A phylogeny of *Iconaster* and *Glyphodiscus* (Echinodermata, Asteroidea, Valvatida, Goniasteridae) with descriptions of four new species

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ABSTRACT
A phylogenetic analysis of 11 taxa and 31 characters resulted in a single most parsimonious tree that supports monophyly of the goniasterid genera *Iconaster* and *Glyphodiscus*. Four new species, *Glyphodiscus magnificus* n. sp., *Glyphodiscus pentagonalis* n. sp., *Iconaster uchelbeluuensis* n. sp., and *Iconaster vanuatuensis* n. sp., are described and two species are synonymized. At least three species within the genus *Iconaster* appear to have invaded shallower water from a deeper-water ancestry. Glassy tubercles, similar to those interpreted as photoreceptors in ophiuroids and other goniasterids, are present in the shallow-water *Iconaster* clade. Glassy tubercles are largely absent in the deeper-water sister and outgroup taxa, suggesting their occurrence is related to photic zone or shallow-water occupation. Biogeographic patterns as presently known suggest that diversification in *Iconaster* and *Glyphodiscus* has been restricted to the central and south Pacific regions.

KEY WORDS
Echinodermata,
Asteroidea,
Valvatida,
Goniasteridae,
Iconaster,
Glyphodiscus,
morphology,
onshore-offshore,
deep-sea,
evolution,
new species.

RÉSUMÉ
*Une phylogénie d'*Iconaster *et de* Glyphodiscus *(Echinodermata, Asteroidea, Valvatida, Goniasteridae) et description de quatre nouvelles espèces.*
Une analyse phylogénétique portant sur 12 taxons décrits par 31 caractères aboutit à un seul arbre de parcimonie maximale. La topologie de cet arbre soutient l'hypothèse de monophylie des genres de Goniasteridae *Iconaster* et *Glyphodiscus*. Quatre nouvelles espèces sont décrites : *Glyphodiscus magnificus* n. sp., *G. pentagonalis* n. sp., *Iconaster uchelbeluuensis* n. sp., et *I. vanuatuensis* n. sp. et deux espèces sont mises en synonymie. Au moins trois espèces du genre *Iconaster* semblent avoir colonisé des milieux peu profonds à partir d'un ancêtre vivant en eaux profondes. Des corpuscules vitreux, similaires aux « photorécepteurs » des ophiures et de certains Goniasteridae, sont aussi présents dans le clade peu profond *Iconaster*. Les corps vitreux sont le plus souvent absents des taxons plus profonds appartenant au groupe frère et aux extra-groupes. Ces résultats suggèrent que la présence des corps vitreux est liée à la zone photique ou à l'occupation de milieux peu profonds. Les distributions géographiques connues indiquent que la diversification des genres *Iconaster* et *Glyphodiscus* est limitée aux régions centrales et méridionales du Pacifique.

MOTS CLÉS
Echinodermata,
Asteroidea,
Valvatida,
Goniasteridae,
Iconaster,
Glyphodiscus,
morphologie,
« onshore-offshore »,
eaux profondes,
évolution,
nouvelles espèces.

INTRODUCTION

New phylogenetic data for two small genera within the family Goniasteridae suggest unusual phylogenetic patterns contrary to those generally observed within the fossil record of echinoderms and other marine invertebrates (Bottjer & Jablonski 1988). Phylogenetic reconstructions within the Asteroidea have historically focused on post-Paleozoic, high-level (i.e. families and above) diversification patterns (e.g., Blake 1987; Gale 1987; Knott & Wray 2000). Mah (2000) argued that more intensive sampling of lower level taxa (i.e. species) is required to further elucidate phylogenetic events within the crown group. Asteroids are ecologically important (e.g., Birkeland 1974). Phylogenetic events in species-level phylogenies can mirror changes in environments over time. For example, phylogenetic histories have been argued as the most useful tools in understanding onshore-offshore evolutionary patterns (Bottjer & Jablonski 1988).
This study was prompted by new phylogenetic data currently being developed for the family Goniasteridae (C. Mah unpublished data), a large and diverse family, including approximately 260 extant species within 70 genera. Goniasterids occur predominantly on deep-water continental shelf habitats in all the world's oceans (A. M. Clark 1993). The greatest number of extant goniasterid species occurs in the Indo-Pacific region (A. M. Clark 1993; C. Mah unpublished data). Considerable work has been published on deep-water asteroids from this area (e.g., Fisher 1919; Jangoux 1981), and new genera and species continue to be discovered (H. E. S. Clark & McKnight 2003). Newly collected material from the Muséum national d'Histoire naturelle in Paris and the Coral Reef Research Foundation in Palau has resulted in discoveries of new taxa and more abundant material than has been available to prior studies.
Iconaster and other ingroup taxa were chosen, in part because of their broad bathymetric range. *Iconaster* occurs within a relatively shallow depth range of 30-208 m, whereas *Glyphodiscus* occurs more deeply, within a depth range of 162-532 m. *Iconaster* and *Glyphodiscus* each possess distinctive suites of characters, suggesting synapomorphies for a species-level analysis. Monophyly of the relationship between *Iconaster* and *Glyphodiscus* was tested to falsify or support the close relation-

ship implied by earlier taxonomic work (e.g., Fisher 1917, 1919).

Astrogonium longimanum was described by Möbius (1859). Sladen (1889: 261) established *Iconaster* based on *A. longimanum* as the type. H. L. Clark (1916: 36) reassigned the species to Perrier's contentious genus *Dorigona* synonymizing *Iconaster*, but Fisher (1919: 304) reaffirmed *Iconaster*. Fisher (1913) described *Iconaster pierectus*, which he later (Fisher 1917: 173) placed within the subgenus *Iconaster* (*Glyphodiscus*). Rowe (1989) elevated *Glyphodiscus* to generic status and described a second species, *Glyphodiscus mcknighti*, from New Zealand. Jangoux (1981) and Aziz & Jangoux (1984) subsequently described *Iconaster elegans* and *Iconaster corindonensis*, respectively.

Little is known of the biology of either *Iconaster* or *Glyphodiscus*. Lane & Hu (1994) described planktonic lecithotrophy without the bipinnaria stage in *Iconaster longimanus*. Coleman (1994) reported that *I. longimanus* feeds on "encrusting invertebrates".

MATERIALS AND METHODS

Phylogenetic data (C. Mah unpublished data) support a monophyletic clade of *Iconaster*, *Glyphodiscus*, *Pontioceramus*, *Pergamaster*, *Astroceramus* and *Lithosoma*, suggesting sister group relationships among them. Identification keys and discussion of putative relationships of *Iconaster* and *Glyphodiscus* within the Goniasteridae (e.g., Fisher 1911, 1919, 1940) have suggested affinities with *Pergamaster*, *Astroceramus*, and *Lithosoma*. The latter three genera, in addition to *Pontioceramus* were therefore included in the analysis as putative outgroups to determine the closest sister taxon to *Iconaster* and *Glyphodiscus*. Ideally, the sister group provides the basis for outgroup comparison (Wiley *et al.* 1991).

Initially, all valid species and potentially new species were included in the analysis. During the investigation, *Iconaster corindonensis* was discovered to be a juvenile of *Lithosoma penichra* (one of the outgroup taxa) and *G. mcknighti* was synonymized with *G. pierectus* (see discussions below). These two taxa were removed from the matrix. Ultimately, 11 taxa were included in the study matrix. Outgroup and ingroup taxa are summarized in Tables 1 and 2, respectively.

A total of 31 morphological characters is included. Characters were partly derived from a character matrix of the Goniasteridae in development (C. Mah unpublished data), and augmented

TABLE 1. — Summary of outgroup taxa included.

Genus and type species	Material examined
Astroceramus Fisher, 1906 *Astroceramus callimorphus* Fisher, 1906	**Hawaii.** TC 33, stn 11, off the Wainae coast, Oahu, 1 dry specimen (BPBM-no #).
Lithosoma Fisher, 1911 *Lithosoma penichra* Fisher, 1917	**New Caledonia.** BATHUS 1, stn CP 658 (MNHN EcAs 11702). **Thailand.** Andaman Sea (Indian Ocean), Malay Peninsula, Phuket, 7°40'N, 097°09'E, 503-512 m, RV *Anton Bruun*, stn 17, 1 dry specimen (USNM E53629).
Pergamaster Koehler, 1920 *Pergamaster synaptorus* Fisher, 1940	**Antarctica.** Joinville Island, 1 dry specimen (NMNH E13416).
Pontioceramus Fisher, 1911 *Pontioceramus grandis* Fisher, 1911	**Philippines.** Cebu Island, 1 dry specimen (NMNH 40578). — MUSORSTOM 3, stn CP 86, 1 dry specimen (MNHN EcAs 11701).

Table 2. — Summary of ingroup taxa included (further details in text).

Glyphodiscus magnificus n. sp.
Glyphodiscus pentagonalis n. sp.
Glyphodiscus perierctus Fisher, 1917
Iconaster elegans Jangoux, 1981
Iconaster longimanus (Möbius, 1859)
Iconaster uchelbeluuensis n. sp.
Iconaster vanuatuensis n. sp.

by additional characters scored from the material studied.

Trees were generated by exporting the character matrix (Table 3) from MacClade 3.08 into PAUP 4.0b10 (Swofford 2003). Unpolarized and unweighted characters were analyzed using the branch-and-bound and exhaustive search options.

Specimens examined (listed below) were collected primarily by the Muséum national d'Histoire naturelle in Paris (MNHN) and the Coral Reef Research Foundation (CRRF) in Koror, Palau. Additional reference material was borrowed from the Department of Invertebrate Zoology, California Academy of Sciences (CASIZ), San Francisco, California, the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, the Western Australian Museum (WAM), and the Smithsonian Institution (NMNH) in Washington, D.C. Taxa analyzed are listed in Table 1. Locality data for material described below refers to general location, collection station data, coordinates, depth, and collection date, followed by where the material is housed and whether the specimen is dried or preserved in alcohol, i.e. wet. *Glyphodiscus pentagonalis* n. sp., *G. magnificus* n. sp., *Iconaster vanuatuensis* n. sp., and *I. uchelbeluuensis* n. sp. were initially recognized as undescribed taxa based on diagnostic morphological characters. They were subsequently included in the cladistic analysis and assigned to genera based on the results.

RESULTS

The analysis resulted in a single most parsimonious tree (Fig. 6) with 52 steps, a Consistency Index (excluding uninformative characters) of 0.673, and a Retention Index of 0.753. The ingroup was assumed to be monophyletic for the analysis. Re-rooting the data as a basal polytomy has no effect on ingroup relationships, tree statistics, number of steps or number of trees recovered but does alter the relationships between the outgroup taxa, supporting a *Pontioceramus* and *Lithosoma* as sister taxa to a basal *Astroceramus*.

TABLE 3. — Data matrix used in analysis. Abbreviation: **OG**, outgroup.

Taxon	**1111111111222222222233** **12345678901234567890123456789 01**
Iconaster elegans	1111110111010011110100220001110
Iconaster longimanus	1111110110000010111000111001111
Iconaster uchelbeluuensis n. sp.	1110111111010010111000111001111
Iconaster vanuatuensis n. sp.	1101110100100010120101110001110
Glyphodiscus perierctus	0000111100210010111000111111101
Glyphodiscus pentagonalis n. sp.	0000111100210110111000111111111
Glyphodiscus magnificus n. sp.	0000111100201010111110111101111
OG: *Pontioceramus grandis*	0000000000100000000000000000000
OG: *Lithosoma penichra*	1001000000000010000000000000000
OG: *Astroceramus callimorphus*	0001000100000000000000001000010
OG: *Pergamaster synaptorus*	0000000100000000000000001101110

Pergamaster no longer emerges as the sister taxon to the ingroup.

Branches show relatively good support values (Fig. 6). Bootstrap support from 300 replicates shows all but *Iconaster* as supported over 50%. *Iconaster* + *Glyphodiscus* are particularly well supported by bootstrap values (96%). The *Glyphodiscus* and *Iconaster* clades each show collapse in one step but the clade including *Iconaster* + *Glyphodiscus* decays in five steps.

CHARACTER ANALYSIS

Characters utilized in the analysis were derived primarily from external anatomy and were grouped below based on body region. Internal characters were derived primarily from the ambulacral plates, a significant but historically underutilized source of character data. The character matrix is included in Table 3. The plesiomorphy or apomorphy of the character is based upon results from the cladistic analysis. Terminology used below follows Spencer & Wright (1966) and Blake (1987).

