Systematics, phylogeny and historical biogeography of the *Pentagonaster* clade (Asteroidea:Valvatida:Goniasteridae)

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Abstract. Morphology-based phylogenetic hypotheses developed for living and fossil goniasterid asteroids have provided several unique opportunities to study bathymetric and biogeographic shifts for an ecologically important group of prominent, megafaunal invertebrates. A cladistic analysis of 18 ingroup taxa employing 65 morphological characters resulted in a single most parsimonious tree. The tree supports assignment of the Atlantic *Tosia parva* (Perrier, 1881) and the Pacific *Tosia queenslandensis* Livingstone, 1932 to new, separate genera. The phylogenetic tree supports offshore to onshore bathymetric shifts between basal and derived taxa. The phylogeny is also consistent with historical events surrounding the separation of Antarctica from Australia and South Africa. *Buterminaster* Blake & Zinsmeister, 1988 from the Eocene La Meseta Formation, Antarctic Peninsula, was included in the phylogenetic analysis and is now supported as the only fossil species in the genus *Pentagonaster* Gray, 1840. *Pentagonaster stibarus* H. L. Clark, 1914 is separated from synonymy with *P. dubeni* Gray, 1847 and resurrected as a valid species. The new genus, *Akelbaster*, gen. nov., shows unusual new structures that resemble cribiform organs, although their function has not been determined. One specific ingroup lineage, including *Tosia* and *Pentagonaster*, attains a much larger adult size than those of its sister-taxa, suggesting that Cope's rule may apply to asteroids within this clade. *Pentagonaster* and related genera are revised. Descriptions of four new genera and three new species are presented, including: *Akelbaster novaecaledoniae*, gen. nov., sp. nov., *Ryukuaster onnae*, gen. nov., sp. nov., *Eknomiaster beccae*, sp. nov., *Pawsonaster parvus*, gen. nov., comb. nov. and *Anchitosia queenslandensis*, gen. nov., comb. nov.

Introduction

Starfishes (phylum Echinodermata, class Asteroidea) are an ecologically important group of marine invertebrates (e.g. Birkeland 1974) that display close relationship between their environmental and biogeographic distributions and their phylogenetic history (Blake 1983, 1987, 1990). Studies of phylogenetic events in modern, post-Paleozoic asteroids within the context of geological tectonic and macroevolutionary events have been based primarily on the interpretation and description of fossils (e.g. Blake and Zinsmeister 1988; Blake and Aronson 1998; Villier and Kutscher 1998; Blake and Jagt 2005) or from phylogenetic analyses of species or population-level DNA sequence data (e.g. Waters and Roy 2003*a*, 2003*b*). Relatively few studies (e.g. Mah 2005*a*, 2005*b*, 2006) have addressed genus and family-level phylogenetic history and events inferred from living asteroid taxa within a historical tectonic context. Studies such as these provide a significant perspective in understanding their present-day distributions.

    Pentagonaster Gray, 1840 and *Tosia* Gray, 1840 comprise a complex of closely related species (Ludwig 1912; A. M. Clark 1953; Fell 1962*b*) occurring primarily in subtropical and temperate Australia and New Zealand with related taxa in South Africa and in the tropical north, central and south Pacific. All occur on the continental shelf in littoral to deeper-water habitats. One species, *Tosia parva* Halpern, 1969, occurs on the continental shelf in the tropical Atlantic.

    Pentagonaster and *Tosia*, described by Gray (1840), were among the first genera described within the Asteroidea. The

formative taxonomic history of *Pentagonaster* and *Tosia* is complex primarily owing to the assignment of a broad array of goniasterid (and other valvatidan) species with similar pentagonal appearance to one or the other genus (Perrier 1875; Sladen 1889), broadening taxon boundaries beyond the original concepts. These difficulties were further complicated by the establishment of the polyphyletic and redundant *Astrogonium* Müller & Troschel, 1842, which was subsequently dismantled and synonymised by Verrill (1899) and Fisher (1911), who later worked to more narrowly define the taxon concepts for *Tosia* and *Pentagonaster*. Ludwig (1912) and later Livingstone (1932) further documented character variation within *Tosia* and helped to further clarify species boundaries. Marsh (1991) synonymised *T. nobilis* Ludwig, 1912 with *T. australis* Gray, 1840 leaving four nominal species, including: *T. australis*; *T. magnifica* Ludwig, 1912; *T. queenslandensis* Livingstone, 1932 and *T. parva*. She synonymised all Australian species of *Pentagonaster* with *P. dubeni* Gray, 1847. A. M. Clark (1993) presented a checklist of all species included within *Pentagonaster*, *Toraster* A. M. Clark, 1952 and *Tosia*. Based on statements by Fisher (1911), *Tosia tuberculata* (Gray, 1847) was established in the new monotypic genus, *Toraster* by A.M. Clark (1952). *Pentagonaster* and *Tosia* were subsequently reviewed and revised by A. M. Clark (1953). Halpern (1969) re-examined the syntypes of the tropical Atlantic *Pentagonaster parvus* Perrier, 1881 and assigned it to the genus *Tosia*.

Biology

Although *Tosia* and *Pentagonaster* are familiar components of the shallow-water fauna of Australia and New Zealand, little is known about their biology and ecology. *Tosia* and *Pentagonaster* apparently devour encrusting invertebrates and/or organic materials. Keough and Butler (1979) and Shepherd (1968) reported *Tosia australis* as feeding primarily on sessile invertebrates, including sponges, bryozoans and compound ascidians. *Tosia magnifica* has been reported feeding on small surface-living microbes (Edgar 1997). Based on field observations, Shepherd (1968: 408) reported that *Pentagonaster dubeni* A. M. Clark, 1933 feeds on encrusting invertebrates, such as sponges, bryozoans and ascidians. No observations on feeding or food items have been reported for *Pentagonaster pulchellus* Gray, 1840, but Crump (1968) reported that *P. pulchellus* elicits no escape reaction from the gastropod *Struthiolaria papulosa gigas* in contrast to the reaction elicited by predatory asteriids, such as *Astrostole* or *Coscinasterias*.

Knowledge of other aspects of the biology of these taxa is scant. Johnson (1973) reported the respiration rate of *P. pulchellus* compared with other New Zealand echinoderms. Brooding was reported in *Tosia australis* by Coleman (1994) and O'Loughlin (1991), making this the sole occurrence of brooding observed within the Goniasteridae. *Tosia magnifica* was dredged from muddy substrates at Port Arlington in southeastern Australia (Currie and Parry 1999).

The biology of the tropical Atlantic *Tosia parva* is also poorly understood. Gonadal cycle, gametogenesis and energy allocation was described by McClintock *et al.* (1995). *Tosia parva* was among several echinoderm taxa that demonstrated significant chemical defences against different predators, but especially against different species of fish (Bryan *et al.* 1997). *Tosia parva* is also reported as one of the dominant asteroid species collected in the northern Gulf of Mexico (Hopkins *et al.* 1991).

Objectives

This study builds on data collected during a phylogenetic revision of the Goniasteridae by Mah (2005*b*) that supported a monophyletic relationship between *Eknomiaster* H. E. S. Clark, 2001, *Pentagonaster*, *Toraster*, *Tosia* and several recently collected specimens that have been putatively identified as new genera and species. Interrelationships among the putative genera, including the Antarctic Eocene *Buterminaster*, were tested and used to reconstruct phylogeny for the clade. Based on this phylogeny, taxonomic revisions and hypotheses for historical biogeography were generated. A comprehensive checklist and diagnostic key to genera and species is also presented.

Materials and methods

Materials

A majority of the specimens examined are housed in the collections of the Division of Invertebrate Zoology (NMNH) and the Department of Paleobiology (NMNH-P) at the National Museum of Natural History in Washington, DC, USA. Additional specimens were obtained from: the California Academy of Sciences (CASIZ) in San Francisco, CA, USA; the Los Angeles County Museum (LACM) in Los Angeles, CA, USA; Museum Victoria (MV) in Melbourne, Australia; and the Muséum national d'Histoire naturelle (MNHN) in Paris, France. Wet and dry specimens were examined across as broad a size and geographic range as possible.

Methods

Character-state data were derived from external and internal skeletal features of the included specimens. New data were collected in addition to and refined from the preliminary data obtained from Mah (2005*b*). A comprehensive list of genera and species is included below and appears in the phylogenetic order outlined in Fig. 10.

Ingroup taxa included all nominal species of *Tosia* and *Pentagonaster* sensu Clark (1953) and the Eocene *Buterminaster* Blake & Zinsmeister, 1988, in addition to specimens supported as sister-taxa by a morphology-based phylogenetic analysis of the Goniasteridae undertaken by Mah (2005*b*). Ingroup taxa as supported by Mah (2005*a*) also included *Toraster* from South Africa, *Eknomiaster* from New Zealand and new genera and species from New Caledonia and Okinawa, Japan.

Four accepted species of *Tosia* were included to test the boundaries of the genus relative to *Pentagonaster*, which showed potential taxonomic overlap. These species were summarised by A. M. Clark (1953, 1993) and represented distinct morphotypes with apparent stability in the taxonomic literature. The inclusion of *Tosia australis* var. *astorlogorum* Müller & Troschel, 1842 and *Tosia nobilis* additionally provided a test for the synonymy of these morphotypes with *T. australis* by Marsh (1991). However, an intensive population-level study of the *Tosia* species-complex across its full range was beyond the scope of this study, which was aimed primarily at establishing lineages within the putative 'pentagonasterine' clade. Treatment and inclusion of the three nominal *Pentagonaster* species in the matrix followed a similar criterion. Morphological variation of *Pentagonaster pulchellus* was studied by Clark and McKnight (2001). The wide range of reported morphological variation suggests that population-level studies would further clarify relationships with *Tosia* and other pentagonasterines.

The Indo-Pacific *Lithosoma* Fisher, 1911 and *Pontioceramus* Fisher, 1911, and the tropical Atlantic *Apollonaster* Halpern, 1970 were utilised as outgroup taxa based on the phylogenetic tree in Mah (2005*b*). The former two genera occur as members of the sister-group to the ingroup lineage. *Apollonaster* occurs more distantly from the ingroup.

Morphological terms and definitions follow those of Clark and Downey (1992). All numerical values for R (distance from centre of disk to armtip) and r (distance from centre of disk to interradius) are given in centimetres.

The final data matrix (Appendix 1) included 18 taxa and 65 morphological characters, which were entered into MacClade 3.08a and analysed using PAUP (Phylogenetic Analysis Using Parsimony) 4.0b10 (Swofford 2003). Character states were run as unordered and unweighted using ACCTRAN optimisation.

Results

Phylogenetic results

A branch-and-bound search resulted in a single most parsimonious tree with a resultant tree length of 145 steps, a consistency index (*CI*) of 0.586 and a retention index (*RI*) of 0.761.

Bootstrap and Bremer values are present for nearly all nodes present (Fig. 1). Basal nodes show the ingroup supported by a bootstrap value of 83% and Bremer value of 2 (node 32). *Eknomiaster* is supported by a bootstrap value of 92% and a Bremer value of 2. The sister-group relationship (node 25) between *Tosia* and *Pentagonaster* is supported by comparable values (bootstrap 92%, Bremer value 3). *Tosia* is supported by a bootstrap value of 84% but decays in two steps. *Pentagonaster* is supported by a bootstrap value of 85% and decays in three steps.

Phylogenetic results and taxonomic congruence

The phylogeny supports a sister-taxon relationship between *Tosia* and *Pentagonaster*, which is consistent with statements by Ludwig (1912), Fisher (1911) and A. M. Clark (1952, 1953). *Tosia* sensu A. M. Clark (1953, 1993) is paraphyletic. *Tosia queenslandensis* is separated from a clade including *T. australis* and *T. magnifica* as sister-taxa. Australian *Tosia* species are supported as monophyletic to a sister-clade to a monophyletic *Pentagonaster*. Both genera are supported as distinct, which is consistent with the A. M. Clark (1953) study but is in disagreement with Livingstone (1932), who believed the two genera should be synonymised.

Our phylogenetic results (Fig. 1) support *Tosia nobilis* and *Tosia australis* var. *astrologorum* and *Tosia australis* on a single branch and agree with the synonymy of these species by Marsh (1991). However, substantial morphological variation has been observed between species in the *T. australis* complex (e.g. Livingstone 1932; A. M. Clark 1953; Marsh 1991). Data presented herein support *Tosia* as separate from *Pentagonaster* and uphold *T. magnifica* as a separate species from the *T. australis* species-complex. However, based on the sampling of morphotypes included herein, the phylogenetic results (Fig. 1) support only two species of *Tosia*: the highly variable *T. australis* and *T. magnifica*, both of which are apparently endemic to Australia.

Monophyly of *Pentagonaster*, including *P. pulchellus*, *P. dubeni*, *P. stibarus* H. L. Clark, 1914 and the Eocene *Buterminaster elegans* Blake in Blake and Zinsmeister 1988, is supported. However, the synonymy of *P. stibarus* with *P. crassimanus* Möbius, 1859 (and consequently with *P. dubeni*) should be re-evaluated. *Pentagonaster stibarus* was believed to be a synonym of *P. crassimanus* (= *P. dubeni*) by several authors, including Mortensen (1925) and A. M. Clark (1953). However, our phylogenetic results present an alternative to this hypothesis, and instead suggest that *P. stibarus* is more closely aligned to the New Zealand *P. pulchellus*.

The original basis for the synonymy of *P. stibarus* with *P. crassimanus* was suggested by Mortensen (1925) and endorsed by H. L. Clark (1946) but lacked any rigorous criteria and was apparently assumed based primarily on a basis of superficial similarity and geographic closeness. As a conservative measure, *Pentagonaster stibarus* is herein retained as a separate species (until additional evidence for its status can be deter-

mined) on the basis that it shows closer affinities with the New Zealand *P. pulchellus* than the Australian *P. dubeni*. Further support for the separation is observed from the increased number of steps (145–148) required with respect to the overall number of steps in the tree, if *P. stibarus* is artificially joined with *P. dubeni* using MacClade.

Pentagonaster stibarus is differentiated from *P. crassimanus* based on the presence of an enlarged penultimate inferomarginal plate (character 38) corresponding to the swollen and elongate penultimate superomarginal plate (characters 27, 28). This enlarged penultimate inferomarginal occurs in *P. pulchellus* but not in *P. dubeni*. Based on the specimens examined and prior historical descriptions (e.g. A. M. Clark 1953) enlarged inferomarginals were not observed to vary among individuals and occurred only in specific taxa. Among the other goniasterid genera with enlarged superomarginals (such as *Sphaeriodiscus*), enlarged inferomarginals have not been frequently observed, with only a single species, *Sphaeriodiscus mirabilis* A. M. Clark 1976, being one of the few known exceptions.

Pentagonaster pulchellus has been further differentiated from *P. dubeni* (and forms identified or considered as *P. crassimanus*) by the presence of four marginal plates per interradius in the former versus six in the latter. Clark and McKnight (2001) noted that among the variation in *P. pulchellus* they examined, some individuals demonstrated six marginal plates (that occur in *P. stibarus*) per interradius versus the typical four. The Eocene *Buterminaster* was supported as the sister-taxon to *Pentagonaster dubeni* based on the presence of identical abactinal and marginal plate characters (e.g. plate shape, furrow spines, granulation, etc.) with a bootstrap value of 74% and a Bremer decay of a single step. This supports *Buterminaster* as a
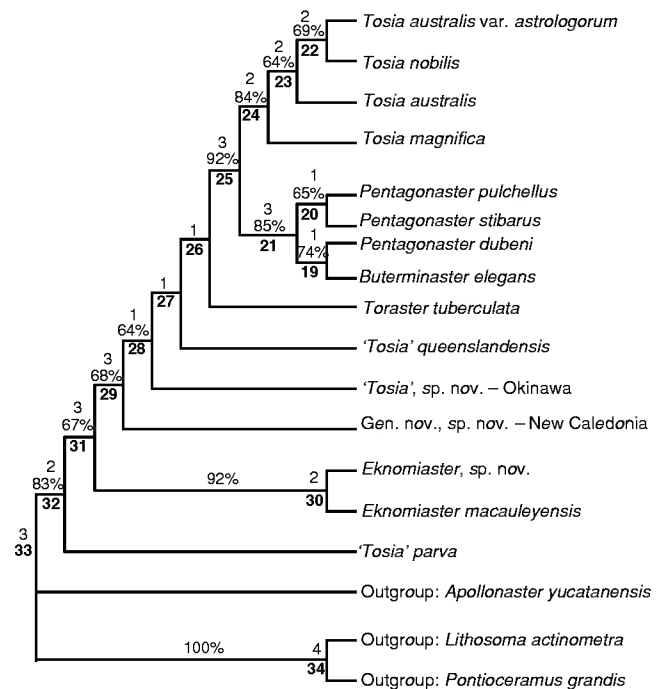

Fig. 1. Phylogenetic tree of the *Pentagonaster* clade. Node numbers in bold. Bootstrap support expressed as %. Bremer support values in outline.

synonym of *Pentagonaster*, extending the range of *Penta-gonaster* to the Eocene of Seymour Island. *Pentagonaster* (formerly *Buterminaster*) *elegans* is distinguished by the presence of an enlarged terminal plate (Blake and Aronson 1998), which remains a putative autapomorphy for *P. elegans*. However, juvenile goniasterids and other valvatidans are frequently observed with an enlarged terminal plate (e.g. *Plinthaster* Verrill, 1899 in Sumida *et al.* 2001) that gradually disappears as the other plate series develop in the adult form. Examination of further specimens of *P. elegans*, displaying a broader range of sizes, would be necessary to ascertain if this feature is growth related or a unique adult characteristic.

The separation of the South African *Toraster* from *Tosia* and *Pentagonaster* by Clark (1952), as initially suggested by Fisher (1911), is also consistent with the phylogenetic hypothesis (Fig. 1). However, the phylogenetic hypothesis disagrees with Clark's (1952) assessment of *Toraster* displaying affinities with *Plinthaster* based on the presence of secondary plates and similar pedicellariae. Secondary plates and pedicellariae occur in several dissimilar and unrelated Goniasteridae (e.g. *Peltaster* Verrill, 1899 and *Hippasteria* Gray, 1840).

