

Phylogeny and biogeography of the deep-sea goniasterid *Circeaster* (Echinodermata, Asteroidea, Goniasteridae) including descriptions of six new species

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ABSTRACT

A phylogenetic analysis of 13 taxa and 32 characters resulted in a single most parsimonious tree that supports monophyly of the goniasterid (Echinodermata, Asteroidea) genus *Circeaster* Koehler, 1909 and supports re-establishment of the genus *Lydiaster* Koehler, 1909. The phylogeny supports monophyly of the ingroup, including 10 species, six of which, *C. kristinae* n. sp., *C. beleanae* n. sp., *C. arandae* n. sp., *C. loisetteae* n. sp., *C. sandrae* n. sp., and *C. pullus* n. sp., are new. Phylogenetic results support diversification into the Indian, Pacific, and Atlantic ocean basins. The phylogeny is constrained by a sister taxon with a Cretaceous fossil occurrence and two geologic events, including the closure of the Indonesian seaway and formation of the Panamanian isthmus. These events formed barriers limiting or preventing larval dispersal between the Indian/Pacific and the Pacific/Atlantic oceans. Larval dispersal through a deep-sea environment was a significant consideration for estimating timing constraints from paleoenvironments. Based on fossil constraints, ancestry for the lineage is suggested as early as the Late Cretaceous with subsequent diversification in the Cenozoic. *In situ* observations of *Circeaster* perched on bare deep-sea coral skeletons and morphological similarities with other known corallivorous goniasterids suggest important ecological roles in the deep-sea.

KEY WORDS

Echinodermata,
Asteroidea,
Valvatida,
Goniasteridae,
deep-sea,
phylogeny,
Panamanian seaway,
Indonesian seaway,
allopatric barrier,
historical biogeography,
evolution,
morphology,
new species.

RÉSUMÉ

Phylogénie et biogéographie des Circeaster profonds (Echinodermata, Asteroidea, Goniasteridae) incluant la description de six espèces nouvelles.

Une analyse phylogénétique portant sur 13 taxons et 32 caractères a produit un seul arbre maximisant la parcimonie. La topologie soutient la monophylie du genre *Circeaster* Koehler, 1909 (Echinodermata, Asteroidea, Goniasteridae) et la restauration du genre *Lydiaster* Koehler, 1909. La phylogénie obtenue soutient la monophylie de l'ingroup qui est constitué de 10 espèces. Six d'entre elles, *Circeaster kristinae* n. sp., *C. helena* n. sp., *C. arandae* n. sp., *C. loisetteae* n. sp., *C. sandrae* n. sp. et *C. pullus* n. sp. sont nouvelles. Les résultats phylogénétiques soutiennent l'hypothèse de diversification dans les bassins océaniques indien, pacifique et atlantique. La phylogénie est contrainte par un groupe frère connu du Crétacé et deux événements géologiques : fermeture du passage indonésien et formation de l'isthme de Panama. Ces événements ont formé des barrières limitant ou empêchant la dispersion larvaire entre les océans Pacifique et Atlantique et les océans Indien et Pacifique. Une dispersion larvaire au sein de milieux profonds a été considérée comme une contrainte forte sur la chronologie des événements évolutifs. L'ancienneté de la lignée évolutive semble remonter au Crétacé supérieur. Elle se serait ultérieurement diversifiée au cours du Cénozoïque. Des spécimens de *Circeaster* ont été observés *in situ* en milieu profond perchés sur les squelettes nus de coraux. De plus, ces spécimens présentent des similarités morphologiques avec d'autres Goniasteridae corallivores ce qui suggère un rôle écologique primordial de ces animaux au sein des environnements profonds.

MOTS CLÉS

Echinodermata,
Asteroidea,
Valvatida,
Goniasteridae,
eaux profondes,
phylogénie,
Route panaméenne,
Route indonésienne,
barrière allopatrique,
biogéographie historique,
évolution,
morphologie,
espèces nouvelles.

INTRODUCTION

The antiquity of deep-sea faunas has been a subject of interest since stalked crinoids were first recovered from Norway in the 19th Century (Thomson 1873). Madsen (1961b) reviewed affinities between fossil taxa and their living abyssal counterparts, including poriferans, scleractinians, octocorals, pycnogonids, crustaceans, brachiopods, molluscs, and stalked crinoids, and concluded that recent deep-sea taxa were relatively young and had differentiated in the Mesozoic. Gage & Tyler (1991: 257) reviewed ideas and hypotheses on the origins and the age of deep-sea faunas. More recent efforts at understanding the evolution of deep-sea faunas have incorporated fossil perspectives (e.g., Jablonski & Bottjer 1988), paleontological data (e.g., Smith 2004), and phylogenetic data from morphology (e.g., Mah 2005), molecules (e.g., Goffredi *et al.*

2003), and a combination of the two (Kano *et al.* 2002). Phylogenetic data has provided additional insight toward understanding the origination of deep-sea lineages (e.g., Kerr 2001; Smith 2004) and the evolution of clades within the deep-sea (e.g., Mooi & David 1996; Mah 1998). The timing and absolute age of diversification events are dependent upon external calibration points for events on the tree, including fossils (Brochu *et al.* 2004; Wiens 2004) and geological events (e.g., Lessios & Weinberg 1994; Lessios *et al.* 2003) as constraints for divergence between clades.

Asteroids have been frequently utilized as model organisms for understanding evolution in the deep-sea (e.g., Madsen 1961a, b; Young *et al.* 1996). Recent phylogenetic studies have emphasized bathymetric gradient shifts in brisingidans (Mah 1998) and goniasterids (Mah 2005). Howell *et al.* (2004) studied genetic divergence between morphotypes of *Zoroaster*

fulgens Thomson, 1873 and discovered reproductive isolation as a result of depth-related factors.

Allopatric speciation in a deep-sea, megafaunal invertebrate genus is interpreted from phylogenetic results of a cladistic analysis, performed on the bathyal-upper abyssal, goniasterid *Circeaster* Koehler, 1909. Fossil dates and geological events provide some timing constraints for phylogenetic events within an exclusively deep-sea asteroid lineage. The goniasterid genus *Circeaster* provides a model organism for studying allopatric evolution within the deep-sea. The genus occupies an exclusively bathyal to upper abyssal distribution (320–3000 m range) (Clark 1993). Habitat was poorly known for the Indian Ocean species, but the Atlantic species were found primarily on the continental shelf. No shallow water species are known. Monophyly for the included taxa was also established from preliminary data for a phylogeny of the Goniasteridae (C. Mah unpubl. data).

Circeaster and the closely related *Lydiaster* Koehler, 1909 were first described by Koehler (1909) based on three species, *C. magdalenae* Koehler, 1909, *C. marcelli* Koehler, 1909 and *L. johannae* Koehler, 1909 from the Indian Ocean. Two additional Atlantic species, *Lydiaster americanus* A. H. Clark, 1916 and *Circeaster occidentalis* H. L. Clark, 1941 were later synonymized by Halpern (1970a: 270) and amended to *Circeaster americanus*. Halpern (1970a: 265) also felt that the characters separating *Lydiaster* and *Circeaster* were “not of generic importance” and synonymized the former into the latter. *Circeaster* was described by Clark & Downey (1992: 237) as “relatively rare”. This has been especially true for the Indian Ocean species, which have not been encountered since their original description by Koehler (1909). Newly collected material described herein has increased the number of specimens available for study, resulting in the discovery of several new species and the re-discovery of additional specimens of Koehler’s (1909) original Indian Ocean species.

MATERIALS AND METHODS

Thirteen terminal taxa and 32 morphological characters (see Appendix 2) were scored largely from dry

specimens. Data was entered into MacClade (Maddison & Maddison 1992) and exported to PAUP* 4.0b10 (Swofford 2003). External endoskeletal features and variation in accessory structures were primary sources of character diversity. Characters were partly derived from a character matrix of the Goniasteridae (Mah unpubl. data), and augmented by additional characters scored from the material studied. Polymorphic characters were used to represent morphological variation where more than one state was present on each species. Thus, if spines were coded as “1” and granules were coded as “0” if spines and granules were variably present, they were coded in the matrix as “01”.

Specimens were obtained as loans from the Department of Invertebrate Zoology, California Academy of Sciences (CASIZ), the Muséum national d’Histoire naturelle, Paris (MNHN), the Division of Echinoderms, Smithsonian Institution (NMNH), the Bernice P. Bishop Museum, Honolulu (BPBM), the Rosenstiel School of Marine and Atmospheric Sciences, Miami (RSMAS) and the Western Australian Museum, Perth (WAM). Specimens and images were also provided by Craig Young, Oregon Institute of Marine Biology (OIMB), Chris Kelley and Edith Chave, Hawaiian Undersea Research Laboratory (HURL). Outgroup choice was based on a phylogeny of the Goniasteridae supporting *Cladaster analogus* Fischer, 1940 and *Floriaster maya* Downey, 1980 as sister taxa (C. Mah unpubl. data) to *Circeaster* (*sensu* Clark 1993). This relationship agreed with comments by Clark & Downey (1992: 244), who observed “undoubted affinities” between *Floriaster* and *Circeaster*. Preliminary data suggested *Cladaster analogus* as plesiomorphic relative to the other recognized species of *Cladaster* Verrill, 1899.

In addition to the outgroup taxa, *Cladaster* and *Floriaster*, 11 terminal taxa were included in the analysis, including the four described species, *Circeaster americanus*, *C. magdalenae*, *C. marcelli* and *Lydiaster johannae*, and six *Circeaster* morphotypes which could not be reconciled with established species descriptions. Specimens of *C. marcelli* were unavailable, and data was scored in the data matrix from the descriptions and figures of Koehler (1909). Newly collected material from the Indo-Pacific Ocean, including specimens from Hawaii, the

Solomon Islands, New Caledonia, Tonga, Western Australia, the Timor Sea, and Madagascar. Furthermore, Clark & Downey (1992: 238) described morphological variation in *C. americanus* and suggested the possibility of an additional unrecognized species of *Circeaster* from the tropical Atlantic. Specimens displaying this variation were included in the matrix. The material described herein for *Circeaster* specimens substantially increases the number of specimens known for non-Atlantic *Circeaster* species.

RESULTS

A branch-and-bound search recovered a single most-parsimonious tree (Fig. 1) with a length of 68 steps (Consistency Index [CI] = 0.7794, Retention Index [RI] = 0.8052). *Circeaster*, as recognized by Halpern (1970a, b), is paraphyletic. The phylogeny supports separation of *Lydiaster* and nine species within a monophyletic *Circeaster* lineage (Fig. 1). *Circeaster* consists of three major lineages, one separating *C. arandae* n. sp., one lineage largely made up of Indian Ocean species, including *C. helenae* n. sp., *C. magdalenae* and *C. marcelli*, and a third lineage consisting of *C. kristinae* n. sp., *C. sandrae* n. sp., *C. pullus* n. sp. and *C. americanus*.

Bremer and bootstrap values (Fig. 1) supported largely identical branches. Highest support was observed in the *Lydiaster* + *Circeaster* clade and the clade including *C. kristinae* n. sp., *C. sandrae* n. sp., *C. pullus* n. sp. and *C. americanus*. Relatively few nodes were unsupported.

Bootstrap analysis (Fig. 1) from 200 branch-and-bound iterations showed several supported nodes. The *Circeaster* + *Lydiaster* sister group relationship is supported by 100% of the bootstrap trees, whereas the *Circeaster* lineage itself is supported by 93% of the trees. *Circeaster helenae* n. sp. + *C. magdalenae* and *C. marcelli* + *C. loisetteae* n. sp. are supported by 67% and 52% bootstrap values, respectively. The clade supporting the former and latter sister taxon pairs is supported by 86% of the trees recovered by the analysis. The Indo-Pacific/Pacific/Atlantic clade is supported by 90% of the trees recovered with support values of 60% for

C. sandrae n. sp., 77% for *C. pullus* n. sp., and 56% for *C. americanus*.

Bremer support (Fig. 1) mirrored bootstrap support values for the *Circeaster* + *Lydiaster* lineage, which collapsed in 10 steps before memory for the search was exhausted. Support for the 10 taxa included in *Circeaster* collapsed in two steps. The sister branch, which included all the remaining *Circeaster* species, to *C. arandae* n. sp. collapsed in two steps. A branch supporting *C. loisetteae* n. sp., *C. marcelli*, *C. helenae* n. sp. and *C. magdalenae* also collapsed in two steps. The node supporting *C. helenae* n. sp. and *C. magdalenae* decayed in a single step. The second clade, which included *C. kristinae* n. sp., *C. sandrae* n. sp., *C. pullus* n. sp. and *C. americanus* collapsed in three steps. *Circeaster pullus* n. sp. and *C. americanus* were supported by a branch that decayed in one step.

CHARACTER ANALYSIS

Character descriptions are listed below in bold, followed by their respective character states and character notes where appropriate. Definitions follow those of Blake (1987) and Breton (1992). A full character matrix is included in Appendix 2. When present, discussion of the plesiomorphy or apomorphy of the characters is based upon results from the cladistic analysis and reflects polarity determinations based on character states in the outgroups. Six characters, including 1.4, 1.5, 1.6, and 1.7 for granule-related features and 4.1 and 4.2 for subambulacral spine features, were coded for absence of these features (i.e. granules or subambulacral spines).

Because absence of presence is not necessarily presence of absence, these are treated as missing data for the analysis and do not necessarily represent homology between the absent characters.

Abbreviations used below include: SM, superomarginal plates; IM, inferomarginal plates; MP, marginal plates; R, length of radius from center of disk to armtip; r, length of radius from center of disk to edge; R/r, ratio of the two lengths, typically used to represent the degree of stellate vs. pentagonal body expression.

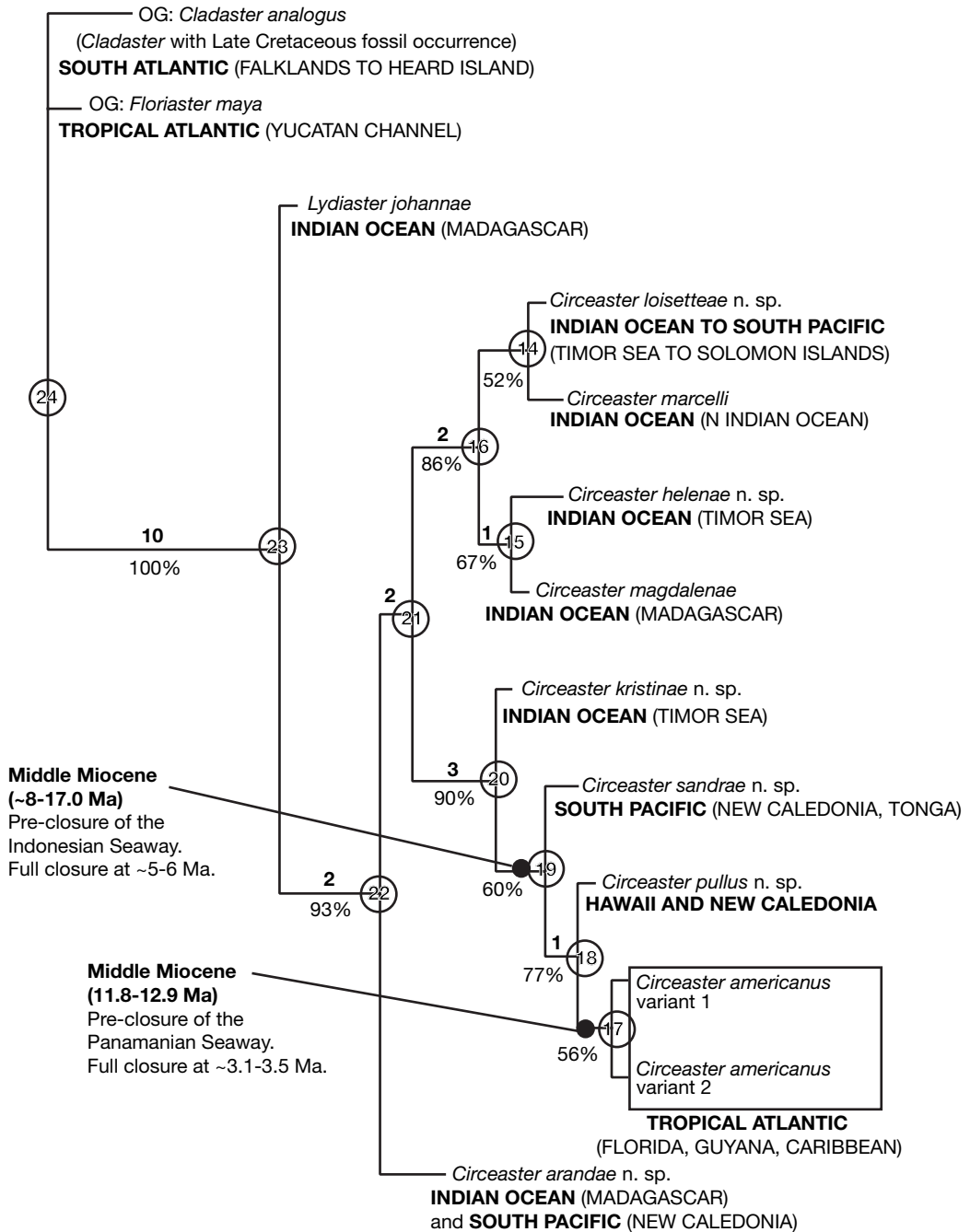


FIG. 1. — PHYLOGRAM INCLUDING *Circeaster* spp., *Floriaster*, and *Lydiaster*. Nodes numbers are indicated into circles. % values signify bootstrap values, values in **bold** signify Bremer support values.

ABACTINAL SURFACE CHARACTERS (1.1-1.9)

1.1 Abactinal arm plate size relative to abactinal disk plate. 0, plates identical or nearly so (e.g., Fig. 2C); 1, arm plates enlarged (Figs 4D; 5C).

Notes: in the derived state, arm plates were 2-6 times larger than those on the disk. Plate size and shape variation is present with some disk and arm plate sizes infrequently overlapping.