Tong-shaped pedicellariae are present in *Glyphodiscus*, but the function of pedicellariae and the selective influences dictating pedicellariae expression are poorly understood. Within a single goniasterid species, number and even presence of pedicellariae can be highly variable among individuals. Evaluation of pedicellarial variation is beyond the scope of this paper; pedicellariae are not included in the character matrix.

ABACTINAL SURFACE CHARACTERS (1-7)

1. Radial regions bearing enlarged accessory plates
0, absent; 1, present (Figs 5B, F; 4C, F)

2. Presence/absence of enlarged accessory plates: in the outgroup taxon *Lithosoma*, enlarged, corner accessory plates are present on all abactinal disk plates. In *I. elegans*, these plates occur on the primary circlet and on other abactinal plates on the disk but in fewer numbers
0, absent; 1, present (Fig. 4A, E)

3. Complete or incomplete ring of peripheral accessories on radial abactinal plates
0, complete ring; 1, incomplete ring (Fig. 4C, F)

4. Presence-absence of glassy tubercles on abactinal plates
0, absent; 1, present (Fig. 5B)

5. Primary circlet plate size
0, not enlarged; 1, enlarged (Fig. 5A)

6. Size of enlarged interradial abactinal plates
0, not enlarged; 1, enlarged (Fig. 4A, E)

7. Elevation of disk and marginal plates: the dorsal marginal plate surface either lies above or flush with the disk surface. Images of living *I. longimanus*, *I. vanuatuensis* n. sp., and *G. magnificus* n. sp. suggest a relatively rigid abactinal disk surface that is not sunken or collapsed in preserved specimens
0, surfaces flush; 1, disk sunken

MARGINAL PLATE CHARACTERS (8-14)

8. Superomarginal plates abutted across arm midline
0, armtip only ; 1, 50% or more of arm's length (Fig. 5A, D)

9. Glassy tubercles on superomarginal plates
0, absent; 1, present (Fig. 4B)

10. Glassy tubercles on inferomarginal plates
0, absent; 1, present

11. Number of interradial marginal plates: character state selection represent perceived differences in plate types observed among taxa. Where marginal plates are most numerous interradially, they also appear to be compressed in shape. Taxa with the fewest plates are largest and tend to be associated with highly pentagonal body forms and low R:r ratios
0, moderate (≈ 6-7); 1, abundant (≈ 9); 2, few (≈ 4-5)

12. Shape of marginal plates
0, wide (W > L); 1, elongate (L > W)

13. Enlarged basal superomarginals: this describes the basal, superomarginal plates present on the arm which are enlarged in size relative to the other superomarginals on the distal region of the arm. They are directly abutting and roughly triangular in shape compared to the quadrate interradial superomarginals
0, absent; 1, present

14. Presence-absence of marginal cones: this describes convex, conical prominences extending

from the dorsolateral edge of the superomarginal and inferomarginal plate series. Pointed marginal plates found in *Amphiaster* and *Goniaster* are convergent (C. Mah unpublished data). Marginal cone development becomes accentuated during ontogeny
0, absent; 1, present (Fig. 3A, B)

ACTINAL SURFACE CHARACTERS (15, 16)
15. Surface granules on actinal plates
0, present; 1, bare
16. Glassy tubercles on actinal surface
0, absent; 1, present

ADAMBULACRAL PLATE AND FURROW CHARACTERS (17-25)
17. Furrow spine length
0, elongate (length ≥ 2 × breadth); 1, not elongate (length < 2 × breadth)
18. Outline shape of furrow spines in cross section
0, thin and flattened; 1, round; 2, quadrate
19. Spacing between furrow spines: crowded furrow spines are densely adjacent to one another and closely abutted. Well spaced furrow spines display about a < 1.0 mm gap between each spine
0, well spaced (Figs 4D; 5C); 1, crowded (Fig. 5G)
20. Subambulacral spines
0, present; 1, absent
21. Flattened subambulacral features: subambulacral ornamentation (i.e. spines, granules, etc.) are flattened, making them flush with the actinal surface
0, absent; 1, present (Fig. 3C)
22. Granular subambulacrals: describes shape and morphology of granular subambulacral ornamentation, including size, overall relief, and roundedness of the granule
0, prismatic ornamentation; 1, spherical ornamentation (Fig. 5C)
23. Subambulacral spines in cross section: describes the shape of subambulacral spine outline in cross-section only, and does not address the overall appearance/morphology of the spine itself
0, round; 1, prismatic-polygonal; 2, absent
24. Gap separating furrow spines from subambulacral spines at fourth adambulacral: a gap is present, where spines or other ornamentation are absent, between the furrow spine series and the subambulacral spine series
0, present; 1, absent; 2, subambulacrals absent
25. Enlarged oral spines: these spines vary in morphology but are 2-3 × the length and approximately 2 × the width at the tip, relative to the surrounding oral and subambulacral spines
0, present; 1, absent (Figs 4D; 5C)

BODY MORPHOLOGY CHARACTERS (26, 27)
26. Interradial arc: the angle present in the interradius between arm tips. Rounded arcs are concave whereas linear arcs describe straight edges between the arms. Direct correspondence between the number of interradial marginal plates (character 11) and the angle of the interradial arc (character 12) is not observed
0, rounded arcs; 1, linear arcs
27. Arm length: this character describes the arm length relative to ingroup taxa. Short arms end relatively near the body and reflect a pentagonal disk and body shape with an R:r ratio of approximately 1:1. Elongate arms extend away from the body resulting in a more stellate body form and a greater R:r ratio. A relationship between the number of interradial marginal plates (character 11) and the angle of the interradial arc (character 12) with this character was not observed
0, elongate (greater than 1:1); 1, short (roughly 1:1)

INTERNAL SKELETAL CHARACTERS (28-31)
28. Shape of ambulacral head: a broad ambulacral head with a flattened lateral surface. Small ambulacral heads are more compressed with a relatively curved lateral surface
0, large (Fig. 1C); 1, small (Fig. 1D)
29. Overlap of ambulacral head flange: the presence or absence of a discrete, curved flange on the ambulacral head that overlaps onto the next ambulacral plate
0, absent (Fig. 1C); 1, present (Fig. 1D)
30. Edge of ambulacral waist: a sharp edge or flattened to rounded surface on the waist region of the ambulacral plate

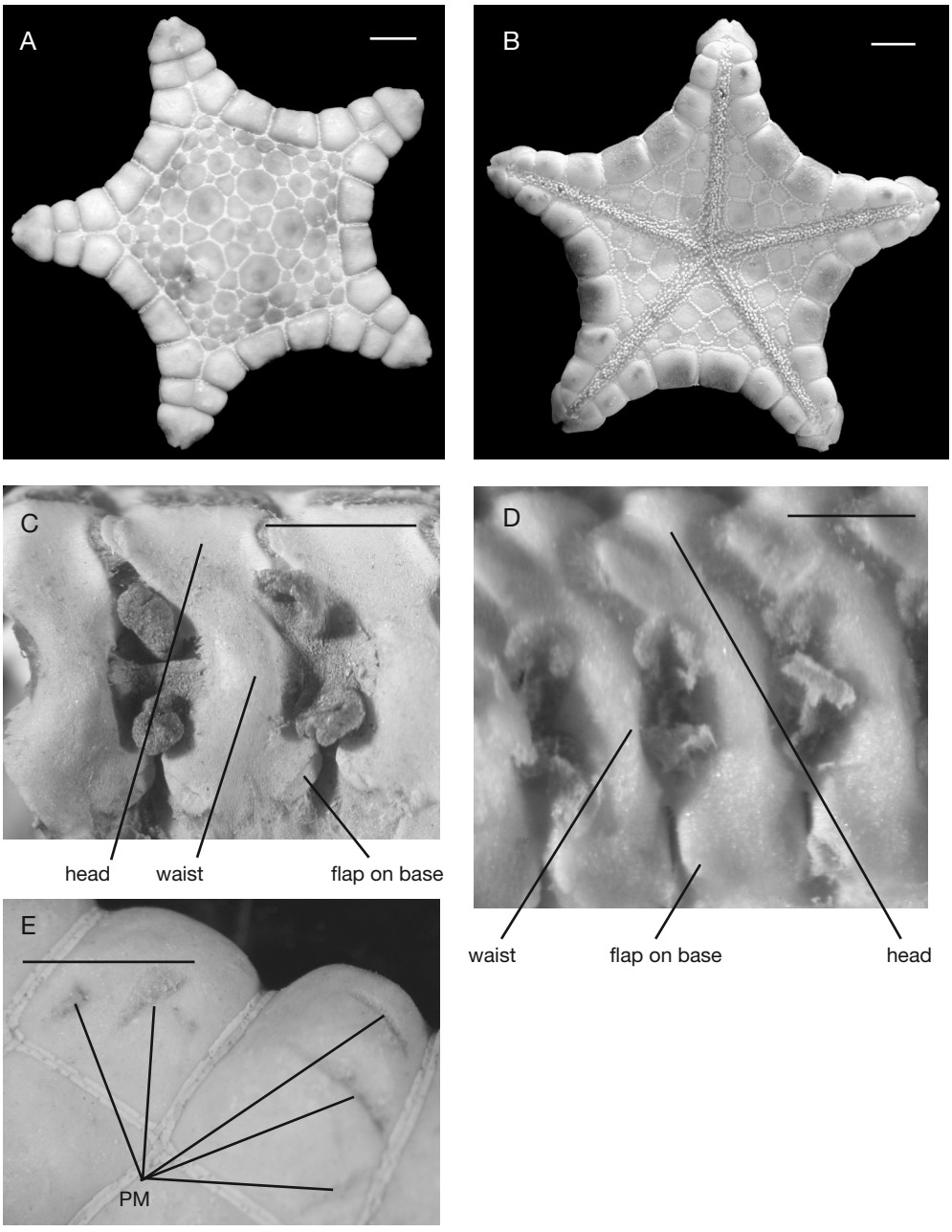

FIG. 1. — **A**, **B**, *Glyphodiscus pierictus* (Fisher, 1917), New Caledonia, juvenile, dry, R = 7.0 mm, r = 4.0 mm (MNHN EcAs 11686); **A**, abactinal surface; **B**, actinal surface; **C**, *Pontioceramus grandis* Fisher, 1911 (USNM IZ-40578), dry, ambulacrals expressing a large ambulacral head (character 28), absence of an overlapping flange on the ambulacral head (character 29), rounded waist surface (character 30), and fan-like flaps on the ambulacral base (character 31); **D**, *Glyphodiscus pentagonalis* n. sp., dry (MNHN EcAs 11690), ambulacrals expressing a small ambulacral head (28), an overlapping flange (29), a sharpened edge on the waist (30), and narrow flaps on the ambulacral base (31); **E**, *Glyphodiscus magnificus* n. sp., paratype (MNHN EcAs 11683), predatory marks (PM) on superomarginals. Scale bars: A, B, D, 1.0 mm; C, 2.0 mm; E, 5.0 mm.

0, rounded waist surface (Fig. 1C); 1, sharp edge on waist (Fig. 1D)

31. Base of ambulacral: the shape of distinct flap-like flanges on the base region of the ambulacral plate. Fan like flaps are broad and rounded extensions on the ambulacral base. Narrow flaps are more elongate and narrower

0, fan-like flaps (Fig. 1C); 1, narrow flaps (Fig. 1D)

SYSTEMATICS

Order VALVATIDA Perrier, 1884
Superfamily GONIASTEROIDEA Forbes, 1841
Family GONIASTERIDAE Forbes, 1841

Genus *Glyphodiscus* Fisher, 1917

Iconaster – Fisher 1913: 642 (in part).

Iconaster (*Glyphodiscus*) Fisher, 1917: 173; 1919: 306. — Spencer & Wright 1966: U58.

Glyphodiscus – Rowe 1989: 273. — Rowe & Gates 1995: 65. — Clark & McKnight 2003: 52.

TYPE SPECIES. — *Iconaster perierctus* Fisher, 1917.

DIAGNOSTIC SUMMARY. — Disk sunken. Primary circlet plates enlarged. Abactinals and superomarginals smooth, bare. Abactinal plates with complete ring of peripheral accessories.

APOMORPHY LIST. — 5, primary circlet plates enlarged. 6, interradial disk plates enlarged. 7, disk sunken. 11, few marginal plates in interradius. 15, actinal plates bare. 17, furrow spines short, squat. 18, furrow spines round to polygonal in cross section. 19, furrow spines crowded. 23, subambulacrals round to polygonal in cross section. 24, subambulacral-furrow spine space absent. 31, narrow flaps on ambulacral base.

Glyphodiscus perierctus (Fisher, 1913) (Fig. 2)

Iconaster perierctus Fisher, 1913: 642.

Iconaster (*Glyphodiscus*) *perierctus* – Fisher 1917: 173; 1919: 306, pls 79, 81, 83, 93.

