitzender Pedizellarien bei Seesternen. *Zoologischer Anzeiger*. **103**: 199–205.
- Hayashi R. 1952.** Sea-stars of Seto and adjacent waters. *Publications of the Seto Marine Biological Laboratory* **11**: 143–159.
- Henry L-A, Roberts JM. 2007.** Biodiversity and ecological composition of the macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep-Sea Research I* **54**: 654–672.
- Hourigan TF, Lumsden SE, Dorr G, Bruckner AW, Brooke S, Stone RP. 2007.** Deep coral ecosystems of the United States: introduction and national overview. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G, eds. *The state of deep coral ecosystems of the United States*. NOAA Technical Memorandum CRCP-3. Silver Spring, MD: NOAA, 1–64.
- Howell K, Rogers AD, Tyler PA, Billett DSM. 2004.** Reproductive isolation among morphotypes of the Atlantic sea star species *Zoroaster fulgens*. *Marine Biology* **144**: 977–984.
- Huesbo A, Nottestad L, Fossa JH, Furevik DM, Jørgensen SB. 2002.** Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* **471**: 91–99.
- Imaoka T, Irimura S, Okutani T, Oguro C, Oji T, Kanazawa K. 1991.** Echinoderms from the continental shelf and slope around Japan. *Japan Fisheries Resource Conservation Association*. **II**: 1–159.
- Imaoka T, Irimura S, Okutani T, Oguro C, Oji T, Shigei M, Horikawa H. 1990.** Echinoderms from the continental shelf and slope around Japan. *Japan Fisheries Resource Conservation Association*. **I**: 1–159.
- Jablonski D, Bottjer D. 1988.** Onshore-offshore evolutionary patterns in post-Paleozoic echinoderms: a preliminary analysis. In: R.D. Burke *et al.*, eds. *Echinoderm Biology*. Balkema, Rotterdam, 81–90.
- Jablonski D, Bottjer DJ. 1990.** Onshore-offshore trends in marine invertebrate evolution. In: Ross RM, Allmon WD, eds. *Causes of evolution: a paleontological perspective*. Chicago, IL: University of Chicago Press, 21–75.

