Phylogeny of the Zoroasteridae (Zorocallina; Forcipulatida): evolutionary events in deep-sea Asteroidea displaying Palaeozoic features

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The Zoroasteridae comprise a small but widespread family of asteroids distributed throughout the deep sea. Although poorly understood, they are often collected in the hundreds, suggesting that they occupy important ecological roles. A phylogenetic analysis including 24 terminal taxa and 70 morphological characters was performed, resulting in a single most-parsimonious tree. The tree separated zoroasterids with open, reticulate skeletons (e.g. *Myxoderma*) as more basal than those with more heavily armored, imbricate skeletons (e.g. *Zoroaster*), which were more derived. In addition to agreement with established genera, a new genus is supported by the phylogeny as the sister taxon to *Myxoderma*. The cladistic analysis was performed in conjunction with a revisionary survey of zoroasterid species, resulting in taxonomic changes to species in nearly every genus. Bathymetric and physiographic shifts were observed between the reticulate and imbricate zoroasterid clades. Zoroasterids possess a single marginal plate series, which occurs in basal sister-group neoasteroids (crown-group asteroids). Phylogenetic results suggest that the morphololgical resemblance between zoroasterids and Palaeozoic taxa, such as *Calliasterella*, is convergent but a paraphyletic Zoroasteride cannot be rejected and remains consistent with basal crown-group affinities. Although the phylogenetic position of the Eocene *Zoroaster* aff. *fulgens* was not strongly supported, its presence within a derived cluster of *Zoroaster* spp. suggests a relatively recent (i.e. Cenozoic) diversification into the deep sea. Taxonomic revisions, and geographical and bathymetric range extensions are also included.   © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150**, 177–210.

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INTRODUCTION

Starfishes within the family Zoroasteridae are prominent members of the deep-sea megafauna, occurring exclusively in bathyal to abyssal habitats (~200–6000 m) in the Atlantic, Pacific and Indian Ocean basins. Zoroasterids are distinctive, possessing a small disc and long tapering arms, and can often reach large sizes with arm length approaching 20.0 cm. Colour in zoroasterids (Alton, 1966: 1709; my unpubl. obs.) varies from white to reddish orange. Zoroasterids are most diverse in the Indo-Pacific but further study (Howell *et al.*, 2004) has indicated that there is greater diversity in the Atlantic than was previously perceived.

Although their ecological role is poorly understood, zoroasterids are frequently collected in high densities, suggesting that they occupy important positions in deep-sea ecosystems. Alton (1966: 1709) reported a collection of nearly 5000 individuals of *Myxoderma platyacanthum* in the Astoria Canyon off the Oregon coast. Verrill (1884: 217) reported approximately 200 specimens of the Atlantic *Zoroaster fulgens* (= *Z. diomedae*) from a single station. *Myxoderma platyacanthum* was one of the five most common invertebrates caught during a 1994 upper continental slope trawl along the west coast of the United States (Lauth, Syrjala & McEntire, 1998). Eocene *Zoroaster* specimens from Seymour Island, Antarctica (Blake &

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Zinsmeister, 1979, 1988) were abundant and did not display any evident transport prior to final burial, suggesting high densities in life.

Zoroasterid biology is poorly known. Seasonality and other aspects of reproductive biology in the Atlantic *Zoroaster fulgens* have been studied by Tyler *et al.* (1984) and Grant (1985). Howell *et al.* (2003) studied feeding in *Zoroaster longicauda* (= *Z. fulgens*) using fatty acid biomarkers. Finamore *et al.* (1991) extracted nine polydrydroxy steroids and two steroid glycosides from the north-east Pacific *Myxoderma platyacanthum*. Oxygen consumption for *Zoroaster evermani* was recorded by Webster (1975). Based on gel electrophoresis, *Myxoderma sacculatum* and three other genera of deep-sea asteroids displayed high genetic variability in contrast to the low variability expected from the deep-sea environment (Ayala *et al.*, 1975). *In situ* observations of the Atlantic *Z. fulgens* have been reported by Rice *et al.* (1982: 66, fig. 2e) and Howell *et al.* (2003: 201, fig. 4E). *In situ* observations by Pawson (1982: 133) revealed population densities of *Z. fulgens* in some sites as high as 3.9 specimens per 1000 m^2. Ascothoracid endoparasites have been observed in Pacific and Atlantic *Zoroaster* species (Grygier, 1985; Stone, 1987).

Taxonomic accounts, keys, and studies in classification of zoroasterids include those of Sladen (1889: 416), Fisher (1919a, 1919b), H.L. Clark (1920: 94); Downey (1970) and McKnight 1977). Fisher (1919b) summarized Indo-Pacific zoroasterids. Zoroasterids in New Zealand were summarized by McKnight (2006). Alcock (1893a, 1893b, 1895) studied zoroasterids in the Indian Ocean. Atlantic zoroasterids were studied by Downey (1970) and Clark and Downey (1992).

Phylogenetic studies including zoroasterids have supported a basal phylogenetic position within the Forcipulatacea (also referred to as forcipulates), suggesting that the zoroasterids may demonstrate characteristics intermediate between Palaeozoic and post-Palaeozoic asterozoans. The Forcipulatacea has been supported as the sister clade to the other two major asteroid lineages, the Valvatacea and the Spinulosacea (Blake, 1987).

Downey (1970) argued for inclusion of the Palaeozoic Calliasterellidae, which includes *Calliasterella*, with the Zoroasteridae within a new order, the Zorocallida. McKnight (1977) disagreed with this placement of the Calliasterellidae and returned the Zoroasteridae to the Forcipulatida. Zoroasterids were included in the first apomorphy-based phylogenic studies to support post-Palaeozoic Asteroidea as a monophyletic group (Blake, 1987; Gale, 1987). Zoroasterids occupy similar positions in both phylogenies. Gale (1987) presented forcipulatidans as derived, including the zoroasterids as the sister clade to the remaining forcipulatidans. Blake (1987)

placed the zoroasterids as the sister clade to the Asteriidae and the Heliasteridae, but placed the Brisingida at the base of the forcipulate clade. Blake (1987) recognized that only a single marginal plate series is present in the Zorocallina, a feature that was also present in asteroids basal to the crown-group Asteroidea, including *Trichasteropsis* and *Calliasterella*. Blake (1990) described two new Jurassic zoroasterid-like asteriids and presented implications for these taxa on a phylogeny of the Forcipulatida.

Based on morphology, Mah (2000) supported zoroasterids as the sister group to *Neomorphaster*, but showed a paraphyletic Pedicellasteridae as basal to the zoroasterids and more derived forcipulates. Comparisons between late Palaeozoic asteroids and zoroasterids were made by Blake & Elliott (2003). A phylogenetic analysis of asteroids from the Ordovician to the Recent, including *Zoroaster* and crown-group sister taxa, was presented by Blake & Hagdorn (2003).

Knott & Wray (2000) presented a tRNA and COI-based molecular phylogeny showing *Myxoderma*, as an exemplar for the Zoroasteridae, as basal to other forcipulate asteroids, including brisingidans. However, their results also display pterasterids and echinasterids on a branch including mostly forcipulate taxa, suggesting the need for further work.

Early hypotheses of phylogenetic relationships among the Zoroasteridae were limited to anecdotal comments. Sladen (1889: 426) observed a close affinity between *Pholidaster* and *Zoroaster*. Fisher (1919a: 485), noted that the plates composing the abactinal skeleton in *Pholidaster* and *Cnemidaster* were similar to those in *Zoroaster*. Downey (1970: 5) perceived *Doraster* as most closely related to *Cnemidaster*. *Myxoderma* was distinguished from other zoroasterid genera based on a phylogenetic hypothesis proposed by Blake (1990). Howell *et al.* (2004) discovered reproductive isolation among morphotypes within the Atlantic *Zoroaster fulgens* from the Porcupine Seabight.

A phylogenetic revision of the Zoroasteridae will establish an evolutionary hypothesis for a major clade of deep-sea invertebrate megafauna, allowing for an assessment of macroevolutionary patterns, such as onshore–offshore migrations (i.e. bathymetric shifts) as outlined by Jablonski & Bottjer (1988) and would establish a phylogenetic framework for the disparate data available for zoroasterids. A phylogenetic hypothesis for the Zoroasteridae also permits exploration of relationships between basal crown-group Asteroidea and its fossil sister taxa, such as *Trichasteropis* (Blake & Hagdorn, 2003), allowing further insight into diversification events near the base of the post-Palaeozoic lineage. In addition to development of a phylogenetic hypothesis, a diagnostic key (Appendix 3) and a taxonomic summary of the Zoroasteridae are presented.

MATERIAL AND METHODS

INGROUP AND OUTGROUP CHOICE

All seven zoroasterid genera currently recognized as valid (summarized by Clark & Mah, 2001) were included as ingroup taxa. *Prognaster* Perrier 1891, described from juvenile individuals, is a synonym of *Zoroaster* (Clark & Downey, 1992: 508) and was not included in the matrix. The type species of each genus was included in the analysis. With the exception of

Zoroaster, all zoroasterid genera included fewer than four putative species each, many of which are morphologically similar to the type. In most genera, differences between species was minimal and monophyly for each genus could be tested from the included species. A full size and geographical range of species was examined where possible.

Although a comprehensive revision of *Zoroaster* was not attempted, a significant number of species were included in the analysis (summarized in Fig. 1,
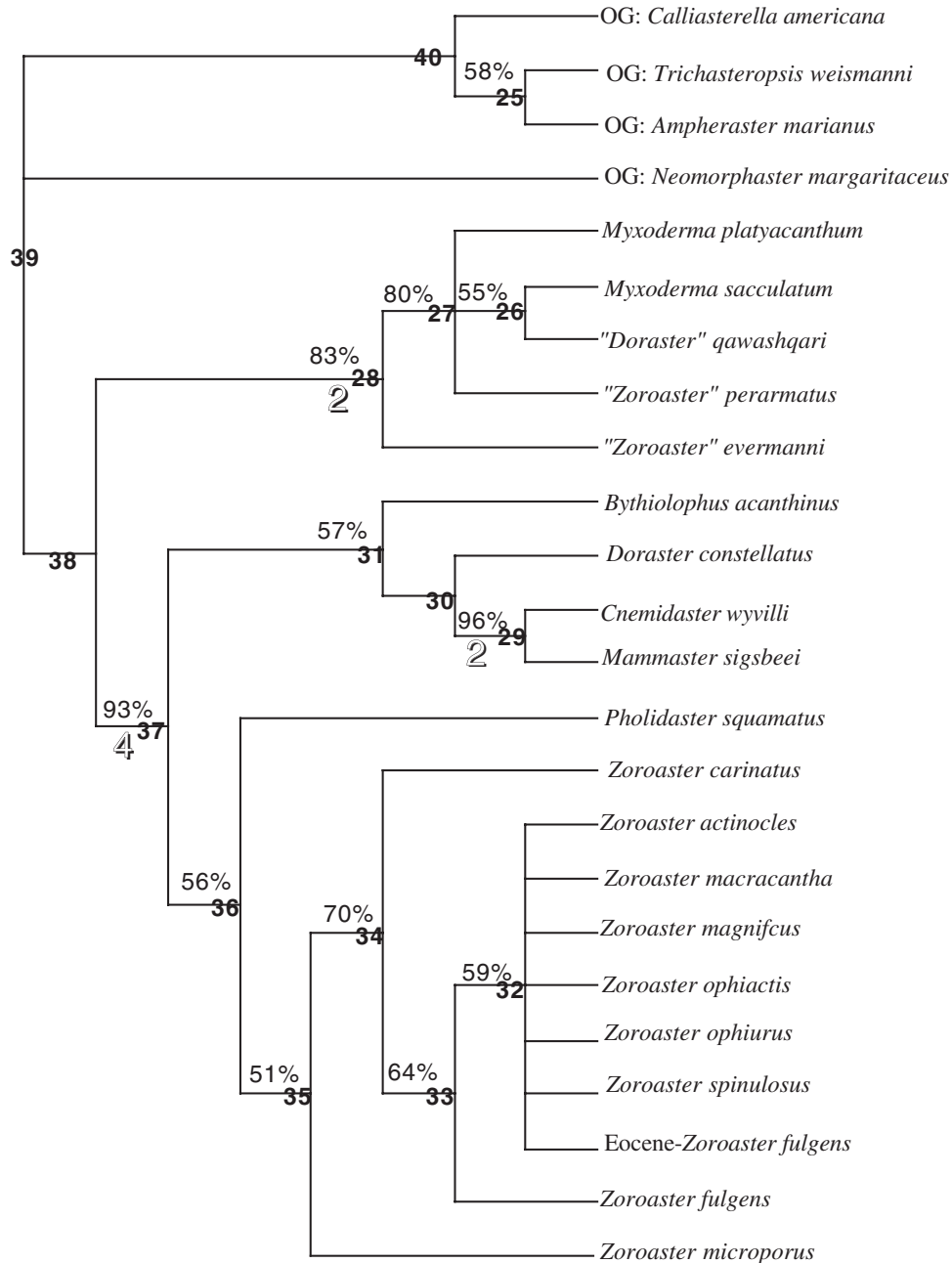

Figure 1. Cladogram of the Zoroasteridae. Node numbers are indicated in bold. Bootstrap support is indicated as %. Bremer values are indicated in shadow font.

Appendix 2), and those which were not were reviewed from the literature and determined to be consistent or not with phylogenetic-based definitions. Downey (1970: 13) provided a checklist summarizing several taxonomic changes in zoroasterid taxonomy up to that time. Although Clark & Mah (2001) summarized 25 putative species and subspecies of *Zoroaster*, their list failed to include several of the taxonomic changes summarized by Downey (1970: 13).

Many species of *Zoroaster* are problematic. Most of the *Zoroaster* species described by Alcock (1893a) are either unavailable for study and/or are incompletely described. Material believed to be Alcock's type series is present in the Muséum national d'Histoire naturelle (MNHN) in Paris, but the status of this material was not confirmed. Zoroasterid material described by Hayashi (1943, e.g. *Z. orientalis*) is apparently lost (T. Fujita, pers. comm.) and may have been destroyed during World War II. *Zoroaster tenuis* is based on juvenile material and was not included in the matrix. All available *Zoroaster* species were entered into the analysis, including the Eocene fossil *Zoroaster* aff. *fulgens* from Seymour Island, Antarctica (Blake & Zinsmeister, 1979, 1988). A key to extant genera is provided (Appendix 3) along with a comprehensive species summary.

Two fossil and two living taxa were included as outgroups. The two fossil species, *Trichasteropsis weismanni* (Münster, 1843) and *Calliasterella americana* Kesling & Strimple, 1966 were supported by Blake (1987, 1990) and Blake & Hagdorn (2003) as taxa basal to the post-Palaeozoic Asteroidea. The Triassic Trichasteropsida, including *Trichasteropsis*, was included as the sister taxon to the extant Forcipulatida. The Pennsylvanian *Calliasterella americana* shows outward morphological similarity with zoroasterids (Downey, 1970) and the genus *Calliasterella* has been supported as proximal to the base of the post-Palaeozoic asteroid lineage (Blake, 1987; Blake & Hagdorn, 2003).

Pedicellasterids have been supported as basal to the derived forcipulate clades by Blake (1990), Mah (2000) and Blake & Hagdorn (2003). Because a comprehensive assessment of the group is unavailable and pedicellasterids display characters plesiomorphic to other forcipulates, pedicellasterids have not been supported as monophyletic by current studies (e.g. Mah, 2000; Blake & Hagdorn, 2003). *Ampheraster marianus* was included as an outgroup based on the presence of shared characters with zoroasterids, including the presence of four rows of tube feet and straight pedicellariae. Fisher (1928: 84) observed morphological resemblance between *A. marianus* and *Myxoderma*.

The monotypic Neomorphasteridae is represented by *Neomorphaster*, which was supported as the sister taxon to *Zoroaster* by Mah (2000). Subsequent review of morphological characters in *Neomorphaster*, including the presence of two rather than a single marginal plate series, suggests convergence rather than close relationship with *Zoroaster*. *Neomorphaster* is included as a test of phylogenetic affinities between the Neomorphasteridae and the Zoroasteridae.

SPECIMEN ANALYSIS

The matrix (Appendix 2) included 24 taxa and 70 morphological characters (summarized in Appendix 1). Data were entered into MacClade 3.08 and exported into PAUP 4.10b10 (Swofford, 2003). Characters were derived primarily from skeletal morphology except for those characters differentiating Palaeozoic from post-Palaeozoic taxa, which were derived primarily from Blake & Hagdorn (2003) and Blake & Elliott (2003). Definitions and terms follow those of Blake (1987) and Clark & Downey (1992). Characters are referred to by numbers indicated in Appendix 1.

Specimens were obtained primarily from collections of the National Museum of Natural History (NMNH, Washington, DC) invertebrate zoology and palaeontology collections. Other material was obtained from the California Academy of Sciences (CASIZ) in San Franciscso, California, the Los Angeles County Museum of Natural History (LACM) in Los Angeles, California, Scripps Institution of Oceanography (SIO) in San Diego, California, and the Museum of Comparative Zoology (MCZ) in Cambridge, Massachusetts. Wet and dry specimens across a broad size and geographical range were examined where possible.

Trees were generated using the branch-and-bound search algorithm with default rooting (tree rooted at internal node with basal polytomy). Alternative rooting assumptions (ingroup assumed monophyletic) did not alter the tree topologies produced. Characters that were unavailable or incompatible between fossil and extant taxa were entered as question marks. Characters were analysed as unordered and run under ACCTRAN character optimization. Bremer support was calculated using PAUP's branch-and-bound search algorithm retaining sequentially higher numbers of trees beyond those which were most parsimonious until branches were observed to decay from consensus tree diagrams. Exploration of other tree topologies was accomplished using the tree editor in MacClade 3.08.

RESULTS

GUT CONTENT ANALYSIS

Wet and dried zoroasterid specimens in the National Museum of Natural History (NMNH) collections in Washington, DC, were examined for gut contents

Table 1. Gut contents from genera of Zoroasteridae

E18505	*Doraster constellatus*	sediment, foraminifera (foram)
E18570	*Doraster constellatus*	bivalve, gastropod
E26549	*Doraster constellatus*	bivalves
E34980	*Doraster constellatus*	gastropods, bivalves
E34933	*Doraster constellatus*	2 gastropods, bivalves
E18511	*Cnemidaster sigsbeii*	sediment, worm tubes
E34073	*Cnemidaster sigsbeii*	gastropod, sediment
E18565	*Cnemidaster sigsbeii*	sediment, gastropod (rissoid?)
E12460	*Cnemidaster sigsbeii*	bivalve (shiny), gastropod (rissoid?)
E12461	*Cnemidaster sigsbeii*	sediment (foram and pteropod tests), crustaceans (cumacean?), gastropods (Rissoidae-cf. *Alvania* sp.)
E14787	*Myxoderma platyacanthum*	bivalves, echinoderm ossicles (ophiuroid)
Fisher, 1928: 49	*Myxoderma sacculatum*	'a shrimp'
E10357	*Sagenaster evermanni*	gastropod, sediment
Alton, 1966	*Sagenaster evermanni*	echinoderm fragments, spicules, crustacean isopods, sediment
Alcock, 1893	*Zoroaster carinatus*	crustaceans, molluscs
E1804	*Zoroaster carinatus philippinensis*	dark mud, sediment, gastropod, bivalve fragments
E4944	*Zoroaster fulgens*	sediment, bivalves
E26348	*Zoroaster fulgens*	bivalves, gastropods, sediment
37009	*Zoroaster microporus* (HOLOTYPE)	bivalve
E15986	*Zoroaster ophiurus*	mud, gastropod, worm tubes, echinoid fragments
Alton, 1966	*Zoroaster ophiurus*	ophiuroid, crustacean fragments, sediment
E18505	*Doraster constellatus*	sediment, foram test? (gastropod)
E18570	*Doraster constellatus*	bivalve, gastropod

(Table 1). Results are consistent with prior accounts by Carey (1972) and Jangoux (1982). Stomach contents were recorded for taxa representing the most diverse zoroasterid lineages. Although all genera were surveyed, gut contents were not available for every genus. Recurring prey items included gastropods (see Figs 3F, 4F) and bivalves, although crustacean remains and ophiuroid and echinoid plate fragments were also present. Inorganic sediment was present in all of the specimens examined. Foraminifera tests, pteropod shells and worm tubes were also present, but it was unclear if these were taken as prey or if these were components of the ingested sediment.