Glyphodiscus perierctus – A. M. Clark 1993: 254.

Glyphodiscus mcknighti – Rowe 1989: 273, figs 8A, B, 9A, 9B. — A. M. Clark 1993: 254 (checklist). — Rowe & Gates 1995: 65. — Clark & McKnight 2003: 53.

HOLOTYPE. — **Philippines.** Sulu Archipelago, Tawitawi Grosimunul Island, Sibutu Passage, 4°56'10''N, 119°46'00''E, 177 m, 24.II.1908 (NMNH 30554).

OTHER MATERIAL. — **New Caledonia.** SMIB 5, stn DW 102, 23°19.6'S, 163°4.7'E, 290-305 m, 9.IX.1989, 1 dry specimen with rough marginals, R = 2.3 cm, r = 1.2 cm (MNHN EcAs 11698). — SMIB 4, stn DW 61, 23°00'S, 167°22'E, 520-550 m, 3 dry specimens, R = 3.3 cm, r = 1.6 cm, R = 1.8 cm, r = 1.0 cm, R = 1.9 cm, r = 1.1 cm (MNHN EcAs 11696). — SMIB 5, stn DW 104, 23°15.7'S, 168°4.4'E, 305-335 m, 2 dry specimens, R = 1.7 cm, r = 0.9 cm, R = 0.8 cm, r = 0.4 cm (MNHN EcAs 11697). — SMIB 5, 13.IX.1989, rocks (= "roche"), 1 dry juvenile specimen, R = 7.0 mm, r = 4.0 mm (MNHN EcAs 11686).

Western Australia. NW of Cape Leveque, Western Australia, 14°57.6'S, 121°40.5'E to 14°56.4'S, 121°42.5'E, 200-235 m, Engel trawl on coral rock bottom, 16.II.1984, 1 specimen, R = 3.7 cm, r = 1.5 cm (WAM Z-20875). — S of Bedwell Is., Clerke Reef, sled stn #LB7, 17°54.2'S, 119°17.5'E to 17°53.3'S, 119°17.1'E, 200 m, rocks and hard sponges, 18.VIII.1995, 1 specimen, R = 4.2 cm, r = 1.5 cm (WAM Z-20944).

DISTRIBUTION. — Philippines to Norfolk Island/New Zealand and to Indian Ocean, Western Australia. 178-550 m.

DIAGNOSTIC SUMMARY. — Body stellate with tapering arms. Marginal plate surfaces smooth to rough. Arms with superomarginal plates abutted across radius.

APOMORPHY LIST. — 12, marginal plates elongate. 27, arms short. 30, ambulacral waist with rounded surface.

REMARKS

The juvenile demonstrates a number of features permitting identification, including smooth, wide marginal plates and relatively short arms. Larger specimens add abactinal, marginal, and actinal plates as well as a greater number of furrow and subambulacral spines.

Terminal plates are enlarged in asteroid juveniles. The small *G. perierctus*, like *Plinthaster dentatus*, described by Sumida *et al.* (2001), is small enough to retain a disproportionately large terminal plate. In the juvenile, the terminal is similar in size to the largest marginal plate. The fossil goniasterid, *Buterminaster elegans* Blake & Zinsmeister, 1988, from the Eocene of Seymour Island, Antarctica also possesses an enlarged terminal plate similar to

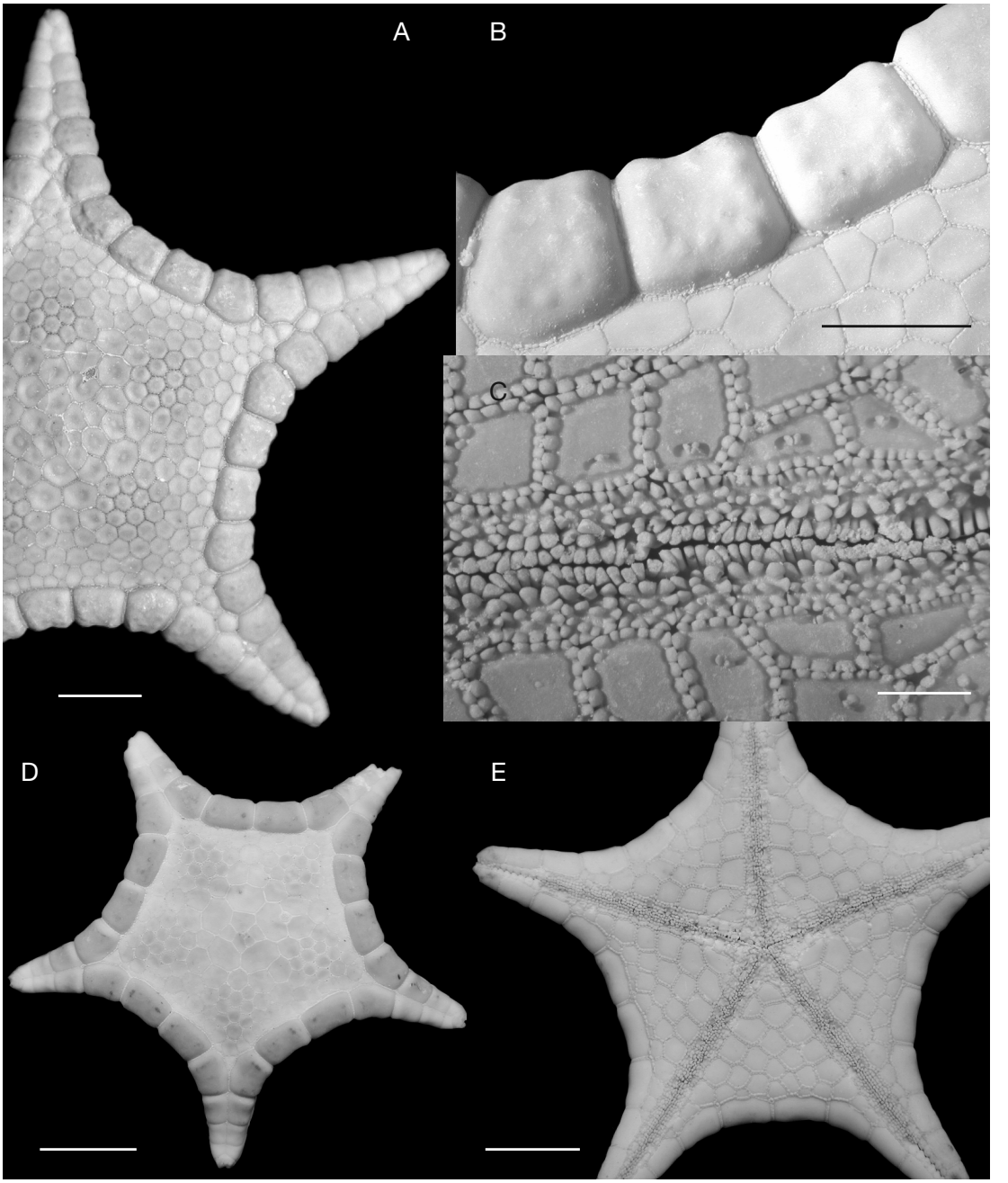

FIG. 2. — **A**-**C**, *Glyphodiscus perierctus* (Fisher, 1917), New Caledonia, SMIB 4, stn DW 61, dry (MNHN EcAs 11686); **A**, abactinal surface, larger specimen with roughened marginal plates; **B**, roughened superomarginal plate; **C**, ambulacral furrow, furrow spines, and adambulacral plates; **D**, **E**, *Glyphodiscus mcknighti* Rowe, 1989 (= *G. perierctus*), New Caledonia, SMIB 5, stn DW 104, dry (MNHN EcAs 11697); **D**, abactinal surface, smaller specimen with smooth marginal plates; **E**, actinal surface. Scale bars: A, B, D, E, 5.0 mm; C, 1.0 mm.

the one observed in *G. perierctus*, suggestive of juvenile morphology. However, the holotype of *Buterminaster* is considerably larger (R = 18-20 mm) than known specimens retaining juvenile morphology (*G. perierctus*, R = 7.0 mm, *Plinthaster dentatus*, R ≈ 4.0 mm). The enlarged terminal plate present in *Buterminaster* and the juvenile specimen of *G. perierctus* completely occupies the distalmost arm tip and differs from enlarged terminals in other fossil species, such as *Comptoniaster* sp. aff. *basseti* (de Loriol, 1887) which only partially occupy the distal arm tip region (Breton 1992: 230).

One of the Western Australian specimens (WAM Z-20944), displays etching and scratching similar in appearance with those caused by predatory fish on Cretaceous goniasterid plates (Neumann 2000).

Body color from freshly collected specimens indicates a deep, brown-orange abactinal surface and a lightly colored actinal surface.

Description of juvenile morphology

A full description of *Glyphodiscus perierctus* is present in Fisher (1919: 306). The juvenile specimen (MNHN EcAs 11686) is described here (Fig. 1A, B) for comparison.

Abactinal plate pattern similar to adult but fewer in number. Paired enlarged primary circlet plates in each interradius present. Additional interradial plates absent. Abactinal plates adjacent to the contact with the marginal plates are smaller and more heterogeneously shaped, directly adjacent to prominent interradial circlet plates.

Terminal plate triangular, enlarged, approximately equal in size to two adjacent superomarginal plates, nearly as large as largest plate in marginal plate series. Larger specimens with terminals comparable in size to one adjacent superomarginal plate, which is smallest (and youngest) in the marginal plate series.

Six marginal plates in each interradius, compared to 12 marginal plates in specimens with R = 2.0 cm and larger. Plate sizes similar, largest and most rectangular interradially, becoming smaller adjacent to the terminal. Distal superomarginal plates wider than long as opposed to elongate in adults.

Actinally, one large chevron present with heterogeneously arranged plates in actinal interradius. Four furrow spines and two enlarged subambulacral spines present versus the five furrow spines and three subambulacrals present in adults. Terminal plate expresses prominent tube foot opening at bottom tip of plate.

Synonymy of *Glyphodiscus mcknighti*

Monophyly of *Glyphodiscus* provides independent support for Rowe's (1989) elevation of *Glyphodiscus* to generic rank. Before *G. mcknighti* was removed from the analysis, *Glyphodiscus perierctus* and *G. mcknighti* were identically coded in the data matrix (Table 3). This is consistent with Rowe's (1989: 274) comments that the two species were very similar. Rowe (1989: 273) distinguished the two based on the presence of roughened superomarginal plates (Fig. 2B), tumid peripheral abactinal disk plates, and papulae distributed over the disk of *I. perierctus*. Although Fisher (1919: 307) described papulae as being "distributed all over the disk", examination of the holotype shows they share a pattern similar to those in other *Glyphodiscus* spp. and are absent from the interradial regions. In fact, Fisher (1919: 307) mentioned that they were absent from one chevron of large interradial plates, but he apparently did not comment on the other interadii. Intermediate degrees of roughening on the superomarginal surface in *G. perierctus* and *G. mcknighti* are observed in MNHN specimens of different sizes (Fig. 2B, D) suggesting that this character is more accentuated with growth. Smaller specimens, up to R ≈ 2.0 mm, demonstrate smooth marginal plates (Fig. 2D), an observation consistent with the size of *G. mcknighti*. Specimens with R > ≈ 2.3 mm demonstrate roughened marginal plates more prominently.

Only one character, tumid peripheral abactinal disk plates, differentiates *G. perierctus* from *G. mcknighti*. Specimens from the South Pacific possess largely flat plates but peripheral abactinal plates are mildly tumid, suggesting that this character varies between geographically disparate populations. Thus, *Glyphodiscus mcknighti* Rowe,

1989, is here considered to be a junior synonym of *Glyphodiscus pierierctus* Fisher, 1913.

Glyphodiscus magnificus n. sp.
(Fig. 3A-C)

HOLOTYPE. — **Palau.** CRECH 146, Mutremdiu 2, Palau, 7°16.41'N, 134°31.43'E, 162 m, 29.III.2001, specimen wet, R = 7.5 cm, r = 2.6 cm (CASIZ 168012).