- Jensen A, Frederiksen R. 1992.** The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe Shelf. *Sarsia* **77**: 53–69.
- Johnson S. 2005.** The red and the black: bioluminescence and the color of animals in the deep-sea. *Integrative and Comparative Biology* **45**: 234–246.
- Jonsson LG, Nilsson PG, Floruta F, Lundälv T. 2004.** Distributional patterns of macro- and megafauna associated with a reef on the cold-water coral *Lophelia pertusa* on the Swedish west coast. *Marine Ecology Progress Series* **284**: 163–171.
- Koehler R. 1909.** An account of the deep-sea Asteroidea collected by the Royal Indian Marine Survey Ship *Investigator*. *Echinoderma of the Indian Museum Part 5*: 115–131.
- Koehler R. 1926.** Echinodermata; Echinoidea. *Australasian Antarctic Expedition 1911–1914. Scientific Reports. Series C, Zoology and Botany* **8**: 1–134. Sydney : David Harold Paisley, Government Printer.
- Koslow JA, Gowlett-Holmes K. 1998.** *The seamount fauna off southern Tasmania: benthic communities, their conservation and impacts of trawling*. Final report to Environment Australia & the Fisheries Research Development Corporation. CSIRO.
- Krieger KJ, Wing BL. 2002.** Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* **471**: 83–90.
- Lambert P. 1978a.** British Columbia Marine Faunistic Survey report: asteroids from the Northeast Pacific. *Fisheries and Marine Service Technical Report* **773**: 1–23.
- Lambert P. 1978b.** New geographic and bathymetric records for some northeast Pacific asteroids (Echinodermata; Asteroidea). *Syesis* **11**: 61–64.
- Lambert P. 2000.** *Sea stars of British Columbia, Southeast Alaska, and Puget Sound*. *Royal British Columbia Museum Handbook*. Vancouver, CA: University of British Columbia Press, 1–186.
- Levina EV, Kalinovsky AI, Andriyashenko PV, Dmitrenok PS, Aminin DL, Valentin A. 2005.** Phrygiasterol, a cytotoxic cyclopropane-containing polyhydroxysteroid, and related compounds from the Pacific starfish *Hippasteria phrygiana*. *Journal of Natural Products* **68**: 1541–1544.
- Linck JH. 1733.** *De Stellis Marinis*. xxiv + 107 pp. Lipsiae.
- Linné C. (1761).** Fauna Svecica sistens animalia Sveciæ Regni: mammalia, aves, amphibia, pisces, insecta, vermes. natalium, descriptionibus insectorum. Editio altera, auctior. – natalium, descriptionibus insectorum. Editio altera, auctior----. *Stockholmiz, Laurentii Salvii*: xlviii + 578 p., 1 pl.
- Love MS, York A. 2005.** A comparison of the fish assemblages associated with an oil/gas pipeline and adjacent seafloor in the Santa Barbara Channel, Southern California Bight. *Bulletin of Marine Science* **77**: 101–117.
- Ludwig H. 1905.** Asteroidea. *Memoirs of the Museum of Comparative Zoology at Harvard* **32**: 1–292.
- Lundsten L, Barry JP, Cailliet GM, Clague DA, DeVogelaere AP, Geller JB. 2009.** Benthic invertebrate communities on three seamounts off southern and central California, USA. *Marine Ecology Progress Series* **374**: 23–32.
- Mah C. 1998a.** New records, taxonomic notes and a checklist of hawaiian starfish. *Bishop Museum Occasional Papers* **55**: 65–71.
- Mah C. 1998b.** Preliminary phylogeny and taxonomic revision of the Brisingida (Asteroidea: Forcipulatata). In: Mooi R, Telford M, eds. *Proceedings of the 9th International Echinoderm Conference*. San Francisco: Ballkema, 273–277.
- Mah CL. 2005a.** A phylogeny of *Iconaster* and *Glyphodiscus* (Goniasteridae; Valvatida; Asteroidea) with descriptions of four new species. *Zoosystema* **27**: 131–167.
- Mah CL. 2005b.** *Cladistic analysis of the Goniasteridae (Asteroidea: Valvatoidea): phylogeny, evolution and biodiversity*. Unpublished PhD Dissertation, University of Illinois.
- Mah CL. 2006.** Phylogenetic analysis and biogeography of the deep-sea goniasterid, *Circeaster* (Echinodermata: Asteroidea) including descriptions of six new species. *Zoosystema* **28**: 917–954.
- Mah CL. 2007a.** Phylogeny of the Zoroasteridae (Zorocallina; Forcipulatata): evolutionary events in deep-sea Asteroidea displaying Palaeozoic features. *Zoological Journal of the Linnean Society* **150**: 177–210.
- Mah CL. 2007b.** Systematics, phylogeny, and historical biogeography of the *Pentagonaster* clade (Goniasteridae, Valvatida, Asteroidea). *Invertebrate Systematics* **21**: 311–339.
- Maluf Y. 1988.** Composition and distribution of the central eastern Pacific echinoderms. Natural History Museum of Los Angeles County, Technical Reports 2.
- Mauzey KP, Birkeland C, Dayton PK. 1968.** Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* **49**: 603–619.
- McKnight DG. 1973.** Additions to the asteroid fauna of New Zealand: family Goniasteridae. *New Zealand Oceanographic Institute Records* **1**: 171–195.
- McKnight DG. 2006.** The Marine Fauna of New Zealand: Echinodermata: Asteroidea (sea stars). 3. Orders Velatida, Spinulosida, Forcipulatata, Brisingida with addenda to Paxillosida, Valvatida. *NIWA Biodiversity Memoir* **120**: 1–187.
- Mercier A, Hamel J-F. 2008.** Nature and role of newly described symbiotic associations between a sea anemone and gastropods at bathyal depths in the NW Atlantic. *Journal of Experimental Marine Biology and Ecology* **358**: 57–69.
- Moore JA, Vecchione M, Collette BB, Gibbons R, Hartel KE. 2004.** Selected fauna of Bear Seamount (New England Seamount chain), and the presence of ‘natural invader’ species. *Archive of Fishery and Marine Research* **51**: 241–250.
- Mortensen PB, Hovland M, Brattegard T, Farestveit R. 1995.** Deep water bioherms of the scleractinian coral *Lophelia perusa* (L.) at 64° N on the Norwegian Shelf: structure and associated megafauna. *Sarsia* **80**: 145–158.
- Mortensen T. 1933.** Echinoderms of South Africa (Asteroidea and Ophiuroidea). *Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening* **93**: 215–400.