Carey (1972) classified the two species of zoroasterids in his survey of asteroid food sources in the north-east Pacific Ocean as omnivores based on the relatively incomplete sampling of food items recovered. A broader sampling of gut contents suggests that zoroasterids are predatory on infaunal invertebrates. Howell *et al*. (2003) showed that although *Zoroaster longicauda* (= *Zoroaster fulgens*) had a fatty acid composition similar to those of three species of brisingid asteroids, which are suspension feeders, gut contents alone indicated a benthic food source, suggesting that *Zoroaster* may derive its food from multiple sources. *Zoroaster longicauda* (= *Zoroaster fulgens*) has also been observed in association with deployed bathyal food falls (carcasses of the porpoise *Phocoena phocoena*) (Kemp *et al*., 2006), suggesting that some zoroasterids also show opportunistic scavenging behaviour.

PHYLOGENETIC RESULTS

The search produced a single most parsimonious tree with a tree length of 139 steps (Fig. 1), a Consistency Index (CI) = 0.6835 and a Retention Index (RI) = 0.8394. The Zoroasteridae is upheld as monophyletic. *Calliasterella* is supported as the sister taxon to a lineage including *Trichasteropsis* + *Ampheraster*. *Neomorphaster*'s relationship to the Zoroasteridae and the more basal forcipulates is unclear.

Three primary ingroup clades resulted from the phylogenetic analysis (Fig. 1). The phylogenetic results indicate that *Zoroaster*, *Myxoderma* and *Doraster sensu* Downey (1970) and Clark & Mah (2001) are paraphyletic. The remaining five zoroasterid genera, *Bythiolophus*, *Doraster*, *Cnemidaster*, *Mammaster* and *Pholidaster*, were not shown to be paraphyletic, but are either monotypic or include few species ($N \leq 3$) showing few morphological differences.

Although paraphyly was observed in *Zoroaster* and *Myxoderma*, characters supporting those clades were largely consistent with taxonomic definitions for those genera as outlined by Clark (1920) and Fisher (1928). *Sagenaster* gen. nov. (= *Zoroaster evermanni*) demonstrated close affinities to *Myxoderma* as originally indicated by Fisher (1905) but was supported as separate from other established zoroasterid genera.

The tree (Fig. 1) is consistent with prior hypotheses of forcipulate phylogeny (Blake, 1990) showing a split between *Myxoderma* and other zoroasterids. The 'reticulate' zoroasterids, *Myxoderma* and *Sagenaster*, display characters plesiomorphic with basal forcipulates (*sensu* Blake, 1990; Blake & Hagdorn, 2003), including *Trichasteropsis*, a Triassic basal post-Palaeozoic asteroid (Blake, 1987), and *Ampheraster*, a pedicellasterid supported as basal to the forcipulates (Mah, 2000). *Sagenaster*'s affinity to *Myxoderma* was outlined by Fisher (1905: 317) who initially placed *Zoroaster evermanni* into *Myxoderma* [= *Zoroaster* (*Myxoderma*)].

Bremer support for all nodes is low (Fig. 1). The node supporting monophyly of the Zoroasteridae decays in one step. Branch support for the reticulate zoroasterids supporting *Myxoderma* + *Sagenaster* gen. nov. decays in two steps. The zoroasterid genera with imbricate (i.e. plates are abutting with overlapping edges) skeletons are upheld by a Bremer value of four, but support for phylogenetic structure within the clade is poor, with the exception of the *Cnemidaster* + *Mammaster* relationship, which decays in two steps. All the remaining branches decay in a single step.

Bootstrap support mirrors Bremer support values (Fig. 1). The reticulate zoroasterids are moderately well supported (83%). *Myxoderma* itself shows similar support (80%). *Myxoderma sacculatum* and *M. qawashqari* are moderately supported (55%). The imbricate zoroasterids are relatively well supported (93%). The *Cnemidaster* + *Mammaster* clade is relatively well supported (96%), but the [{(*Cnemidaster* + *Mammaster*) + *Doraster*} + *Bythiolophus*] clade is moderately to poorly supported (57%). The *Pholidaster* + *Zoroaster* clade is moderately to poorly supported (56%). *Zoroaster* itself is similarly supported (51%). Although resolution within *Zoroaster* is poor, the clades for *Z. carinatus* (70%) and *Z. fulgens* (64%) are moderately well supported. The node containing the remaining *Zoroaster* species included in the analysis was moderately to poorly supported (59%).

Calliasterella is separated from post-Palaeozoic taxa by 33 characters derived from Blake & Hagdorn (2003).

Monophyly of the Zoroasteridae is supported by 16 characters (summarized in Appendix 1). These include squarish-blocky ambulacrals (8.12), the presence of superambulacrals, which are frequently reduced (8.6, 8.7), the presence of straight pedicellariae (7.1), a fan-like array of adambulacral furrow spines (4.4), alternately carinate adambulacral plates (4.1, 4.2), the presence of secondary spines (3.6), enlarged actinolateral spines (3.3), actinolaterally orientated actinal plates (3.2), sharp spine tips (1.24), recurved secondary spines (1.25), flattened abactinal plates (1.26) and the presence of primary and secondary spines (1.5, 1.23).

TAXONOMIC RESULTS – THE RETICULATE ZOROASTERIDS

Zoroasterids possessing reticulate skeletons were supported on node 28 and form the sister clade to the imbricate zoroasterids (Fig. 1, node 37). This included the two nominal species of *Myxoderma* and three species which have not been previously allied with *Myxoderma* (Fig. 1). These taxa were plesiomorphic with basal Forcipulatacea, including the extant *Ampheraster* and the Triassic *Trichasteropsis*. Characters shared between these taxa include but are not limited to reticulated abactinal and actinolateral plate patterns (1.1, 3.4, Fig. 2B, E, F), cruciform–lobate surface, marginal and actinolateral plates (1.2, 1.6, 1.11, 2.6, 3.10, e.g. Fig. 2G), and primary spines present on all plates (1.4, Fig. 2E, F). Taxa on node 28 possess a reticulated abactinal skeleton with relatively undifferentiated cruciform plates all of which bear a primary spine (Fig. 2E, F). Node 28, uniting *Myxoderma* and *Sagenaster* gen. nov., is supported by quadrate–cruciform actinolateral plates (3.10), strongly lobate cruciform marginal plates (2.6, Fig. 2F, G), presence of primary spines on marginal plates (2.4, Fig. 2E, F), presence of primary spines on carinal plates (1.18, Fig. 2E), presence of strongly lobate carinal, disc and other arm plates (1.6, 1.11, Fig. 2G), and low ridged carinal series (1.13, e.g. Fig. 2F).

Although most species of *Zoroaster* were supported together (node 33), one species, *Z. evermanni* (Fig. 2E–G), displayed closer morphological affinities to *Myxoderma* (Fig. 1), having a reticulate skeleton, cruciform disc and body plates, and primary spines on most to all plates. *Zoroaster evermanni* (node 28) is supported as the sister branch to the other four taxa included on the branch (Fig. 1) and is supported here as the new genus, *Sagenaster*, which is defined and summarized below. Fisher (1905) originally described *Zoroaster evermanni* as a member of the genus *Myxoderma* [originally described as subgenus *Zoroaster* (*Myxoderma*)]. However, the internal buttress (character 8.8, Fig. 2D) present in *Myxoderma* is absent in *Z. evermanni*, and Fisher (1919a) eventually placed *Z. evermanni* within *Zoroaster*.

Based on examination of the syntype series, *Zoroaster longispinus* is reassigned to *Myxoderma* (Fig. 1). One syntype (NMNH 34385) falls into what would be considered *Myxoderma* along with a fouth specimen identified by W. K. Fisher (NMNH 9626). NMNH 34385 is designated the lectotype for this species. The remaining syntype specimens (NMNH 34384 and 34386) of *Z. longispinus* are juvenile specimens of *Zoroaster* sp. Those in juvenile *Zoroaster* have imbri-
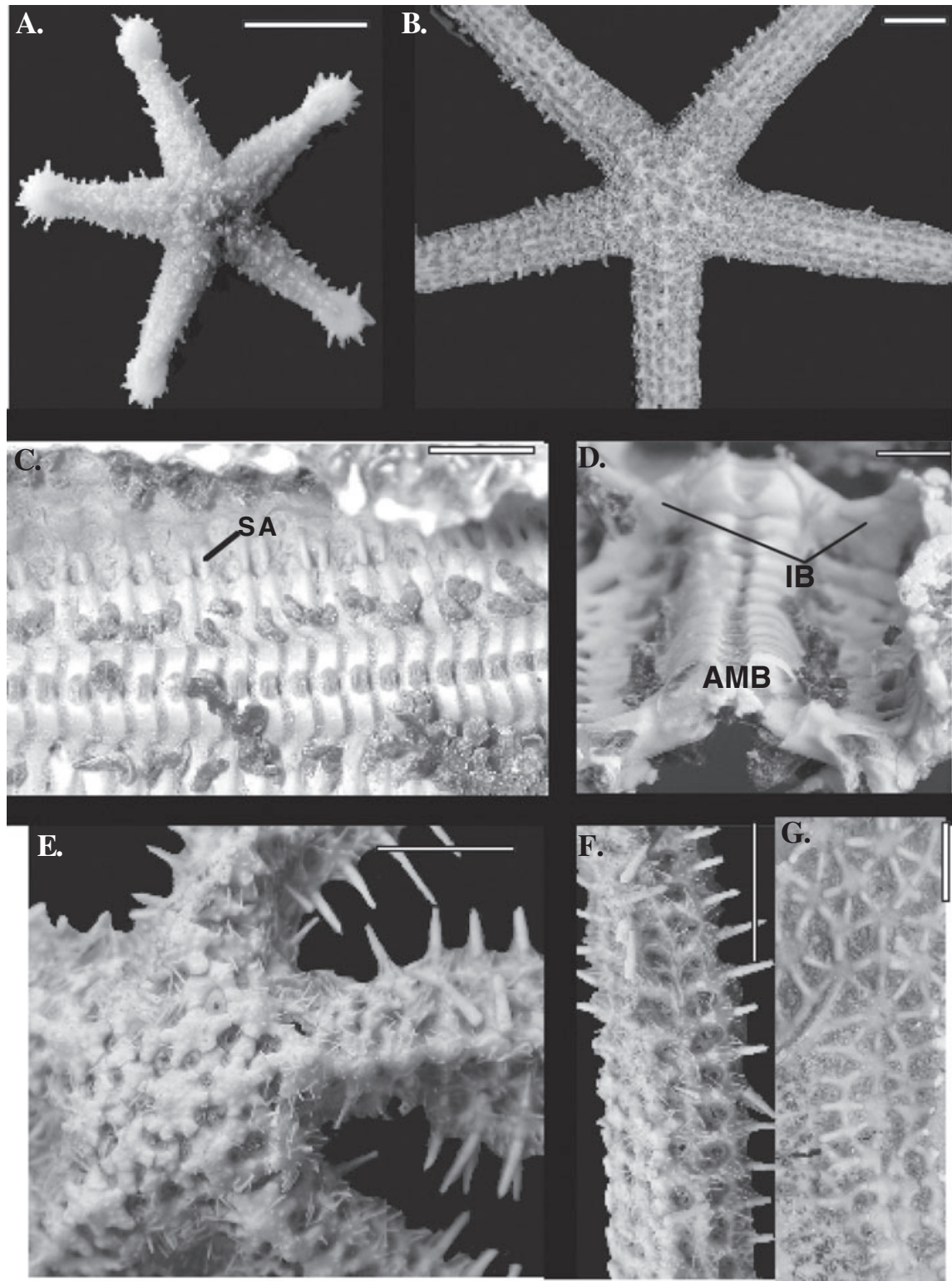
Figure 2. A, abactinal surface juvenile specimen, *Myxoderma sacculatum* (USNM E1149). B, abactinal surface, adult specimen, *M. sacculatum* (USNM E3596). C, ambulacral ossicles and superambulacral ossicles (SA), *M. sacculatum* (USNM E3596). D, same specimen, arm viewed head-on showing ambulacrals (AMB), internal buttress (IB), *Sagenaster evermanni* (USNM 16023). E, abactinal surface, disk and arms. F, arm plates. G, abactinal disk and arm plates showing plate morphology (coelomic view, *M. sacculatum* USNM E13990).

cating polygonal plates (e.g. Fig. 6G, Sumida, Tyler & Billett, 2001). Examination of juvenile specimens of *Myxoderma sacculatum* (R = ~1.0 cm) shows a reticulate skeleton with cruciform plates present in *Z. longispinus* Ludwig, 1905 (Fig. 2A). Examination of syntypes and other material of *Zoroaster longispinus* Ludwig, 1905 and *Zoroaster perarmatus* H. L. Clark, 1920 indicates that *Z. perarmatus* is a junior synonym of *Z. longispinus* Ludwig, 1905. Specimens of *Z. longispinus* are much smaller ($R \leq 4.0$ cm) than the larger *Z. perarmatus* (R = 9.5 cm). However, both specimens show identical numbers of furrow spines (three per plate), similar spination patterns, including a spine on the centrodorsal plate, and identically shaped carinal plates.

Myxoderma derjungini Djakonov, 1950 is a synonym of *Myxoderma sacculatum* (Fisher, 1905). Djakonov (translated from 1950: 91, fig. 87) differentiated this species based on the checkered pattern of 'tubercles' (= spine bases) on alternate series of the longitudinal and transverse rows. However, spine bases in *M. sacculatum*, especially on the actinolateral plates (as figured by Djakonov, 1950: fig. 87) adjacent to the adambulacral series show variable occurrence and are broken off easily in trawl nets. In addition to this single character difference, characters such as the enlarged, sacculate terminal plate, the robust spines and slimy–fleshy membrane are shared with *M. sacculatum*. *Myxoderma sacculatum* occurs over a wide bathymetric (91–2012 m) and geographical range (southern California to Bering Sea) making it co-terminous with *M. derjungini* in the Okhotsk Sea.

Based on phylogenetic results (Fig. 1) *Doraster qawashqari* Moyana & Larrain, 1976 is removed to the genus *Myxoderma*. *Doraster* was diagnosed by Downey (1970) as having enlarged, stellate abactinal plates, and a thickened disc with a smooth, skin-covered surface. A larger size range and greater number of *Doraster* specimens was studied revealing spination over the surface of several specimens. The presence of well-developed adradial plates in large specimens, which are absent to reduced in the smaller type specimens, was also observed. Large-sized *Myxoderma sacculatum* (R < 20 cm) display significant variation relative to smaller specimens, including a more inflated disc and more imbricated arm and disc plates. *Doraster qawashqari* Moyana & Larrain, 1976 has both of these features. Primary disc and arm plates in *Doraster constellatus* differ from those in *D. qawashqari*. Those in the former are more weakly lobate and more imbricate than those in the latter, which are strongly lobate and show a more reticulate pattern. Characters observed by Moyana & Larrain (1976) were distorted by the large size of the specimens, which affected interpretation of the characters used to diagnose *D. qawashqari*.

These characters support placement of *Doraster qawashqari* within *Myxoderma*.

A Miocene specimen identified as *Doraster* by Yamaoka (1987: pl. 2, fig. 4) is also probably *Myxoderma* based on the apparent reticulated skeleton observed on the arms and the shape of the disc and arms. This specimen was not examined.

TAXONOMIC RESULTS – THE IMBRICATE ZOROASTERIDS

Zoroasterids, including *Zoroaster* and the remaining zoroasterid genera possessing imbricate skeletons, were supported on node 37 (Figs 3–6). These taxa are considered derived relative to the outgroup forcipulates and to the reticulate zoroasterids. This clade is supported by 18 characters, including single pores (8.10, Fig. 4A), actinolaterals in transverse series (3.11, Fig. 4B), the absence of quadrate actinolateral plates (3.7), closely distributed secondary spines (3.6), densely distributed imbricate actinolaterals (3.4, 3.5), the presence of weakly lobate marginal plates (2.5), overlapping primary plates (1.22), presence of a lobate centrodorsal (and absence of quadrate centrodorsal, 1.20, 1.21), enlarged disc circlet plates (1.16, Fig. 4A, G), absence of a level carinal series (1.15, Fig. 4E), the presence of lobate carinals (1.12), the presence of polygonal–lobate arm plates (1.7), the presence of primary and secondary abactinal spines (1.4, 1.5), presence of weakly lobate disc plates (1.3), and an imbricate skeletal arrangement (1.1, Figs 3–6).

Taxa on node 37 were separated into two primary lineages, which included *Bythiolophus*, *Cnemidaster* (including synonym *Mammaster*) and *Doraster* on node 31 (Figs 3, 4) and the remaining taxa supported on node 36, which included *Pholidaster* and all 'true' *Zoroaster* species (Figs 5, 6). The former clade (node 31) was supported by three apomorphies, the presence of an internal buttress (8.8, Fig. 2D), weakly lobate actinolaterals (3.8), and a discontinous arm and disc (1.19) whereas the latter clade containing *Zoroaster* and *Pholidaster* is supported by the presence of weakly lobate actinolaterals (3.8). This latter clade also supports the genus *Zoroaster* with one character (8.7, reduced superambulacral plates). *Pholidaster* is supported as the sister taxon to the ten species representing *Zoroaster* in the matrix. *Zoroaster carinatus* and *Z. fulgens* are supported as basal members to a cluster of seven *Zoroaster* spp., which demonstrated few to no character differences at this level of resolution. This cluster included the Eocene *Zoroaster fulgens* described from Seymour Island, Antarctica.