PARATYPES. — **New Caledonia.** BATHUS 1, stn CP 701, 20°57.5'S, 165°35.9'E, 302-335 m, 18.III.1993, 1 dry specimen, R = 4.1 cm, r = 1.5 cm (MNHN EcAs 11682). — MUSORSTOM 4, stn DW 186, 19°07'S, 163°30'E, 190 m, 19.IX.1985, 1 dry specimen, R = 2.5 cm, r = 1.1 cm (MNHN EcAs 11684). — MUSORSTOM 4, stn DW 185, 19°06'S, 163°29'E, 230 m, 18.IX.1985, 7 dry specimens, R = 2.2 cm, r = 0.8 cm, R = 2.4 cm, r = 1.0 cm, R = 2.6 cm, r = 1.0 cm, R = 2.7 cm, r = 1.1 cm, R = 3.4 cm, r = 1.5 cm, R = 3.6 cm, r = 1.8 cm, R = 3.8 cm, r = 1.6 cm (MNHN EcAs 11683). — SMIB 5, 250 m, 13.IX.1989, rocks, 3 dry specimens, R = 2.4 cm, r = 1.0 cm, R = 2.7 cm, r = 1.1 cm, R = 2.9 cm, r = 1.2 cm (MNHN EcAs 11692). — SMIB 5, stn DW 90, 22°19.1'S, 168°41.6'E, 310-340 m 13.IX.1989, 1 dry specimen, R = 2.7 cm, r = 1.2 cm (MNHN EcAs 11693).
Vanuatu. MUSORSTOM 8, stn CP 970, 20°19'S, 169°53'E, 252-310 m, 21.IX.1994, 1 dry specimen, R = 4.3 cm, r = 2.0 cm (MNHN EcAs 11691).

ETYMOLOGY. — The descriptor *magnificus* describes the magnificent and striking appearance of this species.

DISTRIBUTION. — New Caledonia, Vanuatu, and Palau. 162-335 m.

DIAGNOSIS. — A species with interradial marginal (supero- and infero- series) plates bearing conical prominences extended from the plate. Furrow and subambulacral spines are flattened and nearly flush with the actinal surface.

APOMORPHY LIST. — 14, marginal cones (Fig. 3A). 20, subambulacral spines present (Fig. 3C). 21, subambulacral spines flattened (Fig. 3C).

DESCRIPTION

Body relatively flattened. Arms elongate. Interradial arcs broad-linear. Pedicellariae absent on abactinal surface and marginal plate series. Pedicellariae present on actinal surface.

Abactinal surface flat. Disk region stellate. Abactinal plates extend onto the arm base, with one or two plates occasionally present between abutted superomarginal plates. Abactinal plates largely hexagonal in radial regions but rounded to polygonal elsewhere. Plate shapes vary but more heterogeneous near contact between abactinal surface and superomarginal series. Plate size varies with location. Largest plates occur on primary circlet and interradially. Moderate-sized plates occur on radial regions. Smallest plates occur near the superomarginal edge. Primary circlet composed of approximately two prominent polygonal plates for each interradius. One smaller polygon sits between these pairs along each radius, aligned with the carinal plates. Abactinal plates bare, smooth. A complete ring of *c.* 18-45 narrow, rectangular accessories present around each plate. Angular at plate corners, varying in length. Madreporite typically triangular with moderately deep grooves, flanked by three plates. Papular regions restricted to radial regions on disk.

Marginal plates bare, smooth. Roughened surfaces on some (e.g., MNHN EcAs 11683). Marginal plates largest interradially decreasing towards arm tips. Largest specimen (R = 7.5 cm) with 32-35 marginal plates. Smaller specimens (R = 4.1, 4.3 cm) with 23 marginal plates. Smallest specimen (R = 2.2 cm) with 18 marginal plates. Superomarginal-abactinal surface contact forms low rounded angle. Inferomarginal contact similar. Marginal plates abutted along arm. Number of abutted plates range from six to seven pairs (small specimen), nine to 12 pairs (middle-sized specimen) and 13-15 (largest). Abutted plates are more angular in smaller specimens, becoming more round and convex in larger specimens. Marginals largest near the base. Marginal plates matched one-to-one proximally, becoming more mismatched near the tips. Both marginal plate series convex, swollen, forming quadrate mound in cross section. Interradial marginal plates with prominent conical to nubbin-shaped extension on the dorsolateral edge of the plate. Extensions present on 6-7 interradial superomarginal, inferomarginal plates. Cone-like extensions less convex at arm's base. Distinct nubbins on interradial superomarginal and inferomarginal

plates on specimens in MNHN EcAs 11692 (R = 2.4, 2.7, 2.9 cm) from New Caledonia and on distalmost 6-7 inferomarginal plates of smaller specimens. Nubbins sit on inferomarginal swelling. Nubbins absent in the 2.5 cm and 4.1 cm specimens although inferomarginals are swollen. Fully developed conical extensions present on the inferomarginal plates of the regenerated arm of MNHN EcAs 11691 and MNHN EcAs 11683. Accessory granules identical to those on abactinal surface form peripheral borders around marginal plate series. Terminal plate large with one or two spines. Arm tips upturned. Terminals facing dorsally.

Actinal plates on disk only. Actinal plates diamond to polygonal forming two to three chevrons. Plates adjacent to inferomarginals less ordered becoming more polygonal, less diamond shaped. Largest plates adjacent to adambulacral plates. Smallest plates closest to inferomarginals. Larger specimens with additional chevrons. Plates with peripheral granules similar to those on abactinal surface and marginal plate series but thicker and blockier. Peripheral granules on plate corners larger than those along plate sides. Mouth angle plates covered by flattened granules/flattened spines similar to those on the adambulacral plates. Approximately 10 pairs of granules along mouth angle plates. Single large angular granule/spine projects into mouth. Adambulacral plates rectangular with three to five, thick, flattened furrow spines. Diamond to triangular in cross section. Five furrow spines present to distal most arm tip, shows little attenuation. Three large subambulacral granules or flattened spines located directly behind the furrow spines. Remainder of the adambulacral plate covered by flattened, prismatic, polygonal, thickened granules of uneven size, flush with actinal surface. Uneven bare spots present on adambulacral plate. Little variation observed between large versus small specimens and between specimens from different localities. Relatively tiny (blades are *c.* 0.5 mm in length) tong-like pedicellariae located on actinal plate surfaces adjacent to adambulacrals. Pedicellariae slightly larger, more numerous in the R = 7.5 cm specimen.

Ambulacral head small with overlapping facet. Ambulacral waist with sharp edge, Ambulacral base with narrow flaps.

In life, this species is bright yellow with orange papular regions, forming a petaloid pattern. Preserved dry specimens, grayish olive to light brown with light actinal surface. Wet specimens, yellowish white.

An arm tip on MNHN EcAs 11691 shows signs of arm damage and regeneration, displaying a enlarged terminal plate relative to the adjacent superomarginals. Three pairs of marginal plates are present on the arm tip in the process of regeneration. Another arm tip on MNHN EcAs 11691 is parasitized by at least two specimens of the eulimid gastropod, *Stilifer* sp. (A. Warén pers. comm. 2003).

Specimens in paratype lot MNHN EcAs 11683 show superomarginals with roughened surfaces and large numbers of scratches and indentions (Fig. 1E). These marks resemble those described by Neumann (2000), suggesting bite marks from predatory fishes.

Glyphodiscus pentagonalis n. sp.
(Fig. 3D, E)

HOLOTYPE. — **South Pacific Ocean.** SMIB 8, banc Éponge (mont B), stn DW 146, 24°55.2'S, 168°21.7'E, 514-522 m, 27.I.1993, 1 specimen dry, R = 1.6 cm, r = 1.3 cm (MNHN EcAs 11688).

PARATYPES. — **New Caledonia.** LITHIST, banc Stylaster, stn DW 01, 23°37.4'S, 167°42.1'E, 440 m, 10.VIII.1999, 1 specimen dry, R = 2.2 cm, r = 1.5 cm (MNHN EcAs 11690). — SMIB 3, stn DW 05, 24°55'S, 168°22'E, 502-512 m, 21.V.1987, 1 specimen dry, R = 1.6 cm, r = 1.3 cm (MNHN EcAs 11689). — BERYX 11, stn DW 27, 23°37'S, 167°41'E, 460-470 m, 18.X.1992, 1 specimen dry, R = 1.7 cm, r = 1.4 cm (MNHN EcAs 11687). — SMIB 8, banc Éponge (mont B), stn DW 147, 24°54.9'S, 168°21.8'E, 508-532 m, 27.I.1993, 2 specimens dry, R = 1.4 cm, r = 1.2 cm, R = 1.2 cm, r = 1.1 cm (MNHN EcAs 11694). — BATHUS 3, stn DW 819, 23°45'S, 168°16'E, 478-486 m, 28 XI.1993, 1 specimen dry, R = 1.5 cm, r = 1.3 cm (MNHN EcAs 11695).

ETYMOLOGY. — This species is named for its distinctive pentagonal shape.

DISTRIBUTION. — Currently known only from New Caledonia. 460-532 m.

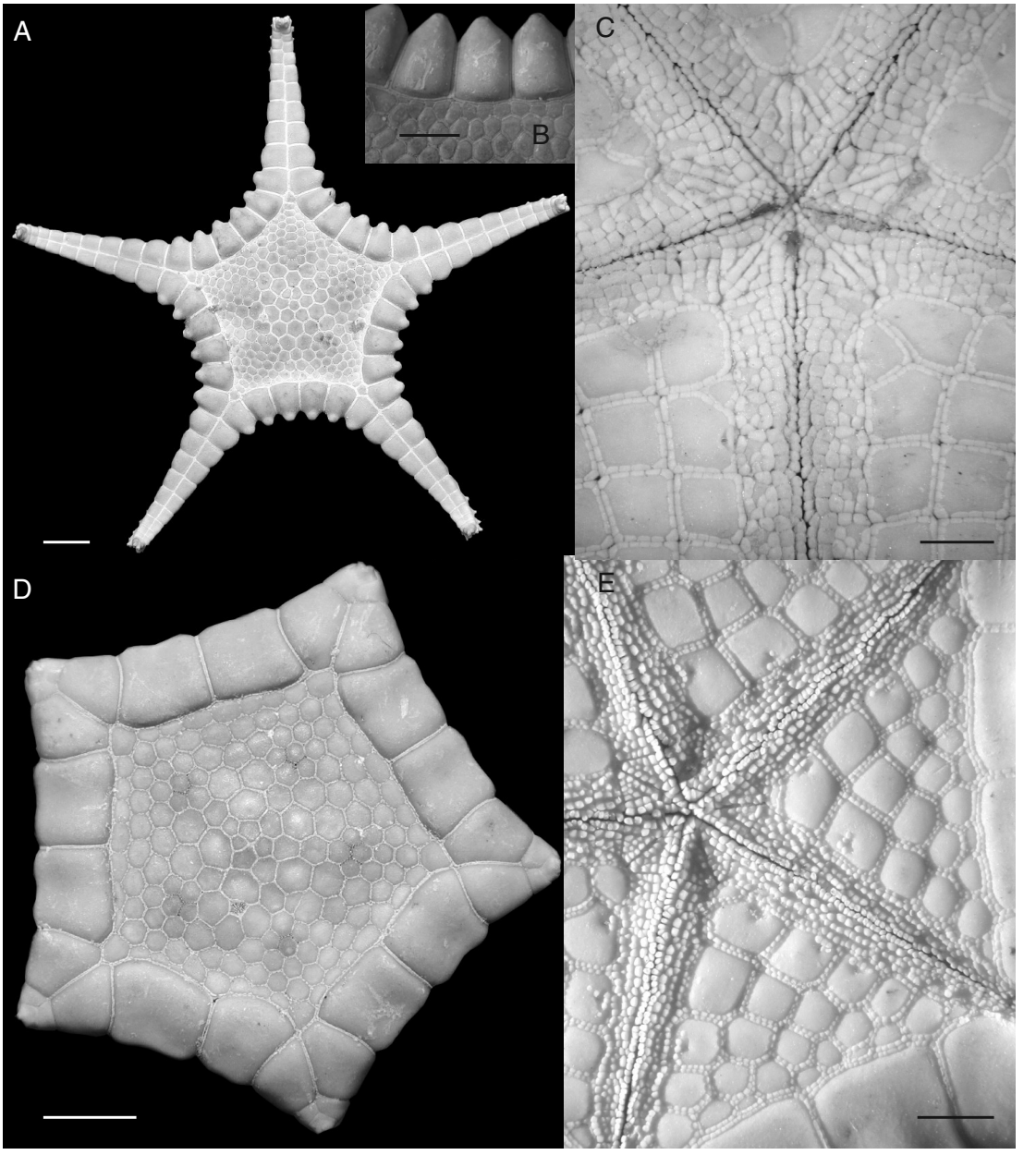

FIG. 3. — **A**-**C**, *Glyphodiscus magnificus* n. sp., New Caledonia, paratype, dry (MNHN EcAs 11682); **A**, abactinal view; **B**, superomarginal plate shape; **C**, oral and adambulacral regions; **D**, **E**, *Glyphodiscus pentagonalis* n. sp., New Caledonia, holotype, dry (MNHN EcAs 11688); **D**, abactinal view; **E**, oral and adambulacral regions. Scale bars: A, 5.0 mm; B, D, 3.0 mm; C, 2.0 mm; E, 1.0 mm.