1.2 Arm-disk transition. 0, no change, disk plates uniform (e.g., Fig. 2C); 1, gradual change; 2, abrupt change.

Notes: in the derived state, the change between the two plates is very abrupt (Figs 4D; 5C) whereas in state 1, a very gradual gradient is present between small and large plates (Fig. 6C). Koehler (1909) first observed this character to distinguish between *Circeaster* and *Lydiaster*. Halpern (1970a, b) later stated that the character was insufficient for separating the two genera and synonymized *Lydiaster* with *Circeaster*. The RI and CI values (1.0) for this character support Koehler's original usage.

1.3 Abactinal plate convexity. 0, plate surface flat; 1, plate surface convex.

1.4 Accessory type. 0, large tubercle; 1, granules; 2, no accessories; 3, pointed, enlarged granules.

Notes: a tubercle (e.g., Fig. 2F) is an enlarged, knob-like process which is typically several times larger than the other smaller, more numerous granules present on the disk surface. Enlarged granules were nearly tubercular in shape but pointed and much larger than granules described in character state 1.

1.5 Accessory distribution. 0, individual accessory; 1, scattered; 2, no accessories.

Notes: this character describes the arrangement of accessories (e.g., tubercles, granules) on the abactinal surface. Individual accessories describe a single structure occupying the majority of the plate surface. Scattered accessories describe multiple accessories, which are moderate to widely spaced on the plate surface.

1.6 Granule size. 0, angular; 1, coarse round; 2, fine, round; 3, absent; 4, enlarged.

1.7 Granule distribution on plates. 0, homogeneous; 1, densely distributed on disk center; 2, absent.

1.8 Accessories on distal arm plates. 0, tubercle; 1, accessories present; 2, accessories absent (Fig. 5C).

1.9 Peripheral accessory position. 0, above plate periphery; 1, accessories form lateral periphery.

MARGINAL PLATE CHARACTERS (2.1-2.11)

2.1 SM plate accessories. 0, tubercles; 1, granules; 2, spinelets.

2.2 IM plate accessories. 0, tubercles; 1, granules; 2, spinelets (e.g., Fig. 4B).

2.3 SM plates abutted at midline. 0, SM plates not abutted; 1, SM plates abutted (Figs 6E; 7C).

2.4 SM spines. 0, absent; 1, present (Fig. 5A, C).

2.5 IM spines. 0, absent; 1, present (Fig. 5A, C).

2.6 Peripheral accessories. 0, coarse (Fig. 2F); 1, fine (Fig. 6A).

2.7 SM granular density. 0, scattered; 1, moderately packed; 2, densely packed.

2.8 IM granular density. 0, scattered; 1, moderately packed; 2, densely packed.

2.9 MP abundance. 0, low, less than 30 per interradius (e.g., Fig. 2E, G); 1, moderate, 30-50 per interradius (e.g., Fig. 6B, D); 2, high, 50-70 per interradius (e.g., Fig. 6A, D).

Notes: marginal plate abundance was counted from arm tip to arm tip and included the plates present within the complete interradius in apparent adult sized animals. Marginal plate number and R/r values mirrored one another, with those species having higher marginal plates per interradius also having higher R/r ratios. Character states were measured from multiple specimens showing R \geq 4.0 cm, including the range between the largest and smallest specimens for each species.

2.10 MP peripheral accessories. 0, coarse granules; 1, fine granules; 2, spinelets.

2.11 SM contact with abactinal arm plates. 0, curved to straight (Fig. 6E); 1, jagged and irregular (Fig. 3D).

ACTINAL SURFACE CHARACTERS (3.1-3.2)

3.1 Actinal accessory type. 0, tubercles; 1, granules (e.g., Fig. 7B); 2, spinelets (Fig. 4B); 3, short spines.

3.2 **Actinal accessory shape.** 0, angular; 1, rounded; 2, spiny; 3, pointed.

Notes: character 3.2 differs from 3.1 based on the surficial appearance of the actinal accessories rather than their overall shape. For example, individual granules might have a round to angular to spiny (i.e. highly tapered) surface with equivocal dimensions whereas a spine or spinelet has a conical shape with a sharpened tip.

ADAMBULACRAL FURROW CHARACTERS (4.1-4.3)

4.1 **Enlarged subambulacral spine.** 0, single spine (Fig. 6A); 1, row of spines (Fig. 5F); 2, spines absent (Fig. 4E).

4.2 **Subambulacral spine location.** 0, present lateral to pedicellariae (Fig. 6A); 1, abradial to furrow spines (Fig. 7B); 2, spine abradial to pedicellariae (Fig. 6F); 3, spine absent (Figs 3C; 4E); 4, pedicellariae absent.

4.3 **Subambulacral accessories.** 0, few (Fig. 6F); 1, abundant (Fig. 3C).

Notes: character 4.3 describes those granules or spinelets present on the adambulacral surface other than the prominent subambulacral spines described above.

BODY MORPHOLOGY (6.1-6.3)

6.1 **Arm length.** 0, arms short (Fig. 2G); 1, arms elongate (Fig. 5A).

Notes: short arms, present only in the outgroup, are based on an R/r ratio of approximately 2.0 whereas long arms are defined as those with an R/r ratio of approximately 2.5-5.0.

6.2 **Arm width.** 0, arms broad (Fig. 4A, C); 1, arms narrow (Fig. 5A).

6.3 **Interradial arc.** 0, interradial curved (Fig. 2G); 1, interradial linear (Fig. 6B).

PEDICELLARIAE (7.1-7.4)

7.1 **Bivalve pedicellariae.** 0, present; 1, absent (Figs 6F; 7B).

7.2 **Paddle-shaped pedicellariae.** 0, present; 1, absent (Figs 2B; 6A).

7.3 **Elongate pedicellariae.** 0, absent; 1, present (Fig. 4E).

7.4 **Sunken pedicellariae.** 0, absent; 1, present (Fig. 4E).

SYSTEMATICS

Order VALVATIDA Perrier, 1884

Superfamily GONIASTEROIDEA Forbes, 1841

Family GONIASTERIDAE Forbes, 1841

NOTES

Lydiaster johannae, *C. marcelli* and *C. magdalanae* were known only from Koehler's (1909) holotypes. The institutional depository of these holotypes was not indicated. Halpern (1970a: 173; 1970b: 265) indicated that he had compared all *Circeaster* species but citations for Koehler's original type specimens were absent from the listing of material studied (Halpern 1970a: 173; 1970b: 265). Koehler's holotypes could not be located in the type collection at the MNHN. Unsuccessful inquiries were made to the collections at the Musée océanographique de Monaco (Michèle Bruni pers. comm. 2002) and to the Indian Museum in Calcutta. Further research was not attempted but could result in discovery of Koehler's *Investigator* asteroid types. As a consequence, neotypes have not been designated.

Descriptions of these species from Koehler (1909), written in French, were incomplete, and re-descriptions with photo images, rather than line drawn illustrations that were presented in the original description, are provided below. Full descriptions and figures for adult specimens of *Cladaster analogus*, *Floriaster maya*, and *Circeaster americanus* were published in Halpern (1970a, b) and Clark & Downey (1992) and are omitted here. Outgroup taxa are described and summarized, followed by the nine *Circeaster* species included in the phylogenetic tree (Fig. 1). A key to species included herein is provided (Appendix 1).

Genus *Lydiaster* Koehler, 1909

Lydiaster Koehler, 1909: 91. — Halpern 1970a: 265.

TYPE SPECIES. — *Lydiaster johannae* Koehler, 1909.

DIAGNOSIS. — Monotypic, see species diagnosis below.

Lydiaster johannae Koehler, 1909
(Fig. 2A-D)

Lydiaster johannae Koehler, 1909: 91, pls III, fig. 9, VII, figs 1, 2, VIII, fig. 1.

Circeaster johannae – Halpern 1970a: 265; 1970b: 173. — Clark 1993: 251.

MATERIAL EXAMINED. — **Madagascar**. 104°15.7'S, 43°01.5'E, 750-810 m, 29.XI.1973, 1 dry spec., R = 11.5 cm, r = 4.1 cm (MNHN EcAs 11724).

DISTRIBUTION. — Previously recorded only from northern Indian Ocean (type locality), 6°31'N, 79°38'45'E, 733 m (401 fms). Occurrence extended south to Madagascar. 733-810 m.

DIAGNOSIS. — $R/r > 2.7$. Abactinal arm plates similar in size to those on disk. Granules two to five, and paddle-like pedicellariae with sharp teeth present (Fig. 2B) on disk and arm plates. Abactinal, marginal, actinal surface/peripheral granules, coarse, angular. Marginal plate surface covered with granular spinelets. Spinelets more abundant on inferomarginals than on superomarginals. Arms broad, elongate. Actinal plates with one or two of any of the following: enlarged tubercles, paddle-like pedicellariae with sharp teeth, spines with roughened tips. Actinal granules angular, coarse with roughened tips. Furrow spines six or seven, angular in cross-section. Enlarged subambulacral spine laterally adjacent to adambulacral paddle-shaped, pedicellariae with sharp teeth. Enlarged subambulacral granules two to five, polygonal in cross-section present abradial to pedicellariae, adjacent to actinal plate region.

APOMORPHY LIST. — Nodes 24 to 23: 1.3, plate surface convex; 1.4, granules present; 1.6, granules coarse, round; 1.7, granule density heavy on central disk; 1.9, accessories form plate periphery; 2.1, SM spinelets present; 2.2, IM spinelets present; 2.6, MP peripheral granules fine; 2.8, IM accessories densely packed; 2.9, MP interradial abundance high; 2.10, MP peripheral granules fine; 3.1, actinal spinelets present; 4.3, subambulacral accessories abundant; 6.1, arms elongate. Nodes 23 to *Lydiaster johannae*: 2.7, SM accessories densely packed.

DESCRIPTION

Disk, large thickened. Interradial arc curved to linear. Arms triangular, upturned. Disk surface swollen, sunken interradially. Disk plates rounded to irregularly polygonal, mound-like, convex. Plate size largest along radial and abradial series, decreasing in size distally. Disk plates smallest adjacent to

superomarginal-disk boundary. Arm plates with no significant difference in size compared to disk plates. Arm plates in three or four series, irregularly distributed along arm. Distinct plate series absent. Granules 1-12 in number, large and coarse, present on plate surface. Granules crowded at disk center (8-12 per plate), decreasing in number (one to two per plate) and becoming more widely scattered closer to the disk-superomarginal boundary. Granules, enlarged, tubercular in appearance. Where granules have been removed or abraded, shallow concavities present. Granules present on disk and arms absent distally, approximately three to five superomarginal plates away from terminal plate. Only one to six granules present on arm plates. Pedicellariae relatively large, three to six teeth per valve, scattered over abactinal plate surface; typically one per plate, more heavily concentrated centrally on disk. Plates lacking surface granulation or pedicellariae smooth. Peripheral granulation, 10-60, typically 20-35, in number, evenly distributed around dorsal plate border. Peripheral granules angular with roughened tips, becoming jagged laterally between inferomarginal and superomarginal series.

Madreporite polygonal, enlarged, swollen, with well-developed grooves. Flanked by eight or nine abactinal plates.

Marginal plates 50-65 in number, from arm tip to arm tip. Largest interradially, decreasing in size distally. Paddle-like pedicellariae with three to six pointed teeth per plate present on surfaces of both marginal plate series. Typically one per plate, found near plate periphery adjacent to actinal intermediate region, or adjacent superomarginal or inferomarginal plate. Marginal series bordered by 20-90 angular-quadrant granules, evenly spaced. Peripheral granules form complete periphery, forming offset double rows between plates, forming shallow grooves between them. Peripheral granules largest along lateral edge between superomarginal and inferomarginal series, becoming finer between superomarginal and inferomarginal series. Peripheral accessories similar in shape and number to those of surrounding superomarginals.

Superomarginals widest interradially, becoming narrower distally with angular to rounded edges. Border with abactinal disk region straight to curved

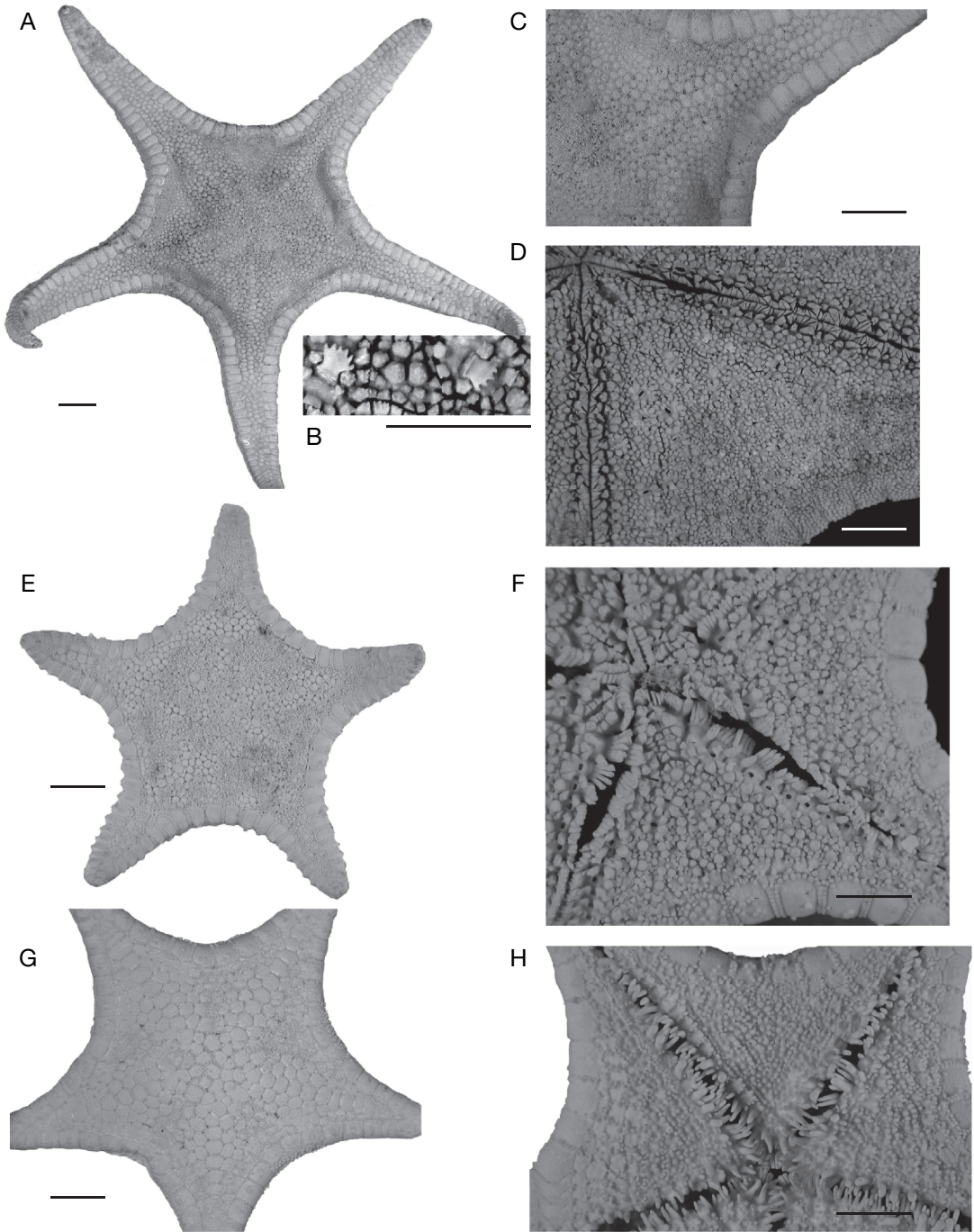


FIG. 2. — **A-D**, *Lydiaster johannae* (MNHN EcAs 11724); **A**, abactinal surface; **B**, pedicellariae; **C**, abactinal arm surface; **D**, actinal surface; **E, F**, *Floriaster maya* (NMNH E38662); **E**, abactinal surface; **F**, actinal surface; **G, H**, *Cladaster analogus* (NMNH E38569); **G**, abactinal surface; **H**, actinal surface. Scale bars: A, C-E, G, 1.0 cm; B, F, H, 0.5 cm.

border. Sharp, thorny, granulose spinelets, 20-80 in number, typically 50-66, uniformly cover superomarginal surface. Spinelets largest, sharpest along lateral edge, becoming rounder, more hemispherical on periphery of plate, adjacent to inferomarginals and abactinal disk surface. Spinelets/granules scattered, highest abundance interradially, decreasing distally toward arm tips. Superomarginals one to six plates away from terminals with zero to eight granules/spinelets.

Inferomarginal series forming lateral ledge below superomarginals. Inferomarginal surface with 0-90 crowded granulose spinelets, covering nearly all open space. Granules/spinelets most heavily cover dorsoventral and lateral surfaces but absent adjacent to superomarginal plates. Abundance of granules/spinelets highest interradially, decreasing distally. Inferomarginals, three to six plates away from terminals, bare or nearly so. Inferomarginal contact with actinal intermediate region straight to concave.

Terminal plate enlarged, two to three times size of adjoining superomarginals; triangular in outline with angles, blunt.

Actinal regions large, with single actinal plate series extending nearly 75% of arm length. Actinal plates polygonal, forming six or seven irregular chevrons. Actinal series adjacent to adambulacral series large; plates hexagonal. Chevrons adjacent to inferomarginal series smaller, more irregular in shape. Actinal plates covered with 2-10 large, block-like, angular to hemispherical granules, many with tips roughened. Several plates with one to four, large, blunt spine-like tubercles, polygonal in cross-section with tip roughened to jagged. Shallow grooves present. Single paddle-like pedicellariae with three to six teeth per valve present on actinal plates, scattered over actinal surface. Granule/spinelets, pedicellariae, tubercles more crowded adjacent to inferomarginal plate series, becoming more evenly spaced adjacent towards mouth and adambulacral series. Actinal accessories crowded along arm plates. Tubercles and pedicellariae continue along plates, decreasing in abundance distally. Distalmost actinal arm plates covered only by two to eight hemispherical granules. Actinal plate bordered by 5-15 granules, evenly spaced, block-like, angular in cross-section, many with tips roughened.

