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New taxa of Valvatida (Asteroidea) with an overview of bivalve pedicellariae proposed form and function

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Abstract

Bivalve pedicellariae are a prominent yet poorly understood morphological feature observed within specific groups within the Valvatida (Asteroidea) and have been used primarily as a taxonomic character. Seven new species, including the new genus *Astrophylax* which features prominent bivalve pedicellariae are described herein. *In situ* observations of shallow and deep-sea taxa provide possible insight into bivalve pedicellariae function. An overview of taxa which contain bivalve pedicellariae, primarily in the Goniasteridae but also the Oreasteridae and the Asteropseidae is also included. A survey of these taxa and their pedicellariae, including trends in abundance, biogeography, and depth provide further context for the understanding of these unusual characters, especially within the Goniasteridae and the Oreasteridae.

Key words: Bivalve pedicellariae, deep-sea, in situ observations, functional morphology, Asteropseidae, Oreasteridae, Hippasterinae

Introduction

Pedicellariae are externally expressed, pincer-like structures (singular=pedicellaria), which are used by echinoderms to interact with the external environment in various ways and are among the many morphologically complex features that characterize the Echinodermata. The role and function of pedicellariae varies widely across echinoderms, including a broad range of functions in asteroids and echinoids, including, but not limited to feeding (e.g. Dearborn *et al*. 1991), defense (e.g. Ghyoot *et al*., 1994), and pest management/prevention of debris settlement (e.g. Campbell & Rainbow, 1976, Lambert *et al*., 1984) although this latter function is not universal (Guenther *et al*., 2007).

In the Asteroidea, pedicellariae are composed of two or more ossicles known as valves and appear to be extensions from the underlying plate or are attached with fleshy stalk. In some cases pedicellariae are associated with a pit or alveolus (derived and modified from Clark & Downey, 1992, Campbell, 1983). The earliest and most prominent consideration of pedicellariae in asteroids and echinoids was undertaken by Perrier (1869) followed by Viguier (1879) who was one of the first to utilize asteroid pedicellariae in a taxonomic context. Campbell (1983) provided a review of pedicellariae form and function in asteroids and echinoids. Among extant echinoderms, pedicellariae are best known in Echinoidea (aka sea urchins and sand dollars, e.g., Coppard *et al.* 2012), Asteroidea (aka sea stars or starfishes, Campbell, 1983; Jangoux & Lambert 1988), and now, in Ophiuroidea (Turner *et al*., 2021, Turner & O'Neill, 2023). Pedicellariae are not known from Crinoidea (feather stars and sea lillies) or Holothuroidea (sea cucumbers). Most accounts (e.g. Coppard *et al*., 2012, Campbell 1983) generally begin with the premise that asteroid and echinoid pedicellariae have been independently derived, a premise which is further followed here.

Pedicellariae are prominent features in the asteroids, so much so that higher taxonomic groupings bear their namesakes, e.g. forcipulate pedicellariae and Forcipulatacea and valvate/valvulate pedicellariae and Valvatacea. Pedicellariae presence and absence has been a consistently used character in diagnosing the major taxonomic groups within the Asteroidea dating back to Viguier (1879). Agassiz (1873) postulated on homologies of asteroid and echinoid pedicellariae, arguing that they were derived from accessory structure such as granules spines. Asteroid pedicellariae variably appear similar to jaws, wrenches, forceps, paddles and clamps (Figs 1A–E), in some cases, these are connected with stalks (Fig. 1A) and in others, flush with the body surface (e.g. Fig. 2F) and/or with an underlying chamber or alveolus (Fig. 2F).

Fossil pedicellariae valves have been recorded from the Middle Ordovician (Tinn & Ainsaar, 2014) with apparent bivalve pedicellariae from the Silurian *Bdellacoma*, classified as an ophiuroid but which shows asteroid affinities (Sutton *et al*., 2005). Blake (2009) documented pedicellariae in the Devonian Helianthasteridae, a Paleozoic asteroid group distant from the crown-group. Gale (2011) has also discussed asteroid pedicellariae within a paleontological/phylogenetic context.

Felipdedal/unguiculate/forcipulate pedicellariae (Fig. 1A, E) are composed of two valves with an underlying

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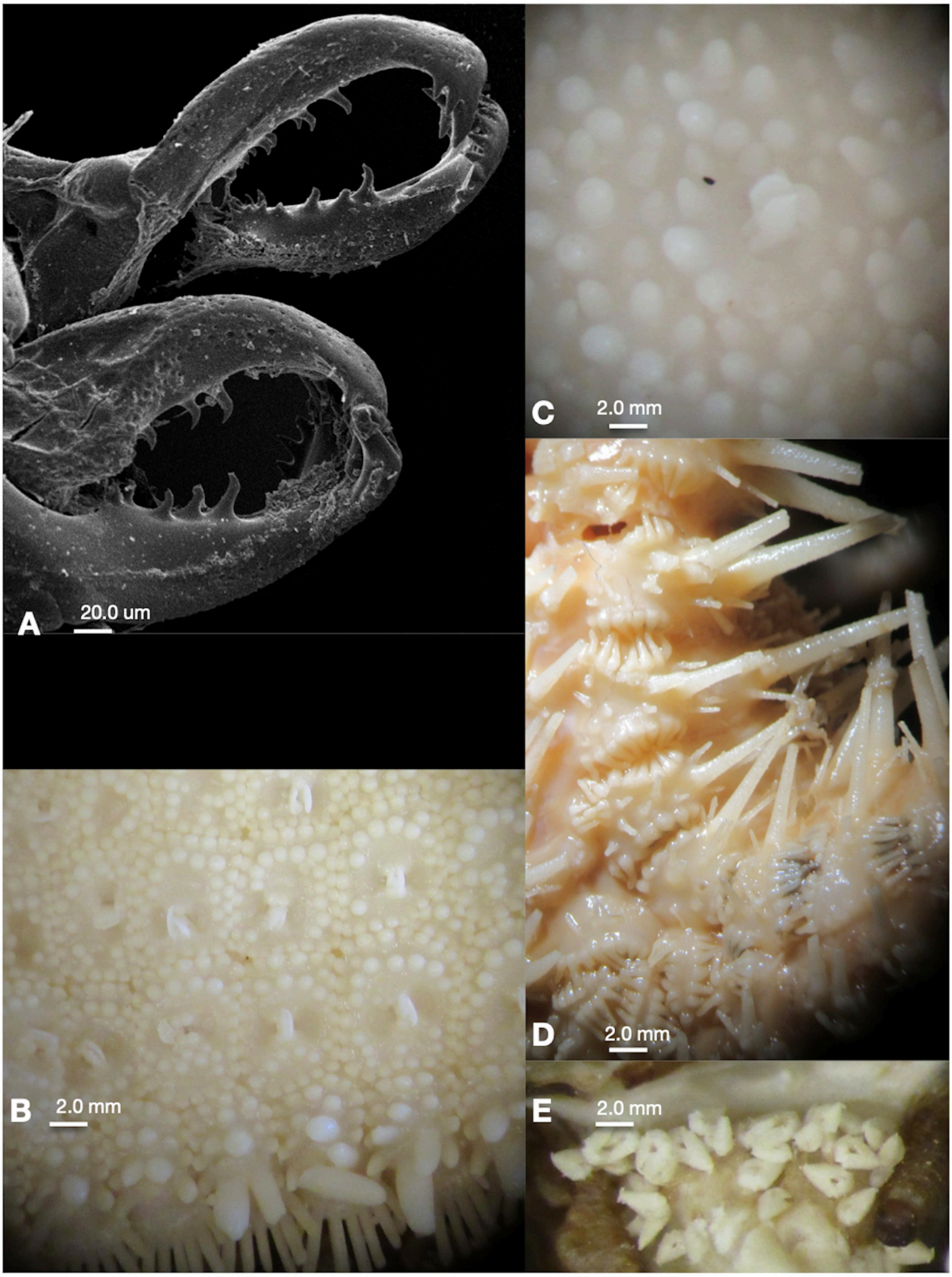

FIGURE 1. Non-bivalve pedicellariae diversity. A. Felipedal/forcipulate pedicellariae in *Labidiaster annulatus*, No Data, USNM collections B. *Astroceramus* sp. Palau, CASIZ 308975, Paddle-shaped pedicellariae on actinal surface. C. *Cladaster rudis* North Atlantic USNM 1607547, Paddle-shaped pedicellariae with square valves on actinal surface. D. Pectinate pedicellariae, *Benthopecten spinuliger* (Ludwig 1905), off Oregon coast, CASIZ 122300. E *Neomorphaster margaritaceus* Bear Seamount, North Atlantic USNM 1016081 Straight pedicellariae on oral plates.

basal piece, generally toothed on the upper valve margin with interlocking claws or points, attached in many taxa with a stalk to the underlying plate, are the most abundant and recognizable diagnostic feature for the Forcipulatacea, a historically well-supported and recognizable group (Mah & Foltz 2011b; Fisher 1928, 1930). Position of these pedicellariae is relevant, as pedicellariae with straight, beak-like valves are present primarily on abactinal, lateral, and adambulacral surfaces whereas the more curved, claw-like pedicellariae occur in tufts around spines on the abactinal and lateral surfaces.

Alveolar, pectinate simple pedicellariae are composed of two or more valves sitting either on the plate surface (Fig. 2A–G) or in association with an underlying chamber or alveolus (Fig. 2F) are present and in some cases diagnose taxa within the Valvatacea. Pectinate and simple pedicellariae are comprised of spines present on the plate surface or edge and are most common in the Paxillosida, especially in the Benthopectinidae (Fig. 1D). More tong-like, paddle or bivalve pedicellariae are present in the Valvatida and especially in the Goniasteridae and Oreasteridae. Some groups, such as the Velatida, including the Pterasteridae, Korethrasteridae, and the Myxasteridae, are completely devoid of pedicellariae (Fisher, 1911; Clark & Downey 1992).

A full understanding of the role and function of pedicellariae in asteroids is an active area of research. Pedicellariae in the Forcipulatacea are better understood than those in the Valvatacea where they are abundant and better studied. Large pedicellariae covering the surface of arms on the Antarctic heliasterid *Labidiaster annulatus*, can capture mobile crustaceans, including krill and amphipods in addition to fish (Dearborn *et al*., 1991). The deep-sea Brisingida utilize numerous pedicellariae on outwardly projecting spines to capture pelagic, swimming crustaceans and other prey (Emson & Young, 1994). Pedicellariae in the temperate Pacific asteriid, *Stylasterias forreri* have been argued as mechanisms for fish-capture (Chia & Amerongen, 1975). Pedicellariae on some nearshore species, such as *Marthasterias glacialis* responds to direct and indirect tactile stimuli, suggesting protective behavior against unwanted materials and organisms (Lambert *et al*., 1984).

Pedicellariae in the Valvatida are among the most poorly understood. Most pedicellariae types in this group have valves that vary in shape from paddle-like, tong-shaped, and especially those that are more bivalve in shape have been used primarily as taxonomic characters without a clear understanding of their function or underlying biology. Fisher (1911: 174) provided a "Note" on pedicellariae providing a key to differentiate the different types of pedicellariae observed within the "Phanerozonia" but more specifically in the Goniasteridae. However, no observations or studies of the function of these types of pedicellariae could be located, at least not to the level of detail observed in forcipulate pedicellariae (e.g. Lambert *et al.,* 1984).

Among the most important questions about pedicellariae concerns their evolutionary relationships and underlying homology which has been a longstanding issue in sea urchins (Agassiz, 1873, Coppard *et al*. 2012) but not in asteroids. A recent survey of Pacific valvatidans, including the Goniasteridae and the Oreasteridae has revealed new species displaying prominent bivalve pedicellariae. Given these specimens and new *in situ* observations, it was deemed timely to survey bivalve pedicellariae, these surveyed here.

Materials and Methods

Specimens, images and videos described herein are housed at the National Museum of Natural History in Washington, D.C. (USNM), the Museum national d'Histoire naturelle (MNHN) in Paris, France, the California Academy of Sciences in San Francisco, CA (CASIZ), the Western Australian Museum in Perth, Australia (WAM) and the National Museum of the Philippines in Manila (PNM).

Videos from the NOAA Ship *Okeanos Explorer* were obtained during expeditions throughout the tropical Pacific during the CAPSTONE expeditions between 2015 and 2017. Full details for these dives are summarized in Mah (2022). Image files cited follow a consistent format, where the first numerical sequence, refers to the expedition number, followed by the date and time, followed by format of the data image. Thus, "EX1702_IMG_20170301T011018Z_ROVHD.jpg" refers to the expedition EX 1702 (to American Samoa), on March 1st, 2017, followed by the time index and file format (jpg. taken by the Remotely Operated Vehicle). Imagery and video are public domain and can be obtained from the author or from the National Oceanic and Atmospheric Administration's (NOAA) Ocean Exploration Division, https://oceanexplorer.noaa.gov/explorations/explorations.html.

NOAA Ship *Okeanos Explorer* images and video cited herein have also been assigned USNM catalog numbers and for the purposes of long-term storage, both USNM and NOAA are file repositories.

Scanning Electron Microscopy (SEM) used herein were taken using a Zeiss EVO MA15 at the Scientific Imaging Lab of the National Museum of Natural History of the Smithsonian Institution. The specimen (USNM 1018861) was dissected following the protocol described by Fau & Villier (2018, 2020).

Morphological terminology not defined herein can be referred to the Glossary in Clark & Downey (1992: xx).

Definitions, and Terms

Comment on Taxonomic Overview (Table 1)

The prominence of bivalve pedicellariae in several of the newly described taxa motivated a comparison of other Valvatida to survey, locate and identify any possible patterns based on abundance, location, size, shape and other variables relative to taxonomy or behavior. A comprehensive survey of taxa with these characteristics is included in Table 1 and an attempt was made to

TABLE 1.

	bvalve size (outlined in Definitions & Terms)	Distribution Trends (outlined in Discssion)	location (outlined in Definitions & Terms)	Bivalve Pedicellariae shape	Depth	Family
Petricia vernicina	medium	diffuse-few	Abactinal, marginal, actinal intermediate	lip-like	Australia, New Zealand, Kermadec islands, 0–70 m	Asteropseidae
Valvaster striatus	large	moderate to abundant	superomarginals	bivalve clam like	Indo-Pacific. 0–58 m.	Asteropseidae
Akelbaster novaecaledoniae	medium	moderate to abundant	Abactinal, marginal, actinal intermediate	lip-like	New Caledonia. 225–400 m.	Goniasteridae
Anthenoides peircei	large	diffuse-few	actinal intermediate-oral	lip-like	Tropical Atlantic, 55–844 m	Goniasteridae
Bathyceramaster kelliottae	large	moderate to abundant	actinal but serial series (adjacent to adambs)	lip-like	North Atlantic, 1386–1699 m.	Goniasteridae
Ceramaster japonicus	small	few	abactinal, marginal, actinal	lip-like	Oregon to Japan, 660–700 m	Goniasteridae
Chitonaster felli	large	clustered	actinal intermediate	elongate and clamp like	South Atlantic-Scotia Sea, 2355–3714	Goniasteridae
Chitonaster johannae	medium	moderate	abactinal, actinal	lip-like	South Atlantic to Scotia Sea 2856–4204 m.	Goniasteridae
Comptoniaster adamsi	medium	moderate to abundant	marginal, actinal	lip-like	Fossil	Goniasteridae
***Fromia baruna* sp. nov.**	large	clustered	abactinal, actinal intermediate-oral	small, short	Indonesia, 15.2 m	Goniasteridae
Fromia eusticha	small	clustered	actinal intermediate-oral	short, round	Philippines, Japan, Indonesia, 44–55 m	Goniasteridae
Fromia labeosa	large	clustered	actinal intermediate	lip-like	Okinawa Japan, 52–137 m	Goniasteridae
Mediaster aequalis	small	diffuse, few	abactinal	small, short	Pacific coast of North America, Alaska to California 0–481 m.	Goniasteridae
Mediaster sladeni	small	diffuse, few	abactinal	small, short	New Zealand, 41–600 m.	Goniasteridae
Peltaster placenta (ex. nidarosensis)	small to medium	moderate	actinal	lip-like	Throughout West and Eastern Atlantic, 10–1007 m	Goniasteridae
Stellaster childreni	small	moderate to clustered	actinal intermediate-oral	lip-like	Indo-Pacific 5–290 m	Goniasteridae
Stellaster princeps	small	moderate to abundant	actinal intermediate-oral	lip-like	Western Australia to Torres Strait, 0–210 m.	Goniasteridae
Wallastra elenderae	medium	abundant	actinal	Valves angular, flat.	Solomon Islands, Western Indian Ocean, 550–836 m	Goniasteridae

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TABLE 1. (Continued)

	bvalve size (outlined in Definitions & Terms)	**Distribution Trends (outlined in Discssion)**	**location (outlined in Definitions & Terms)**	**Bivalve Pedicellariae shape**	**Depth**	**Family**
Weitschataster intermedius (Fossil)	small-medium	moderate to abundant	actinal intermediate	lip-like	Campanian of Germany (Cretaceous). Depth unclear.	Goniasteridae
***Astrophylax accinctus* nov. gen. sp. nov.**	large	clustered, abundant	actinal intermediate	lip like, enlarged	Philippines, 150–250	Goniasteridae-Circeasterinae
***Astrophylax valvata* nov. gen. sp. nov.**	large	clustered, abundant	actinal intermediate	lip like, enlarged	Papua New Guinea, 340–358	Goniasteridae-Circeasterinae
Circeaster americanus	large	abundant	actinal intermediate	bivalve & trivalve	Tropical Atlantic, Gulf of Mexico, 500–1450 m	Goniasteridae-Circeasterinae
Circeaster columnaris **sp. nov.**	medium	abundant	actinal	lip-like	Philippines 150–250 m.	Goniasteridae-Circeasterinae
Circeaster kristinae	large	abundant	actinal	bivalve paddle	Timor Sea to Indian Ocean, 320–610 m.	Goniasteridae-Circeasterinae
Circeaster magdalenae	medium	abundant	actinal	bivalve with teeth	Northwestern Indian Ocean, 850–1703 m	Goniasteridae-Circeasterinae
Circeaster pullus	medium	moderate to abundant	actinal	lip-like	North and South Pacific, 620–2305 m.	Goniasteridae-Circeasterinae
Lydiaster johannae	medium	moderate to abundant	actinal	bivalve with teeth	Northern Indian Ocean and Madagascar, 700–810 m	Goniasteridae-Circeasterinae
Gilbertaster anacanthus	large	abundant	Abactinal, marginal, actinal intermediate	lip-like	Hawaiian Islands to South Pacific 277–868 m.	Goniasteridae-Hippasterinae
Gilbertaster caribaea	large	abundant	Abactinal, marginal, actinal intermediate	lip-like	Off Southeast United States, Gulf of Mexico, 500–886 m.	Goniasteridae-Hippasterinae
Hippasteria californica	medium to large	abundant	abactinal, actinal	bivalve lip-like and with teeth	Japan, Alaska, Pacific coast of North America to Gulf of California, 30–2372 m	Goniasteridae-Hippasterinae
Hippasteria heathi	large	abundant	abactinal, marginal, actinal	lip-like	Aleutian Islands, 214–454 m.	Goniasteridae-Hippasterinae
Hippasteria muscipula	large	abundant	abactinal, marginal, actinal	bivalve with teeth	New Caledonia, New Zealand, Hawaiian Islands, 425–1500 m.	Goniasteridae-Hippasterinae

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TABLE 1. (Continued)

	bvalve size (outlined in Definitions & Terms)	Distribution Trends (outlined in Discssion)	location (outlined in Definitions & Terms)	Bivalve Pedicellariae shape	Depth	Family
Hippasteria phrygiana	large	abundant	actinal intermediate-but also abactinal	bivalve lip-like with large valves	Atlantic, Pacific, Indian Ocean, widely occurring, 10–1221 m.	Goniasteridae-Hippasterinae
Sthenaster emmae	medium to large	abundant	abactinal, actinal	lip-like	Southeast coast of North America (Florida), 252–874 m.	Goniasteridae-Hippasterinae
Eknomiaster beccae	large	clustered	actinal intermediate	bivalve big valves	New Caledonia, 215–1074 m.	Goniasteridae-Pentagonasterinae
Eknomiaster macauleyensis	small to medium	abundant	actinal intermediate	bivalve paddle	Norfolk Ridge, New Caledonia, New Zealand 215–691 m.	Goniasteridae-Pentagonasterinae
Toraster tuberculatus	large	moderate to abundant	abactinal, marginal, actinal	lip-like	South Africa, 75–366	Goniasteridae-Pentagonasterinae
Acheronaster tumidus	large, small	moderate to abundant	actinal intermediate, marginals	lip-like	Australia, New Zealand, Kermadec Islands, New Caledonia, 110–300 m.	Oreasteridae
Anthaster valvulatus	large	moderate to abundant	actinal but serial series (adjacent to adambs)	lip-like	Western to South Australia, 3–40 m.	Oreasteridae
Anthenea aspera	large, small	abundant	actinal, inferomarginals	bivalve and trivalve	Australia, Queensland, Western Australia, 8–40 m	Oreasteridae
Anthenea chinensis	large	abundant	actinal	lip-like	Japan, East China Sea, Thailand, 27–200 m	Oreasteridae
***Anthenea hlan* sp. nov.**	large, small	abundant	actinal intermediate-serial	lip-like	Burma, 22–30 m.	Oreasteridae
***Anthenea nudus* sp. nov.**	large	abundant	actinal intermediate-serial	lip-like	Arafua Sea, Australia. 60 m.	Oreasteridae
***Anthenea serrata* sp. nov.**	large	abundant	actinal but serial series (adjacent to adambs), inferomarginals	lip-like	Okinawa, Palau, Philippines, 6–61 m.	Oreasteridae
Astrosarkus idipi	small	few to many, widely spaced	actinal and furrow	lip-like	Tropical Pacific, southern Japan to New Caledonia, Indian Ocean 67–210 m.	Oreasteridae
Astrosarkus lu	small	few to many, widely spaced	actinal and furrow	lip-like	Timor Sea (Western Australia) 83–84 m	Oreasteridae

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TABLE 1. (Continued)

	bvalve size (outlined in Definitions & Terms)	Distribution Trends (outlined in Discssion)	location (outlined in Definitions & Terms)	Bivalve Pedicellariae shape	Depth	Family
Choriaster granulatus	small	very few to absent	actinal surface	lip-like	Indo-Pacific 0–70 m.	Oreasteridae
Culcita schmideliana	small	few	abactinal	lip-like	Western Indian Ocean to Indonesia, 0–92 m.	Oreasteridae
Goniodiscaster seriatus	small	few to many, widely spaced	actinal	lip-like	Australia, 0–36 m	Oreasteridae
Gymnanthenea difficilis	moderate to large	moderate to abundant	actinal, marginal	lip-like	Southern China, 3–20 m.	Oreasteridae
Halityle regularis	small	few to rare	actinal	lip-like	Indo-Pacific, 3–275 m.	Oreasteridae
Monachaster sanderi	large	few	actinal but scattered	lip-like	Western Indian Ocean to W. Australia to Red Sea and Gulf of Suez, 2–68 m.	Oreasteridae
Nidorellia armata	small-medium	few, widely spaced, sometimes absent	actinal	lip-like	Eastern Tropical Pacific, Baja to Galapagos and Peru 0–73 m.	Oreasteridae
Oreaster reticulatus	small	few, widely spaced	actinal	lip-like	Tropical western Atlantic, 0–69 m.	Oreasteridae
Pentaceraster alveolatus	small-medium	few to many, widely spaced	actinal	lip-like	Indo-Pacific, 1–70 m	Oreasteridae
Pentaster obtusatus	small	few to many, widely spaced	actinal	lip-like	Central Pacific, Philippines to Singapore and Malaysia, shallow.	Oreasteridae
Poraster superbus	small,	few to many, widely spaced	actinal	lip-like	Indo-Pacific, 20–96 m	Oreasteridae
Protoreaster lincki	small, moderate	few to many, widely spaced	actinal	lip-like	Indian Ocean, 0–40 m	Oreasteridae
Protoreaster nodosus	small	few to many, widely spaced	actinal	lip-like	Primarily tropical Pacific to northwest Indian Ocean, 0–30 m	Oreasteridae
Pseudoreaster obtusangulus	small	few to many, widely spaced	actinal	lip-like	Australia, 0–10 m	Oreasteridae
Acodontaster conspicuus	moderate	moderate	abactinal, actinal	angular bivalve and trivalve	Antarctica, Southern ocean 25–665 m	Odontasteridae

summarize as many species with bivalve pedicellariae as possible. This contrasts with exemplars listed herein that demonstrate general trends in pedicellariae distribution. Thus, some taxa, which are exceptional, are elaborated upon, whereas others which show pedicellariae more incidentally are shown in Table 1 for the sake of completeness but not included in the text. Inclusion was subjective but based on the abundance and prominence of the pedicellariae observed.

Bivalve Pedicellariae Size Definitions (Table 1)
Large. Elongate, bisecting the plate on which it sits but occupying the total surface in some. Up to 1.0 cm long and 0.4 cm width.

Medium. Elongate, bisecting most of the plate on which it sits but occupying the total surface in some, approximately 0.3 to 0.4 cm long and 0.1 0.2 cm wide.

Small. Less than half the width of the plate on which it sits. Only approximately 0.1 to 0.3 cm long and 0.1 or so wide.

Bivalve Pedicellariae Location (Table 1)
In the strict sense, bivalve pedicellariae are present in three families within the Valvatida, the Goniasteridae, the Oreasteridae, and the Asteropseidae, but the Odontasteridae possess similar trivalve pedicellariae that vary between two to four valves. Further surveys of other families possessing bivalve pedicellariae were either negative or were due to inconsistent terminology.

Usage for the term "bivalve pedicellariae" across different taxa is inconsistent and differs from that of bivalve pedicellariae herein. Clark & Rowe (1971), Vandenspiegel *et al*. (1998), and Kim *et al*. (2017) have utilized the term 'bivalve" for the elongate, straight pedicellariae present on oral plates and spines distinguishing Doderlein's (1920) "*Luidia quinaria*" group. Cunha & Tavares (2021) used the term "bivalve pedicellariae" for what Campbell (1983) described as either spatulate or excavate pedicellariae.

Literature surveyed includes Fisher (1911, 1919), Clark and Downey (1992), and Marsh and Fromont (2020). Although reported by Fisher (1911), bivalve pedicellariae as were not found in either *Pseudarchaster* or *Luidia*. Assuming that these were not terminological misunderstandings or some other type of error, it is possible that they are simply rarely observed or possibly anecdotal. Bivalve pedicellariae, as circumscribed herein, are observed in only three groups of Asteroidea, the Goniasteridae, the Oreasteridae and the Asteropseidae, all within the Valvatida.

The Goniasteridae contained the greatest number of taxa displaying bivalve pedicellariae, including approximately 25 species in 18 genera, but the Goniasteridae is also the most diverse taxon within the Asteroidea, containing over 70 genera and over 270 species (Mah & Blake 2012). The Oreasteridae display the second most abundant and the Asteropseidae with the fewest. The Odontasteridae includes one species with multiple valves similar to bivalve pedicellariae.

Bivalve pedicellariae were noted as either very prominent and/or are in greatest abundance relative to specific regions on the body surface. Pedicellariae distribution is outlined in the Discussion based on relative size, and abundance on the body surface.

Phylogenetic and Taxonomic Considerations

Taxonomic groups are based on Foltz and Mah's (2011) phylogeny of the Valvatacea. This includes placement of the Pseudarchasteridae within the Paxillosida, separate from the Goniasteridae and the Valvatida in addition to the placement of *Neoferdina* and *Fromia* within the Goniasteridae rather than the Ophidiasteridae (Foltz & Mah 2011, Mah 2017).

Bivalve Pedicellariae Definitions and Distinctions

Bivalve pedicellariae (e.g., Fig. 2G, 34B, C, F) and their diversity of expression across Valvatida provides the impetus for this study. These pedicellariae were described as "pince ou valvulaires" by Viguier (1879). Campbell (1983) reviewed form and function of pedicellariae in asteroids and echinoids describing them as "valve-like" with muscles sunk into the test. Campbell's (1983) account implies that pedicellariae are derived from spines and although this notion is not rejected, treatment here regards components descriptively. Jangoux & Lambert (1988) also provided an overview of asteroid pedicellariae, applied across the Asteroidea, which could only be generally applied herein and will need to be revisited in the future. Figure 2A–G shows a diversity of pedicellariae types observed throughout the Goniasteridae, namely paddle-shaped pedicellariae (e.g. *Calliaster, Astroceramus*), also called "spatulate", which are arguably the most frequently encountered within the Goniasteridae, which can have round (e.g. Fig. 2A) and "toothed" valves (e.g. Fig 2B) and the smaller, tong-like pedicellariae, also called "excavate", with straight or forceps-like valves (e.g. Figs. 1B, 1C, 2C–2D in *Mediaster roanae, Plinthaster ceramoidea*). Paddle-shaped pedicellariae can superficially resemble bivalve pedicellariae but display a substantially narrower element at its base (e.g Fig. 2B).

For purposes herein, bivalve pedicellariae are in most cases, composed of two elongate or rectangular valves (Fig. 2G) which are joined by an underlying plate and multiple tissue bands, presumably muscles and/or connective tissue (Fig. 2F). This definition may also fall under the definition of "bivalve tectiform" as outlined by Jangoux & Lambert (1988). Reference to "bivalve" is considered simpler herein and used throughout.

In a minority of instances, trivalve pedicellariae are observed (e.g. Fig. 8B, D, Fig. 36B, D, E), where three quadrate or blade-shaped valves are present. These are regularly observed only in a single species of Odontasteridae and are otherwise relatively uncommon in the Goniasteridae and Oreasteridae. It is thought that trivalve pedicellariae in these groups are variation relative to more abundantly encountered bivalve pedicellariae.

Bivalve pedicellariae are diverse in form, with

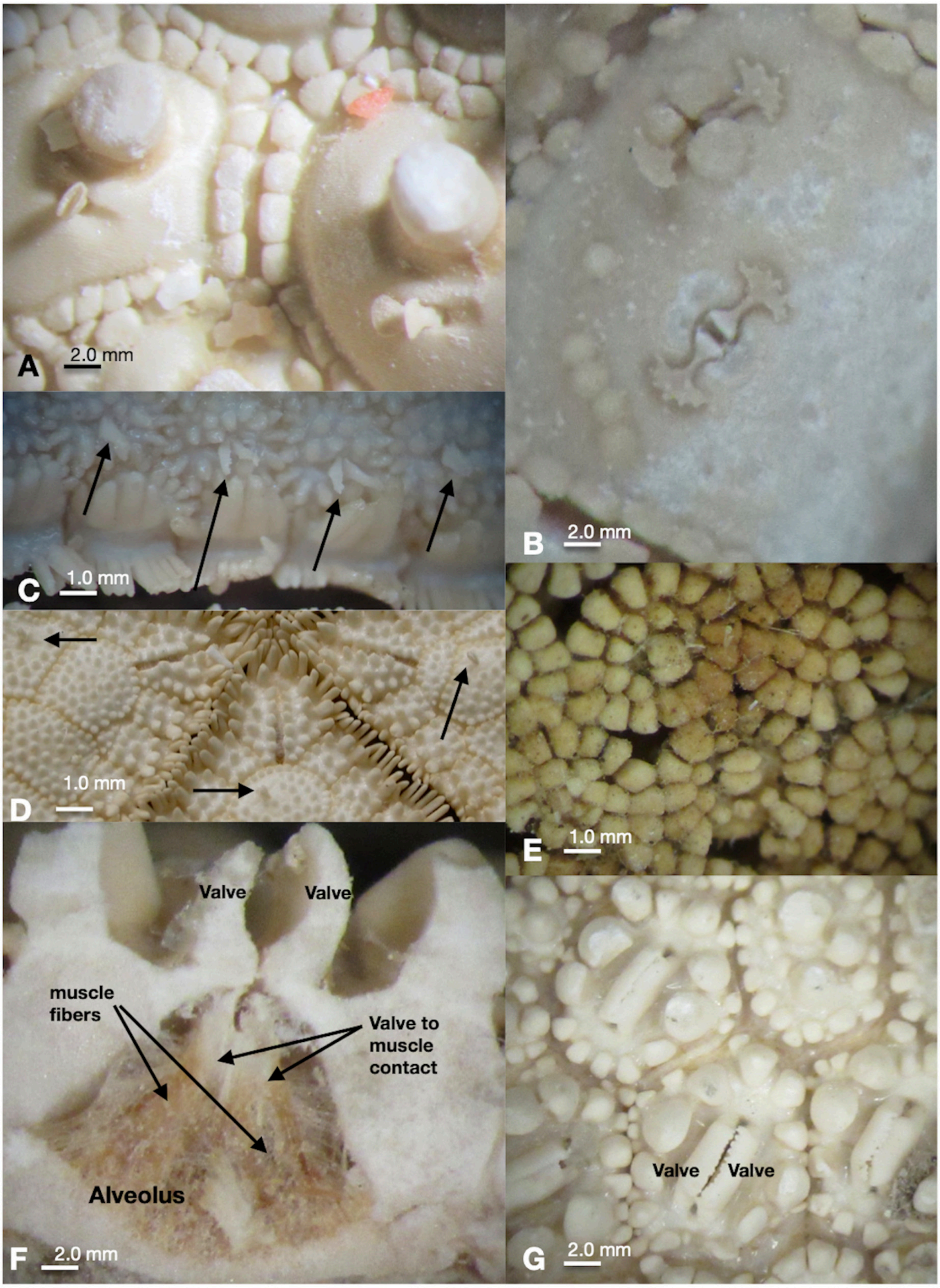

FIGURE 2. Pedicellariae types. A. Paddle-shaped pedicellariae from *Calliaster* **sp. nov.** MNHN 2013-6923. B. Paddle-shaped pedicellariae, narrow neck, valves bearing teeth. Inferomarginal plate surface. *Astroceramus eleaumei* MNHN-IE-2007-1067. C. Tong-shaped straight pedicellariae adjacent to adambulacral spination. *Mediaster roanae*, MNHN-IE-2007-17326. D. Tong or forceps-like pedicellariae, narrow, on oral actinal plates. *Plinthaster ceramoidea*, BPBM W3522. E. Bivalve pedicellariae on surface of tabular plates. *Mediaster sladeni*, USNM 1411305. F. Cross-section through a bivalve pedicellariae with underlying alveolar chamber showing tissue connections in cross-section. *Hippasteria phrygiana* USNM E25102. G. Bivalve pedicellariae from *Hippasteria phrygiana*, USNM E25102.

some taxa demonstrating pedicellariae valves that are nearly flush with the body surface (e.g. Fig. 20A–D, *Gilbertaster*) whereas in other cases, the valves are more squarish or rectangular (e.g. Figs. 13C–D, 11B–D *Eknomiaster, Wallastra*) and are of sufficient height that they are elevated above the body surface. The edges of these valves are variably smooth to weakly or strongly jagged with the valve displaying well-developed multiple teeth.

Bivalve pedicellariae are typified by *Hippasteria phrygiana* (Fig. 2F–G), which are comprised of two thickened valves with an underlying third piece, which sits over an alveolus or pit containing underlying musculature and other tissue. H.E.S. Clark & McKnight (2001) referred to the underlying alveolus as "pedicellarian pits." The thickened valves are embedded at or above the surface of the test, i.e. the body wall, and as with other surface features, are covered by a thin dermis. Valve edges vary from smooth to strongly serrated.

In some usage, bivalve and other alveolar pedicellariae are considered "large", or of such size that they nearly or completely bisect the plate on which they sit or are similar to or larger in diameter to adjacent plates (e.g. Fig. 2G, Fig. 13C, D).

Abundance is also a consideration for the taxa treated here. Specifically "abundance" refers to the overall number of pedicellariae present per plate on each individual. Several taxa display bivalve pedicellariae present on many if not all plates present in a particular series, such as on all the actinal intermediate plates, or on a complete series of actinal plates extending from the disk to the arm terminus. Some pedicellariae are present irregularly and inconsistently within a species, such as *Mediaster aequalis* and seldom do these occur with any abundance.

New goniasterid and oreasterid taxa associated with bivalve pedicellariae are described herein. These species motivated a review of observations and other taxa displaying bivalve pedicellariae exploring possible functional morphology as well as taxonomic diversity. The Goniasteridae are treated most closely with additional reviews in other valvatidan groups displaying bivalve pedicellariae, notably the Oreasteridae and Asteropseidae.

Systematics

Measurements for R and r herein are assumed to be in centimeters.

GONIASTERIDAE Forbes, 1841

Diagnosis

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

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

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

Comments

The Goniasteridae with more than 300 species assigned to approximately 70 genera (updated from Mah & Blake, 2012) is the most diverse family within the Asteroidea. Goniasterids are found throughout the world's oceans, ranging from the intertidal to 4000 m depths (Mah 2016). The fossil record, extending from the Mesozoic, is relatively good, the most notable faunas from the Cretaceous of (e.g. Breton 1992).

Subgroupings within the Goniasteridae have been established, but work remains ongoing. Mah (2007) supported and circumscribed the Pentagonasterinae, provided support for the Hippasterinae (Mah *et al*., 2010, Mah & Foltz, 2011; Mah *et al*., 2014), established the Ferdininae from former Ophidiasteridae (Mah, 2017), and more recently described the Circeasterinae (Mah, 2024). Other groupings, summarized by Spencer & Wright (1966) remain to be tested and not met with full agreement.

The expression of bivalve pedicellariae among the Goniasteridae is varied. Broadly speaking, the taxa with the most prominent and abundant bivalve pedicellariae are observed among the Hippasterinae and the Circeasterinae, those taxa with corallivorous habits. The Pentagonasterinae, which includes a varied number of bivalve pedicellariae bearing taxa, including *Toraster tuberculatus, Akelbaster novaecaledoniae* and

Eknomiaster, which variably express bivalve pedicellariae between different species. Goniasterid taxa demonstrating the most notable expressions of bivalve pedicellariae were selected and illustrated herein. It is anticipated that as a general rule, bivalve and other pedicellariae can show an unusual amount of variation and it is possible that some taxa demonstrate bivalve pedicellariae with such low abundance that they have been overlooked or is simply present with such low frequency that they could be considered anecdotal.

Anthenoides Perrier 1881

Leptogonaster Perrier 1881: 23; 1884: 246; Macan 1938: 401; Bernasconi 1963: 20; Halpern 1970: 272; Sladen 1889: 326; Fisher 1911: 169, 173; Liao & Clark 1995: 90; H.E.S. Clark & McKnight 2001: 13.

Antheniaster Verrill 1899: 173; Fisher 1906: 1067; 1911: 169, 173.

Anthenoides Downey 1973: 48; Liao & Clark 1989: 37; Clark & Downey 1992: 228; H.E.S. Clark & McKnight 2001: 13.

Diagnosis

Goniasteridae with stellate body form, pointed, arms triangular, interradial arcs broad, abactinal plates abutted, papulae present over radial regions on disk and arms, absent interradially. Abactinal, marginal, actinal surface with continuous granule-invested tegument. Marginal plates quadrate forming distinct abactinal-actinal facing border with granules or short spinelets. Pedicellariae variably present or absent within species. Furrow spines, fine slender, subambulacral spination variable but some species with both bivalve and tong-like or excavate pedicellariae.

Comments

A wide-ranging deep-sea genus with 9 species, including the wide-ranging Atlantic species, *Anthenoides peircei, Anthenoides marleyi* in the Indian Ocean, and the remaining species in the tropical Pacific. One species, *Anthenoides dubius* H.L. Clark 1938 is problematic but was described by H.L. Clark as "improbable" that it was actually a member of *Anthenoides*.

Among the *Anthenoides* species, many possess straight and paddle-like pedicellariae, but it is only the Atlantic *Anthenoides peircei* which shows the distinctive, large bivalve pedicellariae which are emphasized herein.

Anthenoides peircei Perrier, 1881
FIGURE 3A–B

Anthenoides peircei Perrier, 1881: 23; 1884: 168, 170, 247, pl. 8 fig. 1; Sladen, 1889: 326, 756 ; Perrier, 1894: 38; Verrill, 1915: 113, pl..3; fig. 2 pl. 10; figs. 1–1b, 2–2f; Fisher, 1911: 328, 331; Fisher, 1919: 328, 331, 332; H.L. Clark, 1941: 49; D. D. John & A.M. Clark, 1954: 139; A.H. Clark, 1954: 375; Halpern, 1970a: 272, figs. 29–30; Florez & Martinez de Rodriguez, 1971: 5; Downey, 1973: 48, pl. 17, figs. A–B; Walenkamp, 1976: 63, figs. 8c, 21, pl. 12, fig. 3, pl. 13, figs. 1–4, pl..14, figs. 1,3,4; pl. 15, fig. 2; Jangoux, 1978: 95; Walenkamp, 1979: 36, figs.11,13, pl. 9, figs. 1–4; Clark and Downey, 1992: 228, pl. 54E; Clark, A.M. 1993: 242.

Anthenoides brasiliensis Bernasconi, 1956: 33, pl. 1; 1958: 131, pl. 3, figs. 4–5; 1961: 24, pl. 2; 1963: 20, pol. 1, fig. 3, pl.2, fig4, pl. 5, fig. 1; 1964: 254 (as part of key); Clark, A.M. 1993: 242.

Diagnosis

Body stellate, arms triangular, sharply tapering. Body surface covered by a distinct dermis, which obscures plates in some individuals. Abactinal plates flat, polygonal, in regular rows along radial regions. Papular pores large, single. Secondary plates present, numerous. Marginal plates blocklike with inferomarginal plates beveled, projecting slightly beyond superomarginal plates. Up to 12 pairs of superomarginal plates abutted medially. Granules close and abundant on actinal surface, absent or reduced on abactinal surface. Adambulacral plates narrow, each with furrow spines, 4 to 8, two conical subambulacral spines present. Pedicellariae bivalve, variably abundant on actinal surface. (Modified from Clark & Downey, 1992).

Comments

This species has been documented *in situ* (Mah, 2024) on soft and hard substrates with the oral region towards the substratum. One image from Puerto Rico (Mah, 2024) shows the oral surface slightly impressed into a sedimentary bottom, suggesting that the bivalve pedicellariae could assist with manipulating sediments or associated organisms/structures. Mah (2024) showed an individual perched on a columnar structure with epizoic organisms, possibly sponges or hydroids.

Figures (Mah, 2024) show especially large bivalve pedicellariae located adjacent to the mouth suggesting association with feeding. Bivalve pedicellariae is varied, more abundant in larger individuals and lacking from specimens less than (R=1.2).

Distribution/Occurrence

Central to Southwest Atlantic Ocean. Virginia, North and South Carolina, Louisiana, Florida, Texas, Gulf of Mexico. Caribbean Sea. Mexico, Columbia, Antillean Islands from Yucatan to Venezuela. Puerto Rico Cuba, Belize, Bahamas, Trinidad & Tobago, Dominican Republic, Guyana, Surinam, Brazil, Uruguay, Cabo Polonio (to 31ºS). 55–844 m.

Material Examined

USNM E 40601 West of Cape Sable, Florida, Gulf of Mexico, North Atlantic Ocean. 25.2817 -83.7197, 88.2 m. Coll. Mote Marine Lab for BLM/MMS. 16 Nov 1980. 3 dry specs.

R=8.3 r=3.3, R=4.7 r=2.0, R=1.2 r=0.6.

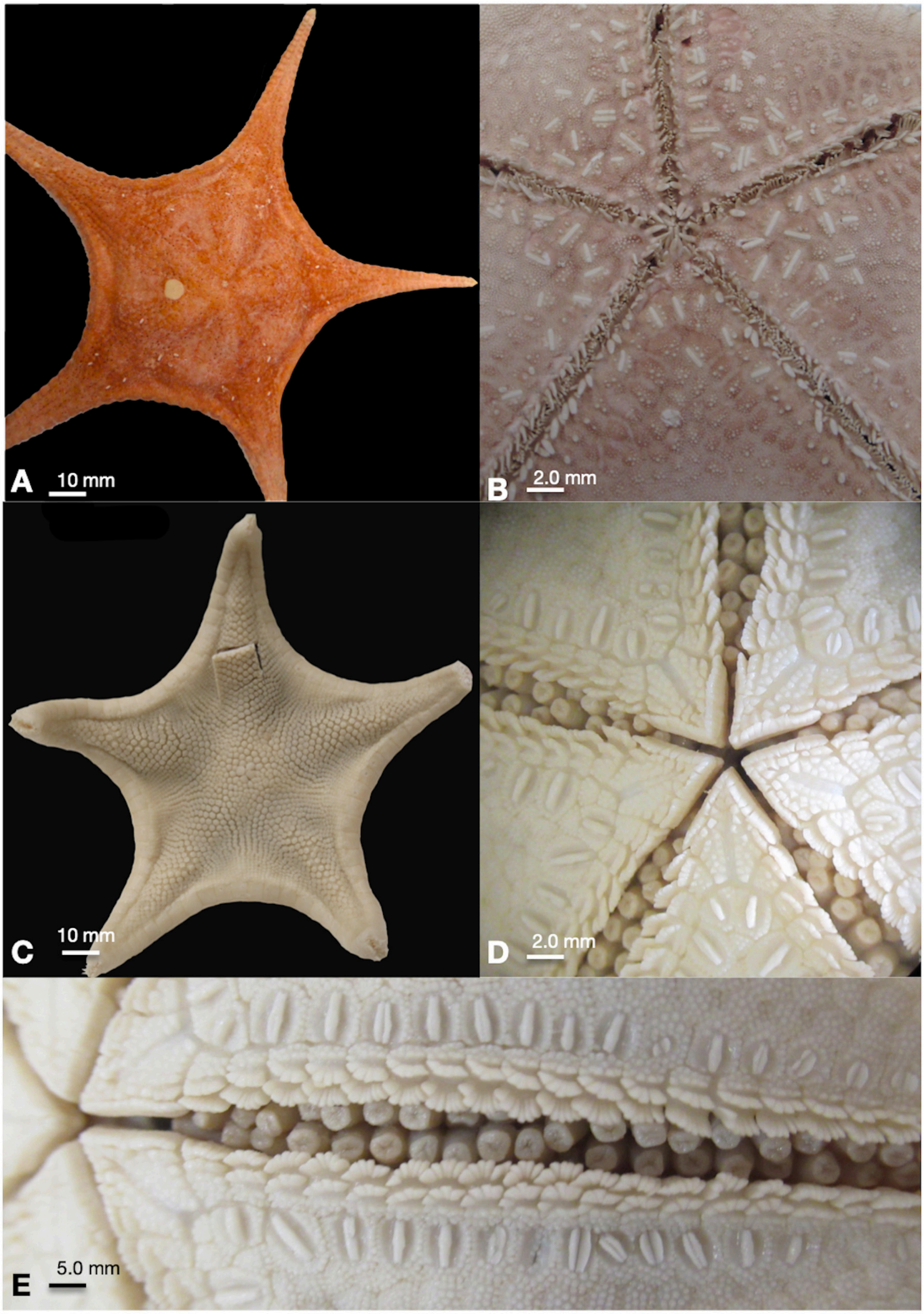

FIGURE 3. *Anthenoides peircei* USNM E40601. A. Abactinal B. Actinal view showing bivalve pedicellariae. *Bathyceramaster kelliottae* C. Abactinal D. Actinal-oral surface featuring bivalve pedicellariae. E. Adambulacral spines and bivalve pedicellariae.