DIAGNOSIS. — Pentagonal body with few, smooth marginal plates (≈ 4-6) in each interadii. Superomarginal plates at each arm tip triangular in outline, and directly abutting across arm.

APOMORPHY LIST. — 12, marginal plates elongate. 13, enlarged basal superomarginals. 27, arms short.

DESCRIPTION

Disk pentagonal. interradial arcs linear. Arms, short and stubby. Body, stout and flat.

Disk area pentagonal. Plates bare, flat. Surface ornamentation absent. Surfaces smooth. Plates more convex on papular regions along radii than on interradial regions of disk. Papular regions composed of six plates surrounding a single seventh plate in the center. Plates flanked at corners by papulae. Abactinals hexagonal to polygonal in shape, especially those around disk center. Plates more elongate, angular at contact between abactinal plates and superomarginal plates. Primary circlet plates at disk center enlarged, plates adjacent to contact with superomarginals smaller. Two enlarged heptagonal plates in each interradius. All plates with complete peripheral border of *c.* 20-60 granular-rectangular plates. Plates adjacent to superomarginal surface with scattered pedicellariae. Madreporite triangular, flanked by three plates.

Approximately six marginals in smaller specimens (R = 1.0 cm) vs approximately eight superomarginal plates (R = 2.4 cm) in larger specimens. Typically about two superomarginals per interradius in specimens above R = 1.0 cm. Marginal plates smooth, devoid of surface ornamentation. Plates flat, largely smooth.

Superomarginals at base of arm enlarged and in direct contact. Shape, asymmetrically pentagonal. Enlarged plates approximately 1.5 times those of the interradial superomarginal plates. Superomarginal plates along arm are four-sided but roughly triangular in shape. No enlarged inferomarginals. Inferomarginals are roughly triangular in shape. All marginal plates bordered by a complete ring of rectangular accessories/granules similar to those of the abactinal and actinal surfaces. Inferomarginals smooth, flat.

Actinal surface region composed of flat, bare actinal plates in approximately two to three concentric chevrons. Plates round to diamond shaped. Plates nearest adambulacrals largest becoming smaller toward the inferomarginal series. Plates closest to adambulacrals are more angular, becoming more rounded closer to marginal plate contact. Plates closer to the inferomarginals more polygonal, less regular in shape. Actinal plates bordered by 20-50 cubic-rectangular shaped, widely spaced accessories, larger than those on the abactinal surface. Some actinal plates near adambulacrals with one narrow-tong shaped pedicellariae rooted in relatively deep pit centered on plate.

Approximately four to five furrow spines medially reduced to two to three at arm tip. Spines thickened and polygonal-triagonal to quadrate in cross section. Furrow spines flanked by three subambulacral spines. Each subambulacral twice thickness of furrow spines. Subambulacrals quadrate to polygonal in cross section, less elongate than furrow spine series. Remainder of adambulacral plate covered by four to six low, relatively large, well spaced, angular granules. Subambulacral granules triangular to quadrate in cross section. Adambulacral side adjacent to actinal plates with three to four low angular granules, triangular to quadrate in cross section.

Ambulacral head small, compressed, with prominent flap overlapping next ambulacral. Waist with sharp edge. Ambulacral base with narrow flaps.

Color observed from freshly collected specimens is a dark grayish-green with light beige-cream disk with red highlights between abactinal disk plates. Dry specimens have similar coloration, but lack red highlights.

Genus *Iconaster* Sladen, 1889

Dorigona – Gray 1866: 7 (in part).

Pentagonaster – Perrier 1875: 190, 192 (in part).

Iconaster Sladen, 1889: 261. — Fisher 1911: 172. — H. L. Clark 1946: 95. — Spencer & Wright 1966: U58. — Aziz 1986: 250.

DIAGNOSIS. — Primary circlet, interradial plates enlarged. Papular plates on radial regions. Abactinal plate corners with enlarged accessories. Glassy tubercles on most but not all species. Superomarginal plates

with glassy tubercles on two species. Arms relatively elongate with superomarginals abutted across midpoint.

APOMORPHY LIST. — 5, primary circlet plates enlarged. 6, interradial disk plates enlarged. 7, disk and marginal plate surfaces flush. 15, actinal plates bare. 17, short and squat furrow spines. 18, furrow spines round and polygonal in cross section. 19, furrow spines crowded. 23, subambulacrals round and polygonal in cross section. 24, subambulacral-furrow spine space absent. 31, narrow flaps on ambulacral base.

SYNONYMY OF *ICONASTER CORINDONENSIS* AZIZ & JANGOUX, 1984

JUVENILE MATERIAL EXAMINED. — **Indonesia.** Tanimbar Is., KARUBAR, stn CP 78, 9°06'S, 131°24'E, 295-284 m, 3.XI.1991, 1 dry specimen (MNHN EcAs 11699).
New Caledonia. Halipro, stn CP 867, 21°26'S, 166°18'E, 720-950 m, 22.III.1994, 1 dry specimen (MNHN EcAs 11700).

Consideration of *Iconaster corindonensis* and *Lithosoma penichra* suggests that the former species consists of juveniles of the latter and therefore *I. corindonensis* is a synonym of *L. penichra*. Although the holotype was unavailable, MNHN specimens that exactly fit the description of Aziz & Jangoux (1984) were available for comparison. Several characters are shared, or plesiomorphic, between *I. corindonensis* and *L. penichra*. These include: glassy tubercles on the abactinal plates present (character 5), superomarginal plates abutted along the arm (character 8), furrow spine length elongate (character 17), furrow spines in cross section thin and flattened (character 18), furrow spine spaced apart (character 19), subambulacrals round in cross section (character 23), enlarged oral spines present (character 25), rounded interradial curve present (character 26), broad ambulacral head shape present (character 28), fan-like flaps on the ambulacral base present (character 31).
Because the type (R = 1.8 cm) and specimens examined (R = 1.1 cm) were all relatively small, it is argued that two features diagnostic for *Iconaster*, including enlarged corner plates (character 1) and an incomplete periphery of accessory plates (character 3), which are present in the description of *I. corindonensis*, change during ontogeny, leading to its erroneous taxonomic placement. After this was determined, "*Iconaster corindonensis*" was removed from analysis.

Iconaster elegans Jangoux, 1981
(Fig. 4A-D)

Iconaster elegans Jangoux, 1981: 467, pl. 3 figs 1-3, text fig. 2. — Aziz 1986: 255. — A. M. Clark 1993: 259.

MATERIAL EXAMINED. — 1 paratype (MNHN EcAs 2776).

DISTRIBUTION. — Known only from the Philippines. 129-222 m.

DIAGNOSIS. — Species with glassy tubercles on all body surfaces, including abactinal, actinal, adambulacral, superomarginal and inferomarginal plate series.

APOMORPHY LIST. — 1, enlarged corner accessory plates present on radial regions. 2, enlarged corner accessory plates present. 3, complete periphery of abactinal accessories. 4, glassy tubercles on abactinal plates. 7, disk and abactinal disk surface flush. 9, glassy tubercles on superomarginal plates. 10, glassy tubercles on inferomarginal plates. 12, wide marginal plates. 16, glassy tubercles on actinal plates. 19, furrow spines spaced apart. 20, subambulacral spines present. 23, subambulacral spines absent. 25, enlarged oral spines present. 26, rounded interradial arc. 31, fan like flaps on ambulacral base.

Iconaster longimanus (Möbius, 1859)
(Fig. 4E-G)

Astrogonium longimanum Möbius, 1859: 7, pl. 1, figs 5, 6.

Astrogonium souleyeti – Dujardin & Hupé 1862: 392.

"*Archaster lucifer*?" – Valenciennes *in* Perrier 1875: 228 (1876: 44) (cited only as MS name in synonymy of *I. longimanus* – Möbius 1859 so not an available name).

Goniaster longimanum – Lütken 1864: 145; 1871: 245.

Dorigona longimana – Gray 1866: 7.

Pentagonaster longimanus – Perrier 1875: 228.

Iconaster longimanus – Sladen 1889: 262. — Koehler 1895: 393; 1910: 268. — Döderlein 1896: 307, pl. 18, fig. 33; 1924: 56, pl. 17, figs 2-2a. — Bedford

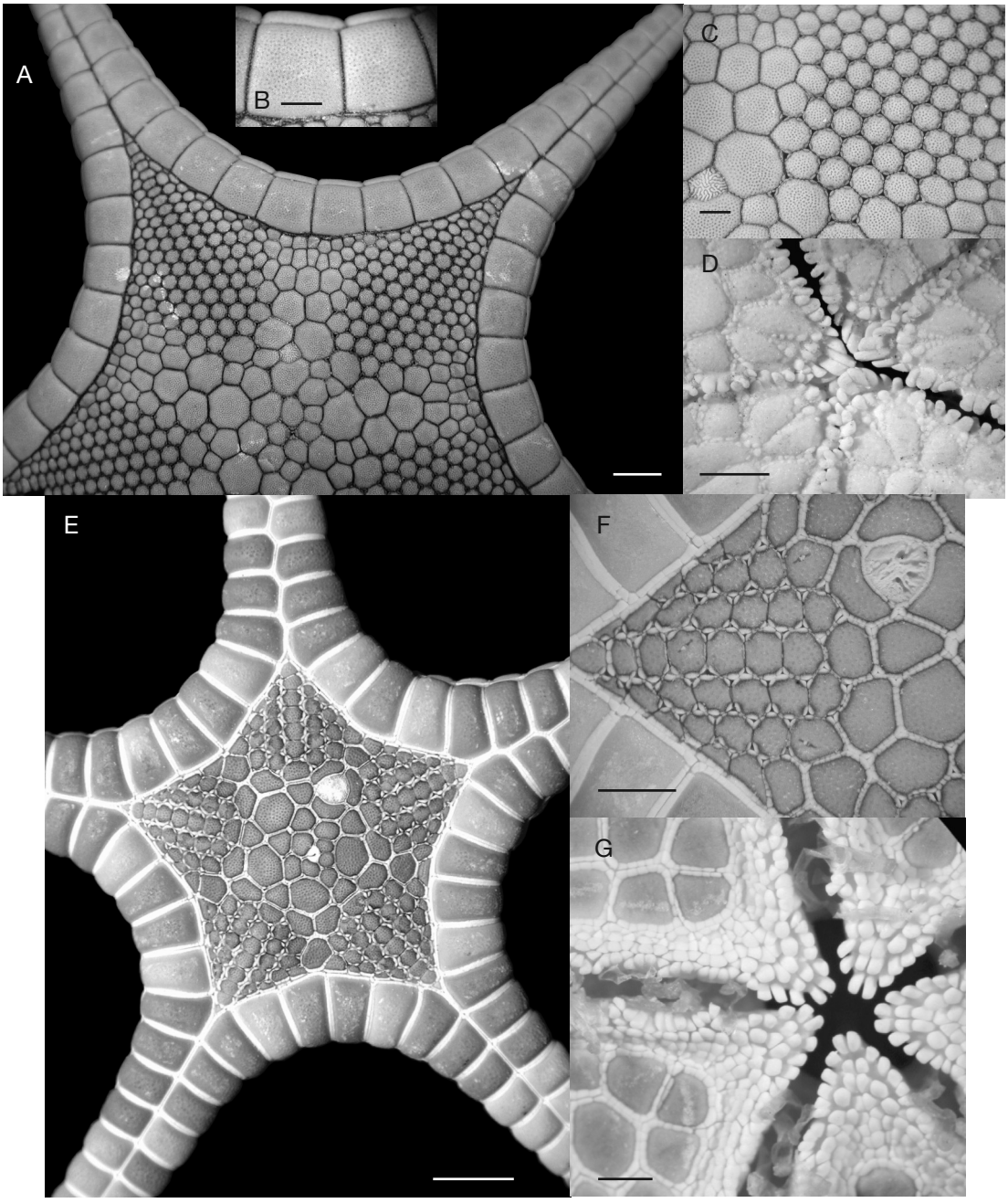

FIG. 4. — **A**-**D**, *Iconaster elegans* Jangoux, 1981, paratype, dry (MNHN EcAs 2776); **A**, abactinal surface; **B**, glassy granules on superomarginals; **C**, enlarged accessories on abactinal plates, papular region; **D**, oral and adambulacral regions; **E**-**G**, *Iconaster longimanus* Möbius, 1859, Singapore, dry (CASIZ 117905); **E**, abactinal surface; **F**, abactinal plates with glassy granules; **G**, oral and adambulacral regions. Scale bars: A, B, 3.0 mm; C, G, 1.0 mm; D, F, 2.0 mm; E, 5.0 mm.