- Mortensen T, Rosenvinge LK. 1933.** Sur une nouvelle algue, *Coccomyxa astericola*, parasite dans une Asterie. *Biologiske Meddelelser* **9**: 1–8.
- Müller OF. 1776.** Zoologiae Danicae Prodomus, seu Animalium Daniae et Norvegiae Indigenarum, characteres, nomina, et synonyma imprimis popularium. Havniae [Copenhagen]: Typis Hallagerii xxxii + 281 p.:
- Müller J, Troschel FH. 1842.** System der Asteriden, 1: Asteriae; 2: Ophiuridae. 134 pp. Braunschweig.
- Nesis KN. 1961.** The routes and periods of formation, of the interrupted area of distribution of amphiboreal species of marine bottom animals. *Okeanologiya* **1**: 894–903.
- O'Connor B, Tyndall P. 1986.** Notes on eight species of rare or deep water echinoderms from Irish inshore waters. *Irish Naturalists Journal* **22**: 96–97.
- Pawson DL, Ahearn C. 2001.** Bathyal echinoderms of the Galapagos Islands. In: Barker M, ed. *Echinoderms 2000, New Zealand*. Netherlands: A.A. Balkema, 41–46.
- Perrier E. 1875.** Révision de la collection de stellérides du *Museum d'Histoire naturelle de Paris*. Paris: Reinwald.
- Perrier E. 1884.** Mémoire sur les étoiles de mer recueillies dans la Mer des Antilles et la Golfe de Mexique. *Nouvelle Archives Museum d'Histoire naturelle de Paris* **6** (2): 127–276.
- Pettibone M. 1969.** Remarks on the North Pacific Harmothoe tenebricosa Moore (Polychaeta, Polynoidae) and its association with asteroids (Echinodermata, Asteroidea). *Proceedings of the Biological Association of Washington* **82**: 31–42.
- Reed JK, Pomponi SA, Weaver D, Paull CK, Wright AE. 2005.** Deep-water sinkholes and bioherms of South Florida and the Pourtales Terrace – habitat and fauna. *Bulletin of Marine Science* **77**: 267–296.
- Reed JK, Weaver DC, Pomponi SA. 2006.** Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the southeastern U.S.: Blake Plateau, Straits of Florida, and Gulf of Mexico. *Bulletin of Marine Science* **78**: 343–375.
- Roberts JM, Henry L-A, Long D, Hartley JP. 2008.** Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic. *Facies* **54**: 297–316.
- Roberts S, Hirshfield M. 2004.** Deep-sea corals: out of sight, but no longer out of mind. *Frontiers in Ecology and the Environment* **2**: 123–130.
- Robson EA. 1961.** The swimming response and its pace-maker system in the anemone *Stomphia coccinea*. *Journal of Experimental Biology* **38**: 685–694.
- Ross SW, Quattrini AM. 2007.** The fish fauna associated with deep coral banks off the southeastern United States. *Deep Sea Research I* **54**: 975–1007.
- Rowe FWE, Gates J. 1995.** Echinodermata. In: Wells A, ed. *Zoological catalogue of Australia* **33**. Australia: CSIRO Melbourne, 63–72.
- Sladen WP. 1889.** Asteroidea. *Report of the Scientific Results of H.M.S. Challenger* **30**: 1–893.
- Smith AG, Smith DG, Funnell BM. 1994.** *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press.
- Spencer WK, Wright CW. 1966.** Asterozoans, Part U: Echinodermata. In: Moore RC, ed. *Treatise on invertebrate paleontology*, Vol. 3. Lawrence: University of Kansas Press, U4–U107.
- Stampanato S, Jangoux M. 2004.** The asteroid fauna (Echinodermata) of Marion and Prince Edward Islands. *Annals of the South African Museum* **112**: 1–16.
- Stimpson W. 1857.** On the Crustacea and Echinodermata of the Pacific Shore of North America. *Boston Journal of Natural History* **6**: 444–532.
- Stone RP. 2006.** Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interaction. *Coral Reefs* **25**: 228–238.
- Swofford DL. 2003.** PAUP*. *Phylogenetic analysis using parsimony (*and other methods)*. Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Trego KD. 2008.** New distribution information for eastern Pacific asteroid and holothuroid species. *JMBA2 Biodiversity Records* **6125**: (no pagination).
- Verrill AE. 1883.** Reports on the Anthozoa, and on some additional species dredged by the Blake in 1877–1879, and by the US Fish Commission steamer 'Fish Hawk' in 1880–1882. *Bulletin of the Museum of Comparative Zoology* **11**: 1–72.
- Verrill AE. 1899.** Revision of certain genera and species of starfishes, with descriptions of new forms. *Transactions of the Connecticut Academy of Arts and Sciences* **10**: 145–234.
- Verrill AE. 1909.** Descriptions of new genera and species of starfishes from the North Pacific coast of America. *American Journal of Science* **28**: 59–70.
- Verrill AE. 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.
- Vogler C, Benzie J, Lessios H, Barber P, Worheide G. 2008.** A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biology Letters* **4**: 696–699.
- Walker CW. 1979.** Ultrastructure of the somatic portion of the gonads in asteroids, with emphasis on flagellated-collar cells and nutrient transport. *Journal of Morphology* **162**: 127–162.
- Wares JP. 2001.** Biogeography of *Asterias*: North Atlantic climate change and speciation. *Biological Bulletin* **201**: 95–103.
- Wood RL. 1958.** Identification and microanatomical study of a new species of Epizoanthus (Zoanthidea). *Dissertation Abstracts* **18** (2): 707–708.