Although some authors (Livingstone 1932) have described *Tosia queenslandensis* as having characters intermediate between *Tosia* and *Pentagonaster*, others (Clark 1953) were more inclined to include it within *Pentagonaster*. The phylogenetic hypothesis supports a basal split of *Tosia queensland-ensis* from the primary *Tosia/Pentagonaster/Toraster* lineage (node 27), which is consistent with Livingstone's (1932) hypothesis. The placement of *T. queenslandensis* in a new genus (described below) is consistent with earlier suggestions (H. L. Clark 1946).

Although *Eknomiaster* occurs distantly from *Pentagonaster* in the phylogeny, its presence within the *Pentagonaster* lineage agrees with H. E. S. Clark's (2001) assessment that the two genera share close affinities.

Tosia parva occurs at the base of the ingroup clade (node 32), very distantly from the Australian *Tosia* lineage (node 24), which is inconsistent with the placement of *Pentagonaster parvus* in the genus *Tosia*, as described by Halpern (1969). A new genus is established for this species below.

The taxa above show reasonable overall Bremer (four steps at node 31) and bootstrap (91% at node 30) support and include genera such as *Tosia* and *Pentagonaster*, which have historically been perceived as being closely related. Results herein support these taxa as members of a discrete clade that is recognised here as the Pentagonasterinae Perrier, 1884, which is herein resurrected from synonymy with the Goniasteridae and restricted. Included members and morphological definition of the subfamily are summarised below. Preliminary data from a family-wide study of the Goniasteridae (Mah 2005*b*) have also supported this clade.

Taxonomy

Family **GONIASTERIDAE** Forbes

Subfamily **PENTAGONASTERINAE** Perrier
(restricted herein)

Type genus: *Pentagonaster* Gray.

Diagnosis

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

Included genera. *Anchitosia*, gen. nov., *Eknomiaster*; *Pawsonaster*, gen. nov., *Pentagonaster*; *Ryukuaster*, gen. nov., *Toraster*, *Tosia*.

Key to the Pentagonasterinae

1.   Enlarged pedicellariae (~5.0 mm in length) present (bivalved pedicellariae visible with naked eye), comparable in size to plate on which it sits 2
     Pedicellariae (~1.0–2.0 mm in length), if present, not enlarged, very tiny (~1/10th size of plate). Pedicellariae tong- or pincer-like, or clam-like, set in pits. 5
2.   Abactinal plates very swollen, convex. Some secondary plates completely covered by large (~1.0 mm) spherical granules present on abactinal, actinal plate surfaces. Two to three papular pores. Marginal plates ~20–40 per interradius. Large bivalved pedicellariae bisecting abactinal plates. Body shape stellate. South Africa . . . .*Toraster tuberculatus*
     Abactinal plates bare. Large spherical granules absent from plate surface. Papular pores single. Marginal plates eight or fewer plates per interradius. Body shape pentagonal. 3
3.   Abactinal plates flattened, essentially flush, smooth. One to three large bivalved pedicellariae, 2–3× size of

actinal plates, centrally located in each actinal inter-mediate region, flanked by large, flattened, scalar spines (Fig. 2*D*–*E*), pedicellariae not consistently present on every actinal intermediate plate. Inter-marginal pit absent. Superomarginal plates, with scattered granules 3–7 per interradius with roughly 1:1 corresponding inferomarginal series. New Caledonia . . . .*Eknomiaster beccae*, sp. nov.

Abactinal plates pointed to tubercular, very convex forming bumpy surface texture. Large bivalved pedicellariae present on every marginal plate and on every actinal intermediate plate (Fig. 3*B*). Intermarginal 'pit' present, covered by flattened, scalar spines (Fig. 3*C*). Three superomarginals, 10 inferomarginals in largest specimens recorded (R = 2.0). Marginal plates completely bare. New Caledonia . . . .
. . . . . *Akelbaster novaecaledoniae*, gen. nov., sp. nov.

4.   Single and double papular pores only, distributed radially, absent interradially. Abactinal plates not convex, not swollen. Penultimate superomarginal plates never enlarged or elongate. Marginal plates gradually decreasing in size. Marginal plates not very swollen or convex in cross section. 9

Multiple papular pores present over complete abactinal surface (radially and interradially). Abactinal plates convex, swollen. Penultimate superomarginal plates enlarged or elongate in most specimens examined. Marginal plates not decreasing in size. Marginal plates swollen, convex in cross section 6

5.   Accessory granules around periphery of abactinal, marginal, actinal intermediate plates relatively large (~2–3 per 1.0 mm at R = 3.5). Enlarged penultimate inferomarginals present or absent. Pedicellariae with long, narrow blades. Actinal intermediate plate surface always bare. Australia and New Zealand . . . .
. . . . *Pentagonaster*

Accessory granules around periphery of abactinal, marginal, actinal intermediate plates relatively small (~4 per 1.0 mm at R = 3.5). Enlarged penultimate inferomarginals absent. Pedicellariae present or absent, when present with short, rounded valves, Actinal intermediate plates covered by granules, bare or with prominent bald centre spot. Australia only. . .
. . . .*Tosia*

6.   Terminal plate enlarged. Penultimate or antepenultimate inferomarginal plates not enlarged. Interradial marginal plates six to eight (frequently six). Body shape stellate (R:r = 2.4). Eocene, Seymour I., Antarctica. . . . . *Pentagonaster elegans*

Terminal plate not enlarged. Penultimate or ante-penultimate inferomarginal plates not enlarged. Interradial marginal plates four. Body shape stellate (R:r = 2.1–2.6). South-west to south-eastern Australia. . . . . *Pentagonaster dubeni*

Terminal plate not enlarged. Inferomarginals enlarged. Interradial marginal plates four. Body shape pentagonal or stellate. Western Australia. . . . .
. . . . *Pentagonaster stibarus*

Terminal plate not enlarged. Inferomarginals enlarged. Interradial marginal plates six. Body shape weakly pentagonal (R:r = 1.5–1.9). New Zealand region. . . .
. . . . *Pentagonaster pulcellus*

7.   Enlarged penultimate superomarginals present or absent. Marginal plates larger with ~6 per interradius at R = 3.8. Marginal plate length > width. Marginal plates highly convex, swollen, sometimes tubercular. Abactinal plates highly convex, swollen to tubercular. Abactinal fasciolar grooves well expressed. Recorded adult body size up to R = 5.1. South-west to south-eastern Australia. . . . . *Tosia australis*

Enlarged penultimate superomarginals never present. Marginal plates smaller with ~15 per interradius at R = 5.5. Marginal plate width > length. Marginal plates swollen, not tubercular. Abactinal plates flat to weakly convex, not as swollen as *T. australis*. Abactinal fasciolar grooves more weakly expressed. Recorded adult body size up to R = 7.7. Southern Australia. . . . . *Tosia magnifica*

8.   Body form stellate (R:r = ~1.8–2.0). Marginal plates smaller, more numerous (~16 per interradii). Terminal plate large, 1–2× size of adjacent superomarginals. Single and double papular pores present 10

Body form more pentagonal (R:r = 1.4–1.6). Marginal plates larger, less numerous (~6–8 per interradius in adult specimens). Terminal plate not enlarged. Single papular pores only. 11

9.   Furrow spines two at R = 2.0. Granules completely absent from marginal plate surface. Tubercular granules never present. Spinelets absent from superomarginal plates. Actinal intermediate plates always bare. Ryuku Is, Japan, Papua New Guinea, Australia, New Caledonia.
. . . *Anchitosia queenslandensis*, gen. nov., comb. nov.

Furrow spines three to five at R = 2.0. Lateral side of marginal plate edge with granular cover. Tubercular granules on abactinal, marginal plate surface. Granular covering on superomarginal and infero-marginal surfaces with bare spot on centre. Actinal intermediate plates covered by granules (at R > 1.5). Short spinelets on distalmost inferomarginal and superomarginal (in larger specimens) plates. Okinawa, Ryuku Is, Japan. . . . .
. . . . *Ryukuaster onnae*, gen. nov., sp. nov.

10.   Peripheral granules around radial abactinal plates discretely spaced around plate. Abactinal and marginal plates bare. Granules absent. Actinal plate surfaces always covered by close fitting granules. Macauley I., Norfolk Ridge, Kermadec Group, South Pacific . . . .
. . . . *Eknomiaster macauleyensis* H. E. S. Clark

Peripheral granules around radial abactinal plates fused into closely articulated ring around abactinal plates. Scattered tubercular granules on abactinal and marginal plate surface. Actinal plate surfaces with or without granular coverings. Tropical Atlantic. . . . .
. . . . *Pawsonaster parvus*, gen. nov., comb. nov.

Genus *Pawsonaster*, gen. nov.

Tosia (restricted to *P. parva*) Halpern, 1969: 503, fig.1. – Halpern, 1970: 168; Clark & Downey, 1992: 267; Walenkamp, 1976: 61; Carrera-Rodriguez & Tommasi, 1977: 96; Walenkamp, 1979: 32.
Type species: *Pentagonaster parvus* Perrier, 1881.

Diagnosis

As for species (below).

Etymology

This genus is named for Dr David Pawson, Curator of Echinoderms at the National Museum of Natural History, Smithsonian Institution in Washington, DC.

Pawsonaster parvus (Perrier), gen. nov., comb. nov.

(Fig. 2*A–C*)

Pentagonaster (*Tosia*) *parvus* Perrier, 1881: 19. – Perrier, 1884: 36, pl. 7, figs 7–8; Sladen 1889: 265.
Goniaster americanus (pt) Verrill, 1899: 154, pl. 26, fig. 6.
Plinthaster dentatus (pt) Gray *et al.*, 1968: fig. 25.
Tosia parva. Halpern, 1969: 503. – Halpern, 1970: 169; Downey, 1973: 54; Walenkamp, 1976: 61; Tommasi & Oliviera, 1976: 84; Carrera-Rodriguez & Tommasi, 1977: 96; Walenkamp, 1979: 32; Jangoux & de Ridder, 1987: 89; Hopkins *et al.*, 1991: 237; Downey in Clark & Downey, 1992: 268; A. M. Clark, 1993: 289; Laguarda-Figueras *et al.*, 2005: 112; Benavides-Serrato *et al.*, 2005: 182.
Tosia clugreta Walenkamp, 1976: 63, pl. 4, fig. 2, pl. 9, fig. 4, pl. 12, figs 1,2,4. – Jangoux & de Ridder, 1987: 89.

Type material

MNHNP EcAh 964, EcAH 3581 (paralectotypes), MCZ 417 (lectotype) (not examined).

Material examined

North Atlantic Ocean: 1 dry spec. body completely disarticulated, 5 dry specs (R = 2.2, r = 1.5; R = 2.3, r = 1.7; R = 2.2, r = 1.5; R = 1.9, r = 1.3; R = 1.8, r = 1.3) (NMNH E12632); 1 dry spec. (R = 1.9, r = 1.2), east of Cape Canaveral, 28°22′30″N, 80°02′00″W, 75–82 m (NMNH E13190); 2 dry specs (R = 1.7, r = 1.1; R = 2.0, r = 1.2), Venezuela, NW of Tortuga, 11°00′N, 65°55′W, 112 m (NMNH E19070); 1 dry spec. (R = 2.1, r = 1.6), SE of Santo Domingo, 18°21′N, 69°14′W, 170–176 m (NMNH E19081); 1 dry spec. (R = 2.2, r = 1.3), south-east of Santo Domingo, 18°21′N, 69°09′W, 130–165 m (NMNH E19082); 1 dry spec. (R = 1.2, r = 1.1), Cay Sal Bank, 23°35′N, 79°34′W (NMNH E19085); 2 dry specs (R = 1.6, r = 1.2; R = 1.6, r = 1.2), NE of Cuba, 20°54′N, 73°37′W, 137–182.8 m (75–100 fms) (NMNH E35025); 1 dry spec. (R = 1.1, r = 0.9), Caribbean Sea, Barbados, 2.5 mi NW of Pelican I., 182.8 m (100 fms) (USNM E53632); 1 dry spec. (R = 1.2 cm, r = 0.8 cm), Brazil, 19°00.33′S, 37°47.65′W, 112 m (MNHN EcAs 11962).

Diagnosis

Body form pentagonal or nearly so (low R/r). Abactinal plates flattened to convex, polygonal to hexagonal in outline. Primary circlet plates distinctive, enlarged. Plates bare or with single tubercular granule at centre. Peripheral granules rectangular to quadrate, snugly arranged around abactinal plate periphery, forming distinct ring around radial plates. Papular pores single, absent interradially. Madreporite triangular. Fasciolar grooves shallow. Marginal plates decreasing in size distally, penultimate superomarginals not enlarged but in contact on distal arm tip. Interradial supero- and inferomarginals wider than long, swollen, convex, symmetrically round in cross section. Marginal plates commonly smooth, but often with scattered or irregular granules, surface texture sometimes uneven or rough. Actinal plates polygonal to round. Surface bare or with bare spot with single to multiple rows of peripheral granules. Complete granular covering sometimes present. Furrow spines 5–7 compressed with 2–4 rows of granular, subambulacral spines. Subambulacrals granular, thickened. Pedicellariae, when present, tong-like. Adambulacral 'dividers' oriented vertically, directed proximally.

Colour in life deep to light orange with lighter coloured oral surface.

Distribution

South Carolina, Florida, Gulf of Mexico, Brazil, to Uruguay; 30–600 m.

Genus *Eknomiaster* H. E. S. Clark

Eknomiaster H. E. S.Clark in Clark & McKnight, 2001: 42.
Type species: *Eknomiaster macauleyensis* H. E. S. Clark, 2001 by original designation.

Diagnosis

Body shape pentagonal. Arms broadly triangular. Body thick, inflated. Abactinal plates, smooth, bare, granulation absent, flat to mildly convex, polygonal to hexagonal in outline. Primary circlet plates distinctive, enlarged. Interradial plates not enlarged. Single papular pores present in radial regions, absent or reduced interradially. Peripheral granules round to polygonal in shape, flush with plate, relatively small in size, tightly arranged. Madreporite triangular in most specimens. Fasciolar channels shallow to absent. Marginal plates blocky, bare, smooth, longer than wide, convex, symmetrically round in cross section. Superomarginal and inferomarginal series correspond nearly 1 : 1, with some plates offset distally. Granules present on marginal plate surface of *E. beccae*, sp. nov., but absent in *E. macauleyensis*. Peripheral granules relatively small, fine, rectangular in shape. Fasciolar channels shallow to absent. Superomarginals neither enlarged or swollen nor elongate, moderately large, 5–8 per interradius. One, or at most two, distal-most superomarginals in contact over midradius. Superomarginal plates not gradually decreasing in size distally. Terminal plate with pointed tip. Arm tip upturned. Actinal plates polygonal, all plates completely covered by evenly spaced coarse granules. Fascioles absent. Peripheral granules polygonal to quadrate. Furrow spines 7–9 compressed. Subambulacral spines thickened relative to furrow. Adambulacral 'divider' oriented vertically, directed proximally (Fig. 7*G*). Pedicellariae, tong-like but variable types occur between species.

Eknomiaster beccae, sp. nov.

(Fig. 2*D–F*)

Material examined

Holotype. 1 dry spec. (R = 3.1, r = 2.4), New Caledonia, Norfolk Ridge, 23°45′S, 168°16′E, 478–486 m, 28.xi.1993, coll. Bouchet, Richer and Waren (MNHN EcAs 11818).

Paratypes. **New Caledonia**: 1 dry spec. (R = 2.0, r = 1.6), southern New Caledonia, 23°21.4′S, 168°4′5 E, 215–260 m, 9.iii.1989, coll. N.O. *Alis* (MNHN EcAs 11819); 1 dry spec. (R = 3.3, r = 2.6), 18°52.80′S, 163°21.70′E, 550 m, 19.ix.1985, coll. MUSORSTOM 4, St. CP 194 (MNHN EcAs 11820).

Other material examined. South Pacific. **East Jumeau Seamount.** 2 dry specs (R = 3.0, r = 2.4; R = 2.4, r = 1.9), 23.809°S, 168.280°E 500–1074 m (MNHN EcAs 11961); 2 dry specs (R = 3.0, r = 2.1; R = 3.3, r = 2.4), 23.791°S, 168.284°E, 422–495 m (MNHN EcAs 11963); 1 dry spec. (R = 3.6, r = 2.6), 23.747°S, 168.281°E, 390–398 m (MNHN EcAs 11964); 5 dry specs (R = 2.4, r = 1.8; R = 1.8, r = 1.3; R = 1.5, r = 1.2; R = 0.7, r = 0.6; R = 0.5, r = 0.3), 23.715°S, 168.257°E, 470–621 m (MNHN EcAs 11965). *Stylaster* **Seamount**: 1 dry spec. (R = 2.6, r = 2.1), 23.668°S, 167.675°E, 517–570 m (MNHN EcAs 11962).

Diagnosis

Marginal plates fewer and larger, smooth, bare, with granules absent from marginal surface. Enlarged pedicellariae on actinal surfaces, other smaller pedicellariae absent or not commonly observed. Colour in life bright orange.

Description

Body shape pentagonal (R/r = 1.2–1.3), stout, with rounded to straight interbrachial arcs. Arm tips upturned.

