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A molecular and morphological revision of genera of Asterinidae (Echinodermata: Asteroidea)

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Abstract

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A molecular phylogeny has inspired a reappraisal of the systematics of the Asterinidae. New morphological characters are defined and illustrated and used to diagnose all genera. A table of the distribution of morphological characters among genera and key for genera of Asterinidae are provided. New genera of Asterinidae are erected: *Aquilonastra* O'Loughlin, *Indianastra* O'Loughlin, *Parvulastra* O'Loughlin and *Pseudopatiria* O'Loughlin. *Patiria* is raised out of synonymy with *Asterina. Allopatiria* is a junior synonym of *Asterina*, *Manasterina* is a junior synonym of *Disasterina*, and *Paxillasterina* is a junior synonym of *Asterinides*. The genus *Asterinopsis* and the genus and species *Desmopatiria flexilis* are nomina nuda. *Patiriella tangribensis* is a nomen dubium. Genera reviewed are: *Anseropoda*, *Asterina*, *Asterinides, Callopatiria, Cryptasterina, Disasterina, Kampylaster, Meridiastra, Nepanthia, Paranepanthia, Patiria, Patiriella*, *Pseudasterina*, *Pseudonepanthia*, *Stegnaster*, *Tegulaster* and *Tremaster*. *Asterina cephea* var. *iranica* is raised to species status. *Enoplopatiria siderea* is a junior synonym of *Asterina stellifera*. *Disasterina leptalacantha* var. *africana* is no longer recognised as a subspecies. *Disasterina spinulifera* is a junior synonym of *Disasterina praesignis*. A synonymy of *Tremaster novaecaledoniae* with *Tremaster mirabilis* is formalised. Asterinid species reassigned on the basis of molecular evidence and morphological congruity are new combinations: *Aquilonastra anomala, A. batheri, A. burtoni, A. coronata, A. minor, A. scobinata, Meridiastra calcar, M. gunnii, M. medius, M. mortenseni, M. occidens, M. oriens, Paranepanthia aucklandensis, Parvulastra calcarata, P. exigua, P. parvivipara, P. vivipara, Patiria chilensis, P. miniata, P. pectinifera*. Species reassigned on the basis of morphological evidence are new combinations: *Aquilonastra cepheus, A. corallicola, A. heteractis, A. iranica, A. limboonkengi, A. rosea, Asterina ocellifera, Asterinides hartmeyeri, A. pilosa, A. pompom, Disasterina ceylanica, D. longispina, Indianastra inopinata, I. sarasini, Nepanthia pedicellaris, Parvulastra dyscrita, Pseudonepanthia briareus, P. gracilis, P. grangei, P. nigrobrunnea, P. reinga, P. troughtoni, Pseudopatiria obtusa, Tegulaster alba, T. leptalacantha, T. praesignis*. Three species remain incertae sedis: *Asterina lorioli, Asterina novaezelandiae* and *Nepanthia brachiata*. A table of asterinid species is provided, with original and current combinations. It is concluded that Asterinidae is a cosmopolitan family, mainly of shallow-water narrow-range genera but including some more widespread in deeper waters of all oceans.

Keywords

Echinodermata, Asteroidea, Asterinidae, new genera, taxonomy, molecular, morphology

Introduction

Traditional systematic studies of asteroids have been confounded, to an extent, by morphological characters that are of dubious phylogenetic value and limited by observable size and historical choice (Clark and Downey, 1992). Some morphological characters currently used in asteroid systematics, for instance, may be subject to strong selection and thus remain stable while evolutionary divergence occurs in other characters (e.g. molecular divergence in living fossils; Avise et al., 1994). Hence taxa that are superficially similar, and perhaps congeneric on traditional morphological criteria, may prove to be unrelated (O'Loughlin et al., 2002; Waters et al., 2004). Some other morphological characters may be plastic and readily diverge among taxa that are closely related (e.g. O'Loughlin et al., 2003). Current taxonomic treatments of asteroids may also be hindered by the possibility that certain morphological characters are phylogenetically informative for some clades but homoplasious and unreliable for others (Mah, 2000). The abundant phylogenetic information provided by DNA sequence data (Avise, 2000) presents a means of reassessing taxonomic relationships and stimulates reappraisal of morphological, behavioural, physiological and ecological traits.

The Asterinidae comprise 21 genera and about 116 species according to the comprehensive index of taxa by A.M. Clark (1993) and the subsequent work of Rowe (in Rowe and Gates, 1995), Campbell and Rowe (1997), O'Hara (1998), VandenSpiegel et al. (1998), A.M. Clark and Mah (2001), H.E.S. Clark and McKnight (2001), O'Loughlin (2002), O'Loughlin et al. (2002, 2003) and Dartnall et al. (2003). The need for a systematic revision was first commented on by Verrill (1913). Recently, Rowe (in Rowe and Gates, 1995), Campbell and Rowe (1997), O'Loughlin (2002) and O'Loughlin et al. (2002) noted continuing conflicting opinions on the systematic status of, and assignment of species to, the genera *Asterina* Nardo, 1834, *Asterinides* Verrill, 1913 and *Patiriella* Verrill, 1913.