APPENDIX 1

DATA MATRIX

Taxon/Node	1111111111222222222233333333334444444
	1234567890123456789012345678901234567890123456
OG: <i>Mediaster aequalis</i>	000000010000000000001000000000000100000000
OG: <i>Peltaster placenta</i>	0111001010000000000100101000000000000000001
OG: <i>Cladaster analogus</i>	0101000010000012000100101000010100000100000001
<i>Hippasteria californica</i>	11111110100111122110001101111000011011111101
<i>Hippasteria heathi</i>	11111110100111122110000101111000011010011101
<i>Hippasteria spinosa</i>	11111110100111122110000101111000011010011101
<i>Hippasteria phrygiana</i>	11111110100111122110000101111000011010011101
<i>Sthenaster emmae</i>	1311031111000022001311103001100100011011011101
<i>Evoplosoma virgo</i>	1101031011110000111111111001111101100101001102
<i>Evoplosoma scorpio</i>	1101111111001122111100111011121101100111001102
<i>Evoplosoma claguei</i>	1101111011001111110100111000011101100110001102
<i>Evoplosoma voratus</i>	1101211011001111110100111001011101100111001102
<i>Cryptopeltaster lepidonotus</i>	1111121021121100110100201010010010011010011111
<i>Gilbertaster caribaea</i>	1212021021120000110211202100000000011020002010
<i>Gilbertaster anacanthus</i>	1212020021120000110211202100000000011020002010

APPENDIX 2

CHARACTER LIST

- | | |
|--|---|
| <p>1.1. Pulpy tissue in body wall. (0) absent, (1) present (Figs 7A, 8A).</p> <p>1.2. Abactinal fasciolar channels. (0) channels well developed, (1) channels shallow, (2) channels absent, (3) channels wide (Fig. 4A, E, H).</p> <p>1.3. Secondary plates. (0) absent, (1) present (Fig. 10E).</p> <p>1.4. Abactinal plate morphology. (0) tabular, (1) flat and platform like (Fig. 4A, E), (2) low (Fig. 3C, E).</p> <p>1.5. Abactinal primary structure, large. (0) absent (Fig. 8B), (1) big spine (Figs 6A, 7C, 10A, C), (2) tubercle present.</p> <p>1.6. Accessory fringe on abactinal plates. (0) granular fringe, (1) spiny fringe (Fig. 10F), (2) angular fringe (Fig. 5B, D), (3) fringe absent.</p> <p>1.7. Carinal series. (0) clearly distinguished, (1) poorly distinguished (Fig. 4A).</p> <p>1.8. Abactinal spinelets. (0) absent, (1) present. (Figs 4E, 9C, 10A, C)</p> <p>1.9. Large, coarse granules. (0) absent, (1) smaller, (2) larger (Figs 3B, C, F, 5B,D).</p> <p>1.10. Abactinal plate articulation. (0) moderately well articulated, (1) tightly articulated (Fig. 4F).</p> <p>1.11. Surface granulation flush between granules. (0) not forming flush surface, (1) forms flush surface with other granules. (Fig. 3B, C, E)</p> <p>1.12. Granular distribution. (0) incomplete cover to absent, (1) complete dense granular cover (Fig. 9C), (2) coarse granules, widely spaced.</p> | <p>2.1. Large superomarginal spines. (0) absent, (1) present. (Figs 5D, 6A, D, 10A–C)</p> <p>2.2. Large inferomarginal spines. (0) absent, (1) present. (Figs 5D, 6A, D, 10B–C)</p> <p>2.3. Superomarginal surface. (0) granules form complete cover (Fig. 9C), (1) bare to partial cover, (2) widely spaced. (Fig. 10A, B, C, G)</p> <p>2.4. Inferomarginal surface. (0) granules form complete cover (Fig. 9C), (1) bare to partial cover (Fig. 10B, C), (2) widely spaced. (Fig. 10B, C, G).</p> <p>2.5. Superomarginal plate shape at inter-radius. (0) wide (Fig. 4H), (1) quadrate (Fig. 10A–C), (2) rounded (Fig. 10G).</p> <p>2.6. Inferomarginal plate shape at inter-radius. (0) wide, (1) quadrate, (2) rounded (Fig. 10G).</p> <p>2.7. Spinelets on marginal plates. (0) absent, (1) present (Figs 4H, D, 9D, 10G).</p> <p>2.8. Fasciolar grooves between marginal plates. (0) well developed, (1) shallow (Fig. 10C, G), (2) absent, (3) wide (Fig. 4C).</p> <p>2.9. Differentiated superomarginal fringe. (0) present (Fig. 10G), (1) poorly differentiated (Fig. 3C).</p> <p>2.10. Differentiated inferomarginal fringe. (0) present (Fig. 10G), (1) poorly differentiated (Fig. 3C).</p> <p>2.11. Surface granule size. (0) absent, (1) smaller (Fig. 9D), (2) larger (Fig. 3C).</p> <p>2.12. Marginal plate series calcification. (0) moderate to heavily calcified (Fig. 10A–C), (1) lightly developed (Fig. 9A).</p> <p>3.1. Actinal fasciolar groove. (0) well developed, (1) shallow, (2) absent, (3) wide (Fig. 4C, D).</p> |
|--|---|