Adambulacral plates pentagonal. Furrow spines, four to six in number, compressed, triangular to prismatic in cross-section, thickened, arranged in continuous linear series. Pedicellariae, large and paddle-like, on adambulacral plate abradial to furrow spines, adjacent to one or two enlarged subambulacral spines. Spines triangular to prismatic in cross-section, with tip roughened. Remainder of adambulacral plate covered by four to eight angular, blockish granules similar to those of actinal plate surface, and one or two spine-like tubercles identical to those on actinal plate surface. Peripheral granules, 8-10, similar to those on actinal plates.

Mouth plate furrow spines, 10-15, similar to those on adambulacral plates, triangular to polygonal/prismatic in cross section. Compressed, blunt with tips roughened. Spines on mouth plates enlarged, triangular in cross-section. Mouth plates covered with blockish-angular granules similar to those on actinal plates. 10-15 granules form edge adjacent to suture between mouth plates, remainder of plate covered by 15-20 enlarged blockish-angular granules with tips roughened.

Genus *Floriaster* Downey, 1980

Floriaster Downey, 1980: 105. — Clark & Downey 1992: 243. — Clark 1993: 253.

TYPE SPECIES. — *Floriaster maya* Downey, 1980.

Floriaster maya Downey, 1980 (Fig. 2E, F)

Floriaster maya Downey, 1980: 105, figs 1, 2. — Clark & Downey 1992: 244, pl. 56G-H. — Clark 1993: 253.

HOLOTYPE. — Caribbean Sea. Southern end of Yucatan Channel, 20°45'N, 86°27'W, 933-1024 m, 6.VII.1970, 1 dry spec., R = 4.0 cm, r = 2.0 cm (NMNH E18324).

OTHER MATERIAL EXAMINED. — Bahamas. Blake Plateau, North Atlantic Ocean, 28°06'N, 77°08'W, 1023-1153 m, 21.IX.1980, 2 dry specs, R = 3.9 cm, r = 2.0 cm; R = 5.1 cm, r = 2.1 cm (NMNH E38662).

DISTRIBUTION. — Caribbean Sea. 933-1153 m.

DIAGNOSIS. — $R/r \approx 2.0-2.5$. Abactinal plates round to polygonal in shape small, irregularly distributed

relative to *Cladaster*. Enlarged, round tubercles covering abactinal, actinal surfaces. Abactinal, actinal plates with coarse, angular peripheral granules. Marginal plates with tubercles and coarse, nubbin-like granules. Approximately 30 marginal plates present from interradius to inter-radius. Interradial arcs linear. Paddle-like pedicellariae on adambulacral plates; subambulacral spine, enlarged, blunt, abradial to pedicellariae. Furrow spines five to seven, compressed, angular in cross-section.

APOMORPHY LIST. — Nodes 24 to *Floriaster maya*: 1.5, single tubercle present; 1.8, tubercles present on distal arm surface.

Genus *Cladaster* Verrill, 1899

Cladaster Verrill, 1899: 175. — Fisher 1911: 221. — Bernasconi 1963: 13; 1963: 255. — Halpern 1970b: 179. — Clark & Downey 1992: 238. — Clark 1993: 251.

TYPE SPECIES. — *Cladaster rudis* Verrill, 1899.

Cladaster analogus Fisher, 1940 (Fig. 2G, H)

Cladaster analogus Fisher, 1940: 123, fig. D, pl. 4, figs 1-3. — Bernasconi 1963: 14. — Clark & Downey 1992: 239. — Clark 1993: 251.

MATERIAL EXAMINED. — **South Atlantic.** Scotia Sea, 53°20'S, 42°42'W, 417-514 m, 29.XI.1986, 1 dry spec., R = 3.5 cm, r = 1.9 cm (NMNH E38569). — Heard Island (near Kerguelen) on rocks, 49°58'75'S, 73°42'04'E, 930 m, III.1983, 1 dry spec., R = 4.2 cm, r = 2.3 cm (MNHN EcAs 11737).

DISTRIBUTION. — The South Atlantic off the Falkland Islands, extending to the Scotia Sea and to Heard Island, near Kerguelen. 147-930 m.

DIAGNOSIS. — R/r ≈ 2.0-2.6. Abactinal plates polygonal, ordered. Abactinal, marginal, and actinal plate surfaces covered with enlarged, well-spaced granules. Enlarged granules also forming border around plates. Less than 30 marginal plates from arm tip to arm tip at R = 3.5 cm. Superomarginals abutted at arm tip. Furrow spines two to three, elongate, blunt, round in cross-section. Subambulacral spine blunt, enlarged. Paddle-like pedicellariae present.

APOMORPHY LIST. — Nodes 24 to *Cladaster analogus*: 1.4, granules enlarged; 1.6, granules, enlarged, pointy; 2.3, SM abutted over midline; 3.2, actinal granules enlarged, pointy; 4.2, abradial to furrow spines.

Genus *Circeaster* Koehler, 1909

Circeaster Koehler, 1909: 83. — Halpern 1970a: 265. — Downey 1973: 47, 55, pl. 21A, B. — Clark & Downey 1992: 237. — Clark 1993: 250.

TYPE SPECIES. — *Circeaster marcelli* Koehler, 1909.

DIAGNOSIS. — R/r > 2.5. Disk swollen, large. Abactinal arm plates two to three times larger than disk plates. Arm plates generally bare. Disk plates with granules, round, hemispherical. Marginal plates wide in most species. Spinelets or granules present along dorsolateral/ventrolateral edges and surfaces of marginal plates. Greater density of spinelets/granules on inferomarginals than on superomarginals. Superomarginal plates abutted over midline in several species. Arms elongate tapering, with tips upturned. Interradial arcs linear to curved. Actinal plates irregular in some species, covered with granules or spinelets. Pedicellariae uncommonly present. Adambulacral furrow spines 6-15. Enlarged subambulacral spine or spines present. Prominent, paddle-like, bivalve, or sunken pedicellariae with jagged teeth present. Pedicellariae present on adambulacral plates.

APOMORPHY LIST. — Nodes 22 to 21: 1.6, granules fine; 2.7, SM density moderately packed.

Circeaster loisetteae n. sp. (Fig. 3)

HOLOTYPE. — **Western Australia.** NW of Tork Sound, soft bottom, 12°54.4'S, 123°0.2'E to 12°50.6'S, 123°0.4'E, 452-462 m, 15.II.1984, 1 dry spec., R ≈ 12.0 cm (arm broken), r = 4.6 cm (WAM Z20670).

PARATYPES. — **Western Australia.** NW of Beagle Bay, Western Australia, soft bottom, 15°08.6'S, 121°3.4'E to 15°6.0'S, 121°6.6'E, 500-504 m, 11.II.1984, 1 dry spec., R = 12.0 cm, r = 5.4 cm (WAM Z20714). — NW of Collier Bay, WA soft bottom, 13°50.3'S, 122°18.5'E to 13°53.4'S, 122°16.7'E, 452-450 m, 13.II.1984, 1 dry spec., R = 12.4 cm, r = 4.2 cm (WAM Z20715). — WNW of Lacepede Archipelago, Western Australia on soft bottom, 15°40.2'S, 120°37.3'E to 15°42.6'S, 120°34.6'E, 500-504 m, 10.II.1984, 3 dry specs, R = 12.7 cm, r = 4.5 cm, R = 11.3 cm, r = 4.1 cm, R = 12.0 cm, r = 4.7 cm (WAM Z20716).

Solomon Islands. 9°6.9'S, 159°53.2'E, 896-912 m, 25.IX.2001, 1 dry spec., R = 16.1 cm, r = 4.5 cm (MNHN EcAs 11726).

ETYMOLOGY. — This species is named for Loisetee Marsh, retired curator of Echinoderms at the Western Australian Museum and collector of many of the specimens examined herein.

DISTRIBUTION. — Western Australia/Timor Sea, Solomon Islands. 452-912 m.

DIAGNOSIS. — $R/r \geq$ approximately 3.0. Abactinal arm plates not enlarged relative to disk plates in specimens with $R \approx 12.0$ cm (Fig. 3B), but present at $R = 16.0$ cm (Fig. 3D). Abactinal granules up to three if present, sparingly distributed over disk center. *Circeaster* with superomarginals abutted at midline. Marginal plate series with granular spinelets, these are more abundant on inferomarginal plates (ventral surface). Actinal surface covered by spinelets, spine-tipped granules. Pedicellariae paddle-shaped. Subambulacral spine absent.

APOMORPHY LIST. — Nodes 16 to 14: 1.5, granules, when present; 1.7, granules distributed heavily on disk center to completely absent; 2.10, MP peripheral spinelets present.

Nodes 14 to *Circeaster loisetteae* n. sp.: 2.3, SM abutted at midline.

DESCRIPTION

Disk thick. Arms elongate ($R/r \approx 3.0$ to ≈ 5.0), tapering. Tips upturned. Interradial arcs rounded. Abactinal plates polygonal to rounded, mound-like, slightly tumid to flat, similar in size, but smaller, more numerous interradially. Disk plates relatively small (*c.* 10-12 across arm base). Abactinal plates largely limited to disk in specimens under $R \approx 12.0$ cm forming acute triangular regions adjacent to proximal superomarginals abutted at midline. Abactinal arm plates, few, bare, two to three times the size of those on disk, present on arm in specimen with $R = 16.0$ cm, occurring irregularly between superomarginals, abutted on abactinal surface. Arm plate arrangement varies from arm to arm. Grooves present over radial regions, becoming shallower interradially. Granules sparingly present (zero to three per plate) but largely absent. Occurrence of granules increases adjacent to madreporite. Peripheral border composed of 12-50 (typically 20-35) coarse, evenly spaced, angular to rounded granules. Paddle-like pedicellariae, about one fifth the size of the plate, with wide, serrated valves, distributed along radial and abradial plates, largely absent from interradial regions. Madreporite hexagonal to polygonal flanked by five or six polygonal plates in the smaller specimens ($R \approx 12.0$ cm), 10-12 plates in the largest specimen.

Marginal plates numerous, 60-70 per interradius (arm tip to arm tip), angular in cross-section,

forming distinct dorsolateral edge. Marginal plates surrounded by *c.* 60-120 angular-rounded granules decreasing distally. Terminal plate rounded, enlarged (approximately equivalent in size to the adjacent terminal superomarginals).

Superomarginals abutting at midradius for over 50% of the arm length. Abactinal plates irregularly present between abutting superomarginals, resulting in angular or polygonal contact boundaries between superomarginal and abactinal disk plates. Contact boundary between superomarginal and disk plates curved to straight, plates with angular to rounded corners. Superomarginal plates narrow. Sharp spinelets, 2-20 in number, scattered, most abundant interradially (*c.* 18) decreasing distally on dorsolateral edge of each superomarginal plate, becoming absent from distalmost superomarginal plate adjacent to tip (approximately 12-15 away from terminal plate). Superomarginal plate surfaces otherwise lacking accessories on both dorsal side adjacent to disk plates, lateral side, adjacent to inferomarginal plate contact.

Inferomarginals rounded-angular in cross-section, forming discrete ventrolateral angle. Inferomarginal surface convex. Lateral surface of inferomarginal plate adjacent to superomarginals bare. Sharp, conical, evenly spaced spinelets, approximately 2-70 (typically about 60) in number, covering all but bare inferomarginal surface adjacent to the superomarginals. Spinelets adjacent to actinal region largest, most prominent.

Actinal region large, composed of approximately six to nine irregular chevrons. Shallow grooves present. Actinal plates limited to disk, with a small series of single plates extended to base of arm. Chevrons adjacent to furrow plate series most ordered, becoming smaller, more jumbled approaching contact boundary with inferomarginal series. Actinal plates more elongate, quadrate in shape proximal to tube foot furrow, becoming more irregularly polygonal at contact boundary with inferomarginal plates. Actinal plates covered by 4-50 coarse, crowded granules. One to eight, typically one to four, sharp, pointed spinelets present on center of nearly every actinal plate. Spinelets stand two to three times over low-rounded granules. Actinal accessories evenly scattered on plate surface. Spinelet abundance higher on plates adjacent to inferomarginal-actinal

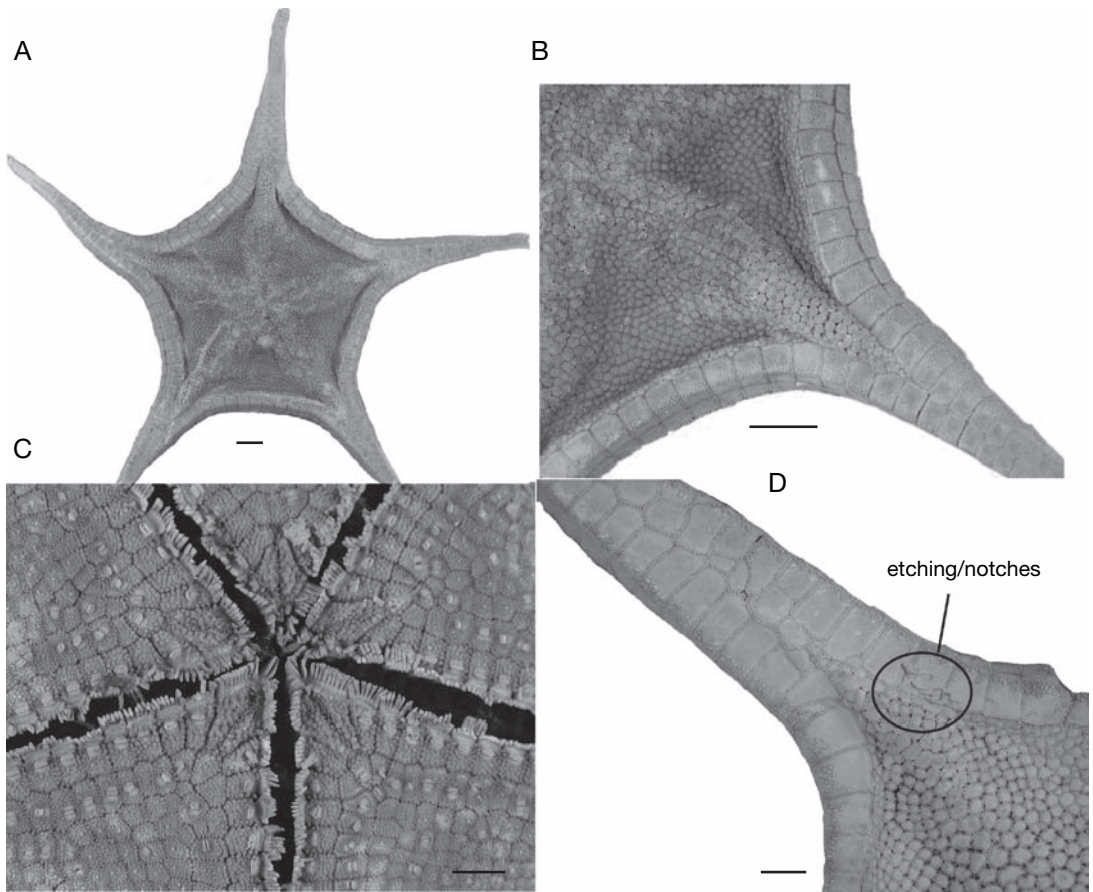


FIG. 3. — *Circeaster loisetteae* n. sp.: **A-C**, WAM 20716; **A**, abactinal surface showing absence of enlarged arm plates; **B**, abactinal surface of arm showing enlarged arm plates; **C**, actinal surface; **D**, MNHN EcAs 11726, Solomon Islands, abactinal arm surface showing etching/notches on marginal plates from possible predation (see Discussion). Scale bars: A, B, D, 1.0 cm; C, 0.5 cm.

plate contact boundary. Periphery of each plate surrounded by 15-50 (usually about 20-30) sharp spinelets, forming close border.

Actinal pedicellariae variably present. When present, one or two pedicellariae present on all adambulacral plates and actinal plates adjacent to adambulacrals. Abundance becoming irregular to absent adjacent to the inferomarginal plate series. Paddle-like pedicellariae present, with serrated valves. Three to seven teeth present on each valve. Pedicellariae positioned on proximal edge of adambulacral. In MNHN EcAs 11726 (from the Solomon Islands) pedicellariae largely absent from intermediate actinal region.

Five to 10 (usually seven to eight) thickened furrow spines, polygonal to quadrate in cross-section with roughened tips. Furrow series straight to curved. Bare region between furrow spines, adambulacral accessories. A single large, paddle-shaped pedicellaria with five to seven prominent teeth sits immediately behind furrow spines, either in bare region or more centrally on adambulacral plate; pedicellariae otherwise absent. One to six sharp spinelets present on adambulacrals, actinal plates additionally covered by 30-40 crowded pointed to round granules. Twenty to 30 spiny to rounded, well-spaced granules forming peripheral border around each plate.

Furrow spines on mouth plates, 8-15, polygonal to quadrate in cross section on mouth plates. Paired, enlarged, thick, triangular in cross-section, with smooth surface at tip of mouth plate. Oral plates covered with 70-80 heterogeneous granules, most with tips, roughened or spiny. Subambulacral spines enlarged, quadrate to polygonal in cross-section. Larger subambulacral spines with clavate tips. Two sets of enlarged granules, 10-15 with rough tips form incomplete to complete edge along groove present between mouth plates.

Circeaster helenae n. sp.
(Fig. 4A, B)

HOLOTYPE. — Western Australia. 145 nautical miles NW off Port Hedland, mud, 18°37'S, 116°14.6'E to 18°38'S, 116°44'E, 696-700 m, 6.IV.1982, 1 dry spec., R ≈ 10-11 cm (arms broken, tips missing), r = 3.9 cm (WAM Z20671).

ETYMOLOGY. — This species is named for Dr Helen Rotman-Clark, National Institute of Water and Atmospheric Research, in honour of her many contributions to asteroid taxonomy.

DISTRIBUTION. — Western Australia, Timor Sea/Indian Ocean. 696-700 m.

DIAGNOSIS. — R/r ≥ 2.5. Granules largely absent from abactinal surface. Superomarginal plates abutted at midline. Superomarginals widest at arm base. Spinelets cover marginals, actinal plate surfaces. Spinelets cover dorsolateral, lateral, ventrolateral marginal plate, actinal surface. Subambulacral spine absent.

APOMORPHY LIST. — Nodes 15 to *Circeaster helenae* n. sp.: 2.3, SM abutted over midline; 2.9, MP abundance, moderate; 7.1, bivalve pedicellariae present.