O'Loughlin (2002) provided a restricted morphological review of Asterinidae and erected a new genus (*Meridiastra*) with three new species (*M. fissura, M. nigranota, M. rapa*). Hart et al. (1997) reported the first molecular phylogeny for 12 asterinid species assigned to the genera *Asterina* and *Patiriella*. The phylogeny indicated that neither *Asterina* nor *Patiriella* is monophyletic. O'Loughlin et al. (2002, 2003) reported two molecular phylogenies and the erection of four new Australasian asterinid species (*Patiriella medius, P. mortenseni, P. occidens, P. oriens*), provisionally assigned to *Patiriella* in the absence of molecular data from other genera. Hart et al. (2003) reported a molecular phylogeny on which Dartnall et al. (2003) erected an additional genus (*Cryptasterina*) and species (*C. hystera* Dartnall and Byrne, 2003). Waters et al. (2004) reported a molecular phylogeny (adapted in Fig. 1) for 31 asterinid species, predominantly Australasian. Their phylogeny showed strong resolution at shallow levels, with six well-supported clades. With additional species included, the polyphyletic assemblages of *Asterina* and *Patiriella* illustrated by Hart et al. (1997) were further elucidated. Some genera, defined on the basis of morphology, have molecular support. Other well-defined clades may deserve generic rank but need morphological support. Some genera as presently conceived appear polyphyletic. They invite reappraisal to explore whether morphology will support division into smaller unrelated genera.

This paper seeks congruence between morphological and molecular data: we evaluate the phylogenetic reliability of characters traditionally used to differentiate asterinid genera and explore the utility of new characters. Ideally, genera are monophyletic groups of species diagnosed by shared character states — morphological, behavioural and molecular — that reflect common descent (De Queiroz and Gauthier, 1992). Here we apply phylogenetically informative morphological characters to define genera anew and recognise new genera. The morphological analysis is extended to many asterinid genera and species for which there are currently no molecular data. Future molecular analyses will help to evaluate the decisions made here on the basis of morphology alone.

In the cladogram of Waters et al. (2004) basal relationships were unclear. It did not demonstrate the monophyly of the family as presently construed. *Dermasterias* (Asteropseidae) was placed within the asterinid clade. It should be noted that this relationship received minimal phylogenetic support. The unresolved affinities of *Demasterias* have little bearing on the objectives of this paper, which are to redefine genera currently assigned to the Asterinidae. On morphological evidence, the genus *Tremaster* Verrill, 1880 appears to be inappropriately included in Asterinidae. But a reassessment of what genera belong in Asterinidae, such as the inclusion or not of *Cycethra* Bell, 1881 (currently in Ganeriidae), and retention or not of *Tremaster*, should await appropriate molecular phylogeny data.

In this revision all of the species of all of the genera were reviewed, except for *Anseropoda* where a sample of species only was examined. Material for three asterinid species, for which the morphological descriptions raise doubts about their generic assignment, could not be found. They are placed incertae sedis.

Terminology follows that defined in the glossary and illustrated by Clark and Downey (1992, figs 2, 3), except that "papular space" ("restricted area with papular pores", fig. 15f) is used for "papular area", and "papulate areas" is used to refer to the parts of the abactinal surface where papulae occur (as defined by O'Loughlin, 2002). The form of spines and spinelets is of ten broad types (form frequently revealed by clearing with bleach): long and thin, needle-like, "acicular" (fig. 5c); round base and apical point, cone-shaped, "conical" (fig. 10g); long, thick, finger-like, "digitiform" (fig. 5e); short and thick, "granuliform" (fig. 5a), which may be subspherical, "globose" (fig. 5b), or "short columnar" (figs 15d, 16h); thin, few prominent points laterally and distally, "splay-pointed" (figs 5d, 6c, 9d); distal pointed glassy tip, "thorn-tipped" (fig. 17d); sac-like base and tapering distally to narrowly rounded end or point, "sacciform" (figs 5f, 8b, 8g, 9c); combination of "sacciform" and "splay-pointed" (fig. 5d). The armature of abactinal plates is consistently referred to as "spinelets", irrespective of size. The armature of actinal plates is consistently referred to as "spines", irrespective of size. Specimen size refers to preserved material, and is categorized as "small" (up to R = 25 mm), "medium" (R = 26–65 mm), and "large" (R greater than 66 mm). All measurements refer to preserved material.