Abactinal plates flat to mildly tumid, bare, smooth. Granules absent from plate surface. Plates pentagonal to polygonal, occasionally irregularly polygonal to trigonal. Primary circlet and central disk plates larger than distal plates adjacent to superomarginal boundary. Peripheral accessories 20–80, angular edges, elongate to squarish in shape, evenly distributed around border. Pedicellariae largely absent from abactinal surface, except for 1–6 small pedicellariae, tong-shaped on plates adjacent to superomarginal border in one specimen (EcAs 11819). Secondary plates absent. Madreporite triangular, bordered by three abactinal plates.
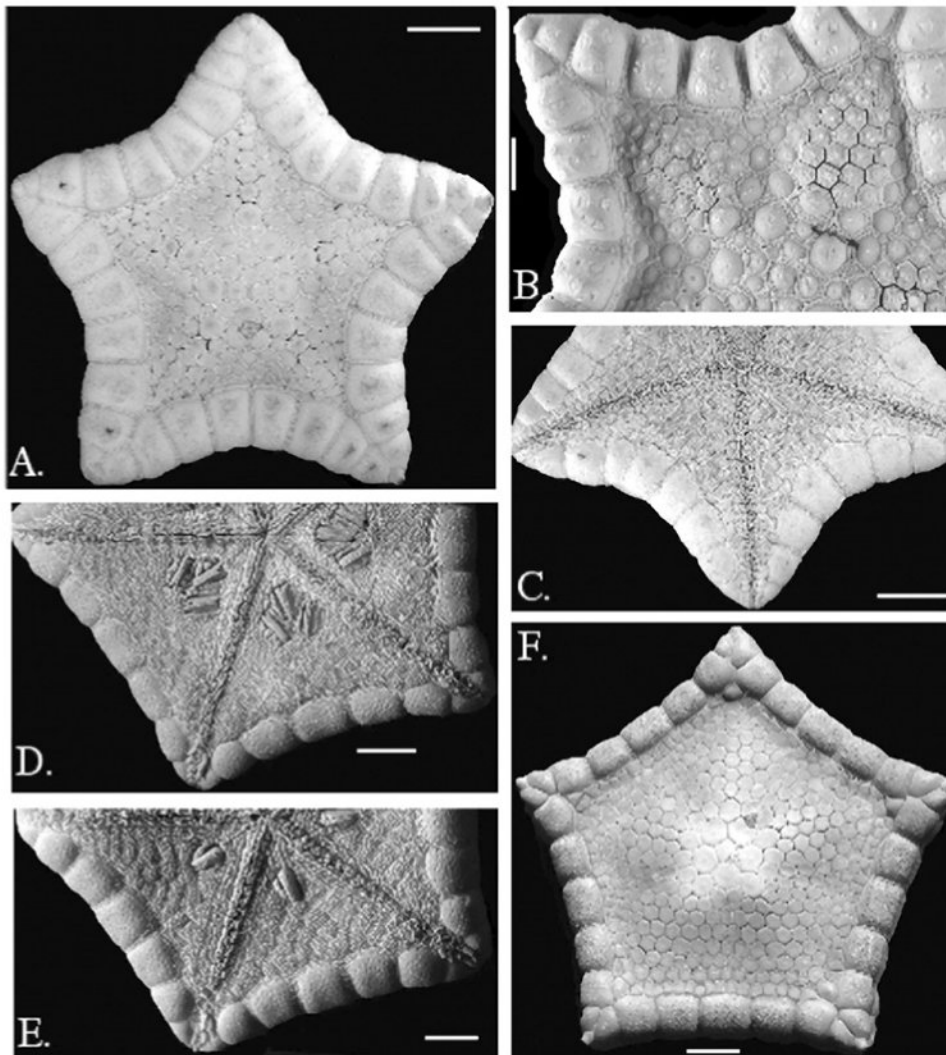

Fig. 2. *Pawsonaster parvus*, gen. nov. NMNHIZ E13190: (*A*) abactinal surface showing gross body outline; (*B*) abactinal surface closeup, showing plates; (*C*) actinal surface. *Eknomiaster beccae*, sp. nov. MNHNP EcAs 11820: (*D*) actinal surface; (*E*) actinal surface of MNHNP EcAs 11818 showing single pedicellariae variant; (*F*) abactinal surface. (Scale bars = 0.5 cm.)

Marginal plates bare except for granules. Granules 80–100, rounded, scattered evenly over all plate surfaces. Absent granules leaving discrete concave pitting on surface. Marginal plates inflated, highly convex in transverse cross section. Greater number of inferomarginals (nine) than superomarginals (seven). Marginal plate series are 1:1 except for those distally where inferomarginals (three) are in contact with single enlarged superomarginal. Granules, 100–125, angular to quadrate in shape from periphery around marginal plates. Middle three superomarginals with equal dimensions (L = W). Distalmost superomarginals enlarged, triangular to rectangular in shape. Superomarginals occasionally vary in shape from arm tip to arm tip on single individual. Distalmost to penultimate superomarginals enlarged to reduced in size relative to inferomarginals. Distalmost superomarginals abutted over midline, directly adjacent to terminal plate. Inferomarginals similar to superomarginals in size distribution. Interradial inferomarginals smaller with even dimensions becoming smaller, more upturned distally adjacent to arm tip. Penultimate and pre penultimate inferomarginal plates triangular or roughly so. Terminal plate triangular, conical with blunt, conical spine at tip. Granules absent from terminal plate.

Actinal surface with chevrons 2–3, arranged in clear series. Actinal plates quadrate to polygonal in shape, some elongate. Largest actinals adjacent to adambulacral furrow becoming smaller, more irregularly shaped, adjacent to inferomarginals.

Actinal surface covered with granules 8–20 (usually 15) evenly distributed, coarse, polygonal. Enlarged bivalved pedicellariae 1–3 set into deep pits present in each actinal interradius. Number of enlarged, actinal bivalved pedicellariae variable. EcAs 11818 with one per interradius. EcAs 11819 with one to two per interradius. EcAs 11820 with three per interradius. Pedicellariae number appears independent of size. Largest pedicellariae sits at middle of each interradius with smaller secondary pedicellariae flanking largest at oblique angles. Each pedicellaria as wide as other actinal plates and flanked by 5–7 (2–5 in smaller specimens) flattened angular spines, triangular to prismatic in cross section. Pedicellariae blades smooth or with minor serrations on each edge.

Furrow spines 7–9 (usually eight), crowded, flattened oval in cross section. Furrow spines in straight to curved series. Smallest distally, tallest at middle. Subambulacral spines enlarged, 2–3 per adambulacral plate, thicker, slightly more elongate than furrow spines. Subambulacrals approximately as wide as 3–4 furrow spines, becoming increasingly larger (3–4×) and more conical distally. Approximately 12 adambulacrals from arm tip, subambulacrals become 2–3× as long as those near the mouth. Adambulacral plate covered with granules 7–12, prismatic to conical in shape, similar to those on actinal plates. Peripheral accessories on adambulacral plates uneven with coarse granules.

Colour in life bright orange.

Remarks

A single or a cluster of three enlarged bivalved pedicellariae were observed to consistently occur in different morphotypes of this species (Fig. 2*D*, *E*). The number of pedicellariae did not show obvious correlation with any environmental factors, such as depth, nor was there any apparent correlation of the pedicellariae

number with size. The number of pedicellariae was the only character that substantially differed among the specimens of these species and was consistently present in all specimens observed.

Distribution

New Caledonia to 'Jumeau Est' seamount at 23°S, 168°E 215–1074 m.

Etymology

Named for Dr Rebecca 'Becca' Price, University of Washington, Bothell, Washington.

Eknomiaster macauleyensis H. E. S. Clark

Eknomiaster macauleyensis H. E. S.Clark in Clark & McKnight, 2001: 42.

Material examined

West Norfolk Ridge. Wanganella Bank: 1 wet spec. (R = 2.5, r = 2.0), 34°37′12″S, 168°57′02″, 521–539 m (MV F122717). **Off New Caledonia:** 4 dry specs (R = 3.2 r = 2.2, R = 3.7 r = 2.4, R = 3.3 r = 2.1, R = 3.5 r = 2.1), 22°58′S, 167°20.4′E, 530–535 m (MNHN EcAs 11761).

Diagnosis

Marginal plates larger (fewer interradially) than those in *E. beccae*, smooth, bare with granules absent from marginal surface. Enlarged pedicellariae absent from actinal surfaces, smaller unenlarged, fan-like, flattened pedicellariae present on many if not most actinal plates.

Colour in life bright orange.

Distribution

New Caledonia and Macauley I., Kermadec Group, Norfolk Ridge, Wanganella Bank; 448–539 m.

Genus *Akelbaster*, gen. nov.

Type species: *Akelbaster novaecaledoniae*, gen. nov., sp. nov.

Diagnosis

As for species description (below).

Etymology

Named for Dr Daniel Blake, Department of Geology, University of Illinois-Urbana Champaign, Illinois. The generic name is an anagram of Blake.

Akelbaster novaecaledoniae, gen. nov., sp. nov.
(Fig. 3*A–F*)

Material examined

Holotype. 1 dry spec. (R = 1.1 cm, r = 0.8), southern New Caledonia, Banc Jumeau east, 23°45.1′S, 168°17′E, 400 m, 30.i.1993, SMIB 8, DW 178, coll. P. Bouchet and B. Richer (MNHN, EcAs 11773).

Paratypes. **Noumea:** 1 dry spec. (R = 2.0 cm, r = 1.6), 23°41.5′S, 167°57.4′E, 338 m, 23.v.1987, SMIB 3, 'VAUBAN' DW 18, coll. ORSTOM (MNHN EcAs 11777); 1 dry spec. (R = 0.9, r = 0.6), 23°40.9′S, 168°00.8′E, 50–270 m, 7.ix.1989, SMIB 5, St. DW 75, coll. ORSTOM (MNHN EcAs 11774); 3 dry specs R = 1.5, r = 1.0; R = 1.3, r = 1.0; R = 1.1, r = 0.8),

23°19.6′S, 163°4.7′E, 290–305 m, 14.ix.1989, SMIB 5. St. DW 102, coll. ORSTOM (MNHN EcAs 11776); 1 dry spec. (R = 0.9,r-0.4), 23°40.8′S, 168°01.1′E, 230–270 m, 7.ix.1989, SMIB 5 St. DW 77, coll. ORSTOM (MNHN EcAs 11783); 1 dry spec. (R = 1.1, r = 0.8), 22°18.7′S, 168°41.3′E, 335–370 m, 13.ix.1989, SMIB 5 DW 87, coll. ORSTOM (MNHN EcAs 11775); 2 dry specs (R = 1.2 cm, r = 0.8 cm/R = 0.7, r = 0.4), 23°21.8′S, 168°4.9′E, 225–270 m, 14.ix.1989, SMIB 5 St. DW 101, coll. ORSTOM (MNHN EcAs 11779); 3 dry specs (R = 1.3, r = 1.1, R = 1.3, r = 1.1, R = 1.0, r = 0.7), 23°40.4′S, 168°00.6′E, 230–240 m, 7.ix.1989, SMIB 5. St. DW 73, coll. ORSTOM (MNHN EcAs 11782). **Noumea. Banc alis roche**: 2 dry specs (R = 1.2 cm; r = 0.8 cm; R = 0.8 cm, r = 0.6), 13.ix.1989, SMIB 5, coll. ORSTOM (MNHN EcAs 11781). **New Caledonia**: 1 wet spec. (R = 1.0, r = 0.8), 2.iii.2003, DW 2124 (MNHN EcAs). **Southern New Caledonia**: 4 spec. (R = 1.6, r = 1.3: R = 1.3 cm, r = 1.1; R = 1.1, r = 0.8; R = 0.9, r = 0.7 cm), 23°42′S, 168°01′E, 260–295 m, 9.iii.1989, SMIB 4. Sta. DW50 (MNHN EcAs 11780); 2 dry specs (R = 1.1, r = 0.7; R = 0.8, r = 0.6), 23°41′S,

168°01′E, 245–260 m, 9.iii.1989, SMIB 4. Sta. DW 51 (MNHN EcAs 11784). **Norfolk Ridge**: 2 dry specs (R = 1.3, r = 1.0 cm; R = 1.8 cm, r = 0.8), 23°42′S, 168°01′E, 308–312 m, BATHUS 3. Stn. CP 806 (MNHN EcAs 11778).

Diagnosis

Intermarginal pits present between supero and inferomarginal plates. All actinal plates with large bivalved pedicellariae. Abactinal and marginal plate surfaces completely bare.

Description

Body thick, pentagonal (R/*r* ~1.1–1.5). Marginal plates form distinct dorsal facing border. Marginal plate periphery represents ~30% of R.

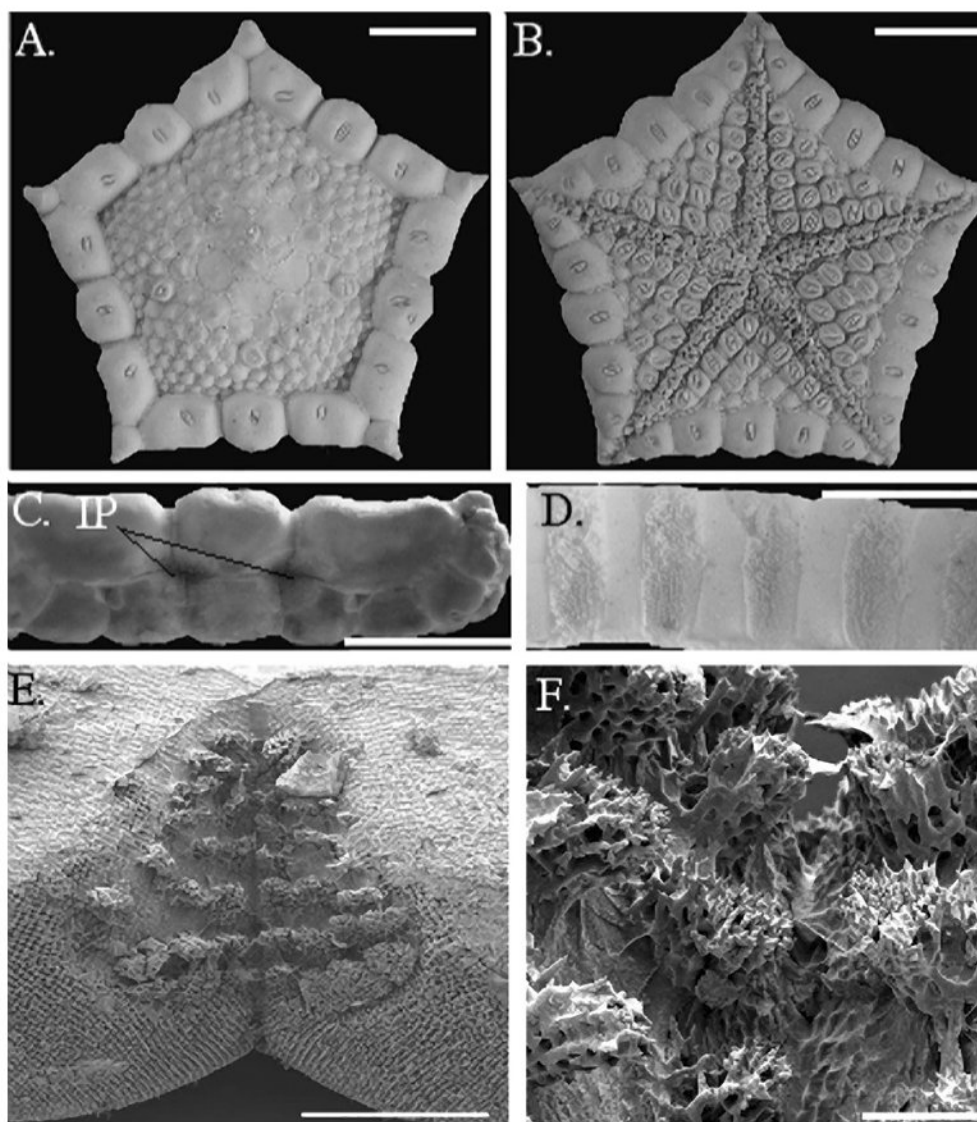Abactinal plates bare, polygonal to rounded. Most plates polygonal, larger proximally becoming more rounded, smaller

Fig. 3. *Akelbaster novaecaledoniae*, gen. nov., sp. nov. MNHN EcAs11782. (*A*) abactinal surface; (*B*) actinal surface; (*C*) lateral side showing intermarginal pits (IP); (*D*) cribiform organs from *Hyphalaster inermis* (Porcellanasteridae – NMNH E38883) (Scale bars = 0.5 cm). (*E*) SEM of intermarginal pits in *Akelbaster* (Scale bar = 500 μm); (*F*) SEM close-up of intermarginal pits in *Akelbaster.* (Scale bar = 100 μm.)

distally, adjacent to superomarginals. Primary circlet plates flat becoming rugose, uneven in larger specimens (R ~2.0). Radial, interradial, and non-circlet disk plates with mound-like convexities round to oblong in shape. Plates with concavities absent from primary circlet region in smaller specimens (R ~1.0) but larger specimens (R ~2.0) with concavities present. Carinal plates with prominent concavity, becoming nearly tubercular, at centre of plate, which becomes less pronounced relative to concavities on interradial and radial plates in larger (R = 2.0) specimens. Angular granules 20–65, evenly distributed, quadrate to elongate in shape. Granules at plate corners angular, approximately twice as large as other granules, forming triangle with granules from other corners. Radial regions swollen, interradial regions depressed. Pedicellariae enlarged, size of an abactinal plate, in each interradius sitting in pits on enlarged interradial plates. Pedicellariae blades flattened, edges smooth.

Madreporite triangular becoming more polygonal to rounded in smaller specimens. Papulae occur completely over entire abactinal surface.

Marginal plates bare, smooth, swollen, convex in cross section. Granules 60–75, quadrate in shape, edges rounded, evenly spaced. Number of interradial superomarginals differs from inferomarginals. Larger specimens (R = 1.5–2.0) with three superomarginals, seven inferomarginals. Supero–inferomarginal series offset except for middle superomarginal that corresponds to middle inferomarginal plate. Superomarginal plates larger than inferomarginal plates. Smaller specimens (R = 0.9) with three superomarginals, five inferomarginals. Superomarginal plates adjacent to terminal largest, elongate. Central superomarginal between distalmost plates with equal length and width. Inferomarginal plates similar in size. Inferomarginal series upturned distally, plates adjacent to terminal smallest in series. All marginal plates with enlarged pedicellariae 1–2 perpendicular to contact between abactinal disk plates and marginal plate boundary. Pedicellaria identical to those on disk, occurring half way between marginal plate edge and contact with abactinal disk plates.