- 3.2. Large pedicellariae on first adambulacral. (0) absent, (1) present (Fig. 3D, G).
- 3.3. Large actinal spines. (0) absent, (1) present (Fig. 6D).
- 3.4. Actinal granules. (0) present (Fig. 3D, G), (1) absent.
- 3.5. Actinal spinelets. (0) absent, (1) present (Figs 4C, D; 6D; 9B).
- 4.1. Subambulacral spines: abundance-size relationship. (0) several, smaller, (1) fewer larger, (2) many (Figs 6B, C, 8D,E).
- 4.2. Furrow spines in cross-section. (0) round (Fig. 5C), (1) angular (Fig. 6C).
- 4.3. Furrow spines compressed. (0) absent, (1) present (Fig. 6B, C).
- 4.4. Pedicellariae replacement of furrow spines. (0) all furrow spines present (Fig. 6D), (1) pedicellariae replaces furrow spines (Fig. 5C, E).
- 4.5. Furrow spines with rough tips. (0) smooth, (1) rough (Fig. 6B, C).
- 4.6. Subambulacral composition. (0) spines only, (1) spines plus pedicellariae (Fig. 7E).
- 7.1. Enlarged pedicellariae. (0) absent, (1) present (Fig. 3C, D, G, 5B, D, E).
- 7.2. Bivalve pedicellariae. (0) absent, (1) present (Figs 3C, D, G, 5B, D, E).
- 7.3. Flat-paddle like pedicellariae. (0) absent, (1) present (Fig. 10F).
- 7.4. Pedicellariae abundance. (0) absent to few, (1) abundant, (2) very abundant (Fig. 3C).
- 7.5. Serrated teeth on pedicellariae. (0) absent, (1) present (Figs 4F, 6C).
- 7.6. Triangular pedicellariae. (0) absent, (1) present.
- 7.7. Pedicellariae on raised base. (0) absent, (1) present (Fig. 4E).
- 8.1. Superomarginal plate facing on abactinal surface. (0) dorsal facing, (1) lateral facing (Fig. 5A, D), (2) dorsolateral facing.
- 8.2. Body-disk swollen. (0) weakly so, (1) strongly so (Fig. 4A, B).
- 8.3. Granules, large & flattened. (0) absent, (1) present (Figs 5C, D).
- 8.4. Arm dimensions. (0) moderate to narrow, (1) broad to short (Fig. 4A, B), (2) narrow and tapering.