Abbreviations for institutions are: AM, Australian Museum, Sydney; BMNH The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand, Te Papa Tongarewa, Wellington; NMV, Museum Victoria, Melbourne, Australia; TM, Tasmanian Museum, Hobart; UF, University of Florida, USA; USNM, United States Museum of Natural History, Smithsonian Institution, Washington; WAM, Western Australian Museum, Perth; YPM, Peabody Museum of Natural History, Yale University, New Haven; ZMUC, Zoological Museum, University of Copenhagen, Denmark. Photography for figures 4–18 was performed using a Leica MZ16 stereomicroscope, DC300 Leica digital camera, and "Auto-Montage" software for composition of images.

Invalid and junior synonyms of genera and species (indexed by A.M. Clark, 1993) are not repeated in this work unless their systematic status is reviewed. The summary distributional data given for the genera below are in part based on more detailed ranges given by A.M. Clark (1993), Rowe (in Rowe and Gates, 1995), O'Loughlin (2002), O'Loughlin et al. (2002, 2003), and Dartnall et al. (2003). Throughout the paper, "Rowe (1995)" refers to "Rowe (in Rowe and Gates, 1995)". The erection of

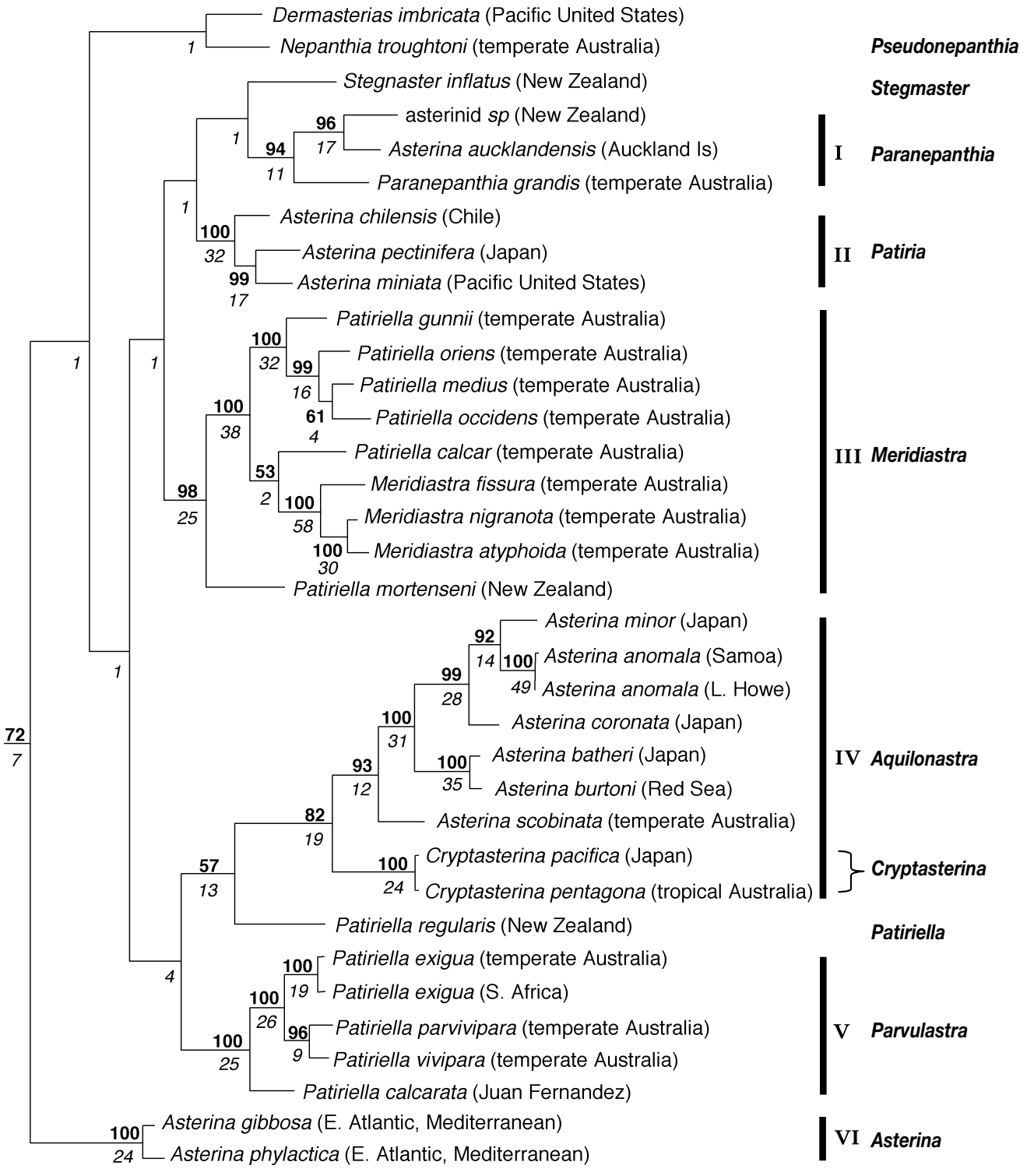


Figure 1. Phylogenetic relationships of asterinid mtDNA sequences (after Waters et al., 2004). Support for particular reconstructions is indicated by bootstrap values (>50%; in bold) and by decay indices (in italics). MtDNA Clades I–VI are identified on the basis of high bootstrap support. Generic assignments made in this paper appear on the right.

new genera and systematic decisions in this work are made by the first author (O'Loughlin).