Two prominent intermarginal openings present on adjacent sides to median supero–inferomarginal plate pairs. Intermarginal openings formed by gap between intersection of four marginal plates composed of two superomarginal and two inferomarginal plates. Intermarginal pits between middle plates largest with most prominent papillae-like covering (Figs 3C, E, F). More distal intermarginal openings smaller with fewer papillar-like structures. Channel present between marginal plates running below rows of papillar granules. Intermarginal plates show apparent connection with fasciolar channel from between marginal plate series. Smaller openings occur between adjacent superomarginal/inferomarginal offset pairings. Pits absent distally. Intermarginal openings covered with flattened, scalar, papillae-like granules, which are largest around periphery becoming smaller and more spinelet-like deeper in opening. Papillar granules flattened and scalar around intermarginal pit periphery becoming more spinelet-like deeper in opening. Viewed using SEM (Fig. 3E, F), papillae granules show fine surface texture covered with fine thorny spinelets in dried specimens. Papillar granules occur in ordered rows perpendicular to cleft between adjacent marginal plates (Fig. 3E). Terminal plate enlarged, triangular with blunt, prominent spine.

Actinal plates convex, quadrate to polygonal becoming more irregular in series adjacent to inferomarginal series. Actinal intermediate chevrons 3–4. Each actinal plate surface completely occupied by an enlarged bivalve pedicellariae, which sits within housing or base identical to those on abactinal, marginal plates. Granules, 20 to 40, evenly distributed, quadrate, angular, form periphery around each plate. No other accessories or primaries present on actinal plate surface.

Furrow spines, 3–4, blunt, quadrate to prismatic in cross section, similar in length. Subambulacrals 2–3 blunt, thickened, increase in length and thickness distally. Near arm tip, subambulacrals are 2–3× as thick as furrow spines and greater in length. Where three subambulacrals present, subambulacral spines on sides twice as thick as middle spine. Where two present, distalmost spine twice as thick as proximal. Subambulacral granules 2–5 in second row, highly angular, polygonal to angular in cross section, less than half length of adjacent subambulacral spine. Third row set off from second by distinct gap or bare spot on plate.

Furrow spines 3–4 on oral plates. Oral plate surface with spines 6–8 thick, blunt, angular to quadrate in cross section, crowded, becoming more granular adjacent to actinal plates. Oral spines continuous with subambulacral spines and have similar length and thickness. More adradial subambulacral spines becoming shorter, more granular, angular to prismatic in cross section. These becoming similar to third row of subambulacral granules on other adambulacral plates. Oral plates narrow, triangular in shape.

Living specimens with deep orange abactinal surface with lighter yellowish highlights, lighter yellow-brown oral surface.

Distribution

New Caledonia; 225–400 m.

Etymology

The species is named for the type locality, New Caledonia.

Genus *Ryukuaster*, gen. nov.

Type species: *Ryukuaster onnae*, gen. nov., sp. nov.

Diagnosis

As for species (below).

Etymology

Named for the Ryuku Is, the type locality and the Latin *aster*, meaning 'star'.

Ryukuaster onnae, gen. nov., sp. nov.
(Fig. 4A–C)

Material examined

Holotype. 1 dry spec. (R = 2.1, r = 1.3), Japan, Ryuku Is, Okinawa, 1 km WNW of Onna village, Horseshoe Cliffs, 26°30′N, 127°50′54″E, 6 m (20 ft), 24.v.1987, coll. R.F. Bolland (NMNH E53610).

Paratypes. **Japan. Ryuku Is:** Okinawa, 1 km WNW of Onna village, Horseshoe Cliffs: 1 dry spec. (R = 1.1, r = 0.7), 26°30′N, 127°50′54″E, 52 m (190 ft), 12.xi.1984, coll. R. F. Bolland (NMNH E53605); 2 dry specs

(R = 1.6, r = 0.9; R = 1.1, r = 0.6), 26°30′N, 127°50′54″E, 52 m (170 ft), 24.v.1984, coll. R. F. Bolland (NMNH E53606); 1 dry spec. (R = 1.3, r = 1.0), 26°30′N, 127°50′54″E, 47 m (155 ft), 20.i.1985, coll. R. F. Bolland (NMNH E53607); 1 dry specs (R = 1.5, r = 0.9; R = 2.0, r = 1.3), 26°30′N, 127°50′54″E, 60 m (190 ft), 3.viii.1984, coll. R. F. Bolland (NMNH E53609); 1 dry spec. (R = 1.1, r = 0.6), 26°30′N, 127°50′54″E, 40–46 m (130–150 ft), 16.iii.1985, coll. R. F. Bolland (NMNH E53611); 1 dry spec. (R = 0.8, r = 0.6), 26°30′N, 127°50′54″E, 67 m (220 ft), 19.vi.1981, coll. R. F. Bolland (NMNH E53612); 1 dry spec. (R = 1.5, r = 0.9), 26°30′N, 127°50′54″E, 60 m (190 ft), 3.viii.1984, coll. R. F. Bolland (NMNH E53681); 1 wet spec. (R = 1.2, r = 0.8), 26°30′N, 127°50′54″E, 60 m (190 ft), 3.viii.1984, coll. R. F. Bolland (NMNH E53706); 1 wet spec. (R = 1.3, r = 1.0), 26°30′N, 127°50′54″E, 60 m (190 ft), in sand, rock, coral rubble, 15.vi.1984, coll. R. F. Bolland (NMNH E53707).

Other material examined. **Japan. Ryuku Is, Okinawa:** 1.3 km ENE of Maeki-zaki, Seragaki Beach: 1 dry spec. (R = 0.9, r = 0.5), 45.75–48.8 m (NMNH 46165); 1 dry spec. (R = 0.8, r = 0.5), 26°30′24″N, 127°52′30″E, 3 m (10 ft) (NMNH E53683).

Diagnosis

Body form stellate. Approximately 16 marginals per interradius. Lateral edge of marginal plates with granular cover. Tubercular granules, granular spinelets on abactinal, marginal plate surface. Actinal intermediate plates covered by granules at R = 1.5 cm. Furrow spines three to five. Terminal plates enlarged.

Description

Body shape weakly stellate (R/r = 1.3–1.5). Arms short, triangular, disk broad. Arm tips upturned.

Abactinal plates flat to mildly convex. Some plates, including those on primary circlet and carinal plates strongly convex. Abactinal plates round to polygonal in outline, becoming irregular adjacent to marginal plate contact. Carinal plate series round to hexagonal. Primary circlet interradial plates enlarged (approximately twice as large as carinals). Plates with 8–50 (typically 20–30) peripheral granules, quadrate, angular to polygonal in shape, discretely separate from one another, but tightly arranged. Plates smooth, bare but in larger specimens (R > 1.5) granules identical to peripheral granules form additional rows on plate adjacent to periphery, becoming very dense, sometimes completely obscuring plate. These larger sized specimens sometimes with large nipple-like tubercle positioned centrally on interradial plates.

Fasciolar channels distinct, but shallow. Papular pores single if present interradially; double on radial regions. Madreporite
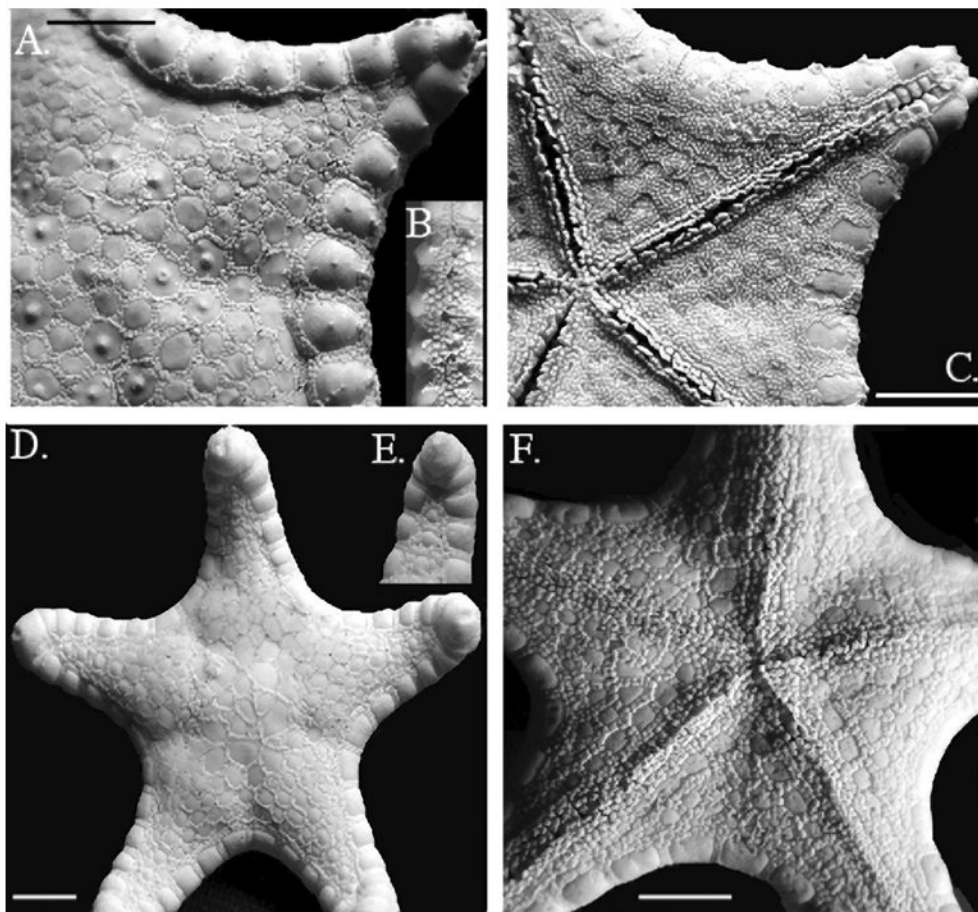

Fig. 4. *Ryukuaster onnae*, gen. nov., sp. nov. NMNH E53610 (Holotype): (*A*) abactinal surface; (*B*) lateral view; (*C*) actinal surface. *Anchitosia queenslandensis*, gen. nov. NMNH E53609: (*D*) abactinal surface; (*E*) close-up of arm tip and enlarged terminal plate; (*F*) actinal surface. (Scale bars = 0.5 cm.)

triangular, commonly bordered by three plates. Four plates are present around more rounded madreporites.

Marginal plates elongate, swollen, quadrate in outline, decreasing in size distally towards terminal. Fasciolar channels distinctly present between marginal plate series. Peripheral granules 20–60, quadrate, rectangular to polygonal, irregularly angular. Larger plates with additional, similar granules forming second and third irregular rows on plate surface adjacent to periphery.

Superomarginals eight (R < 1.7) to 10 (in specimens with R > 1.7). Superomarginals elongate, swollen, with largest, most swollen interradially, decreasing distally. Superomarginal surface generally bare with one, or sometimes more, round tubercular granules on plate surface. Often as single tubercles but also as irregular series following from additional peripheral granular rows. Granules coarser becoming more dense on lateral surface of superomarginal plates with occasional distinct tubercle directed laterally or on lateral edge. One to three large tubercular granules present interradially on lateral surface within dense lateral granular covering. Penultimate supero-marginals generally smaller, but variably occur as larger plates similar to those interradially. Short, tubercular spine sometimes found on lateral surface of distalmost superomarginal plates.

Inferomarginals 10 (R < 1.7) to 12 (in specimens with R > 1.7), slightly less swollen than superomarginals, decreasing in size distally but becoming more swollen adjacent to terminal plate. Short thorny spinelet sometimes flanked by one or more pointed to rounded granule(s) on lateral to actinolateral edge of inferomarginal plate. Multiple additional granular rows present on lateral and ventral surface of inferomarginal plates becoming densest laterally but more evenly spaced ventrally. One to three large tubercular granules present interradially on lateral surface within dense lateral granular covering, located adjacent to iden-tical large tubercular granule on superomarginal series. Ventral surface of inferomarginal plate bare, but bare area varies with degree of granulation, which is greater in larger specimens.

Intermarginal pits located between central two to three inter-radial supero–inferomarginal pairs. Pits bare but flanked on each corner by three to four clavate spines, each with large rounded tips distributed between superomarginal and infero-marginal granules. Spines with fine, roughened surface texture and covered by tissue in dried specimens. Terminal plate enlarged, rounded, swollen, half size of adjacent superomarginal plates in smaller (R < 1.3) specimens. Two to three short spines present on terminal and sometimes as part of peripheral granule series adjacent to terminal.

Actinal plates polygonal with angular edges, flattened in chevron formation. Largest plates in series adjacent to adambu-lacral plates. Second and third series with smaller plates, becoming more irregularly shaped adjacent to inferomarginal contact. Actinal plate surfaces bare in smaller individuals (R ≤1.3), intermediate in moderate sized individuals with plates showing bare spots (R ~1.4), but becoming completely covered in granules in larger specimens (R > 1.4–1.5). Granules, when present, rounded, distributed evenly on plate surface. Fasciolar channels shallow, present on actinal surface. Granules 10–70 on actinal plates, rounded on centre of plate, more angular, poly-gonal around periphery.

Adambulacral plates elongate. Furrow spines, polygonal to quadrate in cross section, slightly compressed 2–4, usually 3–4, weakly concave. Larger specimens regularly with four furrow spines, becoming 2–3 furrow spines distally. Two subambulacral spine series. Subambulacral spines 2–4, usually three, adjacent to furrow spines, weakly concave, oval to round in cross section.

Third subambulacral spine series, 3–4, granular, quadrate to polygonal in cross section, adjacent to granules on actinal plates. Shortest in height relative to furrow spines, separated from remaining actinal granules.

Oral plate with 4–6 furrow spines, quadrate to polygonal in cross section, comparable in thickness to other furrow spines. Spines directed into mouth, triangular in cross section. Oral plate periphery with 10–15 spines. Spines on oral plate seam, paired 1:1 with those on other half of oral plate. Spines on oral plates triangular to polygonal in cross section.

Distribution

Japan, Ryuku Is, Okinawa; 3–67 m.

Etymology

The species is named for Onna Village, near the type locality.

Genus *Anchitosia*, gen. nov.

Type species: *Tosia queenslandensis* Livingstone, 1932.

Diagnosis

As for species (below).

Etymology

The genus name is derived from the Greek *anchi*, meaning 'near' referring to the close association of this species with the genus *Tosia* the original genus designation, which is derived from the Latin for 'inestimable'.

Anchitosia queenslandensis (Livingstone), comb. nov.

(Fig. 4*D–F*)

Tosia queenslandensis Livingstone, 1932*a*: 243. – Livingstone 1932*b*:
    381; H. L. Clark, 1946: 94; A. M. Clark, 1953: 411; Endean, 1957:
    238, 258; Clark & Rowe 1971: 34, 48; Jangoux, 1984: 282, 1986:
    122; Coleman, 1994: 17; Gosliner *et al.*, 1996: 254; A. M. Clark,
    1993: 289; Saba *et al.*, 2002: 25.

Material examined

Japan. Ryukyu Is: Okinawa: 1 dry spec. (R = 1.6, r = 0.9), 1 km WNW of Onna Village, Horseshoe Cliffs, 26°30′N, 127°50′54″E, 6.1 m (20 ft) (NMNH E53610); 1 dry spec. (R = 1.7, r = 0.9), data as for previous speci-men, 58 m (NMNH E53616); 1 dry spec. (R = 1.2, r = 0.7), Seragaki Beach, 1.3 km ENE of Maeki-Zaki, 26°30′24″N, 127°52′36″E, 3–6 m (10–20 ft) (NMNH E53613); 1 dry spec. (R = 1.5, r = 1.0), Makiminato (CASIZ 106985); 1 dry spec. (R = 1.8, r = 0.8), Makiminato, rubble zone (CASIZ 106986); 1 dry spec. (R = 1.7, r = 1.0), Sesoko I. (CASIZ 106987); 1 dry spec. (R = 2.0, r = 1.0), Chatan, reef front (CASIZ 107055). **Papua New Guinea. China Strait:** 1 dry spec. (R = 1.5, r = 1.0) (NMNH E10050). **Australia. Queensland:** 1 dry spec. (R = 1.7, r = 1.0), Great Barrier Reef, Lizard I., south face of reef front, 2–10 m (NMNH E23749).

Diagnosis

Body form stellate, approximately 16 marginals per interradius. Furrow spines two at R = 2.0 cm. Granules absent from marginal plate surface. Tubercular granules, spinelets absent from abactinal, marginal plate surfaces. Actinal intermediate plates always bare.

Description

Body form weakly stellate, overall size relatively small, arm tips rounded. Abactinal plates flattened to convex (especially in carinal series), round to polygonal in outline. Primary circlet plates enlarged, distinctive. Papular pores single or double, present radially, absent interradially. Peripheral granules polygonal to quadrate, discrete from plate (not flush). Madreporite triangular. Fasciolar grooves present, shallow. Marginal plates bare, smooth, mildly convex, granules absent, Marginal plates wider than long, symmetrically round in cross section. Superomarginal to inferomarginals correspond roughly 1:1. Penultimate superomarginal plates neither swollen nor elongate and not abutting over mid radius. Fascioles between marginal plates present, relatively well developed. Superomarginals and inferomarginals 9–12 per interradius (from terminal to terminal), bare, smooth, some specimens with minor surface rugosities. Distalmost superomarginals, more swollen than interradial, symmetrically round in cross section. Peripheral accessory granules discrete (not flush with plate) polygonal to quadrate, rectangular. Terminal plate enlarged, 1–2× size of adjacent superomarginal plates. Actinal plates, relatively large, angular to polygonal, smooth, bare surface, granules absent. Peripheral granules on actinal plates polygonal to quadrate in shape. Furrow spines 2–5 compressed, but thickened, subambulacrals granular, thickened (similar in thickness to furrow spines). Pedicellariae, when present, in pits, with tong-like valves. Adambulacral plates with straight, outward facing surface. Adambulacral 'divider' oriented vertically, directed proximally.

Colour in life deep red to orange with yellow highlights between plates.

Distribution

Japan (Okinawa, Ryukyu Is), Papua New Guinea, Great Barrier Reef, Australia to New Caledonia; 0–58 m.

Genus *Toraster* A. M. Clark

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

Type species: *Astrogonium tuberculatum* Gray, 1847.

Diagnosis

As for species (below).

Toraster tuberculatus (Gray)

Fig. 5*A–C*

Astrogonium tuberculatum Gray, 1847: 79.
Pentagonaster tuberculatus Perrier, 1875: 222. – Perrier, 1876: 38; Bell, 1905: 246.