Bathyceramaster Mah, 2016

Mah 2016: 105; 2022: 31; 2025: 63.

Diagnosis
Abactinal plates tabulate, low to moderate in height with fasciolar grooves, variably shallow to well-developed, plates lacking stellate bases. Abactinal, marginal, actinal surfaces covered by densely arranged polygonal to round granules. Bald patch on marginal plates present on a minority of taxa, absent on most. Body stellate, many species with well-developed arms (R/ r=1.8–4.0). Pedicellariae on most are small or few. (modified from Mah, 2016).

Comments
A genus accommodating *"Mediaster" elegans* Ludwig, 1905, which lacks the distinct internal radiating processes at the base of each abactinal plate (Mah, 2016). Since designation of *Bathyceramaster elegans* (Ludwig, 1905), 7 species have been described primarily from deep-sea Pacific settings (>1000 m) with a single species known from the Atlantic (e.g., Mah, 2024, 2025). Most species show few or weakly developed pedicellariae, with one species showing bivalve pedicellariae.

Bathyceramaster kelliottae Mah, 2024a
FIGURE 3C–E

Mah 2024a: 475, Fig. 6A–G.

Diagnosis
A stellate species (R/r=2.22) distinguished by the presence of short, moderate length tabulate plates topped with round and polygonal granules. Stellate, internally expressed radial ossicles on abactinal plates (as in *Mediaster*) absent. Fasciolar grooves present. Marginal plates, 30 per interradius (at R=6.0) covered with round, coarse granules and small spatulate pedicellariae. Actinal surface covered by granules. Adambulacral plates flanked by a continuous series of actinal plates, each bearing a single large, transversely oriented bivalve pedicellariae, these arranged serially and extending adjacent to the adambulacral plates to the arm tip. Adambulacral plates with spines in four series. Furrow spines, triangular in cross-section, 2 to 6, mostly 5 to 6 decreasing to 2 or 3 distally, adjacent to the terminus. Second and third subambulacral spine series each with four spines with last series showing five spines.

Comments
Large bivalve pedicellariae in this species are arranged transversely in series along the actinal plates adjacent to the adambulacral plates (Fig. 3D–E). Bivalve pedicellariae were absent from the remainder of the actinal intermediate, abactinal and marginal surfaces, although forceps-like pedicellariae occur on the abactinal surface.

Distribution/Occurrence
Deep Mound 2, Blake Plateau and Yakut Seamount, North Atlantic Ocean, 1386–1699 m.

Material Examined
USNM 1660278 Deep Mound 2, Blake Plateau, North Atlantic Ocean. 30.848, -77.3075, 1386 m. Coll. NOAA Ship *Okeanos Explorer* (A. Collins & S. Farrington), EX2107, 2 Nov. 2021, 1 wet spec. R=6.0 cm r=2.7 cm.
EX2107_IMG_20211102T203617Z_ROVHD.jpg.

Other Images

Yakut Seamount (deep), North Atlantic, 35.261862 -48.001104, 1699 m.
EX2104_IMG_20210713T193336Z_ROVHD.jpg
EX2104_IMG_20210713T193321Z_ROVHD.jpg

Chitonaster Sladen, 1889

Chitonaster Sladen, 1889: 282; Spencer & Wright, 1966: U58; A.M. Clark, 1993: 250; Mah 2011: 10.
Pentoplia H.E.S. Clark, 1971: 545; A.M. Clark, 1993: 275.

Diagnosis
Body stellate. Abactinal plates flattened, scalar, overlapping and forming relatively thin body wall. Fasciolar channels weakly present to absent. Plate surface bare in most or with single large granule, blunt cylindrical and/or pointed spines, peripheral accessories absent. Marginal plates face laterally. Large pedicellariae present or absent, either bivalve or with enlarged flange-like valves. Furrow spines one to three, typically two.

Comments
Chitonaster includes four species present at high latitudes in the South Atlantic and adjacent Antarctic waters in relatively deep waters, 102–4204 m (Mah 2011). *Chitonaster johannae* have large, prominent bivalve, or exceptionally trivalve pedicellariae, on the abactinal and actinal intermediate regions whereas *Chitonaster felli* displays prominent bivalve pedicellariae with significantly enlarged valves relative to those in other *Chitonaster* species.

Chitonaster's surface is composed of numerous polylobate imbricating plates, which when compared with more conventional goniasterid morphology, has posed difficulties for clearly establishing affinities. The presence of bivalve pedicellariae and the unusual abactinal plates are similar to those observed in hippasterines but more conclusive tests of relationship are desirable.

Chitonaster felli (H.E.S. Clark, 1971)
FIGURE 4A–E

Pentoplia H.E.S. Clark, 1971: 546; A.M. Clark, 1993: 275.
Chitonaster felli Mah 2011: 13.

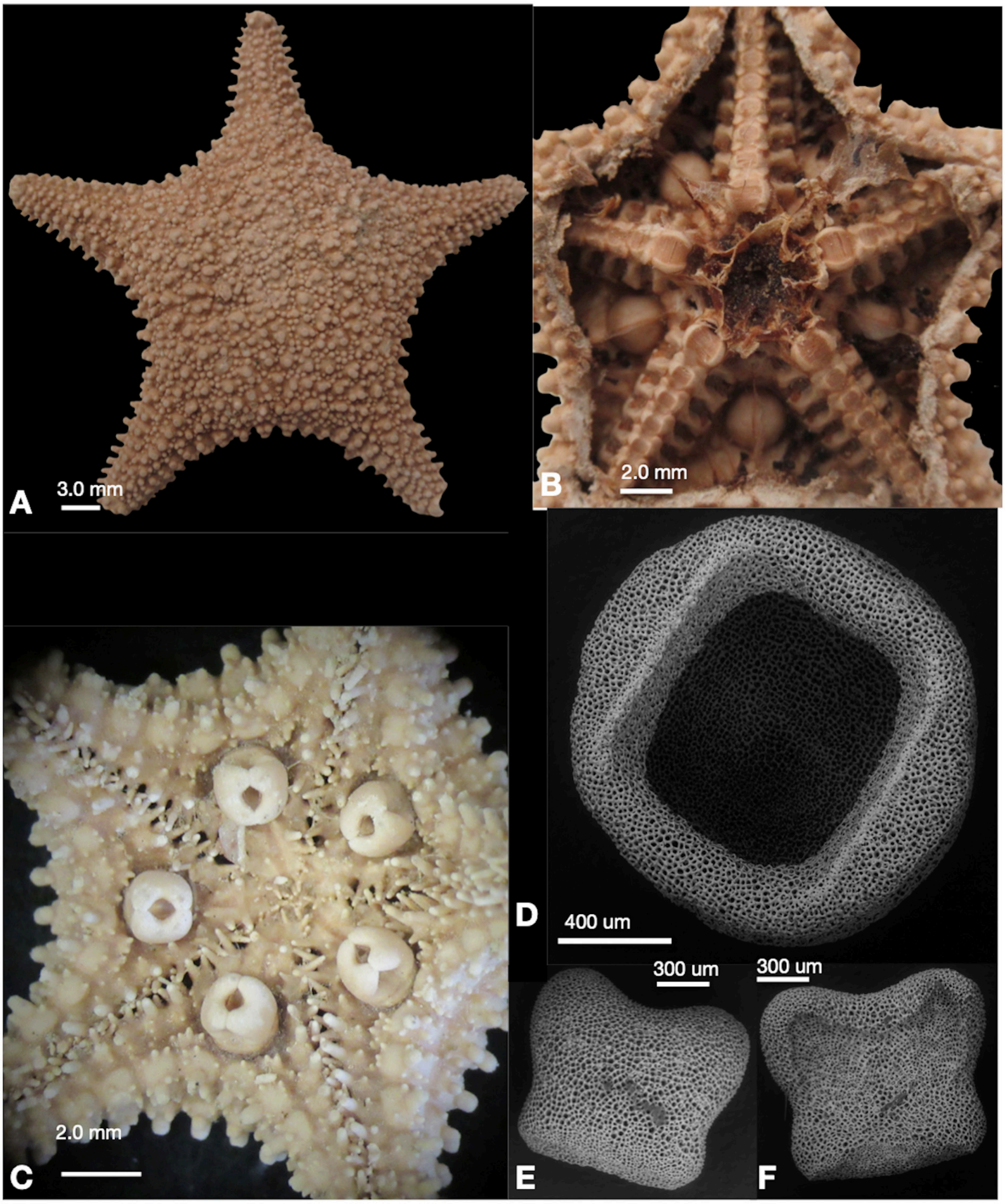

FIGURE 4. *Chitonaster felli* USNM 1018861. A.Abactinal B. Abactinal surface cutaway showing alveolar chambers. C. Actinal surface showing large pedicellariae. D. SEM of Alveolar chamber. E.-F. Valves of large pedicellariae. E shows exterior, F shows interior.

Diagnosis

Body stellate (R/r=1.0 to 2.2), disk strongly arched with triangular arms. Abactinal plates flattened, scalar, forming thin parchment-like body wall. Abactinal plates polygonal in outline, with length and width relatively equidistant. Each plate with one to three (usually one or two) low, blunt, spines with one to 12 small, coarse tubercular granules. Papulae indistinct or absent. Marginal plates, 14 to 24 per interradius (arm tip to arm tip) quadrate in outline. Spines, large, blunt 2 to 3 present on superomarginal and inferomarginal plates with secondary spines conical and pointed. Plates otherwise bare. Each actinal interradial region with a single large clamp-shaped pedicellariae, each with 2 valves each flanked by fewer than 10 small blunt, spine-bearing plates. Valves in contact over one side with two concavities forming an open circle on the ventral-facing surface. Actinal regions with numerous short spinelets or blunt spines. Furrow spines 2 to 3, subambulacral spine single, spaced from furrow by a distinct diastema.

Comments
The pedicellariae in *Chitonaster felli* are exceptional and similar pedicellariae have not been identified in other known asteroid taxa. In terms of overall dimensions, these appear to be the largest pedicellariae known. Pedicellariae valves in this species are thick and paired rising well above the plane of the actinal surface, together showing interlacing digits on the tips of each valve where they are in contact (Fig. 4C–E), each of which are rounded with no apparent serration or other features. The edges of the paired valves display two paired extensions with a central concavity on each valve. An enlarged round, alveolar chamber was present on the interior of each actinal intermediate region (Fig. 4B). Tissue, apparently connective or muscular, underlies each valve within the chamber. Although they display a higher aspect, rising well above the actinal surface, than most other pedicellariae, they appear to be enlarged, more extended bivalve pedicellariae rather than tong-like or paddle-like pedicellariae. Bivalve pedicellariae are also the only type of pedicellariae observed among *Chitonaster* species.

Function of these pedicellariae is unknown, however USNM 1018862 showed a tightly adhered layer of sediment to the actinal surface. This position could face the pedicellariae into the sediment as a means for obtaining food similar to the means hypothesized herein for *Anthenea* and other Oreasteridae bearing large actinal-facing bivalve pedicellariae.

Distribution/Occurrence
South Atlantic-Scotia Sea region near South Georgia/South Orkney Islands. 2355–3714 m.

Material Examined
USNM 1018860 PARATYPE. Southwest of South Georgia Island, Scotia Sea.-55.108 -44.367, 3623–3714 m. Coll. R/V *Eltanin*, Sta. 469, cruise 7. 12 Feb. 1963. 1 dry spec. R=1.3, r=0.5.

USNM 1018861, Northeast of South Shetland Islands, Scotia Sea, South Atlantic Ocean. -59.025 -51.875, 3010–3510 m. Coll R/V *Eltanin,* Sta. 1511, Cruise 22. 26 Jan. 1966. 5 dry specs. R=2.4, r=1.1; R=1.7, r=1.1; R=1.4, r=0.9; R=1.8, r=1.1; R=1.6, r=1.1.

USNM 1018862, Off west tip of South Georgia Island, South Atlantic Ocean, -55.092 -39.842, 2886–3040 m. coll. R/V *Eltanin* Sta. 1537, cruise 22, 8 Feb. 1966, 1 dry spec. R=1.3, r=0.6.

Chitonaster johannae Koehler, 1908
FIGURE 5A–D

Chitonaster johannae Koehler, 1907: 144; 1908: 542; A.M. Clark, 1993: 250; Mah 2011: 15.

Diagnosis
Body form stellate (R/r=2.0–2.6) with arms elongate. Disk swollen, convex. Interradial arcs rounded. Abactinal plates scalar, flattened, overlapping over one another forming mosaic-like pattern. Each plate with spines, one to three, short, blunt, cylindrical and densely clustered on each abactinal plate. Other than short spines, bivalve pedicellariae are the only primary structures present on abactinal surface, usually only on disk rather than on arms. Papulae absent. Marginal plates, 24–36 per interradius, each with blunt cylindrical spines, 2 to 4 in linear series across plate surface. Other accessories absent from plate surface. Actinal region with small thorny spinelets, 1 to 2. Each interradius with large bivalve or trivalve pedicellariae, 1 to 4, similar to those on the abactinal surface. Furrow spines 2, slender, cylindrical, but round in cross-section. Single subambulacral spine present.

Comments
Pedicellariae are variable in this species (Fig. 5C–D), those of USNM 1018953 (at R=2.3) were relatively elongate relative to adjacent plates, approximately 2 to 3X the length of the adjacent plates whereas those on USNM E13501 (at R=3.3) were of half the length, and approximately 1X the length of adjacent plates.

Distribution/Occurrence
South Atlantic-Scotia Sea region near South Georgia/South Orkney Islands. 2856–4204 m.

Material Examined
USNM E13501. South of South Georgia, South Atlantic Ocean. -56.875 -37.542, 3138–3144.0 m. Coll. R/V *Eltanin,* 2 dry specs. R=2.9, r=1.2; R=3.3, r=1.3.

USNM 1018875 South of Burdwood Bank, Argentina, Scotia Sea, -55.025 -58.817, 2782–2891 m. Coll. University of Southern California, R/V *Eltanin* 4 Dec 1962, 1 dry spec. R=2.3 r=0.8.

USNM 1018953 South of South Orkney Islands, Weddell Sea. -63.408 -44.9, 3587–3660 m. coll. US Antarctic Research Program. 1 dry spec. R=2.3, r=1.1.

USNM 1086359 Southern Ocean, Antarctica -66.358 -45.842, 4200–4204 m. Coll. U. Southern California. 1 dry spec. R=2.5, r=1.1.

Fromia Gray, 1840

Fromia Gray, 1840: 286; Fisher, 1919: 373; H.L. Clark, 1921: 38; Rowe & Gates, 1995: 81; Mah & Foltz, 2011: 771, 779, 782; Mah, 2024: 8.
Celerina A.M. Clark, 1967: 193; Rowe & Gates, 1995: 80.
Austrofromia H.L. Clark, 1921: 48; Rowe, 1989: 291; Rowe & Gates, 1995: 81.

Diagnosis
Body strongly stellate (R/r=3.5–5.0), arms elongate, strap-like to triangular in shape. Interradial arcs acute. Arm rectangular in cross-section. Abactinal plates abutted, ranging ranging from flat to convex, covered

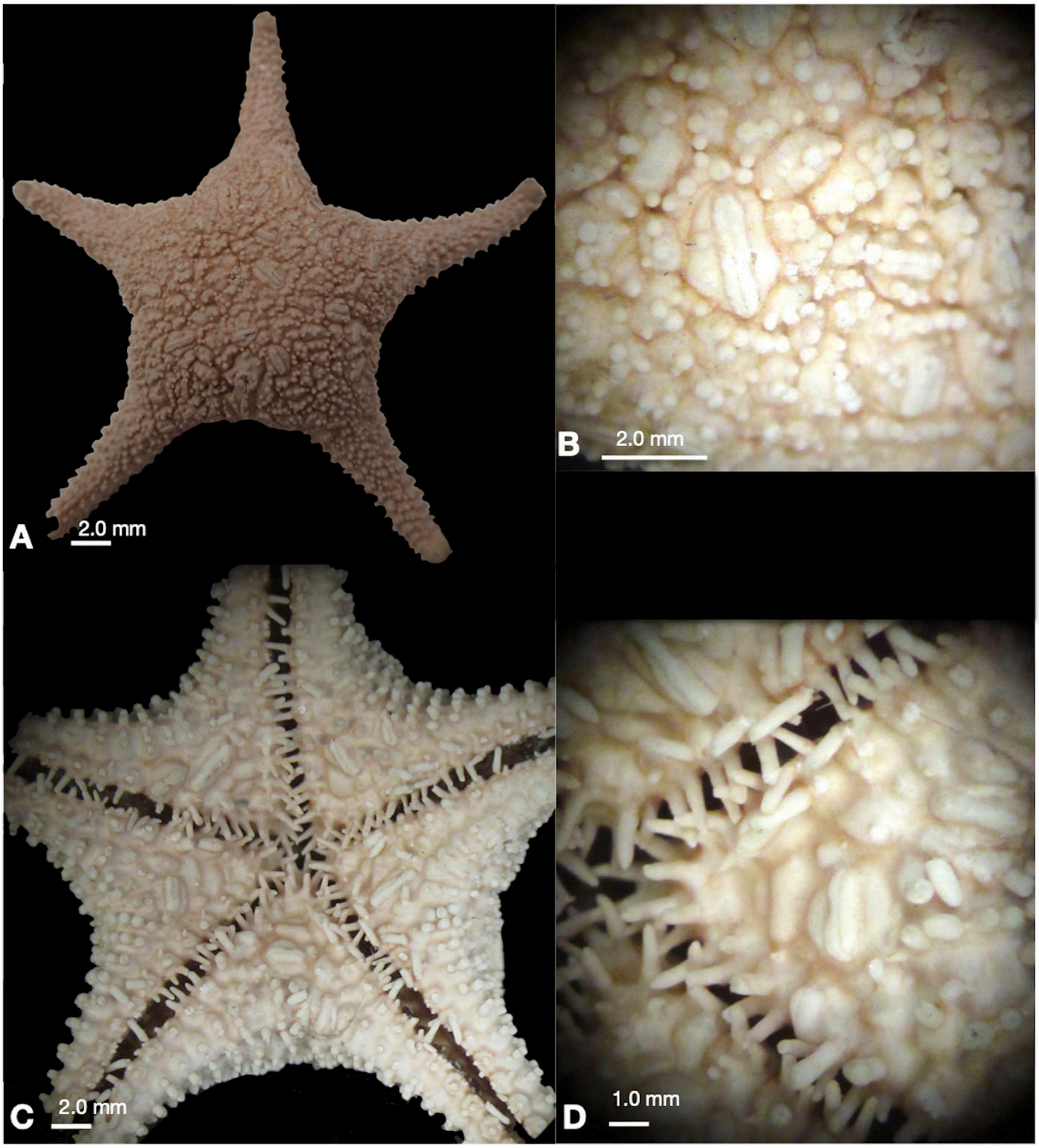

FIGURE 5. *Chitonaster johannae* USNM 1018953. A. Abactinal B. Closeup of bivalve pedicellariae. C. Actinal view showing pedicellariae. D. Closeup on furrow and actinal pedicellariae.

with a distinct continuous granular cover. Marginal plates broadly quadrate in outline forming discrete frame around abactinal lateral outline of body. Marginal plate surface covered by continuous granular cover. Actinal region small, with granule-covered surface. Papulae present at marginal and actinal plate contact. Furrow spines blunt, relatively few, with variable subambulacral armature. (based on Mah 2018).

Comments

Sixteen species of *Fromia* have been described from throughout the Indo-Pacific region. However only *Fromia baruna* **sp. nov.**, *F. labeosa* Arai & Fujita 2021 and *F. eusticha* Fisher 1913, possess pedicellariae. All three species have pedicellariae on their actinal intermediate surface, but pedicellariae are also present on the abactinal surface of *Fromia baruna* **sp. nov.** Two of the three pedicellariae bearing *Fromia* species were collected from mesophotic depths. Although *Fromia baruna* **sp. nov.** was collected from 15.2 m, several *Fromia* species, such as *Fromia monilis* are known from wide-ranging depths extending into the mesophotic.

It is tempting to argue that these three species comprise a separate genus distinct from the other *Fromia* species, however no other distinct, unifying characters could be clearly identified and pedicellariae have been found to be variable among other different goniasterid species, suggesting that such a grouping is premature.

Fromia baruna sp. nov.

FIGURE 6A–F

Etymology

The species epithet, "*Baruna*" is named for the Indonesian god of the sea and rain. Noun held in apposition.

Diagnosis

Body strongly stellate (R/r=4.6), arms elongate and tapering, interradial arcs acute. Abactinal plates large, polygonal in shape, approximately five across arm base, each covered by granules. Pedicellariae on abactinal arm and actinal surfaces with abundant bivalve pedicellariae. Superomarginal plates, approximately 15 to 16 per arm, 30 to 34 per interradius (arm tip to arm tip), Proximal superomarginal plates in consistent series, distal plates irregular, alternating with small or absent plates varying in size, many small, approximately 50% of the size of proximal superomarginals and bearing small conical spine. Proximal actinal region, especially on disk, adjacent to oral plates covered with abundant large bivalve and exceptionally trivalve pedicellariae, each larger than approximately a six count of granules, approximately 0.4 to 0.8 mm in length, approximately 30 to 50 per interradius, covering 4 to 6 plates on disk actinal intermediate region. Remainder of actinal plates covered by granules, 40 to 60, round to polygonal, widely spaced. Furrow spines, mostly 2, exceptionally 3, triangular with blunt pointed tips. Subambulacral spine single, exceptionally two which is smaller on a minority of plates, these pointed with broad-base. Oral plates covered by granules and/or pedicellariae.

Comments

Based on the body/arm shape as well as the size and pattern of superomarginal plates, this species superficially resembles *Fromia monilis* in that the proximal superomarginals are closer and more consistently ordered with distal superomarginals showing alternating large and small, heterogeneous plate morphology. In terms of body shape and superomarginal plate morphology, *Fromia labeosa* and *Fromia eusticha* are more similar in that both show continuous superomarginal plates in a gradually attenuating series.

Pedicellariae valves in *Fromia baruna* **sp. nov.** and *Fromia eusticha* are relatively small, and short compared to those on *Fromia labeosa* which are larger and more elongate. Neither of the other *Fromia* with pedicellariae have them on the abactinal surface (Fig. 6C). *Fromia baruna* and *Fromia eusticha* show a high density of pedicellariae on the actinal surface on the disk around the mouth with pedicellariae present in contrast to *Fromia labeosa,* which shows pedicellariae present in serial position along the arms and disk at transverse to oblique angles relative to the adambulacral plates.

Distribution/Occurrence

Indonesia, 15.2 m.

Description

Body strongly stellate (R/r=4.63), arms elongate, tapering, and triangular (Fig. 6A). Interradial arcs acute. Papulae pores present at each plate angle, between abactinal, superomarginal and inferomarginal plates and between actinal and inferomarginal plates but absent from actinal surface.

Abactinal surface flat, composed of plates, abutted, round to polygonal. Surface covered by continuous granular cover, such that contacts between plates are weakly obscured. Pedicellariae, small bivalve, exceptionally trivalve, abundant, numbering 6 to 20 arranged around periphery of most proximal arm plates and adjacent superomarginal plates, extending approximately 6 to 7 superomarginal plates but absent on distalmost region along arm, approximately corresponding to six superomarginal plates away from arm tip. Pedicellariae large, approximately 0.4 to 0.8 cm in length present on proximal arm regions, but largely absent from central disk (Fig. 6B–C). Granules, 15–30, polygonal to round, widely spaced present on central surface of plates with pedicellariae but expanding to completely cover plates where pedicellariae are absent. Disk also covered by granules, widely spaced. Distalmost abactinal plates mostly flat, but exceptionally one or two per arm, strongly convex. Papulae on disk with 6 enlarged granules present around each pore, approximately twice the size of mosts granules. Madreporite large, flanked by 6 plates, sulci well-developed, surface strongly convex.

Superomarginal plates, approximately 15 to 16 per arm, 30 to 34 per interradius (arm tip to arm tip). Proximal superomarginal plates in consistent series, distal plates irregular, alternating with small or absent plates varying in size, many small, approximately 50% of the size of proximal superomarginals and bearing small conical spine (Fig. 6B). These irregular superomarginal plates approximately correspond with end of pedicellariae on abactinal plate surface. Inferomarginal plates 20 to 22 per arm, 40 to 44 per interradius (arm tip to arm tip), similarly regular proximally becoming more irregular distally. Distalmost inferomarginal plates variably convex, irregular in size shape, with distalmost plates each bearing a small conical spine approximately six plates from terminus. Inferomarginal plates covered with granules forming continuous, even cover over surface. Terminal plate large with short spinelets.

Actinal plate surface composed of two series, both incomplete. One extending approximately 75% of arm distance and a shorter series terminating approximately halfway where superomarginals become irregular. Proximal actinal region, especially on disk, adjacent to oral plates covered with abundant large bivalve and exceptionally trivalve pedicellariae (Fig. 6D, F), each larger than approximately a six count of granules, approximately 0.4 to 0.8 mm in length, approximately 30 to 50 per interradius, covering 4 to 6 plates on disk actinal intermediate region. Remainder of actinal plates covered

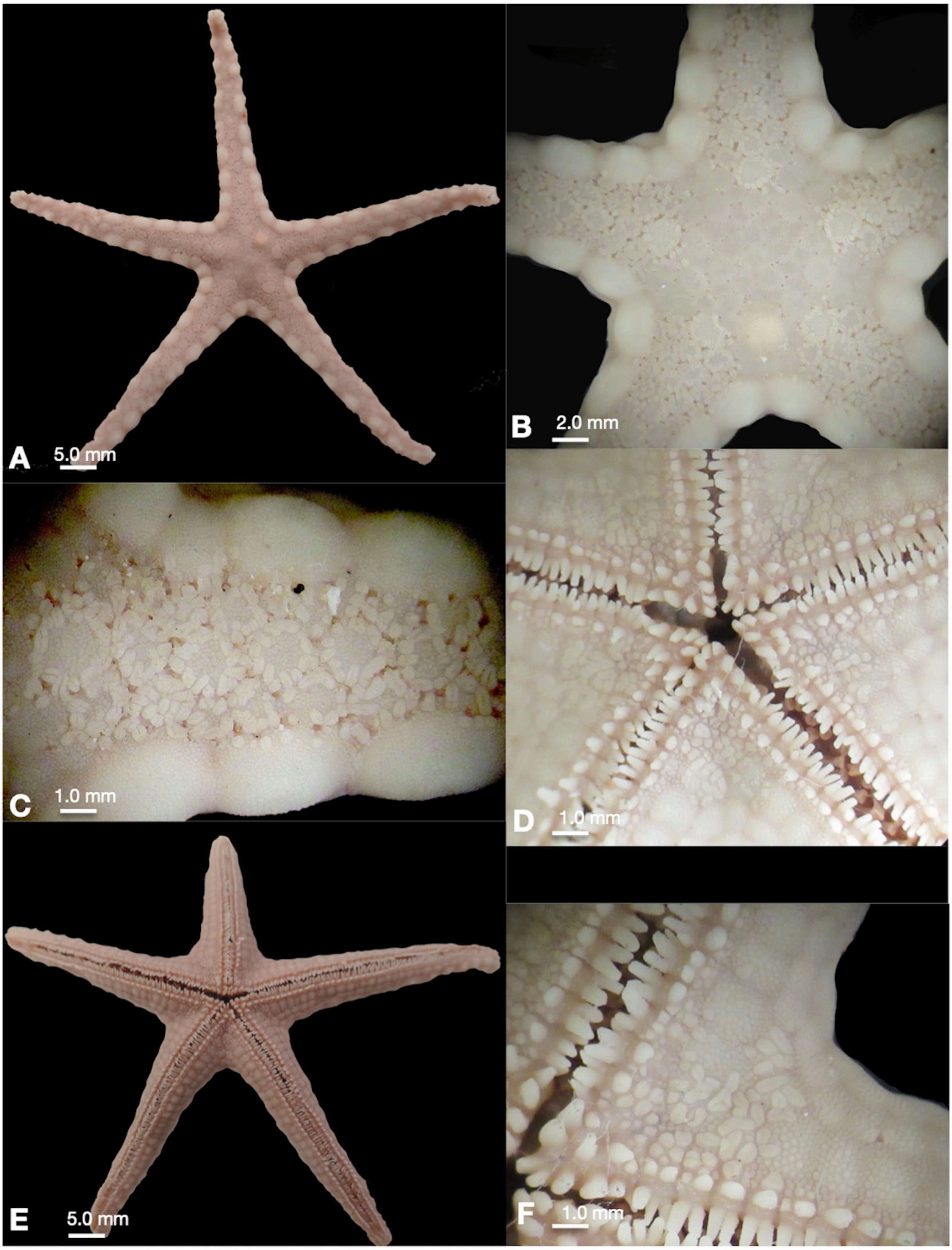

FIGURE 6. *Fromia baruna* **sp. nov.** Holotype USNM E50192. A. Abactinal. B. Closeup of disk and arms surface. C. Abactinal pedicellariae. D. Oral region and furrow spination. E. Actinal. F. Furrow and actinal region.

by granules, 40 to 60, round to polygonal, widely spaced. Overall size coarse proximally becoming smaller distally, overall size approximately 5 to 6 count along a 1.0 mm line. Papular pores present between actinal intermediate and inferomarginal plates.

Furrow spines, mostly 2, exceptionally 3, triangular with blunt pointed tips (Fig. 6D, F). Subambulacral spine single, exceptionally two which is smaller on a minority of plates, these pointed with broad-base. Subambulacral spines separated from furrow spines by a distinct space. Oral plate furrow spines 5 or 6, continued from adambulacral furrow spine series. Subambulacral spines, 4, present on oral plate surface as part of continuous adambulacral spine series. Remaining oral plate surface covered by granules with pointed tips or pedicellariae, 10 to 15 per plate (20 to 30 per interradius).

Material Examined

Holotype. USNM E50192 SW of Banda Besar, Banda Islands, Moluccas, Indonesia, Banda Sea. -4.5433 129.077, 15.2 m, Coll. G. Handler, 8 July 1979, R/V *Alpha Helix.* 1 wet specimen R=3.7 r=0.8 cm.

Fromia eusticha Fisher, 1913

FIGURE 7A, C

Fisher 1913: 213; 1919 375; Domantay & Roxas 1938: 220; A.H. Clark 1952: 286; Jangoux 1978: 294; A.M. Clark 1993: 331; Arai *et al*. 2018: 194; Mah 2024: 11.

Diagnosis

Body strongly stellate (R/r=4.4–4.8) Arms elongate, evenly tapering. Interradial arcs acute. Abactinal surface convex. Abactinal plates round to irregularly polygonal, surface covered by granules. Marginal plates in regular series, regularly decreasing in size with no alternation of large and small plates. Plate surface tumid. Actinal series in three regular series at base of ray. Actinal plates with bivalve pedicellariae, 1 to 8. Furrow spines 3, subambulacrals 2. Subambulacral pedicellariae 1 to 3.

Comments

Fromia eusticha shows a similar morphology and position of pedicellariae with *Fromia baruna* **sp. nov.**, described herein. Actinal pedicellariae are most abundant and predominantly located around the oral region in each interradius (Fig. 7C).

Distribution/Occurrence

Ogasawara Islands, Japan, 96.5–149 m.

Outside Japan. Sulu Archipelago, Philippines, Bikini Atoll, Indonesia, intertidal, 44–55 m.

Material Examined

USNM 32637 Taupe Island, Taupe Group, Sulu Archipelago, Philippines, 5.7778 120.814, 44 m. Coll. USFC Steamer Albatross, Philippines Expedition, 16 Feb 1908. 1 wet spec. R=4.1 r–8.5.

Fromia labeosa Arai & Fujita, 2021

FIGURE 7B, D

Arai & Fujita 2021: 13, Fig. 2.

Diagnosis

Body stellate (R/r=3.6–4.1), arms slender, disk small. Abactinal plates flat, polygonal in shape, abutted. Abactinal, marginal plates covered by continuous granules that obscure plate boundaries. Marginal plates quadrate, uniform, gradually decreasing in size along arm. Large elliptical pedicellariae present on the actinal surface at oblique angle to the adambulacral plates. Furrow spines, 2 to 4, mostly 3; subambulacral spines thick, short, approximately 50% the height of the furrow spines. Adambulacral plates with granules, 2–4 identical with those on actinal plate surface.

Comments

Pedicellariae in *Fromia labeosa* show a distinct difference in size, being easily 3 to 4X the length and position relative to the other two *Fromia* species bearing pedicellariae (Fig. 7D). Pedicellariae in this species are more irregularly present along the plate series adjacent to the adambulacral plates (Fig. 7B, D). In terms of function and/or adaptive significance/taxonomic importance, variation in pedicellariae morphology between *Fromia labeosa* and the other *Fromia* spp. is unclear.

Distribution/Occurrence

Okinawa, Ogasawara Islands, **52**–137 m.

Material Examined

USNM E48903 1 km WNW of Onna village, Horseshoe Cliffs, Okinawa, Ryukyu Islands. 26.5 127.848, 70.0 m. Coll. R.F. Bolland 16 Aug 1981. 1 wet spec. R=2.0 r=0.5.

USNM 1659486 3km WNW of Yuhi Misaki, Okinawa, Ryukyu Islands, Japan. 26.8467, 127.533, 52–55 m. Coll. R.F. Bolland, 14 Nov. 1987. 1 wet spec. R=3.3 r=0.8.

Mediaster Stimpson, 1857

Mediaster Stimpson 1857: 530; Perrier 1894: 377; Verrill 1899: 178; Fisher 1911: 196; Verrill 1914: 295, 1915: 108; Fisher 1919: 255; Macan 1938: 369; H.L. Clark 1946: 83; Bernasconi 1963: 11; Halpern 1970: 202; Clark and Downey 1992: 251; A.M. Clark 1993: 262 (checklist); Rowe & Gates 1995: 65 (checklist); H.E.S. Clark & McKnight 2001: 69; Mah 2016: 118; Mah 2018: 53.

Isaster Verrill 1894: 257.

Diagnosis

Goniasterid genus with tabulate abactinal plates displaying internally radiating ossicles from base of each plate. Abactinal tabulae plates with granules or spinelets. Abactinal plates in most, extending to arm tip, but exceptionally with distalmost superomarginals abutting. Abactinal, marginal, actinal surface covered by granules.

Comments

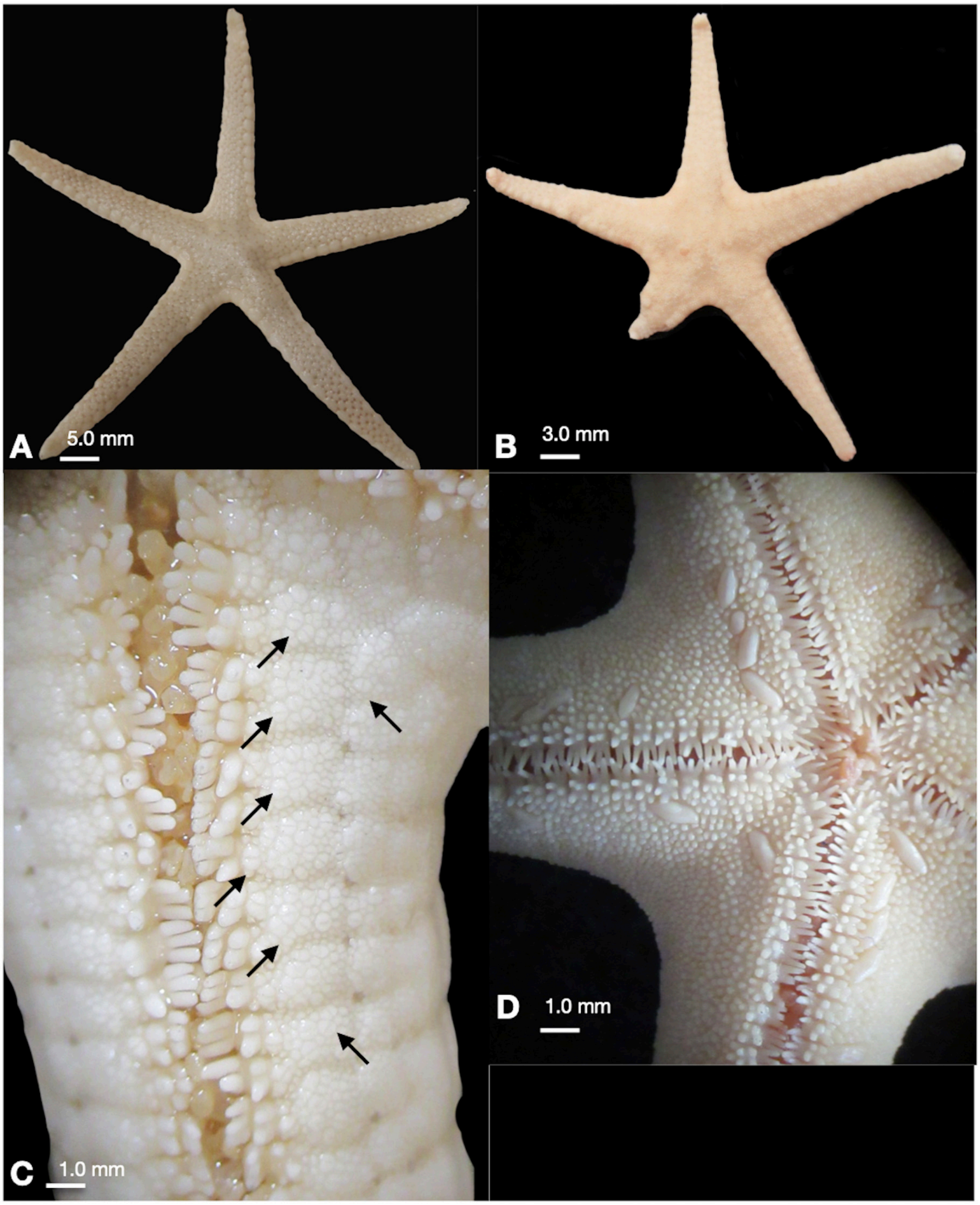

FIGURE 7. *Fromia* spp. with bivalve pedicellariae. *Fromia eusticha* USNM 32637 A. Abactinal. B. Actinal surface showing pedicellariae. *Fromia labeosa* USNM 165486 C. Abactinal. D. Actinal surface showing pedicellariae.

Mediaster includes 18 living and 1 fossil species which occur in cold to temperate water settings in the Atlantic, Pacific and Indian Oceans. As a generality, pedicellariae presence in *Mediaster* species is absent in most species, with relatively low abundance, displaying a variable distribution when present. Among species with pedicellariae, especially bivalve pedicellariae, are widely distributed among species in *Mediaster*, occurring on a minority of plates and in low abundance when present.

Mediaster sladeni Benham, 1909

FIGURE 8A–D

Benham, 1909: 94.

Diagnosis

Body stellate, R/r=2.2, interbrachial arcs weakly curved to linear. Abactinal plates tabulate, forming close cover, each plate with blunt-headed granules, 17–24. Pedicellariae variably present or absent, conspicuous, bivalve or trivalve on abactinal and marginal plate surfaces. Marginal plates covered by small, spaced flat-topped granules/ spinelets. Pedicellariae, 2 to 4 on proximal marginal plates. Furrow spines 5 to 6, blade like, slender, round-tipped. Subambulacral spines 4 to 6, mostly 5, shorter, more angular forming series behind furrow spines, set apart by distinct diastema (Modified from H.E.S. Clark & McKnight 2001).

Comments

Mediaster sladeni was chosen to demonstrate bivalve pedicellariae in this genus owing to the preponderance of pedicellariae of this type (Fig. 8B–D). Species with bivalve pedicellariae include *M. aequalis* Stimpson, 1857 and *M. sladeni* Benham, 1909*,* whereas most of the remainder show more excavate, tong-like pedicellariae (e.g., *Mediaster arcuatus* (Sladen, 1889)*, Mediaster capensis* H.L. Clark, 1923*, Mediaster mollis* Mah, 2018*, Mediaster ornatus* Fisher, 1906*, Mediaster pedicellaris* (Perrier, 1881)*, Mediaster roanae* Mah, 2018*, Mediaster setosus* Mah, 2018*,* and *Mediaster tenellus* Fisher, 1905.) *Mediaster gartrelli* H.E.S. Clark, 2001*,* has both bivalve and tong-like pedicellariae. Pedicellariae have not been reported from the Australian *Mediaster praestans* (Livingstone 1933) and *Mediaster boardmani* (Livingstone 1934).

Distribution/Occurrence

New Zealand, from near Three Kings Island to south of the Snares Islands, 41–600 m.

Material Examined

Mediaster aequalis Stimpson, 1857. USNM 1288441, Outer Bay, Little Port Walter, SE Alaska, Gulf of Alaska, United States. rock rubble. 6.0 m (20 feet). Coll. Lou Barr, via SCUBA. 19 April 1977. 1 dry spec. R=7.3 r=2.7.

Mediaster pedicellaris (Perrier, 1881). USNM E35009, N of Yucatan Peninsula, Gulf of Mexico, North Atlantic. 25º58'N 87º29'30"W, 366 m (200 fms). Coll. R/V Silver Bay, 5 June 1959. 1 dry spec. R=4.3 r=1.1.

Mediaster sladeni (Benham,1909). USNM 1126279, Cook Strait, off Cape Palliser, New Zealand, South Pacific. 73 m. R=8.0 r=3.8.

Peltaster Verrill, 1899

Verrill, 1899: 168; Tortonese & A.M. Clark, 1956: 348; Halpern, 1970: 234; Downey, 1973: 50; Clark & Downey, 1992: 257.

Diagnosis

Body pentagonal to weakly stellate (R/r= 1.1–2.1). Abactinal plates variably weakly tabulate to abutted, irregularly arranged. Secondary plates present or absent. Marginal plates 7 to 30, mostly 15 to 20 per interradius. Abactinal, marginal, actinal plate surfaces covered by abundant to dense cover of granules, in some species, obscuring observable plate boundaries. Adambulacral spination variable, but generally blunt, and thick with subambulacral spines in 2 or more series.

Comments

A genus including 2 species, the Pacific *Peltaster cycloplax* and the widely occurring Atlantic *Peltaster placenta*. *Peltaster micropeltus* (Fisher, 1906) has been reassigned to *Pillsburiaster* (Mah, 2024).

Peltaster placenta (Müller & Troschel, 1842)

FIGURE 8A–E

Goniodiscus placenta Müller & Troschel, 1842: 59.
Pentagonaster nidarosiensis Storm, 1888: 61.
Peltaster nidarosiensis Grieg, 1905: 3, figs. 1–2, 4–5; Fisher, 1911: 162; Verrill, 1915: 28, figs. 4–4a; Tortonese & A.M. Clark, 1956: 348, figs 1a–2a; Halpern, 1970: 235, fig. 14; 1970b: 88.
Peltaster placenta (full synonymy) Clark & Downey, 1992: 257.

Diagnosis

Body form pentagonal to weakly stellate. Abactinal plates flattened, bases stellate, covered with granules. Secondary plates present. Marginal plates flat or nearly concave, covered by granules. A distinct bare or naked area present on superomarginal dorsal surface. Actinal regions large, covered with granules. Furrow spines short, stout, subambulacral granulation grading from furrow spines to actinal granules, crowded. Bivalve pedicellariae variably present or absent. Excavate/tong-like pedicellariae variably present or absent (Modified from Downey in Clark & Downey, 1992).

Comments

Among *Peltaster* species, only the morphospecies, *Peltaster nidarosiensis* (Storm, 1881), synonymized within the widely occurring *Peltaster placenta* possesses bivalve pedicellariae (Fig. 9B,C, E). Pedicellariae of most specimens of *Peltaster placenta* are excavate and tong-like (Clark & Downey, 1992). Downey in Clark & Downey (1992) has argued for one wide-ranging, highly variable species present across the Atlantic Ocean with *Peltaster placenta* including several synonyms representing numerous variation throughout its range. Halpern (1970) provided a recent overview and re-description of this species and identified secondary plates as one of the diagnostic characters. This character, among others, such as marginal plate morphology appears to be variable if the hypothesis of a single wide-ranging species as outlined by Clark & Downey (1992) is accepted.