Morphological diagnostic characters (see Table 1)

The molecular phylogeny of Waters et al. (2004) has provided evidence of relationships between species. Morphological examination of molecular clades has been a starting point for seeking and confirming characters which are useful for generic diagnoses. A significant outcome has been the recognition of internal skeletal plates as good diagnostic characters. Their absence and presence in different combinations vary across genera and are objective criteria.

Clark and Downey (1992) recognised these plates, and defined them collectively as "superambulacral plates". These internal support plates are distinguished here as three independent types, which are each reliable diagnostically. The Clark and Downey (1992) definition of "superambulacral plate" is emended to: an internal plate articulating between the actinal end of an ambulacral plate, and actinal or marginal or abactinal plates (figs 4a, e, 14e, f; illustrated in A.M. Clark, 1983: fig. 5b). Two additional types of plates are defined. A "superactinal plate" is: an internal interradial plate articulating between abactinal plates, and actinal or other superactinal or superambulacral plates (figs 4b, d, 10d, 15c). "Transactinal plates" are: internal plates in transverse series across rays above the actinal plates (fig. 4f; illustrated but not defined in A.M. Clark, 1983: figs 5d, e [*brevis* a junior synonym of *belcheri*]). As with many diagnostic characters, the development and presence of internal plates may be related to size. They have not been observed in the pedomorphic species of some genera.

Body form, in terms of the degree to which rays are discrete and the form of the rays, is useful diagnostically. But both are subject to variation within a species and because of the habit of the animal and preservation artefact. The presence of noticeable body integument is consistent for some genera, but varies in the degree to which it is evident. Whether abactinal plates imbricate, or form regular series, or are irregularly arranged, are useful criteria, but also vary. The presence of single large papulae or numerous small papulae in papular spaces distinguishes some genera but the distinction is not absolute. Whether actinal plates are in longitudinal series parallel to the furrow, or in oblique series from the furrow to the margin, are useful characters, but sometimes a combination of plate arrangements is evident and sometimes there is variation within a species (in one species apparently changing with size). The form of spinelets and spines is broadly useful for generic diagnoses, but there is variation in detail of form among and within species. Whether spinelets are judged to be "opaque" or "glassy" is attempted, but when denuded by bleach all spinelets appear crystalline and thus glassy. There is subjectivity in making diagnostic statements using the above characters.

The occurrence of pedicellariae is diagnostically reliable for some genera but in others they are present in only some of the species. Glassy convexities occur on the plates of many species. They are present on all species of some genera and absent in one genus, but within one genus they are present on one species and absent on another.

Some characters were found to vary within genera and species and are unhelpful for generic diagnostic purposes: extent of development of a carinal series of plates; presence of a border of five large radial and five small interradial plates around the disc; precise numbers of papulae and secondary plates per papular space; numbers of abactinal spinelets and actinal spines per plate; size of plates and spinelets and spines; fissiparity; and gonopore occurrence abactinally or actinally.

We acknowledge the limitations we face in diagnosing genera using morphological characters. These result from examination of few specimens of each species, consequent limited exposure to intraspecific variations and developmental variations, character varability such as noted above, and the subjectivity of decision-making when addressing continuous characters. Table 1 lists some morphological characters judged to be useful diagnostically and their occurrence in the asterinid genera confirmed or erected in this study.

Key to genera of Asterinidae

1. Furrow spines in longitudinal arrangement on adambulacral plates (fig. 16d); 2 series of tube feet in each ambulacrum; lacking internal plated brood chambers 2
— Furrow spines in vertical series on adambulacral plates (fig. 17f); 4 series of tube feet; internal plated brood chambers with abactinal and actinal interradial openings . . . . . ***Tremaster*** Verrill
2. Rays narrow at base, to varying degrees subcylindrical or digitiform (fig. 2j) 3
— Rays broad at base or not discrete, not subcylindrical or digitiform (figs 2b, i) 6
3. Superambulacral series of plates present (fig. 4a) 4
— Lacking superambulacral, transactinal and superactinal plates (fig. 16g) . . . ***Pseudopatiria*** O'Loughlin gen. nov.
4. Superactinal plates present (fig. 4b) 5
— Superactinal plates absent (fig. 14e) . . . . . ***Pseudonepanthia*** A.H. Clark
5. Rays narrowly flat actinally, marginal edge weakly angular; pedicellariae present; transactinal plates present (fig. 4f) . . . . . ***Nepanthia*** Gray
— Rays broadly flat actinally, marginal edge strongly angular (fig. 10d); lacking pedicellariae; lacking transactinal plates . . . . . ***Callopatiria*** Verrill
6. Interradii very thin; abactinal and actinal plates interiorly contiguous throughout the interradii (fig. 7) 7
— Interradii not very thin; abactinal and actinal interradial plates contiguous or connected by superactinal plates distally only (fig. 15c) 9
7. Body arched; furrow spines project actinally, in continuous series, with integument and granule cover (fig. 17c); actinal spines glassy thorn-tipped (fig. 17d) . . . . . ***Stegnaster*** Sladen
— Body not arched; furrow spines not projecting actinally, in webbed groups on adambulacral plates, not covered with integument and granules; actinal spines not glassy thorn-tipped 8