Phylogenetic data support *Mammaster* Perrier, 1894 as a synonym of *Cnemidaster* Sladen, 1889 (Fig. 4). A close relationship between the two has been suggested by Fisher (1928: 32) and Clark (1920: 95). The two genera are relatively well supported as sister
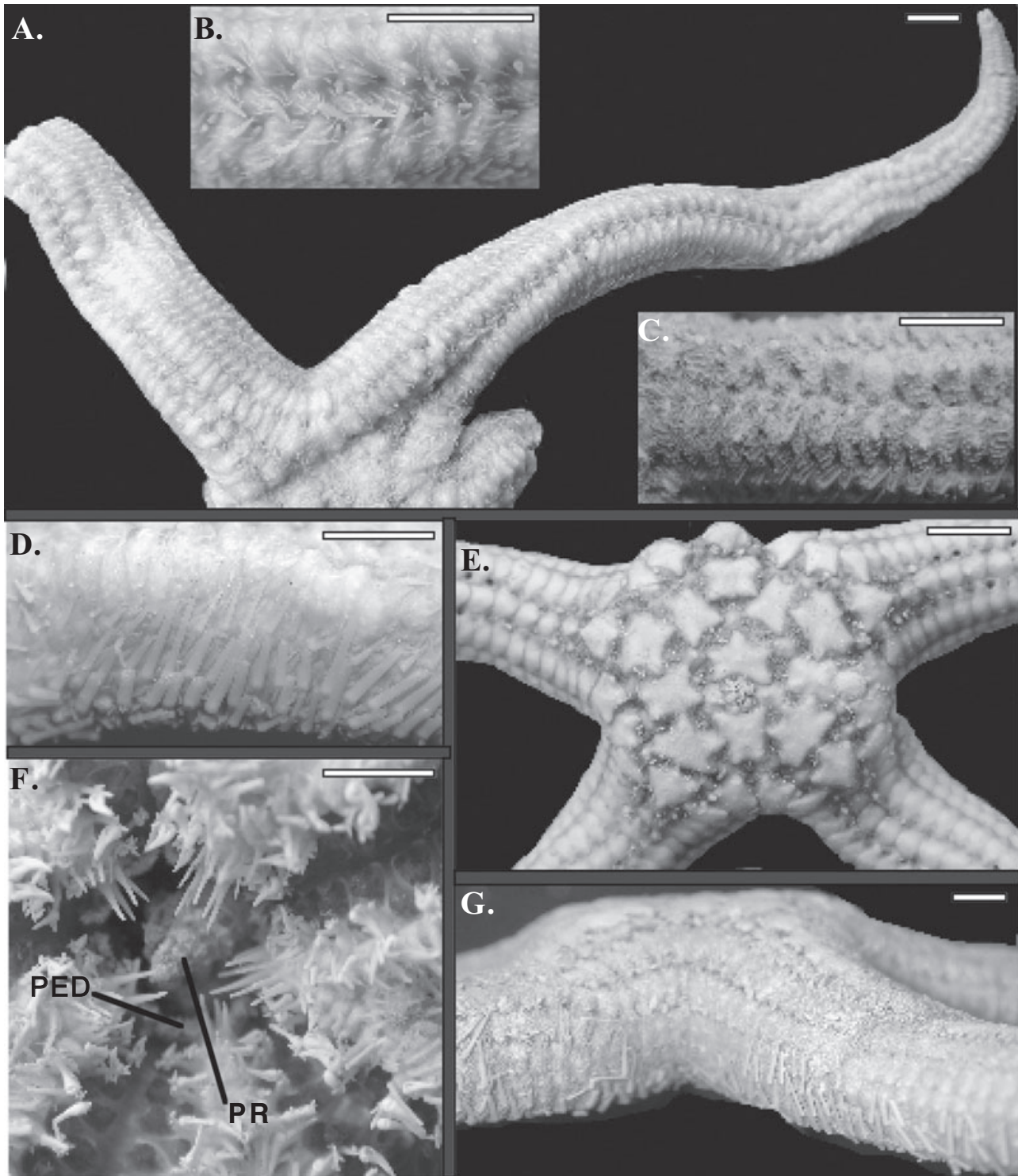
Figure 3. *Bythiolophus acanthinus* Holotype (USNM 37011). A, arm and disk. B, carinal and marginals on close-up of arm. C, carinals and marginals from paratype of *Zoroaster macracanthus*.(MCZ 2499) D, lateral view showing actinolateral spination. *Doraster constellatus* Paratype (USNM E11357). E, abactinal view, disk and arms. F, oral region with prey (PR). Ring of pedicellariae (PED, character #7.3) adjacent (USNM 34980). G, lateral view (USNM 1080506). Scale bar = 0.5 cm.
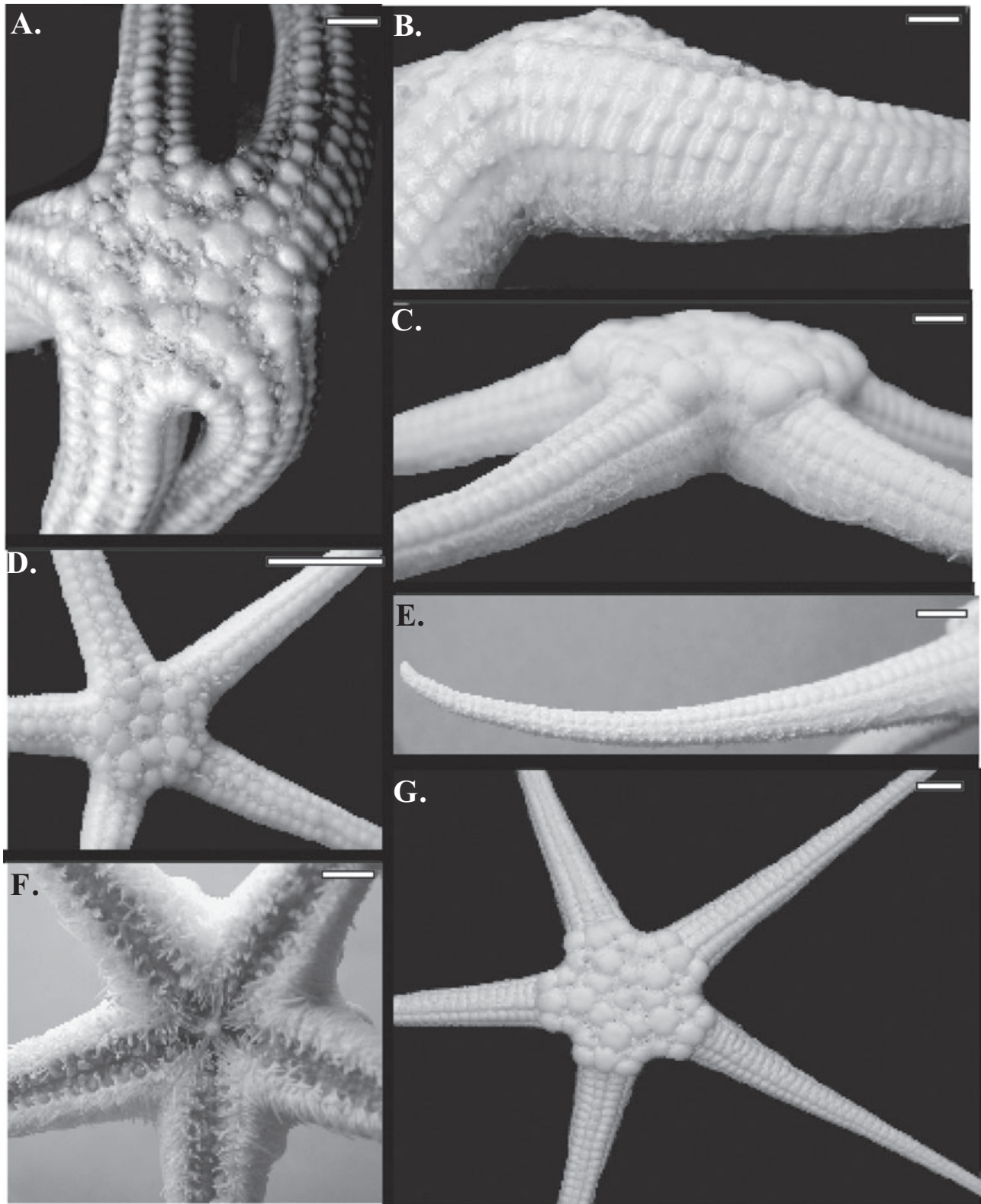
Figure 4. *Cnemidaster wyvillei* (USNM 40566). A, abactinal surface. B, lateral view. C, abactinal surface, juvenile specimen. *Cnemidaster* (= *Mammaster*) *sigsbeii* (USNM E34073). D, lateral view. E, arm showing single marginal plate series. F, oral view showing gastropod prey item in mouth. G, abactinal view, disk and arms. Scale bar = 0.5 cm.
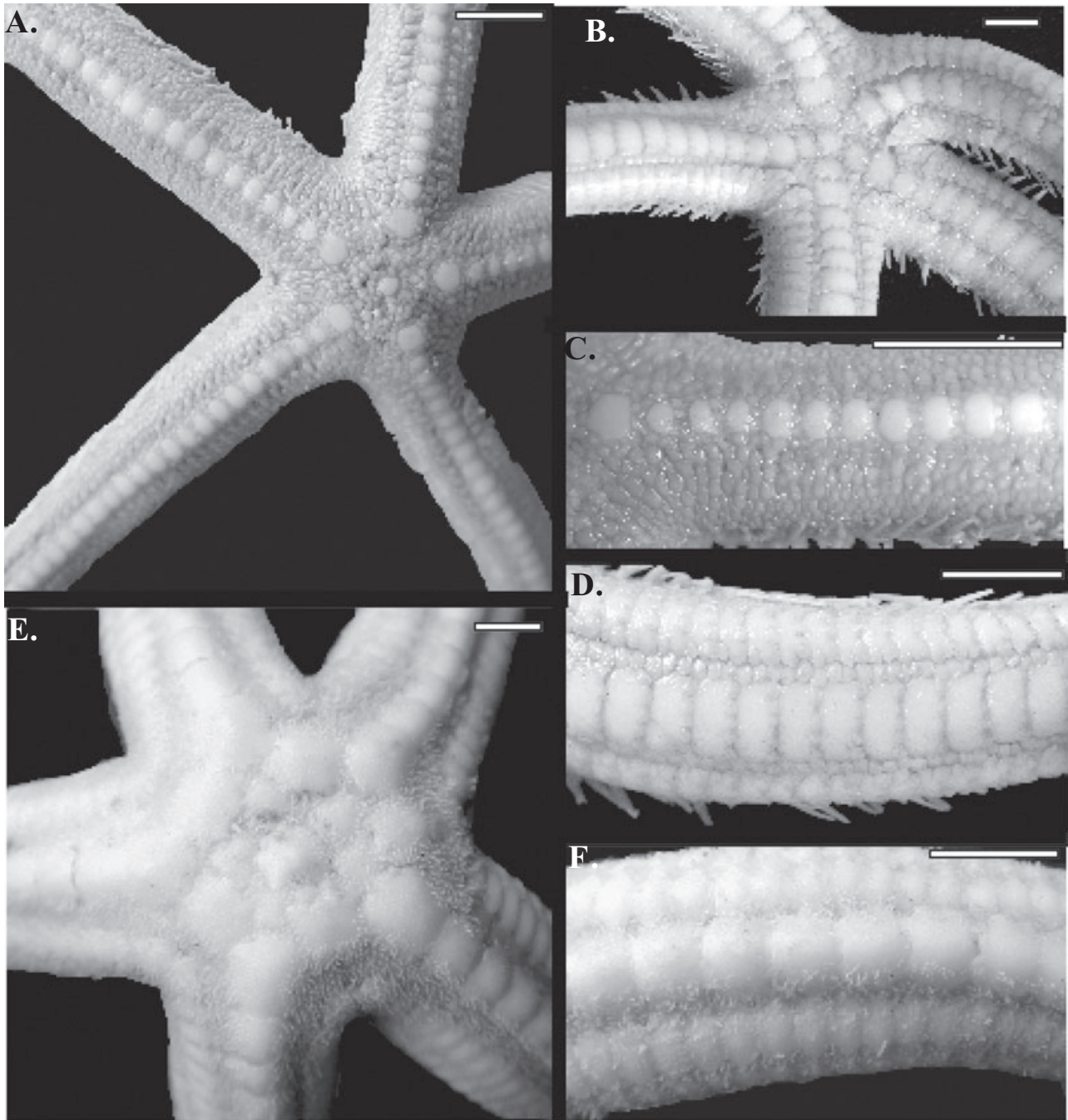
Figure 5. *Pholidaster* A, abactinal surface. *P. squamatus* (USNM 40280). B, *P. distinctus* (Holotype). C, *P. squamatus* arm surface close-up (USNM 40280). D, *P. distinctus* arm surface close up. *Zoroaster microporus* E, holotype, abactinal disk and arms (USNM 37009). F, abactinal arm surface close-up. Scale bar = 0.5 cm.

taxa (bootstrap = 96%, Bremer = 2) but are separated by only two characters, one of which is size-related. The presence of adradial plates (1.8) is described as present in *Cnemidaster* but absent from *Mammaster*. Adradial plates are present in *C. wyvilli* with $R \geq 20.5$ cm but absent from moderate to small specimens ($R \leq 10$ cm). Specimens of *Mammaster* recorded

in Clark & Downey (1992) and those observed in this study do not show R larger than 7.1 cm. Small to moderately sized specimens of *Cnemidaster* display more similarity with comparably sized *Mammaster* than with larger *Cnemidaster*.

Other characters indicated by Clark (1920: 96) to separate the two genera included different numbers of
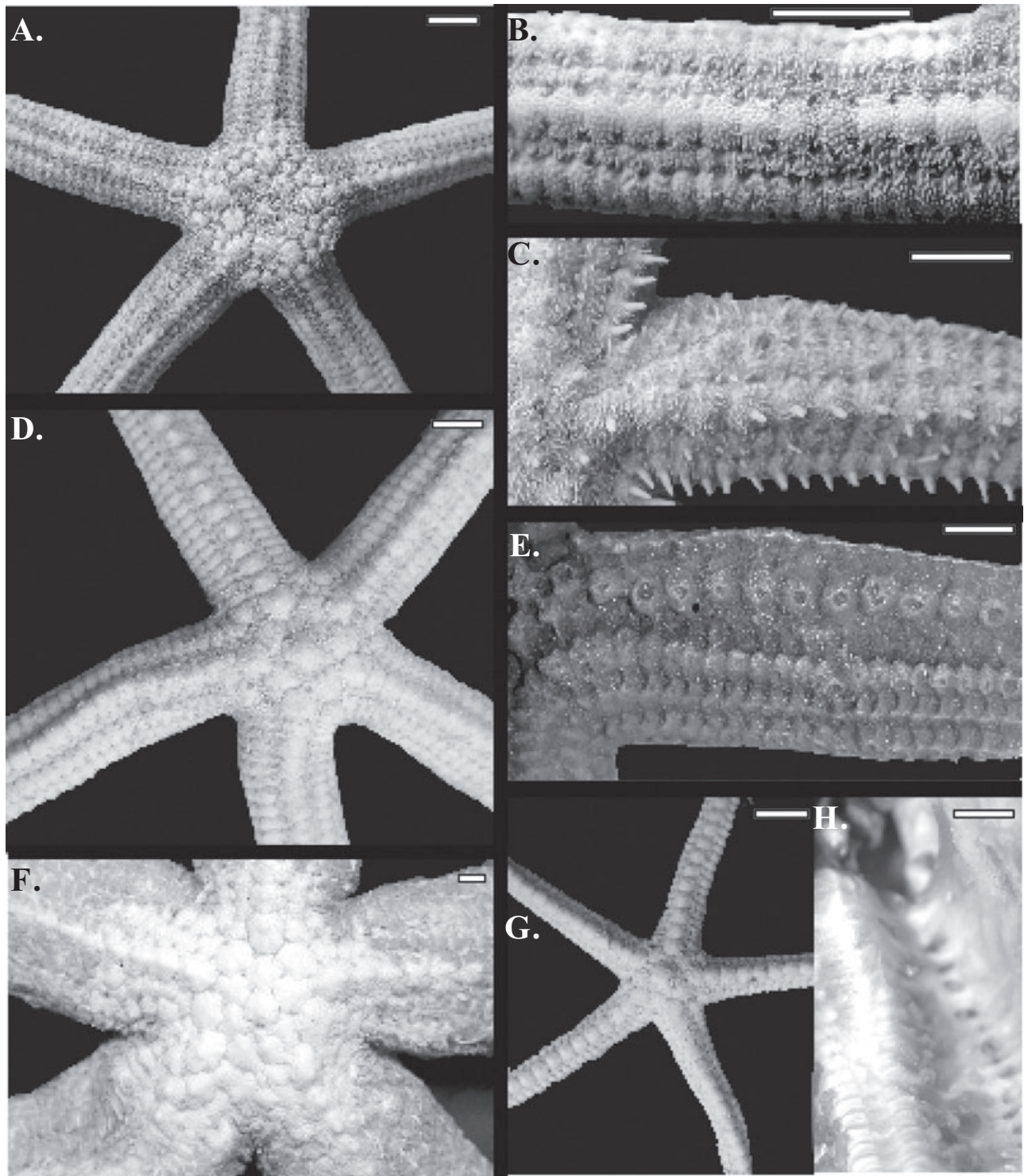
Figure 6. *Zoroaster carinatus* (NMNH E1804) A, abactinal surface, disk and arms. B, close up-arms. *Zoroaster fulgens* C, abactinal surface, disk and arms (NMNH 11264). D, abactinal surface, variant form with spines, disk and arms (NMNH 1017683). E, eocene fossil from Seymour Island, disk and arms. (NMNH 256068). F, deep-water variant morphology from South Atlantic, disk and arms. (NMNH E47615). G, juvenile specimen, abactinal surface. (NMNH E18533). H, internal view showing absence of internal buttress (NMNH E38657). Scale bar = 0.5 cm.

actinolateral rows and an enlarged first carinal plate in *Mammaster*, relative to the marginal plate series. Development of actinolateral rows is size-dependent, making this an unreliable character where the numbers of actinolateral plate series overlap and the presence of an enlarged carinal plate was not observed in the specimens of *Mammaster* examined.

Two species of *Zoroaster* listed in Clark & Mah (2001) have been included in *Cnemidaster* by Downey (1970: 14), including *Z. squameus* Alcock 1893 and *Z. zea* Alcock 1893. A third species, *Z. gilesi* Alcock 1893, is also a likely species of *Cnemidaster* based on the massive semiglobular plates described on the disc (Alcock, 1893a: 108). Alcock (1893a: 110) described *Z. gilesi*, *Z. sqameus* and *Z. zea* as belonging to a well-defined group with shared abactinal plate arrangements.

A second species, *B. macracanthus* (= *Zoroaster macracantha* H.L. Clark 1916) was added to the previously monotypic *Bythiolophus* by Rowe & Gates (1995: 115). Comparison between the holotype of *Bythiolophus* (Fig. 3A) and paratypes of *Z. macracantha* indicate that this assignment is unwarranted and *B. macracanthus* is returned to *Zoroaster*. *Bythiolophus* has alternating large and small marginal plates (Fig. 3B), vs. *Zoroaster* which has consistently sized marginals (Fig. 3C). Return of this species to *Zoroaster* is supported by phylogenetic results (Fig. 1).

Additionally, *Zoroaster macracantha* was considered a synonym of *Z. spinulosus* by Fell (1958: 19), who had not examined type material. Comparison between the paratypes of both species suggests close affinities but with distinct morphologies. *Zoroaster macracantha* has thicker arms with more heavily developed primary spines on the marginal plates.

Digital images of the holotype of *Pholidaster distinctus* (Fig. 5B) were compared with specimens of abraded *P. squamatus* identified by W. K. Fisher (Fig. 5A), which were missing the distinctive scalar spines present on the body surface. Several of these specimens (e.g. NMNH 40573, 40562) showed abrasion, probably from trawl collection, resulting in naked plates identical to those present in *P. distinctus*. *Pholidaster distinctus* is a synonym of *P. squamatus* making the genus *Pholidaster* monotypic.

Howell *et al*. (2004) recognized three reproductively isolated morphotypes in *Zoroaster fulgens* in the Porcupine Seabight where previously *Z. fulgens* was only thought to be a single species with wide morphological variation. *Zoroaster* species included on node 32 show close morphological affinities but are often distributed over large distances. Characters in these *Zoroaster* species are often continuous and show few discrete differences (see matrix in Appendix 2). Several species which were recognized as potential synonyms (e.g. *Z. spinulosus* and *Z. macracanthus*, *Z. hirsutus*

and *Z. magnificus*, *Z. adami* and *Z. carinatus*) were retained as valid pending further phylogenetic data addressing species concepts in *Zoroaster*. Some species (*Z. adami* and *Z. carinatus*) coded identically in the data matrix and were removed.

TAXONOMIC SUMMARY OF THE ZOROASTERIDAE AND OUTGROUP TAXA

SUBORDER ZOROCALLINA DOWNEY, 1970

Zorocallida-Downey 1970: 1; Downey 1973: 95; Moyana & Larrain 1976: 104. Zorocallina-Blake 198: 502, 518.

FAMILY ZOROASTERIDAE SLADEN 1889

Zoroasteridae-Sladen 1889: 416; Alcock 1893b: 173; Perrier 1894: 112; Fisher (1906): 1102; H.L. Clark 1916: 68; Fisher 1919a: 470; Fisher 1919b: 387; Fisher 1928: 32; H. L. Clark 1920: 94; Macan 1938: 414; Hayashi 1943: 161; Fell 1958: 18; Bernasconi 1964: 266; Spencer & Wright 1966: U74; Downey 1970: 1; Downey 1973: 95; Moyana & Larrain 1976: 104; McKnight 1977: 159; Maluf 1988: 124; Clark & Downey 1992: 401; Rowe & Gates 1995: 115; Liao & Clark 1995: 140; Clark & Mah 2001: 230.

Diagnosis: Discs small with elongate, tapering arms. Single row of marginal plates. Papular pores in longitudinal and transverse rows. Disc and arm plates reticulate or imbricate in arrangement. Smaller secondary spines cover most plates. Actinolateral spines (i.e. below marginal plate series) with larger primary spines appressed or facing abactinally. Superambulacral plates present. Pedicellariae straight (absent in *Pholidaster*). Adambulacrals alternately carinate. Tube feet in four rows becoming two rows distally.

BYTHIOLOPHUS FISHER, 1916

Bythiolophus Fisher, 1916: 31; 1919a: 389; 1919b: 2,471, 481, 484; Fisher, 1928: 33 (in key); H.L. Clark, 1920: 99; Downey, 1970: 5 (in key); Spencer & Wright, 1966: U74; Clark & Mah, 2001: 230.

Type species: *Bythiolophus acanthinus* Fisher, 1916.

Diagnosis: Disc broad, arms thick with imbricated plates. Internal buttress present. Marginal plates alternately large and small.

BYTHIOLOPHUS ACANTHINUS FISHER, 1916 (FIG. 3A, B)

Bythiolophus acanthinus Fisher, 1916: 3, 1919b: 25, 485, pl. 135, fig. 1a–c; pl. 139, figs 1, 2; Downey, 1970: 14; Clark & Mah, 2001: 230.

Occurrence: Celebes (Sulawesi), Indonesia, 1022.0 m.