1900: 293. — Fisher 1919: 303, pl. 77, fig. 2, pl. 83, fig. 5, pl. 93, figs 2-2a, pl. 104, fig. 3. — H. L. Clark 1921: 28; 1938: 91. — Engel 1938: 3, pl. 1, fig. 1a-b. — H. L. Clark 1946: 95. — Endean 1957: 238; 1961: 289. — A. M. Clark & Rowe 1971: 47, pl. 5, fig. 4. — Domantay 1972: 79. — Marsh 1976: 217. — Rowe & Gates 1995: 65. — Gosliner *et al.* 1996: 253. — A. M. Clark 1993: 259. — Van Den Spiegel *et al.* 1998: 446, fig. 27A-C, pl. I-4.

MATERIAL EXAMINED. — **Singapore.** Hantu, 10 m, 2 specimens dry (CASIZ 117905).
Philippines. Sulu Archipelago, stn 5174, 2.6 miles west of Jolo Light, Jolo, 36.6 m depth, coarse sand, 1 specimen (NMNH 40546).

DISTRIBUTION. — Indo-Pacific distribution. SE Arabia, Indonesia, N and W Australia and Queensland, Philippine Is, Singapore, South China Seas. 6-85 m.

DIAGNOSIS. — Species with glassy tubercles on abactinal and superomarginal plates. Elongate arms with abutted superomarginals along radius.

APOMORPHY LIST. — 1, enlarged corner accessory plates present on radial regions. 2, enlarged corner accessory plates present. 3, complete periphery of abactinal accessories. 4, glassy tubercles on abactinal plates. 7, disk and abactinal disk surface flush. 9, glassy tubercles on superomarginal plates. 26, rounded interradial arc.

Iconaster uchelbeluuensis n. sp.
(Fig. 5D-G)

HOLOTYPE. — **Palau.** Uchelbeluu (= Augulpelu) Reef, Short Dropoff Bight "Sea Bear Site", 88 m (290 ft), on rocky/sand terrace, 10.V.1997, 1 wet specimen, R = 3.5 cm, r = 1.9 cm (CASIZ 118049).

PARATYPES. — **Palau.** Uchelbeluu (= Augulpelu) Reef, Short Dropoff Bight "Sea Bear Site", 88 m (290 ft), on rocky/sand terrace, 10.V.1997, 4 wet specimens, R = 4.2 cm, r = 1.5 cm; R = 4.0 cm, r = 1.5 cm; R = 3.7 cm, r = 1.6 cm; R = 3.5 cm, r = 1.6 cm (CASIZ 118050).
Philippines. MUSORSTOM 3, stn CP 131, 11°37'N, 121°43'E, 120-122 m, 1 dry specimen, R = 2.8 cm, r = 1.4 cm (MNHN EcAs 11681).
New Caledonia. Nouméa, ORSTOM, *Vauban*, stn 582, 22°45.3'S, 167°26.8'E, 68 m, 18.VII.1985, 1 dry specimen, R = 2.6 cm, r = 1.2 cm with one damaged arm (MNHN EcAs 11685).

ETYMOLOGY. — This species is named for Uchelbeluu Reef, where it was initially discovered and later made available to the author. The "ch" is silent, and the descriptor is pronounced "U- el-be-luu ensis".

DISTRIBUTION. — Philippines, Palau, and New Caledonia. 68-122 m.

DIAGNOSIS. — Species with enlarged accessories at plate corners, but with incomplete ring around abactinal plates. Glassy tubercles absent from abactinal plates.

APOMORPHY LIST. — 1, enlarged corner accessory plates present on radial regions. 2, enlarged corner accessory plates present. 3, complete periphery of abactinal accessories. 9, glassy tubercles on superomarginal plates. 10, glassy tubercles on inferomarginal plates. 12, marginal plate shape, wide. 26, rounded interradial arc.

DESCRIPTION

Stellate disk area. Arms elongate. Interradial angles rounded. Overall body, flat. Arm tips tilting upwards.

Abactinal plates flat, smooth. Surface bare. Glassy tubercles absent on abactinal plates. Abactinals hexagonal to rounded. Primary circlet plates rounded. Abactinal plates heterogeneously shaped at contact between disk and superomarginals. Polygonal plates, paired, enlarged present interradially. Abactinal plates smaller in radial regions, homogeneously sized. Radial regions, swollen. Interradial regions, concave to depressed. Some abactinal plates on arms between superomarginals, elongate, diamond shaped. 30-60 accessory plates form complete border around interradial abactinal plates. Peripheral accessories rectangular to quadrate, larger around corners on the plates. Abactinal plates with corner plates. Complete borders absent around papular regions. Enlarged accessory plates present on abactinal plate corners, forming triads around papulae (Fig. 5F). Accessories absent from lateral sides of radial, papular plates. Enlarged accessory plates absent on primary circlet plates. Madreporite triangular, flanked by three plates.

Approximately 20 marginals present interradially. Marginal plates smooth, convex in cross section, appearing swollen. Superomarginal plates more swollen than inferomarginal plates. Marginal plate surface bare. 30-60 relatively fine glassy tubercles on both marginal plate series on arms only. Glassy tubercles absent from marginal plate series on the disk. Interradial plates largest,

decreasing in size towards arm tips. Distal plates along arm less swollen. Superomarginal plates correspond proximally, becoming more disjunct distally. 30-60 small, rectangular to grain-shaped accessories surround each marginal plate. Accessory plates similar to those present on abactinal surface. Terminal plate triangular to conical. Zero to two spinelets present.

Actinal plates bare. Lacking accessories on plate surface. Abactinal plates diamond to polygonal, forming two to three concentric chevrons. Diamond-shaped actinal plates closer to adambulacrals becoming smaller and more heterogeneously shaped closer to contact with inferomarginal plates. 15-40 quadrate-rectangular shaped accessory plates form actinal plate borders. Small, tong-like pedicellariae present on plates adjacent to adambulacrals. Actinal plates present on disk only, absent on arms. Furrow, subambulacral regions crowded. Two to five thickened furrow spines, oval to triangular-quadrate in cross section. Furrow spine numbers attenuate distally. Two to three subambulacrals, enlarged, flanking the furrow spines. Subambulacrals twice as thick as furrow spines, oval to quadrate in cross section, shorter than furrow spines. Remainder of adambulacral plate covered by angular granules, triangular-quadrate in cross section. Border on adambulacral plate surface enclosing small circular to polygonal bare spot behind the subambulacral series. Wedge to polygonal shaped granule present in the enclosed region. Oral plates covered with relatively thick, prismatic spines, quadrate to triangular in cross section similar to those on subambulacral, furrow spine regions. Approximately nine corresponding thickened granules present on mouth angle plates. Pair of wedge-shaped ossicles on oral plates projecting into mouth.

Ambulacrals with relatively small head. Prominent flap overlapping onto next ambulacral ossicle. Waist with sharp edge. Base with narrow flaps.

Species, bright orange in life. Dry specimens, creamy yellow. Wet specimens, off-white.

MNHN EcAs 11685 with damaged, missing arm. Enlarged abactinal plates have overgrown this region but the marginal plate series have not been replaced. Etching and notching are present on superomarginals of MNHN EcAs 11681 and 11685 suggesting traces of predatory fish as suggested by Neumann (2000) in Cretaceous goniasterids.

Iconaster vanuatuensis n. sp.
(Fig. 5A-C)

HOLOTYPE. — **Vanuatu.** MUSORSTOM 8, stn CP 1018, 17°53'S, 168°25'E, 300-301 m, 27.IX.1994, 1 dry specimen, R = 6.6 cm, r = 2.9 cm (MNHN EcAs 11680).

PARATYPES. — **Vanuatu.** MUSORSTOM 6, stn CP 1017, 17°53'S, 168°26'E, 294-295 m, 27.IX.1994, 2 wet specimens, R = 5.6 cm, r = 2.4 cm, R = 3.2 cm, r = 1.3 cm (MNHN Ech 4685).

ETYMOLOGY. — This species is named for the type locality.

DISTRIBUTION. — Vanuatu. 294-301 m.

DIAGNOSIS. — Glassy tubercles on smooth, abactinal plates. Adambulacral plates covered by flattened scalar granules with short but well spaced furrow spines. Enlarged pair of oral spines, hemispherical in cross section.

APOMORPHY LIST. — 1, enlarged corner accessory plates present on radial regions. 2, enlarged corner accessory plates present. 3, complete periphery of abactinal accessories. 4, glassy tubercles on abactinal plates. 7, disk and abactinal disk surface flush. 9, glassy tubercles on superomarginal plates. 11, high number of marginal plates in interradius. 18, furrow spines, round-polygonal in cross section. 19, furrow spines spaced apart. 20, subambulacral spines present. 22, granular subambulacral spines present. 25, enlarged oral spines present. 26, rounded interradial arc. 31, fan like flaps on ambulacral base.

DESCRIPTION

Overall body convex, relatively flat, broad with tapering arms. Disk stellate. Radial regions swollen with depressed interradial areas. Pedicellariae absent.

50-300 small glassy tubercles present on each plate. Abactinal plates bare, hexagonal to polygonal smooth. Hexagonal plates on the primary circlet and interradial regions, largest. Plate shapes more heterogeneous, smaller at contact with superomarginals. Two large hexagonal plates

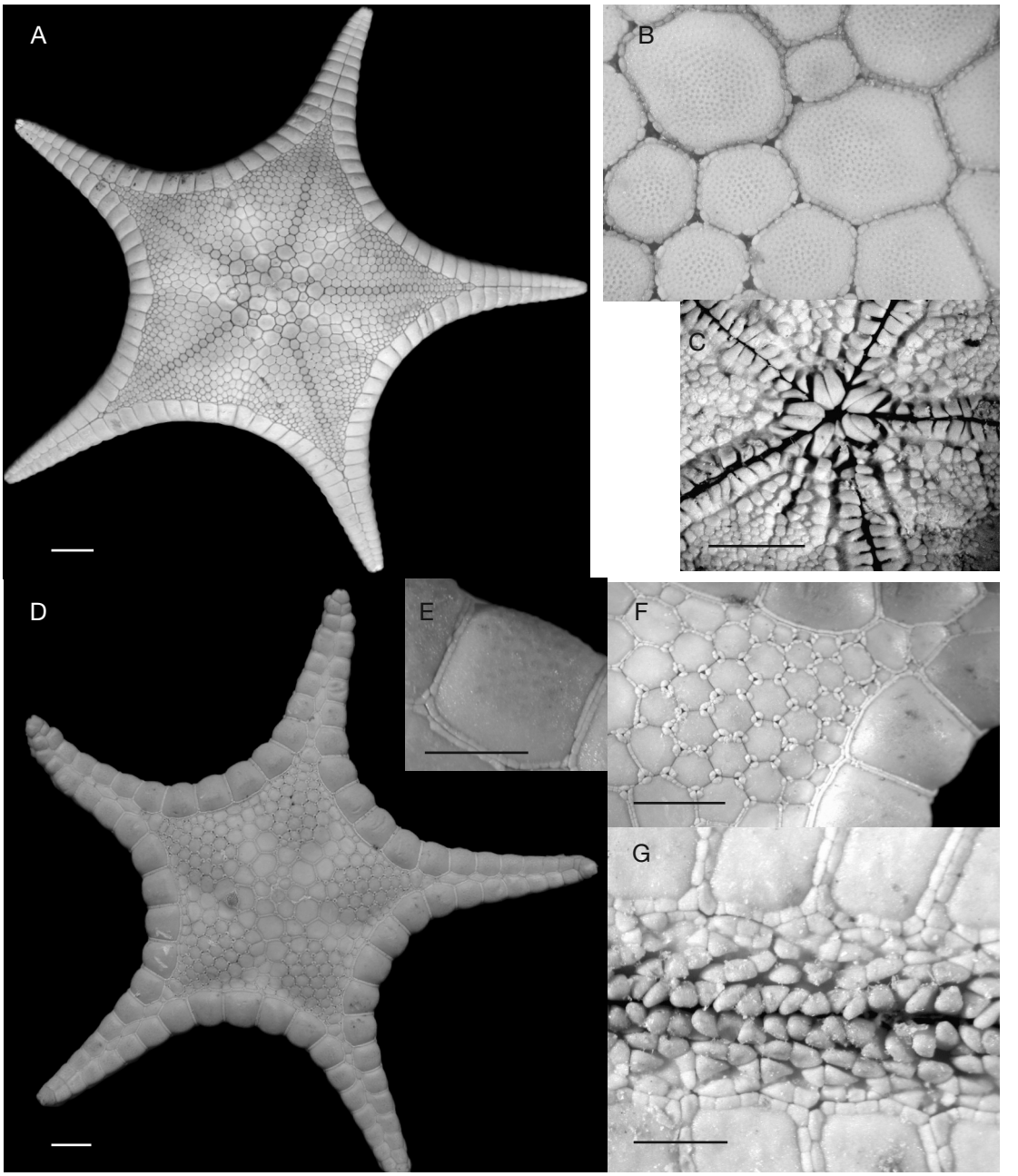

FIG. 5. — **A**-**C**, *Iconaster vanuatuensis* n. sp., Vanuatu, holotype, dry (MNHN EcAS 11680); **A**, abactinal view; **B**, abactinal plates with glassy granules; **C**, oral region showing enlarged spines and adambulacral-subambulacral region; **D**-**G**, *Iconaster uchelbeluuensis* n. sp., Philippines, paratype, dry (MNHN EcAs 11681); **D**, abactinal view; **E**, glassy granules on superomarginal plate; **F**, enlarged accessories on corners of abactinal plates; **G**, adambulacral plates displaying crowded furrow spines and subambulacral spines. Scale bars: A, 10.0 mm; B, G, 1.0 mm; C, E, F, 2.0 mm; D, 5.0 mm.

present in each interradial region. Smaller accessory plates present between larger primary circlet plates. Coloration retained on preserved specimens, marking carinal series. Abactinal plates present between abutted superomarginal plates along base of arm. 30-40 accessory plates form full border around abactinal plates. Enlarged accessories present at plate corners around papular openings. Abactinal plate accessories rounded, rectangular in shape.