8. Abactinal spinelets sacciform; interradii extensively supported by long thin articulating interior projections from abactinal and actinal plates (fig. 7) . . ***Anseropoda*** Nardo
— Abactinal spinelets granuliform; interradii extensively supported interiorly by contiguous imbricating abactinal and actinal plates . . . . . ***Pseudasterina*** Aziz and Jangoux
9. Lacking superambulacral, transactinal and superactinal plates 10
— One or both of superambulacral and superactinal plates present 13
10. Abactinal body covered by thick integument with subgranular spinelets; body typically in high arched (domed) shape (fig. 17e); abactinal interradial plate arrangement irregular . . . . . ***Kampylaster*** Koehler
— Body not covered by thick integument with subgranular spinelets; body rarely in high arched (domed) shape; abactinal interradial plate arrangement regular 11
11. Abactinal spinelets glassy, acicular or subsacciform, in tufts (fig. 8f) or paxilliform (fig. 8i); inferomarginal plates with distal tuft of spinelets (fig. 8h) . . ***Asterinides*** Verrill
— Abactinal spinelets opaque, granuliform or digitiform, not in tufts or paxilliform; inferomarginal spinelets not in distal tufts 12
12. Rays discrete; abactinal spinelets columnar to digitiform (fig. 6a) (Atlantic, Mediterranean) . . . . . ***Asterina*** Nardo
— Rays not discrete, margin straight or slightly incurved; abactinal spinelets granuliform (fig. 5a) (temperate Indo-Pacific) . . . . . ***Meridiastra*** O'Loughlin
13. Abactinal and actinal plates with dense subpaxilliform tufts of glassy acicular subsacciform spinelets and spines (fig. 5c); lacking superambulacral plates (fig. 15c) . . . . . ***Paranepanthia*** Fisher
— Abactinal spinelets and actinal spines not in dense subpaxilliform tufts; superambulacral plates present 14
14. Abactinal spinelets glassy, acicular or sacciform or splay-tipped sacciform or long thin conical (fig. 13c) 15
— Abactinal spinelets opaque, granuliform or digitiform, or short thin to thick columnar (fig. 15d) 18
15. Abactinal plates with numerous firmly attached, glassy spinelets (fig. 9f); superomarginal spinelets same as those on abactinal plates (fig. 9d) . . . . . ***Aquilonastra*** O'Loughlin gen. nov.
— Abactinal plates with very fine glassy spinelets, numerous to none, weakly attached (fig. 13c); superomarginal spinelets few to none (fig. 13d) 16
16. Abactinal plates loosely contiguous leaving non-plated spaces (fig. 12); distal abactinal plates in series perpendicular or zig-zag to margin (fig. 12a); superomarginal plates small, not in regular series; inferomarginal plates with stout sacciform spinelets (fig. 10e) . . ***Disasterina*** Perrier
— Abactinal plates imbricate, always contiguous; distal abactinal plates not in perpendicular series to margin; superomarginal plates in distinct regular series; inferomarginal spinelets not stout sacciform 17
17. Body low; abactinal plates small, thin, deeply notched, up to 6 series along each side of rays (fig. 13b); inferomarginal spinelets acicular, in dense integument-covered tufts (fig. 13d) . . . . . ***Indianastra*** O'Loughlin gen. nov.
— Body high; abactinal plates large, thick, shallow notches or crescentiform, up to 3 series along side of rays (fig. 18a); inferomarginal spinelets discrete, not in dense integument-covered tufts . . . . . ***Tegulaster*** Livingstone
18. Form subpentagonal to medium-rayed stellate; large papular spaces; numerous papulae and secondary plates per space (fig. 15f) 19
— Form pentagonal to subpentagonal; small papular spaces; few papulae and secondary plates per space (fig. 11b). .20
19. Abactinal plates with close subpaxilliform cover of spinelets; spinelets thick to thin, short columnar or sub-globose (figs 15d, e); more than 3 spines on mid-interradial actinal plates . . . . . ***Patiria*** Gray
— Spinelets on abactinal plates not in close subpaxilliform cover; spinelets granuliform or digitiform (fig. 16e); up to 3 spines on mid-interradial actinal plates ***Patiriella*** Verrill
20. Superomarginal plates typically in prominent series, longitudinally subrectangular; inferomarginal plates project narrowly to define the margin; abactinal papular spaces with predominantly 1 papula (fig. 11a); midray and distal actinal interradial plates frequently with 1 spine . . . . . ***Cryptasterina*** Dartnall et al.
— Superomarginal and inferomarginal plates typically subequal; inferomarginal plates project prominently to define margin; abactinal papular spaces frequently with more than 1 papula (fig. 11b); midray and distal actinal interradial plates frequently with 2 spines (fig. 16c) . . . . . ***Parvulastra*** O'Loughlin gen. nov.