DESCRIPTION

Disk thick, broad. Arms thick, wide. Abactinal disk plates form stellate region. Abactinal plates round to polygonal. Plates larger, oblong along radial regions becoming smaller, rounder interradially. Abactinal plates flattened to convex. Hemispherical granules few, scattered across surface, approximately one to four per plate, highest density around madreporite. Some plates with tiny paddle-like pedicellariae bearing approximately four to six teeth. Peripheral granules, 15-40, rounded, forming complete, evenly

spaced border, forming shallow grooves between plates. One interradial with sublethal damage or congenital defect with approximately seven superomarginal plates present between abactinal interradial plates, similar in appearance to those described below. Madreporite polygonal, large, flanked by seven to nine granule covered plates.

Marginal plates, 30-50 arm tip to arm tip (arm tips are missing in the available specimen). Marginal plates wide, quadrate to diamond-shaped in lateral cross-section, edges rounded, peripheral granules, 100-150, distributed evenly around border of marginal plates. Both marginal plate series with spinelets or granules with spiny tips. Marginal plates. Shallow grooves present between marginal plates. Peripheral accessories around ventral inferomarginal surface with spinelets.

Superomarginals largest at arm base where plates about at midline. Superomarginals offset, forming jagged contact boundary. Interradial plates are approximately 40-50% smaller than those at arm base. Superomarginals decrease in size distally along arm. Spinelets, 10-40 per superomarginal plate, highest abundance interradially, decreasing distally. Spinelets present dorsolaterally, absent from region adjacent to contact boundary between superomarginal and abactinal disk and region adjacent to boundary with inferomarginal plates along lateral surfaces on all plates. Superomarginal dorsal surface bare.

Region on inferomarginals adjacent to superomarginal contact bare. Some flattened to hemispherical granules on lateral inferomarginal surface. Remaining inferomarginal surface with 50-100 sharp, conical spinelets and/or spiny tipped granules, covering ventral, ventrolateral surface. Spinelets evenly distributed; greatest abundance on ventral inferomarginal plate surface. Arm tips, terminal plates unknown.

Actinal surface with six or seven chevrons, these irregular interradially, adjacent to inferomarginals. Chevron plates polygonal to rounded, those in series adjacent to adambulacral furrow with largest-sized plates, pentagonal-hexagonal in shape. Consecutive chevron plates elongate, polygonal, becoming more irregular in shape interradially adjacent to inferomarginals. Actinal surface covered with three to eight short, sharp spinelets similar

to those on ventral inferomarginal surface and/or 15-30 pointed-rounded granules. Spinelets, when present, occur centrally on plate with granules or other accessories absent between spinelets. Granules dense, evenly distributed. Large bivalve pedicellariae with thin, flat valves, with 10-15 low serrations across edge, scattered across actinal surface. Largest chevron adjacent to adambulacrals with prominent large spinelets, approximately three to six enlarged pedicellariae on each plate, surrounded by 20-30 accessory granules/spinelets. Actinal plate periphery 20-40 granules similar to those elsewhere on body, forming evenly spaced border, shallow grooves between actinal plates.

Furrow spines, six to eight, flattened, chisel-shaped, arranged in weakly curved to straight series. Discrete bare region present between furrow spines and enlarged pedicellariae on adambulacrals. Adambulacrals pedicellariae composed of either one enlarged, curved pedicellaria or two paddle-shaped pedicellariae closely adjacent to one another. Serration on valves low to absent on single, enlarged valves, but smaller paddle-shaped pedicellariae with seven or eight prominent teeth on each valve. A second space sets off the pedicellaria from remaining accessories on the adambulacrals plate. Adambulacrals plate surface covered by approximately three to five (usually four) large, tapering spinelets, followed by 6-10 short, granular spinelets identical in size, shape to those on actinal surface.

Furrow spines on mouth plates, approximately 10-12, with enlarged blunt, round spines directed into mouth. Spines flattened, triangular to polygonal in cross-section. Enlarged curved pedicellariae similar to others on adambulacrals plate present behind furrow spines, discrete space on adambulacrals plate. Approximately 18-25 enlarged granules, spiny-angular flanking suture on mouth plates. Suture deep. Approximately 20-35 granules covering adambulacrals surface.

Circeaster magdalenae Koehler, 1909
(Fig. 4C-E)

Circeaster magdalenae Koehler, 1909: 88, pl. V, figs 1-3, VI, fig. 2.

MATERIAL EXAMINED. — **Madagascar.** 13°50.0'S, 47°37.0'E, 850-1125 m, 27.II.1975, 1 dry spec., R = 11.6 cm, r = 5.2 cm (MNHN EcAs 11725).

DISTRIBUTION. — Previously recorded only from 15°11'N, 72°28'45'E, 1668-1703 m (912-931 fms). Occurrence extended to Madagascar. 850-1703 m.

APOMORPHY LIST. — Nodes 16 to 15: 7.3, elongate pedicellariae present; 7.4, sunken pedicellariae present. Nodes 15 to *C. magdalenae*: 1.6, granules coarse, round.

DIAGNOSIS. — R/r = 2.2. Transition abrupt, between disk and arm plates with bare abactinal arm plates. Pedicellariae elongate with enlarged jagged teeth, sunken into body surface on actinal surface, adambulacrals plates. Spinelets cover dorsolateral, lateral, ventrolateral marginal plates, actinal surface. *Circeaster* with thick, broad arms. Subambulacrals spine absent.

DESCRIPTION

Disk, thick, large. Arms broad at base. Abactinal plates rounded to irregularly polygonal. Plate surface convex, low, mound-like. Abactinal plates, larger at center of disk, decreasing in size, but not greatly so, adjacent to contact with superomarginal plates, adjacent to the base of the abactinal arm plates. Carinal and primary circling plate series not clearly distinguished. Granules, zero to six in number present on each abactinal plate; coarse, low hemispherical, crowded. Granule abundance heaviest at disk center (five or six per plate), decreasing (one or two per plate) distally adjacent to superomarginals. Granule size increases as granule number decreases. Individual granules can occupy nearly entire abactinal plate surface. Granular-shaped spinelets, one to three in number, also present on disk periphery. Small paddle-like pedicellariae, similar in size to smaller granules with three to five teeth on each valve, rare on abactinal surface (only one or two present on specimen). Disk plates adjacent to superomarginals, largely bare of granules. Arm plates smooth, bare, enlarged three to six times the size of abactinal disk plates, directly abutting forming a mosaic distinctly separated from disk plates (Fig. 4D), few granules present. Abactinal arm plates largest at arm base, decreasing in size until adjacent to terminal plate, extending to arm tip. Plates hexagonal, becoming more irregularly polygonal to rounded distally.

Peripheral granules, 8-60, usually 25-35, forming complete borders around all abactinal plates. Granules form crowded borders around disk plates, evenly spaced around arm plates.

Madrepore polygonal, convex, grooves poorly developed, flanked by eight abactinal plates.

Marginal plates 60-75 (from arm tip to arm tip); widest, largest, interradially becoming smaller, more elongate distally. Superomarginal and inferomarginal series correspond one to one interradially. Superomarginal and inferomarginal series offset, becoming more jagged distally.

Superomarginal corners angular to rounded. Superomarginal dorsolateral border rounded to flattened. Superomarginals forming enlarged, irregular jagged to polygonal contacts intruding onto arm region adjacent to bare arm plates. Bare superomarginal surface identical to abactinal arm disk surface. Sharp, thorny spinelets, 1-35 in number per plate, widely scattered, on dorsolateral, lateral surfaces. Spinelets absent from disk surface adjacent to abactinal disk plates but covering dorsal surface of superomarginal plates on arm plates adjacent to arm disk plates. Spinelets/granules most abundant interradially, decreasing distally. Spinelets adjacent to terminal plate, hemispherical, rounded. Peripheral granules, 20-90, bead-like, becoming more pointed, spine-like along lateral edge adjacent to inferomarginal plates.

Inferomarginal series, slightly extended, forming narrow border, especially along arms. Inferomarginal plates wide, forming prominent ventral border. In cross-section, ventrolateral border rounded contact border with actinal intermediate plates, convex. Ventrolateral surface with 2-100 granule-like spinelets, highest interradially, decreasing distally, arm becoming bare or nearly so one to five plates away from terminal. Spinelets more spine-like interradially, more granule-like distally, scattered widely over plate surface. Spinelets most abundant covering ventral, ventrolateral, lateral plate surfaces, becoming bare laterally, adjacent to superomarginal contact. Inferomarginals adjacent to terminal, short, tiny granular spinelets/granules, 30-150 forming complete border. Total number of peripheral granules decreases distally. Peripheral accessories more spinelet-like interradially, becoming more granule-like distally,

adjacent to the terminal plate. Inferomarginals rarely with one or two bivalve pedicellariae, three to six sharp teeth on each valve.

Terminal plate triangular, smooth, approximately size of adjoining superomarginal plate.

Actinal regions large, extending from disk along approximately 75% of arm distance. Actinal plates in six to eight irregular chevrons, becoming less ordered, more irregular away from the ambulacral furrows, toward interradiar arcs, inferomarginals. Plates in chevron adjacent to adambulacral plates largest, quadrate in shape. Actinal plates covered by 6-40 sharp conical spinelets, crowded but evenly spaced. Size largely homogeneous, but spinelets on actinal arm plates are two to three times larger. Spinelets not forming distinct border but forming nearly continuous cover up to contact with inferomarginals, forming shallow channel between actinal, inferomarginal plate series.

Spinelet cover nearly complete save for 20-30 unusual bivalve pedicellariae, inset into, flush with actinal surface. Pedicellariae shape variable: straight, boomerang-like, T-shaped to sinusoidal, large (may be present over one actinal) valves with 4-20 sharp, interlocking teeth.

Pedicellariae separated from other actinal spinelets by discrete furrows bordered by 14-18 enlarged spines on either side. No clear pattern of pedicellariae distribution evident, but higher numbers appear to be present along actinal arm adjacent to mouth plate regions in single specimen examined

Furrow spines, 8-10, compressed, narrow, triangular to polygonal in cross-section, identical in size. Adambulacral plate quadrate to polygonal, decreasing in size distally. Large pedicellariae, similar to that on the actinal plates, separated by a large gaps separating pedicellariae from furrow spines, other actinal spinelets on adambulacral plate. Furrow pedicellariae transverse to plate length, parallel to furrow spines, valves with 4-20 interlocking teeth. Pedicellariae straight to irregularly curved, few extending onto adambulacral plate adjacent to actinal intermediate region. Pedicellariae becoming smaller distally, shifting from single to two pedicellariae at approximately 30-40 adambulacral plates from terminal. Adambulacral plate covered by 30-50 short, sharp spinelets, largely homogeneous in

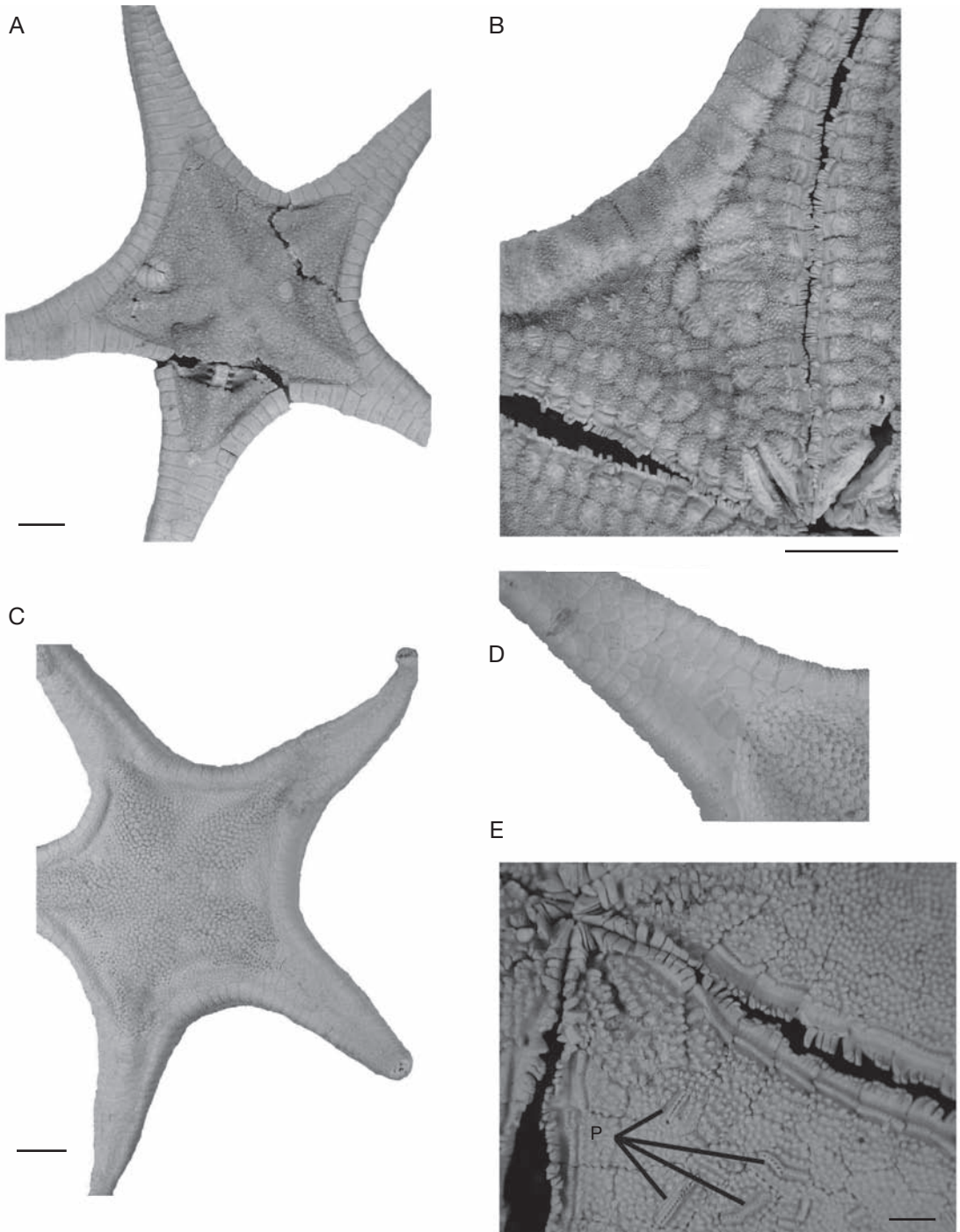


FIG. 4. — **A, B**, *Circeaster helenae* n. sp. (WAM Z20671); **A**, abactinal surface; **B**, actinal surface; **C–E**, *Circeaster magdalenae* Koehler, 1909 (MNHN EcAs 11725); **C**, abactinal surface; **D**, close-up of arm; **E**, actinal surface. Abbreviation: **P**, pedicellariae. Scale bars: A, C, 2.0 cm; B, D, 1.0 cm; E, 0.5 cm.

size, occur with three to six larger spines, two to three times the size of other spinelets, increasing in size and abundance distally. Plates adjacent to mouth plate or closer to mouth region with largely homogenous spinelets, increasing to one to three enlarged spines, approximately five or six plates away from mouth plates.

Furrow spines on mouth plates 12-15; enlarged, thickened, angular to polygonal in cross-section. Enlarged mouth plates directed into mouth; thickened, polygonal in cross-section. Furrow spines separated from mouth plate accessories by discrete furrow. Pedicellariae absent from mouth plates. Mouth plates covered by 30-50 blunt, curved, sometimes conical spines with smooth to jagged tips. Eleven to 12 enlarged spine-like granules form border to suture along each side of mouth plate. Other spines/spinelets on mouth plates similar to those on actinal plate surface.

Circeaster arandae n. sp.
(Fig. 5A-C)

HOLOTYPE. — Madagascar. 13°48.8'S, 47°29.4'E, 1800-2000 m, 27.II.1975, 1 dry spec., R = 9.5 cm, r = 2.2 cm (MNHN EcAs 11727).

PARATYPES. — Madagascar. 13°40.3'S, 47°32.5'E, 1600-1725 m, 28.II.1975, 1 dry spec., R = 10.4 cm, r = 2.3 cm (MNHN EcAs 11728).

New Caledonia. 24°28'S, 168°08'E, 2160 m, 3.IX.1985, 1 dry spec., R = 8.9 cm, r = 1.9 cm (MNHN EcAs 11729).

ETYMOLOGY. — This species is named for my colleague Danielle Aranda from Rio del Valle Junior High in Oxnard, California, in honour of her dedication to science education.

DISTRIBUTION. — New Caledonia to Madagascar. 1600-2160 m.

DIAGNOSIS. — $R/r \geq 4.0$. *Circeaster* with relatively small disk, arms relatively narrow. Abactinal arm plates bare, enlarged 3-5 times disk plates. Transition between disk and arm plates abrupt. Marginal plates with single prominent sharp spine, with secondary spinelets. Marginal plates on disk with high density of sharp spinelets. Ventrolateral edge of inferomarginal plates with several sharp spinelets. Adambulacral with furrow spines, 1-2 paddle-like pedicellariae, subambulacral spine, enlarged.

Tips roughened/fluted adjacent to pedicellariae. Spinelets cover adambulacral, actinal plates.

APOMORPHY LIST. — Nodes 21 to 16: 2.11, SM contact with abactinal plates, curved to straight; 4.1, subambulacral spine, single, enlarged; 4.2, abradial to furrow spines; 6.2, arms narrow.

Nodes 22 to *Circeaster arandae* n. sp.: 2.4, superomarginal spines present; 2.5, inferomarginal spines present; 2.8, IM accessories, few, scattered; 2.10, spinelets present as peripheral accessories on marginal plates.

DESCRIPTION

Disk relatively small. Interradial arcs linear to curved. Abactinal disk plates weakly convex, largely bare; many with granules or moderate-sized tubercles. Abactinal disk plates round to polygonal. Size and shape largely homogeneous, although plate size decreases closer to superomarginals. Granules and nubbin-like tubercles most heavily concentrated on central disk region, decreasing in abundance closer to the edge of the disk, base of arm. Tubercles absent from New Caledonian specimen, present only on Indian Ocean specimens. When present, three to five coarse low-lying to hemispherical granules; angular to polygonal in cross-section, scattered on disk surface but absent from arm plates and peripheral disk regions. Abactinal granules crowded, often densely packed, sometimes obscuring plate surface. Highest density of granules on central region of disk. Granules and tubercles absent on New Caledonia specimen, present on Indian Ocean specimens. Pedicellariae, sugar-tong-like, three or four prominent teeth on valves, uncommon on abactinal surface, randomly distributed. Madreporite large, swollen, highly convex, surrounded by 12-18 abactinal plates.