Material: Indonesia. NMNH 37011 HOLOTYPE Muna Island, Greater Sunda Islands, 5°35′S, 122°20′E, 1022 m. Coll. 16.xii.1909. (1 wet spec. $R = 10.1$, $r = 1.1$)

CNEMIDASTER SLADEN, 1889

Cnemidaster Sladen, 1889: 423; Fisher, 1919a: 389; 1919b: 471, 480, 481, 485; Hayashi, 1943: 174; Spencer & Wright, 1966: U74; Clark & Mah, 2001: 230.
Mammaster Perrier, 1894: 114 (in key); Fisher, 1919a: 389; 1919b: 471, 481; Spencer & Wright, 1966: U75; Downey, 1970: 12; Clark & Downey, 1992: 403; Clark & Mah, 2001: 231.

Type species: *Cnemidaster wyvilli* Sladen, 1889.

Diagnosis: Disc plates enlarged, swollen, rounded. Disc thick, discontinuous with arms in smaller specimens (below $R = 7.0$). Disc and arm plates imbricate. Disc and arm surface largely bare, covered with membranous skin. Internal buttress present.

CNEMDIASTER GILESI (ALCOCK, 1893) COMB. NOV.

Zoroaster gilesi Alcock, 1893: 108; H.L. Clark, 1920: 101; Clark & Mah, 2001: 234; Clark & Mah, 2001: 233; Sastry, 2005: 47 143 174.

Occurrence: Andaman Sea, 896–915 m.

CNEMIDASTER NUDUS (LUDWIG, 1905)

Zoroaster nudus Ludwig, 1905: 164.
Cnemidaster nudus H.L. Clark, 1920: 98; Downey, 1970: 14; Maluf, 1988: 43 124; Nybakken *et al.*, 1998: 1777.

Occurrence: Farallon Islands (Central California), Cabo San Lucas, Mexico to Chile, 1366–2598 m.

Material: Central California. LACM Farallon Islands slope, 37°38.40′N, 123°21.53′W to 37°38.36, 123°19.90′W, 2300–2375 m. Coll. 29.vii.1991. [$R = \sim11.4$, $r = 1.3$ (1 wet spec.)].
   Mexico. NMNH 34381 Offshore of Ventana Bay, Baja California. 23°59′N, 108°40′W, 1820 m. Coll. 20.iv.1891. [1 wet spec. $R = 12.0$, $r = 1.3$ (arms broken)] NMNH 34387, Cerralvo Island, Baja California. 24°22′30″N, 109°3′20″W, 2598 m. Coll. 20.iv.1891. [$R = 3.9$, $r = 0.7$ (arms broken)] LACM 9161, Off Rio Elata, Sinaloa, Mexico. 23°40′30″N, 107°38′30″W to 23°37′N, 107°51′48″W. 1384–1366 m. Coll. 11.v.1959. [1 dry spec. $R = \sim6.5$, $r = 1.1$ (arms broken)] SIO E170, SW of Cabo San Lucas 22°42.5′N, 110°21.0′W to 22°41.4′N, 110°12.0′W. 1893–1957 m, Coll. 28.vi.1965. [2 dry specs. $R = 6.1$, $r = 1.3$; $R = 7.5$, $r = 1.3$ (arm tips broken)] SIO E 1602, SW of Cabo San Lucas, 22°45′N, 110°23.0′W. 1917–2014 m. Coll. 28.vi.1965. [1 wet spec. $R = 9.3$, $r = 1.3$ (arm tips broken)] Chile. NMNH E446 Off Arica, Chile. 18°44.7′S, 70°40.7′W to 18°40.2′S, 70°35.1′W, 1097–1152 m, Coll. 7.v.1972. (1 wet spec. $R = 4.4$ $r = 0.6$).

CNEMIDASTER SIGSBEEI (PERRIER, 1894)

Zoroaster sigsbeci Perrier, 1880: 436 [lapsus for *sigsbeei* (Perrier 1881)]
Zoroaster sigsbeei Perrier, 1881: 5; 1884: 195.
Mammaster sigsbeei Perrier, 1894: 125; Perrier, 1894: 125; H.L. Clark, 1920: 73, 1941: 67; Downey, 1970: 12; Clark & Downey, 1992: 403; Clark & Mah, 2001: 231; Lalana *et al.*, 2004: 10.

Occurrence: Gulf of Mexico-S. Florida, Caribbbean Sea-Bahamas, Puerto Rico, Cuba, Venezuela, Gulf of Guinea, 310–1318 m.

Material: Gulf of Mexico: NMNH E12460 Florida Keys, Gulf of Mexico, 366 m [6 dry specs. $R = 4.0$, $r = 0.9$, $R = 4.9$, $r = 1.0$, $R = 6.6$, $r = 1.0$, $R = 4.4$, $r = 1.0$, $R = 4.7$, $r = 1.1$, $R = 3.7$, $r = 0.9$ cm (arm tips broken)] NMNH E 18510 Vero Beach, Florida, 27°50′N, 79°15′W, 522 m, Coll. 17.vii.1965. (1 dry spec. $R = 6.5$, $r = 1.0$ cm) NMNH E 13208 SE of Pensacola, Florida. 29°27′N, 86°57′W, 752 m, Coll. 23.vii.1967. [1 dry spec. $R = \sim2.2$, $r = 0.5$ cm (arm tips broken)] NMNH E 34922, Off of Florida, 29°14′N, 86°59.42′W, 900 m, Coll. 6.viii.1968. (1 dry spec. $R = 1.2$, $r = 0.3$ cm) Caribbean Sea: NMNH E 18512 Bahamas, SW of Grant Bahama Island, 26°6′N, 79°19′W, 449 m, Coll. 25.ix.1967. (1 dry spec. $R = 7.7$, $r = 1.3$ cm) NMNH E 18513 Bahamas, SW of Grant Bahama Island, Northwest Providence Channel, 26°19′N, 79°00′W, 498 m, Coll. 1.x.1967. (1 dry spec. $R = 2.9$, $r = 0.6$ cm) NMNH E 18511 East of Cay Sal bank, Bahamas, 23°34′N, 79°16′W, 520 m. Coll. 15.vi.1968. (1 dry spec. $R = 6.7$, $r = 1.1$) NMNH E 18514, Cay Sal bank, Bahamas, 24°04′N, 79°42′W, 549 m. Coll. 22.vi.1967. (1 dry spec. $R = 3.0$, $r = 0.7$) NMNH E 18565 East of Cay Sal Bank, 23°35′N, 79°24′W, 516 m, Coll. 27.vi.1970, [2 dry specs. $R = \sim7.0$, $r = 1.3$, $R = 5.3$, $r = 0.9$ cm (arm tips broken)] NMNH E 13662 NE of Honduras, 16°43′N, 82°38′W, 430–613 m, Coll. 12.vii.1970. (1 dry spec. $R = 2.7$, $r = 0.6$ cm) NMNH E 03967 Puerto Rico, coll. 1933. (1 dry spec. $R = 7.3$, $r = 0.9$) NMNH 12459 Testigo Islands, Venezuela 11°35′N, 62°37′W, 402–421 m, Coll. 19.iv.1960. (1 dry spec. $R = 2.0$, $r = 0.5$ cm) Gulf of Guinea: NMNH E 34073 South of Lagos, Nigeria, 4°15′N, 4°27′E, 1280–1318 m, Coll. 26.v.1965. (1 dry spec. $R = 7.1$, $r = 1.0$ cm)

CNEMIDASTER SQUAMEUS (ALCOCK, 1893)

Zoroaster squameus Alcock 1893: 109; 1895: pl. IV, fig. 2.

Cnemidaster squameus H.L. Clark, 1920: 98; Fisher, 1919b: 18, 481; Macan, 1938: 415; Clark & Mah, 2001: 231.

Occurrence: Laccadive Sea and off Aden 1900–2000 m.

CNEMDIASTER WYVILLI SLADEN, 1889

Cnemidaster wyvilli Sladen, 1889: 424; Fisher, 1919b: 18, 25, 480, pl. 134, fig. 3.3a, pl. 138; H.L. Clark, 1920: 98; Hayashi, 1943: 175; Nybakken *et al*., 1998: 1777; Clark & Mah, 2001: 231.

Occurrence: Japan, Celebes, Arafura Sea of Borneo, 1370– 1990 m.

Material: Indonesia-Malaysia. NMNH 40555, NW of Unauna Island, Celebes. Indonesia. 0°08′S, 121°19′E, 1992 m, Coll. 18.xi.1909. [1 wet spec. *R* = ~5.0 *r* = 0.9 (arms broken, spec. disarticulated)] NMNH 40566 South of Darvel Bay, Sabah, Celebes Sea. 4°19′54″N, 118°58′38″E, 1628 m. Coll. 26.ix.1909. (1 wet spec. *R* = 20.5, *r* = 1.7) NMNH 40818 East of Waleabahi Island, Celebes. 0°22′N, 123°3′30″E, 1760 m, Coll. 14.xi.1909. (1 wet spec. arms disarticulated, *r* = 1.0) NMNH 40298 East of Waleabahi Island, Celebes, Gulf of Tomini, 0°22′N 123°3′30″E, 1760 m. Coll. 14.xi.1909, [1 wet spec. *R* = 11.3, *r* = 1.8 (arm tips broken)] NMNH 40299 North of Togian Island, Celebes, Gulf of Tomini. 0°16′28″N, 121°33′30″E, 1525 m. Coll.17.xi.1909. (1 wet spec. *R* = 11.8, *r* = 0.8) CASIZ 8587 Binang Unang Island, Gulf of Tomini, 0°04′00″S, 121°36′00″E, 1392.0 m. Coll. 18.xi.1909. (1 wet spec. *R* = 11.3, *r* = 1.3) Japan. NMNH 31958, Manazuru Zaki, Sagami Bay, Honshu Island. 35°8′N, 39°10′E, 916–1370. coll. 5.v.1900. (2 wet specs. *R* = 3.3 *r* = 0.5; *R* = 2.0, *r* = 0.4) CASIZ 115933 Off Honshu Island, Manazuru Zaki, 916–1370 m, Coll. 5.v.1900. [1 wet spec. *R* = 12.8, *r* = 1.1 (arm tips broken)]

CNEMIDASTER ZEA (ALCOCK, 1893)

Zoroaster zea Alcock, 1893: 110; 1895: Pl. II, 2,2a.; Clark & Mah, 2001: 235.
Cnemidaster zea Fisher, 1919b: 18, 481, 483; H.L.Clark, 1920: 98; Downey, 1970: 14.

Occurrence: S. India, 1090 m.

DORASTER DOWNEY, 1970
(FIG. 3E–G)

Doraster Downey, 1970: 5; Moyanna & Larrain, 1976: 103; Walenkamp, 1979: 87; Clark & Downey, 1992: 402; Clark & Mah, 2001: 231.

Type species: *Doraster constellatus* Downey, 1970.

Diagnosis: Disc and arm plates imbricate. Disc enlarged, swollen. Spinelets cover disc, arm surface (frequently absent). Disc plates strongly stellate. Internal buttress present.

DORASTER CONSTELLATUS DOWNEY, 1970
(FIG. 3E–G)

Doraster constellatus Downey, 1970: 5; Moyana & Larrain Prat, 1976: 103; Clark & Downey, 1992: 402; Clark & Mah, 2001: 231.
D. cancellatus Jangoux, 1978: 98 (lapsus for *D. constellatus*)

Occurrence: SW orf Nantucket Shoals, Gulf of Mexico, Atlantic Panama, Surinam, 350–914 m.

Material: North Atlantic. NMNH 1080502, SW of Nantucket Shoals, Massachsetts, 39°18′30″N, 71°23′30″W, 2601 m, Coll. 11.viii.1885 (13 wet specs.) Gulf of Mexico-NMNH E23145 East of Corpus Christi, Texas. 27°38′N, 95°35′W, 412 m. Coll. 7.v.1956. (1 dry spec. *R* = 12.1, *r* = 1.4) NMNH E34980, East of Mississippi Delta, Louisiana. 29°07′N, 88°11′W, 549 m, Coll. 3.vi.1959. (1 dry spec. *R* = 12.6 *r* = 1.2) NMNH E18554, East of Mississippi Delta, Louisiana. 29°12′N, 88°03′W, 366 m, Coll. 3.vi.1959. (1 dry spec. *R* = 10.1 *r* = 0.9) NMNH E18506, East of Mississippi Delta, Louisiana. 29°14′N, 87°54′W, 366 m, Coll. 22.v.1956. (1 dry spec. *R* = 12.8 *r* = 1.7) NMNH E10742 PARATYPES, Mississippi Delta, Louisiana. 29°03′15″N, 88°16′W, 592 m, Coll. 11.ii.1885. (2 dry specs. *R* = 6.6, *r* = 0.8; *R* = 11.6). NMNH E11353 PARATYPE SW of Grenada, 11°36′N, 62°52′W, 393–421 m, Coll. iv.1960, [1 dry spec. *r* = 10.2, *r* = 1.4 (arms broken)] Caribbean Sea-NMNH E18519, East of Chinchorro Bank, Quintana Roo, Mexico, 18°30′N, 87°37′W, 715–787 m, Coll. 17.iii.1968. (1 dry spec. *R* = 15.4, *r* = 1.9) NMNH 1080556, Gulf of Mosquitos, Panama, 9°20′N, 81°24′W, 860–914 m, Coll. 25.v.1962. [2 dry specs. *R* = 14.3, *r* = 2.1; *R* = 4.8, *r* = 1.0 (arms broken on one spec)] NMNH 26524, Gulf of Mosquitos, Panama, 9°6′N, 81°15′W, 777 m, Coll. 29.x.1970. (1 dry spec. *R* = 4.2, *r* = 0.8). NMNH 1080506, Gulf of Mosquitos, Panama, 9°7′N, 81°10′W, 732 m, Coll. 31.v.1962. (1 dry spec. *R* = 17.1, *r* = 2.1) NMNH E12441 Rosalind Bank between Honduras and Jamaica, Honduras. 16°35′N, 80°04′W, 732 m, Coll. 18.v.1962. [1 dry spec. *R* = 12.6, *r* = 2.4 (arms broken)] NMNH E12447 Rosalind Bank between Honduras and Jamaica, Honduras. 16°35′N, 80°10′W, 576 m, Coll. 18.v.1962 [2 dry specs. *R* = 26.6, *r* = 2.2, *R* = ~13.1, *r* = 1.7. (arms broken)] NMNH E26552 Off Santa Marta, Colombia. 11°13′N, 74°26′W, 631 m, Coll. 9.xi.1970 [1 dry spec. *R* = ~12.6, *r* = 1.7 cm (arm tips broken)] NMNH E18507, North of Aramatka Point, Guajira Peninsula, Colombia, 12°13.18′N, 18°72.52′W, 408–576 m, Coll. 29.vii.1968. [2 dry specs, *R* = ~6.7, *r* = 1.2, *R* = 3.6, *r* = −0.7 (arm tips broken)] NMNH E12443 East of Paraguana Peninsula, Vene-

zuela 15°39′N, 61°10′W, 649 m, Coll. 5.iii.1966 [5 dry specs, $R = 9.5$ $r = 1.6$; $R = 7.1$, $r = 1.3$; $R = 5.6$, $r = 0.9$; $R = 12.7$, $r = 1.4$; $R = 14.6$, $r = 1.5$ (arm tips, arms broken)]. NMNH E12444 East of Paraguana Peninsula, Venezuela 11°53′N, 69°25′W, 640 m, Coll. 3.x.1963. [3 dry specs, $R = {\sim}16.5$ $r = 2.2$; $R = {\sim}18.8$, $r = 2.3$; $R = 16.3$, $r = 2.2$; (arm tips, arms broken)] NMNH E18570 East of Testigo Islands, Venezuela, 11°36′N, 62°46′W (no depth indicated). Coll. 19.iv.1960 [2 dry specs. $R = {\sim}11.2$, $r = 1.4$; $R = {\sim}17.5$ (arm tips broken)] French Guiana. NMNH E18508, North of Cayenne. 7°5′N, 52°47′W, 366 m, Coll. 14.ix.1958. [1 dry spec. $R = {\sim}2.5$, $r = 1.1$ (arms broken)]

MYXODERMA FISHER, 1905

Zoroaster (*Myxoderma)* Fisher, 1905: 316.
Myxoderma Fisher, 1919a: 389, 391; 1919b: 471; 1928: 44; Spencer & Wright, 1966: U75; Aziz & Jangoux, 1984: 193; Clark & Mah, 2001: 231.

Type species: *Zoroaster* (*Myxoderma*) *sacculatus* Fisher, 1905.

Diagnosis: Disc and arm skeleton reticulate. Plates cruciform, forming open papular fields. Primary spines present on all plates. Internal buttress present.

MYXODERMA ACUTIBRACHIA AZIZ & JANGOUX, 1984

Myxoderma acutibrachia Aziz & Jangoux, 1984: 192; Clark & Mah, 2001: 231

Occurrence: Macassar Strait, 01°58′54″S, 119°09′72 E, 715–800 m (no specimens examined).

MYXODERMA LONGISPINUM LUDWIG, 1905
COMB. NOV.

Zoroaster longispinum Ludwig, 1905: 180; Maluf, 1988: 44, 125; Clark & Mah, 2001: 234
Zoroaster perarmatus H.L. Clark, 1920: 102; Maluf, 1988: 45, 125, Clark & Mah, 2001: 235

Occurrence: Gulf of California S to Panama and the Galapagos, off N. Peru, 980–1571 m.

Material examined: Mexico. NMNH 34385 designated herein as LECTOTYPE. Concepcion Bay, Gulf of California. 26°48′N, 110°45′20″W, 1571 m. Coll. 22.iv.1891. (1 wet spec. $R = 2.7$, $r = 0.5$) NMNH E 9626. East of San Marcos, Baja California. 27°9′N, 111°42′W, 1567 m. Coll. 20.iii.1889. (1 wet spec. $R = 3.4$, $r = 0.7$) Peru: NMNH E4905 (HOLOTYPE for *Z. perarmatus*). Aguja Point, Peru, South Pacific. 5°47′S, 81°24′W, 980 m. Coll. 12.xi.1904. (1 dry spec. $R = 9.8$, $r = 1.3$ cm)

MYXODERMA PLATYACANTHUM (H.L. CLARK, 1913)
(W/SYNONYM SSP. RHOMALEUM FISHER, 1919)

Zoroaster platyacanthus H.L. Clark, 1913: 199.
Myxoderma platyacanthum Fisher, 1919a: 392; H.L. Clark, 1920: 99; 1923: 152; Fisher, 1928: 52; Alton, 1966: 1709; Aziz & Jangoux, 1984: 193; Maluf, 1988: 44, 124; Lissner & Hart, 1993: 109; Clark & Mah, 2001: 231.
Myxoderma platyacanthum rhomaleum Fisher, 1919a: 393; 1928: 45, 54, pl. 14, fig. 3.3a, pl. 15, fig. 2; pl. 16, fig. 1; pl. 23, fig. 1; pl. 24, fig. 2; pl. 25, fig. 3.

Occurrence: Queen Charlotte Island (Canada), Oregon, Californa to Mexico, 256–2904 m.