Asterinidae Gray, 1840

Synonymy. See Clark and Downey, 1992.

Diagnosis. See Clark and Downey, 1992.

Genera. See Table 2.

Remarks. We do not revise the family diagnosis of Clark and Downey (1992). Changes to the list of genera in A.M. Clark (1993) are: *Cryptasterina* Dartnall et al., 2003, *Meridiastra* O'Loughlin, 2002, *Aquilonastra* O'Loughlin gen. nov., *Indianastra* O'Loughlin gen. nov., *Parvulastra* O'Loughlin gen. nov. and *Pseudopatiria* O'Loughlin gen. nov. are added; *Allopatiria* Verrill, 1913 is a junior synonym of *Asterina* Nardo, 1834; *Patiria* Gray, 1840 is raised out of synonymy with *Asterina*; *Manasterina* H.L. Clark, 1938 is a junior synonym of *Disasterina* Perrier, 1875; *Paxillasterina* A.M. Clark, 1983 is a junior synonym of *Asterinides* Verrill, 1913, which is maintained as a valid genus; and *Asterinopsis* Verrill, 1913 and *Desmopatiria* Verrill, 1913 are rejected.

We agree with H.L. Clark (1938) that *Asterinopsis* Verrill, 1913 is nomen dubium. Verrill (1913) designated *Asterias penicillaris* Lamarck, 1816 (Indo-Pacific) the type species, and assigned *Asterina pilosa* Perrier, 1881 (West Indies) and *Asterina lymani* Perrier, 1881 (synonymous according to Clark and Downey, 1992) to *Asterinopsis*. Fisher (1919) added *Nepanthia pedicellaris* Fisher, 1913 to *Asterinopsis*. Mortensen (1933) judged that the type of *A. penicillaris* was lost and that no reliable specimens or image were available. H.L. Clark (1938, 1946) pointed out that Mortensen's case for the dubious