Arm plates convex, three to five times the size of disk plates, continuing along arm in multiple rows, two or three plates continue from base distally, attenuating to one row of abactinal plates near arm tip, the 15-18 distalmost abactinal plates. Some tubercles present on base of arm, but plate surface largely bare. Pedicellariae absent from arm plates. Peripheral granules 10-20 (typically 12-15), angular to rounded in cross-section becoming more angular, prominent on New Caledonia specimen, more rounded, polygonal on Indian Ocean specimens. Peripheral granules around arm plates smaller, 20-60 surround smaller to larger plates, respectively. Marginal plates, 50-65

(typically about 55–60) in each interradius. Marginal plates largest interradially, becoming smaller distally. Distalmost superomarginals, often four to eight plates from the terminal plate, abut at arm tip. Marginal plates angular in cross-section, forming distinct lateral edge. Tong-shaped pedicellariae, with three to five teeth, present on Indian Ocean specimens on superomarginal and inferomarginal plates on spine clusters. Spinelets form continuous periphery around each marginal plate.

Superomarginal plate shape quadrate, forming distinct dorsal border, forming convex to linear contact with abactinal disk surface. Prominent, sharp, conical spine or array of conical spinelets present on dorsolateral superomarginal plate surface, which is otherwise bare. Granules or other accessories absent. Spinelets present on three to eight middle interradiial superomarginal plates. Spines present or absent from these plates, but when present, in conjunction with 5–10 sharp spinelets. Superomarginal spines also absent on distalmost 10–15 plates from terminal, but present as continuous series on all other superomarginals.

Inferomarginals attenuate in size but at different rate from superomarginals, retaining a larger size relative to its superomarginal counterpart adjacent to arm tip. Clusters (7–25, usually approximately 15) of sharp, conical spinelets present on 16–25 middle interradiial inferomarginal plates. Low-lying granules with points also present. Prominent spines similar to those on superomarginal spines, present on ventrolateral surface of inferomarginal plates occurring distally along arm, ending three to six plates from terminal. Aside from spinelets, inferomarginal plate surface bare. Terminal triangular approximately two to three times the size of adjacent superomarginal plates.

Actinal regions relatively small, in three or four irregular chevrons. Actinal plate extend to base of arms, rounded to polygonal in shape. Prominent, tongue-like pedicellariae with three to five large teeth, nipple-like tubercles, sharp granular spinelets, and polygonal granules present on actinal plate surface, which is otherwise bare. Granular spinelets absent on New Caledonia specimen, present on Indian Ocean specimens. Actinal spinelets, 3–15 per plate, vary in size, scattered across different plates. Tubercles

uncommon, but with greatest abundance adjacent to inferomarginal plates. Peripheral accessories bead-like but becoming more spinelet-like in Indian Ocean specimens. Peripheral accessories/spinelets form incipient shallow, grooves.

Furrow spines 12–15, flattened, blade-like in linear to slightly convex order parallel to tube foot furrow. Discrete space separates furrow spines from large tongue-like pedicellariae, with three to five large teeth on valves. Additional bare regions surround pedicellariae. Peripheral granules, 12–15 with tips rough to spinelet-like. Adambulacral plate covered by five to seven spinelets/rough-tipped granules.

Furrow spines on mouth plates, 18–25. Mouth plate surface covered with accessory granules identical to those on actinal plates. 12–15 granules present along mouth plate suture, with tips roughened, worn down in Indian Ocean specimens. One or two large pedicellariae present on mouth angle plates adjacent, behind mouth plate furrow spines.

Circeaster marcelli Koehler, 1909

Circeaster marcelli Koehler, 1909: 84, pl. IV, figs 1, 2, pl. VI, fig. 1. — Clark 1993: 251.

MATERIAL EXAMINED. — No specimens available for examination.

DISTRIBUTION. — Recorded from 7°23'N, 75°44'E in the Indian Ocean. 1926 m (1053 fms).

DIAGNOSIS. — $R/r = 2.67$. Arm plates significantly larger than disk plates. Transition abrupt between abactinal disk and arm plates. Abactinal granules absent. Superomarginals not abutting at midline, arm plates continuous to terminal. Interradiial arcs linear. Spinelets and granules with spiny tips cover superomarginal, inferomarginal plates, actinal surface. Seven to eight thick, blunt furrow spines. Prominent paddle-like toothed pedicellariae, separated from furrow spines. Granules identical to actinal surface present on remainder of adambulacral plate.

APOMORPHY LIST. — Nodes 14 to *Circeaster marcelli*: 1.4, abactinal accessories absent; 1.6, no size, accessories absent.

DESCRIPTION

See Koehler (1909; translation in English of the description is available from the author).

Circeaster kristinae n. sp.
(Fig. 5D-F)

HOLOTYPE. — Timor Sea/Indian Ocean. NW Slope, 115 nautical miles NNW of Dampier, WA (Western Australia), 18°46'S, 116°24'E, no depth recorded, 1 dry spec, R = 12.1 cm, r = 3.4 cm (WAM Z20711).

PARATYPES. — Timor Sea/Indian Ocean. Off Port Hedland, WA, 149 nautical miles NW, on mud, 18°43'S, 116°35'E to 18°43'S, 116°33'E, 612-610 m, 7.IV.1982, 1 dry spec., R = 13.1 cm, r = 4.2 cm (WAM Z20672). — 18°38'S, 116°52'E to 18°38'S, 116°54'E, 600-594 m, 7.IV.1982, 1 dry spec., R = 12.3 cm, r = 3.9 cm (WAM Z20694). — W of Roebuck Bay, WA on muddy bottom, 18°04'S, 118°14'E to 18°00'S, 118°19'E, 400-396 m, 24.II.1984, 1 dry spec., R = 13.1 cm, r = 3.9 cm (WAM Z20707). — NW of York Sound, WA, 12°54.4'S, 123°0.2'E to 12°50.6'S, 123°0.4'E, 452-462 m, 15.II.1984, 1 dry spec., R = 13.3 cm, r = 4.2 cm (WAM Z20708). — NW of York Sound, WA, mud bottom, 12°48.1'S, 122°56.7'E to 12°50.6'S, 122°55.2'E, 496-504 m, 15.II.1984, 1 dry spec., R = 14.5 cm, r = 3.4 cm (WAM Z20709). — NW of Augustus Island, WA, on soft bottom, 13°17'S, 122°37.4'E to 13°18'S, 122°35.8'E, 494-484 m, 15.II.1984, 1 dry spec., R = 10.1 cm, r = 3.3 cm (WAM Z20712). — Off Port Hedland, WA, 124 nautical miles NNW, 18°20'S, 118°00'E to 18°19'S, 118°00'E, 320 m, 10.IV.1982, 1 dry spec., R ≈ 8.0 cm (arm broken), r = 3.2 cm (WAM Z20713). — C. 123 nautical miles NNW of Dampier, 18°52'S, 116°00'E, 550 m, 14.III.1992, 3 dry specs, R = 12.3 cm, r = 3.3 cm, R = 11.4 cm, r = 4.6 cm, R = 12.9 cm, r = 3.6 cm (WAM Z20722). — C. 123 nautical miles NNW of Dampier, WA, 18°48'S, 116°07'E, 555 m, 17.III.1992, 1 dry spec., R = 10.6 cm, r = 3.3 cm (WAM Z20723). — C. 23 nautical miles NNW of Dampier, 18°52'S, 116°00'E, 550 m, 14.III.1992, 3 dry specs, R = 11.0 cm, r = 3.5 cm, R = 10.6 cm, r = 3.4 cm, R = 12.6 cm, r = 3.6 cm (WAM Z20724). — C. 123 nautical miles NNW of Dampier, WA, 18°48'S, 116°07'E, 555 m, 17.III.1992, 1 dry spec., R = 11.1 cm, r = 3.6 cm (WAM Z20725). — C. 150 nautical miles WNW of Port Hedland, WA, 18°00'S, 118°09'E, 545 m, 28.II.1992, 1 dry spec., R = 11.1 cm, r = 3.6 cm (WAM Z20726).

ETYMOLOGY. — This species is posthumously named in honour of Dr Kristina Louie, UCLA.

DISTRIBUTION. — Central Pacific (Timor Sea) to Indian Ocean. 320-610 m.

DIAGNOSIS. — $R/r \geq 4.0$. Abactinal arm plates, enlarged, bare. Transition abrupt between arm, disk plates. Abactinal plates extend to arm tip. Marginal plates with scattered, rounded granules. Actinal plates with rounded granules,

small paddle-like pedicellariae with sharp teeth. One to several subambulacral spines present between furrow spines and ambulacral pedicellariae.

APOMORPHY LIST. — Nodes 21 to 20: 2.1, SM granules present; 2.2, IM granules present; 3.1, actinal granules present; 3.2, actinal accessories angular; 6.3, interradial arcs, linear.

Nodes 21 to *Circeaster kristinae* n. sp.: 4.1, row of enlarged subambulacral spines.

DESCRIPTION

Body moderately thickened, disk small. Interradial arcs linear. Abactinal plates polygonal to round. Plates smaller centrally on disk; carinal series wide, enlarged, becoming 1.5-3 times size of central disk plates. Plates smaller, more polygonal with equal dimensions interradially, especially adjacent to superomarginal contact with disk surface. Plate surface convex to flattened. One to 30 coarse, hemispherical granules present on each plate. Granules smaller with greater abundance, larger with fewer abundance. Individual granules nearly tubercle-like in size. Granule abundance lowest (1-10 granules) on disk center, increasing at disk edge and base of arms (10-30 granules). Granules absent on distal abactinal arm plates but can extend midway on arm (c. 12 marginal plates from terminal). Arm plates enlarged, three to four times the size of central disk plates. Two or three series of plates on arm base, gradually decreasing to single series distally. Arm plates wide to quadrate. Some plates more irregularly polygonal. Some arm plates resemble disk plates in size. Most arm plates flattened, enlarged, some specimens (e.g., WAM Z20722) with one to six convex, wart, like carinal plates, often with large number of small granules (c. 20-30) relative to abundance of granules on other arm plates (approximately one to five).

Madreporite polygonal, low, convex, flanked by 8-10 abactinal plates.

Marginal plates, 50-70 (arm tip to arm tip), widest, most enlarged interradially, decreasing in size distally. Both series with blunt, curved dorso-lateral edge. Both plate series with 40-90 bead-like to angular peripheral granules forming evenly spaced border around each plate. Straight to zig-zag border between superomarginal, inferomarginal plate series.

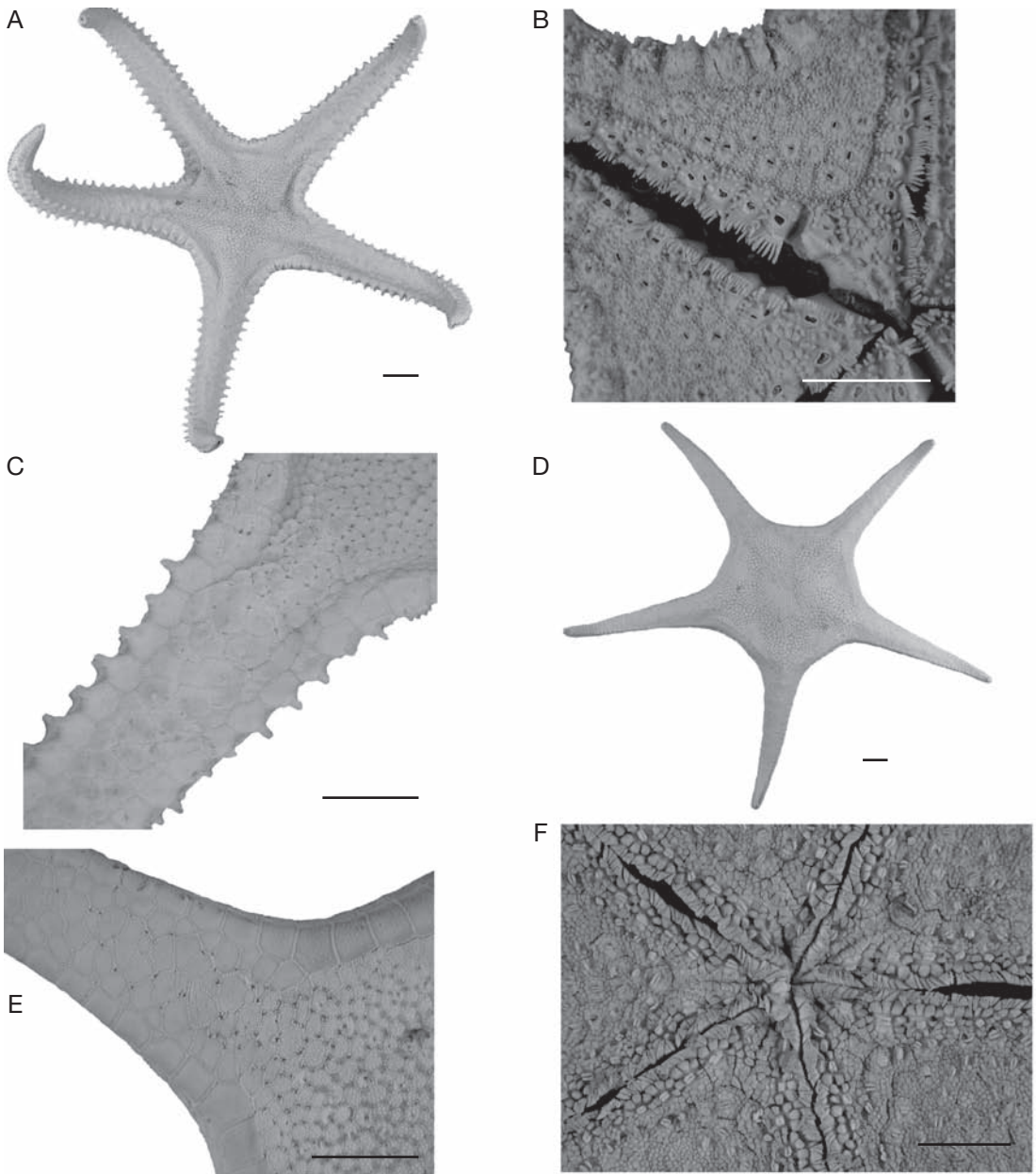


FIG. 5. — **A-C**, *Circeaster arandae* n. sp. (MNHN EcAs 11727); **A**, abactinal surface; **B**, actinal surface; **C**, abactinal arm disk surface; **D-F**, *Circeaster kristinae* n. sp. (WAM Z20694); **D**, abactinal surface; **E**, abactinal arm-disk surface; **F**, actinal surface. Scale bars: A-E, 1.0 cm; F, 0.5 cm.

Supermarginal plates low-convex in cross-section, corners, rounded to angular. Contact boundary with abactinal disk plates, straight to low-curved.

Granules, coarse 1-40, typically 20-35, scattered, covering supermarginal plate surface. Granule abundance highest interradially, decreasing distally.

Granules absent from 6-15th plates adjacent to terminal plate. Granules on superomarginal plate center, periphery of plate bare. Pedicellariae single, small, paddle-shaped, on lateral surface of superomarginal plate adjacent to inferomarginal contact. This area otherwise bare.

Inferomarginal edge rounded, plates low, convex. Contact boundary with actinal intermediate region, straight to low-curved. Granules, 1-55, typically 30-40, identical to those on superomarginals, scattered, covering inferomarginal plate surface. Inferomarginal granules densely packed with greatest abundance interradially, decreasing distally. Greater numbers of granules on interradial inferomarginals (*c.* 50 granules) compared to corresponding superomarginals (*c.* 35 granules). Granules absent from six to 15th plates adjacent to terminal plate. One or two paddle-like pedicellariae identical to those on superomarginal plates on periphery of inferomarginal plate adjacent to actinal intermediate region.

Actinal region composed of six or seven chevrons. Actinal plates rounded-polygonal, largest on chevron adjacent to adambulacral plate series, decreasing in size closer to actinal/inferomarginal boundary. Grooves shallow. Actinal plate surfaces covered by 2-12 scattered, hemispherical granules and/or single, large bivalve pedicellariae with three or four teeth. Actinal regions otherwise bare. Granule density increases closer to inferomarginal plate contact, replaced by pedicellariae closer to mouth plates. Five to 25 angular to polygonal granules forming discrete, well-spaced boundary around each plate.

Furrow spines, six to nine, flattened, polygonal to angular in cross-section. Furrow spines decrease in number distally. Peripheral granules and furrow spines with roughened furrow tips. Discrete gap located between furrow spines and individual, large bivalve pedicellariae. One or two enlarged subambulacral spine present adjacent to furrow spines and pedicellariae. Adambulacral plate covered by 5-20 angular granules some with roughened tips cover remainder of adambulacral plate, forming border around adambulacral plate. Furrow spines on mouth plate, 15-25 flattened, polygonal to angular in cross-section. Spines on mouth plate

tip triangular in cross-section. Pedicellariae, large, identical to those on adambulacrals, one or two, on mouth plates. Mouth plate surface and peripheral border covered by 12-25 angular, polygonal granules with roughened or jagged tips. Granules enlarged angular 8-10, with tips roughened, form border along mouth plate suture.

Circeaster sandrae n. sp.

(Fig. 6A-C)

HOLOTYPE. — Southwest Pacific Ocean. Banc Combe, 12°17'S, 177°28'W, 780-794 m, 18.V.1992, 1 dry spec., R = 14.0 cm, r = 3.6 cm (MNHN EcAs 11730).