Material: British Columbia (Canada): CASIZ 8636, Queen Charlotte Islands: Moresby Island, 2904 m on grey mud, 52°39.00′30.00″N, 132.00°38.00′0.00″W, Coll. 3.ix.1890. (19 wet specs. $R = 6.0$, $r = 0.9$; $R = 7.2$, $r = 1.1$; $R = 7.5$, $r = 0.9$; $R = 6.3$, $r = 0.9$; $R = 5.3$, $r = 0.8$; $R = 6.3$, $r = 0.8$; $R = 5.9$, $r = 1.0$; $R = 4.6$, $r = 0.8$; $R = 5.7$, $r = 0.9$; $R = 4.9$, $r = 0.7$; $R = 6.3$, $r = 0.8$; $R = 3.1$, $r = 0.6$; $R = 5.9$, $r = 0.8$; $R = 5.4$, $r = 0.6$; $R = 6.3$, $r = 0.8$; $R = 5.9$, $r = 0.8$; $R = 4.8$, $r = 0.8$; $R = 6.5$, $r = 0.8$; $R = 6.2$, $r = 1.0$) Oregon: NMNH E10355, SW of mouth of Columbia River, 46°0.1′N, 124°50.8′W. 549 m, Coll. 9.v.1963. (1 dry spec. $R = 6.1$, $r = 1.3$ cm); NMNH E16027, SW of mouth of Columbia River, 46°0.0′N, 124°47′W, 410 m, Coll. 25.i.1963 (1 dry spec. $R = 7.6$, $r = 1.4$); NMNH E10354, SW of mouth of Columbia River, 46°0.0′N, 124°58.8′W, 503 m, Coll. 14.v.1963 (1 dry spec. $R = 2.9$, $r = 1.8$). NMNH E16031, Winchester Bay 43°46′N, 124°57′W, 507 m, Coll. 19.x.1888. [3 dry specs. $R = 7.6$, $r = 1.3$, $R = 8.0$, $r = 1.1$, $R = 6.6$, $r = 1.3$ (arm tips broken)] Washington: NMNH E10353, Astoria Canyon, 46°13.6′N, 124°44.2′W, 1006 m, Coll. 13.iii.1963. (1 dry spec. $R = 4.2$, $r = 1.2$) California: CASIZ 115924 Eel Canyon, Humboldt County, 704 m, on mud, Coll. xii.1966 (6 wet specs. $R = 5.0$, $r = 1.0$, $R = 4.2$, $r = 0.6$, $R = 4.1$, $r = 0.8$, $R = 5.9$, $r = 1.1$, $R = 5.6$, $r = 1.1$ $R = 6.1$, $r = 0.9$) CASIZ 115900 Gulf of Farallones, 37°26.70′N 123°1.30′W, 519–660 m, Coll. 18.xii.1985 (2 wet specs. $R = 5.4$, $r = 0.9$; $R = 5.1$, $r = 0.9$); CASIZ 115911 Gulf of Farallones, 37°35.30′N 123°14.50′W, 1491–1405 m, Coll. 14.xii.1985 [2 wet specs. $R = 4.4$, $r = 0.8$, $R = 5.4$, $r = 1.0$ (arm tips broken)]; CASIZ 115908 Santa Barbara Channel to Santa Cruz Island 91–366 m (2 wet specs. $R = 2.9$, $r = 0.5$, $R = 3.4$, $r = 0.6$); CASIZ 115920 Off San Luis Obsipo County, 35°1.80′N 121°10.20′W, 576 m, Coll. 7.ix.1976 (1 wet spec. $R = 5.7$, $r = 1.3$). Mexico: NMNH 31640 San Pablo Point, Baja California. 27°7.8′N, 114°33.10′W, 519 m, Coll. 15.iii.1911 (1 dry spec. $R = 6.7$, 0.95 cm). SIO E 249 S of Isla San Pedro, Mexico. 27°40′N, 111°29.6′W to 27°32.1′N, 111°20.1′W. 931–952.0 m. Coll. 16.i.1961. [3 wet specs. $R = 7.2$ $r = 1.0$, $R = 7.9$ $r = 1.0$, $R = 7.7$ $r = 0.8$ (arms broken)].

MYXODERMA QAWASHQARI (M<small>OYANA</small> & L<small>ARRAIN</small> P<small>RAT</small>, 1976) **COMB. NOV.**

Doraster qawashqari Moyana & Larrain Prat, 1976: 105; Codoceo & Andrade, 1978: 159; Clark & Mah, 2001: 231.

Occurrence: Mexico, Peru, to S. Chile, 300–2454 m.

Material: Mexico. SIO E 1005 Off Pta. Chivato sur 27°18′N, 111°24′W, 1829–1875 m. Coll. 15.vi.1970 [2 wet specs. R = ~12.4, r = 1.6, R = ~14.5, r = 1.7 (arms broken)]; SIO E1006 Off Pta. Lobos. Sonora, Mexico. 27°13′N, 111°28′W, 1829–1875 m. Coll. 14.vi.1970 [3 wet specs. R = 11.1, r = 1.2, R = 14.3, r = 1.4, R = 14.9, r = 1.7 (arms broken)], Peru. NMNH 1084273 Off Lima, Peru. 11°50′S, 77°58′W, 935–907 m (1 dry spec. R = 16.2, r = 1.3). Chile. NMNH E16255 Paratype, Bahia Tarn Chile, Golfo de Penas. 42°45′S, 75°45′W, 300 m, Coll. 1.x.1972. (1 dry spec. R = 16 cm, r = 1.3 cm) NMNH 1080458, SW of Paita, Piura Peru. 5°07′S, 81°27′W to 4°59′S, 81°27′W, 365–457 m. Coll. 3.vi.1966 (58 dry specs. Size range from R = 5.3, r = 0.7 to R = 2.2, r = 0.4). CASIZ 115935 Off Chile. 42°36′, 75°28′W, 2454.0 m, Coll. 12.ii.1888. [1 wet spec. R = 9.5, r = 1.1 (arm tips broken)] CASIZ 115936 Off Chile. 38°8′00″, 75°53′00″ 1238.0 m, Coll. 14.ii.1888 (1 dry spec. R = 9.2, r = 0.9 (arm tips broken)]. SIO E446 Off Arica, Chile. 18°44.7′S, 70°40.7′W to 18°40.2′S, 70°35.1′W, 1097–1152 m, Coll. 7.v.1972 (2 wet specs. R = 9.6 r = 1.5, R = 13.5 r = 1.3); SIO E620 West Cortz Basin (on escarpment). 32°27.7′N, 119°33.8′W to 32°27.9′N, 119°34.1′W, 1445.0 m. Coll. 7.v.1975. (1 wet spec. R = ~22.0 cm, r = 2.1). SIO E 997, Off Arica, Chile. 18°44.7′S, 70°40.7′W to 18°40.2′S, 70°35.1′W, 1097–1152 m, Coll. 7.v.1972. (1 wet spec. R = 10.5 r = 1.7)

MYXODERMA SACCULATUM (F<small>ISHER</small>, 1905)
(<small>WITH SYNONYM SSP.</small> ***ECTENES*** F<small>ISHER</small>, 1919)

Zoroaster (*Myxoderma*) *sacculatus* Fisher, 1905: 316.
Zoroaster evermanni H.L. Clark (not Fisher) 1913: 198.
Myxoderma sacculatum Fisher, 1919a: 392; H.L. Clark, 1923: 152; Fisher, 1928: 45, 49; Baranova, 1957: 175; Alton, 1966: 1709; Maluf, 1988: 44, 125; Clark & Mah, 2001: 232.
Myxoderma derjungi Djakonov, 1968: 91.

Occurrence: Okhotsk Sea, Bering Sea to southern California. 91–2012 m.

Material examined: Alaska. CASIZ-24100, Bowers Bank, Bering Sea, Aleutian Islands, 54.00°33′N 178°44′W, 1068 m, Coll. 4.vi.1906. (dry specimen-arm fragment only) CASIZ 115903 Bering Sea 57°50.92′N 173°57.72′W, 720–750 m, Coll. 21.vi.1979. (1 wet spec. R = 13.3 r = 2.2) Oregon. NMNH E28078, SW mouth of Columbia River, 45°44′12″N, 125°8′48″W, 1555 m,

Coll. 29.v.1964. [1 wet spec. R = ~25.0, r = 2.1 (arms broken)] NMNH E 14760, SW mouth of Columbia River, 1372 m, coll. 9.vi.1962. [1 wet spec. R = ~30.0, r = 2.6 (arms broken)]. California. NMNH 32451 West of San Nicolas Island, Channel Islands, 33°24.36′N, 120°12.30′W, 1170 m, Coll. 26.iv.1911. (2 dry specs. R = 10.6, r = 1.1, R = 6.6, r = 0.9 cm) NMNH 3596 San Diego. 32°40.30′N, 117°31.30′W, 1504 m. Coll. 19.i.1889. [4 dry specs. R = 8.6, r = 1.1, R = 7.7, r = 0.9, R = 6.1, r = 0.9, R = 6.7, r = 1.0 (arm tips broken)] NMNH E 01149 West of San Nicolas Island, Channel Islands, 33°15′N, 119°30′W, 1983–2012 m, Coll. 13.iv.1904. (8 wet specs. R = 4.0, r = 0.8, R = 3.2, r = 0.7, R = 1.7, r = 0.5; R = 1.8, r = 0.4; R = 1.2, r = 0.3, R = 1.3, r = 0.3, R = 1.2, r = 0.3, R = 1.1, r = 0.2 cm) CASIZ 102207, Humboldt County off Trinidad Head on sandy mud, 329 m, Coll. xii.1966. [3 dry specs. R = 4.7, r = 0.9, R = 4.5, r = 0.7; R = 4.3, r = 0.8 (arm tips broken)] CASIZ 115927, Farallon Islands on mud, rocks, 1280–1500 m, Coll. 12.xi.1950. [1 wet spec. R = 18.1, r = 1.7 (arm tips broken)] CASIZ 115914, Santa Barbara Channel to Santa Cruz Island 91–366 m (1 wet spec. R = 2.1, r = 0.4). CASIZ 117841 Off Humboldt County, 1123.0 m. Coll. 13.xi.1975. (2 dry specs. R = 22.0, r = 1.5, R = 17.6, r = 1.8)

PHOLIDASTER S<small>LADEN</small>, 1889
(F<small>IG</small>. 5A–D)

Pholidaster Sladen, 1889: 426; Fisher, 1919a: 388; 1919b: 471, 484, 485; Spencer & Wright, 1966: U75; Clark & Mah, 2001: 232.

Type species: *Pholidaster squamatus* Sladen, 1889 (designated by Fisher, 1919a).

Diagnosis: Disc and arm plates imbricate. Disc and arms covered by flattened scales covering nearly all plates save for the carinal arm series and primary circlet on disc. Carinal plates along arms bare. Superambulacral plates reduced. Internal buttress absent. Pedicellariae absent.

PHOLIDASTER SQUAMATUS S<small>LADEN</small>, 1889
(F<small>IG</small>. 5A–D)

Pholidaster squamatus Sladen, 1889: 427; Fisher, 1919b: 4,18, 484; H.L. Clark, 1920: 98; Marsh, 1976: 221; Jangoux, 1981: 475; Clark & Mah, 2001: 232.
Pholidaster distinctus Sladen, 1889: 429; Fisher, 1919b: 18; Clark & Mah, 2001: 232.

Occurrence: Philippines, Indonesia, W and NW Australia, 90–256 m.

Material examined: Philippines. NMNH 40573. Masbate Passage, Baleno, Masbate Island. 12°25′18″N, 123°37′15″ Coll. 21.iv.1908. [1 wet spec. R = ~7.0, r = 0.7 (arms broken, spec. partially disartculated)]

NMNH 40562. NE of Cataingan, masbate Island, Samar Sea. 12°4′15″N, 124°4′36″ E (mixed stations). Coll. 20.iv.1908. [6 wet specs. $R = 5.9$, $r = 0.7$; $R = 5.2$, $r = 0.7$; $R = {\sim}5.0$, $r = 0.7$; $R = 5.0$, $r = 0.7$; $R = 3.7$, $r = 0.7$; $R = 3.8$, $r = 0.7$ (arm tips broken)] NMNH 40215 Destacado Island, Northern Samar, Samar Sea, 12°12′35″N, 124°2′48″E, 247 m. Coll. 13.iii.1909. [7 wet specs. $R = 6.1$, $r = 0.8$; $R = 6.1$, $r = 0.7$; $R = 5.8$, $r = 0.7$; $R = 6.1$, $r = 0.7$; $R = 6.2$, $r = 0.7$; $R = 5.6$, $r = 0.6$; $R = 5.5$, $r = 0.6$ (arm tips broken] NMNH E50370, Bohol Strait, Bohol. 90 m. Coll. 22.xi.1979. [2 wet specs. $R = 10.0$, $r = 0.8$; $R = 9.1$, $r = 0.8$ (arm tips broken)]

SAGENASTER MAH GEN. NOV.

Etymology: Latin (*sagena*) for fish-net, referring to the reticulate or net-like skeleton in this genus.

Type species: *Zoroaster evermanni* Fisher, 1905.

Diagnosis: Disc and arm skeleton reticulate. Plates cruciform, forming open papular fields. Primary spines present on all plates. Internal buttress absent.

SAGENASTER EVERMANNI (FISHER, 1905)
(W/SYNONYM *EVERMANNI MORDAX* FISHER, 1919)
(FIGS 2E, F)

Zoroaster (Myxoderma) evermanni Fisher, 1905: 317; not H.L. Clark, 1913: 198 (= *Myxoderma sacculatum*).
Zoroaster evermanni Fisher, 1919a: 390; H.L. Clark, 1920: 100; 1923: 152; Fisher, 1928: 40, pl. 13, fig. 3, pl. 14, figs 1.1a, 1b, pl. 18, fig. 4; pl. 19, fig. 1; pl. 20, figs 3, 4; Alton, 1966: 1709; Carey, 1972: 41; Lambert, 1978a: 23; 1978b: 64; Maluf, 1988: 44, 125; Nybakken *et al.*, 1998: 1777; Clark & Mah, 2001: 233.
Zoroaster evermanni mordax Fisher, 1919a: 391, 1928: 34, 43, pl. 13, fig. 4; pl. 14, fig. 2; pl. 19, fig. 2.

Occurrence: Aleutian Islands (Alaska), Queen Charlotte Island (Canada), Oregon, Washington to S. California, Mexico, 100–2710 m.

Material: Alaska: CASIZ 115898, Aleutian Islands, Unalaska Island, 54.00°21.50″N, 167.00°47.50″W, 905–910 m, Coll. 14.vi.1979 (wet spec. $R = 17.2$, $r = 1.6$). Oregon: NMNH E 10356, SW of mouth of Columbia River, 45°51.5′N, 124°42′W. 823 m, Coll. 6.iii.1962. (1 dry spec. $R = 12.6$, $r = 0.9$ cm) NMNH E 10359 SW of mouth of Columbia River, 45°52.3′N, 124°52′W. 823 m, Coll. 13.v.1963. (1 dry spec. $R = 9.1$, $r = 0.9$ cm) NMNH E16023, SW of mouth of Columbia River, 45°52′N, 124°54′W. 823 m, Coll. 27.v.1962 (1 dry spec. $R = 9.2$, $r = 0.9$ cm); NMNH E 10360, SW of mouth of Columbia River, 45°40.5′N, 124°55′W, 1372 m, Coll. 2.viii.1963. (1 dry spec. $R = 3.2$, $r = 0.35$ cm) NMNH E 10357, SW of mouth of Colum-

bia River, 45°52′N, 124°54′W. 732 m, Coll. 23.i.1963. (1 dry spec. $R = 14.2$, $r = 0.8$ cm) NMNH E 16019, SW of mouth of Columbia River, 45°56′N, 124°51′W. 682 m, Coll. 12.iii.1962. [1 dry spec. $R = {\sim}8.2$, $r = 0.8$ cm (arm tips broken)] NMNH E 10358, SW of mouth of Columbia River, 45°57.3′N, 124°48.7′W. 594 m, Coll. 10.v.1962. [1 dry spec. $R = {\sim}16$, $r = 0.9$ cm (arm tips broken)] NMNH E 16007, SW of mouth of Columbia River, 46°14′N, 124°44′W. 979 m, Coll. 13.iii.1962. [2 dry specs. $R = {\sim}12.5$, $r = 1.0$ cm, $R = 7.2$, $r = 0.8$ cm (arm tips broken)] CASIZ 122302, Off Oregon coast, 44°20′N, 125°5′W, 823–914.0 m, Coll. 10.xii.1961 (1 wet spec. $R = 11.8$, $r = 0.7$). CASIZ 121506 Cascadia Plain, 45°55.50′N, 125°38.8′W, 2030.0 m, Coll. 20.iii.1970. (5 wet specs. $R = 2.0$, $r = 0.3$, $R = 1.1$, $r = 0.2$, $R = 0.8$, $r = 0.2$; $R = 1.1$, $r = 0.2$, $R = 0.4$, $r = 0.1$) California: CASIZ 113317 Humboldt County on mud, 704–841 m, Coll. vi.1977. (3 dry spec. $R = 8.8$, $r = 1.2$, $R = 12.2$, $r = 1.1$; $R = 9.7$, $r = 0.8$) CASIZ 113318 Eureka, Humboldt County on soft green-black mud, 100–1005 m, Coll. i.1977. (2 dry specs. $R = 10.6$, $r = 0.8$, $R = 11.2$, $r = 0.8$) CASIZ 11319, Eureka, Humboldt County on soft green-black mud, 823 m [2 dry specs. $R = 10.5$, $r = 1.1$, $R = {\sim}15$, $r = 1.1$ (arm tips broken)] CASIZ 115950 Off Point Loma Lighthouse, San Diego on green mud, fine sand, 294–933 m, Coll. 5.iii.1904. [1 wet spec. $R = 13.9$, $r = 1.1$ (arm tips broken)] CASIZ 115910 Gulf of Farallones, 913–1000 m, Coll. 16.xii.1985. (2 wet specs., $R = 3.1$, $r = 0.4$, $R = 2.6$, $r = 0.6$) CASIZ 115925 Off Bodega head, Sonoma County, 549–567.0 m Coll. 16.iii.1965. [1 wet spec. $R = {\sim}14.8$, $r = 1.0$ (arms broken)]

TERMINASTER HESS, 1974

Asterias Quenstedt, 1876: 49, pl. 91, fig. 155.
Terminaster Hess, 1974: 647; Hess, 1986: 47.

Type species: *Asterias cancriformis* Quenstedt, 1876.

Diagnosis: Disc small. Disc and arm with imbricate skeleton. Plates polygonal to weakly lobate. Large primary spines present. Terminal plate enlarged.

TERMINASTER CANCRIFORMIS (QUENSTEDT, 1876)

Asterias cancriformis Quenstedt, 1876: 49, pl. 91, fig. 155.
Terminaster cancriformis Hess, 1974: 647; 1986: 47.

Occurrence: English Oxford Clay, Callovian to Middle Oxfordian (Mid to Late Jurassic) marls of the French and Swiss Jura.

TERMINASTER SPINULOSUS KUTSCHER & HARY, 1991

Kutscher & Hary, 1991: 62

Occurrence: Isolated ossicles from the Sinemurien (Early Jurassic) of SE Luxembourg, NE of the Paris Basin.

ZOROASTER THOMSON, 1873
(WITH SYNONYM *PROGNASTER* PERRIER, 1891)

Prognaster Perrier, 1891: 1226; 1896: 22 (Probably not Perrier, 1894 according to Fisher, 1928: 32); Fisher, 1919b: 388; H.L. Clark, 1920: 96, 98; Downey, 1970: 14.

Zoroaster Thomson, 1873: 154; Sladen, 1889: 416; Fisher, 1919b: 471, 484, 485; Verrill, 1915: 27; H.L. Clark, 1920: 100; Fisher, 1928: 33; Bernasconi, 1964: 266; Spencer & Wright, 1966: U74; Downey, 1970: 14; Harvey *et al.*, 1988: 167; Clark & Downey, 1992: 403; Liao & Clark, 1995: 140; Clark & Mah, 2001: 232.

Type species: *Zoroaster fulgens* Thomson, 1873.

Diagnosis: Disc small. Disc and arm with imbricate skeleton. Carinal plates ridge-like. Primary spines present or absent on carinals, marginal plate series. Superambulacrals reduced. Internal buttress absent.

ZOROASTER ACTINOCLES FISHER, 1919

Zoroaster actinocles Fisher, 1919: 390; 1928: 37; Clark & Mah, 2001: 233

Occurrence: Aleutian Islands, California to Chile. 1617–2710 m.

Material examined: Alaska. CASIZ 120350 Patton Seamount, Gulf of Alaska. [1 wet spec. R >15.4, r = 2.1 (arms broken)] NMNH 37039 HOLOTYPE, North of Amukta Pass, Island of Four Mountains, Aleutian Islands, Bering Sea. 53°12′N, 171°37′W, 2226 m, coll. 29.v.1906 (1 wet spec. R = 16.1, r = 1.1) California. CASIZ 769 Monterey Fan Valley, 36.00°33.70″N, 122.00°27.20″W, 2430–2710 m, Coll. 21.iii.1975. (8 wet spec. R = 9.7, r = 0.8; R = 7.6, r = 0.8; R = 8.8, r = 0.8; R = 6.1, r = 0.7; R = 6.1, r = 0.6; R = 5.2, r = 0.6) CASIZ 115905 East Cortes Bank, 32.00°15.90″N 118.00°41.20″W, 1617–1678 m, Coll. 20.i.1985. (2 wet specs. R = 13.4, r = 1.0, R = 12.3, r = 1.0) Chile. CASIZ 115934 Off Chile, 45°35′N, 75°55′W 1920.0 m, Coll. 11.ii.1888. (1 wet spec. R = 11.1, r = 1.1) NMNH 1084274 west mouth of Straits of Magellan. 53°13′S, 75°41′W to 53°16′S, 75°41′W. 1500–1666 m. Coll. 5.i.1966. (2 dry specs. R = 15.1, r = 1.3; R = 12.5, r = 1.0).

ZOROASTER ADAMI KOEHLER, 1909

Zoroaster adami Koehler, 1909: 108; Fisher, 1919b: 18, 472, 175; H.L. Clark, 1920: 101 (in key); Clark & Mah, 2001: 233; Sastry, 2005: 47, 143, 157.