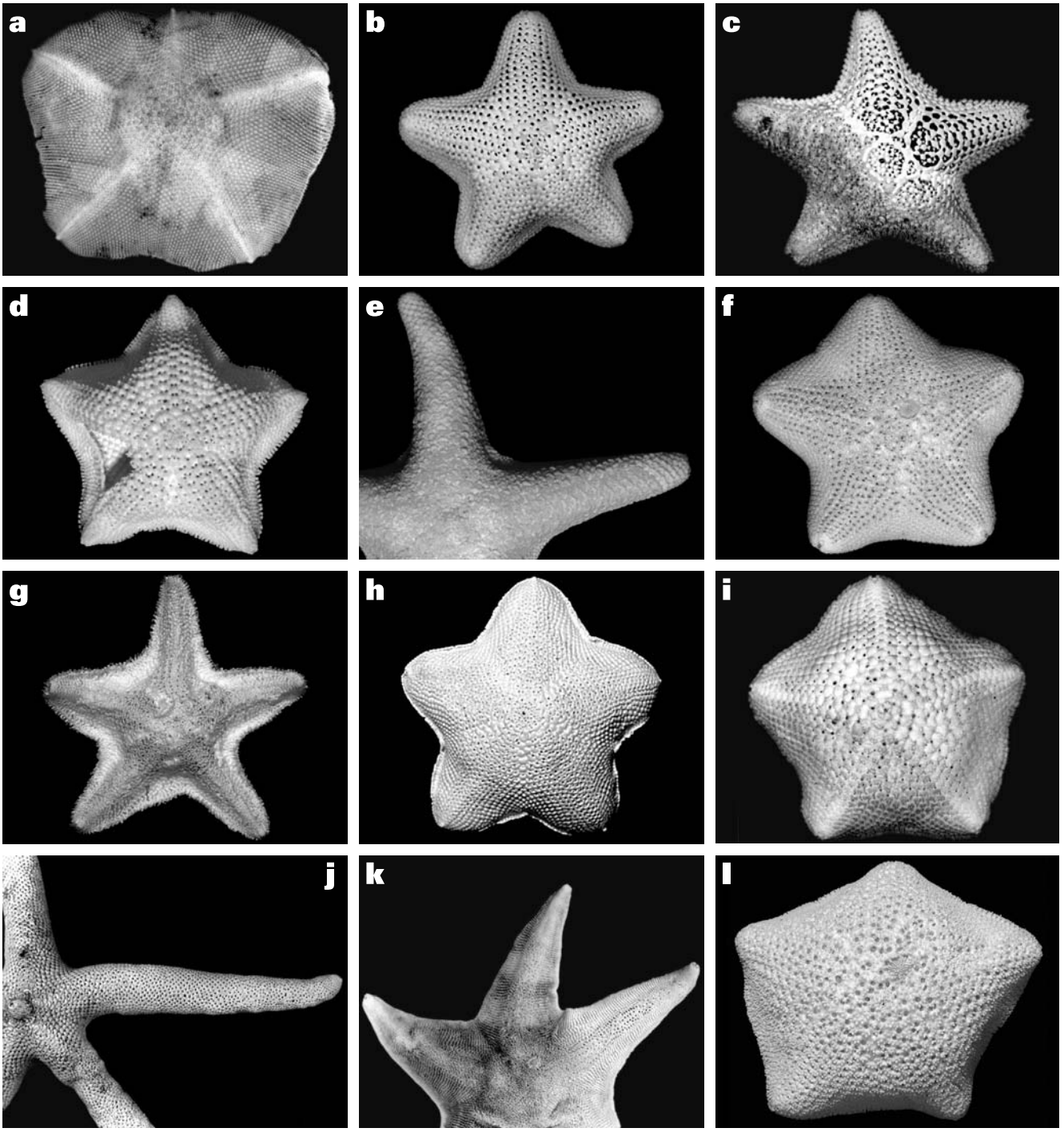


Figure 2. Abactinal views of type species of Asterinidae genera. a, *Anseropoda placenta* (R = 31 mm, AM J10714). b, *Aquilonastra cepheus* (R = 12 mm, AM J8072). c, *Asterina gibbosa* (R = 16 mm, AM G11524). d, *Asterinides folium* (R = 19 mm, USNM E28573). e, *Callopatiria granifera* (R = 50 mm, NMV F98049). f, *Cryptasterina pentagona* (R = 11 mm, NMV F95959). g, *Disasterina abnormalis* (R = 22 mm, WAM Z6754). h, *Indianastra sarasini* (R = 20 mm, NMV F95802). i, *Meridiastra atyphoida* (R = 12 mm, AM J9909). j, *Nepanthia maculata* (R = 73 mm, AM J13918). k, *Paranepanthia platydisca* (R = 57 mm, holotype, USNM 32644). l, *Parvulastra exigua* (R = 11 mm, neotype, TM H508).