Tosia tuberculata Verrill, 1899: 161. – Fisher, 1911: 166; H. L. Clark, 1923*a*: 266, pl. 9, figs 1–2. H. L. Clark, 1926: 11; Mortensen, 1933: 243, pl. 10, figs 5–7.
Toraster tuberculatus A. M. Clark, 1952: 205. – A. M. Clark & Courtman-Stock, 1976: 66; Clark in A. M. Clark & Downey, 1992: 267; A. M. Clark, 1993: 289.

Material examined

South Africa: 1 dry spec. (R = 6.4, r = 3.5), Cape of Good Hope, False Bay (NMNH E19064); 1 dry spec. (R = 4.1, r = 2.3), Cape of Good Hope, 13 miles east of Vasco de Gama (USNM E19060); 1 dry spec. (R = 6.1, r = 4.2), off South Africa, 35°31′S, 21°14′E, 110 m (CASIZ 087576).

Diagnosis

Abactinal plates swollen, complex. Secondary areas completely covered by large spherical granules on abactinal and actinal intermediate plate surfaces. Papular pores two to three. Marginal plates 20-40 per interradius. Large bivalved pedicellariae on abactinal plates.

Description

Body form weakly to strongly stellate, relatively thin relative to *Tosia* or *Pentagonaster*. Arm tip rapidly narrowing, pointed distally. Abactinal plates extremely convex, swollen, mostly bare, smooth, round to polygonal in outline. Abactinal surface covered with large, evenly round, spherical granules covering some secondary plate surfaces and plate periphery, especially at lateral contact with superomarginal plate series. Abactinal plates all relatively uniform in size, radial/interradial plates not distinctive, not enlarged. Primary circlet plates sometimes enlarged. Abactinal plates relatively small compared with *Tosia* or *Pentagonaster*. Large bivalve pedicellariae present, commonly bisect abactinal plates. Madreporite polygonal. Double to multiple papular pores present, but absent interradially. Fasciolar grooves between abactinal plates well developed. Marginal plates convex longer than wide interradially becoming wider distally, relatively small compared with *Pentagonaster* or *Tosia*, decreasing in size distally. Enlarged bivalve pedicellariae similar to those on abactinal plate surface irregularly present on superomarginal plates. Large, spherical granules, similar to those on abactinal surface, form periphery and cover partial superomarginal and inferomarginal surface, especially on lateral marginal plate surface. Granules sometimes distributed patchily over plate surface. Fasciolar grooves between marginal plates well developed. Swollen penultimate marginal plates absent. Multiple (3–6) superomarginal plates in contact across midradius adjacent to arm tip, becoming more swollen, wider distally. Actinal plates polygonal, obscured by spherical granules identical to those on abactinal, marginal plate surface, relatively small in size compared with those in *Tosia* or *Pentagonaster*. Furrow spines enlarged, relatively few (1–3) in number per plate. Subambulacrals also thickened, granular, becoming indistinguishable from actinal granulation. Adambulacral plate surface facing furrow straight in outline. Adambulacral 'divider' directed horizontally, oriented symmetrically.

Living colour described by Mortensen (1933: 243) as a 'beautiful red'.

Distribution

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

Genus *Pentagonaster* Gray

Pentagonaster Gray, 1840: 280. – Perrier, 1875: 190; Sladen, 1889: 264 (pt.); Verrill, 1899: 157; Fisher, 1911: 166; Ludwig, 1912: 8; H. L. Clark, 1946: 88; A. M. Clark, 1953: 398; Spencer & Wright, 1966: U58; A. M. Clark, 1993: 269; Clark in H. E. S. Clark & McKnight, 2001: 92.

Stephanaster Ayres, 1851.

Buterminaster Blake in Blake & Zinsmeister, 1988: 494

Type species: *Pentagonaster pulchellus* Gray, 1840 by original designation.

Diagnosis

Body robust, weakly stellate to pentagonal. Arm tips rounded. Abactinal plates round to polygonal, bare, smooth, surface granules absent. Some abactinal plates flattened, but mostly convex. Plate size large, relative to sister-taxa, Primary circlet distinctive, but interradial plates not enlarged. Peripheral accessory granules relatively large, coarse, compared with sister-taxa (e.g. *Tosia*), well spaced, polygonal to quadrate in shape. Double and multiple papular pores on complete abactinal surface (radial and interradial regions). Fasciolar channels relatively well developed. Madreporite triangular in most specimens. Marginal plates well developed, distinctly forming border around body, smooth, bare, granules absent from plate surface, relatively large, longer than wide, very convex, symmetrically round in cross section. Marginal plates large relative to sister-taxa, 3–8 plates per interradius. Peripheral accessory granules relatively coarse compared with sister-taxa, well spaced, polygonal to quadrate in shape, discrete (not flush with plate), well spaced. Fasciolar channels between marginal plates relatively well developed. Penultimate superomarginals enlarged, elongate, commonly in contact over mid-radius. Penultimate inferomarginals enlarged in *P. pulchellus* and *P. stibarus* but absent in *P. dubeni*. Actinal intermediate plates, large relative to sister-taxa, polygonal in shape, bare, granules absent from plate surface. Peripheral accessory granules relatively large, coarse, compared with sister-taxa (e.g. *Tosia*), well spaced, polygonal to quadrate in shape. Fasciolar channels present between actinal plates. Furrow spines thick, blunt, relatively few (1–3) per adambulacral plate. Subambulacrals thickened, in multiple rows, granular to polygonal in shape. Pedicellariae with slender valves, Adambulacral plate surface facing furrow straight in outline. Adambulacral 'divider' directed horizontally, oriented symmetrically.

Pentagonaster dubeni Gray

(Fig. 6*A*–*B*)

Pentagonaster dubeni Gray, 1847: 79. – Tenison-Woods, 1878: 91; Ludwig, 1912: 18; H. L. Clark, 1928: 380; 1938: 79; 1946: 88; A. M. Clark, 1953: 400; 1966: 308; Shepherd, 1968: 308; Dartnall, 1969: 54; 1972: 75; 1980: 8, 33, Zeidler & Shepherd, 1982: 408; A. M. Clark, 1993: 271; Coleman, 1994: 16; Gosliner *et al.*, 1996: 254; Edgar, 1997: 337; Davie, 1998: 222.
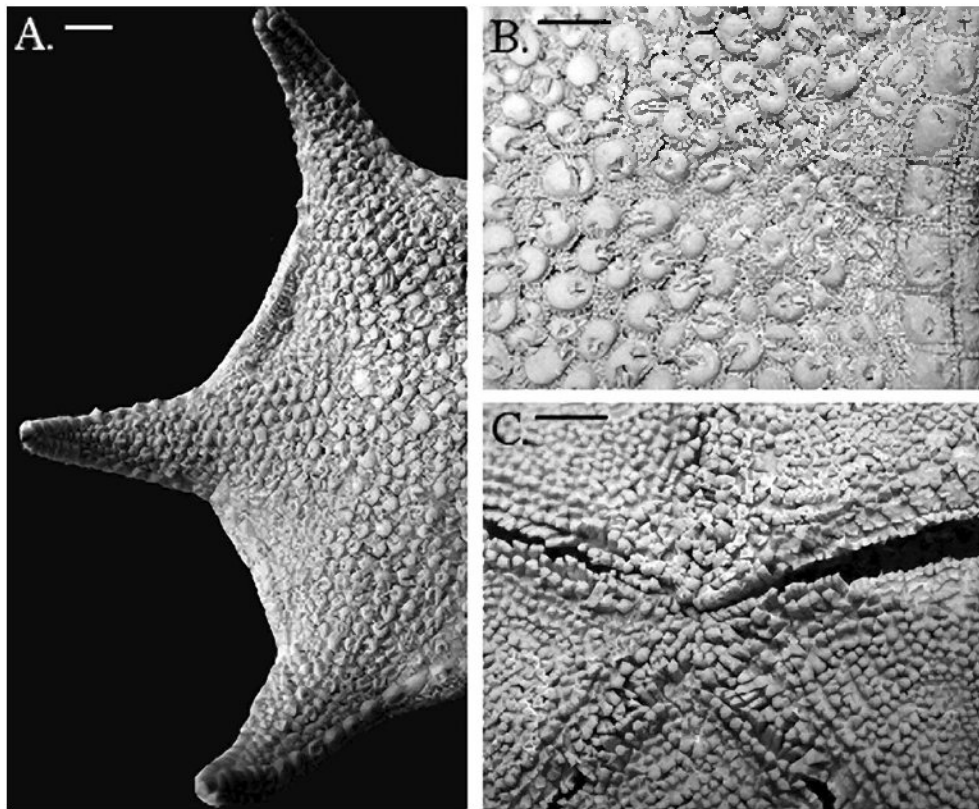

Fig. 5. *Toraster tuberculatus*. NMNHIZ E19064: (*A*) abactinal surface; (*B*) abactinal surface, close-up showing granules, pedicellaria; (*C*) actinal surface. (Scale bars = 0.5 cm.)

Astrogonium crassimanum Möbius, 1859.
Goniaster dubeni Lütken, 1865: 144.
Pentagonaster gunni Perrier, 1875.
Astrogonium dubeni Sladen, 1889: 748.
Stephanaster dubeni Perrier, 1894: 403.
Pentagonaster crassimanus (Möbius, 1859). – Ludwig, 1912: 15; H. L. Clark, 1946: 89.

Material examined

Australia. New South Wales: 1 dry spec. (R = 4.2, r = 1.6), Sydney Harbour, Fairlight, near Manly, subtidal (LACM 1964–291.1); 1 dry spec. (R = 3.7, r = 2.2), Dobroyd Head, near Manly, on rocky bottom, 15 m (50 ft) (NMNH E14291); 1 dry spec. (R = 2.8, r = 1.2), Port Jackson (NMNH 17765); 1 wet spec. (R = 3.7, r = 1.7), Port Jackson (NMNH 17881). **Western Australia:** 1 dry spec. (R = 3.7, r = 1.7), Houtman Abrolhos 1s (LACM 1972–429.1); 1 dry spec. (R = 4.6, r = 2.0), Geographe Bay, Quindalup (LACM 1972–430.1); 3 dry specs (R = 3.1, r = 1.6, R = 3.8, r = 1.6, R = 2.7, r = 1.2), Fremantle, 6.1 m (NMNH E13775).

Diagnosis

Arms elongate, disk small with R/r range = 2.0–2.6. Supero-marginal and inferomarginal plate series mismatched distally (ratio of 7/4). Inferomarginals not enlarged.

Distribution

Central east to south-east coast, Bass Strait, south to south-west and western Australian coast, including Tasmania; 0–200 m.

Pentagonaster elegans (Blake in Blake & Zinsmeister)
(Fig. 6C–E)

Buterminaster elegans Blake in Blake & Zinsmeister, 1988: 495.

Material examined

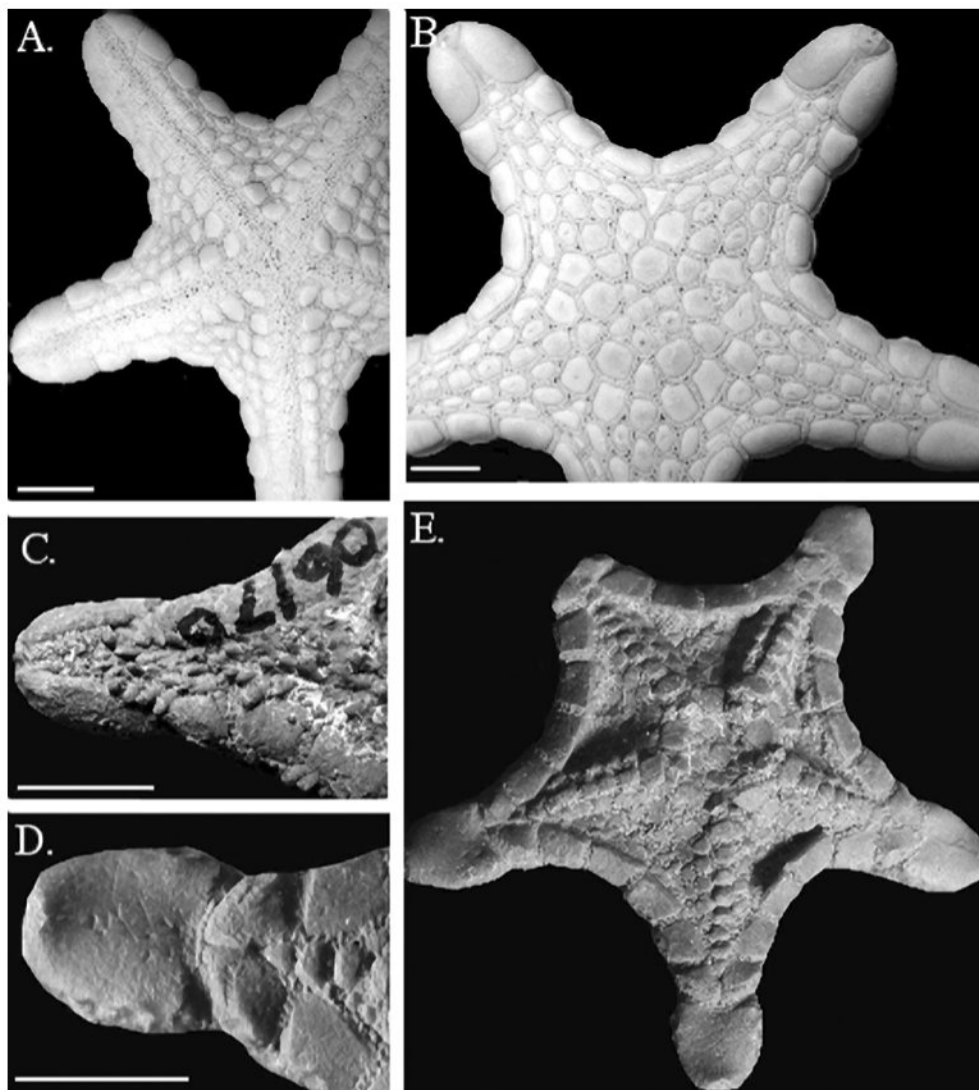*Holotype.*   Antarctica, west side of Seymour 1., Upper Eocene, La Meseta Fm. (NMNH-P 406170).

Fig. 6. *Pentagonaster dubeni.* NMNH1Z E13775: (*A*) actinal surface; (*B*) abactinal surface. *Pentagonaster* (*formerly Buterminaster*) *elegans* NMNH-P 406170: (*C*) actinal surface, arm tip; (*D*) arm tip, enlarged 'terminal' plate; (*E*) abactinal surface. (Scale bars = 0.5 cm.)

Diagnosis

Abactinal plates bare, smooth, polygonal to round in outline. Peripheral granules discrete, polygonal. Primary circlet plates distinctive, interradial primary circlet plates enlarged. Madreporite trigonal. Marginal plates bare, smooth, with length greater than width. Columnar spines described in Blake and Zinsmeister (1988: 494) on inferomarginals, terminals similar to furrow spines and may have simply been displaced. Terminal plate enlarged into toe-shaped single plate. Furrow spines thickened. (More information on morphology and condition of specimen is given in Blake and Zinsmeister (1988).)

Distribution and geologic age

Eocene, La Meseta Formation, Seymour I., Antarctica.

Pentagonaster stibarus H. L. Clark

(Fig. 7*A–B*)

Pentagonaster stibarus H. L. Clark, 1914: 136. – H. L. Clark, 1916: 44; 1923b: 238; Mortensen, 1925: 285; H. L. Clark, 1946: 89; Marsh *et al.*, 1999: 396.

Material examined

Western Australia: 1 dry spec. (R = 1.5, r = 1.4), Indian Ocean, Houtman Abrolhos Is, Wooded Isle (NMNH E6478).

Diagnosis

Abactinal plates smooth, convex, round to polygonal in outline. Six superomarginals per interradius (exclusive of enlarged plates) at R = 5.2 (two per interradius (exclusive of enlarged plates) at R = 1.5). Penultimate or antepenultimate superomarginal and inferomarginal plates enlarged. Furrow and subambulacral spines flattened, nearly flush with actinal surface.

Pedicellariae with two to three (primarily three) slender valves irregularly present on abactinal surface; not recorded from actinal surface.

Colour in life 'bright orange' (H. L. Clark 1914).

Distribution

Western Australia, Houtman-Abrolhos I. region, including Wooded Isle and to the south between Fremantle and Geraldton; 73–183 m.

Pentagonaster pulchellus Gray

(Fig. 7*C–I*)

Pentagonaster pulchellus Gray, 1840: 280. – Hutton, 1872: 8; Perrier, 1875: 202; Tenison-Woods 1878: 91; Benham, 1909: 11; Ludwig, 1912: 9; Mortensen, 1925: 281; Farquhar, 1927: 237; Young, 1929: 159; Fell, 1947: 21, 1952: 8, 1958: 12, 1959: 136, fig. 20, 1960: 56, 1962*a*: 31; A. M. Clark, 1953: 396; McKnight, 1967: 300; H.E.S. Clark 1970: 3, Town, 1978: 52; Fenwick & Horning, 1980: 439; A. M. Clark, 1993: 274; Gill, 1998: 10; H. E. S. Clark in H. E. S. Clark & McKnight, 2001: 92.
Astrogonium pulchellum Müller & Troschel, 1842: 55. – Sladen, 1889: 748; Farquhar, 1895: 200, 1897: 194, 1898: 310.
Stephanaster elegans Ayres, 1851: 118.
Pentagonaster abnormalis Gray, 1866: 11, pl. 8(1, 2). – Benham, 1909: 93, pl. 8(5).
Astrogonium abnormale Farquhar, 1898: 310.