Occurrence: Philippines. Madagascar, Andaman Sea, 700–1040.0 m.

Material examined: Philippines. CASIZ 104213, NE of Calagua Islands. 14°41′7″, 123°24′12″ 435–451.0 m. Coll. 27.ix.1995 (1 wet spec. R = 7.7, r = 0.7). Madagascar. CASIZ 115902 Off Nosy Be. 12°31′30″, 48°5′3″. 700–710.0 m, coll. 24.xi.1988. (3 wet spec. R = 5.2, r = 0.4; R = 6.6, r = 0.6; R = 7.6, r = 0.6)

ZOROASTER ALFREDI ALCOCK, 1893

Zoroaster alfredi Alcock, 1893: 102; 1893: 173; H.L. Clark, 1920: 101 (in key); Macan, 1938: 415; Clark & Mah, 2001: 233.

Occurrence: Bay of Bengal, Arabian Sea, 2380–3350 m.

ZOROASTER ALTERNICANTHUS MCKNIGHT, 2006

Zoroaster alternicanthus McKnight, 2006: 42.

Occurrence: New Zealand region, 33–52°, 150–427 m.

ZOROASTER ANGULATUS ALCOCK, 1893

Zoroaster angulatus Alcock, 1893: 105; Fisher, 1919b: 472, 477; H.L. Clark, 1920: 101 (in key); Macan, 1938: 415; Clark & Mah, 2001: 233.

Occurrence: Gulf of Mannar, Maldive-Laccidive area, 910–1460 m.

ZOROASTER BARATHRI ALCOCK, 1893

Alcock 1893: 103; Fisher, 1919b: 21, 473, 475; H.L. Clark, 1920: 101 (in key); Clark & Mah, 2001: 233.

Occurrence: Bay of Bengal, 2780 m.

ZOROASTER CARINATUS ALCOCK, 1893
(SSP. *PHILIPPINENSIS* FISHER, 1916 SYN. BY JANGOUX & AZIZ, 1988)

Zoroaster carinatus Alcock, 1893: 107; 1895: pl. IV, fig. 1.1a; Rowe & Gates, 1995: 116.; Clark & Mah, 2001: 233; Sastry, 2005: 47, 143, 165; McKnight 2006: 40.

Zoroaster carinatus philippinensis Fisher, 1916: 30; Fisher, 1919b: 18, 472, 477, 479, pl. 116, fig. 3, pl. 135, fig. 3a, pl. 137; H.L. Clark, 1920: 102 (in key); Jangoux, 1981: 459; Jangoux & Aziz, 1988: 648; Rowe & Gates, 1995: 116; Liao & Clark, 1995: 140.

Occurrence: Philippines, South China Sea, New Caledonia, Western Australia, Indian Ocean, Andaman Sea. 152–1104 m.

Material: Central Pacific. NMNH 40297, Deagan Island, Masbate Island, Samar Sea, Philippines. 12°15′N, 123°57.30′E, 146 m. Coll. 20.iv.1908. (1 dry spec. disarticulated). NMNH 40586 Lucena City, Tayabas Bay, Luzon Island, Quezon. 13°49′40″N,

121°40′15″E, 152 m. Coll. 24.ii.1909. [1 wet spec. $R = 6.6$, $r = 0.7$ (arm tips broken)]; NMNH 40380 Ticao Island, Masbate Passage, 12°31′30″N, 123°35′24″E, 1104 m. Coll. 21.iv.1908. (1 wet spec. $R = 7.7$, $r = 0.9$) NMNH E1804 No data (probably Philippines). (5 dry specs. $R = 9.9$, $r = 0.8$; $R = 8.7$, $r = 0.8$; $R = 7.4$, $r = 0.8$; $R = 7.6$, $r = 0.7$; $R = 8.1$, $r = 0.7$). Indian Ocean. NMNH E50357, NE of Mombasa, Kenya. 2°56′S, 40°28′E, 240 m, Coll. 8.xi.1964 (3 dry specs. $R = 7.4$, $r = 0.9$; $R = 8.0$, $r = 0.9$; $R = 8.2$, $r = 0.9$). NMNH E 50358, NE of Mombasa, Kenya. 2°54′S, 40°23′E, 34 m (340 m), Coll. 7.xi.1964. (5 dry specs. $R = 7.5$ $r = 0.9$; $R = 7.7$, $r = 0.9$; $R = 8.1$, $r = 0.9$; $R = 8.2$, $r = 0.9$; $R = 6.5$, $r = 0.7$) NMNH E50371 East of Zanzibar Island, Tanzania. 2°50′S, 40°31′E, 190 m. Coll. 8.xi.1964. (1 wet spec. $R = 8.2$, $r = 1.1$) NMNH 1080461, west of Phuket Island, Malay Peninsula, Thailand. 7°40′N, 97°9′E, 370 m, Coll. 21.iii.1963. [15 dry specs. $R = 1.7$, $r = 0.3$; $R = 3.1$, $r = 0.3$; $R = \sim12.5$, $r = 0.8$; $R = \sim11.0$, $r = 0.8$; $R = 9.5$, $r = 0.8$; $R = \sim10$, $r = 0.8$; $R = \sim11.0$, $r = 0.8$; $R = \sim9.0$, $r = 0.7$; $R = 10.8$, $r = 0.6$; $R = \sim10.8$, $r = 0.8$ (arms broken, twisted)]

ZOROASTER FULGENS Thomson, 1873

Zoroaster fulgens Thomson, 1873: 153; Studer, 1883: 130; Sladen, 1889: 418; 1891: 694; Perrier, 1894: 116; Koehler, 1896: 42; H.L. Clark, 1901: 237; Farran, 1913: 19; Fisher, 1919b: 471; H.L. Clark, 1920: 101 (in key); Mortensen, 1927: 132; Downey, 1970: 14; Rice *et al.*, 1982: 66; Gage *et al.*, 1983: 269, 286; Harvey *et al.*, 1988: 167; Hoz & Garcia, 1991: 135, 136; Hansson, 1998 (checklist); Clark & Mah, 2001: 234; Sumida *et al.*, 2001: 29; Howell *et al.*, 2004: 977.

Zoroaster aff. *fulgens* (Eocene) Blake & Zinsmeister, 1979: 1151; 1988: 495.

Zoroaster ackleyi Perrier, 1880: 436; 1881: 6; 1881b: 59; 1894: 117; Verrill, 1915: 28; H.L. Clark, 1920: 101 (in key); Fisher, 1928: 491; John & Clark, 1954: 139.

Zoroaster diomedeae Verrill, 1884: 217.

Zoroaster longicauda Perrier, 1885: 198; 1894: 120; Howell, Billett & Tyler, 2002: 1906.

Prognaster grimaldii Perrier, 1891: 1226; 1891b: 259; 1896: 23, pl.2; Richard, 1900: 75, fig. 23.

Zoroaster trispinosus Koehler, 1895: 442; 1896: 33; 1909: 108.

Zoroaster bispinosus (as lapsus for trispinosus) Koehler, 1909: 316

Occurrence: North Atlantic (off Massachusetts), Faeroe Channel, Rockall Trough (north-east Atlantic), to Bahamas, Gulf of Mexico, and Surinam. South Atlantic to Shag Rocks, South Georgia Sea, to Indian Ocean (South Africa) 220–4810 m.

Material: North Atlantic. NMNH E 38674 Hudson Canyon, off New Jersey. 38°29′48″N, 72°32′ 54″W, 2625–2640 m. Coll. 30.vii.1975. (2 dry specs. $R = 9.9$, $r = 1.1$; $R = 13.1$, $r = 1.4$) NMNH 14274 Georges Bank, Massachusetts, 41°9′40″N, 66°2′20″W, 2296 m. Coll. 4.ix.1883. [2 dry specs. $R = 11.2$, $r = 1.5$; $R = \sim10$, $r = 1.2$ (arm tips broken)] NMNH E18533, Off Andros Island, Tongue of the Ocean, Bahamas. 24°26′N, 77°34′W, 1565 m, Coll. 28.ix.1967 (4 dry specs. $R = 1.3$, $r = 0.2$; $R = 1.9$, $r = 0.3$; $R = 10.0$, $r = 1.6$; $R = 9.9$, $r = 1.1$). NMNH E18534, North of Little Bahama Bank, 27°30′N, 78°38′W, 490 m. Coll. 5.ii.1964 (1 dry spec. $R = 3.8$, $r = 0.5$). NMNH E38657, East of Virginia Beach, Virginia. 36°42′N, 74°4′30″W, 2400–2450 m, Coll. 24.vii.1975. [3 dry specs. $R = 16.7$, $r = 1.2$; $R = 17.4$, $r = 1.7$; $R = 18.6$, $r = 1.7$ (arms broken, or twisted in several specs.)] Gulf of Mexico. NMNH 1017683, off Florida. 28°16′N, 86°36′16″E, 838–847 m. Coll. 20.v.1985. [16 dry specs. $R = 4.7$ $r = 0.7$; $R = 9.2$, $r = 1.0$; $R = 6.1$, $r = 0.7$; $R = 9.7$, $r = 0.9$; $R = 10.1$, $r = 1.0$; $R = 8.4$, $r = -0.9$; $R = 3.6$, $r = 0.6$; $R = 3.2$, $r = 0.5$; $R = 1.9$, $r = 0.4$; $R = 11.6$, $r = 0.9$; $R = 13.1$, $r = 1.1$; $r = 9.2$, $r = 0.8$; $R = 9.9$, $r = 0.9$; $R = 10.3$, $r = 0.9$ (arm tips broken on several)] Caribbean Sea. NMNH E18538 Off of Roque Islands, Venezuela. 11°50′N, 66°10′W, 1059 m, Coll. 23.vii.1968 (3 dry specs. $R = 2.3$ $r = 0.5$; $R = 1.5$, $r = 0.4$; $R = 1.9$, $r = 0.3$), NMNH E18539, East of St. Vincent Island, 13°20′48″N, 61°2′30″W, 658–841 m (1 dry spec. $R = 0.9$, $r = 0.2$) Guyana-Surinam. NMNH E18529, NE of Paramaribo, 7°21′N, 53°15′W, 549 m. Coll. 21.iii.1965. [2 dry specs, $R = 6.5$, $r = 0.7$; $R = 7.7$, $r = 0.8$ (arms broken on specs.)] NMNH E19310 N of Georgetown, 8°14′N, 57°38′W, 1408 m. Coll. 15.vii.1968. (1 dry spec. $R = \sim10$, $r = 1.3$ (arm tips broken)] NMNH E18536 NE of Paramaribo, 8°33′N, 54°18′W, 1253 m. Coll. 12.vii.1968. (1 dry spec. arms disarticulated, $r = 0.8$) South Atlantic. NMNH E47618, Shag Rocks, South Georgia Island, Scotia Sea. 50°51′12″S, 43°3′12″W, 1351–1362 m. Coll. 9.v.1975. (2 dry specs. $R = 9.6$, $r = 1.1$; $R = 17$, $r = 1.6$) NMNH E47615, NW of South Georgia Island, Scotia Sea. 51°2′12″S, 42°47′36″W, 1481–1546 m, Coll. 9.v.1975. [4 dry specs. $R = \sim23$, $r = 2.0$; $R = 19.6$, $r = 2.1$; $R = \sim24$, $r = 2.1$; $R = 23.4$, $r = 1.8$ (arms twisted, broken on some)] NMNH E47586, Shag Rocks, South Georgia Island, Scotia Sea. 50°51′12″S, 43°3′12″W, 1351–1362 m. Coll. 9.v.1975. [5 dry specs. $R = 17.1$, $r = 1.4$; $R = 20.3$, $r = 2.1$; $R = 17.7$, $r = 1.5$; $R = 16.2$, $r = 1.5$; $R = \sim23$, $r = 1.8$ (arms broken twisted)] Indian Ocean (South Africa). SIO E 2941, off tip of South Africa, 53°21.1′S, 24°56′E, 1100–1400 m. Coll. 21.i.1984 (1 wet spec. $R = 12.1$, $r = 1.6$); SIO E 2943, off tip of South Africa, 46°30.8′S, 33°51′E, 2700–3900 m, Coll. 27.i.1984 ($R = 16.0$, $r = 1.3$).

Fossil material: NMNH 256068. Eocene, Upper La Meseta Formation, Antarctica, Seymour Island. Disc and arm fragments.

ZOROASTER GILESI (SEE *CNEMIDASTER*)

ZOROASTER HIRSUTUS LUDWIG, 1905

Zoroaster hirsutus Ludwig, 1905: 172; H.L. Clark, 1920: 101 (in key); Fisher, 1928: 37; Clark & Mah, 2001: 233.

Comments: Similar to *Zoroaster magnificus*, a possible synonym, but differs in size and primary circlet plate morphology.

Occurrence: Mexico, 3436 m.

Material: Mexico. NMNH 34382, Punta Maldonado, 14°46′N, 98°40′W, 3436 m, Coll. 10.iv.1891. [1 wet spec. $R = 22.0$, $r = 1.3$ (arms broken)]

ZOROASTER MACRACANTHA H.L. CLARK, 1916

Zoroaster macracantha H.L. Clark, 1916 68; 1920: 101 (in key); Fell, 1957: 33; Fell, 1958: 19.
Bythiolophus macracanthus Rowe & Gates, 1995: 115; Clark & Mah, 2001: 230.

Occurrence: South Australia: 146–1006 m.

Material: MCZ 2499-PARATYPE. Great Australian Bight. 129°28′E, 146–219 m (1 dry spec. $R = 16.2$, $r = 1.5$); NMNH 1084275 Chatham Rise, 43°40′S, 179°28′E, 403 m, Coll. 24.i.1954. [1 dry spec. $R = \sim 15.5$, $r = 2.1$ (arms broken)]

ZOROASTER MAGNIFICUS LUDWIG, 1905

Zoroaster magnificus Ludwig, 1905: 159; H.L. Clark, 1920: 104 (in key); Fisher, 1928: 37; Maluf, 1988: 44, 125; Clark & Mah, 2001: 234.
Zoroaster longispina? (in part from syntype series) Ludwig, 1905: 180.
Zoroaster sp. juv.? Ludwig, 1905: 177.

Occurrence: Farallon Islands (Central California), Panama to Galapagos, 2775–3667 m.

Material examined: California. LACM 37°39.05′N, 123°27.36′W to 37°39.20′N, 123°25.60′W. 2775–2840 m. Coll. 28.vii.1992 [1 wet spec. $R = \sim 14.5$, $r = 1.3$ (arm tips broken)]; LACM 37°39.05′N, 123°27.36′W to 37°39.20′N, 123°25.60′W. 2775–2840 m. Coll. 28.vii.1992 [1 wet spec. $R = \sim 16.0$, $r = 1.3$ (arm tips broken)] South and Central America. NMNH E944 SYNTYPE (PARALECTOTYPE) SE of Galapagos Islands, 4°33′S, 87°42′30″W, 3667 m, Coll. 9.xi.1904 [1 wet spec. $R = 29.5$, $r = 14.0$ (arms broken)]; NMNH 34383 SYNTYPE SW of Coiba Island, Panama. 6°17′N, 82°5′W, 3058 m, Coll. 24.ii.1891. [2 wet spec. $R = 27$, $r = \sim 13$; $R = 26.5$, $r = \sim 13$ (arms broken, specs. damaged)]

ZOROASTER MICROPORUS FISHER, 1916

Zoroaster microporus Fisher, 1916: 30; 1919b: 21, 27, 472, 473, 475, pl. 134, fig. 4a, pl. 139, fig. 4; H.L. Clark, 1920: 101 (in key); Hayashi, 1943: 171; Clark & Mah, 2001: 234.

Occurrence: Japan. Indian Ocean-Moluccas. 1280 m.

Material examined: Japan. CASIZ 115932 Honsu, Kinka San Lighthouse 38°11′30″N, 142°12′E, 730 m, Coll. 10.x.1906. [1 wet spec. $R = 10.8$ $r = 1.0$ (arm tips broken)] Indian Ocean. NMNH HOLOTYPE 37009, Buru Island, Moluccas, Indonesia, 3°53′20″S, 126°48′E, 1280 m. Coll. 10.xii.1909. (1 wet spec. $R = 20.5$, $r = 1.2$).

ZOROASTER OPHIACTIS FISHER, 1916

Zoroaster ophiactis Fisher, 1916: 29, 1919b: 18, 27, 471, 472, 473, 475, pl. 135, fig. 2a–b, pl. 136, fig. 1; pl. 139, fig. 3; H.L. Clark, 1920: 101 (in key); Hayashi, 1943: 168; 1973: 94 (english section), 71 (japanese section); Imaoka *et al.*, 1990: 63; Clark & Mah, 2001: 234.

Occurrence: Philippines, Celebes to Japan. 500–1678 m.

Material: Philippines. CASIZ 104217, SE Luzon, Lagonoy Gulf. 13°21′N, 124°12′E, 1037.0 m. Coll. 24.ix.1995. (1 wet spec. $R = 12.8$, $r = 1.1$) Indonesia. CASIZ 18407 HOLOTYPE (partial) Dodepo Island, Teluk, Celebes. 0°16′28′, 121°33′30″, 1525 m, Coll. 17.xi.1909. (1 wet arm fragment) South China Sea. NMNH 40351, SW of Tungsha Island 20°05′N, 116°5′E, 958 m, Coll. 8.viii.1908. (1 dry spec.disarticulated)

ZOROASTER OPHIURUS FISHER, 1905

Zoroaster ophiurus Fisher, 1905: 315; 1919: 390; H.L. Clark, 1913: 199; 1920: 102 (in key), 1923: 152; Fisher, 1928: 34; Baranova, 1957: 175; Alton, 1966: 1709; Carey, 1972: 41; Lambert, 1978a: 23; Maluf, 1988: 45, 125; Clark & Mah, 2001: 233.

Occurrence: Bering Sea, S. to N. Peru, 695–2230 m.

Material: Oregon. NMNH E16008 SW of mouth of Columbia River, 45°42′36″N, 125°12′36″W. 1920 m, Coll. v.1964. [1 dry spec. $R = \sim 21.0$ cm, $r = 1.0$ cm (arms broken)] NMNH E10362 SW of mouth of Columbia River, 45°50.4′N, 125°11.2′W, 1646 m, Coll. 2.ix.1963. (1 dry spec. $R = 2.0$, $r = 0.3$ cm). NMNH E 15986, SW of Mouth of Columbia River, 45°38′36″N, 125°18′W. 2103 m [22 dry specs. $R = 17.5$, $r = 1.1$; $R = 10.6$ $r = 1.1$; $R = \sim 17$ $r = 1.1$; $R = 13.5$, $r = 1.1$; $R = \sim 15$, $r = 1.2$; $R = \sim 17$, $r = 1.4$; $R = \sim 17.6$ $r = 1.3$; $R = 13.6$, $r = 1.1$; $R = \sim 18$ $r = 1.1$; $R = \sim 16.7$, $r = 1.1$; $R = 14.4$, $r = 1.2$; $R = 13.7$, $r = 1.3$; $R = 11.7$, $r = 1.3$; $R = 17.8$, $r = 1.1$; $R = 16.3$, $r = 1.2$; $R = 14.3$, $r = 1.2$; $R = \sim 13.0$, $r = 1.2$; $R = 13.4$, $r = 1.1$; $R = \sim 13.2$, $r = 1.1$; $R = \sim 7.8$, $r = 1.1$; $R = \sim 16.5$ $r = 1.1$ (siX-rays) (arms broken or twisted)] California. LACM Farallon

Islands slope, 37°38.40′N, 123°21.53′W to 37°38.36′N, 123°19.90′W, 2300–2375 m. Coll. 29.vii.1991. (1 wet spec. $R = 3.1$, $r = 0.6$). CASIZ 115916 West Cortes Bank, 32°13′N, 119°15.6′W, 1583–1678 m, Coll. 19.i.1985. (1 wet spec. $R = 8.3$, $r = 0.7$) CASIZ 115918 Monterey fan valley, Monterey Bay, off Point Cypress 36°33.70′N, 122°27.20′W, 2430–2710.0 m, Coll. 21.iii.1975 (1 wet spec. $R = 9.6$ $r = 0.9$). CASIZ 115923 off southern California on grey mud 32°17′N, 119°17′W, Coll. 17.i.1889. [1 wet spec. $R = \sim3.2$, $r = 0.2$ (arms broken)] Mexico. NMNH 32450, SW of San Carlos Point, Baja California. 29°23′N, 116°14′W, 1607 m. Coll. 29.iv.1911. [1 dry spec. $R = 12.5$, $r = 0.9$ (arm tips broken)] NMNH 33252 SW of Punta Abreojos, Baja California. 26°14′N, 114°, 1701 m. Coll. 22.iv.1911. (2 dry specs. $R = 2.6$, $r = 0.5$, $R = 3.0$, $r = 0.5$)

ZOROASTER ORIENTALIS HAYASHI 1943
(WITH FORMA GRACILIS)

Zoroaster orientalis Hayashi, 1943: 162; Clark & Mah, 2001: 234.