PARATYPES. — New Caledonia. 23°10'S, 166°49'E, 870-1000 m, 31.III.1994, 1 dry spec., R = 6.5 cm, r = 2.7 cm (MNHN EcAs 11731). — 21°00'S, 160°50'E, 745 m, 22.X.1986, 1 dry spec., R = 7.4, r = 3.5 cm (MNHN EcAs 11732). — 20°23'S, 166°20'E, 800 m, 17.II.1989, 1 dry spec., R = 7.6 cm, r = 3.0 cm (MNHN EcAs 11733).

Marquesas Islands. Île Nuku Hiva, 8°50'S, 140°10'W, 705-794 m, 9.IX.1997, 1 dry spec., R = 13.0 cm, r = 4.4 cm (MNHN EcAs 11734).

Tonga. NW Tongatapu, 20°58'S, 175°16'W, 869-880 m, 9.VI.2000, 1 dry spec., R = 9.3 cm, r = 4.0 cm (MNHN EcAs 11734).

ETYMOLOGY. — This species is named for my colleague Sandra Brooke (OIMB).

DISTRIBUTION. — South Pacific Ocean, Tonga, New Caledonia, Marquesas Islands. 705-1000 m.

DIAGNOSIS. — R/r = 3-4. Abactinal arm plates similar to disk plates in size, becoming gradually larger on arm. Arm plates only one to two times as large as disk plates. Granules round, low scattered over disk, arm base, disappearing near arm tip. Granules rounded, low, scattered over marginal plate surface. Subambulacral spine enlarged, laterally adjacent to pedicellariae, paddle-like, toothed.

APOMORPHY LIST. — Nodes 20 to 19: 2.3, SM abutted over midline; 2.9, MP abundance, moderate; 3.2, actinal accessories, spiny.

Node 19 to *Circeaster sandrae* n. sp.: 1.2, arm-disk plate transition, gradual; 4.2, subambulacral spine adjacent to pedicellariae.

DESCRIPTION

Disk moderately thick. Arms triangular. Interradiar arcs linear. Abactinal plates round to polygonal, little

variation in shape, size. Plates on disk edge adjacent to superomarginals slightly smaller than those centrally on disk. Abactinal plates convex, appearing flatter in smaller specimen ($R = 6.5$ cm). Pedicellariae paddle-shaped bearing three or four teeth uncommon on abactinal plates. Pedicellariae moderately large (about the size of two or three granules). Granules scattered, 1-30 per plate. Most granules (*c.* 20-30) central on disk, decreasing in abundance adjacent to superomarginals (approximately one to five). Peripheral granules, 10-40 (mostly 20-30), evenly spaced. Peripheral granules polygonal to round. Shallow grooves present. Abactinal arm plates enlarged, approximately twice the size of some disk plates, but some similar in size to carinal disk plates, oval to polygonal in shape. two or three plate series at arm base, forming single series distally along arm. Granules on arm plates few to absent. Distalmost abactinal arm plates bare, convex. Madreporite pentagonal to hexagonal, slightly swollen, convex with rounded edges, flanked by five to eight abactinal plates.

Marginal plates, 35-55, usually about 45-50, per interradius from arm tip to arm tip. Marginal plates with rounded edges, quadrate in transverse cross-section, rounded dorsolateral/ventrolateral edges. Superomarginal and inferomarginal series slightly offset forming zig-zag boundary. Granules absent between superomarginal and inferomarginal plates.

Abutted superomarginals, zero to six. Disk-superomarginal plate contact weakly convex to straight. Interradial superomarginal plates longest, becoming wider/shorter, closer to arm tip. Granules abundant, 20-100 (usually 50-80) coarse scattered, present on superomarginal plate surface. Granules most abundant interradially, decreasing distally. Granules absent on distalmost superomarginal plates.

Inferomarginal plates with higher abundance of granules, 0-200 granules coarse, scattered. Number of granules highest on interradiial plates, decreasing to none adjacent to the terminal plate. Pedicellariae paddle-shaped, small, close in size to adjacent granules. Pedicellariae rarely present (sometimes one per radii) on lateral to dorsolateral plate surfaces.

Actinal plates quadrate, polygonal to irregularly round. Surfaces flat to slightly convex. Plates form

five to eight irregular chevrons. Actinal region limited to disk in smaller specimens ($R \approx 8$ cm) but extending along arm in larger specimens ($R > 10.0$ cm). Chevrons adjacent to adambulacral plates distinct but becoming irregular closer to actinal interradiial region/inferomarginal plate contact. Some plate surfaces bare, or covered with 5-25 coarse, hemispherical, nubbin-like granules, or large, paddle-shaped pedicellariae with three to six teeth on valve. Granule abundance higher adjacent to mouth and adambulacral regions, decreasing adjacent to contact with inferomarginal plates. Granule shape, abundance varies based on size and locality. New Caledonia specimens with slightly larger dense covering of actinal granules in larger specimen (MNHN EcAs 11732), scattered few granules in smaller specimen. Tonga specimen granules with rough tips, more angular in cross-section. Marquesas and Loyalty Ridge specimens closely resemble New Caledonia form, with smaller/fewer actinal granules. Actinal plate periphery surrounded by 4-30 granules, varying in shape from round to angular/polygonal.

Furrow spines 5-15, usually 12-14, vary by size, locality, position along tube foot furrow. Furrow spines laterally flattened, angular to flattened oval-like in cross-section. Tonga specimen furrow spines with roughened tips, foliate. Marquesas specimen with relatively thicker, angular furrow spines. Adambulacral plate with one to two thickened (approximately two to four times the furrow spines) subambulacral spine. Spine tip morphology varies from fluted/roughened (in Tonga specimen) to smooth (in New Caledonia specimen). Intermediate variation exists in New Caledonia and other specimens. Enlarged paddle-like pedicellaria adjacent to subambulacral spine, with three to six interlocking teeth on each valve. Granules 3-10, hemispherical to angular cover remainder of adambulacral plates, otherwise bare. Granules slightly coarser than those on other actinal plates.

Oral region sunken relative to actinal surface. Mouth plates with 15-20 furrow spines along tube foot furrow. One to three large pedicellariae, similar to those on other adambulacral plates, present on mouth plates. Tip of mouth plates with enlarged oral spines consistent in morphology with those on

furrow spines. Tonga SW Pacific specimens with spines, laterally flattened, foliate. New Caledonia, Marquesas specimens mouth, furrow spines, more angular, thickened. Mouth plates covered with 10-15 hemispherical to angular granules with tips rounded to fluted/roughened. Ten to 15 such granules flank either edge of suture on mouth plate. Other granules scattered, distributed over mouth plates. Mouth plates bare where accessories are absent.

Colour in life is a bright red-orange.

Circeaster pullus n. sp.
(Figs 6D-F; 8)

HOLOTYPE. — **Hawaiian Islands.** Off Kona, Hawaii, 19°37.9'N, 156°02.1'W, 585 m, 18.VII.1996, 1 dry spec., R = 8.8 cm, r = 3.3 cm (CASIZ 172875).

PARATYPES. — **Hawaiian Islands.** Off Kona, Hawaii, 19°37.9'N, 156°02.2'W, 535 m, 19.VII.1996, 1 dry spec., R = 8.9 cm, r = 3.3 cm (CASIZ 172876). — Off Oahu, Hawaii, 21°38'N, 158°47'W, 2305.1 m, 16.V.2001, 1 wet spec., R = 6.5 cm, r = 2.9 cm (CASIZ 163326). — Pinnacle north of FFS, NW Hawaii, 24°34.0'N, 166°1.80'W, 1360 m, 19.IX.2001, 1 wet spec., R = 2.7 cm, r = 1.3 cm (BPBM W3510).

New Caledonia. South New Caledonia, 23°02'S, 166°52'E, 620-700 m, 30.III.1994 (MNHN EcAs 11736).

ETYMOLOGY. — The species epithet is "*pullus*" for "young" in honour of its collector, Dr Craig Young (OIMB).

DISTRIBUTION. — Hawaiian Islands to New Caledonia. 620-2305.1 m.

DIAGNOSIS. — R/r = 2.0-3.0. Abactinal arm plates bare, enlarged, at base of arm. Round, hemispherical granules on disk, marginal plate surface. Superomarginal plates abutted over midline. Enlarged subambulacral spine abradial to adambulacral pedicellaria, adjacent to actinal intermediate region. Bivalve pedicellariae present on actinal surface, adambulacral plates.

APOMORPHY LIST. — Nodes 19 to 18: 4.3, subambulacral accessories few; 7.1, bivalve pedicellariae present. Nodes 19 to *Circeaster pullus* n. sp.: 4.2, spine abradial to pedicellariae.

DESCRIPTION

Disk moderately flattened relative to those of other species. Interradial arcs broad slightly curved to linear. Abactinal plates slightly convex, round to

polygonal to quadrate in outline. Carinals polygonal, interradials more rounded. Plates moderate sized on central disk region, becoming smaller, more heterogeneous in shape interradially, adjacent to superomarginal plate contact. Abactinal arm plates, two to three times larger than interradial plates, gradually becoming polygonal to oval, enlarged, before superomarginals abut over arm mid-radii. Arm plates similar in size to carinal disk plates. Plates in central region of disk with 1-18, usually 3-10, coarse, scattered granules. Granules most numerous on largest plates on central disk region, attenuating closer to contact with superomarginal plates. Granules absent on plates nearest superomarginal plate-disk contact and interradial regions on disk. Granules strongly convex, bead-like, resting on plate surface. Abundance of granules less in New Caledonia specimen. Granules limited 1-12 per plate only plates proximal to disk centre, adjacent to madreporite, anus, primary circlet. Other plate surfaces bare. Granules in concave pitting. Jaw-like pedicellariae small, less than 1 mm in width with shanks, well-developed. Two or three teeth present in Hawaiian specimens. Pedicellariae larger, with flatter blades, three to five teeth present in greater abundance in New Caledonia specimen. Oblong pits present where pedicellariae are absent. Madreporite pentagonal with relatively deep-sinusoidal folds flanked by six plates. All abactinal plates, madreporite surrounded with a periphery of smaller bead-like accessory granules, approximately 30-40% smaller than those on the abactinal plate surface. Rounded granules, bead-like, 10-50 depending on plate size.

Approximately 35-50 (usually about 40) marginal plates in each interradius (arm tip to arm tip). Marginal plate surface slightly convex, quadrate rounded to angular in cross-section. Spines absent, rounded granules present on all marginal plate surfaces. Approximately 40-100 spaced, rounded to angular bead-like granules, evenly spaced, forming border around each marginal plate identical to those on abactinal surface. Both series of marginal plates largest at interradii, becoming smaller and narrower closer to arm tip. Pedicellariae, three to six, identical to those on abactinal surface, present on lateral and ventral surface of both marginal plate series.

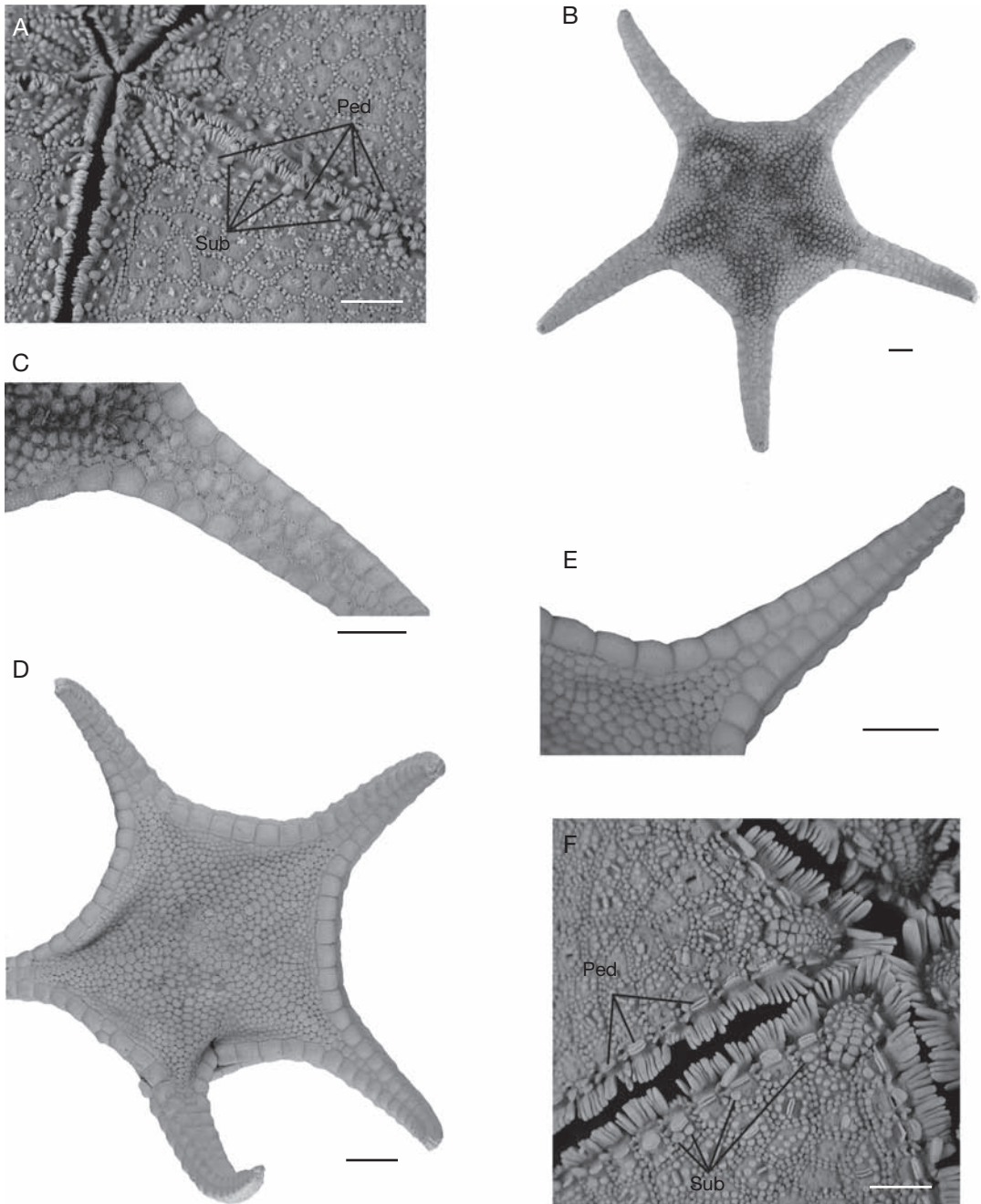


FIG. 6. — **A-C**, *Circeaster sandrae* n. sp. (MNHN EcAs 11730); **A**, actinal surface; **B**, abactinal surface; **C**, abactinal arm-disk surface; **D-F**, *Circeaster pullus* n. sp. (CASIZ 172875); **D**, abactinal surface; **E**, abactinal arm-disk surface; **F**, oral surface. Abbreviations: **Ped**, pedicellariae; **Sub**, subambulacral spine. Scale bars: A, F, 0.5 cm; B-E, 1.0 cm.

The New Caledonia specimen with flatter, broader, toothed pedicellariae versus the Hawaiian specimens with narrower, sugar-tong like morphology.

Approximately 50% of arm, approximately 10-15 distalmost superomarginal plates abutted at midline on arm. Superomarginal plate surface with 3-60 hemispherical scattered granules at plate centre. Granules absent from lateral surface of superomarginal plate adjacent to abactinal disk. Superomarginal plates with linear to low-curved contact with disk. Abundance of granules decreases distally, from *c.* 50 to absent, adjacent to terminal plate.

Inferomarginals slightly offset from superomarginals. Inferomarginals with 3-60 hemispherical scattered granules. Granular abundance highest interradially, attenuating distally. Granules more abundant on ventral surface adjacent to actinal plates. Granules absent from inferomarginal lateral side and plate surface adjacent to superomarginals. Highly convex to straight contact between inferomarginals and actinal plates.

Actinal regions large, extending to base of arms, corresponding to area of abactinal arm plate enlargement. Plates form three to five irregular chevrons. Actinal plates quadrate to polygonal in shape with more rounded, smaller plates adjacent to inferomarginals. Plate surface with 1-15 (typically 3-10), coarse, scattered, hemispherical granules, an enlarged pedicellaria on bare plate surface. Twelve to 20 larger, peripheral bead-like, granules similar to those on other plates. Surficial and peripheral granules in New Caledonia specimen with roughened tips. Incipient grooves present between peripheral granule borders. Pedicellariae with wide flap-like valves, six to eight teeth on each valve. Single pedicellaria or combination of pedicellariae and granules present on actinal plates.

Adambulacral plates similar in size to actinal plates. Furrow spines four to eight, flattened, oval to angular/triangular in cross-section. Furrow spine abundance highest (seven or eight) near mouth lowest at arm tip (three to six). Adambulacral pedicellariae separated from furrow spines by discrete space. Subambulacral granules large, thick, angular to rounded in cross-section. Adambulacral plates surrounded by 12-15 coarse, angular peripheral granules identical to those on actinal plates. Peripheral

granules adjacent to tube foot furrow, angular to triangular in cross-section. Subambulacral surface, peripheral granules in New Caledonia specimen with roughened tips. More discrete spaces separate enlarged subambulacral granules from peripheral granules on adambulacral plates.

Mouth plates flanked by 10-12 furrow spines. First two to three spines on oral plate directed into mouth enlarged, approximately four times thicker, twice as long than typical furrow spine size. Subsequent mouth plate furrow spines attenuated distally. Mouth plate covered by 20-35 coarse, angular granules. Granules six or seven, enlarged, form border on either side of mouth plate depression, some closely abutting. Other granules are lower, and angular, polygonal in cross-section, evenly spaced. Single pedicellaria identical to those on adambulacral plate present or absent on mouth plate adjacent to furrow spine.

The smallest specimen shows several differences. Abactinal plates limited to the disk, absent from arms, similar in size and shape. Granules, pedicellariae largely absent from abactinal plate surfaces. Individual granules present near disk center. Ten to 30 coarse peripheral granules around each abactinal plate border.