The presence/absence of bivalve pedicellariae appears to be a possible discrete character which could support a species such as *Peltaster nidarosiensis*. However, Downey in Clark & Downey (1992) found "no geographic or bathymetric pattern to these variations in pedicellariae, nor any correlation with other characters." This was in relation to both bivalve and "sugar tongs" pedicellariae. Four specimens displaying bivalve pedicellariae were examined. Bivalve pedicellariae were observed on both eastern and western Atlantic specimens (e.g. Fig. 9A–C) in addition to one specimen from the North Atlantic (MNHN-IE-2019-5507) with bivalve pedicellariae consistent

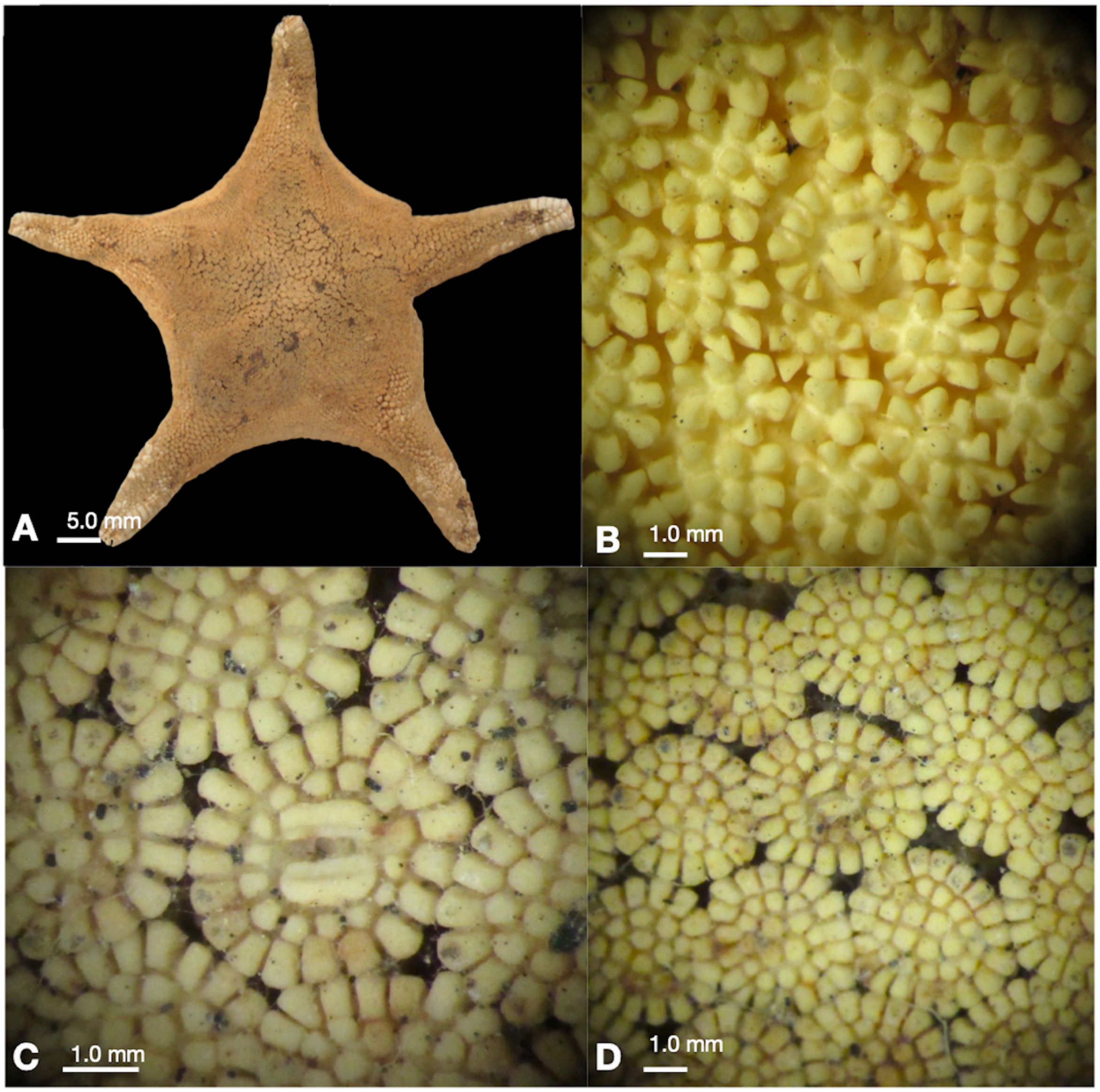

FIGURE 8. *Mediaster sladeni*, New Zealand, USNM 1126279. A. Abactinal. B. Actinal trivalve pedicellariae. C. Abactinal bivalve pedicellariae. D. Abactinal trivalve pedicellariae.

with the "*nidarosiensis*" morphotype (Fig. 9D–E). One tropical Atlantic specimen, USNM 1225448 possessed paddle-shaped pedicellariae on the abactinal surface but abundant bivalve pedicellariae on the actinal intermediate surface. USNM 38229 displayed bivalve pedicellariae on abactinal and actinal surfaces. None of the specimens with bivalve pedicellariae possessed secondary plates, as other *P. placenta* are listed as having (Halpern 1970).

In situ observations of *Peltaster placenta* show feeding on a deep-sea demosponge in the genus *Geodia* sp. in conjunction with the goniasterid *Plinthaster dentatus* and a cidaroid sea urchin. These show the actinal surface of both pentagonal-shaped stars, *Peltaster* and *Plinthaster* splayed out on the sponge surface with stomach extended (Mah 2020). It is possible that pedicellariae, either bivalve or tong-like play a role in predation of this kind via physical damage of the issue prior to digestion by the extended cardiac stomach. Mediterranean individuals of *Peltaster placenta* were observed to feed on antipatharians (Bo *et al*. 2018) Their Fig. 1e shows apparent pedicellariae adjacent to the adambulacral spination. It is argued that these play a role in the feeding process, breaking up the tissue prior to digestion.

Distribution/Occurrence

Western Atlantic: Cape Cod region, Massachusetts, New York, Florida, Georgia, Louisiana, Antigua and Barbados, Bahamas, Jamaica, Puerto Rico, Guadeloupe, Venezuela, Eastern Atlantic: Norway (near Trondheimsfjord) south to the equator, Iceland, Mediterranean, including Tunisia. 10–1007 m.

Material Examined

Peltaster placenta ("*nidarosiensis*" morphotype)

USNM 38229 Off of Key West, Florida Keys, Gulf of Mexico, North Atlantic Ocean, 24.2917 -81.8917 , 232

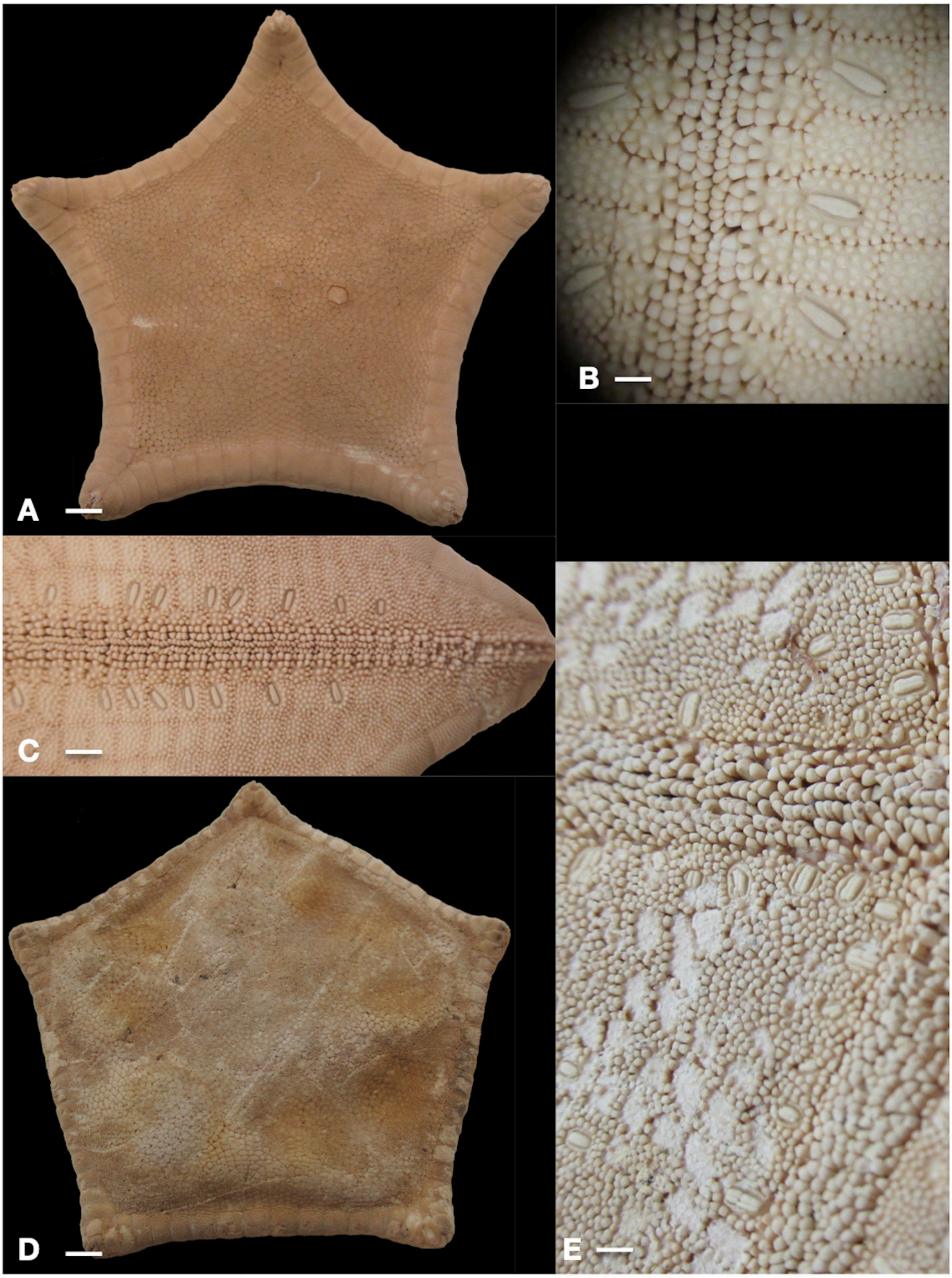

FIGURE 9. *Peltaster placenta* A. Abactinal USNM 1127107. B. Close-up pedicellariae adjacent to adambulacral series. C. Pedicellariae adjacent to adambulacral series. D. MNHN-IE-2019-5507 Abactinal. E. Pedicellariae on actinal surface adjacent to mouth.

m. Coll. R/V *Fish Hawk*, 19 Feb 1902, 2 dry specs. R=4.4 r=3.0, R=4.7 r=3.0

USNM E12588 Marie-Galante, Guadeloupe, Caribbean Sea, North Atlantic Ocean. 15.67 -61.15 , 622 m. Coll. RV *Oregon* II, 1 Dec 1969. 1 dry spec. R=8.0 r=5.7.

USNM 1225448 Lease Blocks VK862/VK906, Gulf of Mexico, North Atlantic Ocean. 29.1065 -88.384, 336–316 m. Coll. S.W. Ross, *Johnson Sea Link* II, 20 Feb 2009. 1 dry spec. R=8.2 r=5.6.

MNHN-IE-2019-5507 Edie Warner Island Faugplatz, North Atlantic 66.0058333333 -25.01194445, Coll. 8 June 1964.1 dry spec.

Stellaster **Gray, 1840**
FIGURE 10A–D

Gray, 1840: 277; Doderlein, 1935: 86; H.L. Clark, 1946: 96; A.M. Clark & Rowe, 1971: 49.

Diagnosis
Body stellate, arms triangular, tapering. Abactinal plates polygonal or substellate, covered by granules, small, crowded. Inferomarginal plate with a flattened mobile spine. Bivalve pedicellariae present, flush on actinal surface. Tong-like pedicellariae also present in some taxa (Modified from Marsh & Fromont 2020).

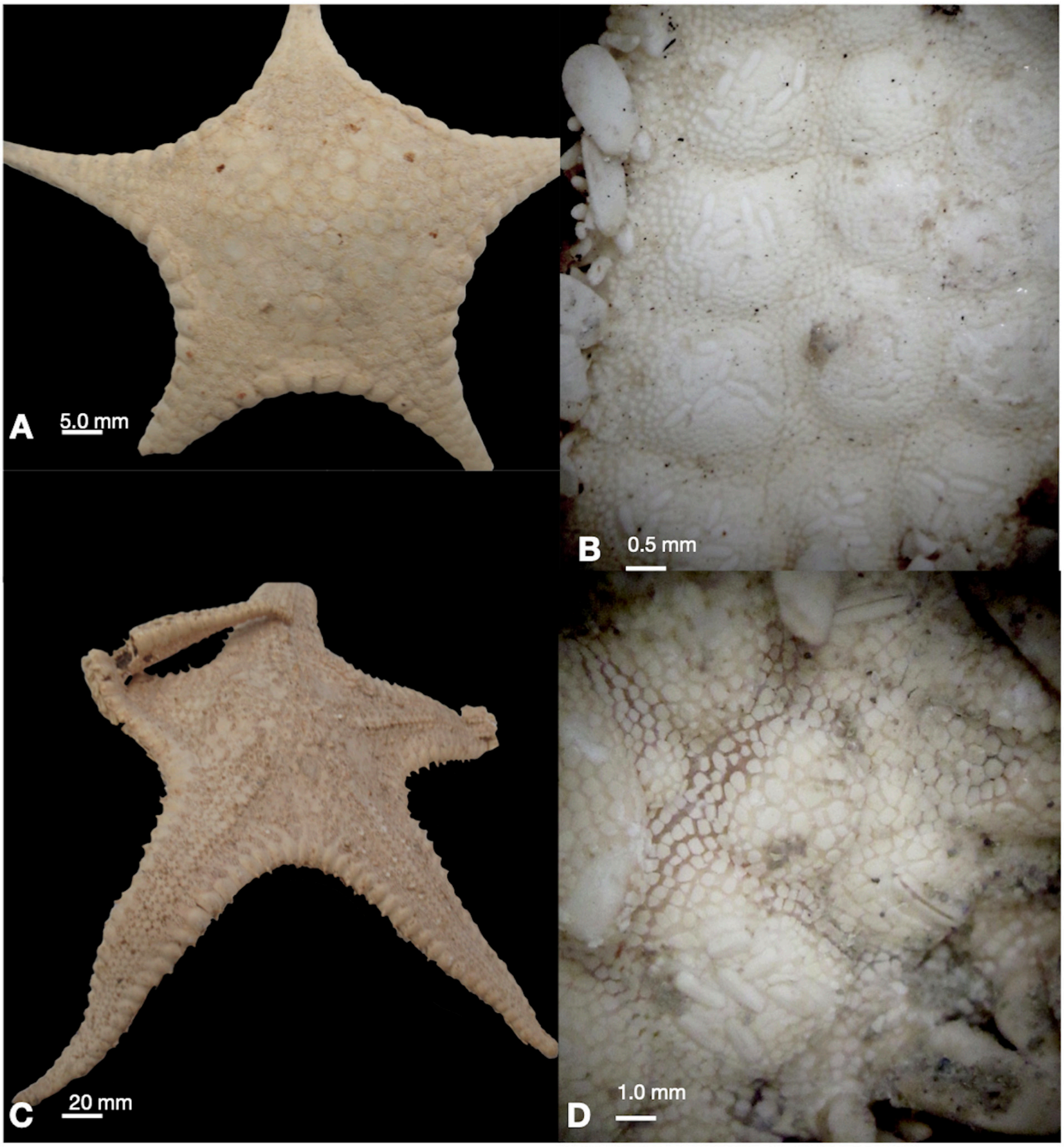

FIGURE 10. *Stellaster* spp. A. *Stellaster childreni*, USNM E46871, Abactinal. B. Closeup on pedicellariae on actinal surface. C. *Stellaster princeps* USNM E38930 D. Closeup on pedicellariae on actinal plates adjacent to mouth.

Comments

Stellaster includes 7 species, present throughout the Indo-Pacific, but particularly in Australian waters. Marsh and Fromont (2020) have documented 4 commonly encountered shallow-water species. One species, *Stellaster childreni* Gray, 1840 occurs widely throughout the Indo-Pacific. Bivalve and small paddle-shaped pedicellariae are widespread on several species of *Stellaster*. Specimens of two species, the widespread *Stellaster childreni* and the Australian *Stellaster princeps* were examined, in addition to descriptions of additional species. Bivalve pedicellariae were observed on specimens of *Stellaster childreni* (USNM E46871) (Fig. 10B) and *Stellaster princeps* Sladen, 1889 (E38930) (Fig. 10D) with bivalve pedicellariae reported on *Stellaster inspinosus* H.L. Clark, 1916 and *Stellaster septemtrionalis* Imaoka *et al*. 1991 by their respective authors. Doderlein (1935) detailed extensive variation among forma of *Stellaster "equestris"* (=*S. childreni* according to A.M. Clark, 1993). However, confirmation of bivalve pedicellariae across this range was beyond the scope of this survey.

Surveyed specimens showed few bivalve pedicellariae on the abactinal surface but in high abundance on the actinal surface with multiple pedicellariae present on the surface of plates adjacent to the adambulacral plates and the mouth (Fig. 10B, D). These occur in an unordered, irregular fashion in contrast to the more serial transverse oriented pedicellariae of other Goniasteridae (e.g. *Bathyceramaster kelliottae*).

Material Examined

Stellaster childreni Gray, 1840 USNM E46871 Namp'odong, Pusan, Western Channel, Korea Strait, South Korea. Coll. B.J. Rho, 26 May 1981. 3 dry specs (arm tips broken). R=6.3 r=2.5, R=6.2 r=2.6, R=6.7 r=2.4.

Stellaster incei Gray, 1947 (=*Stellaster childreni)* USNM E10226 Off east coast Malay Peninsula, Thailand Gulf of Thailand. Coll. R/V *Tongkol*, 1926. 1 dry spec.

Stellaster princeps Sladen, 1889 USNM E38930, North of Wessel Islands, Arnhem Land, Northern Territory, Australia, Arafura Sea, South Pacific. -10.4333 136.433, 56.0 m. coll. W. Houston, 9 March 1985. 1 dry spec. R=17.5 r=5.5.

Wallastra Mah, 2018

Wallastra elenderae Mah, 2018

FIGURE 11A–D

Mah 2018: 98, Fig. 37A–G.

Diagnosis

Body strongly stellate (R/r=3.46) with elongate, slender arms, weakly curved interradial arcs. Abactinal plates bare, surface mostly bare and smooth, especially on distal disk regions adjacent to superomarginals and along arms. Central disk plates with one to several, widely distributed button-like granules. Superomarginals wide to quadrate in shape, with mostly bare surface, or widely distributed coarse granules occur. Each actinal plate covered with closely articulated granules, most plates with a single large bivalve pedicellaria. Furrow spines four or five, large bivalve pedicellariae present.

Comments

Prominent bivalve pedicellariae are present on nearly every actinal plate in this species (Figs. 11B–C) as well as on each adambulacral plate (Fig. 11D) with very few to none on the abactinal or marginal plate surfaces. As discussed by Mah (2018) this species shares similarities with *Astroceramus*, differing primarily in lacking glassy granules from the abactinal surface and in displaying numerous bivalve pedicellariae.

Although never observed alive and *in situ*, the bivalve pedicellariae pattern and valve morphology is very similar to that observed in multiple species of *Circeaster*.

Distribution/Occurrence

Solomon Islands and Western Indian Ocean, between Mayotte and the Glorioso Islands, 550–836 m.

PENTAGONASTERINAE Perrier, 1884

Diagnosis

Abactinal plates smooth or with discrete smooth surface, flattened, to very convex, hexagonal to polygonal in clearly delineated outline. Primary circlet plates well defined, interradial plates enlarged in most taxa. Bare (i.e. ornamentation is absent), smooth (i.e. flat, frictionless surface) abactinal plates in most, but with partial granular covering in some genera (e.g. *Toraster, Ryukuaster*, gen. nov.). Fasciolar grooves between abactinal marginal plates shallow to well developed. Double to multiple papular pores in most taxa. Madreporite triangular. Superomarginal and inferomarginal plates swollen, blocky, length >width in most specimens examined. Marginal plates commonly smooth to bare, but some taxa with few to scattered granules. Penultimate superomarginals swollen or elongate in many taxa. Actinal plates relatively large, polygonal, smooth, bare, with occasional granular covering. Bare spot on granulated surface sometimes present. Furrow and subambulacral spines few in number, usually two to three, blunt and thickened in most taxa. Pedicellariae bivalve or tong-like, enlarged to basal plate-sized in some genera. Adambulacral plates with horizontally oriented, symmetrical 'divider' in most. Overall body shape with low R/r, pentagonal or weakly stellate with rounded arm tips. Test robust, heavily calcified (from Mah 2007).

Comments

The Pentagonasterinae was defined with a morphology-based phylogenetic analysis to include *Tosia, Pentagonaster, Toraster, Anchitosia, Ryukyuaster, Eknomiaster*, and *Akelbaster* (Mah 2007) and is comprised almost entirely of species that occur in the Southern Hemisphere.

The Pentagonasterinae is diagnosed from the more

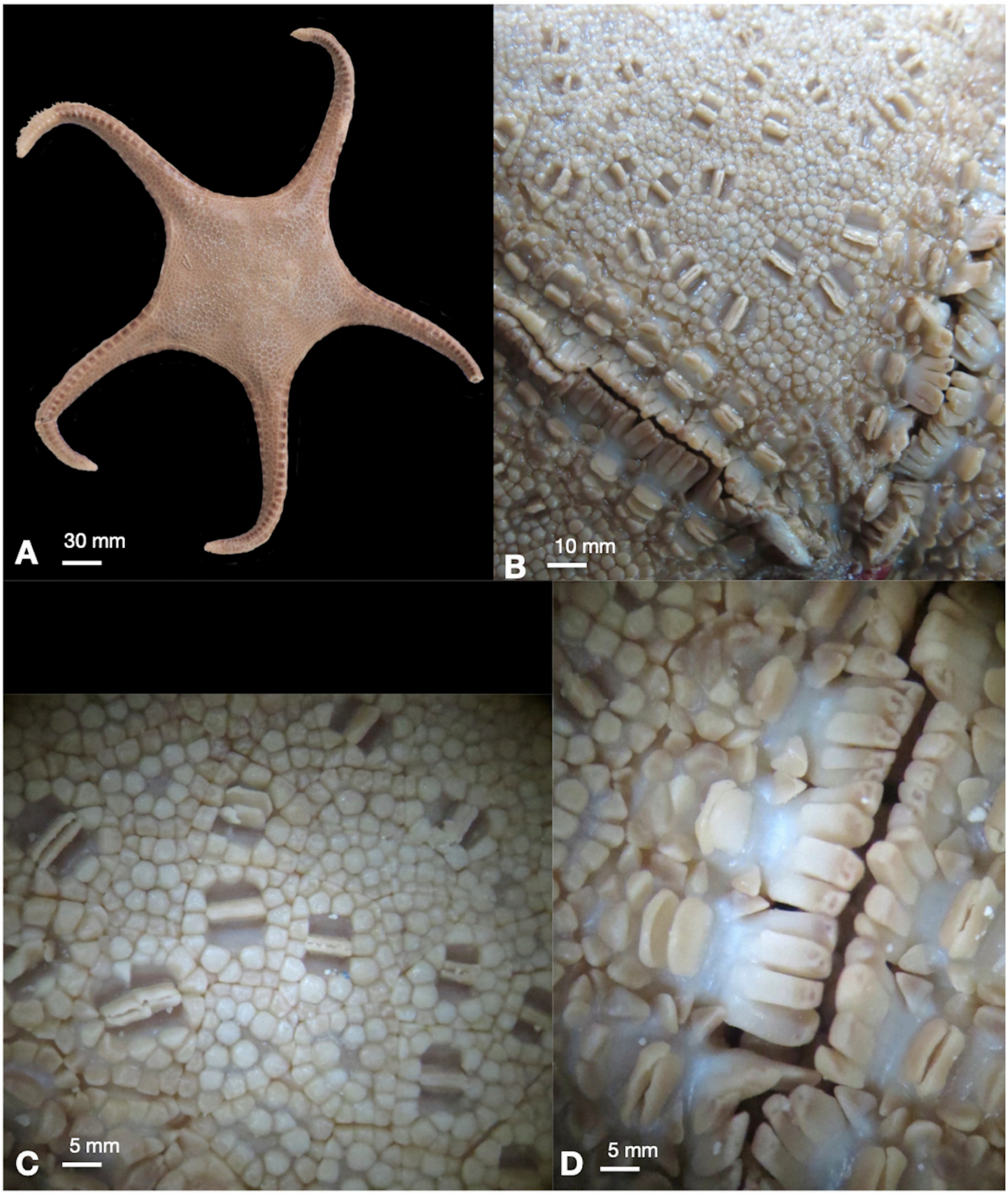

FIGURE 11. *Wallastra elenderae* MNHN-IE-2013-17165. A. Abactinal. B. Actinal and furrow areas. C. Closeups on actinal pedicellariae. D. Adambulacral pedicellariae.

broadly defined Goniasteridae based on the presence of abactinal, marginal and actinal plates with a smooth surface and in many taxa with well-defined fasciolar grooves. Marginal plates are relatively few and enlarged with body shape often pentagonal or weakly stellate.

Three species in two genera, *Akelbaster novaecaledoniae* Mah, 2007, *Eknomiaster macauleyensis* Clark & McKnight, 2001, and *Eknomiaster beccae* Mah, 2007 display very numerous and/or very prominent bivalve pedicellariae.

***Akelbaster novaecaledoniae* Mah, 2007**
FIGURE 12A–B

Akelbaster novaecaledoniae Mah, 2007: 318, Figs. 3A–F.

Diagnosis

Body thick, rigid, pentagonal in shape, R/r=1.1–1.5. Abactinal plates smooth, bare, pointed to tubercular, very convex forming bumpy surface texture. Large bivalved pedicellariae present on every marginal plate

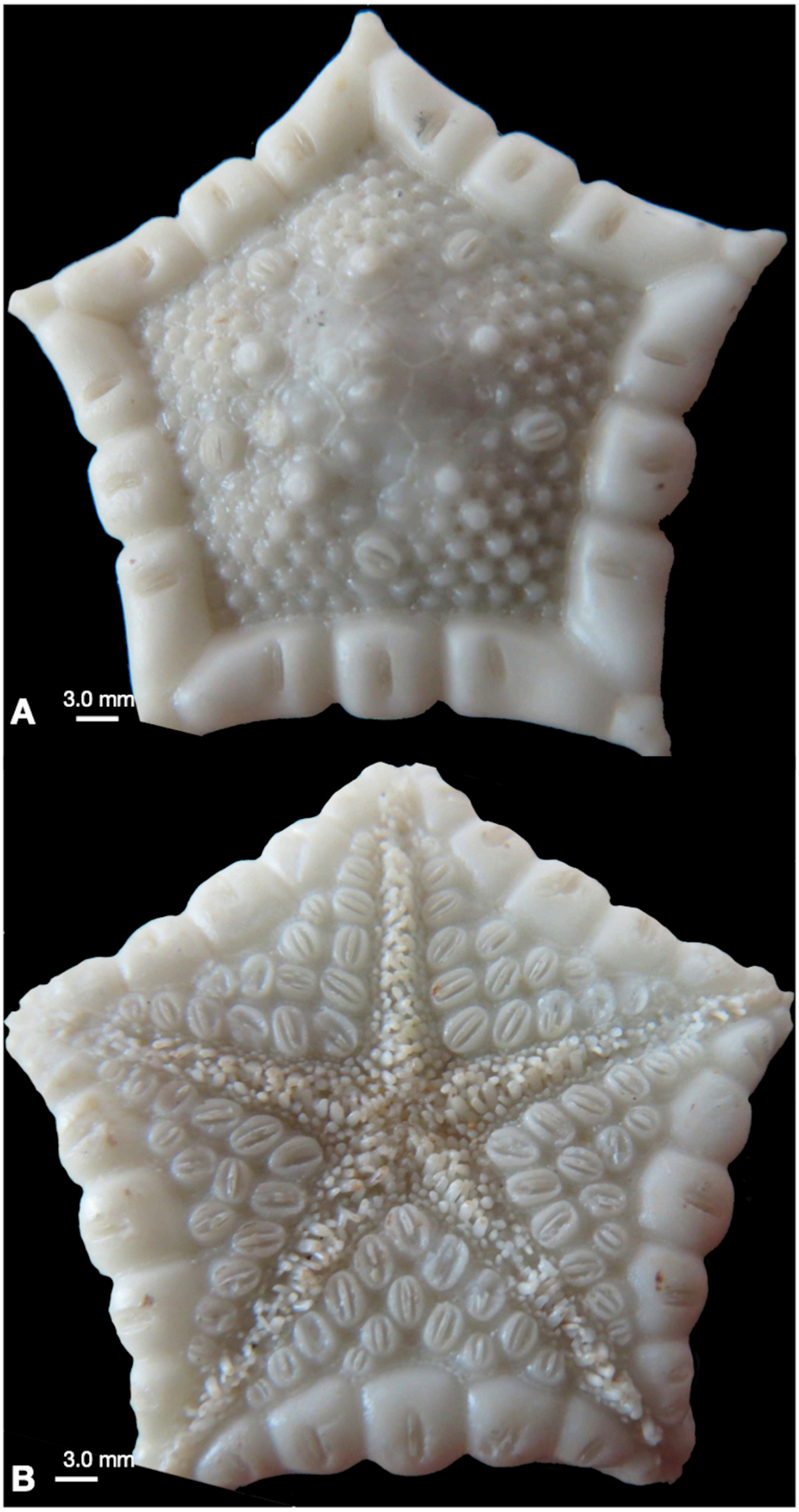

FIGURE 12. *Akelbaster novaecaledoniae* MNHN-IE-2007-6650. A. Abactinal. B. Actinal.

and on every actinal intermediate plate. Intermarginal 'pit' present, covered by flattened, scalar spines. Three superomarginals, 10 inferomarginals in largest specimens recorded (R = 2.0). Marginal plates completely bare. Dorsal and ventral-facing surface of every superomarginal and inferomarginal plate each with a single, centrally located bivalve pedicellariae. All actinal plates entirely bare save for a bivalve pedicellariae occupying nearly the complete surface of each. Furrow spines 3 to 4.

Comments on pedicellariae

Pedicellariae distribution and abundance in *Akelbaster novaecaledoniae* is unusual, even for the observed patterns in the Goniasteridae in that nearly every actinal plate is occupied primarily by a bivalve pedicellariae and its alveolus, in addition to identical pedicellariae present in each interradius on the abactinal surface as well a transversely arranged pedicellariae on every marginal plate. (Fig. 12A–B).

Actinal pedicellariae in *Akelbaster* appear similar in abundance to that of the Cretaceous *Weitschataster intermedius*, but is otherwise very different in terms of marginal plate shape and ornamentation. Biology and life mode of this species are unknown. However, the SEM of structures present between the marginal plates of *Akelbaster* are reminiscent of cribriform organs of porcellanasterids, possibly suggesting a similar buried life mode.

Distribution/Occurrence

Known only from New Caledonia, many specimens from seamounts, 225–400 m

Material Examined

MNHN-IE-2013-7023 New Caledonia, -23.3 168.25, 270 m. Coll. NORFOLK 2, DW 2124, 11 Feb. 2003. 1 wet spec. R=1.1 r=0.7.

MNHN-IE-2007-6345, New Caledonia, -22.313333 168.686667, 340–345 m. Coll., EXBODI DW 3855, 14.09.11, 2 wet specs. R=1.0 r=0.8 R=0.9 r=0.8.

MNHN-IE-2007-6650, New Caledonia, -22.22 167.155, 353–365 m. Coll. EXBODI DW3784, 9 Feb, 2011 1 wet spec.

Eknomiaster H.E.S. Clark in H.E.S. Clark & McKnight, 2001

Eknomiaster H.E.S. Clark, 2001: 40; Mah, 2007: 316; 2018: 32.

Diagnosis

Body shape pentagonal (R/r=1.47–1.55), interradial arcs weakly curved to straight. Abactinal plates, polygonal, bare, smooth with no surficial accessories. Marginal plates, blocky, smooth with no surficial accessories, enlarged with five to eight per interradius. Actinal surface covered by granules, pedicellariae of varying types. Furrow spines three to seven.

Comments

Eknomiaster was described by H.E.S. Clark in H.E.S. Clark & McKnight (2001) from the New Zealand region (South Pacific). Two additional species have subsequently been described, including *Eknomiaster beccae* Mah 2007 from the New Caledonia region and *Eknomiaster horologium* from the Indian Ocean. *Eknomiaster* species are differentiated based on the morphology of pedicellariae present on the actinal surface. *Eknomiaster macauleyensis* and *E. horologium* both possess a paddle-shaped pedicellaria present on each actinal plate. These differ from *Eknomiaster beccae* which possesses a large bivalve pedicellariae, each 2 to 3X the size of adjacent actinal plates, variably 1 to 3 in each interradius.

Eknomiaster beccae Mah, 2007

FIGURE 13A–F, 14A–B

Eknomiaster beccae Mah 2007: 316, Fig. 2D–F.

Comments

As described in Mah (2007), this species is separated from other species of *Eknomiaster* by the 1 to 3 enormous pedicellariae present in each actinal intermediate region (Fig. 13C–F).

Pedicellariae Variation

Additional specimens of *Eknomiaster beccae* allowing a survey of pedicellariae variation in this unusual species. As indicated by Mah (2007), the actinal pedicellariae varies in number from 1 to 3. However subsequent observation suggests that among individuals with three pedicellariae length and morphology varies between the central and the two adjacent pedicellariae among different individuals (Figs 13B–F). In specimens such as MNHN-IE-2013-6613, pedicellariae on either side of the central pedicellaria are much shorter and approximately half its size (Fig. 13D), whereas in MNHN-IE-2014-297, all three pedicellariae are more slender, distinctly elongate and similar in length to one another (Fig. 13C). Other than pedicellariae and associated actinal characters such as granules, observed abactinal and marginal characters were similar to *Eknomiaster macauleyensis* specimens

Among examined specimens, size was apparently not a factor associated with pedicellariae number. A total of 4 individuals, 2 lots plus the holotype, displayed a single pedicellariae in each interradius (Fig. 13B). The smallest *E. beccae* specimens (R=0.5 and 0.7 cm, MNHN-IE-2014-515) displayed a single pedicellaria in each actinal interradius (Fig. 14A–B). The adjacent pedicellariae were absent, suggesting that the central one is the first to form. Specimens with R=1.4 and 1.7 showed 3 pedicellariae, but with no size and pedicellariae overlap, suggesting the possibility the further two lateral pedicellariae could simply arise as individuals increase in size (R> 0.7).

Although most specimens examined displayed a consistent number and similarly sized pedicellariae per actinal interradius, not all of them did. Three specimens in MNHN-IE-2013-7300 have only 1 or 2 pedicellariae

FIGURE 13. *Eknomiaster beccae* variation. A. MNHN IE-2014-505, Abactinal. B. Actinal. showing single pedicellariae. C. MNHN-IE-2014-297 pedicellariae elongate. D. MNHN-IE-2013-6613 small lateral pedicellariae E. MNHN-IE-2013-7300. variation showing two pedicellariae in one interradius. F. variation showing single and two pedicellariae in two interradii, respectively.

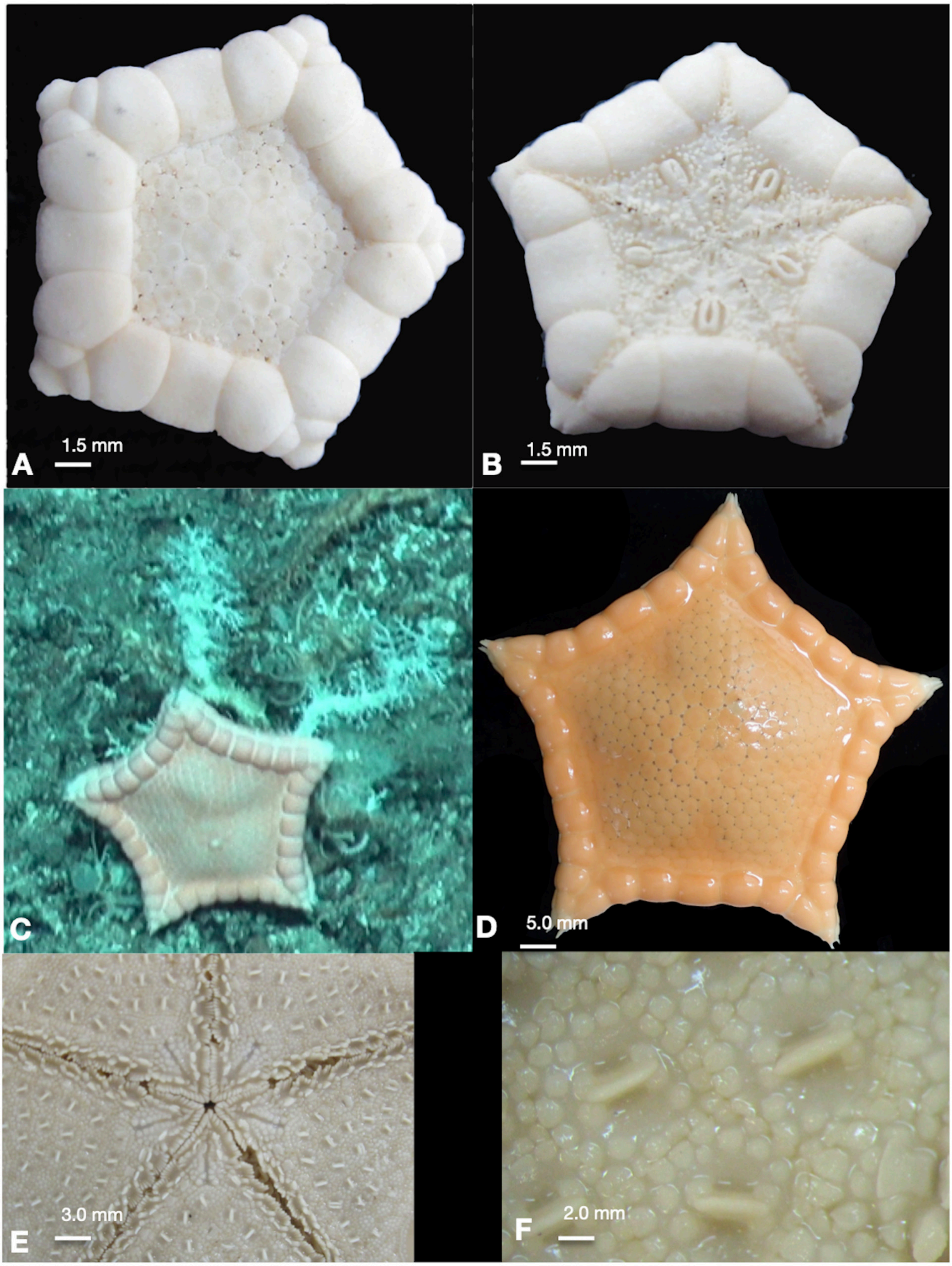

FIGURE 14. *Eknomiaster beccae* small size MNHN-IE-2014-515 A. Abactinal B. Actinal. C. *Eknomiaster macaulayensis* MNHN-IE-2019-3019, *in situ* D. Abactinal surface. E. Closeup of actinal surface. E. Paddle-like actinal pedicellariae.

in one interradial region (Fig. 13E, F), with the typical 3 pedicellariae present in the other 4 areas. In all these instances, the central pedicellariae in the identical consistent position was present but lacking lateral pedicellariae (Fig. 13F).

Distribution/Occurrence
New Caledonia. 215–1074 m.

Material Examined
MNHN-IE-2013-6613 New Caledonia, 460–470 m, Coll. CHALCAL 2, DW 77, 1 wet spec. R=2.7 r=2.1.

MNHN-IE-2013-6721 Norfolk Ridge, New Caledonia, -23.766667 168.283333, 400–439 m. Coll. Lozouet, Boisselier, Richer, IRD, NORFOLK 1, CP 1711, N/O *Alis,* 1 wet spec. R=2.7 r=1.9.

MNHN-IE-2013-6722 Banc Jumeau est, New Caledonia, -23.766667 168.283333, 400–465 m, Coll. Lozouet, Boisselier, Richer, IRD, NORFOLK 1,CP 1705, N/O *Alis*. 4 wet specs. R=3.1 r=2.0, R=2.7 r=2.0, R=3.2 r=2.2, R=2.7 4=1.9.

MNHN-IE-2013-4734 Banc Jumeau est, New Caledonia, -23.775333 168.285339 , 403–440 m, Coll. Lozouet, Samadi & Richer-IRD, NORFOLK 2, N/O) *Alis*. 1 wet spec. R=3.6 r=2.3.

Eknomiaster macauleyensis H.E.S. Clark in H.E.S. Clark & McKnight, 2001
FIGURE 14C–F

Eknomiaster macauleyensis H.E.S. Clark, 2001 & McKnight: 42, Plate 9; Mah, 2007: 318.

Comments
A species described from a damaged specimen collected from near Macauley Island in the Kermadec group (H.E.S. Clark & McKnight, 2001). Further specimen occurrences are reported herein and throughout the New Caledonia region (Mah 2007). Depth has been extended from 215 to 691 m depth.

***In situ* Observation and Pedicellariae Notes**
During the KANADEEP 2 expedition, exploring New Caledonia, the ROV *Victor II* observed and collected a specimen of *Eknomiaster macauleyensis* (MNHN-IE-2019-3019) perched on a stylasterid coral (MNHN-IK-2015-3099) identified as *Stephanohelia praecipua* Cairns, 1991 upon which it was likely feeding (Fig. 14 C).

The *E. macauleyensis* specimen may have been feeding on polyps of the stylasterid or alternatively, if the stylasterid was moribund, it may have been feeding on epizoic taxa, such as hydroids, growing on its surface. Bivalve pedicellariae were present on nearly every actinal plate (Fig. 14E–F). The distances between them may show a relationship with the polyps on the stylasterid.

Distribution
Norfolk Ridge, Wanganella Bank, Jumeau East, *Stylaster* Bank, Grand Passage, 215–691 m.

Material Examined
MNHN-IE-2013-4690 Banc Zorro, New Caledonia, -25.400167 168.332672, 623–691 m. Coll. P. Lozouet, S. Samadi & Richer, IRD. NORFOLK 2, 27 Oct. 2003, 1 wet spec.

MNHN-IE-2019-2158 Banc Antigonia, New Caledonia, -23.346666 168.080002, 215–260 m. Coll. B. Richer de Forges, IRD, SMIB 4. March 9, 1989. 1 wet spec.

MNHN-IE-2019-3019 New Caledonia, 23.616667 167.7333333, 559 m. Coll. ROV *Victor* II, KANADEEP 2 Pl. 743.04, PBT-I-06, 13 Sept. 2019 1 wet spec. (*in situ* image).

MNHN-IE-2009-2159 Grand Passage, New Caledonia, -18.870001 163.354996, 550 m. Coll. N/O *Vauban*, MUSORSTOM 4, 19 Sept. 1985. 1 wet spec.

MNHN-IE-2009-2187 Banc Stylaster, New Caledonia, -23.6675 167.675003, 517–570 m. Coll. P. Lozouet, S. Samadi & Richer, IRD. NORFOLK 2. 1 wet spec.

MNHN-IE-2009-2190, Banc Jumeau east, New Caledonia, -23.6675 167.675003, 470–621 m. Coll. P. Lozouet, S. Samadi & Richer, IRD. NORFOLK 2. 1 wet spec.

MNHN-IE-2013-7300 Jumeau Est, Ride de Norfolk, New Caledonia, -23.79583 168.28883, 410–530 m, Coll. S. Samadi, P. Lozouet & M. Castelin, N/O *Alis*, TERRASSES, 19 Oct 2008. 1 wet spec.

Toraster A. M. Clark, 1952

Toraster A.M. Clark 1952: 205; A.M. Clark, 1993: 287; Clark in A.M. Clark and Downey 1992: 267.

Diagnosis & Comments. Monotypic, as for species.

Toraster tuberculatus (Gray, 1847)
FIGURE 15A–D

Astrogonium tuberculatum Gray, 1847: 79.
Pentagonaster Perrier, 1875: 222 (1876: 38); Bell, 1905: 246.
Toraster tuberculatus A.M. Clark, 1952: 205; A. M. Clark & Courtman-Stock, 1976: 66. A.M.
Clark, 1993: 289; Clark in A.M. Clark & Downey, 1992: 267; Mah, 2007: 314, 323. Atkinson & Sink, 2018: 425.
Tosia tuberculata H.L. Clark, 1923a: 266; 1926: 11; Mortensen, 1933: 243.

Diagnosis
Body form weakly to strongly stellate, relatively thin relative to *Tosia* or *Pentagonaster*. Arm tip, rapidly narrowing, pointed. Abactinal plates extremely convex, swollen, mostly bare, smooth, round to polygonal in outline. Abactinal surface covered with large, evenly round, spherical granules covering some secondary plate surfaces and plate periphery, especially at lateral contact with superomarginal plate series. Abactinal plates all

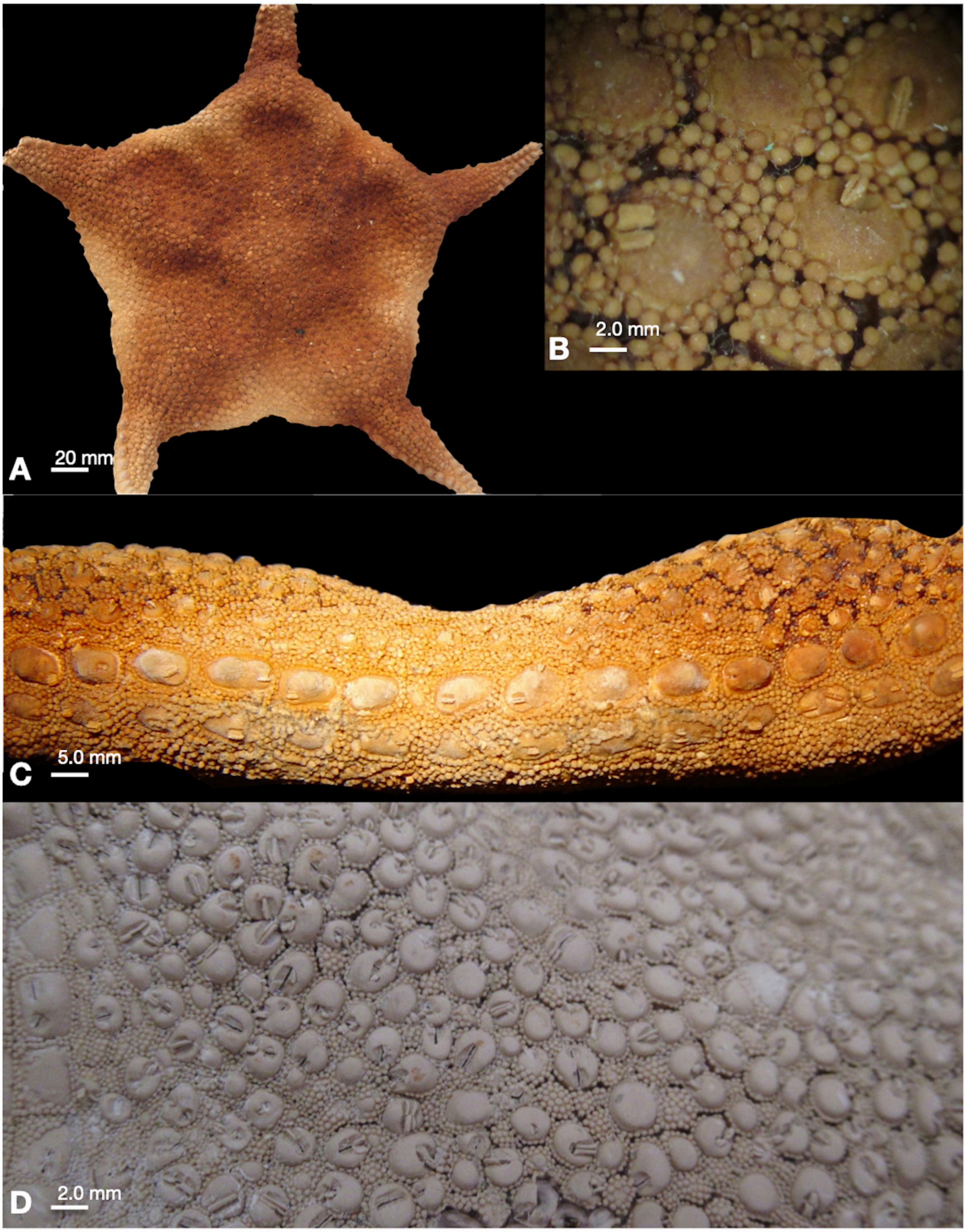

FIGURE 15. *Toraster tuberculatus* USNM 1666413. A. Abactinal B. Closeup on abactinal pedicellariae. C. Lateal view showing marginal plate pedicellariae. D. USNM E19060. Abactinal closeup on plates.

relatively uniform in size, radial/interradial plates not distinctive, not enlarged. Primary circlet plates sometimes enlarged. Abactinal plates relatively small compared to *Tosia* or *Pentagonaster*. Large bivalve pedicellariae present, commonly bisect abactinal plates. Madreporite polygonal. Double to multiple papular pores present, but absent interradially. Fasciolar grooves between abactinal plates well-developed. Marginal plates convex, longer than wide, interradially, becoming more wider distally, relatively small compared to *Pentagonaster* or *Tosia*, decreasing in size distally.