Occurrence: Off Omaesaki Japan, 274–869 m.

Comments: Holotype material is probably lost.

ZOROASTER PLANUS ALCOCK, 1893

Zoroaster planus Alcock, 1893: 104; Fisher, 1919b: 472, 477; H.L. Clark, 1920: 101 (in key); Clark & Mah, 2001: 234; McKnight, 2006: 43.

Occurrence: Laccadive Sea, 2200 m.

ZOROASTER SINGLETONI MCKNIGHT, 2006

Zoroaster singletoni McKnight, 2006: 41.

Occurrence: New Caledonia Basin, 1392–2162 m.

ZOROASTER SPINULOSUS FISHER, 1905

Zoroaster spinulosus Fisher, 1906: 1102; 1919b: 472; H.L. Clark, 1920: 101 (in key); Fell, 1958: 19; 1960: 65; McKnight, 1967: 292, 302; H.E.S. Clark, 1970: 4 (in checklist); McKnight, 1975: 59; 1993: 185; Rowe & Gates, 1995: 116; Chave & Malahoff, 1998: 87; Mah, 1998a: 69; Clark & Mah, 2001: 234; McKnight, 2006: 42.

Occurrence: Alaska, Hawaiian Islands, S. Australia, and Tasman Sea, White Island, New Zealand, 350–1680 m.

Material: Alaska. CASIZ 113329, West point of Yunaska Island 53°46′N, 171°37′W, 2226.0 m, Coll. 29.v.1906. (1 dry spec-arm fragment only) Hawai'i. NMNH 21187 HOLOTYPE, West of Kalaupapa, Molokai Island. 21°14′45″N, 157°5′5″W, 600–757 m.

Coll. 18.iv.1902 (1 wet spec. $R = 11.7$, $r = 1.1$) NMNH 31382 PARATYPE, Hanamaulu Bay, Kauai Island. 22°2′10″N, 159°18′15″W, 620–936 m. Coll. 2.viii.1902. (1 wet spec. $R = 11.8$, $r = 1.0$) NMNH 32210 PARATYPE, Between Molokai and Oahu Islands, Kawai Channel. 21°22′35″N, 157°24′40″W, 792–817 m, Coll. 24.vii.1902 (1 wet spec. $R = 15.0$, $r = 1.2$); CASIZ 171711 Pioneer Bank, 25°48.12′N, 173°25.92′W. 1797 m. Coll. 8.x.2003 (1 wet spec. $R = 17.3$, $r = 1.2$). New Zealand. NMNH 1084276, 8 miles east of White Island, Bay of Plenty, North Island. 630–550 m, Coll. 30.ix.1963. [4 dry specs. $R = 10.3$, $r = 1.4$, $R = 8.5$, $r = 1.3$, $R = 8.8$, $r = 1.2$, $R = 10.2$, $r = 1.1$ (arms broken)]

ZOROASTER TENUIS SLADEN, 1889

Zoroaster tenuis Sladen, 1889: 421; Koehler, 1907: 141; 1908: 566; Fisher, 1919b: 472; H.L. Clark, 1920: 101 (in key); A.M. Clark, 1962: 67; Clark & Mah, 2001: 234.

Occurrence: N. of New Guinea and Southern Ocean between Gough and Bouvet Islands, 3190– 1960 m.

Comments: Based on juvenile specimens. A likely synonym of *Z. fulgens*.

ZOROASTER VARIACANTHUS MCKNIGHT, 2006

Zoroaster variacanthus McKnight, 2006: 39.

Occurrence: Challenger Plateau, western-central New Zealand, 914 m.

ZOROASTER SP. 1

Zoroaster sp. A.M. Clark, 1977: 134.

Occurrence: Indian Ocean, east coast of Africa, 200–1000 m. Noted by A.M. Clark (1977: 134) as being a 'poor specimen' (and presumably unidentifiable).

ZOROASTER SP. 2

Zoroaster sp. McKnight, 2006: 44.

Occurrence: Cavalli Seamount, east of northern New Zealand, 560–630 m.

OUTGROUP TAXA: MATERIAL EXAMINED

PEDICELLASTERIDAE PERRIER, 1884
AMPHERASTER FISHER, 1923

Ampheraster Fisher, 1923: 253; 1928: 80; Downey, 1971: 51; 1973: 90; Clark & Downey, 1992: 407; Clark & Mah, 2001: 237.

AMPHERASTER MARIANUS (LUDWIG, 1905)

Sporasterias mariana Ludwig, 1905: 231.

Ampheraster marianus Fisher, 1923: 253; 1928: 81; Clark & Downey, 2001: 237

Occurrence: W. Mexico north to Washington. 510–1240 m.

Material examined: California. NMNH E 8926 Off Poinht San Pedro, Channel Islands, Santa Cruz. 34°, 119°, 818–933. Coll. 14.iv.1904. (2 dry specs. $R = 4.3$, $r = 0.5$; $R = 4.6$, $r = 0.5$, and other arm fragments, disarticulated specimens).

NEOMORPHASTERIDAE FISHER, 1923
NEOMORPHASTER SLADEN, 1885

Glyptaster Sladen, 1885: 612 (nom. nudum, no species named) (non *Glyptaster* Hall, 1852 (Crinoidea)].
Calycaster Perrier, 1891: 1226; 1891: 258.
Gastraster Perrier, 1894: 102; Fisher, 1918: 103; 1923: 250; 1930: 206; Mortensen, 1927: 137.
Neomorphaster Sladen, 1889: 436; Fisher, 1923: 596; 1930: 211; Clark & Downey, 1992: 405; Clark & Mah, 2001: 236.

NEOMORPHASTER FORCIPATUS VERRILL, 1894

Neomorphaster forcipatus Verrill, 1894: 269; 1895: 206; Clark & Downey, 1992: 405; Clark & Mah: 236.

Occurrence: S of Nantucket to Hudson Canyon, 1400–2000 m.

Material examined: Bahamas. NMNH E18509. South of Pinders Point, Grand Bahama Island. 26°17′N, 78°41′W. 513–715 m. Coll. 3.iii.1965. (1 dry spec.s $R = 9.1$, $r = 1.7$ cm).

DISCUSSION

CHARACTER ANALYSIS AND PALAEOZOIC AFFINITIES

Body morphology within the Zoroasteridae is broadly similar to the morphology observed in several Palaeozoic asteroids. Comparisons between the Zoroasteride and ancient asteroid taxa can be traced to Thomson (1873: 154), who observed similarity between *Zoroaster fulgens* and *Arthraster dixoni* (Cretaceous), which had previously been classified in the fossil Calliasterellidae. Downey (1970) observed a close similarity between *Doraster* and *Calliasterella*. Comparisons between zoroasterids and Palaeozoic taxa within a phylogenetic context have been addressed by Blake (1987, 1990), Blake & Elliott (2003) and Blake & Hagdorn (2003). Initially, the similarity of the imbricated skeleton provided the basis for initial comparisons (e.g. Downey, 1970) but has become more focused on homologous plate series and skeletal structures shared between taxa (e.g. Blake & Elliott, 2003; Blake & Hagdorn, 2003).

Marginal plates have been regarded as significant in studies of asteroid classification and evolution. For example, the Phanerozonia, a major group of asteroids including the Valvatida, Paxillosida and Notomyotida (Sladen, 1889), was defined largely on the basis of the enlarged marginal plate series present in those groups. The marginal plate series was traditionally defined as the single or double horizontal series defining the ambitus of the body in most asteroids (Spencer & Wright, 1966: U29; Clark & Downey, 1992: xxi). However, a formal criterion for recognizing marginal plate series was absent, until Blake (1978: 241) established marginal plates as the series of plates (usually two) along each side of the arm extending from either side of the terminal plate. This placed marginal plates within an ontogentic framework rather than a strictly locational one.

A single marginal plate series (Fig. 4E) was recognized in the Zoroasteridae (Blake, 1987, 1990), where previously it had been assumed that all living asteroids possessed two series of marginal plates. Scanning electron microscopy of marginals in post-settlement and juvenile specimens of *Zoroaster fulgens* (Sumida *et al*., 2001) shows no indication of a second marginal series in early ontogeny.

A single row of marginal plates is apparently present in the enigmatic *Xyloplax* (Infraclass Concentricycloidea, Mooi, Rowe & David, 1998; Mah, 2006a, b) and suggests affinity with crown-group Asteroidea. A single marginal plate series is present in several Palaeozoic asteroids and somasteroids (Blake & Elliott, 2003), suggesting that the character is plesiomorphic for the crown group. This is consistent with distribution of this character in the resultant phylogenetic tree. It is important to note that Palaeozoic asteroid faunas are poorly known. Preservational bias can be a significant factor when considering character distributions for phylogenetic estimation between post-Palaeozoic and Palaeozoic taxa.

Although zoroasterid genera have only a single plate series, they show significant variation. Marginal plates in *Myxoderma* and *Sagenaster* (node 28) are more cruciform-lobate (character 2.6, Fig. 2G) and are therefore similar to marginal plates in forcipulataceans with reticulated skeletons (e.g. *Asterias*, *Ampheraster*). Marginal plate shape in the clade containing *Zoroaster*, *Bythiolophus*, *Doraster* and *Cnemidaster* (node 37) are rounded to polygonal and similar in shape (Figs 3G, 4B, C, E) to those in Palaeozoic taxa, such as *Calliasterella* or *Neopalaeaster* (see Blake & Elliott, 2003). Several other characters, such as enlarged primary disc and carinal plates (e.g. characters 1.14, 1.16, Fig. 4A, G), a sharply demarcated disc (1.19, Fig. 4G), and the imbricated arrangement of the skeleton (character 1.1, Figs 3–6) also show apparent similarity between

the crown-group zoroasterids and Palaeozoic taxa (Blake & Elliott, 2003).

Disc and arm plates in Palaeozoic genera such as *Calliasterella* or the Triassic *Trichasteropsis* (Blake & Elliott, 2003; Blake & Hagdorn, 2003) are blockier and much more massive (characters 1.16, 1.26, 8.11) than those observed in adult imbricate zoroasterids. Juvenile imbricate zoroasterids also have large, blocky plates (Sumida *et al.*, 2001; Blake & Elliott, 2003) but juvenile asteroids often show disproportionately enlarged structures that become more proportional as ontogeny develops.

Distribution of characters among zoroasterid genera suggests that the outward appearance observed is only superficially similar to the appearance observed in Palaeozoic taxa. Two characters, the imbricate skeleton (1.1) and the single marginal series (2.1), are reconstructed as plesiomorphic to crown-group asteroids. Other characters showing apparent similarity are interpreted as non-homologous or potentially convergent. As indicated above, there are significant character differences between Palaeozoic and post-Palaeozoic asteroids.

Alternative tree topologies present other possible hypotheses for post-Palaeozoic diversification within the forcipulatacean lineage. *Calliasterella* was placed as the sister clade to the Zoroasteridae and to the imbricate zoroasterids (node 35-*Zoroaster*, etc.). Either tree topology added only one step to the total tree length. Similarly, a tree topology uniting all the taxa with reticulate skeletons, placing *Myxoderma* + *Sagenaster* as the sister group to *Ampheraster* + *Trichasteropsis* on a monophyletic clade leading to a paraphyletic Zoroasteridae adds only one step more to the tree length. The relatively low Bremer and bootstrap values supporting zoroasterid monophyly would not be inconsistent with these tree topologies. The relatively low support values might also be attributable to plesiomorphy of characters in the Zoroasteridae, similar to the character distribution of *Xyloplax* (Mah, 2006). A paraphyletic Zoroasteridae would be consistent with affinities to basal post-Palaeozoic asteroids.

Mah (2000) placed *Neomorphaster* as the sister branch to the Zoroasteridae. *Neomorphaster* was also supported by this analysis as the sister group to the Zoroasteridae. However, *Neomorphaster* can be joined to node 38 at the base of the clade containing *Trichasteropsis* and *Ampheraster*, or as the sister clade to *Calliasterella* with the addition of one extra step. Adding *Neomorphaster* as the sister branch to *Ampheraster* adds five extra steps ($N = 142$). Although putatively basal to the Zoroasteridae and other forcipulates, the phylogenetic position of *Neomorphaster* remains unclear pending further research.

BATHYMETRIC SHIFTS AND THE SIGNFICANCE OF POST-PALAEOZOIC FOSSILS

If bathymetric ranges are mapped onto the phylogenetic tree (Fig. 7), a significant shift is observed between the clade containing those zoroasterids with a reticulate skeleton (*Myxoderma*, *Sagenaster*, node 26) and those zoroasterids with an imbricate skeleton (*Zoroaster*, *Cnemidaster*, *Doraster*, *Bythiolophus*). Clades with a delicate reticulate skeleton inhabiting shallow-water environments are basal relative to the more derived taxa with a more heavily armored imbricate skeleton in deeper, abyssal environments. The morphological shift between the reticulate and the imbricate zoroasterids is similar to the pattern observed in the Brisingida (Mah, 1998b). Reticulate brisingidans, such as *Odinella* and *Brisingaster*, occur within a shallower depth range relative to the more heavily armored members of the Freyellidae, which occupy almost exclusively abyssal habitats.

Bathymetric ranges (Fig. 7) for the reticulate clade are 91–2904 m, whereas the bathymetric range for the imbricate clade is 90–4810 m. Reticulate and imbricate zoroasterids display overlapping bathymetric ranges. However, for asteroid species recorded from the Porcupine Seabight, Howell *et al.* (2002) observed that there is a much narrower centre of distribution in which abundance of adult individuals is highest, despite much wider total adult depth ranges. Alton (1966: 1688) observed the peak abundance of *Myxoderma platyacanthum* and *M. sacculatum* between 397–878 m and 1372–1555 m, respectively. Peak abundance in *Sagenaster* (= *Zoroaster*) *evermanni* was observed between 502 and 1490 m, whereas abundance in the imbricate *Zoroaster ophiurus* was only observed below 1865 m. Howell *et al.* (2002) observed peak abundance for *Zoroaster fulgens* and *Z. longicauda* (considered by Clark & Downey, 1992 as a synonym of *Z. fulgens*) at 1450–1550 m and 3650–3750 m, respectively. The range of occurrence in reticulate zoroasterids is shallower than that observed in the imbricate zoroasterids.

Incomplete preservation of features in the Jurassic *Terminaster cancriformis* (Quenstedt) precluded its inclusion in the matrix. However, characters figured by Hess (1974, 1986) suggested placement on the phylogenetic tree. Hess (1986) figures several prominent enlarged primary spines in *Terminaster* and compares the enlarged terminal plates with those in *Myxoderma sacculatum*. Enlarged terminals occur in both juvenile zoroasterids and across several phylogenetically disparate zoroasterid genera (e.g. *Myxoderma* and *Zoroaster*). The primary spines apparently occur on nearly all arm and disc plates, a feature present in *Myxoderma* and *Sagenaster*. However, *Terminaster* possesses only polygonal to slightly lobate
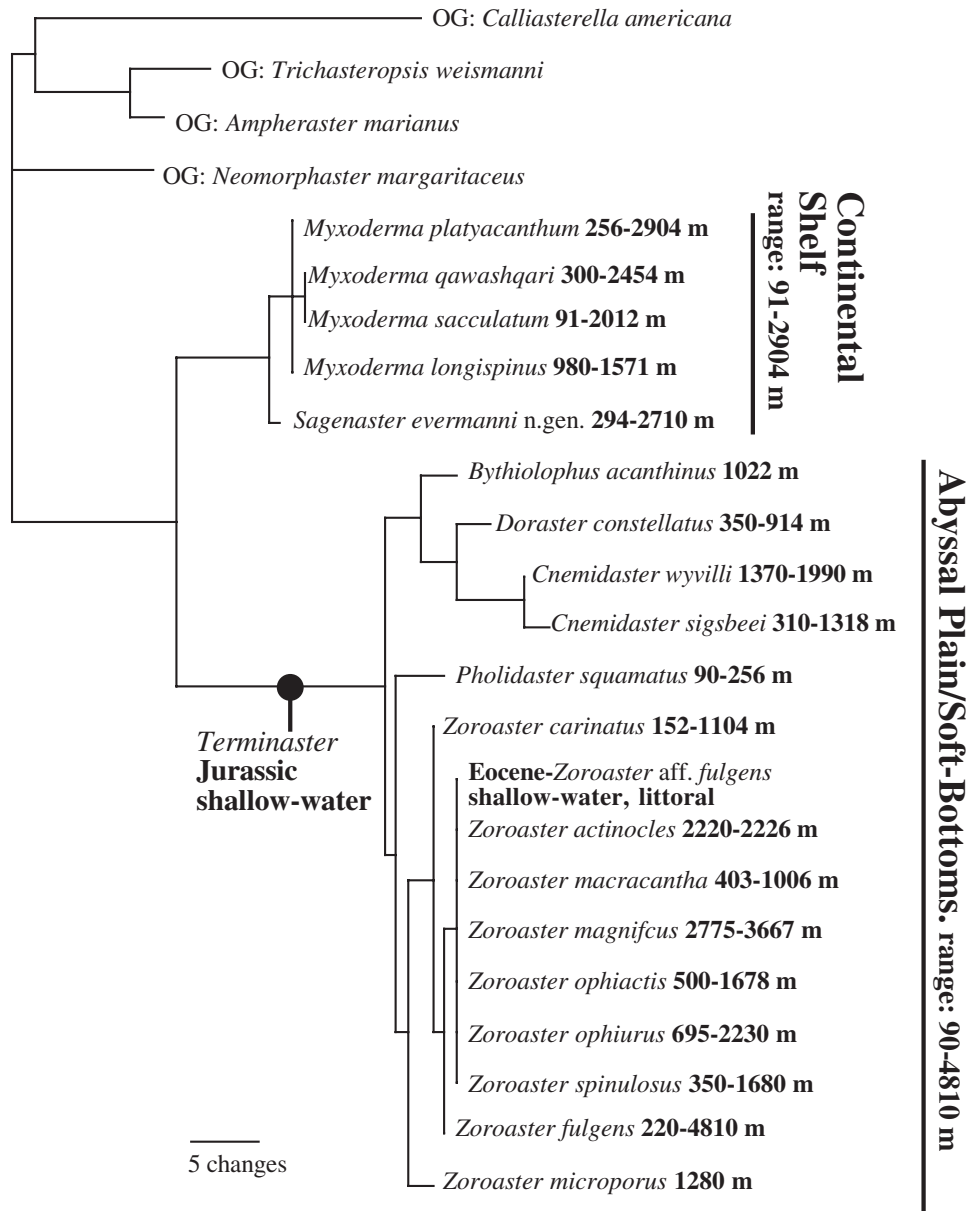
Figure 7. Phylogram of the Zoroasteridae with bathymetric ranges mapped for each taxon. Note taxonomic revisions applied to included taxa (tree and node positions parallel to those in Fig. 1).

plates, which are present only in the 'imbricate' zoroasterids (node 37). The absence of enlarged disc plates and relatively small disc size do not support affinities with the taxa included on node 29 (*Bythiolophus*, *Doraster*, *Cnemidaster*). This suggests a position basal to node 35 or close to node 34 near the base of *Pholidaster* + *Zoroaster*. *Terminaster* was collected from marls, which have been interpreted as shallow (< 100 m, Hallam, 1998: 684), suggesting a shift between shallow- to deep-water environments (> 100 m) after the Jurassic.

Onshore–offshore trends within individual zoroasterid lineages were less well defined. Several taxa displayed shallower bathymetric occurrence relative to their sister taxa (Fig. 7), but patterns suggesting diversification of multiple taxa into either shallow- or deep-sea environments was unclear. For example, *Doraster* occurs in a shallower bathymetric range (350–640 m) relative to the deeper-water *Cnemidaster* (including synonym *Mammaster*) (310–1990 m). However, *Bythiolophus*, the sister clade to the *Doraster* + *Cnemdiaster* clade, occurs in a much deeper bathymet-

ric range (450–1006 m) relative to *Doraster*. *Pholi-daster* is supported as the sister taxon to *Zoroaster*, and occurs in relatively shallow depths (90–256 m). Although *Zoroaster carinatus* occurs in relatively shallow depths (152–1104 m), *Z. microporus*, the sister taxon to the remaining *Zoroaster* species, does not (1280 m).