Marginal plates *c.* 20 per interradii from arm tip to arm tip. *C.* 70-80 coarse granules form periphery around marginal plates. Seven to eight superomarginals abutted at midline, with slightly jagged contact. Two to six coarse, scattered granules present on superomarginal surface near dorsolateral edge. Inferomarginals with 2-20 coarse scattered granules, one or two paddle-shaped pedicellariae, teathed. Terminal plate approximately three times the size of adjacent superomarginal plates. Actinal surface with two or three chevrons, actinal plates periphery bordered by 6-20 large, angular granules, tips blunt to pointed. Actinal plates with single to few granules resembling peripheral granules and/or paddle-shaped pedicellaria with 8-11 sharp teeth along lateral side of each valve. Pedicellaria uncommon on actinal plates. Remainder of actinal plate surface bare. Six to eight (mostly seven or eight) compressed furrow spines. Adambulacral plate with paddle-like pedicellariae, single enlarged subambulacral spine.

The Hawaiian specimens were recorded *in situ* as orange. Living colour of the New Caledonia specimen is unknown. *In situ* observations of *C. pullus* n. sp. (C. Kelley, HURL, unpubl. data) show the abactinal disk surface substantially inflated.

Circeaster americanus (A. H. Clark, 1916)
(Fig. 7)

Lydiaster americanus A. H. Clark, 1916: 141; 1954: 376.

Circeaster occidentalis H. L. Clark, 1941: 46, pl. 4, fig. 2. — A. H. Clark 1954: 376.

Circeaster americanus — Halpern 1970a: 265, figs 26-28; 1970b: 174. — Downey 1973: 47, 55, pl. 21A, B. — Walenkamp 1979: 52, figs 14, 18, pl. 12, figs 1, 2. — Clark & Downey 1992: 237. — Clark 1993: 250.

MATERIAL EXAMINED. — SM joined-variant 1 (Fig. 7A-C): **Caribbean Sea.** Saint Christopher and Nevis, SE of Nevis, 17°06'N, 62°17'W, 322 m. 8.X.1969, 1 dry spec., R = 8.2 cm, r = 3.3 cm (NMNH E12712). — Netherlands Antilles, North of Saint Eustatius, 17°46'N, 62°59'W, 355-365 m, 18.V.1967, 1 dry spec., R = 7.8 cm, r = 2.8 cm (NMNH E12798). — Leeward Islands, Dominica, Dominica Passage, 15°38'N, 61°7'W, 808 m, 5.III.1966, 1 dry spec., R = 5.4 cm, r = 2.2 cm (NMNH E12801). — Off SE coast of Martinique, 14°18'N, 60°45'W, 1235 m, 7.VII.1969, 1 dry spec., R = 3.9 cm, r = 1.9 cm (NMNH E19072). — Caribbean Sea, no other data, 1 dry spec., R = 9.9 cm, r = 4.2 cm (NMNH E19076). — Off East central coast Nicaragua, 13°31'N, 81°54'W, 549 m (300 fms), 12.IX.1957, 1 dry spec., R ≈ 6.5 cm (arm broken), r = 3.2 cm (NMNH E19077). — 24°15'N, 80°02'W, 545 m, 1 dry spec., R = 7.8 cm, r = 3.3 cm (RSMAS UMML 40.216). — Off Columbia, 10°13'N, 76°6'W, 814-1050 m, 15.VII.1966, 1 dry spec., R = 7.1 cm, r = 2.4 cm (RSMAS UMML 40.231). — 16°35'N, 80°10'W, 577 m, 18.V.1962, 1 dry spec., R = 9.7 cm, r = 4.3 cm (RSMAS UMML 40.573). — Off Venezuela, 11°50'N, 66°10'W, 1059 m, 23.VII.1968, 2 dry specs, R = 6.0 cm, r = 2.0 cm, R = 2.5 cm, r = 1.3 cm (RSMAS UMML 40.574). — Off Suriname, 8°14'N, 57°38'W, 1408 m, 15.VII.1968, 3 dry specs, R = 6.3 cm, r = 2.4 cm, R = 5.1 cm, r = 2.1 cm, R = 4.3 cm, r = 1.6 cm (RSMAS UMML 40.575).

Florida. SW of Apalachicola Bay, 28°17'N, 86°21'W, 671 m (367 fms), 20.VI.1969, 2 dry specs, R = 8.9 cm, r = 3.6 cm, R = 8.2 cm, r = 3.2 cm (RSMAS UMML no number).

SM free-variant 2 (Fig. 7D-F): **Guyana.** NE of Georgetown, 8°33'N, 54°18'W, 675-1253 m, 12.VII.1968, 1 dry

spec., R = 8.7 cm, r = 3.1 cm (NMNH E19046).

Caribbean. Saint Vincent, off Georgetown 13°21'N, 61°02'W, 708 m, 6.VII.1969, 1 dry spec., R = 8.5 cm, r = 3.5 cm (NMNH E21156). — Quintana Roo, off Espiritu Santo Bay, 18°57'N, 87°9'W, 1143 m (625 fms), 7.VII.1970, 1 dry spec., R = 6.2 cm, r = 1.5 cm (NMNH E19048).

Florida. Straits of Florida, 23°42'N, 80°43'W, 1083 m, 30.IV.1969, 1 dry spec., R = 5.9 cm, r = 1.3 cm (NMNH E19073).

DISTRIBUTION. — Tropical Atlantic-Florida, Louisiana, and North Carolina and the Caribbean, including Columbia, the Grenadines, Leeward Islands, Nicaragua, Netherlands Antilles, St. Vincent, Suriname, and Venezuela. Additional specimen records (not examined, NMNH E19052, E19074, E19075) extend the depth range of this species to 500-1450 m.

DIAGNOSIS. — R/r ≈ 2.4-4.0. Granules round, scattered over abactinal disk, arm surfaces. Arm plates enlarged, bare relative to disk plates; arm plates similar to disk plates in overall size and shape. Superomarginal plates abutted at midline. Row of enlarged subambulacral spines present adjacent to furrow spines. Bivalve pedicellariae present on actinal and adambulacral plates.

APOMORPHY LIST. — Nodes 18 to 17: 6.3, interradial arcs curved; 7.2, paddle-like pedicellariae, absent. Node 17 to *Circeaster americanus*-variant 1: 2.3, SM abutted over midline.

Node 17 to *Circeaster americanus*-variant 2: 4.1, row of enlarged subambulacral spines.

DESCRIPTION

Note on descriptions

As indicated above, full descriptions of adult *C. americanus* are summarized in Halpern (1970a, b) and Clark & Downey (1992). Several smaller specimens (RSMAS UMML 40.574, R = 2.5 cm, RSMAS UMML 40.575, R = 4.3 cm and NMNH E19072, R = 3.9 cm) were not included in these earlier studies but display significant information on growth and illustrate size range within the species and are described below.

Smaller specimens

Smaller specimen from RSMAS UMML 40.574 with 21 superomarginal inferomarginals per interradius from arm tip to arm tip, increasing to *c.* 30 in NMNH E19072 and *c.* 31-32 marginal plates in RSMAS UMML 40.575. The RSMAS UMML 40.574 specimen shows a continuous or nearly

continuous series of carinal plates from disk to terminal. Plate series on arm, slightly enlarged, convex; becoming smaller, elongate distally. Where carinal series is discontinuous, distalmost superomarginals adjacent to terminal abut at midline. Continuous, discontinuous carinal series varies from arm to arm on a single individual and across different specimens but pattern appears consistent between smaller and larger specimens. In larger individuals where arm carinals absent distally, additional superomarginals abut over midline adjacent to terminal. Marginal plate granules with identical distribution pattern in smaller specimens, with higher granule density interradially decreasing distally, present on all plates, including those adjacent to the terminal. Terminal plates enlarged, with two short spines present. Spines absent in larger specimens with terminal plate comparable in size to adjacent superomarginal plates. Marginal plate patterns suggest an ontogenetic change as carinal plate series along the arm are discontinued proximally followed by subsequent addition of abutted superomarginals distally, in larger individuals ($R \geq 3.5$).

Furrow spines in RSMAS UMML 40.574, three or four with a single enlarged subambulacral spine and pedicellariae, immediately adjacent on the adambulacral plate. The slightly larger, RSMAS UMML 40.575 with four or five furrow spines, a variable full row of subambulacral spines or single subambulacral spine and a single enlarged bivalve pedicellaria. Specimen NMNH E19072 shows five or six furrow spines with variable rows or single subambulacral spine.

In situ observations of *C. americanus* show it as light tan above but off white below with brown-red tube feet (D. Pawson, NMNH, pers. comm. 29.VIII.2004).

TAXONOMIC CONCLUSIONS

The present phylogeny disagrees with Halpern's (1970a, b: 265) decision to synonymize *Lydiaster* with *Circeaster*, and supports *Lydiaster johanna* within a separate, distinct genus. *Lydiaster americanus*, the original name for *Circeaster americanus*, is further supported herein within the *Circeaster* lineage and

retained as a member of the genus *Circeaster* in agreement with Halpern (1970a, b).

The phylogeny supports *Circeaster* as monophyletic. Four of the previously undescribed terminal taxa included in the analysis are supported as new species and are described above. The two morphological variants of *Circeaster americanus* discussed by Clark & Downey (1992: 238) were included in the matrix and supported *C. americanus* as monophyletic. Clark & Downey (1992: 238) argued that abutting superomarginal plates at the midline (character 2.3) correlated with other characters, including the number of furrow spines (four or five spines present) (character 4.4) and the shape of the pedicellariae. The proposed correlation in pedicellariae morphology was not confirmed. The difference in furrow spine number cited by Clark & Downey (1992) was observed, but examination of additional specimens suggests that the character varies among individuals. The variation in furrow spine number (Clark & Downey 1992) differed from arm to arm within a single individual (e.g., NMNH E19046) and is considered variable. A single enlarged subambulacral spine was consistently present in those specimens of *C. americanus* lacking abutted superomarginal plates whereas a series of subambulacral spines was present in specimens with abutted superomarginal plates. Number and position of multiple enlarged subambulacral spines varied from arm to arm on some individuals (e.g., RSMAS UMML 40.574).

DISCUSSION

BASAL DIVERSIFICATION

A morphological phylogeny of the Goniasteridae (Mah unpubl. data) supports *Cladaster*, *Floriaster*, and *Lydiaster* as sister taxa to the *Circeaster* clade. *Lydiaster* is further supported as the immediate sister group to the *Circeaster* clade (Fig. 1). Ideally, the sister group provides the basis for outgroup comparison (Wiley *et al.* 1991). Occurrence and fossil data suggest a southern Tethys/South Atlantic range for sister taxa to the *Lydiaster* + *Circeaster* lineage. The phylogeny supports either a biogeographical shift between the South Atlantic/southern Tethys or an

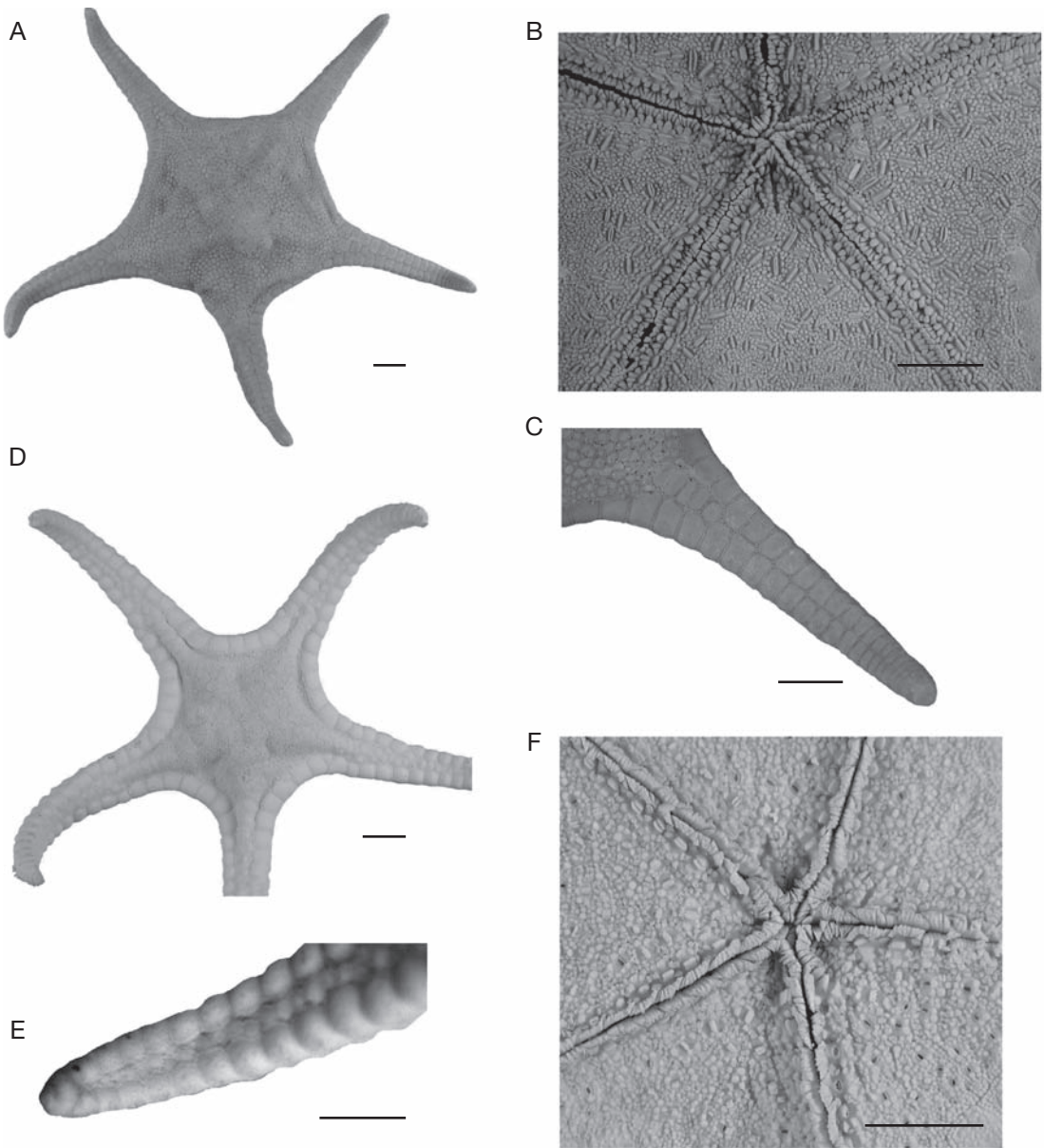


FIG. 7. — *Circeaster americanus* (A. H. Clark, 1916): **A-C**, variant 1 (NMNH E19076); **A**, abactinal surface; **B**, actinal surface; **C**, abactinal-disk showing arm tip with supermarginals abutted over midline; **D-F**, variant 2 (NMNH E19073); **D**, abactinal surface; **E**, arm tip showing plates to terminal plate; **F**, actinal surface. Scale bars: A-C, 1.0 cm; D-F, 0.5 cm.

extinction event associated with the sister/outgroup taxa relative to the basal taxa within the ingroup with Indian Ocean occurrence.

Three of the five known (four recent, one fossil) *Cladaster* species occupy a South Atlantic/southern Ocean distribution and one fossil species suggests

a Cretaceous occurrence for the genus. *Cladaster validus* occurs in the North Pacific, *C. rudis* occurs in the tropical Atlantic, *C. macrobrachius* occurs in the Indian/Atlantic Ocean regions, and *C. analogus* occurs in the South Atlantic/southern Ocean region. The fossil species, *C. carrioni* (Medina & Del-Valle, 1983), was described from the Campanian-Maastrichtian (Upper Cretaceous [c. 70-80 Ma]) of Isla Vicecomodoro Marambio (= Seymour Island), Antarctic Peninsula. Preliminary phylogenetic data (C. Mah unpubl.) suggest *Cladaster validus* and *C. rudis* are derived relative to the South Atlantic species, *C. macrobrachius* and *C. analogus*. *Cladaster carrioni* was considered by Medina & Del-Valle (1983) to share most similarities with the N Pacific *C. validus*. However, comparison of the description of *C. carrioni* with specimens of *C. validus* indicate that *C. carrioni* lacks features present in *C. validus*, including a raised square-shaped, bare spot on the superomarginal plate surface and comparably shaped marginal plates. *Cladaster carrioni* lacks the greater arm length and bivalve pedicellariae present in *C. macrobrachius* and shows greater morphological similarity with the South Atlantic *C. analogus*. Occurrence of *Cladaster analogus* in the South Atlantic and the presence of *C. carrioni* from the Antarctic Peninsula (southern Tethys Ocean) are consistent with the Indian Ocean occurrence of basal taxa within the *Circeaster* + *Lydiaster* lineage. The Campanian-Maastrichtian age for *Cladaster carrioni* suggests a minimum age for the *Cladaster* branch on the phylogeny in the Late Cretaceous.

Floriaster maya is supported as the immediate sister group to the *Circeaster* + *Lydiaster* clade but is known only from the Yucatan Channel in the tropical Atlantic. Its apparent absence from the southern Atlantic/Indian Ocean region implies either a broader geographic occurrence than is currently known, or a historical migration between the southern and tropical Atlantic regions. The latter pattern is observed in other goniasterid genera. *Tessellaster clarki* was described from shallow-water Eocene sediments from Seymour Island (Blake & Aronson 1998), whereas the extant *Tessellaster notabilis* inhabits exclusively deep-water habitats (329-575 m) from the tropical Atlantic (Clark

& Downey 1992). *Floriaster's* distribution is not inconsistent with a biogeographical shift from an outgroup occupying the South Atlantic/southern Tethys to the Indian Ocean occurrence of plesiomorphic *Lydiaster* + *Circeaster*.

BIOGEOGRAPHY AND HISTORICAL BARRIERS

Lydiaster johannae, the sister taxon to *Circeaster*, occurs in the Indian Ocean. *Circeaster arandae* n. sp., the sister branch to the clade including the other *Circeaster* species, occurs in the Indian Ocean and New Caledonia, suggesting a broad southern hemisphere distribution.

Within the most diverse *Circeaster* branch, four species, *C. loisetteae* n. sp., *C. marcelli*, *C. helenae* n. sp., and *C. magdalenae*, are included in one of the two included sister clades, suggesting a diversification throughout the Indian Ocean. The sister clade to these latter taxa includes *C. kristinae* n. sp., *C. sandrae* n. sp., *C. pullus* n. sp., and *C. americanus*; the clade shows diversification from the Timor Sea to the South Pacific, Hawaii/New Caledonia, and tropical Atlantic. Three species occurring westward of Indonesia, *C. sandrae* n. sp., *C. pullus* n. sp., and *C. americanus*, demonstrate a morphological break from those occurring in the Indian Ocean.