Material examined

New Zealand: 1 dry spec. (R = 4.1, r = 2.6), Stewart 1. (CASIZ 028704); 6 dry specs (R = 5.4, r = 3.5; R = 5.6, r = 3.8; R = 5.8, r = 3.4; R = 5.7, r = 3.2; R = 4.2, r = 2.7; R = 4.2, r = 3.0) (NMNH E9988); 3 dry specs (R = 3.0, r = 1.6; R = 3.0, r = 2.1; R = 2.7, r = 1.7), South 1., east of Omaru, 45°37′S, 170°48′E, 51 m (NMNH E13482); 1 dry spec. (R = 2.7, r = 1.8) between South 1. and Stewart 1., Foveaux Strait, 22–37 m (NMNH E10143); 3 dry specs (R = 3.8, r = 2.4; R = 3.8, r = 2.5; R = 3.2, r = 1.9), Wellington, Island Bay, intertidal (NMNH E16334).

Diagnosis

Body weakly stellate to pentagonal with short arms, rounded arm tips. Four, but up to six or seven, pairs of marginal plates (exclusive of enlarged penultimates) per interradius. Penultimate superomarginals and inferomarginals enlarged.

Colour in life brown, red, orange, yellow, grey or purple with lighter coloured oral surface.

Distribution

North of Auckland to ~48°S (Snares Is), Cook Strait, east coast of South Island, New Zealand, Chatham Is; 0–215 m (peak occurrence 0–50 m).

Genus *Tosia* Gray

Tosia Gray, 1840: 281. – Gray, 1847: 80, 1866: 11; Verrill, 1899: 148, 158, 160 (emended); Fisher, 1906: 1052, 1911: 166; Ludwig, 1912: 1, 22; H. L. Clark, 1946: 93; A. M. Clark, 1953: 396; Spencer & Wright, 1966: U58; Halpern, 1970: 168; Downey in Clark & Downey, 1992: 268.
Astrogonium Müller & Troschel, 1843: 116.
Stephanaster Perrier, 1894: 403.
Type species: *Tosia australis* Gray, 1840.

Diagnosis

Body, robust, thickened. Pentagonal to weakly stellate. Arm tips rounded. Abactinal plates bare, granules absent, convex to swollen with tubercular points, relatively large compared with those in other sister-taxa. Radial regions with swollen, very convex plates. Primary circlet distinctive, interradial plates enlarged. Peripheral accessories polygonal to quadrate, discrete from plate, closely distributed, smaller, finer, than those in *Pentagonaster*. Madreporite triangular. Double to multiple papular pores present across complete abactinal surface (radial and interradial). Well developed fasciolar channels present between abactinal plates. Marginal plates blocky, bare, swollen, convex, symmetrically rounded in . Peripheral accessory granules polygonal to quadrate, relatively small, fine compared with those in *Pentagonaster*. Fasciolar channels well developed between plates. Penultimate superomarginals enlarged, swollen, sometimes elongate. Penultimate inferomarginals never enlarged, never swollen or elongate. Actinal plates relatively large, polygonal in outline, flattened to mildly convex, bare, smooth, granules absent from surface. Fasciolar channels poorly developed. Peripheral accessory granules relatively fine, smaller relative to those in *Pentagonaster*, discrete from plate, polygonal to quadrate in shape. Furrow spines thickened, few in number (typically 1–3 per plate). Subambulacral spines, often granular, blunt, thickened, in multiple rows. Pedicellariae, when present, with paddle-like valves. Adambulacral plate surface

facing furrow straight in outline. Adambulacral 'divider' directed horizontally, oriented symmetrically.

Tosia australis Gray

(Figs 8*D–E*, 9*A–F*)

Tosia australis Gray, 1840: 289. – Ludwig, 1912: 23; H. L. Clark, 1928: 381, 1938: 77, 1946: 94; A. M. Clark, 1953: 404; Dakin, 1960: 321; Shepherd, 1968: 741; Marsh, 1976: 216; Dartnall, 1969: 54, 1972: 75, 1980: 8, 33; Zeidler & Shepherd, 1982: 408; Marsh, 1991: 445; A. M. Clark, 1993: 288; Coleman, 1994: 17; Edgar, 1997: 337.

Astrogonium geometricum Müller & Troschel, 1842: 54.
Tosia astrologorum Müller & Troschel, 1842: 54. – Tenison-Woods, 1878: 92; Verrill, 1899: 161.
Tosia australis var. *astrologorum* Müller & Troschel, 1842: 54.
Astrogonium nobilis Müller & Troschel, 1843: 116.
Tosia rubra Gray, 1847: 81.
Tosia tubercularis Gray, 1847: 80. – Livingstone, 1932: 378.
Pentagonaster australis Perrier, 1875: 200.
Pentagonaster minimus Perrier, 1875: 207.
Tosia nobilis Tenison-Woods, 1878: 92. – Ludwig, 1912: 30; A. M. Clark, 1953: 406, pl. 45, figs 3, 4, 6, 7, pl. 46, figs 1–2; Marsh, 1976: 217; A. M. Clark, 1993: 289.
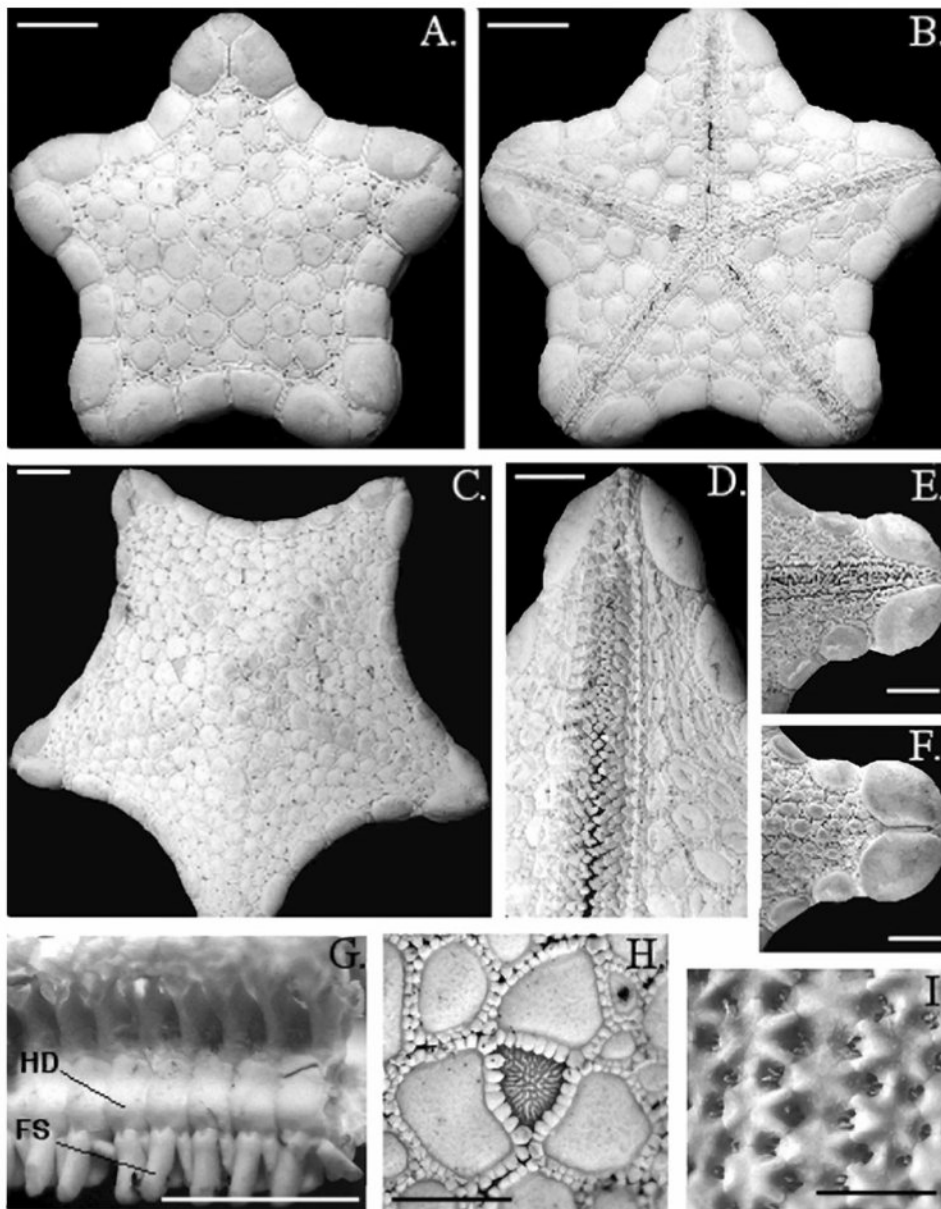

Fig. 7. *Pentagonaster stibarus* NMNH E6478: (*A*) abactinal surface; (*B*) actinal surface. *Pentagonaster pulchellus* NMNH E16334: (*C*) abactinal surface; (*D*) actinal surface, ambulacral furrow, spines. CASIZ 028704: (*E*) enlarged penultimate inferomarginal plates; (*F*) enlarged penultimate superomarginal plates. NMNH E13482: (*G*) adambulacral plates showing furrow spines (FS) and horizontal divider (HD); (*H*) triagonal madreporite; (*I*) multiple papular pores (viewed from coelomic side). (Scale bars = 0.5 cm.)

Material examined

Australia. Victoria: 1 dry spec. (R = 2.9, r = 1.8), Sorrento (LACM ECH-46); 1 dry spec. (R = 1.0, r = 0.8), Lorne, Point Grey, intertidal rocks and algae (NMNH 3102); 2 dry specs (R = 2.4, r = 1.8; R = 1.2; r = 0.8), Lorne, Point Grey, intertidal rocks and algae (NMNH E47792). **Tasmania:** 2 dry specs (R = 2.0, r = 1.4; R = 1.8, r = 1.3), Tasmania, (NMNH 17895). **South Australia**: 2 dry specs (R = 3.1, r = 2.1; R = 2.3, r = 1.7), Great Australian Bight, Gulf of St Vincent near Adelaide (NMNH E9601); 1 dry spec. (R = 2.6, r = 2.0), Indian Ocean (NMNH E37372); 3 dry spec. (R = 2.6, r = 2.0; R = 2.3, r = 1.7; R = 2.3, r = 1.7), Indian Ocean, Kangaroo I. (NMNH E47791); 1 dry spec. R = 3.2 r = 2.4), Indian Ocean (NMNH E47794). **Western Australia:** 1 dry spec. (R = 5.1, r = 2.9), Esperance, Esperance Bay, 10 m (CASIZ 116087); 1 dry spec. (R = 2.2 r = 1.4), Geographe Bay off Dunsborough (CASIZ 116089); 1 dry spec. (R = 1.8, r = 1.3), Indian Ocean (NMNH E01359); 2 dry specs (R = 3.7 r = 2.2, R = 2.6, r = 1.5), Garden I., near Fremantle (NMNH E10568).

Diagnosis

Body form variable; pentagonal to weakly stellate with curved interradial arcs. Radial papular abactinal plates variably convex, from evenly round in cross section to tubercular with pointed tips. Marginal plates enlarged, typically 6–8 per interradius, often longer than wide interradially. Penultimate superomarginal plates commonly enlarged, swollen, and/or elongate. Superomarginal plate series swollen convex to tubercular. Furrow spines typically 1–3 (usually two) per plate. Pedicellariae, when present, paddle-like in shape.

Colour in life orange, brown, to purple-grey with lighter highlights and mottled patterns on abactinal surface.

Distribution

Bass Strait, Tasmanian coast, southern to south-western coast, western coast to Kalbarri, Western Australia; 0–40 m.

Tosia magnifica (Müller & Troschel)

(Figs 8*A–C*)

Astrogonium magnificum Müller & Troschel, 1842: 53, pl. 4, fig. 1.
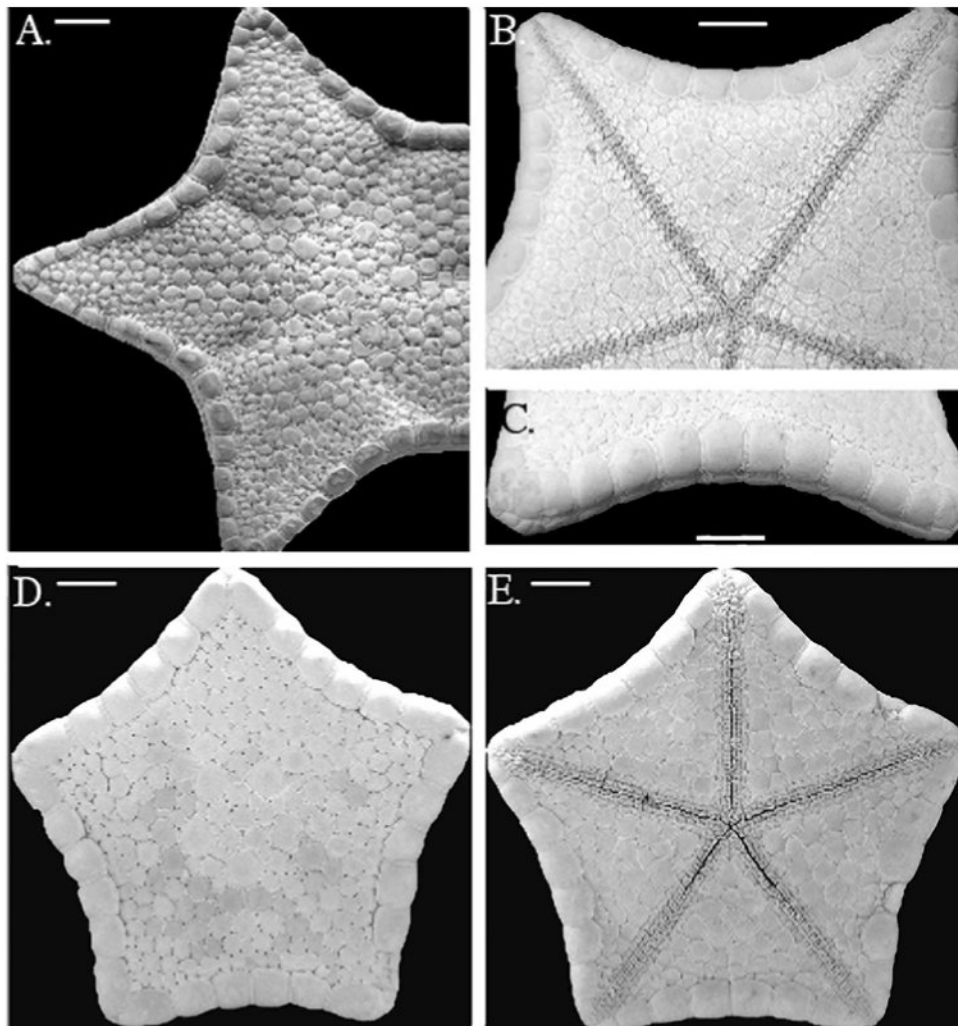*Astrogonium australe* Müller & Troschel, 1842: 55.

Fig. 8. *Tosia magnifica*: (*A*) abactinal surface NMNHIZ 33114; (*B*) actinal surface NMNHIZ 47790; (*C*) dorso-lateral view of abactinal and superomarginal plates. *Tosia australis* CASIZ 116088: (*D*) abactinal surface 'pentagonal form'; (*E*) actinal surface. (Scale bars = 0.5 cm.)

Astrogonium ornatum Müller & Troschel, 1842: 55.

Tosia aurata Gray, 1847: 80. – Gray, 1866: 11, pl. 16, fig. 2; Tenison-Woods, 1878: 92; Ludwig, 1912: 34;H.L. Clark, 1916: 43; Livingstone, 1932: 377, pl. 43, figs 3–9, pl. 44, fig. 3.

Tosia grandis Gray, 1847: 80. – Gray, 1866: 11, pl. 3, fig. 1; Livingstone, 1932: 380.

Astrogonium emili Perrier, 1869: 84

Pentagonaster auratus Perrier, 1875: 204 (1876: 20)

Pentagonaster magnificus Perrier, 1894: 390.

Tosia magnifica Ludwig, 1912: 36. – A. M. Clark, 1953: 408; Shepherd, 1968: 742; Dartnall, 1980: 8, 33; Zeidler & Shepherd, 1982: 410; Jangoux & deRidder, 1987: 90; A. M. Clark, 1993: 289; Coleman, 1994: 17; Edgar, 1997: 336.

Material examined

Australia. Tasmania: 1 dry spec. (R = 2.6 r = 2.0), Kettering, 23 miles S of Hobart, on jetty piles, 0–1 m (CASIZ 116086); 1 dry spec. (R = 6.8, r = 4.2) (NMNH 40042); 1 dry spec. (R = 2.5, r = 1.8), Maria I., 27.4 m (15 fms) (LACM 1939–286.1). **Victoria:** 1 wet spec. (R = 2.8, r = 2.1), Port Phillip Bay, Balcombe Bay (NMNH 10599); 1 dry spec. (R = 5.8, r = 3.7), Bass Strait (NMNH 33114); 1 dry spec. (R = 5.2, r = 3.1), Bass Strait, between Victoria and Tasmania (NMNH 38200); 1 dry spec. (R = 3.8, r = 2.8), Port Phillip Bay, Sandringham, 4.5 mi SW of Picnic Point 12 m (6.5 fms)

(NMNH E47789); 1 dry spec. R = 3.8, r = 2.7), Port Phillip Bay, Fawkner Beacon, 3 miles off Brighton, 18 m (10 fms) (NMNH E47790). **Western Australia:** 1 dry spec. (R = 2.6, r = 1.6), Cockburn Sound, N side of Jervois Groyne, under rocks, 2.4 m (LACM 1964–290.1).

Diagnosis

Superomarginal width greater than length, fewer in number and smaller in size relative to *T. australis*. Neither penultimate superomarginals or inferomarginals enlarged or swollen. Superomarginal plate series decreasing in size distally.

Colour in life red to white with darker mottled patterns on abactinal, superomarginal plate series.