APPENDIX 3

ARTIFICIAL KEY TO INCLUDED TAXA (INCLUDING TERMINOLOGY)

Pulpy tissue covering abactinal plates. Abactinal plates tightly articulated with secondary plates. Fasciolar grooves between plates often shallow to absent. Body coelom swollen, thick. Large primary conical spines, coarse granules and/or pedicellariae (equivalent to diameter of plate base) present on abactinal, marginal, and actinal plate surface. Bivalve pedicellariae are common. Marginal plates quadrate to ovalate, often bare but surrounded by peripheral accessories. Furrow spines often thickened, large and relatively few in number (two to four in most). Adults often large with heavy skeletons, body shape is frequently stellate but smaller individuals can be weakly pentagonal (but never pentagonal as adults).....Hippasterinae (proceed to 0/0a)

Pulpy tissue absent. Abactinal plates not tightly articulated. Secondary plates present or absent. Paxillae or tabulae present or absent, often with well-developed fasciolar grooves present or absent. Large conical spines and pedicellariae may be present but not on all plate surfaces and not generally observed together. Marginal plates variable but may be bare to completely covered by granules. Furrow spines may number from few (two to three) to very high (over ten) per plate. Body skeleton more dorsoventrally flattened. Marginal plates abutting over midradius present or absent. Body shape can be completely pentagonal or stellate as adults.....Other Goniasteridae

(0) Spines and/or spinelets absent from abactinal, marginal, and actinal plate surface (Fig. 3A, E). Secondary plates absent. Marginals never bare – always covered by closely articulated, blunt, flattened granules (Fig. 3C). Large, bivalve pedicellariae, abundant, flush with surface (Fig. 3A, C, D, G). First adambulacral with enlarged bivalve pedicellariae on entire length of plate (Fig. 3D, G), superceding the furrow spines. Two to three furrow spines per plate.....*Gilbertaster*

Abactinal plates with one to five smaller plates enclosed by peripheral plates (Fig. 3E, F). Multiple, smaller subambulacral spines present (Fig. 3G). $R : r = 2.68$. Tropical Pacific: Hawaii, New Zealand. *Gilbertaster anacanthus* Fisher, 1906 (Fig. 3E–G)

Abactinal plates dominated by pedicellariae, small tubercles, and ruffled processes (Fig. 3A, B). None enclosed by peripheral plates. Single triangular wedge-like subambulacral spine present (Fig. 3D). $R : r = 2.5$. Tropical Atlantic: off Florida/Carolinian coast.....*Gilbertaster caribaea* (Verrill, 1899) (Fig. 3A–D)

(0a) Spinelets or large, prominent conical spines present on most abactinal, marginal, and actinal plate surfaces (e.g. Figs 6A, D, E, 10B, C). Secondary plates present (Fig. 10E). Marginals completely bare (Fig. 10B, C) or sometimes partially covered by spinelets (Fig. 6D) or granules. Up to ten furrow spines per plate, but often fewer than four, often thick and round in cross-section but sometimes compressed (Fig. 6C).....(1)