Enlarged bivalve pedicellariae similar to those on abactinal plate surface irregularly present on superomarginal plates. Large, spherical granules, similar to those on abactinal surface form periphery and cover partial superomarginal and inferomarginal surface, especially on lateral marginal plate surface. Granules sometimes distributed patchily over plate surface. Fasciolar grooves between marginal plates, well-developed. Swollen penultimate marginal plates absent.

Multiple (3–6) superomarginal plates in contact across midradius adjacent to armtip, becoming more swollen, wider distally. Actinal plates polygonal, obscured by spherical granules identical to those in *Tosia* or *Pentagonaster*. Furrow spines enlarged, relatively few (1–3) in number per plate. Subambulacrals also thickened, granular, becoming indistinguishable from actinal granulation. Adambulacral plate surface facing furrow-straight in outline. Adambulacral "divider" directed horizontally, oriented symmetrically (from Mah 2007) Living color described by Mortensen (1933: 243) as a "beautiful red'.

Comments

Toraster tuberculatus is unusual because the pattern of pedicellariae abundance is the reverse of what is observed in most other Goniasteridae. Bivalve pedicellariae in this species are most numerous on the abactinal side, but largely absent from the actinal surface (Fig. 15B–D). Pedicellariae where present nearly always occur in dome-like enclosures (Fig. 15D). Based on dissection, these are the alveolus for the pedicellariae where the valves attach internally to connective or muscle tissue.

Distribution/Occurrence

South Africa, South Africa: Natal to western Cape Province; 75–366 m.

Material Examined

USNM E19064 Cape of Good Hope, False Bay. 1 dry spec. R=6.4, r=3.5.

USNM E 19060 Cape of Good Hope, 13 Mi, east of Vasco de Gama. 1 dry spec. R=4.1, r=2.3. CASIZ 087576, Off S. Africa -35.520556 21.3333, 110 m, coll. J. Korrubel, 38 Sta. A12008, 15 Sept. 1991. 1 dry spec. R=6.1, r=4.2.

USNM 1666413 From wellhead on South coast, South Africa, 120–248 m. Coll. by SAT (saturation divers) 11 Aug 2012, A32223. 1 dry spec. R=11.6 r=6.1.

CIRCEASTERINAE Mah 2024b

Diagnosis

Body strongly stellate (R/r=3.0–4.0), arms elongate, slender to broad based. Abactinal plates variably flat to weakly convex, covered by large, coarse granules. Abactinal plate surfaces mostly smooth but with large granules, scattered to absent. Distinctly coarse granules mark periphery. Arm plates in *Circeaster* and *Atheraster* 2–3x the size of those on the disk but more consistent in size in *Lydiaster* and *Armaster*. Marginal plates blocky, wide, forming prominent border variably bare or with pronounced large conical spine and/or spinelets; granules on plate surfaces, scattered. Actinal surface covered by spinelets or granules. Adambulacral spination with enlarged, thickened subambulacral spine(s), alveolar pedicellariae with variable morphology but valves spoon to flattened with teeth or prongs. Furrow spine number, ranging from 6 to 20, mostly 7 to 15.

Comments

The Circeasterinae, established by Mah (2024b) includes 16 species in 4 genera, including *Circeaster* Koehler, 1909 and three other genera, known primarily from deep-sea settings in the Pacific, Indian and Atlantic oceans. *Circeaster* and *Atheraster* Mah, 2022 have been observed *in situ*, feeding on colonial octocorals.

Bivalve pedicellariae are present in multiple species of *Circeaster* and *Atheraster* as well as *Astrophylax* **gen. nov.** Other genera possess various types of pedicellariae, but primarily paddle or tong-like morphologies. *Circeaster* was initially diagnosed based on the presence of enlarged abactinal plates on the arms relative to those on the disk, a character shared with *Atheraster*. Other genera, including *Lydiaster* and *Armaster* were recognized based on the similarity of abactinal and marginal plate morphology but further distinguished by spination, pedicellariae and other characters. *Astrophylax* lacks enlarged abactinal arm plates but is consistent with abactinal and marginal plate morphology as observed in *Circeaster* suggesting a close relationship.

Astrophylax gen. nov.

Etymology

The genus name is taken from the Greek *astron* for star and *phylax* for "guard" in reference to the many pedicellariae present on the actinal surface.

Included species. *Astrophylax valvatus* n. gen, sp. nov. (type species), *Astrophylax accinctus* n. gen, sp. nov.

Diagnosis

Abactinal plates, polygonal to round, convex with widely-spaced distinct, round granules. Marginal plates abutted over mid radius along arm. Marginal plate surface with numerous, widely spaced coarse granules. Actinal plates each with a large bivalve pedicellariae with teeth on each valve. Pedicellariae present along diameter of each plate, periphery surrounded by quadrate, spines, with jagged tips. Each interradius with large pedicellariae, large, 2 to 6 (although see description), either in series or present interradially. Furrow spines curved, 2 to 3, large with shorter, but angular, pointed subambulacral spines.

Comments

The convex abactinal and marginal plate shape and overall body shape are similar with those observed in several species of *Circeaster*, including *C. pullus*, *C. sandrae* and *C. americanus,* which also shows similarly shaped abactinal plates with a smooth surface and widely spaced coarse granules (Mah 2006). *Astrophylax* **gen. nov.** is therefore placed as a member of the Circeasterinae based on these characters, in addition to the morphology of the numerous actinal bivalve pedicellariae.

Although the abactinal and marginal plate surfaces of *Astrophylax* **gen. nov.** are similar to those of *Circeaster*, it can be distinguished from *Circeaster* by the very large actinal pedicellariae, the absence of enlarged abactinal arm plates (or any arm plates), the abutted superomarginal plates along the arm, and the presence of enlarged, and curved furrow spines.

Species within *Astrophylax* are distinguished primarily based on the distribution and location of enlarged pedicellariae on the actinal surface. *Astrophylax valvatus* **gen. nov. sp. nov.** is the type species for *Astrophylax* **gen. nov.**

***Astrophylax accinctus* sp. nov.**

FIGURE 16A–E

Etymology

The species name is taken from the Latin *accinctus* which means "well girded, armed, equipped" alluding to the pedicellariae on the actinal surface.

Diagnosis

Abactinal plates, polygonal to round, convex with widely-spaced distinct, round granules. Marginal plates abutted over mid radius along arm. Marginal plate surface with numerous, widely spaced coarse granules. Actinal plates with a pair of large bivalve pedicellariae, 5 to 10X the size of others on the actinal surface, each with smooth valves in each interradius. Pedicellariae present on each plate, periphery surrounded by blunt, thick spines, some with jagged tips. Furrow spines curved, 2 to 3, large with shorter, but angular, pointed subambulacral spines.

Comments

The description of this species is similar to the Papua New Guinea *Astrophylax valvatus* **gen. nov. sp. nov.**, specimen and is nearly identical in size (R=7.2 vs. 7.6) to the *A. valvatus* holotype and the larger paratype but differs significantly in that this species possesses only two enlarged pedicellariae per actinal interradial region (Fig. 16D). This is consistent within all four specimens examined. Each of these pedicellariae lacks the periphery of blunt spines as in *A. valvatus* **sp. nov.**

As discussed herein, the pedicellariae in *A. valvatus* occurs in a series with the largest culminating proximally whereas those in *A. accinctus* are located as a consistent pair in each interradius across different sizes (Fig. 16C).

Abactinal plates on *A. valvatus* are more angular and hexagonal in shape (Fig. 16B) compared to the Philippines specimens, which have more rounded edges and are closer to quadrate in outline.

Distribution/Occurrence

Philippines, 150–250 m.

Description

Body stout, strongly stellate (R/r=2.2–2.5), arms triangular, interradial arcs broadly curved (Fig. 16A, C).

Abactinal surface flat, level with superomarginal plate surface (interradial regions weakly sunken in dry specimen). Plates present only on disk up to point where superomarginals join over arm midline. Abactinal plates range from larger, quadrate plates to smaller more irregular shaped. Most plates on radial regions quadrate to round, large, becoming smaller and more irregular (quadrate, polygons and rounded) in shape interradially adjacent to superomarginal contact (Fig. 16B). Abactinal plate on distalmost disk region adjacent to abutted superomarginals slightly larger than adjacent carinals and with one irregular plate beyond first or second plate abutment. Plate surface covered by circular, evenly spaced, round granules, four to 40, most with between 10–30 (Fig. 16B). In the paratype, at R=2.7 one to six granules present, widely spaced. Granules numbering approximately three along a 1.0 mm line. Granule absence leaves corresponding pitting on plate surface. Plates peripherally surrounded by 15–60 quadrate shaped granules, approximately four to six per side. At R=2.7, four to 32 granules surround each plate. Two to four (mostly three) moderately sized (about 1.0 mm in length) pedicellariae observed, each bivalve shaped with rounded valves bearing jagged edges. Papulae present on radial regions, absent interradially. Madreporite pentagonal with well developed sulci; flanked by one abactinal plate per side. Shallow fasciolar grooves strongly developed radially, weak to absent interradially.

Superomarginals 16 to 38, inferomarginals 18 to 38 per interradius (Fig. 16A). Superomarginals and inferomarginals with slight offset resulting in a zig-zag shaped contact between them. Marginal plates rectangular and elongate in outline. Superomarginals 2 (in paratype) to 11 (in holotype) abutting over midline. Contact between superomarginals over midline is similarly jagged. Marginal plates relatively flat. Superomarginals and inferomarginals covered with round, evenly distributed granules, 20–300, most with 25–250 present on the surface of each plate (Fig. 16B). Granules most abundant interradially becoming less abundant and more widely spaced distally. Granules proximally dense and more closely arranged but similar overall to those on abactinal surface. Absent granules results in corresponding granular pitting present on plate surface. No pedicellariae on marginal plates observed. Shallow fasciolar grooves present among marginals. Terminal plate large, triangular with smooth surface.

Actinal surface with three to five plate series in chevron formation. Nearly all actinal plate series covered with a very prominent series of large bivalve pedicellariae (Fig. 16C–E), each with roughened to jagged valves, each surrounded by 6 to 12 blunt, round tipped granules. Those plates without pedicellariae, adjacent to the oral plate are round in shape with nine blunt spines around the edge of each. On the holotype, pedicellariae

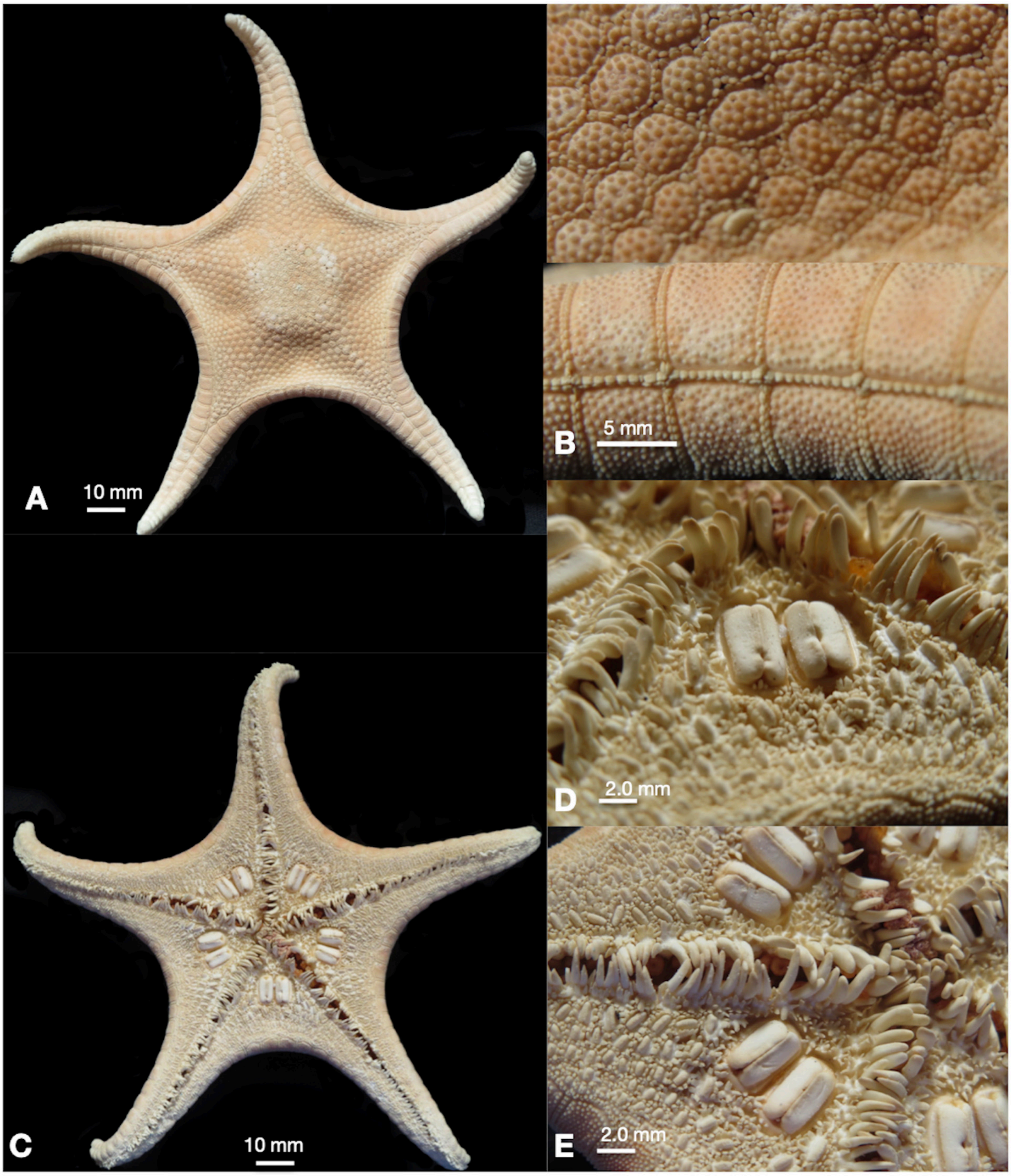

FIGURE 16. *Astrohylax accinctus* **sp. nov.** Holotype PNM 7153. A. Abactinal B. Abactinal-Marginal contact. C. Actinal. D. closeup on actinal intermediate pedicellariae. E. Adamblacral-oral region showing pedicellariae.

number approximately one per plate, with two largest pedicellariae, centrally on each interradius, on plates adjacent to mouth. Pedicellariae number approximately 30 from central proximal actinal plate along arm to arm tip. In the smaller specimen, pedicellariae occupy only a minority of actinal plates. Pointed granules, three to nine, mostly four to six, cover the surface of most actinal plates, especially adjacent to the inferomarginals. Large paired pedicellariae approximately 6.0 mm in length on paired plates adjacent to oral plate to 1.5 mm length pedicellariae more distally along arm (Fig. 16E). Each pedicellariae valve smooth but with weak to low irregularities along edge. No spines or other accessories directly around each pedicellariae. A wide, clear space is present between each of these pedicellariae and between the pedicellariae and the accessory covered actinal surface. Other actinal plate surfaces covered by bivalved pedicellariae of moderate size (1.0–2.0 mm in length) present in parallel series along actinal plates. Smaller sized pedicellariae with 10–15 jagged teeth. More distally and adjacent to the inferomarginals are actinal plates showing bivalve pedicellariae but also pointed granules, present one to three per plate surface. Shallow fasciolar groove present.

Furrow spines two, large and curved inwards toward the furrow with blunt tip, round in cross-section, interweaving with spines from either side (Fig. 16E). At R=2.7, furrow spines are more weakly curved and many are straight. Furrow spines are thickened proximally becoming more flattened distally. Subambulacral spinelets set off from furrow spines by a discrete space; highly variable in size and shape, numbering six to eight in two very irregular series of one to four, mostly two to three, behind the furrow spines. Some adambulacral plates with spinelets only on periphery of plate, absent from surface. Subambulacrals adjacent to furrow spine with one to two enlarged spines, irregular in shape, angular in cross-section. Subambulacral spinelets adjacent to actinal side quadrate to polygonal round in cross-section, smallest of the subambulacral spinelets. No pedicellariae observed. Oral plates with four furrow spines, curved, blunt. One large spine from oral plates projecting into mouth. Oral plate surface covered by seven to 10 blunt spines, triangular in cross-section.

Material Examined

Holotype. National Museum of the Philippines PNM 7153 Balut Island, Mindanao, Philippines. 200–250 m. 1 dry spec. R=7.6 r=3.0.

Paratypes. National Museum of the Philippines PNM 7154 Balut Island, Mindanao, Philippines, 150–250 m. 1 dry spec. R=5.7 r=1.9.

Further Material.

USNM 1762034 Balut Island, Mindanao, Philippines, 150–250 m. 1 dry spec. R=6.7 r=2.4.

USNM 1762035 Balut Island, Mindanao, Philippines. 200–250 m. 1 dry spec. R=2.7 r=1.2.

USNM 1740717 Balut Island, Mindanao, Philippines, 200 m. Coll. 2015. 1 dry specimen. R=7.3 r=2.9.

***Astrophylax valvatus n. gen,* sp. nov.**

FIGURE 17A–F

Etymology

The species epithet *valvata* is Latin for "folding door" or valve, alluding to the multiple pedicellariae present on the actinal surface.

Diagnosis

Body stout, strongly stellate (R/r=2.5), arms triangular, interradial arcs broadly curved. Plate surface covered by circular, evenly spaced, round granules, six to 50, most with between 20–40. Granules moderate in size, numbering three to four along a 1.0 mm line. Superomarginals 9 or 10 abutting over midline. Marginal plates relatively flat. Superomarginals and inferomarginals covered with round, evenly distributed granules, 20–300, most with 25–250 present on the surface of each plate. Actinal surface covered on nearly every plate by an enlarged bivalve pedicellariae with the primary series showing enlarged pedicellariae proximal to the oral region (Fig. 17E–F). Remainder of actinal surface covered by numerous low, rounded granules. Pedicellariae flanked by blunt, spines forming peripheral boundary. Furrow spines 2 to 3, large and curved inwards. Subambulacral spines 3, set off from furrow spines by a distinct space.

Comments

This species is distinguished by the presence of enlarged, serial bivalve pedicellariae arranged transversely to the ambulacral furrows with the largest pedicellariae present proximally adjacent to the oral region (Fig. 17E–F). Pedicellariae continue along the arm on the actinal surface to the distalmost tip. This is in sharp contrast to those enlarged actinal pedicellariae on *Astrophylax accinctus* **sp. nov.** which appears to be present as a fixed pair in each interradius.

Distribution/Occurrence

Papua New Guinea, 340–358 m.

Description

Body stout, strongly stellate (R/r=2.5), arms triangular, interradial arcs broadly curved (Fig. 17A, D).

Abactinal surface flat, level with superomarginal plate surface. Abactinal plates primarily hexagonal but ranging from polygonal to quadrate in outline (Fig. 17B). Most plates on radial regions hexagonal, becoming smaller and more irregular (quadrate, polygons and rounded) in shape interradially adjacent to superomarginal contact. Abactinal plate on distalmost disk region adjacent to abutted superomarginals slightly larger than adjacent carinals and with one irregular plate beyond first or second plate abutment. Plate surface covered by circular, evenly spaced, round granules, six to 50, most with between 20–40. Granules moderate in size, numbering three to four along a 1.0 mm line. Granule absence leaves corresponding pitting on plate surface. Plates peripherally surrounded by 15–60 quadrate shaped granules, approximately four to six per side. Three moderately sized (about 1.0 mm in length) pedicellariae observed, each bivalve shaped with rounded valves bearing jagged edges. Papulae present on radial regions, absent interradially. Madreporite pentagonal with well developed sulci; flanked by one abactinal plate per side. Shallow fasciolar grooves strongly developed radially, but weakly so interradially.

Superomarginals 34, inferomarginals 32 per interradius (Fig. 17A). Superomarginals and inferomarginals with slight offset resulting in a zig-zag shaped contact between them. Marginal plates rectangular and elongate in outline. Superomarginals 9 or 10 abutting over midline. Contact between superomarginals over midline is similarly jagged. Marginal plates relatively flat. Superomarginals and inferomarginals covered with round, evenly distributed granules, 20–300, most with 25–250 present on the surface of each plate (Fig. 17C). Granules most abundant interradially becoming less abundant and more widely spaced distally. Granules proximally dense and more

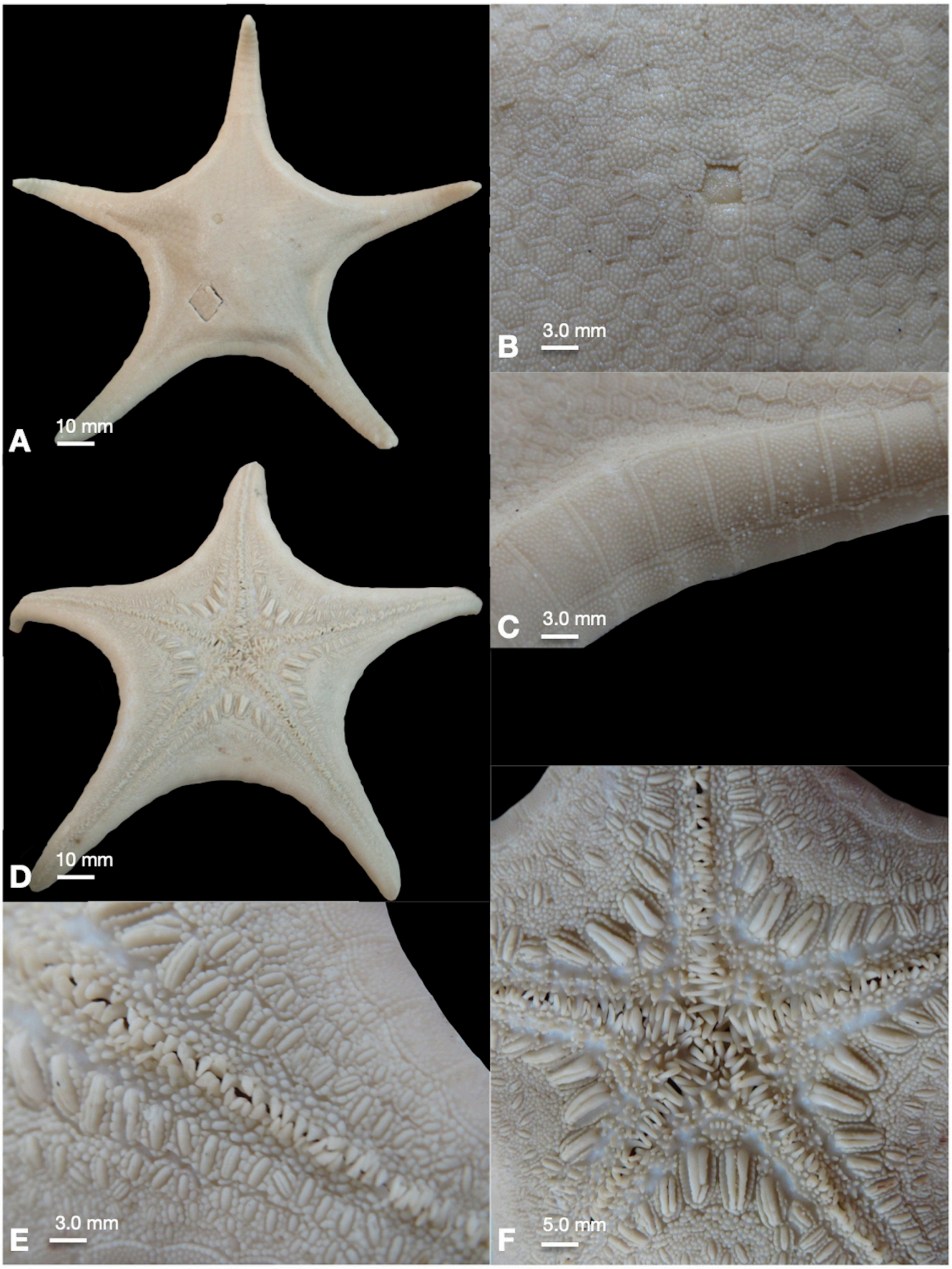

FIGURE 17. *Astrophylax valvata* **sp. nov.** Holotype MNHN IE-2007-3208. A. Abactinal B. Abactinal closeup, including madreporite. C. Lateral view of marginal plates. D. Actinal. E. Pedicellariae and furrow spination. F. Actinal-oral region showing pedicellariae.

FIGURE 18. *Circeaster columnaris* **sp. nov.** Holotype PNM 7152. A. Abactinal B. Abactinal closeup, including madreporite. C. Lateral view of marginal plates. D. Abactinal closeup at disk and arm. E. Actinal. F. Closeup of adambulacral spination.

closely arranged but similar overall to those on abactinal surface. Absent granules results in corresponding granular pitting present on plate surface. No pedicellariae on marginal plates observed. Shallow fasciolar grooves present among marginals. Terminal plate large, triangular with smooth surface.

Actinal surface with three to five plate series in chevron formation, most plate surfaces covered by coarse, polygonal granules, coarse proximally becoming smaller and finer distally. Pedicellariae, very prominent, present in abundance on actinal intermediate surface present in ordered, transverse to oblique series relative to adambulacral plates (Fig. 17D–F). Pedicellariae number approximately one per plate, largest on plates adjacent to mouth. Largest pedicellariae ranges from 5.0 mm in length on paired plates adjacent to oral plate to 1.0 mm length pedicellariae more distally along arm (Fig. 17E). Pedicellariae number approximately 30 from central proximal actinal plate along arm to armitp. Each pedicellariae asymmetrically thickened proximally, surrounded by series of six to 24 quadrate granules set off from the pedicellariae itself. The space between the pedicellariae and the granular periphery is most prominent proximally but largely disappears distally along the arm. Large empty spaces present between granular periphery and spines on adambulacral surface. Subsequent actinal series covered by coarse, smooth polygonal granules, numbering approximately three to six per plate but irregularly arranged. Other actinal plate surfaces covered by bivalved pedicellariae of moderate size (1.0–2.0 mm in length) present in parallel series along actinal plates. Some pedicellariae with rough edged valves but others with 10–15 jagged teeth.

Furrow spines two or three, large and curved inwards toward the furrow with blunt tip, round to weakly angular in cross-section, interweaving with spines from either side (Fig. 17E–F). Subambulacrals three, set off from furrow spines by discrete space. Subambulacral granules/spinelets numbering six to eight in two series of three or four present behind these larger subambulacrals. These lattermost subambulacrals quadrate to polygonal in cross-section. All adambulacral armature set off from proximalmost pedicellariae series by discrete space. This space is most pronounced proximally but "pinches out" distally. Oral plates with four furrow spines, curved, blunt. One large spine from oral plates projecting into mouth. Oral plate surface covered by seven to 10 blunt spines, triangular in cross-section. Space between oral plates and pedicellariae with oval arrangement of seven to 10 granules in four of the interradii, but with a large bivalve pedicellariae in the fifth.

Material Examined

Holotype. MNHN-IE 2007–3208. Papua New Guinea, Offshore islands and reefs from Lancasy (Au large des îles et récifs Lancasay) -8.273167 150.490997, 340–358 m Coll. Samadi *et al*. BIOPAPUA DW 3732, 9 Oct, 2010. 1 wet spec. R=7.2, r=2.8.

Circeaster Koehler, 1909

FIGURE 19A–F (pedicellariae diversity)

Circeaster Koehler, 1909: 83. Halpern, 1970a: 265. Downey, 1973: 47, 55, pl. 21A, B. Clark & Downey, 1992: 237, A.M. Clark, 1993: 250; Mah, 2006: 927; 2024: 13.

Diagnosis

Body weakly stellate to stellate, R/r > 2.5. Disk strongly arched, large. Arms elongate, tapering. tips upturned. Interradial arcs linear to curved. Abactinal arm plates two to three times larger than disk plates, changing gradually to abruptly between disk to arm. Abactinal arm and disk plates bare. Superomarginal plates abutted over midline in several species. Marginal plates bare, but variably with spinelets or granules present along dorsolateral/ventrolateral edges and surfaces of marginal plates. Greater density of spinelets/granules on inferomarginals than on superomarginals. Pedicellariae present in all known species, variably paddle-like, bivalve, or recessed within alveolar chambers, valves toothed to smooth mostly on actinal and adambulacral plate surfaces. Adambulacral furrow spines 6–15. Enlarged subambulacral spine or spines present in addition to pedicellariae.

Comments

Circeaster was initially described from deep-sea settings in the Indian Ocean to include *C. marcelli* Koehler (1909) and *C. magdalenae* Koehler 1909, and has since grown to include seven additional species, totaling nine total accepted species present throughout the Pacific, Indian, and Atlantic Ocean. Diversity of *Circeaster* and related taxa, such as *Lydiaster* and others (see Mah 2024 and *Astrophylax* herein) has led to establishment of a subfamily, the Circeasterinae, including five genera (Mah 2024). As has been indicated elsewhere, many species within *Circeaster* and the Circeasterinae have been observed *in situ* feeding on deep-sea colonial octocorals throughout the Atlantic and the Pacific (e.g. Mah 2020a, 2020b).

Pedicellariae, especially bivalve pedicellariae are a prominent feature among the Circeasterinae and *Circeaster* in particular. Species showing bivalve pedicellariae include the Indian Ocean *Circeaster helenae* Mah 2006*, Circeaster marcelli, Circeaster magdalene* , the Pacific *Circeaster pullus* Mah 2006, and the Atlantic *Circeaster americanus* (A.H. Clark, 1916). Valves of most species are smooth (Fig. 19A–C, E–F), but some species, such as *Circeaster magdalenae* (Fig. 19D) are more elongate with valves bearing prominent teeth. Many species show pedicellariae as part of the armature of the adambulacral plates. The tropical Atlantic *Circeaster americanus* demonstrates bivalve and trivalve pedicellariae (Fig. 19A–B).

Material Examined

Circeaster americanus USNM E19076 Caribbean Sea, no other data.1 dry spec., R ≈ 6.5 cm (arm broken), r = 3.2 cm. USNM E12712 SE of Nevis, St. Kitts and Nevis, Caribbean Sea, North Atlantic. 17.1 -62.28, 589 m. Coll. RV Oregon II, 8 Dec 1969. 1 dry spec. R=8.2, r=3.3.

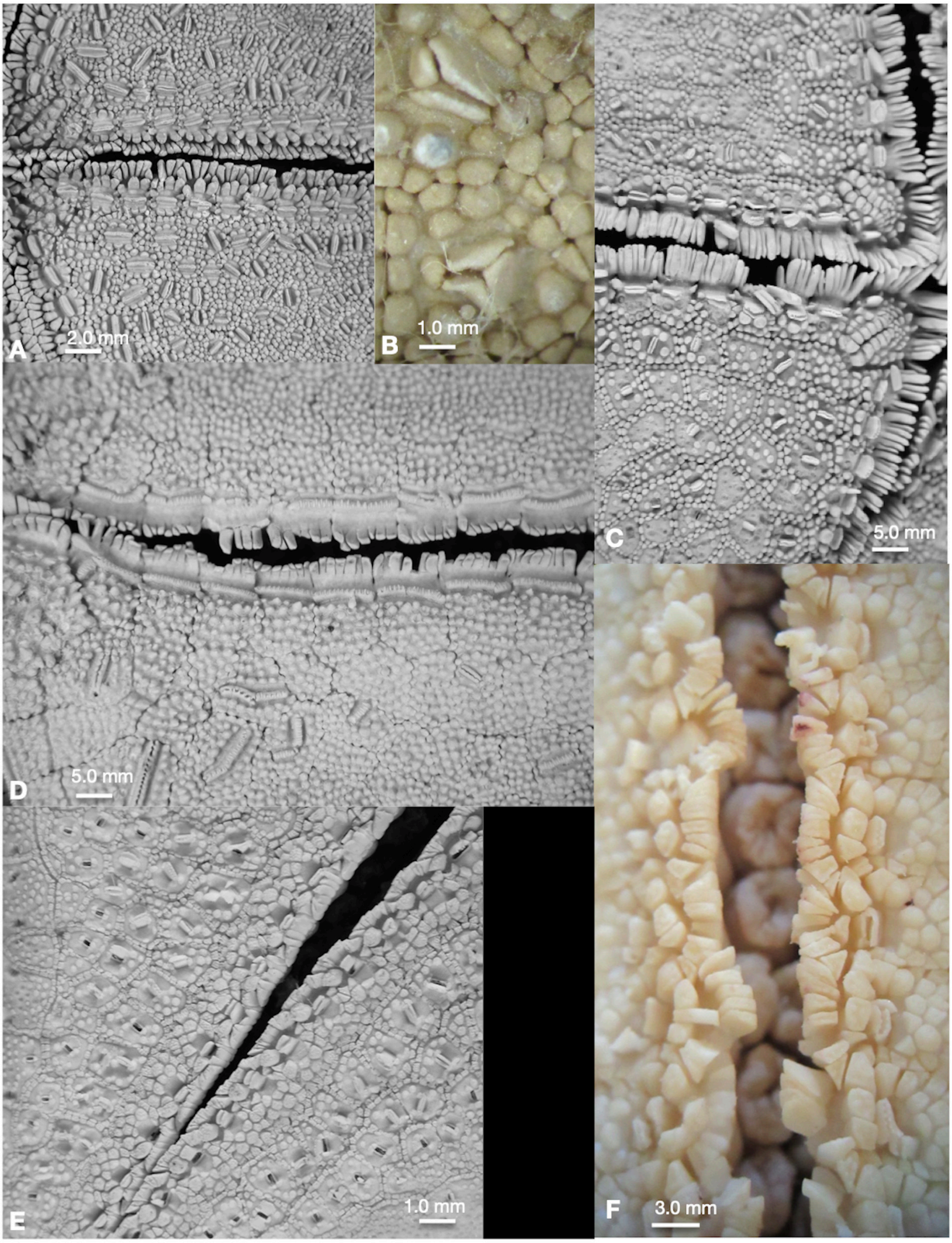

FIGURE 19. *Circeaster* spp. pedicellariae variation. A. *Circeaster americanus* USNM E19076 Oral and adambulacral spines-pedicellariae. B. *Circeaster americanus* USNM E12712 Trivalve pedicellariae. C. *Circeaster pullus* MNHN-IE-2009-2117, Bivalve pedicellariae with short, jagged valves. D. *Circeaster magdalenae* MNHN-IE-2019-4637, Bivalve with elongate, toothed valves. E. *Circeaster kristinae* WAM Z20694 Bivalve, nearly paddle-shaped with toothed valves. F. *Circeaster dux*, WAM Z110163, Adambulacral furrow showing bivalve pedicellariae with smooth to jagged valves.

Circeaster dux Mah 2024 WAM Z110163 Site 30 Gascoyne Marine Park, 19 km W. Lakeside, 22.00276 -113.733333, 794 m, coll. RV *Investigator*, 8 Dec. 2022, 1 wet spec. R=13.2 r=4.3.

Circeaster kristinae Mah 2006 WAM Z20694 Timor Sea, Indian Ocean, 18º38'S 116º52'E to 18º38'S 116º54'E, 600–594 m. R=12.3 r=3.9.

Circeaster magdalenae Koehler 1906 MNHN-IE-2019-4637 Madagascar, 13° 49' 59.9988'' S ; 47° 36' 59.994'' E, 850–1125 m. R=11.6 r=5.2 .

Circeaster pullus MNHN-IE-2009-2117 SW Ille des Pins, New Caledonia, South Pacific, 23° 2' 48.1812'' S ; 166° 52' 31.2636'' E, 620–700 m.

Circeaster columnaris sp. nov.

FIGURE 18A–F

Etymology

The specific epithet *columnaris* is derived from the Latin for "pillar" in reference to the thickened subambulacral spine.

Diagnosis

Body stellate, R/r=2.54, rigid, arms triangular, broad at base, interradial arcs curved. Abactinal plates polygonal, variably equidimensional to elongate. Surface covered by coarse, round granules, widely spaced, 5 to 30 per plate. Abactinal arm and disk plates show gradual transition with no change in granulation. Superomarginal plates abutted, approximately 4 to 6 distalmost plates, totaling about 13% of total "r". Bivalve pedicellariae in abundance on actinal surface, but few (n=2 observed) on abactinal surface. Furrow spines 3, with blunt, rounded tips. Subambulacral spines thick, 3 to 5X the thickness of a single furrow spine, with a rounded, tip.

Comments

A species with closest similarity to *Circeaster sandrae*, *C. pullus*, and *C. americanus*, all of which showing weakly expressed abactinal arm plate size difference, but also bivalve pedicellariae. Although the abactinal and marginal plates are similar, *C. columnaris* **sp. nov.** shows the enlarged subambulacral spine and the absence of pedicellariae from the adambulacral plate region.

This species invites comparison with *Astrophylax* **gen. nov.** described herein. Abactinal and marginal plates with coarse granules as well as the presence of multiple bivalve pedicellariae present on the actinal plates. The furrow and subambulacral spination clearly distinguishes this taxon from *Astrophylax*.

Distribution/Occurrence

Balut Island, Philippine Islands, 150–250 m.

Description

Body stellate, R/r=2.54, rigid, arms triangular, broad at base, interradial arcs curved (Fig. 18A).

Abactinal plates variably polygonal, ranging from more equi-dimensional to more elongate. Larger plates proximally, smaller plates distally adjacent to superomarginal contact. Plate surfaces weakly convex to flat, covered with coarse, round granules, widely spaced from one another, approximately 5 to 30 per plate but becoming more densely arranged adjacent to superomarginals. Abactinal plates extending from disk to approximately 50% of arm distance, gradually attenuating where superomarginals are abutted across mid radius on distal half of arm distance (Fig. 18C). Bivalve pedicellariae present on abactinal surface but only sparingly with only n=2 counted on the holotype. Madreporite triangular, deeply inset on surface, sulci well developed, flanked by 3 adjacent abactinal plates (Fig. 18B).

Marginal plates 25 to 26 per interradius, plate shape wide, with rounded abactinal-lateral edge. Superomarginal plates distinct, forming approximately 13% of total r (=0.3/2.2) with 4 to 5 distalmost superomarginal plates abutted, some slightly offset forming zig-zag contact. Superomarginal plate surface with coarse, round granules, approximately 350–450, widely spaced, deciduous, leaving weakly developed distinctly convex pitting on plate surface where granules are absent (Fig. 18C–D). Peripheral granules, round on abactinal-actinal facing, 20 per side, laterally approximately 30, more quadrate in shape. Inferomarginals largely identical to superomarginals in terms of granule covering, peripheral granules. No pedicellariae on marginal plates. Terminal plate triangular with rounded edges, smooth surface.

Actinal surface well developed in approximately 3 complete series, extending to arm base, arranged in chevron formation (Fig. 18E). Each plate with a prominent bivalve pedicellariae with smooth valves, each as wide as the plate on which it sits (Fig. 18E–F). A minority of plates with two pedicellariae. Pedicellariae proximally larger becoming smaller adjacent to inferomarginal contact, all oriented irregularly with no distinct orientation. Pedicellariae prominent, but none are oversized as in *Astrophylax*.

Furrow spines 3, thick, with blunt rounded tips, oval to round in cross-section (Fig. 18F). A single, large subambulacral spine, approximately the thickness of 3 to 4X the furrow spines sits adjacent to the furrow spines, surrounded by peripheral spines, 4 to 6, short, blunt and thick in palmate formation. Oral plate with 9 to 11 furrow spines, thickened, blunt with rounded tip with a single paired spine directed into oral opening. Oral plate surface with approximately 4 to 8 pointed spinelets present on either side of the interradial diastema. =

Material Examined

Holotype. PNM 7152, Balut Island, Mindanao, Philippines, 150–250 m. 1 dry spec. R=5.6 r=2.2.

HIPPASTERINAE Verrill 1899

Verrill, 1899: 174; Fisher, 1906: 1165; 1910: 223; Spencer & Wright, 1966: U58; Mah *et al*., 2010: 270; Mah *et al*. 2014: 425.

Diagnosis
Based on Mah (2024). Pulpy tissue present, covering plates. Abactinal plates with spiny-granular or angular accessory fringe. Abactinal plates tightly abutted. Superomarginal and inferomarginal plates, variably round to quadrate with large, prominent spines or tubercles in most taxa. Pedicellariae enlarged, abundant, and on raised base. Disk thick and strongly arched in most.

Comments
Although only 4 genera are included within the Hippasterinae, there appears to be a rich species diversity within *Evoplosoma* and *Hippasteria* as further species have been described as deep-sea settings have been further explored. *Hippasteria* is known from 12 species distributed throughout the Pacific, Atlantic, and Indian oceans from wide-ranging depths. *Evoplosoma* is known 14 species, primarily collected from deep-sea settings (1000–4000 m). Revisions to *Hippasteria* in conjunction with further specimens have resulted in the discovery of the wide-ranging *Hippasteria phrygiana* as well as several previously undescribed species (Foltz *et al*. 2013; Mah *et al*. 2014; Mah, 2020). *Evoplosoma*, a deep-sea octocoral predator has similarly been found to include numerous species, including some with wide distributions, such as *Evoplosoma voratus* (Mah, 2020; 2024).

Hippasterines are known primarily as predators on cnidarians, especially colonial octocorals but also including sea anemones and antipatharians (Mah *et al*., 2010, Mah 2020, 2024)). The morphology in hippasterines has been argued as associated with this predatory behavior (Mah 2024) but how spines and pedicellariae function in this regard is poorly understood. Pedicellariae various types are present in all 4 genera, with *Gilbertaster, Sthenaster* and *Hippasteria,* with all having prominent and numerous bivalve pedicellariae on abactinal, marginal and actinal surfaces versus *Evoplosoma* with tong-like or paddle-shaped pedicellariae.

Gilbertaster Fisher, 1906

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

Diagnosis
Arms triangular, narrow and tapering. Disk weakly swollen. Thick and pulpy tissue covering abactinal, marginal and actinal plates. Abactinal plates low, polygonal, covered by 1–12 closely articulated angular granules elongate to round in shape, flattened, surface texture smooth to rough. Fasciolar grooves shallow. Secondary plates present. Abactinal plates with angular accessories. Pedicellariae large, bivalved with smooth valves, the length of one to two plates and abundant on abactinal surface. Marginal plates, 50–70 per interradius (arm tip to arm tip), squarish in outline with edges rounded, covered by angular granules similar to those on abactinal surface. Variable surfaces smooth (on *Gilbertaster anacanthus*) to roughened (on *Gilbertaster caribaea*). Pedicellariae large, bivalve similar to those on abactinal surface on marginal plate surface, many bisecting the width of the plate. Spines absent from superomarginal and inferomarginal plate series. Granules, densely arranged, covering superomarginal and inferomarginal plate series. Superomarginal and inferomarginal plates quadrate at interradius. Fasciolar grooves on marginal and actinal surfaces absent. Fringe of accessories on marginal plates poorly differentiated. Superomarginal plates forming prominent dorsolateral fringe. Actinal plates covered by 1–15 flattened, polygonal, angular granules. Large bivalve pedicellariae similar to those on abactinal and marginal plate surfaces, abundant on actinal plates. Actinal plates with granules but lacking large spines or spinelets. Pedicellariae, bivalved, present on plate series at perpendicular angle, adjacent to ambulacral furrow. Pedicellariae, flat-tong shaped, with serrated blades present on actinal plates. Pedicellariae on raised bases, abundant. Furrow spines two to four (usually three) blunt, thickened spines, horizontally flattened (*G. anacanthus*) to triangular/quadrate in cross-section (*G. caribaea*). Subambulacral spines, 1–4, blunt, flattened. Round to quadrate (*G. anacanthus*) to triangular in cross-section (*G. caribaea*). Pedicellariae, bivalved, enlarged on first adambulacral (similar to others) replacing subambulacral spination and sometimes replacing furrow spination. Subambulacral spines smaller in size, more abundant. Furrow spines round in cross-section.

Comments
Gilbertaster includes two species, *Gilbertaster anacanthus* Fisher 1906 and *Gilbertaster caribaea* (Verrill, 1899), in the tropical Pacific and tropical Atlantic respectively. *Gilbertaster* is unusual for the sheer abundance of large, bivalve pedicellariae present on the abactinal, marginal, and actinal surfaces (Figs 20A–D), perhaps more so than any other valvatacean asteroid.

Gilbertaster caribaea (Verrill, 1899)
FIGURE 20A–D

Hippasteria caribaea Verrill 1899: 174, pl. 28; Halpern 1970: 190; Clark & Downey 1992: 246.
Gilbertaster caribaea Mah *et al*., 2010: 273; 2020: 228.

Diagnosis
Modified from Mah *et al*. (2010). Disk broad, arms short, R/r=2.1 to 2.4, interradial arcs weakly curved to straight. Marginal plates 40–50 per interradius. Furrow spines 2 to 4, mostly 3. subambulacral spines 1 to 4, blunt and flattened.