Distribution

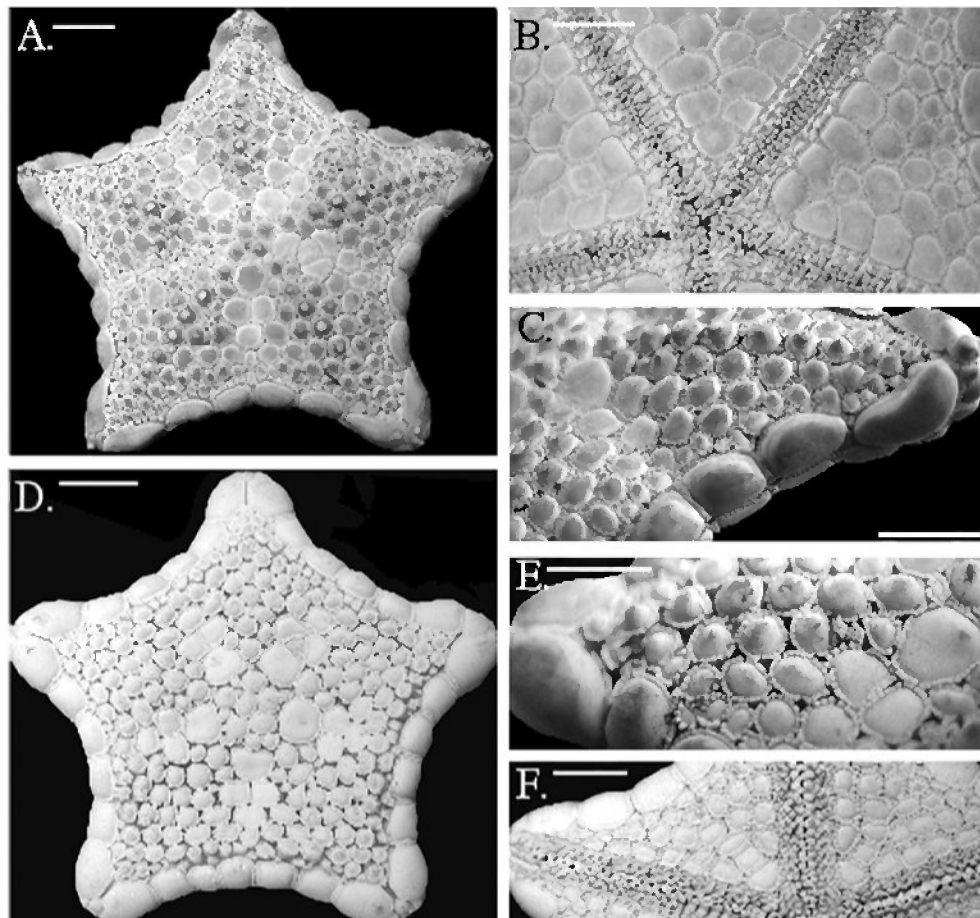Southern Australia: South Australia, Tasmania, Victoria; 0–200 m.

Fig. 9. *Tosia australis* (ex. *T. nobilis*) NMNHIZ E10568: (*A*) abactinal surface; (*B*) actinal surface; (*C*) lateral view showing tuberculate carinals and superomarginal plates. *Tosia australis* (= *T. astrologorum*) NMNHIZ E 47792: (*D*) abactinal surface; (*E*) actinolateral view showing swollen convex carinals; (*F*) actinal surface. (Scale bars = 0.5 cm.)

Outgroup taxa

Apollonaster yucatanensis Halpern

Material examined

Holotype. 1 dry spec. (R = 3.6, r-2.4), Gulf of Mexico, Yucatan, Arrowsmith Bank, 20°57′N, 86°34′W, 40–165 m, 10.ix.1967 (NMNHIZ #11285).

Lithosoma penichra Fisher

Material examined

Indian Ocean. Thailand: 1 dry spec. (R = approx. 8.5, r = approx 3.0 cm, specimen is damaged), 7°40′N, 97°9′E, west of Phuket, 503–512 m (NMNHIZ #53629).

Pontioceramus grandis Fisher

Material examined

Philippines. Cebu I.: 1 dry spec. (R = approx. 10.7, r = approx. 4.5, specimen damaged), Bohol Strait, Naga, 10°9′15″N, 123°52′E, 296 m (NMNHIZ 40578).

Discussion

Bathymetric shifts

Phylogenetic patterns (Fig. 10) support a general offshore to onshore or 'shallowing' trend, as defined by Jablonski and Bottjer (1988; and others), between basal and derived members of the ingroup. Offshore to onshore trends have been observed in other goniasterid taxa, including the tropical Pacific *Iconaster* (Mah 2005*a*). Basal members of the ingroup showed continental shelf distributions in relatively deep water (roughly 200–600 m). *Ryukuaster* and *Anchitosia* occur in relatively shallow water relative to *Akelbaster*, *Eknomiaster* and *Pawsonaster*.

Node 26 supports *Toraster* from deep-water (75–366 m) continental shelf habitats as basal to the largely shallow-water *Pentagonaster+Tosia* clade. *Tosia magnifica* has been reported within a wider and deeper depth range (0–200 m) compared with the more derived *T. australis* complex, which occurs in a narrower, shallower bathymetric range (0–40 m). This is consistent with the biogeographic hypothesis outlined above.

Bathymetric patterns (Fig. 10) are more ambiguous in *Pentagonaster*, as *P. dubeni* and *P. pulchellus* are reported as occurring over similar bathymetric ranges (0–200 m). The derived *P. pulchellus* has been reported by Clark and Mcknight (2001) as mainly occurring between 0–50 m, but peak occurrence data for *P. dubeni* is unavailable. *Pentagonaster stibarus* is reported from moderate depths (60–183 m), which is consistent with the ranges of other *Pentagonaster* species.

Biogeography, Buterminaster and historical events

Continental positions reconstructed by Dingle and Lavelle (2000) show Australia, Antarctica, the southern tip of Africa and the pre formed New Zealand in close proximity with nearly coterminous continental shelves in the mid-Cretaceous

(110 Mya). These positions are consistent with the geographic distributions of the ingroup taxa. *Eknomiaster* and *Akelbaster* show basal divergence and have been collected from the continental shelf off New Caledonia. *Eknomiaster macauleyensis* was collected from the Kermadec group near Macauley I. and Wanganella Bank, suggesting that the distribution for *Eknomiaster* is more widespread in the South Pacific. However, asteroid biodiversity in the south and central Pacific region remains poorly known and full distribution data for four of the genera included in the tree (*Eknomiaster*, *Akelbaster*, *Ryukuaster* and *Anchitosia*) are most likely incomplete.

The tree supports a basal split between *Pawsonaster* (that occurs in the tropical Atlantic) and the remaining Indo-Pacific taxa on node 32. The known occurrence of *Pawsonaster* extends from the tropical North Atlantic to Uruguay (Clark and Downey 1992). Connection between the North Atlantic and the South Atlantic was established by at least the Cenomanian (95 Mya) (Smith *et al.* 1994). The development and opening of the Atlantic Ocean would be consistent with ancestral populations of *Pawsonaster* on the coterminous continental shelf between South America and Antarctica (Dingle and Lavelle 2000). The coterminous shelf continued north throughout the South Atlantic and into the North Atlantic as South America and Africa separated in the Cenomanian. Full separation of South America and Antarctica in addition to development of the circum-Antarctic current with associated climatic events at the Eocene-Oligocene boundary may have cut off the northern populations and resulted in a localised polar extinction. Although fossils of *Pawsonaster* have not been recorded from Antarctica, other asteroid taxa, such as the goniasterid *Tessellaster*, have been recorded from Eocene fossils from Seymour I. and living in deep-water settings in the tropical North Atlantic (Blake and Aronson 1998).

Ryukuaster and *Anchitosia* have both been collected from the Ryuku Islands in Japan. *Ryukuaster* has been collected only from Okinawa in the Ryuku Is, whereas *Anchitosia* has been collected from Okinawa, Japan in addition to New Caledonia, Papua New Guinea, and Queensland, Australia. All specimens of *Ryukuaster* and *Anchitosia* examined and those described in the literature (e.g. Livingstone 1932; H. L. Clark 1946) indicate that adult specimens are relatively small in size. It is possible that this species has been overlooked in surveys of the Indo-Pacific region. If it is assumed that *Ryukuaster*'s occurrence in Okinawa is not a sampling artefact, its distribution may be explained as a consequence of extinction or endemism. The former hypothesis, which is most consistent with the phylogenetic tree (145 steps), suggests *Ryukuaster* was widespread throughout the south and central Pacific before an extinction event, removing it from most of its prior distribution, leaving a relictual population in Japan. If two more steps are added to the tree (147 steps), and *Ryukuaster* were placed as the sister-taxon to *Anchitosia*, the tree topology would be consistent with *Ryukuaster* as a derived regional endemic rather than a member of a basal divergence.

Toraster represents a basal split from the *Tosia+Pentagonaster* clade in Australia and New Zealand. Distribution data for *Toraster* suggest that it is restricted to the South African region. Although its distributional limits are unclear, other faunal accounts of the African coast (e.g. Walenkamp 1990) and the

adjacent Indian coast (e.g. Jangoux and Aziz 1988) and the Atlantic (Clark & Downey 1992), do not report *Toraster* occurring further north. The phylogeny is consistent with *Toraster* showing divergence from *Tosia+Pentagonaster* during the mid-Cretaceous. Africa shows substantially more movement away from the coterminous Antarctic/Australian shelf, which would be consistent with the marked morphological divergence of *Toraster* from *Tosia* and *Pentagonaster* (taxa included on node 26).

Pentagonaster pulchellus in New Zealand and *Pentagonaster stibarus* from the Abrolhos Is region in Western Australia are supported as sister-taxa to a branch including *P. dubeni*, which occurs along the east, west, and southern coasts of Australia (Rowe and Gates 1995) and *Pentagonaster* (formerly *Buterminaster*) *elegans* from the Eocene of Seymour I. (Antarctica).

The phylogenetic position of *P. elegans* supports an association between the biogeographic patterns observed in the ingroup taxa and the historical southern break-up of southern Gondwana between 90 and 30 Mya, as outlined by Dingle and Lavelle (2000) and Lawver and Gahagan (2003). The occurrence of *Pentagonaster elegans* on the Antarctic Peninsula and potentially throughout the Antarctic continental shelf in the Late Eocene (56–34 Mya) would be consistent with the resultant tree topology (Figs 1, 10). A coterminous continental shelf was

present between Australia and the pre formed Antarctic Peninsula up to the Paleogene (30 Mya) (Dingle and Lavelle 2000). The migration of Australia away from Antarctica and the development of the circum-Antarctic current in addition to perceived changes in climate (Clarke and Crame 1992) could have been associated with the extinction of *P. elegans* relative to its living sister-species. The movement and isolation of New Zealand away from Australia is argued as a potential mechanism resulting in the subsequent separation of *P. pulchellus* from the other *Pentagonaster* species. If a sister-group or otherwise close phylogenetic relationship between *P. stibarus* and *P. pulchellus* remains supported, several hypotheses including subsequent dispersal or extinction of a *P. stibarus* type ancestor are possible.

The phylogeny suggests *Tosia* (Fig. 10) is an Australian endemic. The geographically widespread *Anchitosia queenslandensis* (formerly *Tosia queenslandensis*) is interpreted as phylogenetically distant and separate from the exclusively Australian *Tosia*.

Tosia magnifica, which is distributed primarily along the southern Australian coast, is supported as basal to a derived *Tosia australis* species-complex. The *T. australis* species-complex occurs today in a shallower bathymetric range and across a wider geographic range than *T. magnifica*. This includes the variant morphologies that encompass *T. nobilis* and
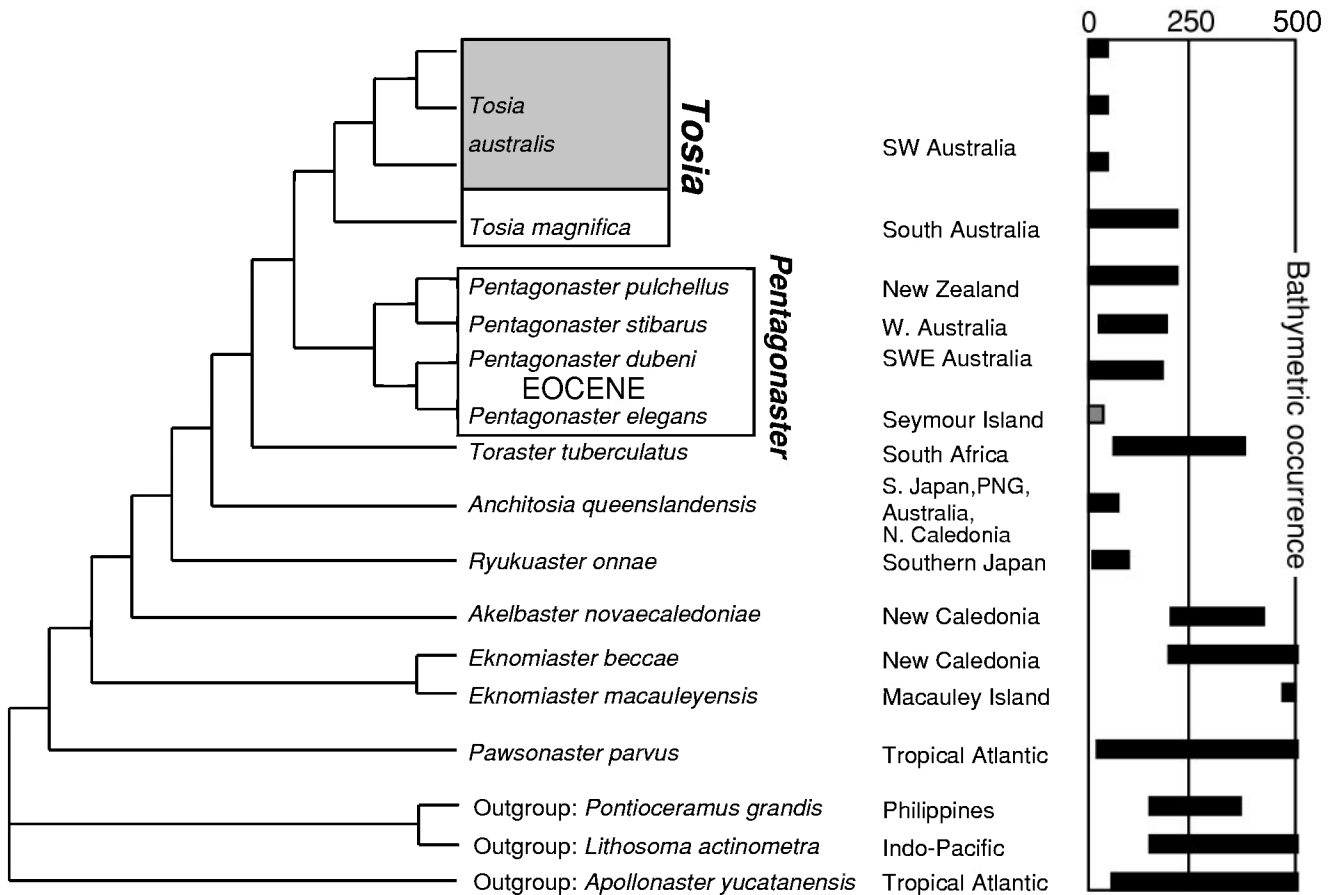

Fig. 10. Depth and occurrence mapped onto the phylogenetic tree. *Tosia australis* species-complex in shaded box. Grey bar for *Pentagonaster elegans* indicates shallow water sediment, but exact paleobathymetry is unclear.

T. australis var. *astrologorum*, which occur throughout southern and western Australia. Based on the wide range of morphological variability in *T. australis* across the extensive Australian coast (e.g. Livingstone 1932; A. M. Clark 1953), there remains strong potential for the discovery of cryptic species. Other shallow-water brooding asteroids (e.g., *Leptasterias*) showing wide morphological variability have demonstrated this potential (e.g., Hrincevich et al. 2000).

The Eocene/Oligocene development of the Antarctic circumpolar current, subsequent climate shift and the isolation of Antarctica from Australia (outlined in Clarke et al. 2004) are consistent with bathymetric and geographic shifts in *Tosia* and *Pentagonaster*. *Tosia magnifica*'s deeper bathymetric range and southern distribution is potentially relictual, derived from a more broadly distributed ancestor occurring throughout the continental shelf coterminous with Antarctica until the two continents were geographically and oceanographically separated.

Phylogenetic results for the ingroup (Figs 1, 10) do not agree with Fell's (1962*b*) West Wind Drift (WWD) dispersal hypothesis. This hypothesis outlined an east to west, Australia to New Zealand pattern of larval dispersal-based evolution as an explanation for the relationship between *Tosia* and *Pentagonaster*, implying that the latter was derived from the former. O'Hara (1998) presents a summary of outdated aspects and critical examination of the WWD hypothesis with respect to more recent knowledge of echinoderm and especially ophiuroid distributions and biodiversity. Phylogenetic evidence agrees with some very specific aspects of WWD with regards to larval dispersal at the species and population levels (e.g. Waters and Roy 2003*a*, 2003*b*) but meets with disagreement on a broader scale (e.g. O'Hara 1998). The WWD hypothesis also pre dates knowledge of plate tectonics (O'Hara 1998). Geographic distributions mapped onto the tree (Fig. 10) do not show an unambiguous east to west trend of diversification. The WWD hypothesis also assumes strict separation between the Australian/New Zealand and Antarctic faunas. This notion is starkly contradicted by the inclusion of the Eocene *Pentagonaster* (= *Buterminaster*) *elegans*, which strongly ties the *Pentagonaster* clade with the Antarctic. Other asteroid genera, such as *Sclerasterias*, which occur in New Zealand, have also been identified as Eocene fossils on Seymour I. in Antarctica.

Size: Cope's rule in asteroids?

Available specimen size data suggest that *Toraster*, *Tosia*, and *Pentagonaster* attain a larger adult body size than other ingroup taxa, especially the immediate sister-taxa, *Anchitosia* and *Ryukuaster*, which show a maximum *r* = ~2.0. It had been incorrectly assumed in early accounts of *Anchitosia* (as *Tosia queenslandensis*) that specimens were juvenile *Pentagonaster dubeni* (e.g. H. L. Clark 1946: 95; A. M. Clark 1953: 411). *Anchitosia* shows distinct morphological differences (Fig. 4 and Appendix 1) and has been recorded from New Caledonia and Okinawa, Japan – regions well outside *Pentagonaster* or *Tosia*'s known distribution. Recorded adult sizes for other sister-group taxa, including *Pawsonaster*, *Akelbaster*, and *Eknomiaster* suggest a smaller adult size (in terms of R) than those above node 26, although some do come close to overlapping in size (*P. dubeni* and *E. beccae*). Taxa included above node 24 also show stronger expression of stellate body form (i.e. R:r is closer to 2:1 and

generally greater than 1:1, which represents the pentagonal body form). Adult *Toraster*, *Tosia* and *Pentagonaster* attain an adult R < 3.0, ranging up to ~4.0.