- (1) Abactinal, marginal, actinal plates covered by small, conical spinelets (Fig. 4A, B, C, D, E, H). No single large spines present (Fig. 4A, B). Marginal plates at inter-radius wide in outline (Fig. 4H).....*Sthenaster emmae* (Fig. 4A–H)
- (1a) Abactinal, marginal, actinal plates may or may not be covered by large conical spines (Figs 6A, 7A, C, 10A, C). Spinelets present or absent. Marginal plates at inter-radius equidistant quadrate to ovaloid in shape.....(2)
- (2) Tight fitting, angular granules cover abactinal (Fig. 5B, D), marginal (Fig. 5D), actinal plates (Fig. 5E). Prominent spines on marginal plates (Fig. 5D). Large pedicellariae adjacent to adambulacral plates (Fig. 5E).....*Cryptopeltaster lepidonotus* (Fig. 5A–E)
- (2a) Tight fitting, angular granules absent. Large pedicellariae present or absent.....(3)
- (3) Marginal plates large, heavily calcified, facing dorsally (Fig. 10A) or are visible dorsolaterally. Large bivalve pedicellariae present with smooth blades (Fig. 10D). Spines typically blunt or conical ((Figs 10A–C). Furrow spines enlarged, rounded in cross-section (Fig. 10B). Body wall thick, swollen.....*Hippasteria* (Fig. 10A–G)
- (3a) Marginal plates more lightly calcified, facing laterally (Figs 6A, 7A). Smaller palmate tong-like pedicellariae, with teeth on blades (Fig. 6C). Sharp spines and spinelets on abactinal, actinal surface (Fig. 6A, D). Furrow spines small and numerous, often angular to quadrate in cross-section with furrows (Figs 6B, C, 9B). Body wall relatively thin.....*Evoplosoma* (Figs 6–9)
- (4) Spinelets present on marginal plates, sometimes in abundance.....(5)
- (4a) Spinelets absent from marginal plates, which are largely bare of accessories (Figs 7B, 8C), except for pedicellariae and blunt granules.....(8)
- (5) Abactinal, marginal, and actinal plate surfaces covered by densely packed, spiny granules (Fig. 9A, C). Larger, prominent abactinal, marginal, and actinal intermediate spines absent.....*E. virgo* Downey, 1982 (Fig. 9A–D)
- (5a) Abactinal, marginal, and actinal plate surfaces *not* covered by densely packed granules. Large, prominent abactinal, marginal and actinal intermediate spines present.....(6)
- (6) Overall disk large, gradually tapering into arms. Adults ($R = 11.0$ cm) with 70–90 marginal plates per inter-radius. Known only from Indian Ocean.....*E. augusti* Koehler, 1909
- (6a) Overall disk smaller relative to arms, which are tapering and more sharply set off from disk. Adults ($R \leq 8.0$ cm) with 60–66 marginal plates per inter-radius. North Atlantic and Hawaii.....(7)
- (7) Furrow spines five to seven, mostly six or seven on adambulacrals proximal to mouth. Spinelets on marginal plates cover surface of plate (Fig. 6D). Approximately 60–66 superomarginals per inter-radius (approximately 30–33 from midline to tip). North Atlantic.....*E. scorio* Downey, 1981 (Fig. 6A–E)
- (7a) Furrow spines three to five (six on first, five on second, three or four on rest). Spinelets do not evenly or completely cover surface of superomarginal plate (conical or pointed granules may be clustered, however). Approximately 30 superomarginals per inter-radius (approximately 15 from midline to tip). Hawaiian Islands (based on the size of the specimen described, this is possibly a smaller/sub-adult specimen. Larger adult specimens may show character variation.).....*E. forcipifera* Fisher, 1906
- (8) Abactinal, marginal, actinal surface covered by prominent cover of thickened, blunt spines evenly distributed over body. Furrow spines five to six. Superomarginal plates per inter-radius ~50–70 Indo-Malaysian region.....*E. timorensis* Aziz & Jangoux, 1985
- (8a) Body surface covered by short, round bullet-like tubercles or prominent, conical spines (Fig. 7A). Superomarginal plates per radius per inter-radius ~58–60. Rodriguez Seamount & Islas Tres Marias (Mexico). North Pacific region.....*E. claguei* sp. nov. (Fig. 7A–F)
- (8b) No prominent conical spines on abactinal plates (although tubercles are present). Abactinal plates are mostly bare of larger, primary spines or tubercles (Fig. 8B). Superomarginal plates per radius per inter-radius ~44–45 (greater number of smaller-sized inferomarginals = 54–55 per inter-radius). Superomarginals larger, fewer than inferomarginals. More rounded, ovalate in shape (Fig. 8C) Davidson Seamount, North Pacific region.....*E. voratus* sp. nov. (Fig. 8A–F)

TERMINOLOGY USED IN KEY

Abactinal – The surface above the superomarginal series that includes the primary cirlet, carinal, and dorsal surface plate series, as well as accessories and primaries that sit on those plates.

Accessories – Smaller structures, relative to the primaries, such as spinelets and granules, that are mounted on or adorn a plate surface. Accessories are primarily mounted on other plates and are smaller

than the plate they adorn and as such, occur in large numbers compared to primaries, described below.

Actinal – The surface below the inferomarginal series that includes the mouth, actinal, oral, and adambulacral plate series, as well as all accessories and primaries, which sit on these plate series.

Bivalve pedicellariae – Pedicellariae with two low valves inset in a depression in a plate, often resembling a bivalve mollusc.

Carinal plate series – Abactinal plates in series along midradial line along abactinal arm surface, often flanked along arm's length by adjacent lateral series.

Fasciolar channels – Channels between two rows of plates lined with ciliated epithelium. Fasciolar grooves are most easily distinguished between tall, shaft-like plates, but occur on lower mound-like plates as well. Channels are created between any two series of accessories (spinelets, granules, etc.) or plates.

Furrow spines – Series of spines present on furrow margin of adambulacral plate.

Granules – A small round, hemispherical or irregular grain of calcite present on the plate surface. (Granules are frequently lost during preservation or rubbed off specimens over time.)