Comments
Both species of *Gilbertaster* strongly resemble one another, differing only in body shape (R/r) and in number of marginal plates per interradius from arm tip to arm tip. Distribution of *Gilbertaster* species, one in the tropical Atlantic and one in the tropical Pacific suggests a widespread occurrence which may have been separated

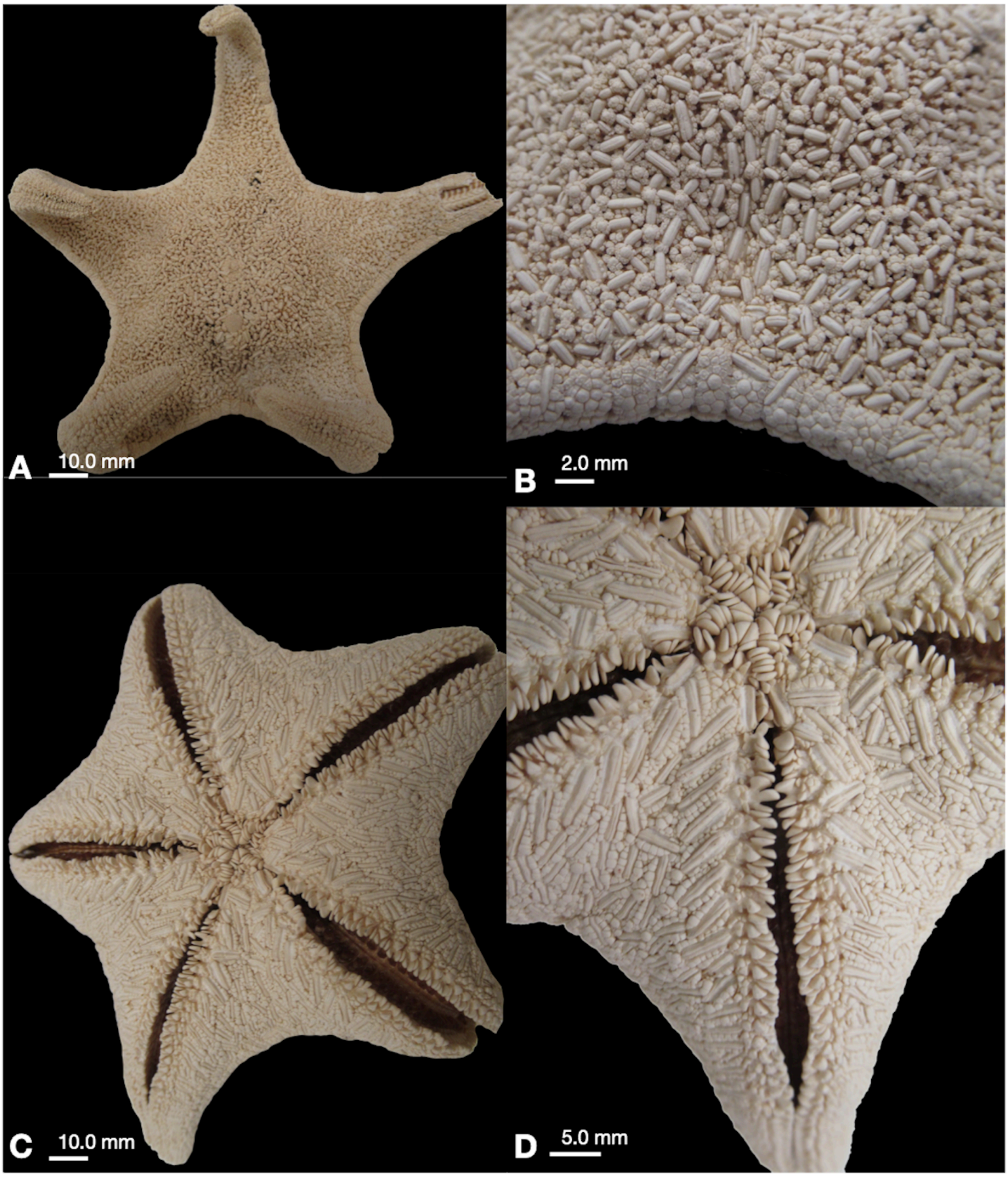

FIGURE 20. *Gilbertaster caribaea* USNM 1126236. A. Abactinal B. Closeup on surface, plates and pedicellariae C. Actinal. D. Closeup on actinal surface.

by the formation of the Panamanian isthmus (Mah *et al*., 2010). Both species share numerous and conspicuous bivalve pedicellariae covering the abactinal, marginal and actinal surfaces suggesting a similar function.

Observations of *G. caribaea in situ* showed this species feeding on primnoid octocorals and in association with amphipods possibly demonstrating kleptoparasitism (Mah, 2020).

Distribution/Occurrence

Off SE coast of United States, Grand Bahamas Gulf of Mexico, 500–886 m.

Material Examined

Gilbertaster caribaea (Verrill, 1899) USNM 1126236 Jacksonville Lithoherms, North Atlantic Ocean, 30.5169 -79.6612, 543–581 m. coll. Ross, S. W.; Sulak, K. J.; Nizinski, M. S.; Baird, E. Johnson Sea Link I, 10 June 2004. 1 dry spec.

Hippasteria Gray, 1840

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

Diagnosis
Modified from Mah *et al*. (2010, 2014) and Mah (2024). Body weakly pentagonal to stellate (R/r=1.5–2.3). Disk and arms thick. Arms relatively broad and short. Tissue with pulpy texture covers abactinal plates. Shallow fasciolar grooves present. Secondary plates present. Abactinal plates, tightly articulated, polygonal to irregular in outline, flat and elevated over surface. Carinal series are poorly distinguished. Abactinal spinelets (sometimes granular) forming fringe around abactinal plates. Spines, large, conical; granules common on abactinal plates. Large spines present on superomarginal and inferomarginal plates of most species. Superomarginal and inferomarginal plates 1) bare, quadrate to rounded in outline at interradii with no other accessories other than 2) large spines. 3) 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 species, Actinal fasciolar grooves shallow. Large actinal spines and spinelets present. Subambulacral spines large (and thus few in number). Furrow spines large, blunt, and round, usually few. Enlarged bivalved pedicellariae on raised bases on body surface.

Comments
Hippasteria currently includes 13 species, including *Hippasteria phrygiana* (Parelius, 1768)*,* which was found to be widely distributed throughout the Atlantic, Pacific, and Indian Ocean (Foltz *et al*., 2013). Three species of *Hippasteria* are subjects here for features associated with their unusual pedicellariae valve morphology. *Hippasteria californica* Fisher, 1905 and *H. phrygiana* are widely distributed and show variable pedicellariae valves across their range, whereas *H. muscipula* show valves which are unusual relative to other *Hippasteria* species.

Relevant to pedicellariae morphology, most if not all *Hippasteri*a spp. have been recorded *in situ* feeding on octocorals, although *Hippasteria phrygiana* has been reported attacking sea anemones, zoanthids and other invertebrate prey (summary in Mah *et al*., 2010) with detailed accounts of *Hippasteria phrygiana* (as *Hippasteria spinosa* Verrill, 1909) in the North Pacific feeding on the sea pen *Ptilosarcus*. Individiuals of what appear to be *Hippasteria muscipula* and possibly *Hippasteria phrgyiana* have been observed by the NOAA ship *Okeanos Explorer* in the North Pacific/Hawaiian Islands region feeding heavily on colonial octocorals such as so-called "bamboo corals" (family Isididae) as well as on Atlantic octocoral species (Mah, 2020, 2022, pers. observation). As outlined herein, pedicellariae were observed being active during feeding suggesting they play a role, but exactly how they participate is unclear.

Pedicellariae Across *Hippasteria* spp.
Bivalve pedicellariae are present in all *Hippasteria* species and display a relatively consistent appearance, with most species displaying valves with variably smooth (e.g. Fig. 2F, G) to more serrated edges (Fig. 22B, C). *Hippasteria phrygiana,* which was shown to be widely distributed (Foltz *et al*., 2013; Mah *et al*., 2014) across the Pacific, Atlantic, and Indian Ocean demonstrates the least variation of character. Other species showing smooth valves include *H. falklandica* Fisher, 1940, *H. heathi* Fisher, 1905, *H. lepidonotus* (Fisher, 1905), *H. tiburoni* Mah *et al*. 2014, and *H. capstonei* Mah, 2022.

Hippasteria muscipula have valves with strongly expressed serration on the abactinal and actinal surfaces and teeth on the marginal plate surfaces.

Pedicellariae morphology varies at depth in *Hippasteria californica*, with deeper-water forms showing more toothed or otherwise variable valve morphology relative to those observed from shallower settings, which are smooth and more elongate (e.g. CASIZ 113375). One deep *Hippasteria californica* specimen (USNM 1418240) displayed actinal pedicellariae with valves that narrow at the apex and abactinal pedicellariae with toothed valves. An *H. californica* specimen (CASIZ 120096) from Patton Seamount at 2373 m has pedicellariae with strongly toothed valves on the abactinal and actinal surface.

Hippasteria californica Fisher, 1905
FIGURE 21A–F

Hippasteria californica Fisher, 1905: 310; 1911: 233; H.L. Clark, 1913: 194; Alton, 1966: 1702; Lambert, 1978b: 62; Maluf, 1988: 34, 118; Mah *et al*., 2010: 285; Clark & Jewett, 2011: 53. Mah *et al*., 2014: 426, Figs 2A–F, 3A–F.
Cryptopeltaster lepidonotus Imaoka *et al*., 1991: 52.

Diagnosis
Disk arms, broad, short, tapering with pointed tips. Interbrachial arcs wide, rounded. Abactinal pedicellariae with serrate valves. Ossicles on most surfaces denticulate. Marginal plates oblong-elliptical in shape, separated by encroaching abactinal, actinal plates, most with a single, pointed, conspicuous spine. Furrow spines 2 to 3, mostly 2, thick, blunt, oval in cross-section. Adambulacral plate with large, single bivalve, clamp-like pedicellariae, valves smooth in addition to two irregular rows of short, heterogeneous blunt to pointed spines and granules (Modified from Fisher, 1911).

Comments
Hippasteria californica was supported as monophyletic by molecular data and inhabits a wide distribution, from the Gulf of California to Alaska and Japan and with a broad bathymetric range, occurring between 30 to 2373 m (Mah *et al*., 2014). *In situ* observations suggest this species feeds on sponges and colonial octocorals (e.g. Stone, 2014) similar to other Pacific species in contrast to Carey *et al*. (1972) who reported sediment in the gut contents of this species. Pedicellariae on this species are

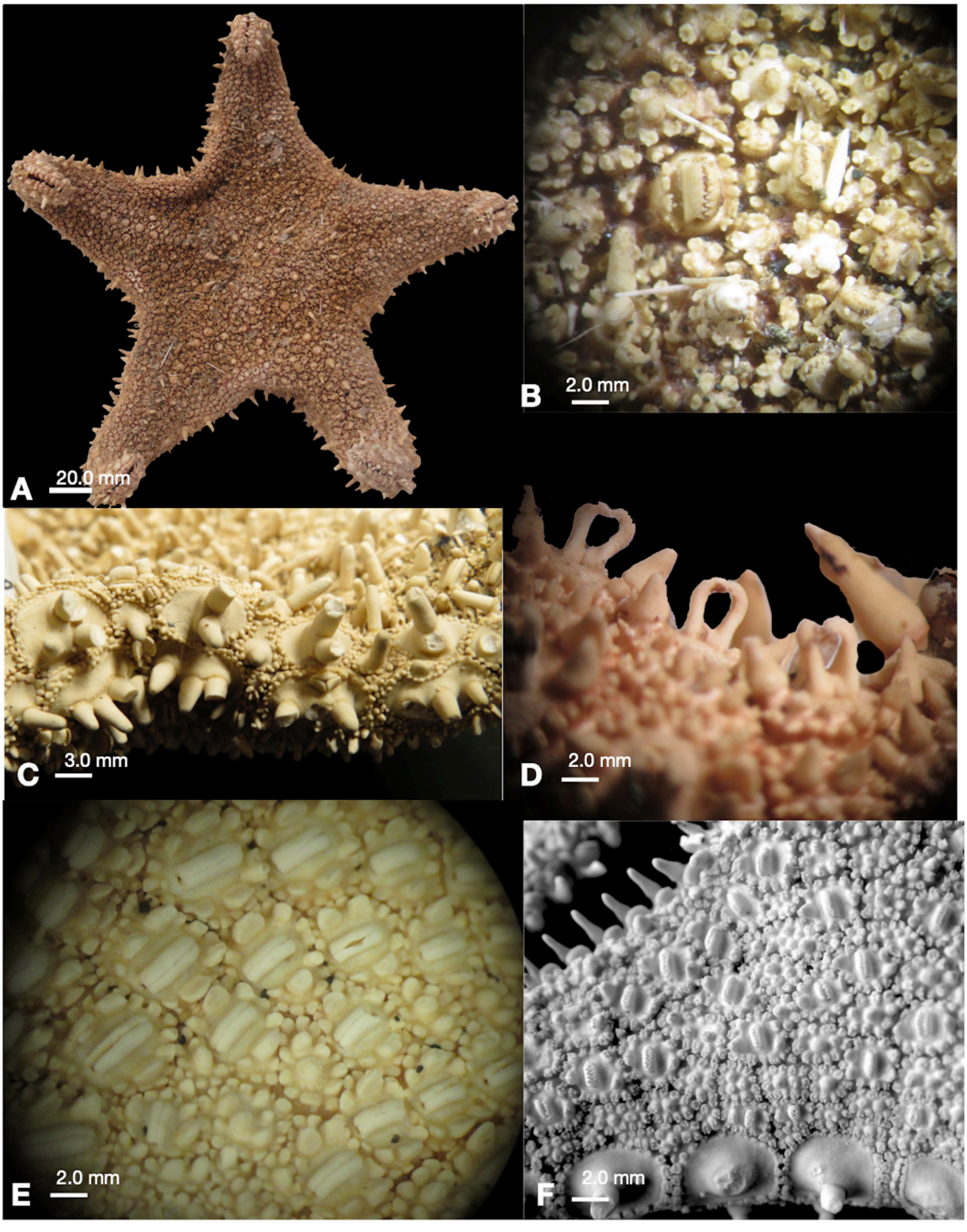

FIGURE 21. *Hippasteria californica* pedicellariae diversity. A. Abactinal surface. USNM 1418240 (west of Monterey Bay, 1293 m) B. Abactinal pedicellariae, bivalve with teeth. C. Actinal pedicellariae, tong-like. D. CASIZ 113375. Circular marginal plates. E. USNM 1288433 (Aleutian Islands) pedicellariae on actinal surface, smooth valves. F. CASIZ 120096 Actinal pedicellariae with teeth.

diverse and abundant (Fig. 21 B, D, E), suggesting diverse function.

Distribution/Occurrence

Gulf of California (Baja), Southern California, Washington to British Columbia, Aleutian Islands (Alaska) to Patton Seamount, Gulf of Alaska and Hokkaido, Japan 110–2373 m. As shallow as 30 m in British Columbia.

Material Examined

USNM 1418240. West of Monterey Bay, California, North Pacific. 36.683333 N 122.233333 W, 1293 m. Coll. R/V *Point Sur*, 10 April 2009. 3 dry specs. R=10.6 r=3.6 R=9.4 r=3.4 R=7.8 r=3.3.

CASIZ 113375 vicinity of Fitzburgh Channel, off Hakai Channel, British Columbia 42.0 m, coll. W.F. Thompson. 1 dry spec. R = 12.0, r = 5.8.

CASIZ 120096 Patton Seamount, Gulf of Alaska, (start) 54.345972 N, 150.338972 W to (end) 54.326 N, 150.365 W, 2373 m. R V Alvin, Dive 3432, 24.vii.1999. one dry spec. R = 9.2, r = 4.6.

Hippasteria muscipula Mah, Neill, Eleaume & Foltz, 2014

FIGURE 22A–C, 23A–C

Hippasteria muscipula Mah, Neill, Eleaume & Foltz, 2014: 438, Figs 6A–F.

Diagnosis

Disk tumescent, body stellate (R/r=2.0–2.19), arms triangular. Body covered by pulpy membrane. Abactinal surface covered by prominent conical spines sitting on

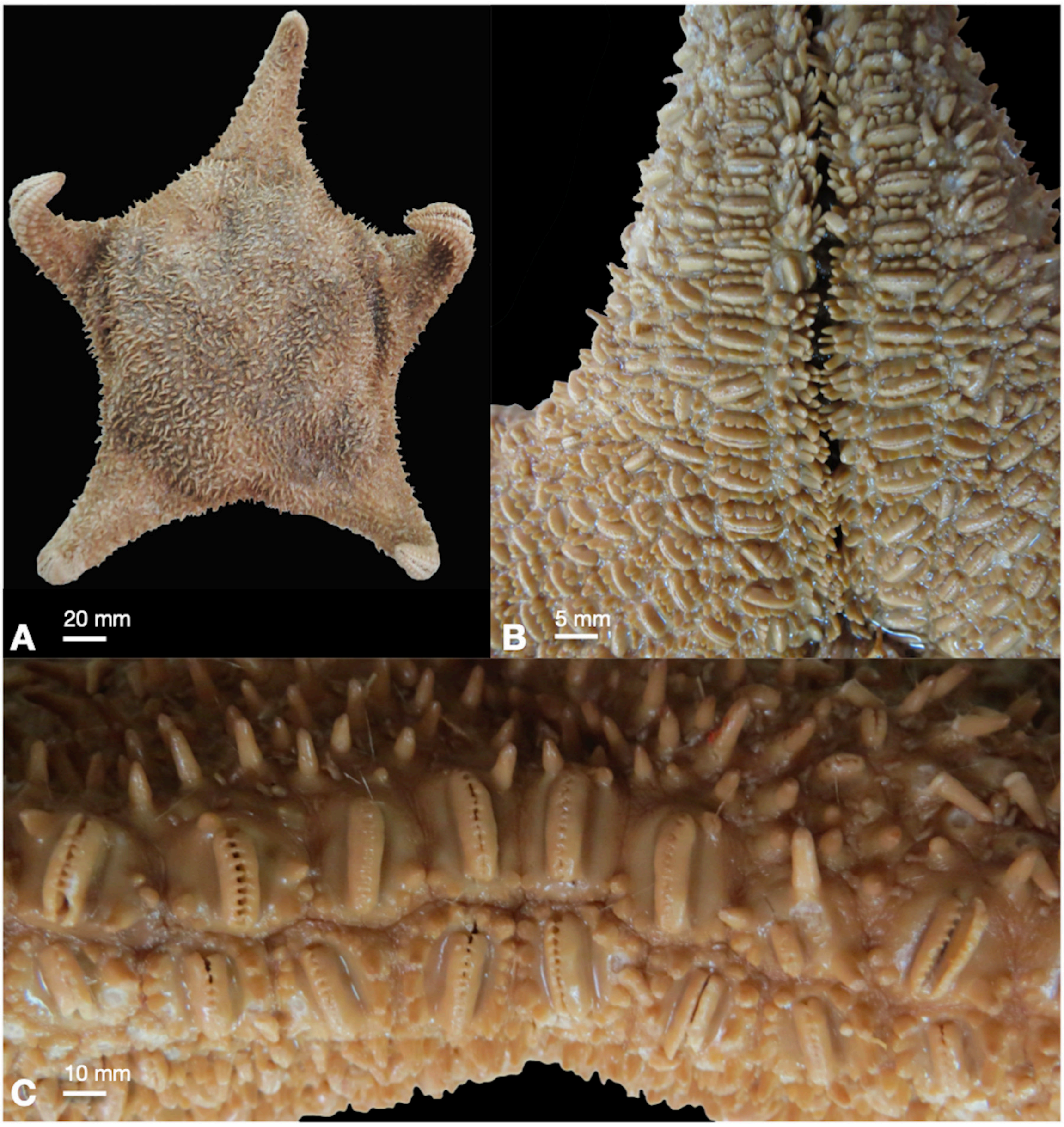

FIGURE 22. *Hippasteria muscipula* MNHN IE-2007-2362 A. Abactinal. B. Actinal and adambulacral closeup. C. Lateral view showing pedicellariae on marginal plates.

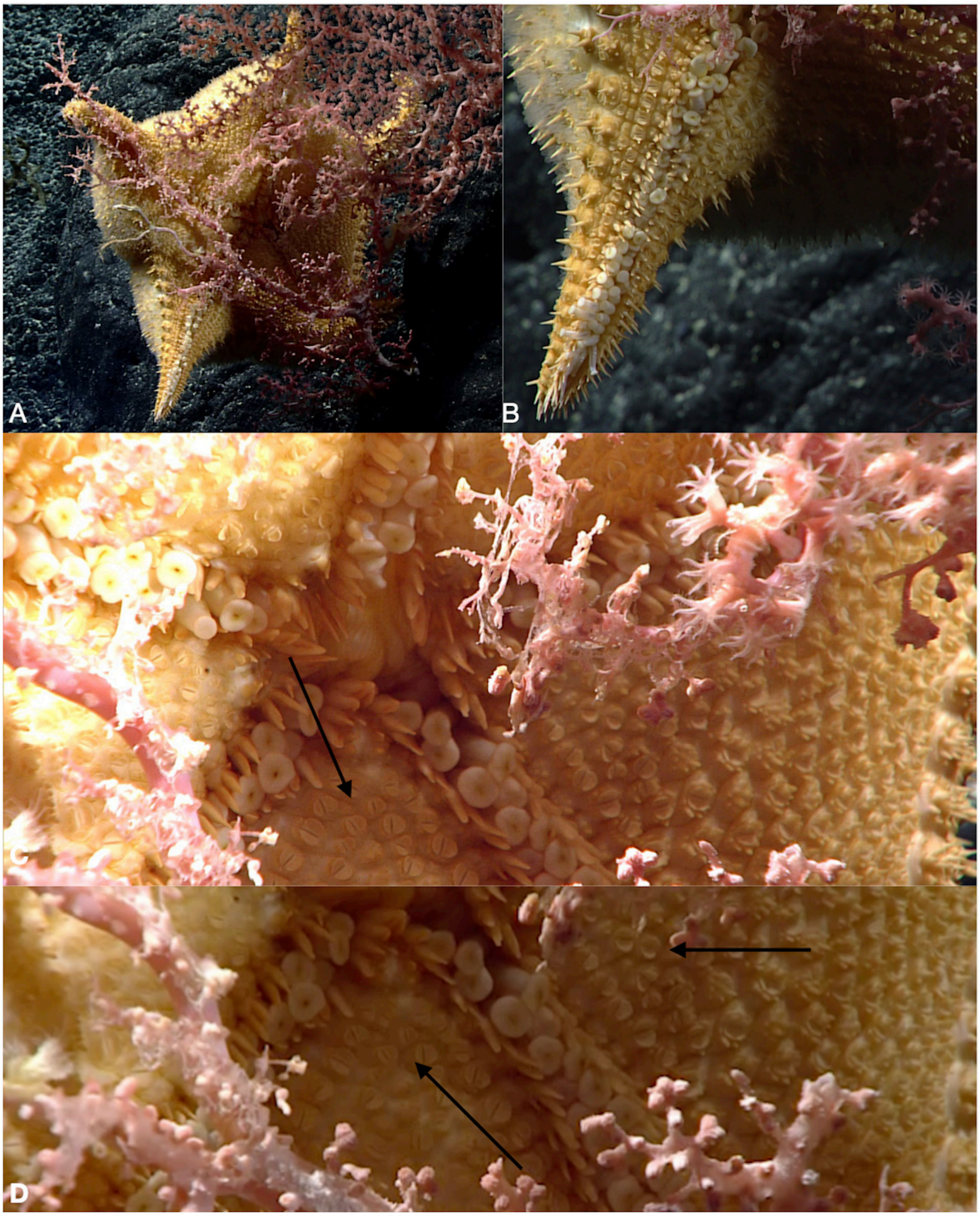

FIGURE 23. *Hippasteria muscipula in situ* (specimens not collected). A. Oral view of individual predating on *Corallium*. B. closeup of tube feet. C. Closeup showing open bivalve pedicellariae during predation.

convex bases. Secondary plates present. Large bivalve pedicellariae, clam-like each with serrated valves, sitting on a distinct base. Marginal plates variably circular to irregularly round or polygonal, each with spines and a large, prominent toothed pedicellariae, each valve bearing distinct, pointed teeth. Actinal region with multiple elongate bivalve pedicellariae, each valve with 8 to 12 interclasping teeth present on each plate. Furrow spines 2 to 4, every third adambulacdral plate with a bivalve pedicellariae each with smooth valves, behind each furrow spine.

Distribution/Occurrence

New Caledonia, New Zealand, Hawaiian Islands, 425–1500 m.

Observations

Open actinal pedicellariae-video. USNM 1762335 Johnson Atoll region, 15.67984944 -170.3711033, 1180.5 m, EX1706_VID_20170721T215000Z_ROVHD_Low.mp4.

Open abactinal pedicellariae.feeding.

USNM 1762334 North Pacific, 22.7543098 -160.9285389, 460.5 m. 26 Sept 2017. EX1708_IMG_20170926T200827Z_ROVHD.jpg

USNM 1762332 North Pacific 26.4306455 -177.8013935, 2008.9 m. 10 March, 2016.

EX1603_IMG_20160310T210526Z_ROVHD_COR_ASR_AUD.jpg

USNM 1762331 North Pacific 18.30747089 -158.4541544, 980.8 m, 2 Sept 2015.

EX1504L3_IMG_20150902T003304Z_ROVHD_ASR.jpg

Open abactinal pedicellariae. feeding & polynoid associates.

USNM 1762330, North Pacific 19.23077253 -157.6117326, 2112.1 m. 2 Sept 2015.

EX1504L3_IMG_20150902T203458Z_ROVHD_ASR_COR.jpg

USNM 1762333, North Pacific 28.68037023 -162.6091477 1771.4 m 19 Sept. 2017, EX1708_IMG_20170919T234444Z_ROVHD.jpg Closed pedicellariae. No feeding.

Hippasteria phrygiana (Parelius, 1768)

FIGURE 24A–D

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

Comments

Although many populations of *Hippasteria phrygiana* have relatively similar bivalve pedicellariae (Figs 2F–G,

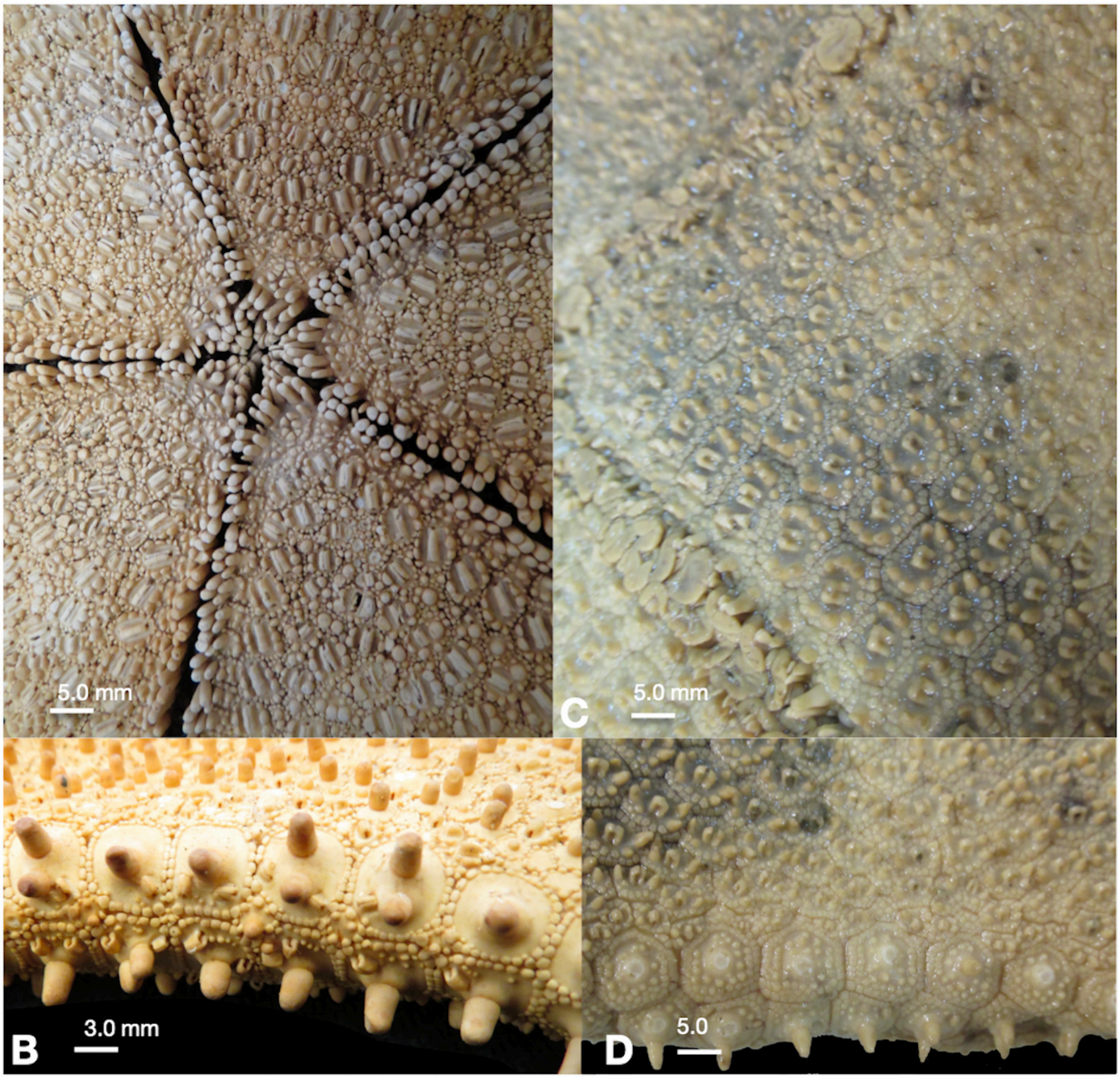

FIGURE 24. *Hippasteria phrygiana* pedicellariae variation. A. USNM 14361 Atlantic, Actinal B. Marginal plates. C. MNHN IE-2007-1311, Solomon Islands, Abactinal. D. Actinal.

24A–B), there are individuals which show significant divergence. MNHN-2007-1311 from the Solomon Islands for example has actinal pedicellariae which are more forcipiform, (Figs 24C–D) similar in shape to the actinal pedicellariae on deep-sea *Hippasteria californica* as seen in CASIZ 1418240 from deep-sea settings outside Monterey Bay (Fig. 21A–B) .

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

Material Examined
(North Atlantic) USNM E25102 Off Cape Cod Lighthouse, Massachusetts, 61.3–68.6 m. Coll. R/V Jenny B, 23 Nov 1966. 1 dry spec. R=10.0 r=4.8.

(Pacific) USNM 1288439 Portlock Bank, Gulf of Alaska, Alaska, 58.2661 -148.7483, 149 m. Coll. R. Stone, 21 June 2001. 1 dry spec. R=6.9 r=3.7.

(South Pacific) USNM 13768. East of Banks Peninsula, South Island, New Zealand, South Pacific.- 43.9 174.598, 585 m. Coll. J. Cook. 1 dry spec. R=11.5 r=6.4.

MNHN IE-2007-1311 Solomon Islands 9.2 S, 160.916667 E, 722 m, coll. Richer de Forges & Boisselier, SALOMONBOA 3 aboard N/O *Alis*. 1 wet spec. R = 12.4, r = 7.6.

Sthenaster Mah *et al*., 2010

Diagnosis. Monotypic. as per genus below.

Sthenaster emma Mah *et al*., 2010

FIGURE 25A–D

Mah *et al.,* 2010: 274: Fig.4A–H.

Diagnosis
Disk large, broad. Body stout, weakly stellate, R/r=1.9–2.1. Disk broad, arms triangular in outline. Interradial arcs weakly curved to straight. Abactinal plates, high-aspect, mound-like, round to polygonal with secondary plates, embedded in a thick, pulpy dermis, covered with blunt conical granules. Pedicellariae, large, bivalve each with prominent teeth, 9–12, on each valve occupying nearly complete plate diameter present across abactinal surface. Marginal plates 42–25, wide, covered by conical spinelets, 20–35 per plate. Bivalve pedicellariae, 1 to 4, present on nearly all marginal plates, similar to those on abactinal surface, peripherally with small conical spinelets. Actinal surface with plates covered by granule-like spines, conical in shape. Bivalve pedicellariae present in abundance, especially adjacent to oral region and along plates adjacent to the adambulacrals. Valves with smooth or weakly serrated edges. Furrow spines, 3 to 4, blunt tipped. subambulacral spines in 2 to 3 series, each with blunt spines, 2 to 4.

Comments
Sthenaster emmae is predatory on octocorals and other encrusting metazoans and has been observed feeding *in situ* (Mah, 2010; 2020). Bivalve pedicellariae are present on abactinal, marginal and actinal surfaces (Fig. 25A–D). Abactinal pedicellariae show valves with 9 to 12 pronounced teeth (Fig. 25B) as opposed to those on the actinal surface which are largely smooth or with more weakly developed serration. This could suggest that these pedicellariae serve different functions relative to their orientation. *In situ* images (Mah, 2020) show this species hunched over presumptive prey or food items suggesting that smooth edged or weakly serrated pedicellariae on the actinal surface may play a role in feeding given their proximity to the tube feet and the mouth. Those pedicellariae with teeth on the abactinal surface may serve a defensive purpose, possibly repelling asteroid predators, namely *Solaster*, which generally attack by moving over the abactinal surface (Mauzey *et al*., 1968) or other mobile pests or predators, such as small swimming crustaceans.

Distribution/Occurrence
Savannah Banks and off the coast of Jacksonville, FL, Central Plateau Scarp and Richardson's Jellyfish, 252–874 m.

Material Examined
Holotype. USNM 1124468, Savannah Banks, North Atlantic Ocean, 31.7044 -79.1314 498 m, coll. T. Casazza, JSL 4902, 26.x.2005. 1 wet spec. R = 9.6, r = 4.7.

FOSSIL TAXA

Comment
Two clear examples of apparent bivalve pedicellariae were located and are presented herein. Villier (2008) identified apparent bivalve pedicellariae alveoli from indeterminate goniasterid marginal plates (disarticulated) from the Callovian (Jurassic). A survey of Breton (1992) and Jagt (2000) records apparent bivalve pedicellariae traces from marginal plate ossicles, including *Parametopaster, Cenomanaster, Comptoniaster, Ophryaster, Talecaster*, and *Tomidaster*. Breton (1996) observed that alveolar pedicellariae appear in *Comptoniaster* at the Hautverian (in the Cretaceous) with further occurrence "suddenly" throughout taxa in the Cenomanian and provides a list of species showing traces of the alveoli or chambers. Villier *et al*., (2004) recorded one Cretaceous occurrence in the fossil Stauranderasteridae.

Comptoniaster adamsi Blake, 2010

Blake 2010: 179, 184.

Diagnosis
Species of *Comptoniaster* with comparatively short, broad arms and a broadly rounded interbrachial arc. Abactinals uniform in appearance, many with elongate pedicellariae,

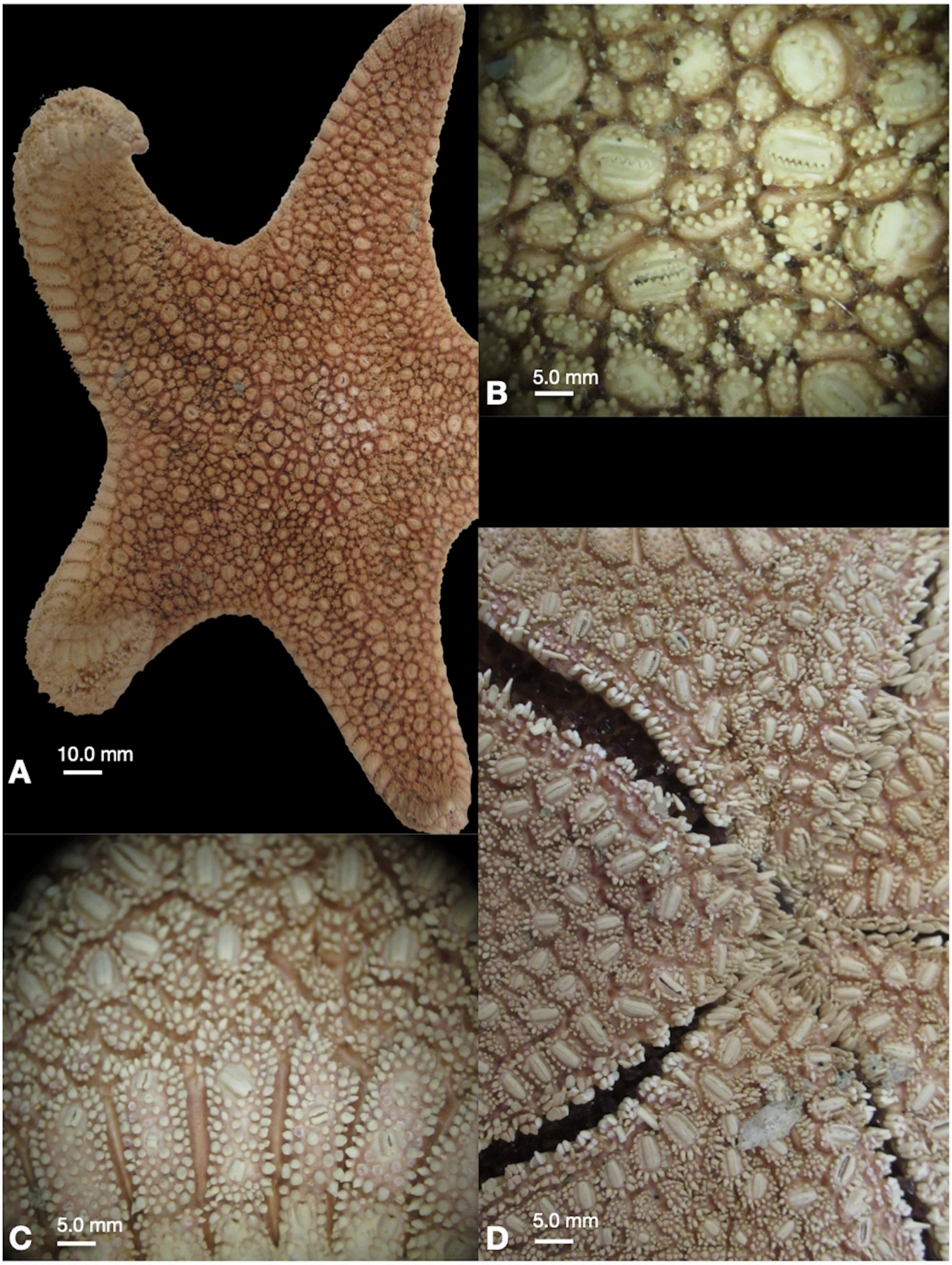

FIGURE 25. *Sthenaster emmae* USNM E15539 A. Abactinal B. Abactinal closeup showing pedicellariae. C. Actinal-inferomarginal contact. D. Actinal-oral region showing pedicellariae.

especially at arm radii; abactinals low, tabular. Marginals robust, many bear elongate pedicellariae near their abradial margins. Adambulacrals short, wide, adradial face flat (i.e., podial prominence lacking), furrow adambulacral spines in linear series, furrow and lateral spine bases differentiated. (From Blake 2010)

Comments

Large bivalve pedicellariae are present on the abactinal and marginal surfaces, with actinal surface out of view, in this species, These appear most common on inferomarginal plates with fewer on the superomarginals with relatively large pedicellariae on the abactinal surface.

This distribution is similar to pedicellariae distribution on *Anthenea* spp. but pedicellariae data for this species are absent from the actinal surface and precludes a definitive conclusion.

Weitschataster intermedius Neumann & Girod, 2018

Neumann & Girod, 2018: 425, 427.

Diagnosis
A small goniasterid with pentagonal to subpentagonal outline. Sides of each arm with 3 SMs (2 median SMs plus the USM). Central field of marginal ossicles raised and confluent with surrounding margin. Surface of marginals covered with pits and tubercles. SMs and IMs may possess single alate pedicellariae scars on the adradial part. Actinal ossicles with large elongate rimmed pedicellariae scars. IMs are slightly longer than median SMs, resulting in a compound, shifted pattern where IM 1 and IM 2 correspond with two SMs. (based on Neumann & Girod, 2018).

Comments
The Cretaceous *Weitschataster* has numerous alveolar pits indicating traces of bivalve pedicellariae observed on the actinal plate surface, similar to those in *Akelbaster* (Neumann & Girod 2018). The authors noted the significance and presence of bivalve pedicellariae shared between *Weitschataster* and other Goniasteridae, especially in the Hippasterinae.

OREASTERIDAE Fisher, 1908

Diagnosis
Modified from Marsh & Fromont (2020). Body massive, ranging in shape from pentagonal and nearly spherical to strongly stellate, R/r ranging between 1.0 to 4.0. Disk strongly arched with disk large. Abactinal skeleton reticulate with secondary plates in contact with primary plates forming conspicuous papular regions. Marginal plates well developed but obscured or inconspicuous in some taxa. Actinal papulae absent. A calcareous internal septum present.

Comments
Oreasterids includes 75 species within 18 genera present primarily throughout the tropical Indo-Pacific with 1 genus and 2 species in the tropical Atlantic. Most oreasterids occur in shallow-water, but can occur in mesophotic and deep-sea settings, as deep as 300 m (e.g. Mah 2023, 2021).

Although many oreasterids remain poorly understood, the feeding ecology of several species has become better understood in recent years. The tropical Atlantic *Oreaster reticulatus* (Linnaeus, 1758) has been documented feeding on sponges (Wulff 1995) as well as "microphytes", such as microalgae (e.g. Scheibling, 1982) in the sediment. The Indo-Pacific *Protoreaster nodosus* has similarly been documented as feeding on meiobenthos and microbial/microalgal film by extra-oral feeding on sediments and sea grass (Scheibling & Metaxas 2008). Castello y Tickell *et al*. (2022) reported east tropical Pacific *Pentaceraster cumingi* and *Nidorellia armata* as feeding on the cidaroid urchin *Eucidaris* and unbleached crustose coralline algae, respectively.

Bivalve Pedicellariae in the Oreasteridae

A complete list of all bivalve pedicellariae bearing Oreasteridae is included in Table 1. Selected genera are included here that demonstrate noteworthy expression, in terms of size, abundance, etc. of bivalve pedicellariae across the Oreasteridae. A complete list of oreasterids with bivalve pedicellariae is summarized in Table 1. At least one species in every genus of Oreasteridae has bivalve pedicellariae, but not always in abundance. Most taxa show pedicellariae on the actinal intermediate surface to varying degrees. The more "goniasterid-like" genera, such as *Anthenea* and *Gymnanthenea* show large pedicellariae, i.e. equal to size of the plate on which it sits, in distinct series on actinal plates adjacent to the adambulacral plate series, extending from the disk along the length of the arm (e.g. Fig. 30 E–G), but in contrast, the more strongly arched, massive forms with large, coarse granules and spination such as *Choriaster, Culcita*, *Pentaceraster*, or *Protoreaster* display relatively small and fewer pedicellariae, which are more widely spaced and irregularly positioned on the actinal surface.

Although ecological data is incomplete, Marsh & Fromont (2020) have described *Anthenea, Goniodiscaster,* and *Gymnanthenea* as present on muddy or soft sedimentary bottoms, in contrast to the larger forms, such as *Pentaceraster* or *Protoreaster* which are largely present on sandy bottoms, especially near mangroves. *Culcita* and other oreasterids with thick body walls, such as *Choriaster* are recorded from coral reefs, reef flats and adjacent habitats. Pedicellariae position in *Anthenea* and related taxa may be closely associated with life habits. For example, one *in situ* image of *Goniodiscaster pleyadella* (Lamarck, 1816) shows the actinal surface and the inferomarginal plates buried below the sediment with the abactinal and superomarginal plates nearly flush with the bottom surface (Marsh & Fromont 2020: 407). Further *in situ* observations of *Anthenea* show possible feeding (Marsh & Fromont 2020: 381, 389, Fig. 28A–B, 29A–B). Pedicellariae on the actinal surface may be involved with feeding in some direct or indirect way, as has been suggested for Goniasteridae, such as *Bathyceramaster kelliottae*. A discussion of possible pedicellariae function in the Oreasteridae is presented in the Discussion.

Acheronaster H.E.S. Clark, 1982

Comments & Diagnosis
Monotypic. As for species

***Acheronaster tumidus* H.E.S. Clark, 1982**
FIGURE 26A–D

H.E.S. Clark, 1982: 39; H.E.S. Clark & McKnight, 2001: 180; Mah, 2021: 439.

Diagnosis
Modified from H.E.S. Clark (1982). Body stellate, arms elongate, interbrachial arcs rounded. Abactinal plates forming reticulum, plates small rounded spines. Abactinal, marginal surface covered by granules. Papular regions distinct. Marginal plates without enlarged spines. Actinal areas large, adambulacral plates with 2 to 3 spine series. Bivalve pedicellariae present on abactinal, marginal, actinal surfaces.

Comments
Aside from *Anthenea* species, the related *Gymnanthenea, Anthaster* and *Monachaster*, *Acheronaster* has the most numerous and largest of bivalve pedicellariae observed in the non-"goniasterid" shaped Oreasteridae (Figs 26 B, D).

Distribution/Occurrence
Kermadec Islands, north of New Zealand and coast of New South Wales, Australia, New Caledonia,110–300 m

Material Examined
MNHN IE-2013-6608. Kaimon-Maru Bank, Norfolk Ridge, New Caledonia, 24.734617 S,168.164368 E, 269–300. Coll. Lozouet, Boisselier & Richer-IRD, aboard N/O *Alis,* NORFOLK 1. CP 1678, June 22 2001,1 dry spec. R=18.1, r=7.7.

***Anthaster* Döderlein, 1915**

Comments & Diagnosis
Monotypic. As for species.

***Anthaster valvulatus* (Müller & Troschel, 1843)**
FIGURE 27A–D

Oreaster valvulatus Müller, J. & Troschel, F. H., 1843: 115.
Pentaceros valvulatus Sladen 1889: 345.
Anthaster valvulatus Döderlein, 1915: 30; 1935: 105; H.L. Clark 1928: 386; 1938: 102; Shepherd 1968: 743 (food); Ziedler & Shepherd 1982:411, figs. 5e–f, 10; Marsh & Fromont 2020: 362.

Diagnosis
Modified from Marsh & Fromont (2020). Body weakly stellate (R/r=1.9–2.0), arms elongate, disk surface convex. Body surface covered with small polygonal granules. Abactinal plates convex with bare, rounded tubercles. Interradial plates with medium sized pedicellaria rather than a tubercle, which are more prominent on primary circlet and along radial series. Superomarginal plates convex, covered by variably sized/shaped tubercles and pedicellariae. Inferomarginals lacking tubercles but with bivalved pedicellariae, up to 4.0 mm long. Most proximal actinal plates with large bivalve pedicellariae (up to 4.0 mm long). Adambulacral plates with slender furrow spines, 9 to 10, subambulacral spines in two series, one with 3 thick spines with blunt tips and an outer subambulacral spine series of 3 to 5 irregular spinelets. A prominent pedicellariae sits between the inner and outer subambulacral spine.

Comments
A species with bivalve pedicellariae on abactinal, marginal, and actinal surfaces (Fig. 27C–D). Those on the abactinal surface are smaller, easily less than 50% the pedicellariae length of those on the marginal and actinal surfaces. While abundant, pedicellariae appear evenly distributed, approximately one associated with each plate.

Marsh and Fromont (2020) describe this species on rock, sand, sea grass beds, or on muddy bottoms where they devour sponges and ascidians.

Distribution/Occurrence
From Encounter Bay, South Australia to near Lancelin, Western Australia. 3 to 40 m depth.

Material Examined
USNM E04678. South Australia, Australia, South Pacific. 1 dry spec. R=7.7 r=4.0.

***Anthenea* Gray, 1840**

Diagnosis
Modified from Marsh & Fromont (2020). Body weakly stellate to stellate (R/r=1.5–2.1), arms short, interradial arcs weakly curved to straight. Surface flattened to convex. Surface covered by distinct dermis overlying abactinal plates forming widely meshed reticulations with large papular spaces. Some plates with crystal bodies. Marginal plates well-developed. Granules present with varying expression in size, abundance. Inferomarginal plates each with one or more large bivalve pedicellariae. Actinal plates, especially those adjacent to the adambulacral series, each with a large bivalve pedicellariae. Actinal pedicellariae each surrounded by a single or double row of granules. Adambulacral spination, furrow and subambulacral spines, form 3 rows.