Marginal plates flat. Mildly convex in cross section. Abundant between arm tips. 36-38 marginal plates present in each interradius. Marginal plates smooth, bare. Marginal plates bordered by accessories identical to those surrounding abactinal plates. Marginal plates wide. Superomarginals abutted across most of arm's distance, 11-12 plates abutted across arm. Contact between abactinal plates, superomarginals convex. Inferomarginals identical in shape. Marginal plates largest interradially becoming smaller distally along arm. Terminal plate large, unevenly oval. Pedicellariae absent on marginal plates.

Actinal plates diamond to polygonal. Plates bordered by small oval-rectangular accessories similar to but larger than those on abactinal surface. Actinal plates present, disk only, absent on arm. Actinal plates form chevrons becoming more disorganized closer to inferomarginal contact. Actinal plates largest adjacent adambulacral plates.

Smallest, most heterogeneously shaped closest to inferomarginals. Adambulacral plates rectangular. Five to seven furrow spines present. Furrow spines short, quadrate to triangular in cross section. Furrow spines well spaced in convex-palmate pattern becoming more prominent distally. Several series of flattened, almost scalar granules adjacent to furrow spines. Seven to eight large, polygonal-unevenly shaped granules immediately flank furrow spines, gradually intergrading into *c.* 30-50 smaller, flatter, polygonal granules covering adambulacral plate, actinal plates. Small circular to unevenly shaped bare spots present on adambulacral plates. Bare spots absent proximal to mouth becoming larger distally. Paired mouth angle plates partly covered by smaller granules adjacent to actinal plates, covered by coarser blockish granules closer to tube foot groove/mouth. Oral spines, paddle shaped, enlarged, thickened, hemispherical in cross-section, flanked by curved-angular furrow spines.

Ambulacral head shape small. Ambulacral facet overlapping onto next. Sharp ridge present on ambulacral waist. Ambulacral base with broad-fan like flaps.

Preserved dry specimen with beige, light brown abactinal surface and dark brown carinal plate series. Carinal color pattern retained in dry, wet specimens.

DISCUSSION

Patterns observed in several, major invertebrate groups display onshore-offshore patterns of evolution (i.e. shallow water ancestry) (Bottjer & Jablonski 1988). Although full phylogenetic histories for crown-group asteroids are incomplete, similar patterns are observed. For example, a phylogenetic analysis of the deep-sea Brisingida supported a shallow-water ancestry (Mah 1998). For fossil species, Blake & Zinsmeister (1988) documented Eocene members of the extant zoroasterid *Zoroaster fulgens* Thomson, 1873 from shallow water sediments at Seymour Island in Antarctica. *Zoroaster fulgens* occurs today only in deep-water habitats, below 200 m. When depth ranges for ingroup taxa are mapped back onto the tree (Fig. 6), a split between deep and shallow-water members of the ingroup is observed. Outgroup taxa and the sister clade, *Glyphodiscus*, both occupy deep-water environments, suggesting deep-water ancestry for the shallow-water *Iconaster* clade.

A greater number of apomorphic changes is present among the species within *Iconaster* relative to *Glyphodiscus* (Fig. 6), suggesting character evolution associated with shallow water habitation, as has been suggested by Jablonski & Bottjer (1988: 86). For example, glassy tubercles (characters 4, 9, 10, 16) are present on abactinal and actinal surfaces of *I. elegans*, disk and marginal plate surfaces of *I. longimanus* and *I. uchelbeluuensis* n. sp.

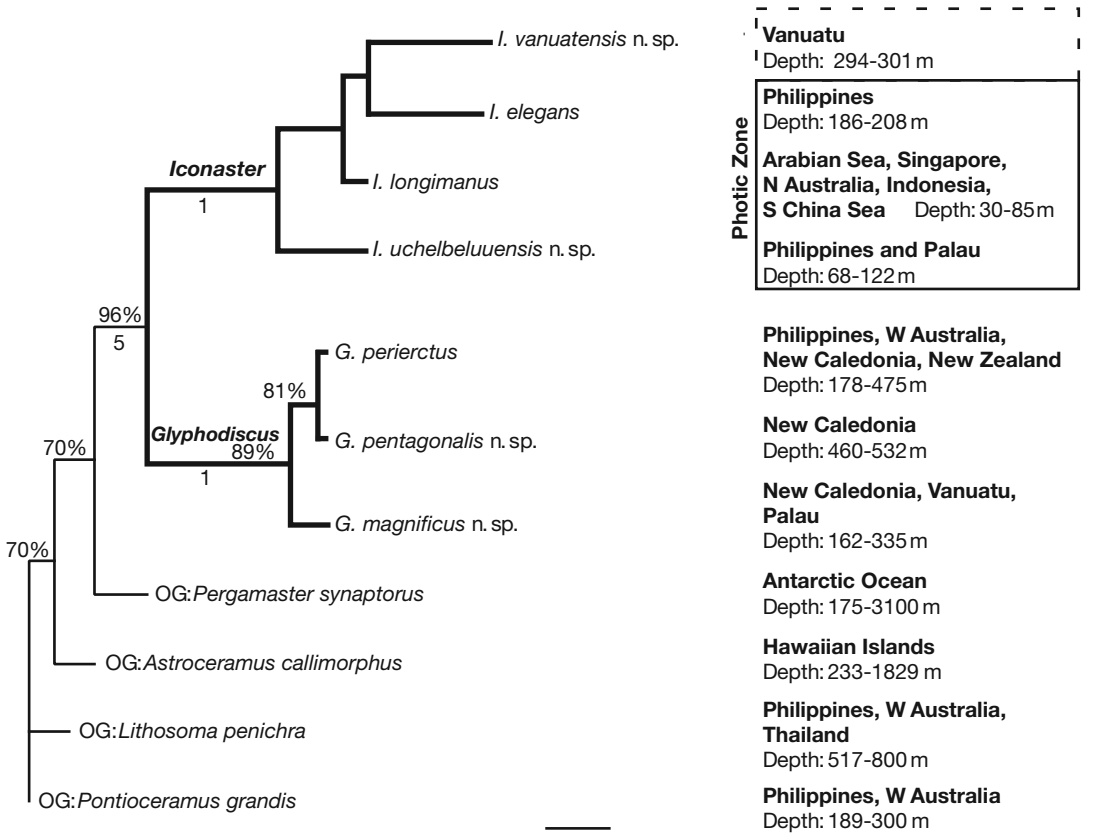

FIG. 6. — Phylogram of *Iconaster* + *Glyphodiscus*, plus outgroup taxa. Numbers with % above branches are bootstrap values (300 replicates). Single numbers below branches are Bremer support values. Lines shown in bold are ingroup taxa. Geographic and bathymetric range data shown to right of tree. Dotted line around Vanuatu indicates possible photic transmission to deeper depths (see Discussion). Abbreviation: **OG**, outgroup taxon. Scale bar: 5 changes.

and on the abactinal surface only of *I. vanuatuensis* n. sp. Glassy tubercles have been interpreted as photoreceptors in the goniasterid starfish *Ogmaster* by Dubois & Hayt (1990), and in ophiocomid ophiuroids (Aizenberg *et al.* 2001), and are convergently expressed in shallow-water valvatidans, including goniasterids, oreasterids, and ophidiasterids (C. Mah unpublished data). Expression may be associated with exposure to sunlight. Three of the four species of *Iconaster*, *I. elegans*, *I. longimanus*, and *I. uchelbeluuensis* n. sp., occur within the range of the photic zone (30-208 m depth) (Fig. 6) and the remaining species, *Iconaster vanuatuensis* n. sp., from Vanuatu, occurs in deeper water (294-300 m depth). Although this initially appears inconsistent, significant levels of light remain present at intermediate depths between 200-900 m (Denton 1990), especially in the relatively clear water of the South Pacific.

Interpretation of biogeographic patterns in *Iconaster* and *Glyphodiscus* must be tentative given that occurrence data for each taxon's geographic range is probably incomplete and influenced by collection bias.

The basal species of *Glyphodiscus* (*G. magnificus* n. sp.) has been recorded in New Caledonia, Vanuatu, and Palau, whereas the more derived

G. perierctus occurs as far north as the Philippines, as far west as Western Australia, and as far south as New Zealand. Distribution suggests that derived taxa dispersed north to the Philippines (central Pacific region), west to the Central Pacific-Indian Ocean and south to New Zealand from a basal divergence in the South Pacific region.

Iconaster uchelbeluuensis n. sp. is supported as basal to *I. longimanus*, *I. elegans*, and *I. vanuatuensis* n. sp., suggesting basal divergence in the central Pacific region with *I. vanuatuensis* n. sp. occurring in the south Pacific. *Iconaster longimanus* occurs widely throughout the Indo-Pacific region and is the only other species of *Iconaster*, aside from *I. vanuatuensis* n. sp., known outside the Philippines, central Pacific area.

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REFERENCES

AIZENBERG J., TKACHENKO A., WEINER S., ADDADI L. & HENDLER G. 2001. — Calcitic microlenses as part of the photoreceptor system in brittlestars. *Nature* 412: 819-822.

AZIZ A. 1986. — *La faune d'astérides (Echinodermata) de la région indo-malaise : taxonomie, zoogéographie, et bathymétrie*. Ph. D. Dissertation from the Marine Biology Laboratory, Université libre de Bruxelles, Belgium, 598 p.

AZIZ A. & JANGOUX M. 1984. — Description de quatre nouvelles espèces d'astérides profonds (Echinodermata) de la région Indo-Malaise. *Indo-Malayan Zoology* 2: 187-194.

BEDFORD F. P. 1900. — On the echinoderms from Singapore and Malacca. *Proceedings of the Zoological Society of London* 1099: 271-299.

BIRKELAND C. 1974. — Interactions between a sea pen and seven of its predators. *Ecological Monographs* 44: 211-232.

BLAKE D. B. 1987. — Classification and phylogeny of post-Paleozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History* 21: 481-528.

BLAKE D. B. & ZINSMEISTER W. J. 1988. — Eocene asteroids (Echinodermata) from Seymour Island, Antarctic Peninsula. *Geological Society of America Memoir* 169: 486-498.

BOTTJER D. J. & JABLONSKI D. 1988. — Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* 3: 540-560.

BRETON G. 1992. — *Les Goniasteridae (Asteroidea, Echinodermata) jurassiques et crétacés de France : taphonomie, systématique, biostratigraphie, paléobiogéographie, évolution*. Thèse de Doctorat d'État es Sciences, Université de Caen, France, 588 p.

CLARK A. M. 1993. — An index of names of recent Asteroidea Part 2: Valvatida. *Echinoderm Studies* 4: 187-366

CLARK A. M. & ROWE F. W. E. 1971. — Monograph of shallow-water Indo-West Pacific echinoderms. *British Museum (Natural History) Publications* 690: i-ix + 1-238, 31 pls.

CLARK H. E. S. & MCKNIGHT D. 2003. — The marine fauna of New Zealand: Echinodermata: Asteroidea (Sea-stars). Order Valvatida. *NIWA Biodiversity Memoir* 117: 1-270.