Inferomarginal plate – A plate of the lower of the two marginal series.

Marginal plates – A plate of one of the two horizontal series usually defining the ambitus extending to the terminal plate. Facing of the ambitus may be directed dorsally, ventrally, or laterally, depending on the size and shape of the marginal plate series, which varies from taxon to taxon. Marginals can be paired or offset and are often, but not always, equal in number.

Pedicellariae – Small pincer-like organs on the body surface, which are variously modified in shape and number of components. Individual pieces are known as blades or valves.

Pointed granule – A small rounded granule with a sharp or pointed tip.

“R” and “r” – measurements of the radius as defined from the center of the disk, usually by the anus. “R” is the distance from the center of the disk to the armtip whereas “r” is the distance from the center of the disk to the interradius. The ratio of R:r is often a means of determining overall shape of the body (with 1:1 being pentagonal).

Secondary plates – Smaller plates (less than half to one quarter of other plate size) found between abactinal.

Spinelets – Similar to a pointed granule but more conical at the base with a sharp or pointed tip.

Spines – A prominent, externally expressed conical or pointed shaft-like primary structure, usually articulated on the surface of a plate.

Superomarginal plates – A plate of the upper marginal series.

Tong-like pedicellariae (aka alveolar pedicellariae) – Pedicellariae with two slender, or toothed valves, usually opened out and lying in alveolus of matching shape.

Tubercle – Swollen, enlarged, blunt, and rounded calcified primary structure, parallel to a spine, but spherical to club-like in shape

APPENDIX 4

SUMMARY LIST OF GENERA, SPECIES, AND SUMMARY NOTES

Genus	Species	Notes
<i>Cryptopeltaster</i>	<i>lepidonotus</i>	Range extended, neotype designated.
<i>Cryptopeltaster</i>	<i>philippii</i>	Synonymized with <i>Cryptopeltaster lepidonotus</i>
<i>Evoplosoma</i>	<i>augusti</i>	Type may be lost.
<i>Evoplosoma</i>	<i>claguei</i>	New species.
<i>Evoplosoma</i>	<i>scorpio</i>	Range extended.
<i>Evoplosoma</i>	<i>timorensis</i>	
<i>Evoplosoma</i>	<i>virgo</i>	
<i>Evoplosoma</i>	<i>voratus</i>	New species.
<i>Evoplosoma</i>	sp. 1	From Fujikura <i>et al.</i> , 2008. From off Java (Indonesia).
<i>Gilbertaster</i>	<i>anacanthus</i>	Range extended to Palau.
<i>Gilbertaster</i>	<i>caribaea</i>	Species placed into <i>Gilbertaster</i> . Range extended.
<i>Hippasteria</i>	<i>antiqua</i>	Cretaceous fossil. Probably not true <i>Hippasteria</i>
<i>Hippasteria</i>	<i>californica</i>	
<i>Hippasteria</i>	<i>colossa</i>	Part of <i>H. spinosa</i> complex
<i>Hippasteria</i>	<i>derjungini</i>	Part of <i>H. spinosa</i> complex
<i>Hippasteria</i>	<i>falklandica</i>	
<i>Hippasteria</i>	<i>heathi</i>	
<i>Hippasteria</i>	<i>imperialis</i>	
<i>Hippasteria</i>	<i>kurilensis</i>	Part of <i>H. spinosa</i> complex
<i>Hippasteria</i>	<i>leiopelta</i>	
<i>Hippasteria</i>	<i>mammifera</i>	Part of <i>H. spinosa</i> complex
<i>Hippasteria</i>	<i>nozawai</i>	
<i>Hippasteria</i>	<i>pedicellaris</i>	Part of <i>H. spinosa</i> complex
<i>Hippasteria</i>	<i>phrygiana argentinensis</i>	Part of <i>H. phrygiana</i> complex
<i>Hippasteria</i>	<i>phrygiana phrygiana</i>	Part of <i>H. phrygiana</i> complex
<i>Hippasteria</i>	<i>phrygiana capensis</i>	Part of <i>H. phrygiana</i> complex
<i>Hippasteria</i>	<i>phrygiana strongylactis</i>	Part of <i>H. phrygiana</i> complex
<i>Hippasteria</i>	<i>spinosa</i>	Species complex in North Pacific
<i>Hippasteria</i>	<i>tasmanica</i>	
<i>Sthenaster</i>	<i>emmae</i>	New genus, new species