Comments
The genus *Anthenea* Gray 1840 currently comprises 23 species distributed throughout the Indo-Pacific region, but primarily occurring in Australia and the central Pacific/ Indonesian area with none known from the Atlantic.

Anthenea has several closely related genera, such as *Gymnanthenea* and *Goniodiscaster* which demonstrate strong morphological affinities. Distinctions between genera which are members of the "*Anthenea*" group are sometimes based on relatively few characters and have not been reviewed since H.L. Clark (1938), although Marsh & Fromont (2020) have recently reviewed Australian

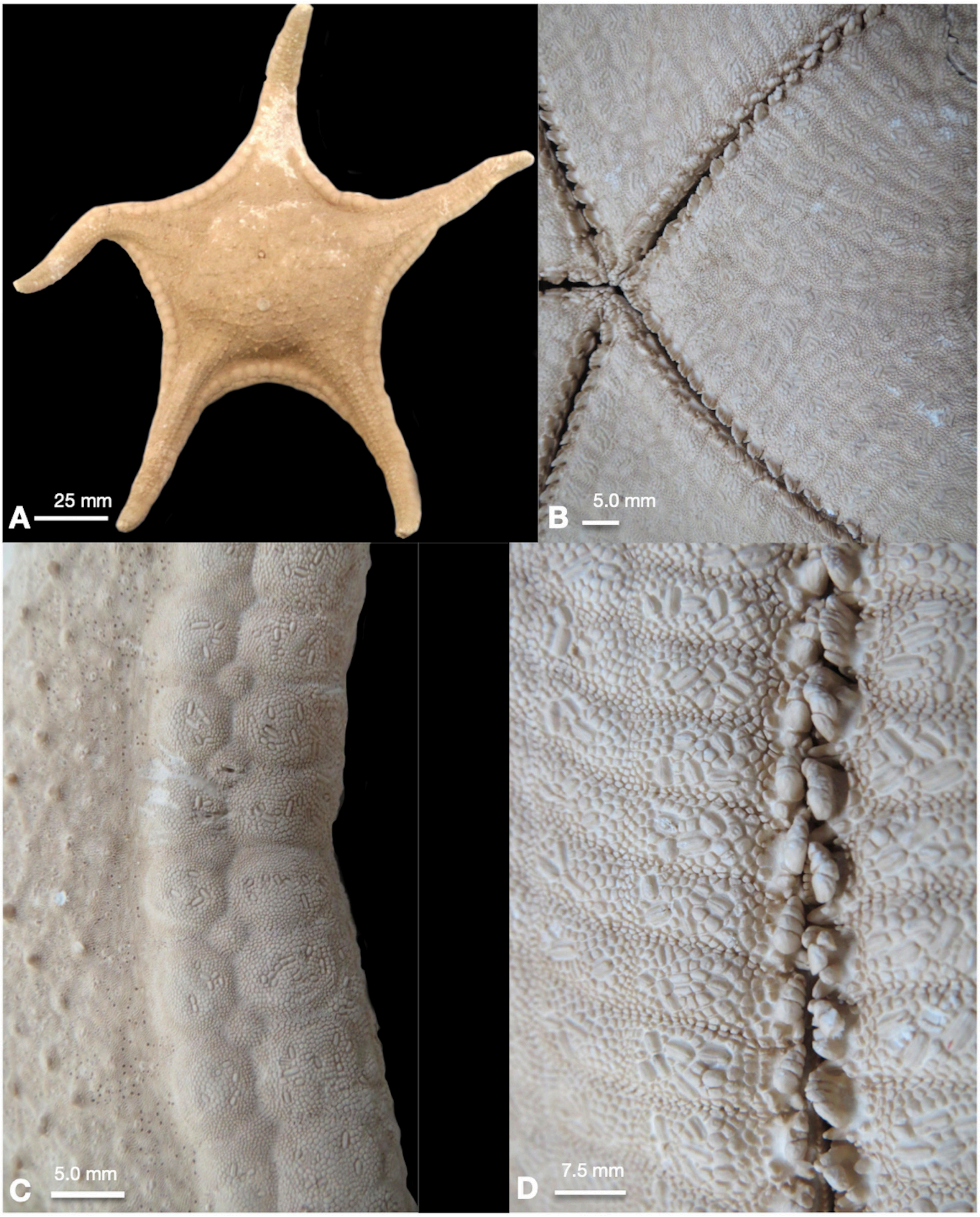

FIGURE 26. *Acheronaster tumidus* MNHN IE-2013-6608 A. Abactinal B. Actinal closeup. C. Abactinal-marginal showing pedicellariae. D. Actinal adambulacral closeup.

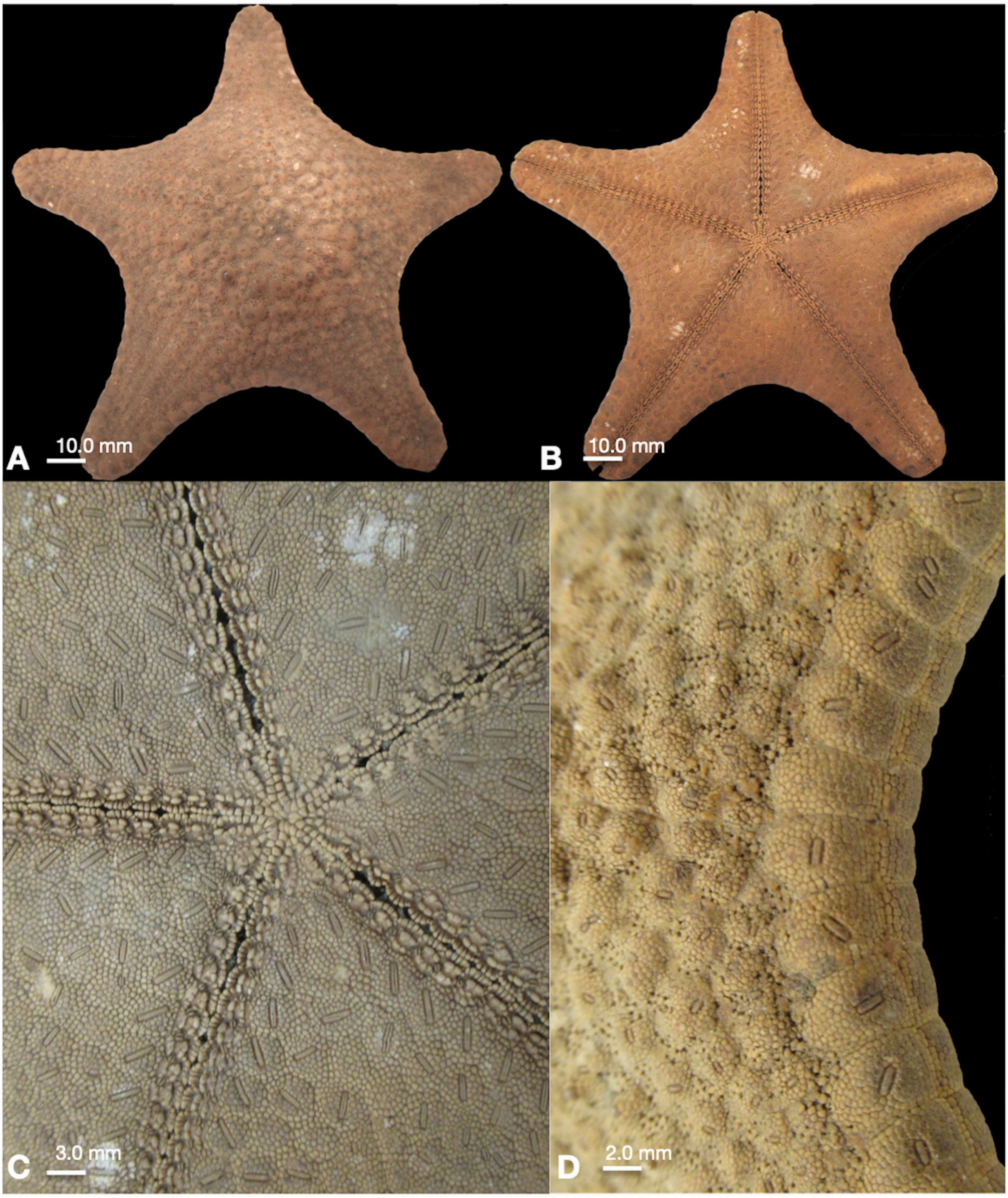

FIGURE 27. *Anthaster valvulatus* USNM E04678 A. Abactinal B. Actinal. C. Actinal-oral region. D. Abactinal-superomarginal contact.

species. *Anthenea* for example was identified based on the presence of three "adambulacral spine series" versus *Gymnanthenea* which was identified based on only two. Following the usage of "adambulacral spine series" in Döderlein (1915, 1935, 1936) and subsequent use by Clark and Rowe (1971), Liao and Clark (1995) and Marsh and Fromont (2021), the "spine series" includes the furrow spines, and the one or two spines series adjacent to the furrow spines (these latter adjacent spines are also known as subambulacral spines). Subambulacral spines re composed of one larger blunt spine, round in cross-section and approximately twice the width of but slightly shorter than the furrow spines. Two or more smaller subambulacral spines, half the height and thickness, sit adjacent to this primary spine, sometimes adjacent to or at oblique angles to the larger subambulacral spine. This character varies with respect to what is considered a "series" depending on number of spines and whether they possess a distinct linear arrangement. The dependence of historical accounts on this variable character to distinguish *Anthenea* from other genera, mainly *Gymnanthenea*, has led to some skepticism (e.g., Liao and Clark, 1995). It is beyond the scope of this work to treat a revision of *Anthenea* and related taxa, and so for now, taxon definitions are based on those of recent treatments, such as Liao and Clark (1995) and Marsh and Fromont (2021).

Although bivalve pedicellariae vary among species, they are generally large and abundant on marginal and actinal surfaces with relatively few to no pedicellariae on the abactinal surface. Pedicellariae are almost always present on the actinal series adjacent to the adambulacral plates and variably present on the remainder of the actinal series, depending on species.

Anthenea chinensis **Gray, 1840**

FIGURE 28A–B

Anthenea chinensis Gray, 1840: 279; 1866: 8.

Goniodiscus pentagonulus Muller & Troschel, 1842: 57, pl. 4, fig. 2.

Goniodiscus articulatus Perrier, 1869: 279.

Anthenea pentagonula Perrier 1875: 275 (1876: 90); Doderlein, 1915: 32, pl. 4, figs 3,4, pl. 5, fig. 1; Smith,1927: 276; Chen, 1932: 67; H.L. Clark, 1938: 115; Clark & Rowe, 1971: 32, 51, 52; Liao & Clark, 1995: 98.

Diagnosis

Body form stellate, R/r=1.6–2.1. Arms triangular, disk broad with proximal arm variably wide. Interradial arcs weakly curved to curved. Surface covered by conical, pointed tubercles present at interstices of where reticulate plates overlap, especially prominent on radial regions on arm. Abactinal covered by thick dermis, infused with small prickle-like spinelets, homogeneous in size, widely spaced on complete surface, approximately 4 to 6 count along a 1.0 mm line. Clamp-like pedicellariae, approximately 1.0 mm wide x 0.5 mm tall, common on abactinal surface, widely spaced, 2 to 6 present along a 5.0 mm line. Marginal plates wide, forming distinct periphery, approximately 16% (1.0/6.0) of distance “r”. Superomarginal plates, approximately 22–24 per interradius (11–12 per arm), inferomarginals approximately 30 per interradius (15 per arm). Inferomarginal plates wide, covered by coarse granules, 50 to 80, adjacent to contact with superomarginals on lateral surface, becoming smaller, more densely packed and abundant on actinal side of the inferomarginal plate surface. Adambulacral spines in three series, furrow spines and two subambulacral spine series. Furrow spines 4 to 5, blunt, oval to round in cross-section, three central spines thick and tallest versus peripheral spines which are approximately 10% of the height of the central furrow spines. Subambulacral spines set off from furrow spines by a distinct space, each series contains approximately 2 to 3 tubercle-like spines, each at least 2 to 3x the thickness of a furrow spine.

Comments

Consideration of the ecological comments prompted the need to address taxonomic questions associated with the relevant taxa. Among the most significant was raised by Liao and Clark (1995) who questioned whether the species present in China were the same species recorded from Australia. Their work outlined four species of *Anthenea* in southern Chinese waters, *Anthenea dificilis, Anthenea aspera, Anthenea chinensis* and *Anthenea viguieri*. Their work included reinstating *Anthenea chinensis* Gray 1840 as a separate name from the Australian *Anthenea pentagonula* into which *A. chinensis* had been synonymized. In their summary of Australian *Anthenea*, Marsh and Fromont (2020) further agreed that records of “*Anthenea pentagonula*” from South-East Asia were “questionable.” Liao and Clark (1995) also noted that regional representatives of two species, *Anthenea aspera* Doderlein, 1915 and *Anthenea viguieri* Doderlein, 1915 were also possible synonyms of *Anthenea chinensis* in the Chinese region. Adjacent regions, such as Singapore (e.g., Vandenspiegel *et al*., 1998) and Vietnam (Antokhina & Britayev, 2012) show that *Anthenea aspera* is used widely used throughout the region for species similar to *Anthenea chinensis*. Chinese and Taiwanese (USNM E1203 and others) specimens and one specimen from Japan (CASIZ 106930) suggest overlap in characters between concepts outlined for *Anthenea aspera* and *Anthenea chinensis* as summarized in Liao and Clark (1995). This includes overlapping R/r ratios, the broad triangular arms as well as the subjective assessment of granules and tubercles as “coarse” and “broad” which appeared to overlap between specimens examined and Liao and Clark’s (1995) description.

However, comparison between specimens from Japan and Thailand suggests that *Anthenea chinensis* shows sufficient character differences, including adambulacral spination morphology and number as well as distinctly different marginal plate number and abactinal spination/accessories to preclude clear agreement with Doderlein (1915). Full molecular phylogenetic revision of *Anthenea* from across its range is desirable, but for now, *A. chinensis* is argued as a distinct species.

Distribution/Occurrence

Okinawa, Japan, East China Sea (Taiwan), Thailand, 27–200 m.

Description

Body, thick, stout, weakly stellate (R/r=1.97) in shape, arms short, triangular, disk large. Interradial arcs wide, armtips upturned.

Abactinal surface reticulate forming quadrate to triangular meshwork, papular regions poorly differentiated but approximately 10–30 per region. Papulae present only on radial regions, absent from narrow interradial strip. Surface covered by conical, pointed tubercles present at interstices of where reticulate plates overlap, especially prominent on radial regions on arm. Abactinal covered by thick dermis, infused with small prickle-like spinelets, homogeneous in size, widely spaced on complete surface,

FIGURE 28. *Anthenea chinensis in situ*. Hong Kong. A. Abactinal B. Actinal surface showing pedicellariae with sediment. Photo credit: Johnny So.

approximately 4 to 6 count along a 1.0 mm line. Clamp-like pedicellariae, approximately 1.0 mm wide x 0.5 mm tall, common on abactinal surface, widely spaced, 2 to 6 present along a 5.0 mm line. Interradial regions on disk characterized by a distinct seam which is confluent with contact between interradial superomarginal plates. Interradial regions largely bare, save for prickle-like spinelets, lacking tubercles or pedicellariae. Distalmost surface on arms with mound-like plates, 2 to 4, covered by granule-like tubercles, similar in size to those on adjacent superomarginals.

Marginal plates wide, forming distinct periphery, approximately 16% (1.0/6.0) of distance "r". Superomarginal plates, approximately 22–24 per interradius (11–12 per arm), inferomarginals approximately 30 per interradius (15 per arm), numbers are estimates due to some inter-radii with damaged or incomplete marginals. Superomarginals covered by thick dermis, infused with stout, round granules, ranging from 60 to 150 in number, increasing distally. Granules widely spaced on plate surface, approximately 7 to 9 along a 5.0 mm line, variable in size, ranging from approximately 0.2 mm to 0.7 mm in diameter. Bivalve pedicellariae on one or two superomarginals per interradius, occurring on lower end of plate adjacent to contact with inferomarginal plates. Inferomarginal plates wide, covered by coarse granules, 50 to 80, adjacent to contact with superomarginals on lateral surface, becoming smaller, more densely packed and abundant on actinal side of the inferomarginal plate surface. Approximately 10 bivalve pedicellariae per interradius with one or two pedicellariae occurring at irregular and oblique angles on each inferomarginal plate, each surround by approximately 15–30 granules. Terminal plate triangular, with granules ranging from smaller spine-like in size and low, glassy incipient granules. Pre-terminal superomarginal plates small relative to other proximal superomarginal plates.

Actinal surface with three full series, one or two incomplete series in chevron formation. Individual plates round to polygonal in shape, separated by shallow fasciolar grooves. Each plate covered by large round granules, widely spaced, approximately 12–30 (mostly 14–19) per plate. Large bivalve pedicellariae, ranging from 2 to 4 mm in length, sometimes occupying the entire diameter of the plate on which it sat. Pedicellariae most abundant on actinal plates adjacent to adambulacral plates, and on proximal actinal intermediate plates, with few to none distally adjacent to inferomarginal plate contact.

Adambulacral spines in three series, furrow spines and two subambulacral spine series. Furrow spines 4 to 5, blunt, oval to round in cross-section, three central spines thick and tallest versus peripheral spines which are approximately 10% of the height of the central furrow spines. Subambulacral spines set off from furrow spines by a distinct space, each series contains approximately 2 to 3 tubercle-like spine, each at least 2 to 3x the thickness of a furrow spine. One subambulacral, facing distally smaller than the other but both thicker relative to the furrow spines. Oral plates with 9 furrow spines, thick and round in cross-section with an 10th spine on each plate (two total) , triangular in cross-section projecting into the mouth. Oral spines densely packed. Subambulacral spines on oral plate similar to those on adambulacral in being twice to three times as thick as the furrow spines. Oral surface with approximately 16 quadrate to blocky granules, roughly paired in half with 8 granules on each side.

Material Examined

Japan. CASIZ 106930 Nakagusuku Bay, Okinawa, Ryukyu Islands. Coll. by fishermen, 20 July 1985, 1 dry spec. R=11.8 r=6.0.

East China Sea (Taiwan). CASIZ 108097, N. of Taiwan, 28.00ºN 121º00E, 73.1–110 m (40–60 fms), 2 wet specs. R=6.7 r=3.4; R=4.3 r=2.1.

CASIZ 108101, N and NW of Taiwan, East China Sea, 50–90 m. Coll. F.B. Steiner, June 1973. 3 wet specs. R=6.7 r=3.2, R=4.4 r=2.1, R=4.6 r=2.3.

CASIZ 113390, N and NW of Taiwan, East China Sea, 60 m, Coll. F.B. Steiner, Feb 1972. 1 wet spec. R=6.6 r=3.3.

CASIZ 113394, Off Taiwan, 60 m. Coll. commercial fisherman, 1 Feb. 1972. 7 wet spec. R=7.6 r=3.5, R=5.3 r=2.4; R=4.6 r=1.9, R=4.0 r=2.0, R=4.2 r=1.9, R=4.7 r=2.2, R=3.7 r=1.6

Thailand. CASIZ 113396, approximately 15 miles offshore E of Kau Sarmroiyord (via Bangkok Fish Market) sand and mud, 12.00º8.00'N 100.00º 14'E, 26–28.0 m, Coll. Thai fishermen, of F/V *Datechalothorn 20991,* 30 July–1 Aug 1960. 1 wet spec. R=8.9 r=4.3.

Anthenea hlan sp. nov.

Figure 29A–G

Etymology

The species epithet "hlan" is the Burmese word for spear, taken in apposition, alluding to the pointed abactinal spines that characterize this species.

Diagnosis

Body shape weakly stellate to stellate, arms triangular. **Abactinal plates with spines or pointed conical tubercles.** Abactinal pedicellariae small, paddle-like, relatively few. Marginal plates 26 superomarginal plates per interradius (arm tip to arm tip) with 13 per side, 27 inferomarginal plates. **Large bullet-shaped tubercles/spines, present proximally and along arms on dorsal/dorsal-lateral superomarginal plate surface**. Furrow spines 5 to 6, central spines, closely arranged especially at the base, most elongate, blunt, round in cross-section, those on end of each side approximately 20% of height of central spines. A single subambulacral spine series present with the central spine enlarged, blunt, round in cross-section, flanked by smaller spines approximately 50% of the height and the thickness.

Comments

This species shows similarity with *Anthenea regalis* Koehler 1910 which has "cylindrical tubercles" in contrast

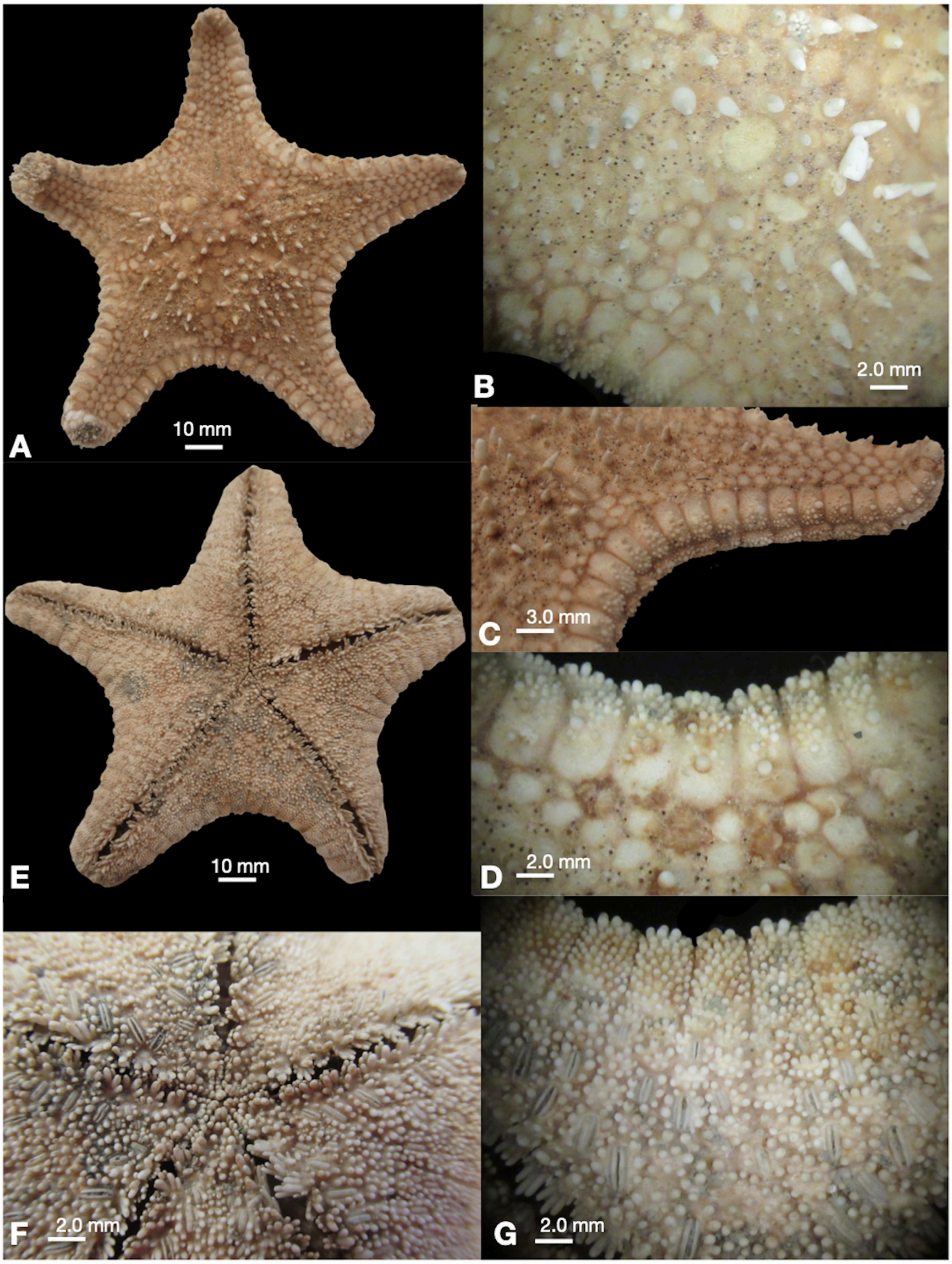

FIGURE 29. *Anthenea hlan* **sp. nov.** Holotype USNM E53676 A. Abactinal B. Closeup on abactinal surface. C.Abactinal-superomarginal contact. D.Abactinal-lateral closeup. E. Actinal. F. Actinal oral view with sediment in pedicellariae. G. Closeup actinal pedicellariae with sediment.

to the distinctly pointed conical spines observed herein. Superomarginals on *Anthenea hlan* **sp. nov.** also display conical spines on the dorsal surface of the superomarginal plates, which are absent in *A. regalis*. Marginal plate number per interradius, furrow spine and subambulacral spine number are similar with that of *A. regalis*.

Distribution/Occurrence
South of Boronga Islands, Burma, 22–30 m.

Description
Body stellate (R/r=1.7–2.15), disk broad, arms triangular, tips weakly pointed. Interradial arcs weakly curved to straight (Fig. 29A).

Abactinal plates round to irregularly polygonal, forming an abutted pavement, covered by distinct dermis. Secondary plates present. Primary circlet plates, each approximately 3 to 5X the size of the adjacent disk plates, flattened, with approximately six associated paired plates forming a distinct "fold" in each interradius, lacking papulae between them. Plates 6 to 10 proximally across arm base, decreasing to approximately three series along arm tip. Papular regions large, up to 6 surrounding each plate, each region with papulae, 1 to 5, especially proximally. Papulae fewer along arm, diminishing to a single papulae around plates adjacent to arm tip or else completely absent. Minute ossicles or spinelets present completely covering epidermal surface. Prominent, pointed conical spines present on disk and proximally on arm, especially along primary circlet and carinal series (Fig. 29A–C). Spines largest and most abundant, widely spaced, in up to three roughly linear series proximally, diminishing to a single spine, approximately midway along arm, and completely absent distally, around arm tip. Variably, USNM E9299 has prominent spines on the primary plates but is covered by pointed conical tubercles on other proximal plates. Small pedicellariae present, but relatively few to absent with rectangular to quadrate shaped valves, larger (approximately 0.75 mm length) proximally shrinking in size with pedicellariae more distally along arms similar in size to a papular pore (0.25 mm length) and eventually absent adjacent to arm tip. Anus with six short pointed spines, directed inwards. Madreporite polygonal, large, flanked by approximately six plates.

Marginal plates 26 superomarginal plates per interradius (Fig. 29A) (arm tip to arm tip) with 13 per side, 27 inferomarginal plates. Superomarginal plates wide, especially interradially becoming more elongate distally. Dorsal superomarginal plate surface covered only by dermis and small minute spinelets/ossicles as covering the abactinal surface. Superomarginals with mostly one enlarged short, cone-shaped spine, bullet-shaped, approximately 1.0 mm height), standing well above the surface of the marginal plate, in series along the dorsal and/or dorsal-lateral surface of the superomarginal plates, especially proximally. Superomarginal lateral surface covered by 8 to 20, mostly 10 to 15 prominent, cylindrical to conical shaped, pointed granules of varying sizes, ranging from very small, <0.3 mm to up 0.75 mm in height (Fig. 29C–D). Inferomarginal plates covered by similar types of conical pointed granules, approximately 20 to 200, widely spaced with larger granules adjacent to the contact with the superomarginal plates. A single large bivalve pedicellariae present on a single distal inferomarginal plate, approximately two to three plates from the terminus. Terminus large, broadly diamond-shaped, surface smooth.

Actinal intermediate region in 3 series, chevron-like arrangement with a single series extending onto the arms. Wide bivalve pedicellariae with smooth valves on the actinal plate series adjacent to the adambulacral series and on approximately 50% of the plates in the actinal intermediate region (Figs. 29 E–G). Actinal plates with large, round granules, 4 to 15, widely spaced, on those with pedicellariae (Figs. 29F–G). When present the pedicellariae nearly bisect the plate with granules on either side. Fasciolar grooves weakly present.

Furrow spines 3 to 6, (Fig. 29F) but mostly 3 to 4 proximal, central spines, closely arranged especially at the base, most furrow spines thick, blunt, round in cross-section, those on end of each side approximately 20% of height of central spines with shortest spines at distal edges. 6 furrow spines present only present on adambulacrals near arm tip. A single subambulacral spine series present with the central spine enlarged, blunt, round in cross-section, flanked by smaller spines approximately 50% of the height and the thickness. Remainder of adambulacral plate with a single series of irregularly arranged blunt granules widely spaced. Oral plate with furrow spines 7, blunt, round in cross-section, blunt tipped. Two spines, one per plate, triangular in cross-section per interradius projecting into mouth. Oral plate surface covered by approximately 15 thick, blunt round spines similar to the subambulacral spines, approximately 4 to 6 paired along the center of each plate one other side of the diastema between the oral plates.

Material Examined
Holotype. USNM E53676 South of Boronga Islands, Boronga Islands, Burma, Bay of Bengal, Indian Ocean. 19º50'N 92º55'E, 22–30 m. Coll. R/V *Anton Bruun,* IIOE, 5 April 1963. R=4.3 r=2.0l.

Paratypes. USNM E9299. Pakistan, vicinity of Karachi, Arabian Sea, Indian Ocean. Coll. M.A. El-Husseini. 27 March 1963. 1 dry spec. R=4.0 r=2.3.

CASIZ 28705, Madras, Tamil Nadu, Bay of Bengal, India. Coll. F. B. Steiner, Feb 1968. 1 dry spec. R=5.3 r=2.4 (6 armed variant).

Anthenea nuda **sp. nov.**
FIGURE 30A–G

Etymology
The species epithet, *nuda* is Latin for nude or naked, alluding to the absence of tubercles or pedicellariae on the abactinal surface. Gender is female.

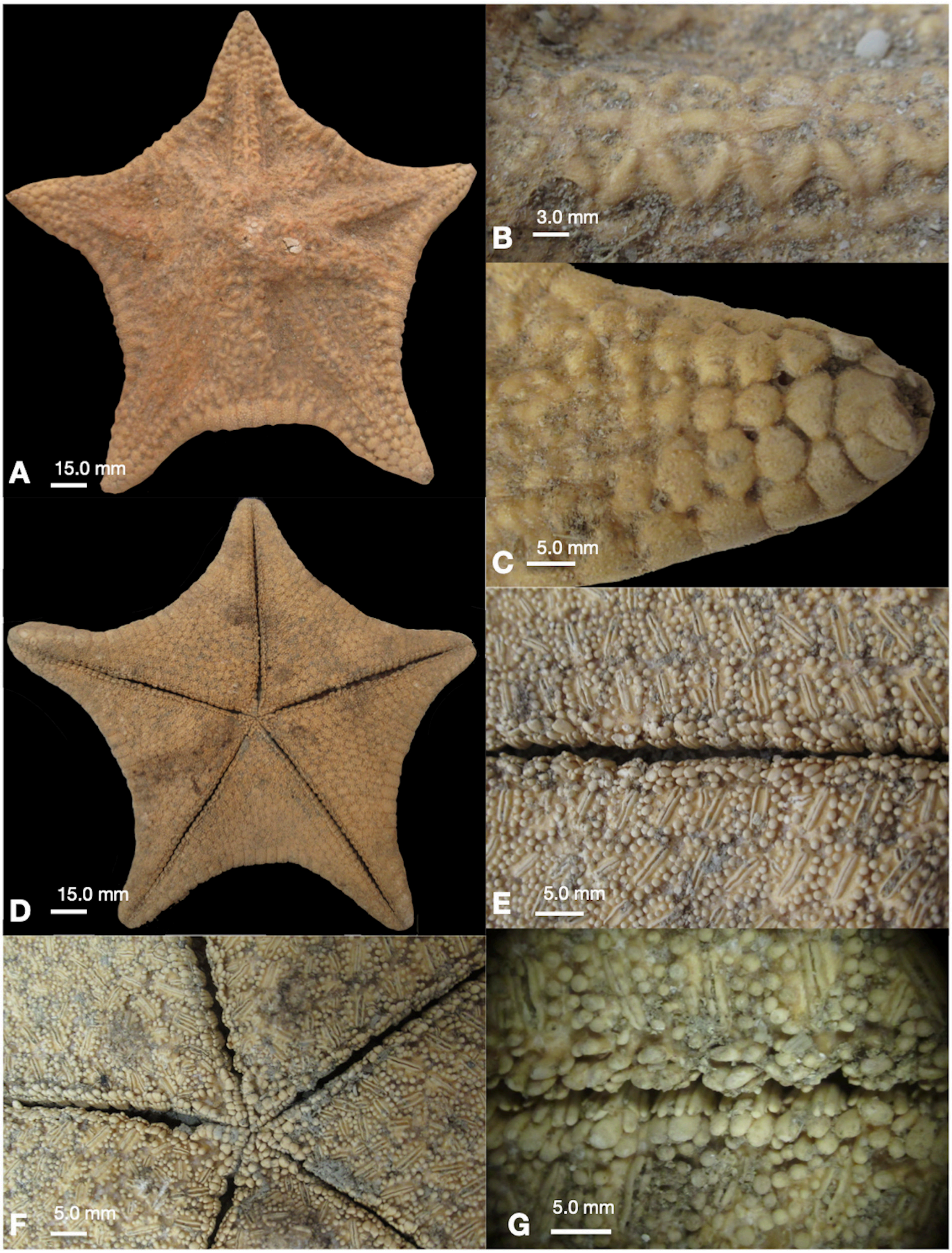

FIGURE 30. *Anthenea nuda* **sp. nov.** Holotype USNM E38927 A. Abactinal B. Closeup on carinal plates. C. Closeup on armtip plates. D. Actinal. E. Closeup on actinal and adambulacral pedicellariae. F. Actinal-oral region. G. Adambulacral-furrow closeup showing pedicellariae with sediment between valves.

Diagnosis
Body stellate to weakly stellate, R/r=1.69–2.06. Disk broad, arms triangular. **Abactinal surface devoid of tubercles, granules or pedicellariae, covered by distinct dermis,** extending to marginal plates. Abactinal plates distally on arms, abutted rather than reticulate, strongly convex. Marginal plates covered by round granules, pedicellariae present on inferomarginal plates but absent on superomarginal plates. All actinal plates with a large bivalve pedicellariae. Furrow spines 4 to 6, central 2 to 3 thickened, all blunt tipped in palmate formation. Subambulacral spines, very thick, blunt, large relative to furrow spine's in two irregular series, each with 2 to 3 spines.

Comments
This species invited immediate comparison with the Indian Ocean *Anthenea mertoni* Koehler, 1910 with which it shares enlarged, abutted distalmost abactinal plates in addition to similar numbers of furrow spines. However, *A. nudus* **sp. nov.** has no tubercles or pedicellariae on the abactinal surface (Fig. 30A–C) and has much larger and thicker subambulacral spines (Figs. 30E–G) than those illustrated by Koehler (1910). The absence of tubercles and pedicellariae similarly differentiates this species from *A. aspera* Döderlein, 1915 and A. *pentagonula* (Lamarck, 1816).

Occurrence/Distribution
Arafua Sea, Northern Territory, Australia. 60 m.

Description
Body weakly stellate to stellate, R/r=1.69–2.06, disk broad, arms short, triangular, interradial arcs weakly stellate to straight. Body with overlying dermis (Fig. 30A).

Abactinal surface composed of thick plates forming open reticulate network on disk (Figs. 30A–B), but with more closely abutted/imbricate plates distally on arm (Fig. 30C). Proximal disk plates forming triangular shaped open papular regions, each with 3 to 6 papular pores. Plates in hexagonal arrangement with a round to polygonal center with six radiating bar-shaped ossicles meeting with other hexagonally arranged ossicles. Distal plates at arm tip strongly convex, closely abutted, enlarged with approximately three plates across distal arm region. Central interradial plates with thickened, closely articulated plates, no papulae. Abactinal surface with no granulation, no tubercles, no pedicellariae. Madreporite round to polygonal, sulci well developed.

Marginal plates, approximately 26 to 30 per interradius (arm tip to arm tip), approximately 13 to 16 along each arm (Fig. 30A). Superomarginals, occupy a relatively small proportion (14%=1.0/6.8) of the total "r" with inferomarginal plates jutting outward. Both marginal plates distinctly wider than long with rounded abactinal-lateral and actinal-lateral edges. Surface convex, covered with coarse, round granules, widely spaced. Contact between marginal and abactinal plates obscured by dermis covering over surface. Granules become more diffuse distally and surface of superomarginal plates adjacent to abactinal surface with granules absent. Pedicellariae absent from superomarginal plates. Inferomarginal plates covered with 20 to 60 granules, coarse, widely spaced in addition to elongate bivalve pedicellariae, 1 to 2 positioned at oblique angles on ventral surface of each plate. Fasciolar groves present between superomarginal and inferomarginals, as well as at contact with actinal plate series. Terminal plate triangular, pointed tip.

Actinal region broad, with approximately 6 to 8 full series in chevron like formation (Fig. 30D). Each plate round to polygonal in shape, fasciolar grooves present between actinal plates, aligned with those on inferomarginal plates. Actinal plates with a large, elongate bivalve pedicellariae with smooth valves, approximately 3.0 mm in length, bisecting the length of the plate on which it sits (Fig. 30E–G). These surrounded by round, spherical granules, smooth, approximately 10 to 20 in irregular single series, evenly spaced. Actinal plate otherwise smooth. Pedicellariae are present on nearly all actinal plates, save for a minority of small, irregular plates adjacent to the inferomarginal contact.

Furrow spines 4 to 6, central 2 to 3 thickened, all blunt tipped in palmate formation. Subambulacral spines in two irregular series, each with 2 to 3 spines (Fig. 30F–G). Subambulacral series adjacent to the furrow spines very thick, approximately the thickness of 2 to 3 furrow spines, tipped with blunt tips. Subambulacral spines adjacent to the actinal spines shorter, more similar to adjacent granules on actinal plates. Oral plates with furrow spines, 10, thickened, round to quadrate in cross-section, with blunt to rounded tips. Two shorter, blunt, angular spines thick directed into mouth. Oral plate spines covered by large, thick blunt spines, each 2 to 4 times the thickness of the furrow spines concealing the oral region around the mouth.

Material Examined
Holotype. USNM E38927. North of Arnhem Land, Northern Territory, Australia, Indian Ocean. -10.667 133.833, 60.0 m. Coll. T. Ward, 11 April 1986. 1 dry spec. R=11.5 r=6.8.

Paratypes. USNM E38926. North of Wessel Islands, Northern Territory, Australia, Indian Ocean, -10.3667, 136.517. Coll. Northern Territory Fisheries, 12 Nov. 1986. 1 dry spec. R=12.4 r=6.0.

USNM E38928. North of Wessel Islands, Northern Territory, Australia, Indian Ocean, -10.05 136.833, 60.0 m.Coll. J. Baxter, 7 Feb 1986. 1 dry spec. R=12.6 r=6.9.

Anthenea serrata sp. nov.
FIGURE 31 A–F

Vandenspiegel, *et al*., 1998:458 (as *Gymnanthenea laevis*).
Saba *et al*., 2002: 32 (as *Gymnanthenea globifera*).

Etymology
The species epithet "*serrata*" alludes to the serrated appearance formed by the spines present on the marginal plates along each arm. Gender is female.

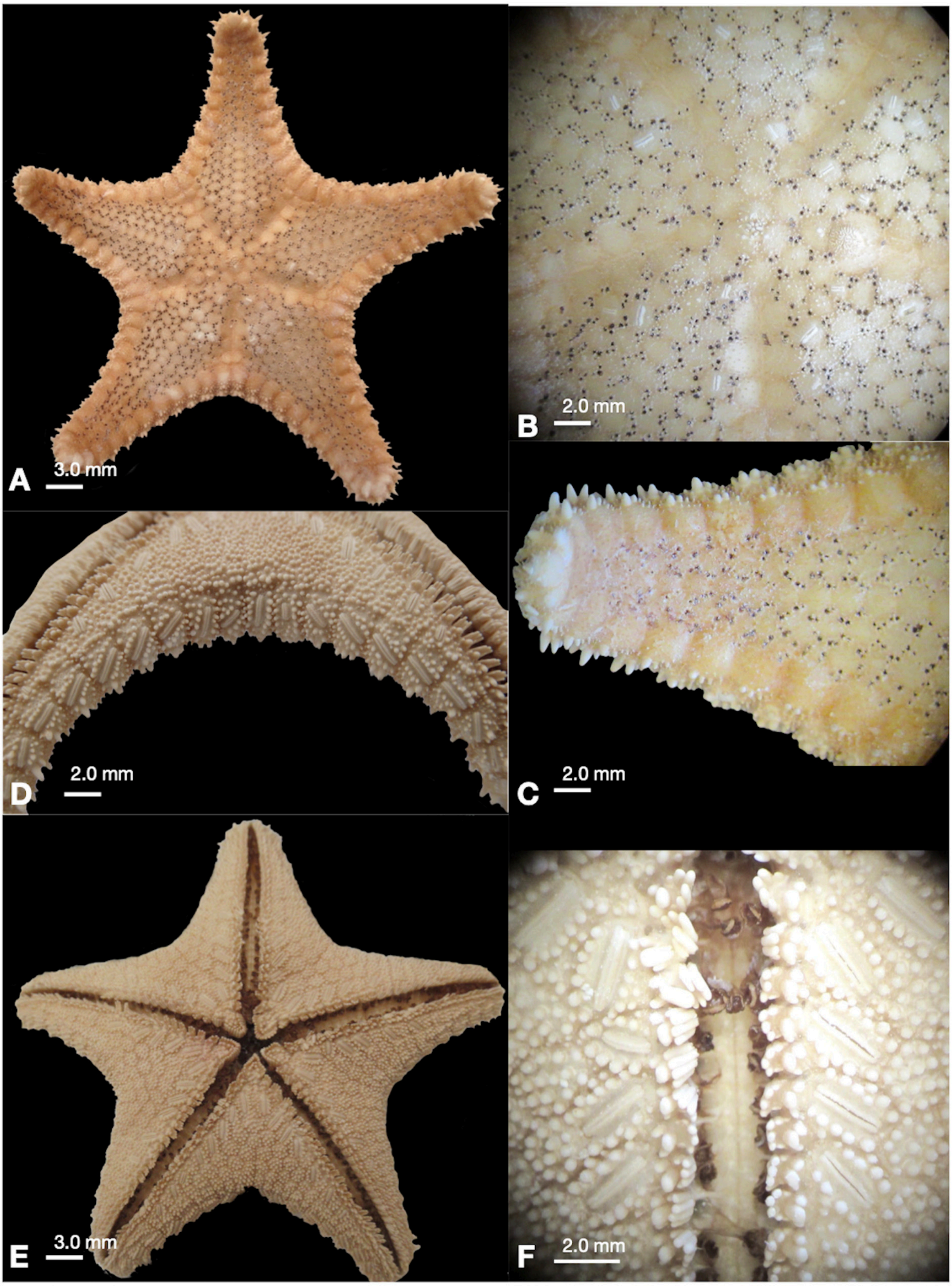

FIGURE 31. *Anthenea serrata* **sp. nov.** Holotype USNM E45263 A. Abactinal B. Closeup of abactinal surface. C. Closeup of arm tip. D. Inferomarginal-actinal contact with pedicellariae. E. Actinal. F. Actinal-adambulacral region showing pedicellariae.

Diagnosis

Body stellate, R/r=1.8–2.2, arms triangular in shape, disk broad, interradial arcs curved. Body planar, marginals forming serrated outline. Thin dermis present over body surface. Minute spiny granules widely occurring over abactinal surface. Bivalve pedicellariae present, perhaps two to each radial region. Superomarginal plates forming distinct abactinal border, making up 20% of distance "r". Superomarginal plate surface with distinct conical (bullet-shaped) spines, 1 to 6 with smaller secondary cone-like granules, 8–12, also present. Inferomarginals with large bivalve pedicellariae, one per plate occupying nearly complete distance of each plate surface. Large bivalve pedicellariae on actinal plates adjacent to adambulacral plates. Two series of adambulacral spines. Furrow spines five, blunt, weakly clavate, round in cross-section, one large subambulacral, approximately twice the thickness of but slightly shorter than the furrow spines, flanked by two smaller subambulacral spines, 1/3 the height and half the thickness of the large primary subambulacral spine.

Comparisons with *Anthenea flavescens*

Anthenea serrata **sp. nov.** invites immediate comparison with *Anthenea flavescens*, with which it shares many similarities as outlined in Doderlein (1915). Both species display the same distinctly planar body form with triangular arms with similar R/r ratio (*A. flavescens* with 2.17, *A. serrata* with 1.8–2.2), as well as similar types of abactinal and marginal plate arrangement and morphology. Marginal plate number per interradius is similar (16–20). Both species display a large bivalve pedicellariae on each of their inferomarginal plates (Fig. 31D) as well as five furrow spines on their adambulacral plates.

Anthenea serrata **sp. nov.** is distinguished by the distinct and consistent presence of one to six short, conical spines on the lateral and lower surface of the superomarginal plates, (Fig. 31C) as well as a numerous short conical tubercles on the abactinal surface of the superomarginal plates where the surface of *A. flavescens* is conspicuously bare or else covered with small granules as outlined in Doderlein (1915). Subambulacral spines in *A. serrata* are in indistinct rows with one large, thick blunt spine easily two to three times the thickness of one furrow spine flanked by two smaller spines approximately 40% of the height of the large single subambulacral spine. This is in contrast to the two rows of subambulacrals, each bearing two to three spines (Fig. 31F).

The overall similarity and the smaller size shared between *Anthenea flavescens* and *Anthenea serrata* suggests close affinity. Both species share abactinal and marginal plate characters which set them apart from the other, more massive *Anthenea* species, as outlined in Doderlein (1915). Further investigation may support these species as part of a further distinct taxon.

Comparisons with small *Anthenea chinensis*

The largest *Anthenea serrata* **sp. nov.** specimen (R=3.5) has a relatively small size compared to other known *Anthenea* species, which typically display R=6.0 to 10.0 cm. *Anthenea serrata* **sp. nov.** was compared with smaller individuals of another species of *Anthenea, Anthenea chinensis*, (R=3.8 from USNM E1203) known to occur in the local area.

Anthenea serrata **sp. nov.** shares the numerous embedded crystal bodies which are present on the abactinal and marginal plate surfaces as outlined by Doderlein (1915) as well as the large bivalve pedicellariae on the actual surface as well as similar marginal plates forming a wide border around the periphery.