Larger body size in these taxa would be consistent with Cope's Rule, which has been stated as the tendency for evolutionary lineages to increase in size over time (Hone and Benton 2005). Several selective advantages have been attributed to large body size (summarised in Hone and Benton 2005) but many were based on interpretations from bilateral metazoans such as mammals and insects. Not all of these generalisations are appropriate (e.g. increased intelligence, success in mating, or potential for thermal inertia) for application to the non-endothermic adult pentameral body plan observed in asteroids. However, some of the selective advantages listed by Hone and Benton (2005) are consistent with aspects of the phylogenetic hypothesis. For example, larger size and survival through lean times and resistance to climatic variation and extremes would be consistent with the phylogenetic interpretation of the timing of events for the taxa above node 26 as continental shifts and climate changes (such as the separation of Australia from Antarctica) would have affected marine environments (as indicated above). Increased defence against predation could be interpreted as increased effectiveness of the closure of larger, more thickened adambulacral furrow spines as outlined for *Pentagonaster dubeni* and other valvataceans by Blake (1983). The development of brooding in *Tosia australis* would be consistent with the switch from r- to K-selection strategies as fewer offspring are produced with higher parental investments relative to non-brooding asteroid species.

Several patterns relating size, respiration, and temperature were consistent with the observations of body size in the ingroup taxa. A review of studies of environmental temperature versus organism size in ectotherms (Atkinson 1994) reported that 83.5% of the studies surveyed showed a significant reduction in size associated with increased rearing temperatures during development and also indicated a decrease in temperature as the cause of a majority of ectotherms to attain a larger size at a given stage of development. A recent study by Kingsolver and Pfennig (2004) shows that selection on individual organisms apparently favours larger body sizes. They argue that positive directional selection on individuals could translate into a macroevolutionary trend towards increased size of an entire lineage. This would be consistent with the size patterns observed among the ingroup taxa. *Anchitosia* and *Ryukuaster* occur in shallow-water tropical reef environments (Rowe and Gates 1995), which have higher water temperature relative to the habitats of other members of the clade that either inhabit deep continental shelf waters (e.g. *Eknomiaster*, *Akelbaster* and *Pawsonaster*) or subtropical temperate, shallow-water environments (e.g. *Pentagonaster*, *Tosia* and *Toraster*).

In amphipods, maximum potential size showed an increase as temperature decreased (Chapelle and Peck 1999). An association between larger body size and colder temperatures (resulting from climatic cooling during the Cenozoic) has also been shown in podocopid ostracods (Hunt and Roy 2006). Climate change events in association with development of the circum-Antarctic current at the Eocene/Oligocene boundary (~30–40 Mya: Zachos *et al.* 2001) that likely isolated *Tosia* and *Pentagonaster* from *Buterminaster* and other sister-taxa could have also affected overall body size of those taxa.

Large size and lower temperature have been associated with increased levels of dissolved oxygen in other invertebrates (Chapelle and Peck 1999). Although this has notion has met with some contention (Spicer and Gaston 1999), the pattern is also apparently observed in deep sea turrid gastropods (McClain and Rex 2001). Two derived morphological characters related to gas exchange (the widespread distribution of papular pores on the abactinal surface and the presence of multiple papular pores) occur in *Tosia* and *Pentagonaster* suggesting a relationship between larger body size in these taxa and increased opportunities for oxygen uptake. Some echinoids also have well developed respiratory papulae probably associated with an increased metabolic rate and decreased gas exchange efficiency in higher temperature shallow shelf habitats (Smith 1984; Villier *et al.* 2001). In the spatangoid *Heteraster*, well developed respiratory structures and increased size is similarly correlated with decreasing depth (Villier *et al.* 2001).

Intermarginal pits: their function and evolution

Relatively well developed pits covered with spines or granules are present at the junctions between the superomarginal and inferomarginal series in *Ryukuaster* (Fig. 4*B*) and *Akelbaster* (Fig. 3*C*, *E*) respectively. These structures are superficially similar in appearance to cribiform organs, which occur between superomarginal and inferomarginal series within particular families in the Paxillosida, including the Porcellanasteridae and the Goniopectinidae (Madsen 1961; Clark and Downey 1992). In the infaunal goniopectinid asteroid *Ctenodiscus*, it was observed (Shick *et al.* 1981) that cribiform organs acted as 'turbines' to drive current flow over its body into the fasciolar channels over the papulae and out the excurrent opening of its burrow. Ciliary driven feeding in other asteroids, such as the valvatacean *Porania* has also been observed (Gemmill 1915). The flattened granular spines in the intermarginal pit in *Akelbaster* sit openly (Fig. 3*C*, *E*), as they are in some porcellanasterids (e.g. *Hyphalaster*, see Fig. 3*D*), and are not closed in by lamellae as they are in *Ctenodiscus*. Well developed fasciolar channels between the marginal and abactinal plates are present in *Akelbaster* and cribiform organ-bearing paxillosidans suggesting that these intermarginal pits in conjunction with ciliary currents serve to irrigate the papulae and may possibly present fine particles to the mouth as a source of nutrition. The high numbers of bivalved pedicellariae present in *Akelbaster* may also be involved with prey capture or defence against small organisms drawn into the fasciolar channels, such as amphipods. However, no connections between the intermarginal pits and the coelom were evident. It is unknown if *Akelbaster* occurs in soft sediment substratum analogous to those inhabited by the Paxillosida.

The intermarginal pits in *Ryukuaster* are bare (Fig. 4*B*) and show less granular spine development than those of *Akelbaster*. Clavate spines occur on the periphery of these pits at the junctions between marginal plates in *Ryukuaster* but are absent on the surface of the pit itself. As in *Akelbaster*, the surface of these pits and spines are thought to be ciliated and capable of generating a current through the fasciolar channels. The functional significance of this simplified morphology is unclear.

Intermarginal pits on the tree were supported as plesiomorphic for the clade at node 27 occurring in *Akelbaster* and

Ryukuaster but subsequently showing loss in the more derived clades at node 24. The less developed intermarginal pit in *Ryukuaster* would be consistent with a reduction of this structure in the more derived members of the clade. Similar pits or cavities have been observed in the Cretaceous goniasterid *Haccourtaster hrbac* by Zitt (2005). However, the structures in *Haccourtaster* appear to be directed inwards rather than outwards and appear much larger and more elaborate relative to plate size than those in *Akelbaster* or *Ryukuaster*. *Haccourtaster* was also described as showing affinities with *Metopaster* (Zitt 2005), which, as indicated above, is phylogenetically distant from taxa on the *Pentagonaster* lineage. Interestingly, *Akelbaster* and *Ryukuaster* have relatively small adult sizes and a relatively pentagonal body shape similar to that of *Haccourtaster*. If functional interpretations for these intermarginal pits or cavities are considered as similar and/or analogous or homologous traits the similarities in size and shape may reflect functional or phylogenetic significance.

The unique intermarginal spination observed in *Akelbaster* is a novel morphological feature and represents a new expression of biological complexity with unknown significance. This further underscores the importance of the undiscovered biodiversity of the south and central Pacific Ocean (e.g. New Caledonia, etc.) and the overall importance that such discoveries may have on interpretations of phylogeny and traits seen in fossil taxa.

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Appendix 1.　Data matrix

Taxon	Characters						
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	66666
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345
Lithosoma actinometra	0000000100	0000111001	0001000000	0000000000	0000100011	0000000000	00010
Pontioceramus grandis	0000000100	0000011001	0001000000	0000000000	0000000001	0000000000	00010
Apollonaster yucatanensis	0000100100	0100011001	2001000000	0010000000	0010000101	1001200000	00100
Buterminaster elegans	110010????	1111110?01	001010??11	1111110?11	1111?????	11?10110?0	0????
Pentagonaster dubeni	1100101001	1111110101	0010111111	1111110011	1111111111	1111011000	00101
Pentagonaster stibarus	1100101001	1111110101	0010101011	1121110111	1121111111	1111131000	00101
Pentagonaster pulchellus	1100101001	1111110101	0010101011	1111111111	1111111111	1111131000	00101
Tosia australis	1100111001	1111010101	0000111111	0111111011	0111211101	1111221000	00011
Tosia australis var. *astrologorum*	1111111001	1111010101	0000111111	0211112011	0211211101	1111131000	00011
Tosia nobilis	1111111001	1111010101	0000111111	1211112011	1211111101	1111131000	00001
Tosia magnifica	1100111001	1111010101	0000100011	0111111011	0111211101	1111131000	00011
Toraster tuberculatus	1120000110	1102220102	2020200010	1100100010	1101000122	1111000100	01001
"Tosia" sp. nov. Okinawa	0100110110	0111010111	2100100011	0111110011	0111011101	1121220000	00000
Tosia queenslandensis	0100110110	0111010101	0000100011	1111120011	1111111101	1121110000	00001
"Tosia" parva	0000100100	0110111001	2010000001	0110110001	0111201001	1001221000	00010
Eknomiaster macauleyensis	0000100100	0110001000	0000000001	1111110001	1111001011	1001221000	00010
Eknomiaster beccae	0000100100	0110001000	1000000001	1111110001	1111001011	1001221100	01010
Gen., sp. nov. New Caledonia	1001110100	0111010011	0000110101	1121110001	1121101001	1121221111	11000

<div align="center">**Appendix 2.   Character list**</div>

Abactinal surface

(*1*)   *Plate convexity*: 0, flat (Figs 2*F*, 4*D*); 1, convex (Figs 5*B*, 9*C*, *E*).

(*2*)   *Plate shape*: 0, angular to hexagonal (Fig. 2*B*, *F*); 1, rounded to multi-sided (Fig. 7*H*).

(*3*)   *Degree of plate convexity*: 0, not swollen; 1, moderately swollen; 2, strongly swollen (Fig. 5*B*).

(*4*)   *Radial area plate development*: 0, not distinctive; 1, radial regions distinctive (Fig. 9*A*).

(*5*)   *Overall plate size*: 0, small (~20 carinal plates from disk to arm tip); 1, large (<15 carinal plates from disk to arm tip) (Fig. 6*B*, *E*).

(*6*)   *Interradial plate size*: 0, not enlarged; 1, enlarged relative to radial plates (Fig. 9*A*, *C*, *D*, *E*).

(*7*)   *Papular distribution*: 0, absent interradially; 1, present radially and interradially.

(*8*)   *Single papular pores*: 0, absent; 1, present.

(*9*)   *Double papular pores*: 0, absent; 1, present.

(*10*) *Multiple papular pores*: 0, absent; 1, present (Fig. 7*I*).

(*11*) *Fasciolar channels*: 0, shallow; 1, well developed (Fig. 9*D*, *E*).

(*12*) *Primary circlet plate size*: 0, similar in size relative to other plates; 1, enlarged (Fig. 3*A*).

(*13*) *Madreporite shape*: 0, polygonal; 1, triangular (Fig. 7*H*).

(*14*) *Peripheral granule-plate articulation.* 0, tightly articulated (Fig. 2*B*); 1, crowded (Fig. 5*A*, *B*); 2, well spaced (Fig. 9*E*)

(*15*) *Peripheral granule size*: 0, fine; 1, coarse; 2, very coarse (Fig. 5*B*, *C*).

(*16*) *Peripheral granule shape*: 0, rectangular; 1, quadrate to polygonal (Figs 7*H*, 9*E*); 2, spherical (Fig. 5*B*, *C*).

(*17*) *Peripheral granule flush*: 0, granules not flush (Figs 7*H*, 9*E*); 1, granules flush with plate (Fig. 2*B*).

(*18*) *Internal plate morphology*: 0, round to polygonal; 1, with stellate projections (Fig. 7*I*).

Marginal plates

(*19*) *Intermarginal pit*: 0, absent; 1, present (Fig. 3*C*, *E*, *F*).

(*20*) *Granular accessories*: 0, rectangular; 1, quadrate to polygonal; 2, spherical (Fig. 5*B*).

(*21*) *Granule distribution*: 0, absent (plate bare); 1, granules scattered (Fig. 2*B*, *D*, *E*, *F*); 2, granules clustered together (Fig. 4*A*, *B*, *C*).

(*22*) *Ganular spinelets*: 0, absent; 1, present (Fig. 4*B*).

(*23*) *Peripheral granule size*: 0, fine; 1, coarse; 2, very coarse (Fig. 5*B*).

(*24*) *Peripheral granule flush*: 0, granules not flush (Figs 4*B*, 5*B*); 1, granules flush with plate.

(*25*) *Peripheral granule articulation*: 0, tightly articulated; 1, crowded; 2, well spaced.

(*26*) *Marginal plate series correspondence*: 0, superomarginal to inferomarginal series correspond 1:1 or nearly so (Fig. 4*B*); 1, marginal plate series offset (Fig. 3*C*).

(*27*) *Penultimate superomarginal swollen*: 0, not swollen; 1, swollen (Figs 6*B*, 7*A*, *C*, *F*).

(*28*) *Penultimate superomarginal elongate*: 0, not elongate; 1, elongate (Fig. 7*C*).

(*29*) *Superomarginal fasciolar channels*: 0, absent; 1, present.

(*30*) *Superomarginal plate density*: 0, moderate; 1, blocky.

(*31*) *Superomarginal plate dimensions*: 0, width > length (Fig. 2*A*, *B*); 1, length > width (Figs 2*F*, 6*B*, *E*).

(*32*) *Superomarginal plate in cross section*: 0, angular; 1, rounded, symmetrical (Fig. 2*A*, *B*, *F*); 2, rounded-asymmetrical (Fig. 9*C*).

(*33*) *Superomarginal plate size*: 0, small (>20 per side); 1, moderate (6–15 per side); 2, large (three per side) (Fig. 3*A*, *B*, *C*).

(*34*) *Superomarginal plate size distribution*: 0, size decreasing distally (Fig. 2*A*, *B*); 1, size not decreasing distally (Fig. 3*A*, *C*).

(*35*) *Superomarginal plate convexity*: 0, not convex; 1, convex (Fig. 9*A*, *D*).

(*36*) *Superomarginals in contact along midradius*: 0, >3 plates; 1, single plate (Figs 2*A*, *B*, *F*, 6*B*); 2, no plates in contact (Fig. 4*D*).

(*37*) *Superomarginal plate tumid*: 0, not tumid; 1, tumid; 2, sharply tumid (Fig. 9*A*, *C*).

(*38*) *Penultimate inferomarginal enlarged*: 0, absent; 1, present (Fig. 7*B*, *D*, *E*).

(*39*) *Inferomarginal fasciolar channels*: 0, absent; 1, present.

(*40*) *Inferomarginal plate density.* 0, moderate; 1, blocky.

(*41*) *Inferomarginal plate dimensions*: 0, width > length; 1, length > width (Fig. 2*D*, *E*).

(*42*) *Inferomarginal plate in cross section*: 0, angular; 1, rounded-symmetrical (Fig. 2*D*, *E*); 2, rounded-asymmetrical.

(*43*) *Inferomarginal plate size*: 0, small (>20 per side); 1, moderate (6–15 per side); 2, large (three per side).

(*44*) *Inferomarginal plate convexity*: 0, not convex; 1, convex.

Actinal surface

(*45*) *Actinal plate granulation*: 0, complete granular covering (Fig. 5*C*); 1, plate bare (Fig. 9*B*, *F*); 2, combination bare and covered.

(*46*) *Actinal plate shape*: 0, angular; 1, polygonal to round (Fig. 9*B*, *F*).

(*47*) *Actinal plate size*: 0, small; 1, large (Fig. 9*B*, *F*).

(*48*) *Fasciolar channels*: 0, absent; 1, present.

(*49*) *Granule size.* 0, fine; 1, coarse; 2, very coarse (Fig. 5*C*).

(*50*) *Granule shape*: 0, rectangular; 1, polygonal to quadrate; 2, spherical (Fig. 5*C*).

(*51*) *Adambulacral plate in outline*: 0, palmate; 1, straight.

(*52*) *Furrow spine thickness*: 0, compressed; 1, thick (Fig. 7*G*).

(*53*) *Furrow spine number*: 0, many spines (5–15); 1, two spines (three in large specimens) (Fig. 7*D*, *G*); 2, three to four spines (four to five in large specimens).

(*54*) *Subambulacral spine thickness*: 0, not thick; 1, thick.

Appendix 2.   (continued)

Body morphology

(*55*) *Body shape*: 0, strongly stellate; 1, weakly stellate (Figs 7*A*, *C*, 8*A*, 9*A*, *D*); 2, pentagonal (Figs 2*A*, *F*, 3*A*, 8*D*).

(*56*) *Arm shape*: 0, acutely narrowing; 1, elongate and rounded; 2, broadly triangular; 3, short and rounded (Figs 7*A*, *B*, 9*D*).

(*57*) *Disk thickness*: 0, thin to moderate; 1, inflated.

Pedicellariae

(*58*) *Pedicellariae enlarged*: 0, not enlarged; 1, enlarged (Figs 2*D*, *E*, 5*B*).

(*59*) *Pedicellariae on all actinal plates*: 0, absent; 1, present. (Fig. 3*B*).

(*60*) *Single pedicellariae on each superomarginal*: 0, absent; 1, consistently present (Fig. 3*A*).

(*61*) *Single pedicellariae on each inferomarginal*: 0, absent; 1, consistently present (Fig. 3*B*).

(*62*) *Bivalve pedicellariae*: 0, absent; 1, present (Figs 2*D*, *E*, 5*B*).

(*63*) *Slender valved pedicellariae*: 0, absent; 1, present.

(*64*) *Elongate valved pedicellariae*: 0, absent; 1, present.

Skeletal character

(*65*) *Adambulacral plate 'dividers'*: 0, with proximal directed asymmetrical tilt; 1, lacking asymmetrical tilt (Fig. 7*G*).