CLARK H. L. 1916. — A report on the sea-lillies, starfishes, brittlestars, and sea-urchins obtained by the FIS *Endeavor* on the coasts of Queensland, New South Wales, Tasmania, Victoria, South Australia, and Western Australia. Biological results of the fishing experiments carried on by the FIS *Endeavor*, 1908-1914. *Endeavor Research* 4: 1-123.

CLARK H. L. 1921. — The echinoderm fauna of Torres Strait: its composition and its origin. *Carnegie Institution of Washington Publication* 214: 1-223.

CLARK H. L. 1938. — Echinoderms from Australia, an account of collections made in 1929 and 1932. *Memoirs of the Museum of Comparative Zoology* 55: 1-596.

CLARK H. L. 1946. — The echinoderm fauna of Australia. Its composition and its origin. *Carnegie Institution of Washington Publication* 566: 1-567.

COLEMAN N. 1994. — *Sea Stars of Australasia and their Relatives*. Underwater Geographic Pty Ltd, Brisbane, 64 p.

DENTON E. J. 1990. — Light and vision at depths greater than 200 meters, *in* HERRING P. J., CAMPBELL A. K., WHITFIELD M. & MADDOCK L.

(eds), *Light and Life in the Sea*. Cambridge University Press, Cambridge, UK; New York: 127-148.

DÖDERLEIN L. H. 1896. — Bericht über die von Herrn Prof. Semon bei Amboina und Thursday Island gesammelten Asteroidea. *Denkschriften Gesellschaft Jena* 8: 301-322.

DÖDERLEIN L. H. 1924. — Die Asteriden der *Siboga*-Exped. II. Pentagonasteridae. *Siboga-Expedition* 46 (2): 49-69, pls 14-19.

DOMANTAY J. S. 1972. — Summary of a monographic study and checklist of Philippine littoral Echinodermata. *Acta Manilana* 5A (3): 46-94.

DUBOIS P. & HAYT S. 1990. — Ultrastructure des ossicules d'échinodermes à stéréome non perforé, *in* DE RIDDER C., DUBOIS P., LAHAYE M.-C. & JANGOUX M. (eds), *Echinoderm Research*. Balkema, Rotterdam: 217-223.

DUJARDIN M. F. & HUPÉ M. H. 1862. — *Histoire naturelle des Zoophytes. Échinodermes*. Libraire encyclopédique de Roret, Paris, 627 p.

ENDEAN R. 1957. — The biogeography of Queensland's shallow-water echinoderm fauna (excluding Crinoidea), with a re-arrangement of the faunistic provinces of tropical Australia. *Australian Journal of Marine & Freshwater Research* 8: 233-273.

ENDEAN R. 1961. — Queensland faunistic records. VII. Additional records of Echinodermata (excluding Crinoidea). *Papers of the Department of Zoology, University of Queensland* 1: 289-298.

ENGEL H. 1938. — Résultats scientifiques du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. Le Prince et la Princesse Léopold de Belgique. Astéries et Ophiures. *Mémoires du Muséum royal d'Histoire naturelle de Belgique* 18 (3): 1-31.

FISHER W. K. 1911. — Asteroidea of the North Pacific and adjacent waters. 1. Phanerozonia and Spinulosida. *Bulletin of the U.S. National Museum* 76: 1-420.

FISHER W. K. 1913. — Four new genera and fifty-eight new species of starfishes from the Philippine Islands, Celebes, and the Moluccas. *Proceedings of the U.S. National Museum* 43: 599-648.

FISHER W. K. 1917. — New starfishes from the Philippines and Celebes. *Proceedings of the Biological Society of Washington* 30: 89-93.

FISHER W. K. 1919. — Starfishes of the Philippine seas and adjacent waters. *Bulletin of the U.S. National Museum* 100 (3): 1-547.

FISHER W. K. 1940. — Asteroidea. *Discovery Reports*, Cambridge 20: 69-306.

FORBES E. 1841. — *A History of British Starfishes and Other Animals of the Class Echinodermata*. John Van Voorst, London, 267 p.

GALE A. S. 1987. — Phylogeny and classification of the Asteroidea (Echinodermata). *Zoological Journal of the Linnean Society* 89: 107-132.

GOSLINER T. M., BEHRENS D.W. & WILLIAMS G. C. 1996. — *Coral Reef Animals of the Indo-Pacific*. Sea Challengers Press, Monterey, 314 p.

GRAY J. E. 1866. — *Synopsis of the Species of Starfish in the British Museum*. British Museum, London, 17 p.

JABLONSKI D. & BOTTJER D. J. 1988. — Onshore-offshore evolutionary patterns in post-Paleozoic echinoderms: a preliminary analysis, *in* BURKE R. D., MLADENOV P. V., LAMBERT P. & PARSLEY R. L. (eds), *Echinoderm Biology*. Balkema, Rotterdam: 81-90.

JANGOUX M. 1981. — Échinodermes : astéroides, *in* Résultats des campagnes MUSORSTOM I : Philippines, 18-28 mars 1976. *Mémoires ORSTOM* 91: 457-476.

KNOTT K. E. & WRAY G. A. 2000. — Controversy and consensus in asteroid systematics: new insights to ordinal and familial relationships. *American Zoologist* 40 (3): 382-392.

KOEHLER R. 1895. — Catalogue raisonné des échinodermes recueillis par M. Korotnev aux îles de la Sonde. *Mémoires de la Société zoologique de France* 8: 374-423.

KOEHLER R. 1910. — An account of the shallow-water Asteroidea, *in Echinoderma of the Indian Museum*. Trustees of the Indian Museum, Calcutta, 192 p.

LANE D. J. W. & HU J. M. L. 1994. — Abbreviated development in *Iconaster longimanus* (Möbius): planktonic lecithotrophy in a tropical goniasterid sea star, *in* DAVID B., GUILLE A., FERAL J.-P. & ROUX M. (eds), *Echinoderms Through Time*. A.A. Balkema, Rotterdam & Brookfield, 343-346.

LORIOL P. DE 1887. — Notes sur quelques échinodermes fossiles des environs de La Rochelle. *Annales de la Société des Sciences naturelles de Charente-Inférieure* 23: 313-332.

LÜTKEN C. 1864. — Kritiske Bemaerkniger om forsjellige Søstjerne (Asteriderne), med Beskrivelse af nogle nye Arter. *Videnskabelige Meddelelsefra Dansk Naturhistorisk Forening* 1863: 368-371.

LÜTKEN C. 1871. — Fortasatte kritiske og beskrivende Bidrag til Kundskab om Sostjernerne (Asteriderne). *Videnskabelige Meddelelsefra Dansk Naturhistorisk Forening* 1871: 227-304.

MAH C. L. 1998. — Preliminary phylogeny and taxonomic revision of the Brisingida (Asteroidea), *in* MOOI R. & TELFORD M. (eds), *Echinoderms: San Francisco*. A.A. Balkema, Rotterdam & Brookfield: 273-277.

MAH C. L. 2000. — Preliminary phylogeny of the forcipulatacean Asteroidea. *American Zoologist* 40: 375-381

MARSH L. M. 1976. — Western Australian Asteroidea since H. L. Clark. *Thalassia Jugoslavica* 12: 213-225.

MÖBIUS K. 1859. — Neue Seesterne des Hamburger und Ieler Museums. *Abhandlungen und Verhand-*

lungen. *Naturwissenschaftlicher Verein in Hamburg* 4 (2): 1-14.
NEUMANN C. 2000. — Evidence of predation on Cretaceous sea stars from north-west Germany. *Lethaia* 33: 65-70.
PERRIER E. 1875. — *Révision de la collection de stellérides du Muséum d'Histoire naturelle de Paris*. Reinwald, Paris, 384 p.
PERRIER E. 1884. — Mémoire sur les étoiles de mer recueillies dans la mer des Antilles et le golfe du Mexique. *Nouvelles Archives du Muséum d'Histoire naturelle de Paris* 6 (2): 127-276.
ROWE F. W. E. 1989. — Nine new deep-water species of Echinodermata from Norfolk Island and Wanganella Bank, northeastern Tasman Sea, with a checklist of the Echinoderm Fauna. *Proceedings of the Linnean Society of New South Wales* 111 (4): 257-291.
ROWE F. W. E. & GATES J. 1995. — Echinodermata, *in* WELLS A. (ed.), *Zoological Catalogue of Australia* 33. CSIRO, Melbourne, 510 p.
SLADEN W. P. 1889. — Asteroidea. *Report of the Scientific Results of H.M.S.* Challenger 30: 1-893.
SPENCER W. K. & WRIGHT C. W. 1966. — Asterozoans, Part U: Echinodermata, *in* MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology* 3 (1). University of Kansas Press, Lawrence: U4-U107.
SUMIDA P. Y. G., TYLER P. A. & BILLETT D. S. M. 2001. — Early juvenile development of deep-sea asteroids of the NE Atlantic Ocean, with notes on juvenile bathymetric distributions. *Acta Zoologica* 82: 11-40.
SWOFFORD D. L. 2003. — *PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts, software.
VAN DEN SPIEGEL D., LANE D. J. W., STAMPANATO S. & JANGOUX M. 1998. — The asteroid fauna (Echinodermata) of Singapore, with a distribution table and an illustrated identification to the species. *Raffles Bulletin of Zoology* 46: 431-470.
WILEY E. O., SIEGEL-CAUSEY D., BROOKS D. R. & FUNK V. A. 1991. — The compleat cladist: a primer of phylogenetic procedures. *University of Kansas Special Publication* 19: 1-158.

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APPENDIX
Key to *Iconaster* and *Glyphodiscus*

1. Substantially enlarged accessory plates on abactinal plate corners. These most pronounced on radial regions of disk. Glassy tubercles present or absent on abactinal plates, but may be present on marginal, actinal, or adambulacral plates . . . . . *Iconaster*. 2

— All accessory plates on abactinal surface essentially identical in size. Corner plates not significantly enlarged. Glassy tubercles absent from all plates . . . . . *Glyphodiscus*. 5

2. Full ring of accessory granules border all abactinal plates. Glassy tubercles on abactinal plates only. Flattened, almost flush polygonal granules present on adambulacral plate surface. Disk broad with round interradial arcs. Surface of disk between abactinal and superomarginal plates are flush. Oral spines enlarged, hemispherical in cross section. Color, dark, on carinal series in preserved specimens . . . . . *Iconaster vanuatuensis* n. sp. (Fig. 5A, B)

— Incomplete ring of accessory plates around abactinal plates on radial papular regions. Glassy tubercles present or absent on abactinal, marginal, actinal, and adambulacral plates. Polygonal to prismatic granules/spines can be present or adambulacral plate surface, can be bare and devoid of any surface ornamentation. Relatively small disk with linear interradial arcs. Surface of disk sunken relative to the superomarginal plates. Oral spines identical in size to other furrow and subambulacral spines, polygonal in cross-section 3

3. Superficial ornamentation (e.g., granules, etc.) absent from adambulacral plates. Furrow spines conical. Glassy tubercles present on all surfaces (abactinal plates, marginal plates, actinals, and adambulacrals) . . . . . *Iconaster elegans* (Fig. 4A-C)

— Polygonal to prismatic spines present on adambulacral plates. Furrow spines thickened. Oval to polygonal in cross section 4

4. Glassy tubercles absent from actinal surface but present on abactinal and marginal plates. Marginal plates flattened in cross section . . . . . *Iconaster longimanus* (Fig. 4D-G)

— Glassy tubercles absent from abactinal surface but present on marginal plates along arms only. Absent on superomarginal plates near disk. Marginal plates relatively tumid and round-quadrate in cross section . . . . . *Iconaster uchelbeluuensis* n. sp. (Fig. 5C-G)

5. Superomarginal and inferomarginal plates with conical extensions of the marginal plates. Arms relatively elongate. Marginal plates elongate and moderately abundant . . . . . *Glyphodiscus magnificus* n. sp. (Fig. 3A, B)

— Marginal plates smooth to rough. No spines or prominences present on the marginal plate series. Arms short to absent. Marginal plates wide and relatively few (3-4 per interradius) 6

6. Body pentagonal. Arms short (≈ 2 superomarginal plates), triangular. Enlarged plates at base of arm. Only *c.* 2-4 superomarginal plates per interradius . . . *Glyphodiscus pentagonalis* n. sp. (Fig. 3C-E)

— Body stellate. Arms elongate (≈ 4-6 superomarginal plates). Superomarginal plates at arm base identical in size to other superomarginal plates. About 6-7 superomarginal plates per interradius . . . . . *Glyphodiscus pierctus* (Figs 1A, B; 2)