Anthenea serrata differs from similarly sized *Anthenea* in that the abactinal plates are directly abutting and lack the numerous secondary plates, which apparently develop into the reticulate networks which characterize species within *Anthenea* and other Oreasteridae, the disk has is flattened and planar in shape, the lower inferomarginal plates occupy a position which juts out from under the superomarginal plates, and there are numerous spines present on the lateral surfaces of the superomarginals of *A. serrata* **sp. nov.**, absent from *A. chinensis* and other *Anthenea* from the region.

Comparisons with *Gymnanthenea*

Vandenspiegel *et al*. (1998) and Saba *et al* (2002) were among the earliest to have documented this species, which was identified as belonging to different species in the genus *Gymnanthenea*, from Singaporean and Japanese waters respectively. Examination of this species from specimens in the NMNH collections obtained from Okinawa ultimately permitted further confirmation and description.

Specimens of *Anthenea chinensis* show only "two series" of adambulacral spines, including relatively few furrow spines (five to six) and only 3 subambulacral spines. When this character is followed using Clark and Rowe's (1971) key, which was based on Döderlein's (1915, 1935, 1936) key to *Anthenea* and other oreasterids results in the erroneous conclusion of *Gymnanthenea.* This appears to be the path taken by the two early accounts of this species (Vandenspiegel *et al*., 1998, Saba *et al*., 2002). Comparison with the original description of the two original species of *Gymnanthenea* (e.g. Döderlein, 1915; H.L. Clark, 1938) shows *Gymnanthenea laevis* with much more massive and blocky marginal plates, spines absent on the distalmost marginal plates, as well as "slender" (versus thick) furrow spines and differing shape and number of subambulacrals. Tubercles on *Anthenea serrata* **sp. nov.** are also completely absent but present on both *Gymnanthenea laevis* and especially prominent on *Gymnanthenea globifera* where prominent, large round tubercles occur widely on the abactinal surface (e.g. Marsh and Fromont 2021). *Gymnanthenea laevis* was synonymized with *G. globigera* by Marsh (1976) a decision that was further agreed upon by Rowe and Gates (1995). This synonymy was based on Australian specimens which are not the same as the tropical Pacific Asian species indicated by Vandenspiegel *et al*. (1998), Saba *et al* (2002) and Antokhina and Britayev (2012). Marsh's (1976) synonymy should be upheld, provided the Asian accounts of "*Gymnanthenea*" are removed from consideration.

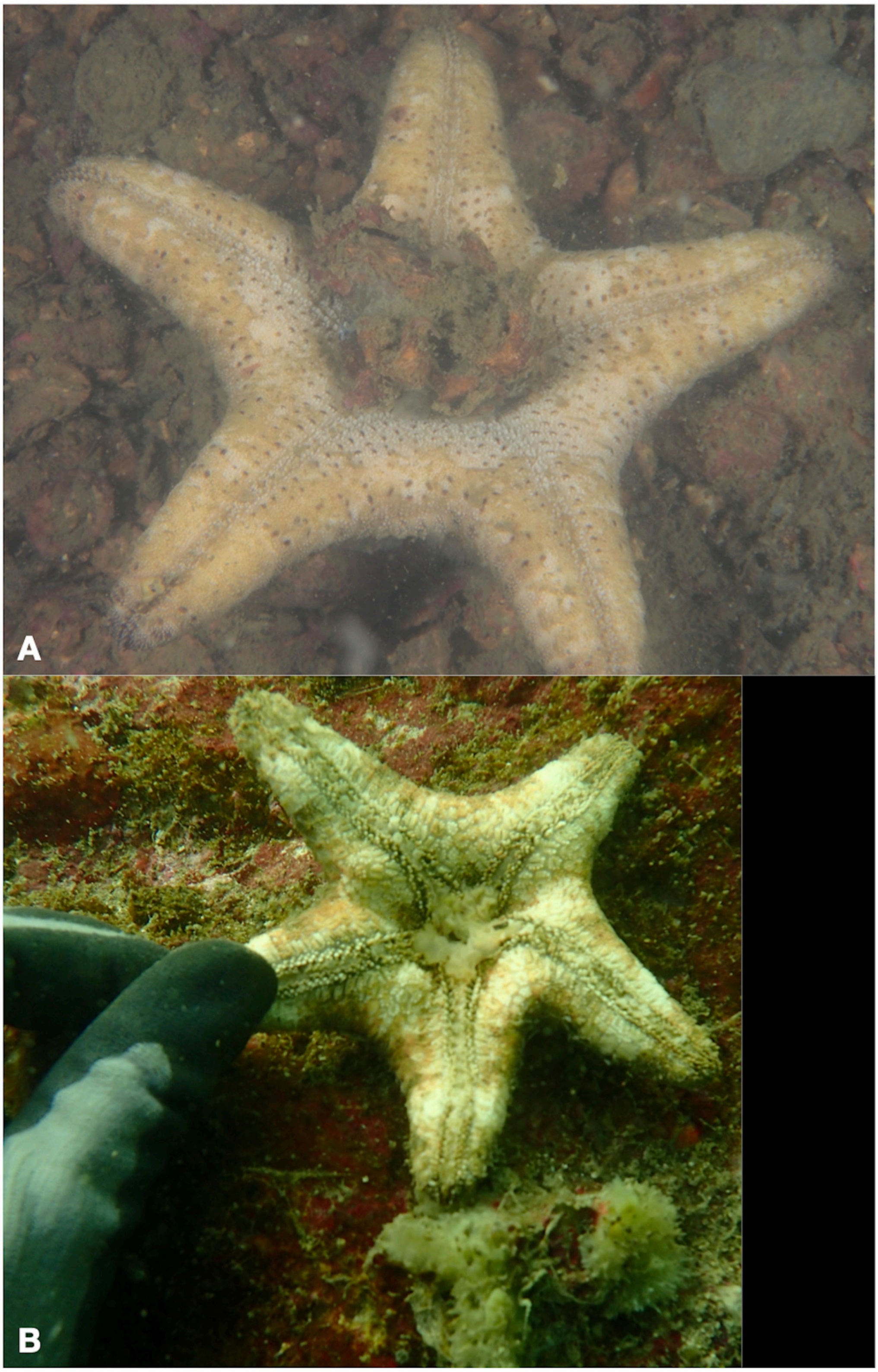

FIGURE 32. *Gymnanthenea difficilis* i*n situ* feeding, Hong Kong. A. *s*ponges and debris around oral region. Note darkened bivalve actinal pedicellariae. B. Sponges? around oral region. Photo credit: Sam Yiu.

A further complication was introduced by Liao and Clark (1995) who described *Anthenea difficilis* Liao and Clark which possessed "two adambulacral spine rows." This species was later moved to the genus *Gymnanthenea* by Fujita and Marsh (2002).

Distribution/Occurrence

Okinawa, Ryukyu Islands;Palau, Philippines, 6–61.0 m.

Description

Body stellate, R/r=1.8–2.2, planar in form, body surface flat (Fig. 31A). Arms triangular in shape, armtips upturned, interradial arcs weakly curved. Thin dermis covers body surface. Spines on distal marginals presents a serrated outline for each armtip. Lateral edge rounded.

Abactinal plates round to polygonal in shape, abutted forming flat surface (Fig. 31B). Abactinal plates flush with superomarginal plate surface. Abactinal surface covered by numerous small prick-like microspinelets, widely spaced, approximately 10–50, each less than half a millimeter in length. Microspinelets most widely spaced centrally but most heavily arranged around papulae, with some papular pores showing 10–15 microspinelets surrounding each pore. Other than these microspinelets, no large tubercles or other primary accessories present on abactinal surface on specimens up to R=3.5. Larger specimens at R>5.0, when denuded, plates show small glassy tubercles embedded in plate surface, approximately 10–60 per plate. Papulae two or three proximally on disk but decreasing to one distally along arm, present all over abactinal disk surface except for paired plates in each interradius. Each interradius with approximately 3 to 4 paired interradial plates (R=1.5 to R=3.0, respectively), closely articulated with no papulae present along each interradial midline. Interradial midline corresponds to contact between interradial superomarginals (Fig. 31A). These track from a single plate on the interradius of the primary circlet. Bivalve pedicellariae, two to four per radial section, each approximately 2.0 mm in length, occupying approximately 40% of the diameter of the plate on which it sits. Madreporite round, convex with well developed sulci, flanked by two plates. Anus with 6–8 spines, bent down over opening, approximately three or four plates present around opening.

Marginal plates 16–26 per interradius (arm tip to arm tip) at R=1.5 to R=3.0. Superomarginals and inferomarginals slightly offset with inferomarginals jutting out slightly beyond superomarginals. Superomarginals almost entirely dorsal-facing with very minimal lateral facing. Abactinal-lateral surface of superomarginal plates with short primary spinelets, relatively squat, 1 to 10. There are additionally to three to 15 smaller secondary tubercles with rounded tips which are flanked by 10–30 microspinelets identical to those on the abactinal plate surface. The distalmost along the arm of these primary spines along the superomarginal edge, is demonstrably larger than other accessories on the superomarginal plate surface, culminating in a distinctly large conical spine on the pre-terminal superomarginal plate (Fig. 31C). No pedicellariae observed on superomarginal plates. Inferomarginals wide, each with a large bivalve pedicellariae present (Fig. 31D) at variable oblique angles along the distance of the inferomarginal plate surface extending to the armtips. Pedicellariae flanked by 10–16 short spinelets (5 to 8 on either side of the pedicellariae). Upper surface of inferomarginal plate surface with enlarged, blunt conical spinelets, 2–5 rising above the surface of the inferomarginal plate surface and presenting the marginal plates with a serrated appearance. Remainder of inferomarginal plate with 10–20 short conical, spines, closer in size to those on marginal and acting plate surface. Irregularly, one or two plates missing a pedicellariae leaving an empty space filled with spinelets identical to those on the abactinal surface. Marginal plates when denuded show 20–50 small glassy tubercles identical to those on the abactinal plates. Spination and tubercles on inferomarginals dense, obscuring plate boundaries between inferomarginals and actinal plates. Terminal plate large, approximately the size of one of the adjacent superomarginals. Triangular in shape with three spines on the tip.

Actinal surface composed of two to three chevron like series (Fig. 31E) with several irregular plates present adjacent to inferomarginal plates. Actinal plates round to polygonal in shape, separated by distinct grooves. Each actinal plate with round bullet shaped granules, 4 to 15, widely spaced on each plate. Distinct trench-like space formed between actinal plates and inferomarginal plate boundary (Fig. 31E). Actinal plates with microspinelets similar to those on abactinal surface. Actinal series adjacent to adambulacral plates each a large prominent bivalve pedicellariae extending from the proximalmost, oral-adjacent plates to the armtip. Pedicellariae large, at oblique to transverse angles, bisecting approximately 30% of the plate on which they sit. A minority, approximately 2 to 6 of these plates lacking pedicellariae and instead with bullet-shaped granules identical to those on other actinal plate surfaces. Pedicellariae flanked by 12 to 20 pointed cylindrical granules some with slightly enlarged tips. Plate plus pedicellariae separated by grooves.

Furrow spines 3 to 6, mostly 4 or 5 proximally (Fig. 31F), spines decreasing until only two are present on plates adjacent to the terminus. Central furrow spines largest and thickest with those on either side of central spines shorter and narrower. Furrow spines palmate in arrangement. Subambulacral spines set off from furrow spines by discrete space. Primary subambulacral spine large, approximately twice to three times the thickness of the furrow spines with two smaller spines offset behind the primary larger subambulacral spine. These smaller spines 1/3 the length, approximately the thickness of the furrow spines or less. On the adambulacral adjacent to the oral plate these smaller spines are as thick as the primary subambulacral spine. Oral plate with 14 to 20 (10 on either side at R=3.0, 7 on either side at R=1.5) thick furrow spines enclosing the oral plate surface, each of these round in cross-section. The two paired furrow spines projecting into the mouth triangular in cross-section. Oral plate surface with 8 total thick spines (similar to the primary subambulacral spine) totaling 16 per paired

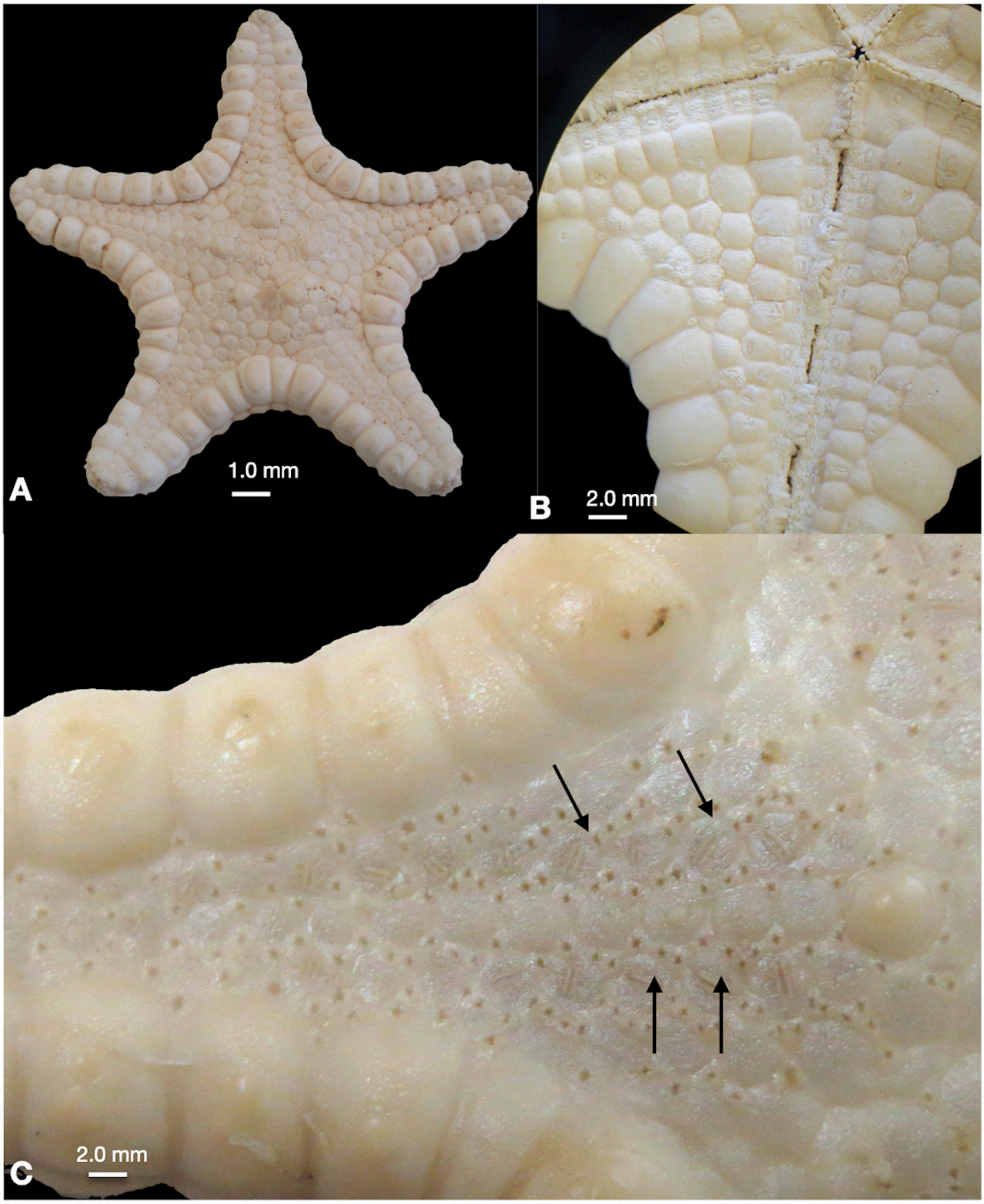

FIGURE 33. *Monachaster sanderi* WAM Z5556. A. Abactinal. B. Actinal view with closeup. C. MNHN IE-2007-5123.

plate at R=3.0. At R=1.5, there are 4 total spines, totaling 8 for the paired plates. A further 8 secondary oral spines (comparable to secondary subambulacral spines) per oral plate, totally 16 per pair sit along either side of the fissure between the paired oral plates.

Color in life variable, ranging from yellow or red on each arm with white interradii to orange, white or grey with speckled grey. A range of colors is documented in Saba *et al*. (2002).

Philippine Variation (at R=4.6 cm)

Abactinal surface with prominent, single tubercular spines on radial regions, bivalve pedicellariae also more abundant, 2 to 6 per arm, than in Japanese specimens where pedicellariae are few to absent at R=3.5 or less.

Superomarginal plates with 2 to 7 prominent spines or tubercles, approximately 3x the size of granules, 10 to 12 on the superomarginal plate surface. Spines becoming more conical and spine-like along the arm with the distalmost superomarginal plates bearing two elongate, pointed spines. Inferomarginal spines, 2 to 7, similarly with much more elongate, prominent spines distally along the arm especially adjacent to the arm tip with accessories on inferomarginal plates more granular or tubercular proximally, especially interradially.

Actinal and furrow characters are similar to those on Okinawan specimens.

Palau Islands Variation

Abactinal surface with single, prominent tubercular spine on proximal most carinal series (absent in Japanese specimens).

Superomarginal spines, 5 to 8 on specimens from Palau (CAS 107524) show a much more distinct, elongate conical shape with 6 to 10 smaller granules on superomarginal plate surface. Japanese specimens with a much more squat cone-like shape. Inferomarginal spines also much more elongate and conical versus those on Japanese specimens which are rounder and more tuberculate.

Granules on actinal surface appear more crowded than those on Japanese specimens with actinal plates narrowing and "pinching out" approximately six marginal plates away from armtip.

Furrow spines six to seven, in fan-like arrangement, weakly webbed at base. Subambulacral spine, distinct pointed, conical and elongate with two small granules on either side of the spine. Most adambulacral plates with one subambulacral spine, a minority of them with two. Japanese specimens with more blunt, almost tubercular subambulacral spine. Subambulacral set apart from furrow spines by discrete space. Japanese specimens more crowded relative to the subambulacral spines.

Material Examined

Japan. Holotype. USNM E45263, Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan. 26.5, 127.848, 40–46 m. Coll. R.F. Bolland, 8 May 1995. 1 dry spec. R=3.7 r=1.6. **Paratypes.** USNM E45262, 1.3 km ENE of Maeki-Zaki, Seragaki Beach, Okinawa, Ryukyu Islands, 26.5067, 127.877, 6.1 m. Coll,. R.F. Bolland, 12 March 1989. 1 dry spec. R=2.7 r=1.2.

USNM E45279 Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan. 26.5, 127.848, 52 m. Coll. R.F., Bolland, 4 Oct 1986. 2 dry specs. R=2.4 r=1.1, R=2.5 r=1.1.

USNM E45280, 1.3 km ENE of Maeki-Zaki, Seragaki Beach, Okinawa, Japan. 26.5067, 127.877. 6.1 m. Coll. R.F. Bolland, 2 April 1989. 1 dry spec. R=3.2 r=1.4.

USNM E46162 Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan. 26.5, 127.848, 52 m. Coll. R.F. Bolland 29 March 1981. 1 dry spec. R=1.4 r=0.7

USNM E46166 Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan. 26.5067, 127.877, 43 m. Coll. R.F. Bolland 18 Dec. 1995. 1 dry spec. R=2.2 r=1.0.

USNM E53608 1.3 km ENE of Maeki-Zaki, Seragaki Beach, Okinawa, Ryukyu Islands 26.5067, 127.877, 49 m. Coll. R.F. Bolland 12 June 1984 1 dry spec. R=1.2 r=0.5.

USNM E53614, Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan. 26.5, 127.848, 0–61 m. Coll. R.F. Bolland, 15 March 2001. 1 dry spec. R=2.8 r=1.4.

USNM E53615, Horseshoe Cliffs, 1 km WNW of Onna Village, Ryukyu Islands, Okinawa, Japan. 26.5, 127.848, 52–58 m. Coll. R.F. Bolland, 1 dry spec. R=1.1 r=0.6.

USNM 1740290 1 km WNW of Onna Village, Horseshoe Cliffs, Okinawa, 26.5 127.848, 64.0 m, Coll. R.F. Bolland 1 dry spec. R=0.7 r=0.4.

CASIZ 106980 Uken, Okinawa, Ryukyu Islands. Coll. M. Yamaguchi, 13 Nov. 1987. 1 dry spec. R=5.3 r=2.0

CASIZ 106971 Makiminato, Okinawa, Ryukyu Islands. Coll. M. Yamaguchi, 13 May 1982. 1 dry spec. R=3.7 r=1.4.

Palau. CASIZ 107524, Reef flat, Ngederrak Reef, Koror, Palau. Caroline Islands, 1–2 feet. Coll. G.C. Williams 10 Jan. 2017. 1 wet spec. R=3.2 r=1.4.

CASIZ 107525, Sea grass beds, sand flats, on south side of Malakai Channel, Ngederrak Reef, Koror, Palau. Caroline Islands. 1–4 m (3 to 12 feet). Coll. G.C. Williams 19 Sept. 1996. 1 wet spec. R=2.7 r=1.3.

Philippines. CASIZ 167873. Philippines. Coll. T. Gosliner. 1 wet spec. R=4.6 r=1.8.

CASIZ 217963. On coral rubble, Muriel's Rock (Kitchen Rock) Maricaban Island. Batangas, Luzon Island. Philippines. Coll. C. Piotrowski, 20 April 2016. 1 wet spec. R=1.1 r=0.5.

Culcita schmideliana (Bruzelius, 1805)

FIGURE 34A–C

Asterias schmideliana Bruzelius, 1805: 11.

Culcita schmideliana Gray, 1840: 276; Perrier, 1875: 266 (74); Doderlein, 1896: 315 (with varieties); Simpson & Brown, 1910: 53; Clark & Rowe, 1971: 41; Jangoux, 1973: 18; A.M, Clark & Courtman-Stock, 1976: 67; Marsh & Marshall, 1983: 675; Jangoux, 1985: 31; Rowe & Gates, 1995: 99; Marsh & Fromont, 2020: 402.

Diagnosis

Distinct papular free area laterally adjacent to the marginal plates. Distinct prominent tubercles and/or spines present on the skeletal ridges between the papular regions, lacking armament on the papular regions. Pedicellariae variably present on actinal surface (Fig 34B–C). (Modified from Marsh & Fromont 2020)

Comments

Figure 34A–C shows a smaller individual (USNM E47982) prior to its transformation to the large, cushion-shaped form which shows a difference in abundance of bivalve pedicellariae on the actinal surface. Bivalve pedicellariae are small and show a relatively low abundance over the surface.

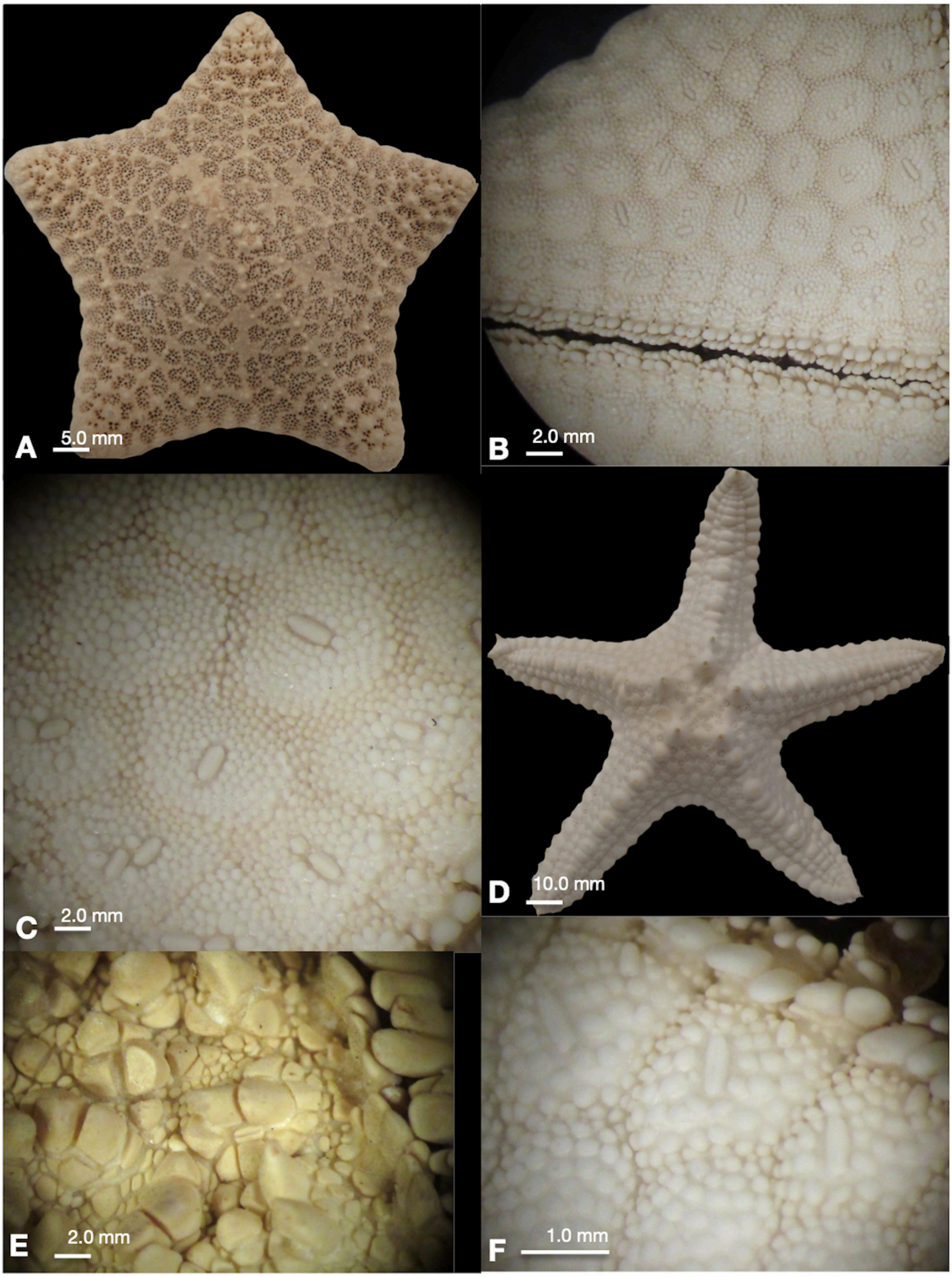

FIGURE 34. Bivalve Pedicellariae Oreasteridae. A. *Culcita schmideliana* USNM E47982 Abactinal B. Actinal and furrow region. C. Closeup on pedicellariae on actinal plates. D. Abactinal *Pentaceraster alveolatus*, USNM E45440 E. Pedicellariae on larger individual, USNM E 09956, F. Pedicellariae, adjacent to adambulacral plates, smaller individual (E45440).

Prey of this species has been listed as hard and soft corals, echinoids, encrusting sponges, ascidians, and algal biofilm on reef sand or seagrass substrates (Marsh and Fromont 2020).

Distribution/Occurrence
Primarily Western Indian Ocean, east Africa, including Madagascar, Maldives, to the Lakshadweep Islands, Indonesia, north east coast of Australia Western Australia to New Townsland and Cocos (Keeling) Islands. 0–92 m.

Material Examined
USNM E47982, Mombasa, Kenya, Indian Ocean. -4.08 39.68, Coll. S.A. Earle, 18 Nov 1964, RV *Anton Bruun*. R=3,5 r=2.3.

Gymnanthenea H.L. Clark, 1938

Diagnosis
Overall morphology similar to *Anthenea*, but displaying 2 rather than 3 furrow spine series. Tubercles present on abactinal surface. Bivalve pedicellariae present on actinal surface (Modified from Marsh and Fromont 2020).

Comments
A genus containing only 3 species diagnosed primarily by the presence of 2 rather than 3 furrow spines with relatively few other characters that apparently support a separate genus *Gymnanthenea*. Many of the species assigned to *Gymnanthenea* are morphologically similar to those in *Anthenea*. It is unclear if subsequent treatments demonstrating greater variation and additional data will support its validity.

*Gymnanthenea difficilis (*Liao & Clark, 1995)
FIGURE 32A–B

Anthenea flavescens Chen, 1932: 67; A.M. Clark, 1982: 487, 490 [non *A. flavescens* (Gray 1840)].
Anthenea pentagonula Chang, Liao et a. 1964: 53 [non *A. pentagonula* Doderlein, 1915].
Anthenea difficilis Liao in Liao & Clark, 1995: 99.
Gymnanthenea difficilis Fujita & Marsh 2002: 162, 170, Fig. 5; Yiu & Mah 2024: 56.

Diagnosis
Body stellate (R/r=2.38), arms triangular, wide at base, interradial arcs curved. Disk and arms thickened. Body surface covered by thick dermis. Armtips upturned, overall shape curved, terminating at a fine point. Abactinal surface covered by dermis with widely spaced coarse granules. Skeleton reticulate. Granules larger, most widely spaced on distalmost arm surface but most coarse surrounding papular pore regions along arms. Papular pores, 6 to 30, present on disk and arms, but absent interradially. Carinal series composed of one or two conical spines per plate, 11 to 16 along each arm at R=6.2, with largest spines present proximally, tapering out at approximately 80% of distance along the arm before the tip. Large bivalve pedicellariae, approximately 1–2 mm in length, each flanked by 4 to 6 blunt spines. Marginal plates, approximately 28–30 per interradius (15 along each arm), call covered by thick dermis. Superomarginals with large, round tubercles, 1 to 4 with 6 to 40 smaller tubercles (approximately 20% of the size of larger tubercles) present on the plate surface. No pedicellariae observed on superomarginals. Inferomarginal plates covered by large, round tubercles, up to 40 on plate surface. One large bivalve pedicellariae bisecting plate at an oblique angle flanked by tubercles.

Actinal surface composed of quadrate to polygonal plates in chevron-like formation in 3 to 4 incomplete series. Surface covered by coarse conical, weakly pointed granules, 6 to 15, close-set, irregularly arranged. Large bivalve pedicellariae, 6 to 8 present on intermediate plates, each approximately 2 mm in length. Actinal plate series adjacent to adambulacral plates each with a large bivalve pedicellariae. Furrow spines 5 to 6, webbed, subambulacral spines in 2 irregularly arranged rows.

Comments
A species assigned to *Gymnanthenea* by Fujita & Marsh (2002) following identification of 2 rather than 3 series of subambulacral spine series. This species is one of two prominent "*Anthenea*-like" oreasterids in Hong Kong (Yiu & Mah 2024).

Distribution/Occurrence
Hong Kong. Southern China, Guangdong and Fujian Province. "shallow water" Observed on rocky wall, 3–20 m.

Material Examined
USNM 3036 Hong Kong, China. Coll. W. Stimpson. 3 wet specs. R=5.8 r=2.6 R= 6.1 r=2.8 R=5.1 r=2.4.

CASIZ 308834, on rock. Breaker reef in Mirs Bay NE of Hong Kong Island, Hong Kong, China, 22º27.78'N, 114º25.11'E. 3 m. Coll. Coral Reef Research Foundation, 4 Oct. 1994 1 wet spec. R=6.2 r=2.6.

Monachaster Döderlein, 1916

Döderlein, 1916: 412; 1935: 103; Clark & Rowe 1971: 48; Tortonese 1976: 271; A.M. Clark 1993: 304; Mah 2018: 65.

Diagnosis. Monotypic, as for species.

Comments
Although placed within the Goniasteridae by Mah (2018), molecular data (Mah & Foltz, 2011) showed *Monachaster* as a member of the Oreasteridae rather than the Goniasteridae with possible close affinity to *Asteropsis* and the Asteropseidae.

Monachaster sanderi (Meissner, 1892)
FIGURE 33A–C

Goniodiscus Meissner, 1892: 185; Ludwig, 1899: 539

Monachaster sanderi Döderlein, 1916: 412; 1935: 103; Clark & Rowe, 1971; 48; Tortonese, 1976: 272; 1980: 113; Walenkamp, 1990: 32; Gosliner *et al*., 1996: 256; Mah, 2018: 65.

Monachaster umbonatus Macan, 1938: 399; Tortonese, 1949: 31

Diagnosis

Body weakly stellate to stellate (R/r=1.6–1.8). Abactinal, marginal, actinal surface covered by low, closely distributed granules. Abactinal regions variably with large, conical tubercles along radial regions. Superomarginals with large, quadrate bald patches (Fig. 33C). Furrow spines four or five in straight series (Fig. 32B). Subambulacral variably present or absent. Bivalve pedicellariae present on abactinal (Fig. 33C) and actinal surface (Fig. 33B).

Comments

Bivalve pedicellariae in this species were observed to be variable across different populations. A new occurrence of Australian specimens of this species shows pedicellariae present regularly along the adambulacral series as well as on the abactinal surface, but more irregularly on plates in the actinal intermediate region. In contrast, specimens examined from Madagascar show pedicellariae to be more abundant around the papular regions on the abactinal surface (Fig. 33C), but were smaller and less abundant on the actinal surface (Döderlein, 1916, 1935).

Distribution/Occurrence

Enderby Island, Dampier Archipelago, Western Australia, Mozambique (Inhaca Island), Madagascar, Tanzania, Somalia, Red Sea to the Gulf of Suez, 2–68 m.

Material Examined

WAM Z5556 Enderby Island, Dampier Archipelago, Western Australia. 20º35.15'S 116º35.62'E, 17 m. Coll. S. Morrison *et al*., 2 Sept. 1999. 1 dry spec.

MNHN-IE-2007-5123 Madagascar, 25° 12.6 'S, 44° 8.6' E, 13–27 m. Coll. ATIMO VATAE TA 21, JS-195. 1 wet spec. R=5.0, r=3.0.

Pentaceraster Döderlein, 1916

Döderlein, 1916: 424; 1936: 331; Clark & Rowe, 1971: 55; A.M. Clark, 1993: 310 (checklist).

Diagnosis

Body stellate (R/r=2.0–3.0, seldom >3.0) with strongly arched disk, elongate, triangular arms.

Distal abactinal, actinal and especially marginal plates covered with distinct, even sized, projecting granules. Abactinal-lateral regions with distinctly reticulate plates showing well-defined pore areas. Primary plates with spines or conical tubercles arranged in longitudinal series in most species. Distal inferomarginal plates with an enlarged spine or conical projection in most species. Intermarginal pore areas weakly developed or absent. Modified from Marsh and Fromont (2020).

Comments

As summarized elsewhere (e.g. Mah 2023, Marsh & Fromont 2020) *Pentaceraster* is a commonly encountered, widely occurring oreasterid primarily from tropical Indo-Pacific shallow to mesophotic settings. There are approximately 15 species, several of which display difficult taxonomic boundaries. Morphological variation for spination and other characters is widespread but bivalve pedicellariae do not appear to be prominent. Marsh and Fromont (2020) for example, do not list them as an identifying diagnostic character for *Pentaceraster* but do indicate bivalve pedicellariae throughout Australian species, referring to them as small in size or as weakly developed.

Pentaceraster alveolatus (Perrier, 1875)

FIGURE 34D–F

Pentaceros Perrier, 1875: 243 (1876: 59); Koehler, 1910: 95.

*Oreaste*r Bell, 1884: 73; Domantay & Roxas, 1938: 212.

Pentaceraster Döderlein, 1916: 428; Jangoux, 1986: 126; Kohtsuka *et al*., 2019: 2020: 58.

Diagnosis

Primary circlet and carinal series bearing large, conical spines, dorsolateral armament present primarily on the disk. Superomarginals and inferomarginals with prominent spines. Spination on disk and arms variably absent to abundant with lateral regions on disk and arms. Arms slender and elongate. Based on Marsh and Fromont (2020), Clark and Rowe (1970).

Comments

Pedicellariae are few and observed primarily on the actinal surface. They vary in size across taxa and relative to the development of adjacent accessories, such as granules or spines (Fig. 34E–F).

Distribution/Occurrence

Widely occurring throughout the Indo-Pacific. Southern Japan, China, Guam, New Caledonia, Samoa, Indonesia, Philippines, Western Australia (single occurrence), 1–54 m.

Range & depth extension. Somalia, 60–70 m.

Material Examined

USNM E37286 SW of Gas Jinnah, Somalia, Indian Ocean. 9.68 51.05, 60–70 m. Coll. R/V Anton Bruun, 16 Dec. 1964. 1 dry spec. R=12.1 r=3.9

ASTEROPSEIDAE Hotchkiss & Clark, 1976

Diagnosis

Body stellate, covered by a thickened dermis obscuring the skeleton. Abactinal skeleton variably imbricating, reticulate or apparently tessellate in juveniles. Plates with or without spines.Pedicellariae, when present are bivalve, granuliform, or elongate and tong-shaped. Marginal plates well-developed with actinal plates in longitudinal series parallel to the ambulacral groove. (Modified from Marsh & Fromont 2020)

Comments
A family of five genera, *Asteropsis, Dermasterias, Petricia*, *Poraniella*, and *Valvaster*. Studies of morphological data have supported *Valvaster* as a member of the Asteropseidae (Blake, 1980, 1987) but other overviews of the Valvatida have suggested that the Asteropseidae is likely paraphyletic, grouped largely owing to the strongly developed dermal covering over the test and its apparently homoplastic presence in other groups, such as the Poraniidae and the Asterinidae (Hotchkiss & A.M. Clark, 1976; A.M. Clark, 1984). For example, molecular phylogenetic data indicate *Dermasterias* to be phylogenetically distant to *Asteropsis* and *Petricia,* which show close affinity to the Oreasteridae (Mah & Foltz 2011). The phylogenetic status of *Poraniella* is currently unknown.

Petricia Gray, 1847

Petricia vernicina (Lamarck, 1816)
FIGURE 35 A, C

Asteropsis vernicina Lamarck, 1816:554.
Petricia punctata Gray, 1847: 81.
Asteropsis imperialis Farquhar, 1897: 193, pl. 13; Benham, 1911: 141.
Petricia vernicina Fisher, 1908: 357; H.L. Clark, 1946: 110; Rowe, 1989: 290; A.M. Clark 1993:321; H.E.S. Clark & McKnight, 2001: 181.
Pectria imperialis [sic] McKnight 1968: 506.
Petricia imperialis H.E.S. Clark, 1970: 5; Keable & Reid, 2015: 248, 273.

Diagnosis
Body form stellate, R/r=1.8–2.8), surface smooth, covered by thick, rubbery dermis with no granules, spines or other accessories. Abactinal skeleton reticulate, individual plates close fitting, plates lobate, separated in larger individuals. Large bivalve pedicellariae commonly but not always present in each interradius and on a minority of specimens on each abactinal and actinal surfaces. Abactinal plates lobate or irregular. Furrow spines 2, subambulacral spines 1 to 2 [modified from Marsh & Fromont (2020) and H.E.S. Clark & McKnight (2001)].

Comments
Petricia is currently considered monotypic, including only *Petricia vernicina* (Lamarck, 1816). A second species, *Petricia imperialis* (Farquhar, 1897) from the Kermadec Islands was synonymized without explanation by H.E.S. Clark & McKnight (2001) with disagreement by Keable & Reid (2015). However, Farquhar's original description of *P. imperialis* was based on the presence of bivalve pedicellariae, which occur variably in *P, verncina* and does not serve as consistent differentiation for a separate species, supporting Clark & McKnight's decision to synonymize *P. imperialis*.

Distribution/Occurrence
Australia, New Zealand and Kermadec Islands, 0–70 m.

Comments on Pedicellariae
Petricia vernicina possess prominent, but very few bivalve pedicellariae (Fig. 35C), located primarily in each interradius. Marsh & Fromont (2020) reported that 76% of this species' diet consists of encrusting sponges, bryozoans, colonial ascidians and coralline algae. Pedicellariae are seldom reported as present on the oral surface, although Marsh & Fromont (2020) do report them from "near the mouth" in some individuals.

Material Examined
Petricia vernicina USNM E14289, Near Manly Dobroyd Head, New South Wales, Australia. 12.2 m. Coll. C. Prigge, June 1967. 1 dry spec.

Valvaster Perrier, 1875

Diagnosis & Comments. Monotypic, as for species

Valvaster striatus (Lamarck, 1816)
FIGURE 35 B, D, E

Asterias striatus Lamarck, 1816: 564.
Asteracanthion striatus Muller & Troschel, 1842: 18.
Valvaster striatus Perrier, 1875: 112 (376); de Loriol, 1885: 11; Fisher 1906: 1093; Koehler, 1910: 175; Clark & Rowe, 1971: 71; Marsh, 1974: 94; Blake, 1980: 165; Marsh & Fromont 2020: 217.
Valvaster spinifera H.L. Clark, 1921: 102 pl. 6, fig. 6, pl. 36, figs 8–9; 1946; 151.

Diagnosis
Modified from Marsh & Fromont (2020). Body stellate, arms triangular. Abactinal plates form reticulate skeleton with individual plates bearing conical spines up to 3.0 mm in length presenting a bristling abactinal surface. Pincer like pedicellariae among spines. Superomarginal plates prominent, each with a single large bivalve pedicellariae (but absent in small specimens). Inferomarginal plates bear a prominent single spine and accessory spines. Actinal plates with heterogeneous spines, large and small. Furrow spines, 4 to 5, with a single subambulacral spine for a plate.

Pedicellariae in *Valvaster striatus*
Marsh & Fromont (2020) have described *Valvaster striatus* with a pedicellaria on every superomarginal plate, but examination of further specimens listed herein shows that while at least a single pedicellariae is present along the superomarginal arm series (Fig. 35D–E), their presence is not as numerous as described elsewhere (e.g. Marsh & Fromont, 2020). Pedicellariae in *V. striatus* has

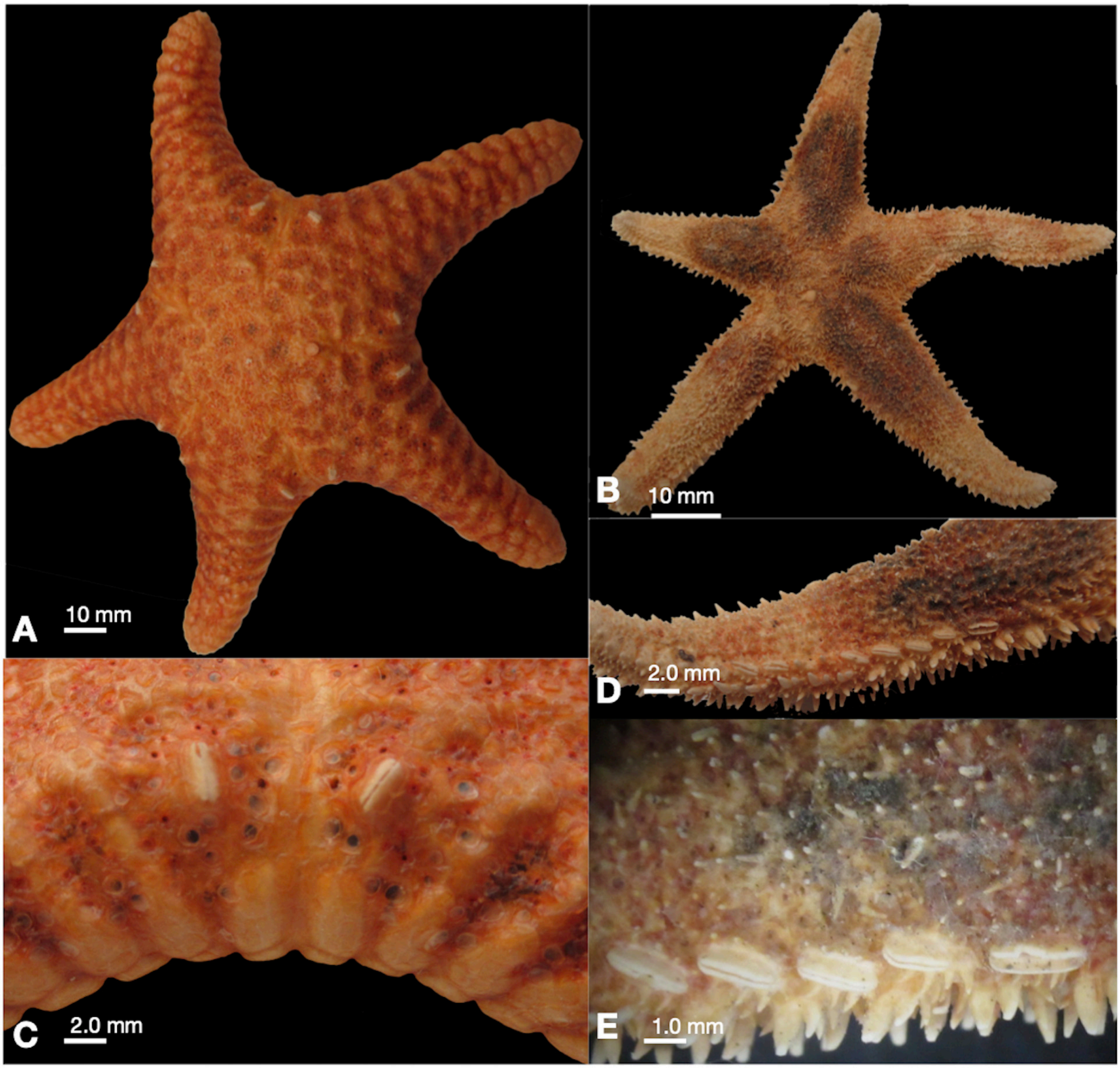

FIGURE 35. Asteropseidae. *Petricia vernicina* USNM E14289 A. Abactinal C. Closeup on pedicellariae. *Valvaster striatus* USNM E42760 B. Abactinal. D. Lateral view showing marginal pedicellariae. E. Closeup of pedicellariae.

been largely utilized as a taxonomic character in literature reviewed (e.g. Marsh & Fromont, 2020; Clark & Rowe, 1971).

Valvaster has shown close affinity with the Oreasteridae, shown initially from morphology (e.g. Blake, 1979) and later from molecular data (Collin *et al.*, 2020).

Distribution

Valvaster striatus. Widespread throughout the Indo-Pacific. Hawaiian Islands, Okinawa, Fuji, New Caledonia, Philippines, Papua New Guinea, Australia, including Western Australia, Timor Sea, Torres Strait, Great Barrier Reef, Bay of Bengal, Mauritius. 0–58.0 m.

Material Examined

USNM E42760. Reef slope off Avarua, Rarotonga Island, Cook Islands, South Pacific.

12–15 m. Coll. B. McCormack, 25 Sept. 1984, 2 dry specs. R=6.3 r=1.5; R=6.2 r=1.7.

USNM E44861 1.3 km East north east of Maekizaki, Seragaki Beach, Okinawa, Ryukyu Islands, 26.5067 N 127.877 E, 36.6 m. Coll. R.F. Bolland, 3 Sept 1989, 2 dry specs.

USNM E45007 1.0 km WNW of Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands. 26.5 N 127.848 E, 58.0 m. Coll. R.F. Bolland, 13 June 1987. 1 wet spec.

USNM E44965 1.0 km WNW of Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands. 26.5 N 127.848 E, 42.7 m. Coll. R.F. Bolland, 7 Jan 1985. 1 dry spec. R=2.1 r=0.7.