Two major historical geological events, the closure of the Indonesian seaway (for review see Hall 2001) and the development of the Panamanian isthmus (for review see Jackson *et al.* 1996), were potential allopatric barriers separating these three species from those in the Indian Ocean and have provided potential timing constraints for the phylogenetic tree. The Indonesian seaway separated *C. sandrae* n. sp., *C. pullus* n. sp., and *C. americanus* from the Indian Ocean species. Closure of the Panamanian isthmus separated *C. pullus* n. sp. (Hawaii and New Caledonia) from *C. americanus* (tropical Atlantic). The final closure of these seaways presents a conservative estimate for isolation between species. However, establishment of these barriers can last several million years, which represents a significant period of evolutionary time. Also, during this transitory period, paleoenvironments undergo shifts between the original environments and those associated with the development of the barrier. Direct

evidence (e.g., fossils) will not be available for all species. However, establishing paleoenvironments appropriate for the dispersal and/or migration of the organisms affected by these barriers presents a significant consideration for timing divergence between species.

Living *Circeaster* occupy exclusively deep-sea (c. 300-3000 m) habitats and are not known from shallow-water habitats. While bathymetric shifts, as outlined by Bottjer & Jablonski (1988), have been observed in other asterooids (e.g., Mah 1998; Blake & Aronson 1998), no onshore-offshore trends are apparent from the phylogenetic trends observed in *Circeaster* and fossils for *Circeaster* are unknown. Timing estimates for the phylogenetic hypothesis below, assumes that species within the *Circeaster* lineage have occupied exclusively deep-water environments throughout its phylogenetic history. This has important considerations for timing estimates associated with the two geologic events mentioned earlier.

That larval dispersal in *Circeaster* is restricted to deep-water habitats is supported by available data and precludes the possibility of transport through shallow waterways. These data more tightly constrains possible timing of larval transport within deep-water paleoenvironments. The known range of vertical distribution in deep-sea asteroid larvae is incomplete but experiments on the deep-sea astropectinid, *Plutonaster bifrons* (Young *et al.* 1996) have suggested that embryonic pressure tolerances were closely tied to the upper and lower bathymetric ranges in that species (c. 2000 m). Studies in two species of deep-water echinoids (Young *et al.* 1998) further suggested that larval depth limits may parallel the depth ranges present in the adults.

Howell *et al.* (2002: 1914) observed that the juveniles of some deep-sea asteroid species extend outside the adult range. Several of these species possess either planktotrophic or lecithotrophic modes of reproduction, which offer the capability for broad vertical dispersal. However, Sumida *et al.* (2000) found that growth of juveniles is slower outside the adult range. Gage & Tyler (1981) observed that the larvae of *Ophiocten gracilis*, which settled outside the adult depth range, did not survive to the following year.

SEAWAY CLOSURE, PALEOENVIRONMENTS AND PHYLOGENETIC TIMING

Evidence for appropriate paleoenvironments, e.g., deep-water sediments, should also be consistent with known bathymetric occurrence in *Circeaster*. The timing of closure and paleoenvironments associated with each seaway for each historical event are reviewed below within the context of the phylogenetic hypothesis.

The Indonesian seaway is found between the southern tip of Indonesia and northwestern Australia and occurs today as a relatively shallow-water connection, effectively separating the Indian from the Pacific Ocean. A full review of Indonesian seaway closure events (i.e. tectonics, etc.) is found in Hall (2001). Based on paleomagnetic evidence, Ali *et al.* (1994) suggested that the seaway began to close c. 22 Ma, roughly in agreement with Smith *et al.* (1994) who supported the beginning of the seaway closing within c. 20-30 Ma. Foraminiferal distribution data for localities throughout the Indo-Pacific associated with the seaway at 22 Ma, 16 Ma, and 8 Ma show paleobathymetry in the 1000-4000 m range (Srinivasan & Sinha 1998). Nishimura & Suparka (1997) reported the absence of the Pacific deep-water (> 200-300 m) planktic foraminiferan *Pulleniatina spectabilis* from the Indian ocean, suggesting that a biogeographic barrier was present at the beginning of the Pliocene (c. 5.1 Ma). Precise timing of the Indonesian seaway closure and understanding of its role as a barrier to dispersal remains incomplete. However, the studies are consistent with a middle Miocene (c. 5-17 Ma) closure of the seaway as suggested by Ogasawara (2002). Conservatively, isolation of Pacific and Indian oceans populations could have occurred as early as c. 17 Ma and as late as c. 8 Ma when paleobathymetry was compatible with bathymetric occurrence in living *Circeaster*.

The closure of the Panamanian seaway (also called the Tropical American seaway or the Central American seaway) between North and South America isolated the East Pacific from the tropical western Atlantic. Duque-Caro (1990) summarized events leading to the development of the Panamanian isthmus and the closure of the seaway. Deep-water connections between the Pacific and

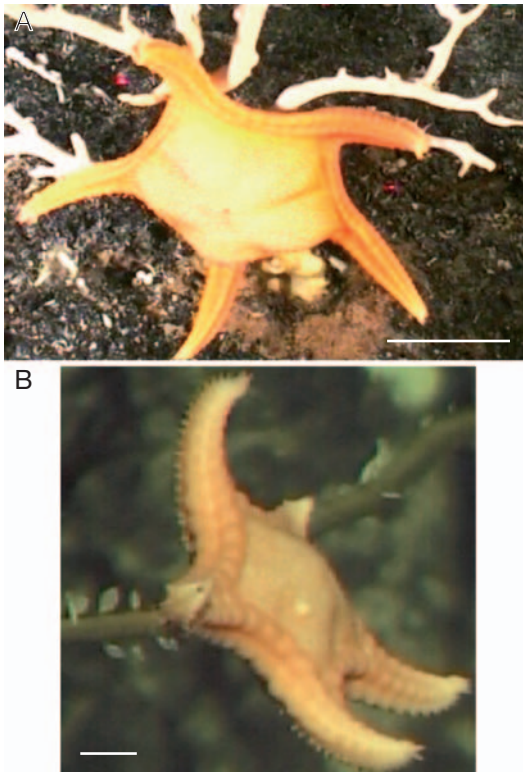


FIG. 8. — *Circeaster pullus* n. sp., Hawaiian Islands *in situ* video captures: **A**, CASIZ 172876 on octocoral/gorgonian skeleton; **B**, BPBM W3510 on *Iridogorgia superba* stalk. Scale bars: A, \approx 3.0 cm; B, 1.0 cm.

the Atlantic ended in the early to middle Miocene (16.1–15.1 Ma) and Caribbean faunal affinities on the Pacific side of South America ended in the middle Miocene (12.9–11.8 Ma). Regional shallowing to upper bathyal depths occurred in the late Miocene (8.6–7.0 Ma), with a restricted shallow-water connection (< 150 m) later in the late Miocene to early Pliocene (6.3–3.7 Ma). Miocene sediments and microfossils suggest that the paleobathymetric depth would have been approximately 2000 m in the earlier middle Miocene, shallowing to 1000 m in the middle Miocene (Duque-Caro 1990), suggesting a depth consistent with *Circeaster*'s known bathymetric range.

Fossil coral and sediment/microfossil evidence indicates that current flow in the early middle Miocene was strongly directed from the east to west

(Duque-Caro 1990; Grigg & Hay 1992), suggesting that dispersal from west to east, as suggested by the phylogeny, would have been unlikely during this time. However, during the middle to late Miocene (12.9–11.8 Ma), the partial emergence of the isthmus and the appearance of the California Current in the coastal areas of NW South America disrupted the surface water circulation between the Atlantic and the Pacific oceans providing an interval for dispersal from the Pacific to the Atlantic.

Isolation between *C. pullus* n. sp. and *C. americanus* might have occurred as late as 12.9 Ma (early-middle Miocene) in contrast to a shallow-water species constrained to complete closure of the seaway 3.1–3.5 Ma (early Pliocene, e.g., Lessios *et al.* 2003). Based on paleobathymetric data, the possibility of exchange through deep-water channels in *Circeaster* between the Pacific and the Atlantic appears unlikely after the late Miocene or early Pliocene.

The effect of the seaway on the evolution of organisms in the East Pacific/West Atlantic has long been recognized (Jackson *et al.* 1996 and references therein). Shallow water taxa, such as isopods (Lessios & Weinberg 1994) and especially echinoids (Lessios *et al.* 1999, 2003), have been the primary focus for studies examining the role of the isthmus as a barrier between populations and/or species. The closure of the Panamanian isthmus has been associated with the evolution of deep-water species (e.g., George 2004), but phylogenetic studies associated with trans-isthmian deep-water taxa were not evident from the literature.

Circeaster has not been recorded from the East Pacific based on surveys or summaries of the regional deep-sea fauna (e.g., Ludwig 1905; H. L. Clark 1920; Maluf 1988). Other shallow-water echinoderms with Indo-West Pacific/Atlantic distributions, such as the echinoid *Euclidaris* (Lessios *et al.* 1999) or the asteroid *Linckia* (Williams 2000), form a continuously distributed lineage occurring from the Indo-West Pacific to the East Pacific to the tropical Atlantic. If *Circeaster*'s absence is not simply a lapse in taxonomic knowledge, this discontinuity in distribution might represent localized extinction of the genus, or the result of an unknown environmental barrier preventing larval settlement or development in the East Pacific.

The phylogeny supports Halpern (1970a: 278), who suggested that the tropical Atlantic goniasterid fauna consists of “Tethyan relicts” with ancestry in the Indo-Pacific Ocean region. Two members of the *Circeaster* lineage occur in the tropical Atlantic, including *Floriaster maya*, which occupies a basal position within the lineage, and *C. americanus*, which occupies a highly derived one. This supports a paraphyletic composition of the tropical Atlantic goniasterid fauna.

The biogeographic pattern present in *Circeaster* is similar to that observed in the exclusively deep-sea brisingidans (Mah 1998: 274) displaying basal taxa in the southern hemisphere and more derived taxa occurring northward. The break between Pacific and Indian Ocean species is identical to those seen in the shallow-water tropical valvatidans *Acanthaster* (Benzie 1999) and *Linckia* (Williams & Benzie 1998; Williams 2000) in addition to other shallow-water species distributed throughout the Indo-Pacific (e.g., Lacson & Clark 1995; Wallace 2001). Wallace (2001) attributed a phylogenetic separation between Pacific and Indian Ocean species in the scleractinian coral *Acropora* to the closure of the Indonesian seaway.

POSSIBLE PREDATION

Two of the southern species, *C. magdalenae* and *C. loisetteae* n. sp. (MNHN EcAs 11726, WAM Z20714), are scratched and notched (e.g., Fig. 3D), consistent with marks made by predatory fish as described by Neumann (2000). Although this study reviews only a few specimens, these marks in addition to other characters, such as teeth on the pedicellariae and the superomarginals abutted at midline could be associated with defense. Blake (1990) has interpreted valvatidans as defensive specialists and cited use of armor and pedicellariae in other valvatidan asteroids. Predatory marks and indications of sublethal predation are largely absent or much less evident from the species in the more northerly taxa.

CIRCEASTER AND DEEP-SEA CORALS

Conservation and management of deep-sea coral reefs, which include scleractinians, hydrocorals, octocorals, and other reef forming cnidarians,

has been on the forefront of recent international marine conservation efforts (George 2003; Roberts & Hirshfield 2004). Concern has focused on the importance of deep-sea coral reefs as habitats for economically important fish and crab species (Husebø *et al.* 2002; George 2004) and their potential as undiscovered “hotspots” of marine biodiversity. Several goniasterid taxa have been observed feeding on octocorals or deep-water cnidarians, including *Calliaster pedicellaris* (Chave & Malahoff 1998), *Hippasteria spinosa* (Birkeland 1974), and *Hippasteria imperialis* (C. Mah unpubl. obs.). Studies on these ecosystems are still in their infancy, but early data suggests that predation on deep-sea corals by goniasterid predators is significant. Krieger & Wing (2002) have observed *Hippasteria* spp. as a predator on the gorgonian *Primnoa* species in the Gulf of Alaska, where it was observed to feed on up to 45% of the polyps at the sites studied.

In situ observations of *C. pullus* n. sp. (Fig. 8) show this species (C. Kelley & E. Chave, HURL, unpubl. obs. 2004) perched upon bare cnidarian stems, suggesting predation. Specimen BPBM W3509 was observed on the stalk of the gorgonian *Irridogorgia superba* (Chrysogorgiidae) (Fig. 8B). Specimens do not show apparent suspension feeding morphology or posture as observed in other asteroids, such as brisingidans (Emson & Young 1994).

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APPENDIX 1

Key to *Circeaster* Koehler, 1909, *Floriaster* Downey, 1980, and *Lydiaster* Koehler, 1909 species.

1. Adambulacral pedicellariae absent or mostly absent (exceptionally 1 or 2 on *Cladaster rudis*). Body surface covered with coarse, deciduous granules. Spinelets, tubercles, absent. Carinal series in clear, distinctive series along arm radii. Abactinal plates relatively large, approximately 3-6 across arm base *Cladaster* spp.
 — Adambulacral pedicellariae, typically with prominent teeth. Body surface not covered by coarse, deciduous granules. Tubercles, spinelets, or low, embedded granules may be present. Carinal series indistinct, often jumbled, not clearly evident along arm radius. Abactinal plates relatively small, approximately 7-9 across arm base 2
2. Tubercles present. Abactinal arm plates small. Plates on disk and arm surface similar in size. Superomarginals never abutting at midline, abactinal plates continue to terminal 3
 — Tubercles absent. Abactinal arm plates 2-4 times larger than disk plates. Superomarginals may or may not abut at midline 4
3. 25-30 marginal plates from arm tip to arm tip. $R/r \approx 2.0$. Tubercles on abactinal, actinal, marginal plates. Marginal plates largely bare except tubercles and granules on lateral edge. Tropical Atlantic *Floriaster maya*
 — 60-70 marginal plates from arm tip to arm tip. $R/r \geq 2.7$. Tubercles limited to actinal surface. Marginal plate surfaces covered by coarse hemispherical granules, many with spiny tips. Indian Ocean *Lydiaster johannae*
4. Large, prominent, sharp spines on nearly all superomarginal, inferomarginal plates. Sharp spinelets present interradially and on several plates in addition to those with spines. Prominent spinelets on actinal and adambulacral plates *Circeaster arandae* n. sp.
 — Spines absent from marginal plates. Spinelets or granules present. Spinelets not as prominent, actinal and adambulacral plates covered with round to spiny tipped granules 5
5. Spinelets (or granules with spiny tips) on marginal, actinal surfaces. Spinelets, more numerous, more pronounced on inferomarginals. Enlarged subambulacral spine(s) absent 6
 — Coarse, smooth granules on marginal plates with blunt to angular granules on actinal surface. Spinelets absent. Enlarged subambulacral spine(s) present 9
6. Elongate, sunken pedicellariae absent 7
 — Elongate, sunken pedicellariae present. Paddle-like pedicellariae present with teeth on actinal, adambulacral plates 8
7. Elongate, sunken pedicellariae with prominent jagged teeth. Superomarginals not abutted at midline. Clear, multiple series of abactinal arm plates. 8-10 furrow spines *Circeaster magdalenae*
 — Elongate, sunken pedicellariae without teeth. Superomarginals abutted at midline. Irregular abactinal arm plates occurring between abutting superomarginals. 6-8 furrow spines *Circeaster helenae* n. sp.
8. Superomarginals not abutted at midline *Circeaster marcelli*
 — Superomarginals abutted at midline *Circeaster loisetteae* n. sp.
9. Bivalve pedicellariae only. Paddle-like pedicellariae absent. 4-7 short, stout furrow spines. Tropical Atlantic Ocean *Circeaster americanus*
 — Paddle-like pedicellariae present. 6-12 (counted proximally) narrow furrow spines ... 10

- 10. Multiple enlarged subambulacral spines. Arms elongate, $R/r \approx 3.0-4.0$, $c. 50-70$ marginal plates per interradius (arm tip to arm tip) *Circeaster kristinae* n. sp.
- Single enlarged subambulacral spine. Arms moderate in length. $R/r \approx 2.0-3.0$, $c. 30-50$ marginal plates per interradius (arm tip to arm tip) 11

- 11. Enlarged subambulacral located laterally adjacent to adambulacral pedicellaria. Bivalve pedicellariae absent. Paddle-like pedicellariae only. Gradual transition between abactinal disk, arm plates *Circeaster sandrae* n. sp.
- Enlarged subambulacral located abradial to the adambulacral pedicellaria. Bivalve pedicellariae present in addition to paddle-like pedicellariae. Abrupt transition between abactinal, disk, arm plates *Circeaster pullus* n. sp.

APPENDIX 2

Character data matrix.

Taxon/Node	1	11111	11112	22222	22223	33	
	12345	67890	12345	67890	12345	67890	12
OG: <i>Cladaster analogus</i>	00031	40100	01000	00000	03040	00000	00
OG: <i>Floriaster maya</i>	00000	00000	00000	00000	00000	00000	00
<i>Lydiaster johannae</i>	00111	11112	20001	22210	00001	10000	00
<i>Circeaster loisetteae</i> n. sp.	12111	21212	21001	12221	22231	10000	00
<i>Circeaster marcelli</i>	12122	32212	20001	12221	22231	10000	00
<i>Circeaster helenae</i> n. sp.	12111	21212	21001	12111	22231	10010	11
<i>Circeaster magdalenae</i>	12111	11212	20001	12211	22231	10000	11
<i>Circeaster arandae</i> n. sp.	12101	11212	20111	00220	22011	11000	00
<i>Circeaster kristinae</i> n. sp.	12111	21111	10001	12210	10111	11100	00
<i>Circeaster sandrae</i> n. sp.	11111	21111	10001	12110	11001	11100	00
<i>Circeaster pullus</i> n. sp.	12111	21211	11001	12110	11020	11110	00
<i>Circeaster americanus</i> var. 1	12111	21211	11001	12110	11110	11011	00
<i>Circeaster americanus</i> var. 2	12111	21211	10001	12110	11010	11011	00