Also included in the matrix was the Eocene *Z.* aff. *fulgens* described by Blake & Zinsmeister (1979), which occurred in littoral, shallow-water sediments. Although identified as *Z. fulgens*, assessment of its species affinities was considered tentative (Blake & Zinsmeister, 1979). All modern *Zoroaster*, including *Z. fulgens*, occupy deep-water environments (≥ 200–4000 m) indicating a bathymetric shift between the Eocene *Zoroaster* from shallow-water sediments at Seymour Island and those *Zoroaster* living today in bathyal to abyssal depths. Deep-sea taxa are often documented from shallower depths (e.g. Pearse & Lockhart, 2004) in the Southern Ocean as a result of the cold-water masses extending to shallow shelf regions. However, schlerochronology of the bivalve *Cucullaea raea*, which co-occurred with *Z.* aff. *fulgens* at the La Meseta formation (Buick & Ivany, 2004), and stable istope proxies (Dutton & Lohmann, 2002) support warmer, more temperate, waters in the Eocene relative to those at Seymour Island today. Evidence from these studies is consistent with palaeoenvironmental changes in Antarctica (reviewed in Dingle & Lavelle, 2000) associated with the development of the circum-Antarctic current (Kennett, 1977) following the separation of eastern Antarctica from Australia (summarized in Clark & Crame, 1989), which resulted in glaciation and cooling events at the Eocene/Oligocene boundary (Zachos *et al.*, 2001). Although the phylogenetic position of the Eocene species on node 30 is equivocal, its derived placement suggests a possibly terminal offshore–onshore migration. The phylogenetic position would be consistent with a localized extinction of *Zoroaster* in Antarctica. Benthic taxa have been considered particularly vulnerable to temperature change (Peck, 2005). With the exceptions of the Eocene *Z. fulgens* and a listing of a juvenile specimen of *Zoroaster tenuis* Sladen from between Gough and Bouvet Islands (on the periphery of the South Atlantic) (Koehler, 1909), zoroasterids have not been recorded from the Southern Ocean (A. M. Clark, 1962).

Placement of the Eocene *Z. fulgens* (Fig. 6E) as the sister taxon to the extant *Z. fulgens* adds a single step, whereas adding it to the base of node 31 or at the base of *Z. carinatus* adds two steps. Moving the Eocene *Z. fulgens* to the base of *Z. microporus* or any further away from node 32 adds at least five steps to the total. Thus, it seems that a more basal position for the Eocene *Z. fulgens* is plausible. Such a position would be consistent with scenarios outlining Antarctica as a 'diversity pump' for distribution of species into the deep-water environments of the Atlantic, Indian and Pacific Oceans (Gage, 2004). Blake & Zinsmeister (1979, 1988) and Blake & Aronson (1998) described several asteroid taxa from Seymour Island, Antarctica, recorded from shallow-water sediments that today occupy continental shelf (~20–180) or deep-water (> 200 m) environments, including *Ctenophoraster*, *Tessellaster*, *Paragonaster* and *Sclerasterias*.

TIMING OF EVENTS, PHYSIOGRAPHY AND HISTORICAL BIOGEOGRAPHY

The two fossil taxa considered in the tree constrain phylogenetic events within the Zoroasteridae. Timing dictated for these constraints was compared with shifting Mesozoic and Cenozoic coastlines (Smith, Smith & Funnell, 1994), including significant geological events such as the opening of the Atlantic Ocean. Fossil occurrence and geological events are broadly consistent with the phylogenetic tree.

Global occurence patterns suggest a hypothesis of Pacific and Indian ocean taxa colonizing the younger Atlantic. An identical pattern also was observed in the Goniasteridae (Halpern, 1970; Mah, 2006a). The phylogeny is consistent with a shift between reticulate zoroasterids (*Myxoderma* and *Sagenaster*) and imbricate zoroasterids (e.g. *Zoroaster*, *Cnemidaster*) from the continental shelf to slope and abyssal plain environments.

In conjunction with onshore–offshore patterns described above, the phylogeny (Fig. 7) supports a physiographic shift between those zoroasterids with reticulated skeletons (*Myxoderma* and *Sagenaster*) living almost exclusively on the continental shelf or on continental slopes vs. the imbricate taxa (e.g. *Zoroaster*), which are found primarily on soft-bottom abyssal plains.

Myxoderma forms a species complex along shelf or near-shelf regions along the perimeter of the Northeast–Central Pacific; from the Okhotsk Sea and the Aleutians along the North and South American coasts extending south to Chile. This is consistent with Aziz & Jangoux (1984: 193) who stated that *Myxoderma* composed a species complex based on *M. platyacanthum*, *M. sacculatum* and *M. acutibranchia*. *Myxoderma acutibrachia* Aziz & Jangoux, 1984 extends the range of the complex to Macassar Straight (between Borneo and Sulawesi). *Myxoderma* has not been recorded from the Indian Ocean, the Hawaiian Islands, Japan or off mainland Asia. *Sagenaster*, the sister taxon to *Myxoderma*, also occurs on shelf or near-shelf regions along the Northeast Pacific coast from Alaska to Mexico. Reticulate zoroasterids have not been recorded from the Atlantic.

Taxa within the imbricate zoroasterid clade show diversification into the Pacific, Indian and Atlantic Ocean basins and occur primarily on muddy bottoms on slope or near-slope regions and abyssal plains and are not commonly recorded from the continental shelf. *Bythiolophus* has been collected only in the central Pacific. *Doraster* is known only from the Atlantic. *Pholidaster* has only been recorded from the Philippines and off the coast of Western Australia (Indian Ocean). *Cnemidaster* and *Zoroaster* occur in the Atlantic, Pacific and Indian oceans. The widespread geographical distribution and the relatively few morphological differences between species are consistent with other deep-sea asteroids, such as the Porcellanasteridae, a cosmopolitan group in abyssal depths (Madsen, 1961). Although *Myxoderma* and *Zoroaster* are recorded from the Aleutian Islands and in the Gulf of Alaska, none is recorded from the Arctic Ocean.

Body fossils of *Terminaster* (Hess, 1974, 1986) are interpreted as morphologically intermediate between reticulate and imbricate zoroasterids. If placed at node 34 (Fig. 7) it suggests a minimum age for the node of 155–160 Ma (Callovian–Oxfordian). At this stage during the Jurassic, the South Atlantic had not yet opened and several continents in the Southern Hemisphere, including Antarctica, Australia, South America and Africa, were still conjoined (Smith *et al*., 1995). The presence of *Doraster* in the formative northern region of the Atlantic Ocean is not inconsistent with the age of the imbricate zoroasterid lineage indicated above.

Cnemidaster was the only zoroasterid studied which displays morphological continuity across the Panamanian Seaway. Although full seaway closure has been estimated at 3.1–3.5 Ma (early Pliocene, Duque-Caro, 1990), exchange between the Indo-Pacific and Atlantic populations of *Cnemdiaster* probably occurred earlier, with deep-water connections between the Pacific and the Atlantic ending in the early to middle Miocene (16.1–15.1 Ma) and Caribbean faunal affinities on the Pacific side of South America ending in the middle Miocene (12.9–11.8 Ma, Duque-Caro, 1990). Support in the phylogeny for *Doraster* as *Cnemidaster*'s sister taxon suggests diversification into the Indo-Pacific region from the tropical Atlantic.

ACKNOWLEDGEMENTS

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APPENDIX 1

LIST OF CHARACTERS

1. Abactinal surface characters

1.1. *Abactinal plate arrangement*. 0, reticulate (Fig. 2B, E–G); 1, imbricate (Figs 3A, E, 4A, B, 5A, E, etc.); 2, highly imbricate (only in *Neomorphaster*).

1.2. *Disc plates*, *strongly lobate*. 0, absent; 1, present (Fig. 2E–G).

1.3. *Disc plates*, *weakly lobate*. 0, absent; 1, present (Figs 3A, E, 4A, B, 5A, E, etc.).

1.4. *Primary abactinal arm spine distribution*. 0, absent; 1, present on all plates (Fig. 2E, F); 2, few spines present; 3, present, but irregular.

1.5. *Secondary abactinal arm spine distribution*. 0, absent; 1, distributed evenly (Fig. 2E, F); 2, distributed densely (Fig. 3B, C).

1.6. *Arm plates cruciform*. 0, not cruciform lobate; 2, strongly cruciform lobate (Fig. 2E–G).

1.7. *Arm plates polylobate*. 0, plates not poly lobate; 1, plates polylobate (Figs 3E, 4A–G, 6 A, D, F).

1.8. *Adradial plates*. 0, absent; 1, present (Fig. 4A–C).

1.9. *Carinal plates*, *peripheral*. 0, absent; 1, present (Fig. 5A–D).

1.10. *Carinal plates*, *quadrate*. 0, absent; 1, present (Fig. 5A–E).

1.11. *Carinal plates*, *strongly lobate*. 0, absent; 1, present (Figs 2B, E–G).

1.12. *Carinal plates*, *weakly lobate*. 0, absent; 1, present (Fig. 4A, C, D, G).

1.13. *Carinal series*, *low ridged*. 0, absent; 1, present (Fig. 2A, E, F).

1.14. *Carinal series*, *ridged*. 0, absent; 1, present (Fig. 6B, C, D, G).

1.15. *Carinal series*, *level*. 0, absent; 1, present (Figs 4A, C, E, 5E, F).

1.16. *Circlet disc plate size*. 0, similar to other disc plates (Fig. 2B, E); 1, enlarged (Figs 3A, E, 5A, E, 6D, F); 2, enlarged and swollen (Fig. 4C, G); 3, robust, blocky (only in *Calliasterella*).

1.17. *Compared primary disc-arm plate size*. 0, similar (Fig. 2B, E–G); 1, dissimilar (Fig. 4C, G).

1.18. *Primary carinal spines*. 0, absent; 1, present (Fig. 6C).

1.19. *Arm-disc continuity*. 0, continuous (Figs 2E, 5A); 1, discontinuous (Fig. 4C, G).

1.20. *Centrodorsal plate*, *strongly lobate*. 0, absent; 1, present (Fig. 2E–G).

1.21. *Centrodorsal plate*, *weakly lobate*. 0, absent; 1, present (Fig. 6D, F, G).

1.22. *Primary disc plates*, *prominence*. 0, continuous with skeleton (Fig. 2B, E–G); 1, overlapping other plates (Figs 3A, E, 4A, B, 5A, E)

1.23. *Number of spine types*. 0, one spine type; 1, two spine types.

1.24. *Spine tip morphology*. 0, granular; 1, blunt; 2, sharp (Figs 2E–F, 6C).

1.25. *Secondary spine morphology*. 0, straight; 1, recurved.

1.26. *Abactinal plate morphology*. 0, blocky-robust; 1, cruciform-reticulate; 2, laterally flattened (only in *Neomorphaster*); 3, dorsoventrally flattened (Fig. 2B, E–G).

1.27. *Carinal plates thickened*. 0, absent; 1, present (only in *Neomorphaster*).

2. Marginal plate characters

2.1. *Number of marginal plate series*. 0, single series (Fig. 4E); 1, two series.

2.2. *Marginal plate robustness*. 0, phanerozonate; 1, cryptozonate.

2.3. *Marginal plate size distribution*. 0, sizes sequential (Fig. 3C); 1, sizes alternating (Fig. 3B).

2.4. *Primary spine on marginal plate*. 0, absent; 1, present (Figs 2E–F, 6C).

2.5. *Marginal plate, weakly lobate*. 0, absent; 1, present.

2.6. *Marginal plate, strongly lobate*. 0, absent; 1, present (Fig. 2F).

2.7. *Marginal plates thickened*. 0, absent; 1, present (only in *Neomorphaster*).

3. Actinal surface characters

3.1. *Actinal plates*. 0, absent; 1, present.

3.2. *Actinal plate orientation*. 0, absent; 1, facing actinally; 2, facing actinolaterally

3.3. *ctinolateral spines*, enlarged. 0, absent; 1, present (Fig. 3D, G).

3.4. *Actinolateral plate arrangement*. 0, reticulate; 1, imbricate; 2, tightly imbricate.

3.5. *Actinolateral plate density*. 0, evenly distributed; 1, densely distributed, esp. near adambulacrals; 2, absent.

3.6. *Secondary spination*. 0, evenly distributed; 1, closely distributed; 2, absent.

3.7. *ctinolateral plates quadrate*. 0, absent; 1, present; 2, actinal plates absent.

3.8. *Actinolateral plates weakly lobate*. 0, absent; 1, present; 2, actinal plates absent.

3.9. *Actinolateral plates polygonal*. 0, absent; 1, present (Fig. 3G); 2, actinal plates absent.

3.10. *Actinolaterals strongly lobate*. 0, absent; 1, present; 2, actinal plates absent.

3.11. *Actinolateral plates in transverse series*. 0, absent; 1, present; 2, actinal plates absent.

3.12. *Actinolateral plates thickened*. 0, absent; 1, present; 2, actinal plates absent.

4. Furrow and adambulacral region characters

4.1. *Adambulacral plates carinate*. 0, weakly carinate; 1, strongly carinate (Fig. 4F); 2, non-carinate.

4.2. *Adambulacral plates alternately carinate*. 0, not alternating; 1, alternating (Fig. 4F).

4.3. *Adambulacrals overlap*. 0, proximally; 1, distally.

4.4. *Adambulacral spine series*. 0, not in array-like formation; 1, array-like formation.

5. Soft tissue characters

5.1. *Pulpy membranous covering*. 0, absent; 1, present.

5.2. *Smooth membranous covering*. 0, absent; 1, present (Fig. 4A, B).

6. Body morphology characters

6.1. *Disc thickness*. 0, moderately thickened; 1, heavily thickened (Fig. 4B, C).

6.2. *Number of tube foot rows*. 0, two; 1, four (proximally).

6.3. *Oral region depressed*. 0, level with oral surface; 1, oral region deeply sunken (Fig. 3F, 4F).

7. Pedicellariae characters

7.1. *Pedicellariae types*. 0, absent; 1, straight and crossed; 2, straight only (Figs 3F, 4F).

7.2. *Pedicellariae distribution*. 0, absent; 1, body surface and adambulacral furrow.

7.3. *Dense oral ring of pedicellariae*. 0, absent; 1, present (Fig. 3F).

8. Internal skeletal characters

8.1. *Oral ring fused*. 0, not fused; 1, fused.

8.2. *Axillary plate*. 0, absent; 1, present.

8.3. *Body ossicle size and number*. 0, large and few; 1, small and numerous.

8.4. *Ambulacral pores deflected*. 0, proximally deflected for pore; 1, podial pore deflects both sides.

8.5. *Adoral carina*. 0, absent; 1, weakly expressed; 2, strongly expressed.

8.6. *Superambulacral plates*. 0, absent; 1, present (Fig. 2C, D).

8.7. *Superambulacral reduction*. 0, not reduced (Fig. 2C, D); 1, reduced; 2, absent.

8.8. *Internal buttress*. 0, absent (Fig. 6H); 1, present (Fig. 2D).

8.9. *Papular rows*. 0, reticulate; 1, ordered rows (Fig. 6A–D).

8.10. *Papular fields*. 0, enlarged field (Fig. 2B, E–G); 1, single pore (Fig. 6B, C).

8.11. *Blocky skeleton*. 0, blocky, robust; 1, not blocky, robust.

8.12. *Ambulacral shape*. 0, compressed; 1, squarish-blocky (Fig. 2C, D); 2, broad rectangular.

APPENDIX 2

DATA MATRIX

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                    1111111111222222222233333333334444444444555555555566666666667
Taxon               1234567890123456789012345678901234567890123456789012345678901234567890
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Taxon	
Calliasterella	100?000000000003001001???00000000000012?2222222000??10000?000000201?02
Trichasteropsi	000?1101001010000001000000?10000001011000?0101000110??01000?111110200010
Ampheraster	0101010100101000000100010101101010110002110000011000010110111110200010
Neomorphaster	2001001100000100000100010211100101110202100001011000011110111120201110
M. platyacanthu	0101110100101000010100121300101010121000110000111110011210111121011011
M. sacculatum	0101110100101000010100121300101010121010110000111110011210111121011011
Z. evermanni	0101110100101000010100120300101010121000110000111100011210111121001011
Z. longispinu	0101110100101000010100121300101010121000110000111110011210111121011011
D. qawashqari	0101110100101000010100121300101010121010110000111??011210111121011011
B. acanthinus	1011201000010011000101112130011010012111100011011110001210111121011111
D. constellatus	1013201100010101000011121300100100121111000100111100111211111121011111
C. wyvillei	1012001100010012101021121300100100121111000100111101111211111121011111
M. sigsbeii	1012001000000012101021121300100100121111000100111101111211111121011111
P. squamatus	1010201100100110000111213001001001211100101011100011000111121001111
Z. carinatus	1013201100010101000011121300100100121111001010111000112101111211101111
Z. actinocles	1013201100010101010011121300101100121111001010111000112101111211101111
Z. fulgens	1013201100010101000011121300101100121111001010111000112101111211101111
Z. macracantha	1013201100010101010011121300101100121111001010111000112101111211101111
Z. magnificus	1013201100010101010011121300101100121111001010111000112101111211101111
Z. microporus	1013201101000011000011121300100100121111001010111000012101111211101111
Z. ophiactis	1013201100010101010011121300101100121111001010111000012101111211101111
Z. ophiurus	1013201100010101010011121300101100121111001010111000112101111211101111
Z. spinulosus	1013201100010101010011121300101100121111001010111000112101111211101111
Z. fulgens-EOC	1013201100010101010011121300101100121111001010111000112101111211101111

APPENDIX 3

KEY TO THE ZOROASTERIDAE

(0a) Two series or marginal plates with both series continuing from interradius to terminal plate. Primary spines present. Secondary spines absent. Adambulacral plates weakly carinate (i.e. carinal projection close to surface of the adambulacral plate-not projecting furrow), not alternating. Superambulacrals absent. Crossed and straight pedicellariae present. Actinolateral spines not enlarged. Abactinal plates reticulate, ordered or unordered. Discs size variable. Arm number five or more. ....**Asteriadina**

(0b) One series of marginal plates. Adradial plate series discontinues distally before reaching terminal plate. Primary and secondary spines present. Adambulacral plates strongly carinate (i.e. carinal projection markedly above surface of adambulacral plate, projecting into furrow), alternately in large (adult) specimens, completely carinate (but slightly lower, more angular) in smaller specimens. Superambulacrals present in all, but reduced distally in *Zoroaster*. Enlarged actinolateral spines. Straight pedicellariae present in all but *Pholidaster*. Plates in well-ordered longitudinal, transverse rows. Discs small, arms elongate, tapering. Arm number always five. ....**Zorocallina (Zoroasteridae)** 1

(1a) Squamulate spines (Fig. 5A, C), pedicellariae absent. ....*Pholidaster* (Fig. 5A–C)

(1b) Spines not squamulate. Straight pedicellariae present 2

(2a) Skeleton reticulate (Fig. 2B, E–G). Primary spines on all plates (Fig. 2E–F). Plates quadrate to cruciform-like (Fig. 2G). Abactinal, actinolateral plates all similar or identical in form. 3

(2b) Skeleton imbricate. Primary spines absent from all plates, but present on primary series (carinals, marginals, etc.). Skeleton well developed. Actinolateral plate series differentiated from adradial, carinal series. 4

(3a) Buttress present (Fig. 2D). .... *Myxoderma* (Fig. 2A, B)

(3b) Buttress absent (Fig. 6H). .... *Sagenaster* (Fig. 2E, F)

(4a) Buttress absent (Fig. 6H). Disc small, arms slender, not thickened proximally, elongate. ....*Zoroaster* (Figs 5E, 6)

(4b) Buttress present (Fig. 2D). Disc thickened, enlarged, arms thickened proximally. 5

(5a) Marginal plate series alternating in size. Sharp spines on adradials. ....*Bythiolophus* (Fig. 3A)

(5b) Marginal plates all of one size. Adradials, if present, never with enlarged spines. 6

(6a) Disc thickened, but plates not swollen. Plates stellate (Fig. 3E). Disc surface continuous with plane of arms (Fig. 3G). Fine spination covers body surface (sometimes denuded) (Fig. 3G). Adradials present in larger specimens, residual in smaller ones. Distinct ring of pedicellariae in mouth (Fig. 3F). ....*Doraster* (Fig. 3E, G)

(6b) Disc plates swollen, polygonal to rounded, enlarged, rising above plane of arms, sharply set off from arms. Abactinal spines few to absent. Thick layer of skin overlies surface...........*Cnemidaster* (*Mammaster* is a synonym) (Fig. 4)