ODONTASTERIDAE

Diagnosis

Body shape pentagonal to strongly stellate. Abactinal plates variably convex and flat ranging to paxillate or tabulate with surface covered by accessories, variably granules or spinelets. Papulae single, limited to abactinal surface. No enlarged spines. Marginal plates blocky, quadrate in shape; appearing variably as a wide distinct border around body periphery to a narrow, lateral-facing series present along a crenulate actinolateral-ridge. Marginal plate accessories, ranging from granules to spinelets, present in some species in high density, abundance. Actinal plates in chevron-like formation, intermediate areas variable in size. Actinal plate accessories variably granules to spinelets. Spines on adambulacral plates in most with transverse series. No superambulacral plates. Most genera with one or two large hyaline-tipped recurved spine or spines on the oral plate. These spines absent in *Hoplaster* and *Diabocilla*.

Comments

The Odontasteridae is a small family containing six genera with most diversity present in the Southern Hemisphere, especially at high-latitudes, although some deep-sea species of *Odontaster* do occur in the Northern Hemisphere. Outside of *Acodontaster*, pedicellariae, if present are simple.

Many members of the Odontasteridae superficially resemble goniasterids as marginal plates are large and blocky and body form is pentagonal in such genera as *Odontaster* and *Hoplaster,* but surfaces are often paxillate or covered by spinelets or granules. Molecular data supports the Odontasteridae as monophyletic on a sister clade to a larger clade containing the Goniasteridae, Asterinidae, and Oreasteridae (Mah & Foltz 2011).

Acodontaster Verrill, 1899

Gnathaster (part) Sladen 1889: 285.
Acodontaster Verrill, 1899: 204; Fisher, 1904: 109 (type *Gnathaster elongatus* Sladen).
Heuresaster Bell, 1908: 8 (type *H. hodsoni* Bell).
Pseudontaster Koehler, 1912: 85 (type *P. marginatus* Koehler).
Odontaster (part) Koehler, 1912 (*et al.*).
Metaodontaster Koehler, 1920: 191, 193 (type *M. waitei* Koehler).
Tridontaster Koehler, 1920: 191, 193 (type *T. laseroni* Koehler).

Diagnosis

Body stellate to strongly stellate. Abactinal plates flat to weakly convex, covered primarily by dense granulation. Papulae restricted to a central region with a patch in each radius; each jaw with only a single recurved spine, variably with smaller, paired accessory spines. Pedicellariae present but variable among genera. (modified from Clark & Downey, 1992).

Comments

Acodontaster is a genus containing five species present almost entirely at high latitudes, especially in the Antarctic where some species have been shown to be ecologically significant, as sponge predators (e.g. Dayton *et al.* 1974). A survey of *Acodontaster* did not immediately show other species with pedicellariae other than *Acodontaster conspicuus*, but a review of species suggests that some species concepts (e.g., A.M. Clark, 1962; Fisher, 1940) are overlapping and a further overview is desirable.

Acodontaster conspicuus (Koehler, 1920)

FIGURE 36A–E

Pseudontaster conspicuus Koehler, 1920: 202, pl. 42, figs. 1–7; pl. 43, figs. 1–10, pl. 70, fig. 1; Koehler 1923: 88, pl. 13, figs. 4–6.
Acodontaster elongatus var. *abbreviatus* Koehler, 1923: 81, pl. 10, figs. 1–3.
Metadontaster waitei Koehler, 1920: 219–226, pl. xlvi, figs. 1–6, pl. xlvii, figs. 5–6, pl. xlviii, fig. 8, pl. lxxi, figs 1–2.
?*Pseudontaster conspicuus* (part) Koehler, 1920: 203, 208, pl. xlii, figs. 3–4, pl. xliii, fig. 2.
Acodontaster waitei Fisher 1940: 114–115; A.M. Clark 1962: 21.

Diagnosis

A species distinguished by the presence of primarily 3 to 4 part with large granuliform, angular valves variably distributed on the abactinal, marginal, and actinal surfaces. On the actinal surfaces these are present in proximity to the oral region and adjacent to the adambulacral plates and furrow spine series.

Comments

Acodontaster conspicuus is the only *Acodontaster* species known that displays pedicellariae, each with 2 to 4, mostly 3, angular granuliform valves. Fisher (1940) has remarked on their resemblance to flat-topped granules and is reminiscent of Agassiz's (1873) comments that pedicellariae are homologous with, and derived from granules, an abundance character on the surface of *Acodontaster*. Although the multiple valves would seem to discount them as being considered as bivalve, valve number varies with a minority of pedicellariae bearing only 2 valves (Fig. 36D), but up to 4. Pedicellariae appearance also shares a resemblance with bivalve pedicellariae in the Goniasteridae. Jangoux & Lambert (1987) also observed similarity between the pedicellariae in this species and that of the goniasterid *Chitonaster johannae*.

Pedicellariae position in *A. conspicuus* is highly variable, but has been observed on abactinal, marginal, and actinal plate surfaces (Fig. 36B, D, E). Actinal pedicellariae location is similar to those in the Goniasteridae and Oreasteridae with pedicellariae present proximally near the mouth and present adjacent to and on either side of the adambulacral plate series as well as on the surface of the superomarginal and inferomarginal plate surfaces. Unusual to *A. conspicuus* is that on USNM 11047631 pedicellariae are also present along the radii of each arm on the abactinal surface, an unusual location for pedicellariae of any type within the Valvatacea.

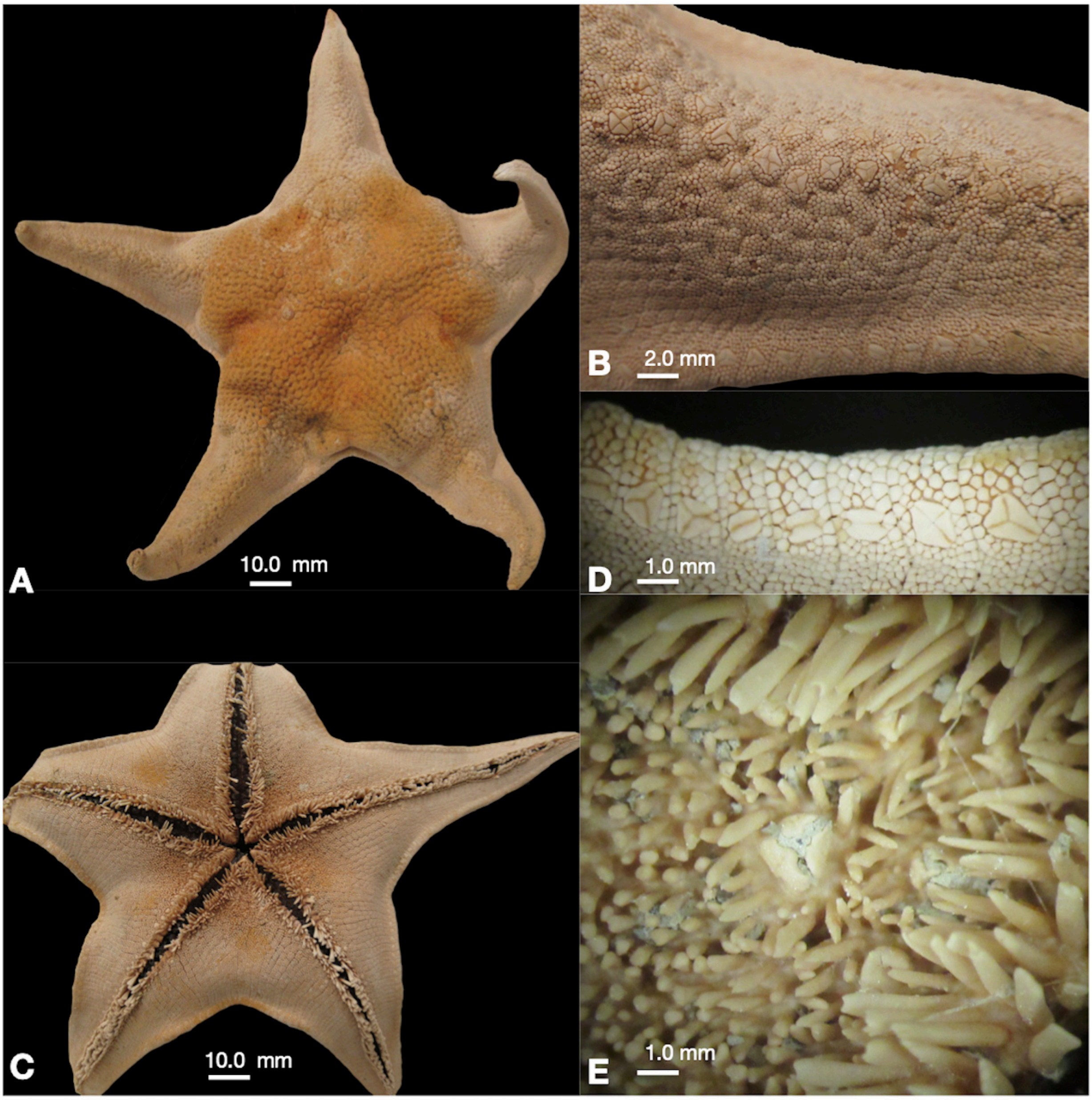

FIGURE 36. Odontasteridae. *Acodontaster conspicuus*. A. Abactinal. B. Abactinal surface with pedicellariae along radius, superomarginal plates. C. Actinal D. Pedicellariae with grey sediment or other material proximal to mouth on actinal intermediate plate.

Distribution

South Sandwich Islands, Antarctic Peninsula, Adelie Land, Graham Land, Victoria Land (Ross Sea), 25–664 m

Material Examined

USNM E13691 NE of Joinville Island, Antarctic Peninsula, Southern Ocean, -62.683 -54.717, 210–220 m. Coll. RV *Eltanin*, 15 March 1964. 5 dry specs.

USNM E13705 "*A. waitei*" Off Vassal Bay, Queen Maud Land, Weddell Sea, Southern Ocean, -77.67 -35.5, 393 m. Coll. RV *Edisto*, 28 Jan 1959. 1 dry spec. R=14.0 cm r=5.0 cm.

USNM 1082938 east of Roosevelt Island, Ross Sea, Southern Ocean, -78.383 -173.067, 473–475 m. Coll. RV *Eltanin*, 26 Jan 1968. 1 dry spec. R=8.3 r=3.0.

USNM 1121457

Discussion

Bivalve Pedicellariae Distribution Trends (Summarized in Table 1)

Clustered

Among the most conspicuous of groupings are those taxa with pedicellariae distribution and abundance identified as "clustered," a group observed only in the Goniasteridae.

This arrangement places large and/or prominent bivalve pedicellariae in abundance and in close arrangement, most often centrally on the actinal intermediate surface, notably adjacent to the mouth with relatively few or absent bivalve pedicellariae elsewhere on the same surface (e.g. Fig. 3B, 13B–F). Clustered bivalve pedicellariae have not been observed on the abactinal or marginal plate surfaces. This includes *Anthenoides peircei*, *Astrophylax* **gen. nov.**, *Eknomiaster beccae*, *Chitonaster felli*, and the two the *Fromia* species with pedicellariae. *Fromia baruna* **sp. nov.** and *Fromia eusticha.*

Abundantly Distributed

The most frequently encountered pattern of bivalve, or indeed most pedicellariae distribution/abundance is described as "abundant" or "numerous." Bivalve pedicellariae are prominent on a majority of plates including on one or multiple plate surfaces, i.e., abactinal, marginal, actinal plates (e.g. Fig. 12A–B). The most common expression would be those taxa showing large or otherwise distinct bivalve pedicellariae on the actinal plate surface (e.g. Fig. 11A–D, 29A–G, 30A–G) seen in most taxa on plates adjacent to the adambulacral plate series along the tube foot groove (e.g., Fig. 30E, F, G) but also on plates close to or adjacent to the mouth (e.g., Fig. 26B, 36E). Pedicellariae are consistently observed in these two locations in the Goniasteridae, Oreasteridae, and the Odontasteridae.

This pattern is observed frequently throughout the Goniasteridae, nearly always with the actinal surface displaying bivalve pedicellariae on several or nearly every actinal plate with few to no pedicellariae on the abactinal or marginal surfaces. Examples include *Wallastra elenderae* (Fig. 11B–D)*, Circeaster americanus* (Fig. 19A–C) or *Cladaster katafractarius* . *Akelbaster novaecaledonia*e has a pedicellariae sitting in its alveolus apparently replacing nearly every actinal plate (Fig. 12B), in addition to a single bivalve pedicellariae present on all superomarginal and inferomarginal plates.

Where bivalve pedicellariae are abundant on the actinal surface some taxa also have bivalve pedicellariae abundantly present on abactinal and marginal surfaces. Extreme forms might include the hippasterine *Gilbertaster,* which shows elongate bivalve pedicellariae on nearly all body surfaces (Fig. 20A–D) save for a small minority of small actinal intermediate plates. Many species of hippasterines, especially *Hippasteria* show abundant bivalve pedicellariae (e.g. Fig. 24) present the abactinal, marginal and actinal plate surfaces, although not as completely as on *Gilbertaster*. Pedicellariae in the odontasterid *Acodontaster conspicuus* also has widely distributed pedicellariae on abactinal, marginal, and actinal surfaces in some abundance, but not comparable to those in *Gilbertaster*.

"Abundant" bivalve pedicellariae patterns are less frequently observed across the Oreasteridae, but primarily on"goniasterid" analogs such as *Anthenea* and the related *Gymnanthenea* (Fig. 31D–F)*, Anthaster* (Fig. 27C–D), and to a lesser extent *Monachaster* where they occur largely on the actinal surface (Fig. 33B–C). Among the more "arched" oreasterids, the deeper occurring *Acheronaster* (Fig. 26B–D) has multiple numbers of pedicellariae on a single plate.

Few Present

There are pedicellariae whose presence are described as "few" or more weakly present. This group shows very few and relatively small or inconspicuous pedicellariae present on the body surface relative to the total number of plates present. This includes those taxa with pedicellariae that occur in relatively low numbers or else, are widely distributed, and diffuse, occurring irregularly and inconsistently on the body surface. This level of pedicellariae presence is most observed in the Asteropseidae (Fig. 35A–E) in species such as *Petricia vernicina,* within the Oreasteridae in strongly arched genera such as *Culcita* or *Pentaceraster*, (Fig. 34A–F) or in the Goniasteridae, where pedicellariae are few, such as in *Mediaster.*

Summary of Distribution Trends

Two parameters dictate the appearance of pedicellariae when observed among the taxa surveyed, relative size and number of pedicellariae present on the surface of each taxon. At the extremes, this involves a high abundance of homogeneous or at least, similar sized pedicellariae present on the abactinal, marginal and actinal surfaces versus the opposite, relatively few but extremely large and prominent pedicellariae (heterogeneous relative to other serial or regular features), isolated to a specific area. These groupings are intended as a guideline, rather than a comprehensive listing.

High abundance present on multiple surfaces, similar sized pedicellariae. *Anthaster valvulatus*, *Gilbertaster anacanthus, Gilbertaster caribbaea*, *Hippasteria phrygiana, Hippasteria heathi, Hippasteria lepidonotus, Hippasteria mcknighti, Sthenaster emmae, Weitschataster intermedius* (fossil).

Pedicellariae abundant to moderately abundant but localized to primarily one surface or region. *Akelbaster novaecaledoniae, Acodontaster conspicuus*, ***Anthena hlan*** **sp. nov.**, ***Anthenea nuda*** **sp. nov.** , ***Anthenea serrata*** **sp. nov.**, *Anthenea* spp, *Anthenoides peircei, Bathyceramaster kelliottae*, *Circeaster americanus*, *Circeaster helenae*, *Circeaster magdalenae, Circeaster marcelli, Comptoniaster adamsi* (fossil)*,* ***Fromia baruna*** **sp. nov.***, Fromia eusticha, Fromia labeosa*, *Lydiaster johannae, Peltaster nidarosensis, Toraster tuberculatus, Wallastra elenderae.*

Few abundance, pedicellariae small. *Culcita* spp. (adult), *Mediaster* spp., *Petricia vernicina*, *Pentaceraster alveolatus* (adult).

Low abundance, large pedicellariae. ***Astrophylax accinctus*** **sp. nov.** , ***Astrophylax valvatus*** **sp. nov.,** *Chitonaster felli*, *Eknomiaster beccae*,

Phylogenetic Trends? Are Bivalve Pedicellariae Monophyletic?

The Valvatacea appears to be supported as a monophyletic clade within the crown group Asteroidea based on phylogenies inferred from morphology (e.g., Blake, 1987) and molecules (Mah & Foltz 2011; Linchangco *et al*., 2017), albeit with differing taxonomic composition. Within the Asteroidea, some lineages, such as the Forcipulatacea, display pedicellariae as reasonably evident synapomorphies for the clade. This invites similar comparison for valvatacean asteroids with bivalve and/or similar types of pedicellariae for groups within the Valvatacea. Valvatacean asteroid groups do not possess pedicellariae as uniformly as those in the Forcipulatacea, but most express "valvate" alveolar, spiniform, or elementary pedicellariae of sufficient diversity and with sufficient regularity that simple "presence" of pedicellariae is a plausible synapomorphy. However, bivalve pedicellariae are expressed on widely different lineages, with many groups lacking them altogether and many appear to vary between related groups that do and do not possess them (Fig 37).

In the Forcipulatacea, three-piece claw-like straight and/or forcipiform pedicellariae (Fig. 1A) are present throughout all taxa and information on ecology and morphology is relatively well-known. Molecular and morphological phylogenetic data have consistently supported the Forcipulatacea as monophyletic (Mah & Foltz 2011, Blake 1987). Pedicellariae distribution patterns are phylogenetically consistent, with three-piece forcipiform pedicellariae in tufts associated with spines restricted to the monophyletic Asteriidae *sensu* Mah & Foltz (2011) in contrast to straight and other pedicellariae present on the body surface or in the ambulacral groove.

The second major taxonomic grouping in the Asteroidea is the Valvatacea (Fig. 37), whose membership has varied over its history. As indicated herein the Valvatacea, includes the Valvatida, Paxillosida and the Echinasteridae (formerly the Spinulosida) (Mah & Foltz 2011a, Linchangco *et al*., 2017, unpublished data)which all express bivalve, tong-like, pectinate, simple and other types of pedicellariae. Pedicellariae are absent in the Echinasteridae.

Bivalve pedicellariae are present on multiple, disparate lineages within the Valvatida and although consistently present, appear to be variable across individuals when observed. Groups within the Valvatida expressing pedicellariae include the Goniasteridae, Oreasteridae+Asteropseidae (=Oreasteracea), and the Odontasteridae. Members of the Goniasteridae are a distinctly different lineage than the members of the clade containing the Oreasteridae+Asteropseidae (=Oreasteracea). Mah & Foltz (2011) agreed with Blake (1987) on the relationship of the Oreasteridae+Asteropseidae as members of the same clade, but Mah & Foltz (2011) showed the Oreasteridae+Asteropseidae clade as the sister clade to the Asterinidae, containing the Ganeriidae and Solasteridae, which for the most part lack pedicellariae. This differs significantly from the relationship supported by Blake (1987) showing the "oreasterid clade" (=Oreasteracea) as sister to the older "Ophidiasteridae." The Ophidiasteridae from this period is now understood to be paraphyletic containing a mix of members from the Goniasteridae and more "typological" ophidiasterids. Goniasterids occupy a much larger and more phylogenetically distant cluster relative to Blake's Oreasteracea (i.e. Oreasteridae+Ophidasteridae). Pedicellariae in the more typological Ophidiasteridae are primarily tong-like or excavate in shape.

Bivalved pedicellariae appear to be associated with two distinct major lineages, the Goniasteridae and the Oreasteridae+Asteropseidae (Fig. 37) and in multiple subgroupings within the Goniasteridae. Available phylogenetic data shows the Hippasterinae, a subfamily in the Goniasteridae, as monophyletic. Bivalve pedicellariae are abundantly present and well-developed in *Hippasteria, Gilbertaster* and *Sthenaster* but absent from *Evoplosoma* which appears consistent with forthcoming molecular phylogenetic data (Mah, in prep). Similarly, bivalve pedicellariae are abundantly present and well-developed in *Circeaster* and several related members of the Circeasterinae Mah, 2024 and includes the unusual *Astrophylax* **gen. nov.** However, bivalve pedicellariae also occur, albeit in differing sizes and distributions, on separate clades, including on *Mediaster* and *Fromia* suggesting that pedicellariae arose on disparate clades within the Goniasteridae.

Outside the Goniasteridae, bivalve pedicellariae also occur in the Oreasteridae+Asteropseidae, and in the Odontasteridae which express trivalve and four-part pedicellariae. Pedicellariae are mostly absent from the Asterinidae+Solasteridae (Fig. 37) save for the presence of non-bivalve pedicellariae present in the genus *Nepanthia*. Within the Asteropseidae, bivalve pedicellariae are prominent in *Valvaster* and *Petricia,* but not recorded from *Asteropsis* and within the Oreasteridae, bivalve pedicellariae are abundant and prominent among the "goniasterid" like forms such as *Anthenea* and *Anthaster* but are less so in the more thickened and arched forms such as *Culcita* and *Pentaceraster.* The Odontasteridae are supported as the sister clade to the Valvatida, including the Goniasteridae, the Asterinidae and the Oreasteridae+Asteropseidae.

Within a phylogenetic context, only four clades completely lack pedicellariae, the Velatida, including four families, Pterasteridae, Korethrasteridae, Myxasteridae and the Xyloplacidae, the Spinulosida, monotypic including the Echinasteridae which includes 8 genera and 133 species, and the Caymanostellidae, which includes 2 genera and 12 species.

Pedicellariae are also absent or rarely observed within the Asterinidae, which has recently been shown to include subgroups than was historically recognized, including the "Solasteridae," Ganeriinae, and the Hyalinothricinae (Mah & Foltz 2011; Mah & Fujita 2020). However, only *Nepanthia* sp. within the Asterinidae has pedicellariae (O'Loughlin & Waters 2004) with nearly all other members lacking pedicellariae. No known asterinids display bivalve pedicellariae.

A further consideration is that of a possible physical

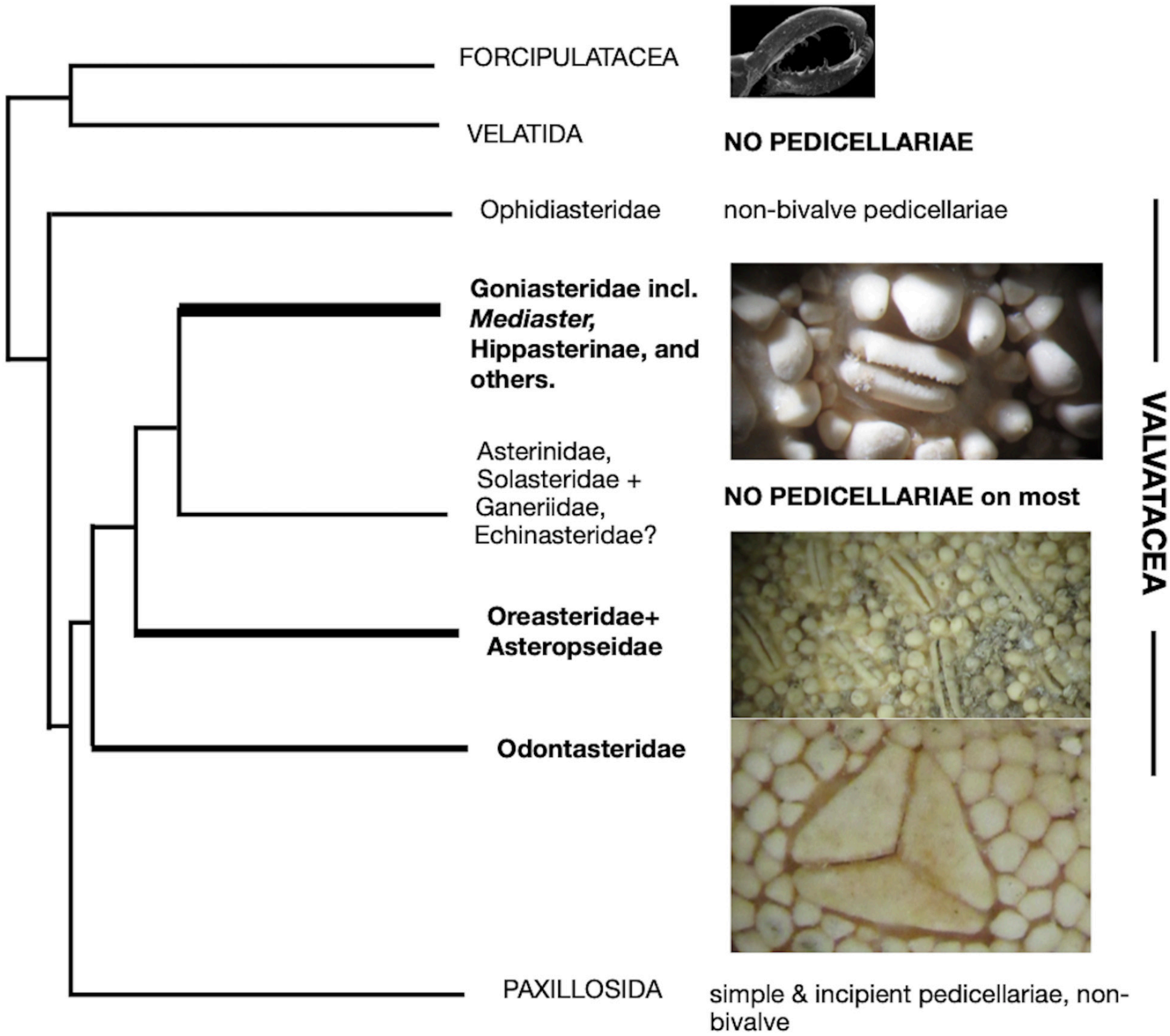

FIGURE 37. Phylogenetic Tree (modified from Mah & Foltz 2011) showing major lineages of Valvatacea with bivalve/tectiform pedicellariae.

constraint considering the presence and/or development of other types of alveolate pedicellariae, including those with smaller less developed pedicellariae with forceps-like or more slender valves when compared against those taxa with larger more strongly developed or broader valves. A full survey of pedicellariae types with comparative presence/absence across the surveyed Valvatacea herein was beyond the scope of the current work, but this is likely an important consideration especially relative to environmental factors, such as ease of calcification and phenotypic effects from predation or other ecological factors when considering physical constraints and developmental tradeoffs.

Bathymetric Trends

No general (i.e. across all taxon) trends showing morphological distinction across depth was evident, but at least three genera were recognized as differing with depth. In some cases, it seems there are distinctions for different species, perhaps as adaptations for differing deeper-water habitats. For differences within populations at different depths, it is unclear if these could be indicators of cryptic species or population-level phenotypic variation across different environmental settings.

Based on observations from specimens herein and in Mah *et al*. (2014) there are distinct differences between shallower and deep-sea members of *Hippasteria californica*. Shallow water members of this species show straight valves with smooth edges whereas deeper-water, >1000 m, individuals show more round, broad valves bearing teeth or in other instances more triangular-shaped valves on the actinal surface.

Similarly, the Antarctic/high-latitude *Chitonaster* shows elongate bivalve pedicellariae in the shallow (104–412 m) *Chitonaster trangae* as well as the deeper-water *Chitonaster johannae* (2856–4204 m) in contrast to the unusually enlarged, claw-shaped pedicellariae in *Chitonaster felli* (2355–3714 m).

Shallower mesophotic species also show this pattern. Only three species of the shallow-water *Fromia* display bivalve pedicellariae, *F. baruna* **sp. nov.**, *F. eusticha* and *F. labeosa*, and the latter two are present at deeper, mesophotic depths, 96–149 m and 52–137 m, respectively. This is in marked contrast to the remainder of pedicellariae-free *Fromia* species, which occur in much shallower settings, 0–44 m (Mah *et al*., 2024).

Biogeographic Trends

Taxonomic and greatest number of taxa displaying unusually abundant or prominent pedicellariae relative to normal pedicellariae presence for their respective groups appear to be highest in the "Golden Triangle" region (e.g. Briggs & Bowen, 2013) where the tropical Pacific and the Indian Ocean come into contact, including Indonesia, the Philippines and adjoining regions.

Members of the Circeasterinae, including *Astrophylax* **gen. nov.** and multiple species of *Circeaster* appear to be particularly diverse in this central/Indo-Pacific region, with nearly all of these species, including *C. loisetteae, C. helenae, C. kristinae*, and *C. columnaris* **sp. nov.** displaying numerous, prominent and ornate bivalve pedicellariae. South Pacific species, such as *C. sandrae* and *C. pullus* display similar but less prominent and fewer pedicellariae. This is consistent with the phylogenetic pattern in Mah (2006) suggesting central Pacific versus a south Pacific/tropical Atlantic clades within *Circeaster*. There were no Atlantic taxa which demonstrates the same levels of pedicellariae abundance or prominence observed in the Pacific or Indo-Pacific taxa.

All members of the oreasterid *Anthenea* and related taxa have bivalve pedicellariae present on most if not all the actinal plates and thus, are argued to have the most abundant bivalve pedicellariae among the Oreasteridae. *Anthenea* species display a distribution that also shows highest diversity in the so-called "Golden Triangle" area, in the central Indo-Pacific region between the northern coast of Australia and north to the south Asian coast. Two of the three *Fromia* species, *F. eusticha* and *F. baruna* **sp. nov.** that display pedicellariae, are present in the Indonesian/central Pacific region with the third, *F. labeosa*, present in southern Japan, which is adjacent to these areas. No other species of *Fromia* are known to show pedicellariae.

Pedicellariae Functional Considerations

The Hippasterinae & other Corallivores

During the NOAA ship *Okeanos Explorer*'s CAPSTONE expeditions in the North Pacific (EX 1504, 1603, 1606, and 1706) several *in situ* observations of *Hippasteria muscipula* were recorded, providing possible insight into pedicellariae function. Details on collection and protocols during this expedition are summarized in Mah (2022). Observations were not made under experimental conditions and are presented here subjectively as zooms on these subjects was opportunistic.

One of the clearest observations took place during EX 1706, the expedition to Johnston Atoll, during a dive to Edmondson Seamount at 1124–1300 m, a specimen of *Hippasteria muscipula* was observed perched on a specimen of *Corallium* sp. (Fig. 23A–C). Although not observed feeding at that moment, absent polyps and other disrupted tissue indicated that it had been predating on that particular individual. A zoom by the ROV's camera focused on the actinal surface of the asteroid and showed several of the large bivalve pedicellariae open and apparently in active motion. Valves of these pedicellariae are approximately 0.5 to 1.0 cm in length and were observed gaping during the video survey of the individual (Fig. 23C). No abactinal pedicellariae were observed.

Other observations of *Hippasteria muscipula* during feeding do show pedicellariae on the abactinal surface open with the valves gaping in a similar fashion to those on the actinal surface during the 1706 observation. In contrast, one non-feeding observation of this species from the Musicians Seamounts shows most visible pedicellariae closed.

Interpretation

There are multiple interpretations of pedicellariae as observed. This includes interaction of at least some pedicellariae directly with the prey items (i.e. cnidarian polyps) and/or a non-feeding related, defensive function, forming defense against possible predators or kleptoparasitic species taking advantage of feeding on the prey items.

Although predation on the octocoral or other cnidarian prey appears largely dependent on the extension of the cardiac stomach in conjunction with movement by the tube feet, it is plausible that the pedicellariae on the actinal surface serve in some kind of supplementary, physical capacity, such as the destruction or damage of defensive polyps or other tissue to facilitate digestion. This might explain the preponderance of pedicellariae on the actinal surface, while abactinal pedicellariae might serve to operate as defense against polyps projecting from different directions or further small predators.

However, most of the CAPSTONE observations did not reveal any aggregations of potential predators or any indirect evidence caused by such species. Mah (2020) observed small amphipods in conjunction with the Atlantic *Gilbertaster caribbaea* which were described as possibly commensal or kleptoparasites. *Gilbertaster* has an abundance of large bivalve pedicellariae on its body surface but there was no evidence of damage to tube feet or other tissue on the star. *Gilbertaster* was not feeding in the amphipod observation cited in Mah (2020) and pedicellariae were closed but did display open or slightly agape pedicellariae in some images of *G. caribbea* feeding. Observations of *Hippasteria* and *Evoplosoma* *w*here pedicellariae were active did not reveal traces of any mobile prey, such as small crustaceans.

Goniasteridae: Abundant small to medium sized pedicellariae

Abundant bivalve pedicellariae in the Hippasterinae and related corallivores are argued as being associated with corallivory. As discussed herein with *in situ* observations of *Hippasteria muscipula* in Johnson Atoll, these pedicellariae were observed opening and closing while the star was predating on its octocoral prey. Many corallivorous goniasterid taxa also tend to demonstrate pronounced spination on the abactinal, marginal and in some cases, actinal surfaces, suggesting functions associated with predation, possibly defense against outside predators or kleptoparasites which are present while the star is feeding. The *Okeanos Explorer* video of *Hippasteria muscipula* from EX 1706 (Fig. 23A–C) provides one of the few *in situ* observations of widespread, abundant bivalve pedicellariae motion during the animal feeding, allowing insight and speculation on possible function.

The observation most likely showed recent feeding since the pyloric stomach was not extended during the observation. However, the pedicellariae were opening and closing during apparent feeding. No small micro predators or other possible threats were observed on the surface during the ROV's closeup on the surface. There was an abundance of partially damaged tissue on the octocoral in addition to what appears to be worn or eroded material on the coral stalk's surface. This is consistent with the notion that at least in this species, bivalve pedicellariae could function to assist the physical breakdown of the coral's tissue, assisting in the external digestion by the cardiac stomach when the star is ready to feed. Similar to brisingid sea star feeding, tube feet might also play a role in conveying food to the mouth (Emson & Young 1994). The alveolar chambers below the pedicellariae themselves display no known connection to the gut or to the interior system of the animal.

The physical posture of most hippasterine and circeasterine Goniasteridae, when feeding on octocorals, generally has the oral surface, and thus the cardiac stomach, always directed towards toward tissue on the octocoral prey. On multiple hippasterines and circeasterines, large bivalve and/or paddle-shaped pedicellariae occur primarily on the actinal surface. For example, *Evoplosoma nuku* Mah 2022 showed numerous straight pedicellariae on its abactinal disk surface (Mah 2022) but showed paddle-shaped pedicellariae on the actinal and adambulacral plates. Many species of *Circeaster,* such as *C. loisetteae* or *C. kristinae* show a similar trend with bivalve or paddle-shaped pedicellariae present primarily on the actinal surface (Mah 2006) to the exclusion of similar pedicellariae on the abactinal surface. Bivalve pedicellariae size and position varies among different taxa with some displaying patterns in stark contrast to the notion of actinal-directed pedicellariae. *Gilbertaster*, for example, shows extremely abundant bivalve pedicellariae on the abactinal, marginal and actinal plate surface. *In situ* observations of this species show it attacking the primnoid octocoral *Plumarella*. Atlantic observations of *Gilbertaster caribaea*, also showed amphipods, possibly kleptoparasites, in association among the tube foot grooves (Mah, 2020). Pedicellariae, in addition to assisting with feeding in some taxa, may serve to deter these amphipods or similar pests.

Pedicellariae in other Predatory goniasterids

Eknomiaster macauleyensis, which has numerous paddle-shaped pedicellariae on its actinal surface (Fig. 14C) was observed perched on a stylasterid hydrozoan, *Stephanohelia praecipua* Cairns, 1991 in New Caledonia, suggesting that pedicellariae could play a role in predation, perhaps assisting or having an indirect role in capturing polyps or other soft-tissue similar to the means outlined for *Hippasteria*.

The presence of serial bivalve pedicellariae along the actinal plate series adjacent to the adambulacral plates on *Bathyceramaster kelliottae* and the "*nidarosensis*" form of *Peltaster placenta* could be explained as part of a hypothesis that explains bivalve pedicellariae for tissue breakdown in conjunction with feeding. *In situ* observations of *Peltaster* on a demosponge (Mah 2020) suggest the greater part of their actinal surface is appressed onto the prey surface, suggesting the pedicellariae could work at physically processing the sponge tissue prior to digestion.

In these latter two species, feeding is argued as much more likely explanation than other types of functions, such as defense, largely because the pedicellariae are directed downward and few to no pedicellariae are present on the abactinal surface. In the examples with corallivorous goniasterids, *in situ* observations also show many examples of *Hippasteria, Circeaster* and other related taxa feeding on the higher branch tips of coral colonies at oblique angles. It is unclear if pedicellariae on abactinal and marginal surfaces are simply directed to assist in tissue processing at different, difficult angles or are perhaps used in some kind of defense. It seems difficult to argue how pedicellariae that are in many instances flush with the body surface could be used in a defensive fashion.

Clustered and Enlarged Pedicellariae

Perhaps the most striking but most enigmatic of bivalve pedicellariae patterns are those species which display relatively few, clusters of enlarged pedicellariae on the actinal intermediate surface, including *Chitonaster felli* (Fig. 4A–E)*, Eknomiaster beccae* (Figs 13A–F; 14A–B) and both species of *Astrophylax* (Figs. 16A–E; 17A–F).

Based on the observation of bivalve pedicellariae open and closing during feeding in *Hippasteria muscipula*, it is argued that these pedicellariae function in a similar fashion, as accessories to feeding, serving to tear or rend prey tissue, possibly from cnidarians or sponges so that the cardiac stomach can more easily digest it.

In addition to observations of activity during feeding, position is a further basis for this notion, since large sized pedicellariae are absent from the abactinal or marginal surfaces as they are in other Goniasteridae or Oreasteridae. *Eknomiaster beccae* is morphologically similar to *Eknomiaster macauleyensis* which was observed perched on a stylasterid coral and showed numerous paddle-shaped bivalve pedicellariae on its actinal surface (Fig. 14E–F). *Eknomiaster beccae* differs primarily in the consistent possession of enlarged, relatively few pedicellariae on the actinal intermediate surface (Figs 13A–F; 14A–B).

Conceivably, these pedicellariae might be used in part for assistance anchoring the individual animals to the substratum, perhaps on a prey organism with a stalk. However, there are no precedents for pedicellariae to be used in this fashion. Defense, as has been argued for other pedicellariae, seems to be difficult to interpret based on this same positional basis. The pedicellariae are essentially fixed and flush with the surface, and unable to be directed towards moving organisms.

Functional Considerations: Oreasteridae, Asteropseidae, and Odontasteridae

Ecological comments

One specimen of *Anthenea chinensis* from Hong Kong were observed *in situ* (Fig. 28A–B) with its actinal surface overturned, covered with sediment and detrital remains, and showing the bivalve pedicellariae open and its cardiac stomach partially extended. It is argued that this is part of the feeding process in this species, as the pedicellariae function to capture or process material capture on this sedimented bottom, facilitated perhaps by the tube feet, with the food ultimately directed towards the mouth.

Specimen USNM E38927 of *Anthenea nuda* **sp. nov.** showed sediment and debris, including sediment grains and possibly foraminifera, were still present on the specimen interspersed between granulation and the pedicellariae valves on the actinal surface (Fig. 30E–G). While it is true that collection by trawl net can result in impacted debris and sediment, it is argued that the extent to which specific materials are present within the pedicellariae valves is more than can be explained by random trawl collection.

The actinal surface of the holotype of *Anthenea hlan* **sp. nov.**, USNM E53676, shows sediment and debris retained on the actinal surface between granules and especially between the valves of the bivalve pedicellariae (Figs. 29F–G), presumed to have been present during collection, but could also be interpreted as possible prey collection.

Figure 32A–B shows two observations of feeding by *Anthenea serrata* **sp. nov.** in Hong Kong on sponges and/or detritus being devoured by this species. Both images show actinal views illustrating open pedicellariae, especially Fig. 32B, in addition to the presence of food and detritus around the mouth.

Pedicellariae in *Acodontaster conspicuus* are broadly similar in location with goniasterids and oreasterids. One specimen USNM 1104731 (Fig. 36E) showed at least two actinal pedicellariae adjacent to the mouth filled with sediment or other material, similar to those observed in *Anthenea* on the actinal intermediate surface, suggesting a similar role in assisting with feeding as outlined herein. *Acodontaster conspicuus* has been documented as an ecologically significant predator on sponges (Dayton *et al.* 1974) and has pedicellariae located on the actinal surface in similar locations to Goniasteridae with similar predatory preferences, such as *Bathyceramaster kelliottae* and *Peltaster "nidarosensis."* Thus, function may serve in a similar fashion.

Oreasteridae, Odontasteridae, and "Abundant" Pedicellariae

Oreasteridae with flattened disks, including *Anthenea, Gymnanthenea* and *Anthaster* display this same, or at least similar, pattern of abundant pedicellariae with pedicellariae present on nearly every plate on the actinal surface, or else in regular series adjacent to the adambulacral plate series. As indicated herein, Oreasteridae occur on a more distant phylogenetic location from the Goniasteridae than has been argued in earlier studies and so function and morphology as well as habitat of *Anthenea* and related are further considerations. The sole odontasterid with "bivalve" or tectiform pedicellariae, *Acodontaster conspicuus*, have pedicellariae located in similar positions proximal to the mouth and in series along the actinal intermediate plates adjacent to the adambulacral plates.

It is argued that *Anthenea* and related taxa inhabit shallower depths with actinal surfaces directed downwards and use their bivalve pedicellariae to assist in gathering and/or facilitating capture of digestible items, including food-containing sediment and other organic materials, on bottom settings which the cardiac stomach and/or the tube feet further process for digestion. Brisingid sea stars use elongate spines and a combination of pedicellariae and elongated tube feet to convey captured prey, mostly crustaceans, to the mouth where they are devoured (Emson & Young, 1994). Tube feet in *Anthenea*, while capable of some flexure, do not appear to show the length necessary to extend beyond areas adjacent to the adambulacral plate series. Furrow and subambulacral spines in *Anthenea* are also well-developed with the former forming interlacing networks across the tube foot groove. This strategy could also be used in the Goniasteridae which feed primarily on soft-sediment bottoms, such as has been observed in *Anthenoides peircei,* which has pedicellariae centered on the actinal surface adjacent to the oral region.

In situ images of two species from Hong Kong (Figs. 28A–B, 32A–B) show one species predating on an apparent sponge and a second devouring a cluster of debris. Damage to the sponge appears widespread and would be consistent with predation by a larger area than the cardiac stomach alone. One image of *Anthenea chinensis* (identified as *A. pentagonula*) shows an *in situ* image immediately following the individual flipped over with the actinal surface displaying sediment and debris closely covering the actinal surface, but especially over the pedicellariae.

Two specimens included herein, USNM E38927, *Anthenea nuda* (Fig. 30E, F, G) and the holotype of *Anthenea hlan* **sp. nov.** (Fig. 29F, G) show sediment and debris remaining on each specimen's actinal surface, jammed between the actinal granules and spination but also within several of the bivalve pedicellariae valves. A survey of the genus *Anthenea* on iNaturalist and habitat summaries from Marsh & Fromont (2020) notes that all species are observed on soft bottoms or some kind of unconsolidated sedimentary habitat suggesting a consistent habitat.

Goniasterids, such as *Fromia* or *Stellaster*, and oreasterid genera, such as *Culctia, Pentaceraster* or the unusual mesophotic *Astrosarkus*, show relatively small but abundant pedicellariae on the actinal surface and for many species, adjacent to the tube foot grooves. These are positionally consistent with function as argued above, but their size seems prohibitively small.

In some Anthenea and other oreasterids there are fasciolar grooves present between the actinal plates and these surfaces are covered by ciliated epidermis. Cilia could convey sediment and sediment-related food, such as foraminifera, to the tube feet or to the mouth, following capture by the actinal pedicellariae. Figures 28B and 32A show the actinal surface of different *Anthenea* sp. *in situ* covered by sediment and flocculent material which occupies interstitial areas between the actinal plates and the tube foot grooves.

Weakly Abundant Pedicellariae Function

Those taxa with the fewest and most irregularly distributed pedicellariae are perhaps the most difficult to explain. Bivalve pedicellariae are least abundant but prominent in the Asteropseidae. Position of the pedicellariae in *P. vernicina* suggests possible function. USNM 13774 shows two pedicellariae per interradius on the abactinal surface, but on this and other specimens the pedicellariae sit centrally on plates, surrounded by a large fields of papular pores (Fig. 34A–C). Bivalve pedicellariae may provide protection against small crustaceans or other micro predators.

The second asteropseid with bivalve pedicellariae, *Valvaster striatus*, could also be considered to show only weakly present pedicellariae, which occur only along the superomarginal plates and nowhere else on the body surface. Although Marsh & Fromont (2020) have reported this species as occurring in coral reef settings, much of its biology appears to be unknown and the role of its pedicellariae are poorly understood.

Some goniasterids, such as *Mediaster* show bivalve pedicellariae present in relatively low abundance on different body surfaces with no apparent centralization or heavy concentration in any specific region and their function seems difficult to interpret. Defensive roles are one possibility but it is unclear how, given the size and location of these pedicellariae provide any functional defense against possible predators or pests.

Conclusions

One new genus of Goniasteridae and seven new species of Valvatida, including four goniasterids and three oreasterids are described herein. Prominent and/or bivalve pedicellariae are significant to the description of this and other valvatidan asteroids. An overview of the Valvatida shows three families, particularly the Goniasteridae which show the largest, most abundant most prominent bivalve pedicellariae in addition to the Oreasteridae and the related Asteropseidae which display smaller, less abundant bivalve pedicellariae (see Table 1).

Among surveyed valvatidan taxa, at least four genera, including *Astrophylax* **gen. nov.** present in the central Indo-Pacific region demonstrate unusually high abundance of pedicellariae.

Taxa from deep-water southern hemisphere settings, such as *Chitonaster* and *Eknomiaster* appear to have among the largest and most prominent pedicellariae, located in similar positions centrally on the actinal intermediate regions. Taxa with more widely distributed, smaller bivalve pedicellariae, usually present along the oral surface are more commonly encountered in shallower, warmer-water settings (e.g. most Oreasteridae).

Bivalve pedicellariae function remains poorly understood, but the positioning on oral surfaces, especially around the mouth suggests an association with feeding. Although a full phylogenetic analysis was beyond the scope herein, review of taxonomic and phylogenetic treatment suggests bivalve pedicellariae are independently derived in the Goniasteridae and the Oreasteridae+Aster opseidae clades.

New Taxa Described

Goniasteridae

***Astrophylax accinctus* gen. nov. sp. nov.**
***Astrophylax valvatus* gen. nov. sp. nov.**
***Circeaster columnaris* sp. nov.**
***Fromia baruna* sp. nov.**

Oreasteridae

***Anthenea hlan* sp. nov.**
***Anthenea nuda* sp. nov.**
***Anthenea serrata* sp. nov.**

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