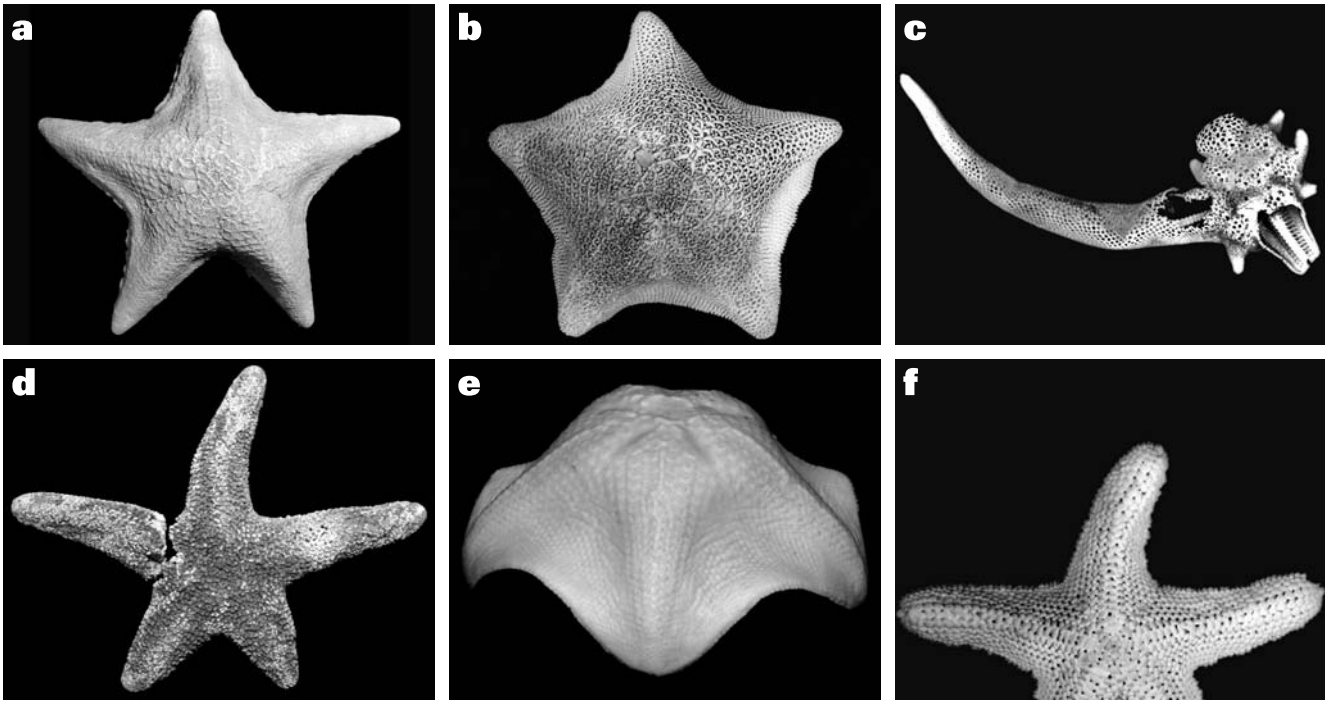


Figure 3. Abactinal views of type species of Asterinidae genera (continued; *Tremaster mirabilis* is figure 17e). a, *Patiria miniata* (R = 67 mm, NMV F98040). b, *Patiriella regularis* (R = 31 mm, AM J5594). c, *Pseudonepanthia gotoi* (R = 74 mm, holotype, USNM 36899). d, *Pseudopatiria obtusa* (R = 54 mm, holotype, BMNH 1938.6.23.24). e, *Stegnaster inflatus* (R = 45 mm, NMV F95675). f, *Tegulaster emburyi* (R = 19 mm, holotype, AM J5605).

state of *penicillaris* would render *Asterinopsis* also dubious. He further pointed out that *Asterinopsis* included both West Indian and Indo-Pacific species. A.M. Clark (1993) awaited reassessment, and listed *N. pedicellaris* and *A. pilosa* under *Asterinopsis*. In this work *N. pedicellaris* is referred to *Nepanthia* and *A. pilosa* is assigned to *Asterinides*.

A.M. Clark (1993) listed *Desmopatiria* Verrill, 1913, but noted "validity doubtful since identity of type species doubtful". The genus was erected for the new species *D. flexilis* Verrill, 1913. It was described from a single dry specimen, without a label, found in the YPM collections with some asteroids from Chile. A recent search of the YPM collections by Eric Lazo-Wasem (pers. comm.) failed to find the specimen. No subsequent specimen has been referred to the species or genus. In the absence of both type specimen and record of type locality, the species *D. flexilis* and genus *Desmopatiria* are judged to be nomina nuda.

Anseropoda Nardo

Figures 2a, 7, 8a-b

Anseropoda Nardo, 1834: 716.—Bell, 1891: 234–235.—Fisher, 1906: 1088.—Clark and Downey, 1992: 174–175.—A.M. Clark, 1993: 204–205.—Liao and Clark, 1995: 128.—Rowe, 1995: 32–33.—McKnight (in Clark and McKnight), 2001: 161. (For complete synonymy and discussion see Clark and Downey, 1992).

Diagnosis. Rays 5–18; body very thin, margin variably curved, rays short or not discrete, broadly rounded or pointed; narrow raised radial areas with single papulae, in scattered or single longitudinal series, sometimes ringed by secondary plates; abactinal plates thin, in longitudinal and oblique series, not notched, each with subpaxilliform glassy, sacciform spinelets, few or tuft; pedicellariae over papulae; actinal plates in longitudinal and oblique series; actinal spines few to numerous per plate, glassy, sacciform; lacking superambulacral plates, superactinal plates present or absent; interradial plates meet internally by long thin articulating projections, extensive in interradii.

Type species. Asterias placenta Pennant, 1777 (subsequent designation by Bell, 1891) (junior synonym: *Asterias membranacea* Retzius, 1783, by Bell, 1891).

Other species. A. antarctica Fisher, 1940; *A. aotearoa* McKnight, 1973; *A. diaphana* (Sladen, 1889); *A. fisheri* Aziz and Jangoux, 1985; *A.* (*Palmipes*) *grandis* Mortensen, 1933; *A. habracantha* H.L. Clark, 1923; *A. insignis* Fisher, 1906; *A. lobiancoi* (Ludwig, 1897); *A. ludovici* (Koehler, 1909); *A. macropora* Fisher, 1913; *A. novemradiata* (Bell, 1905); *A. pellucida* (Alcock, 1893); *A. petaloides* (Goto, 1914); *A. rosacea* (Lamarck, 1816); *A. tenuis* (Goto, 1914).

Material examined. A. placenta. NE Atlantic, off Great Britain, NMV F98043 (2).

A. rosacea. NW Australia, Broome, NMV F95811 (1); AM J7718 (1); Queensland, AM E1814 (1); Tasmania, AM E5037 (1).

Description with some species variations. Body very thin; rays 5 (*grandis, placenta*) or 6 (*insignis*) or 15–18 (*rosacea*), margin variably curved; rays not discrete or short, broad basally,

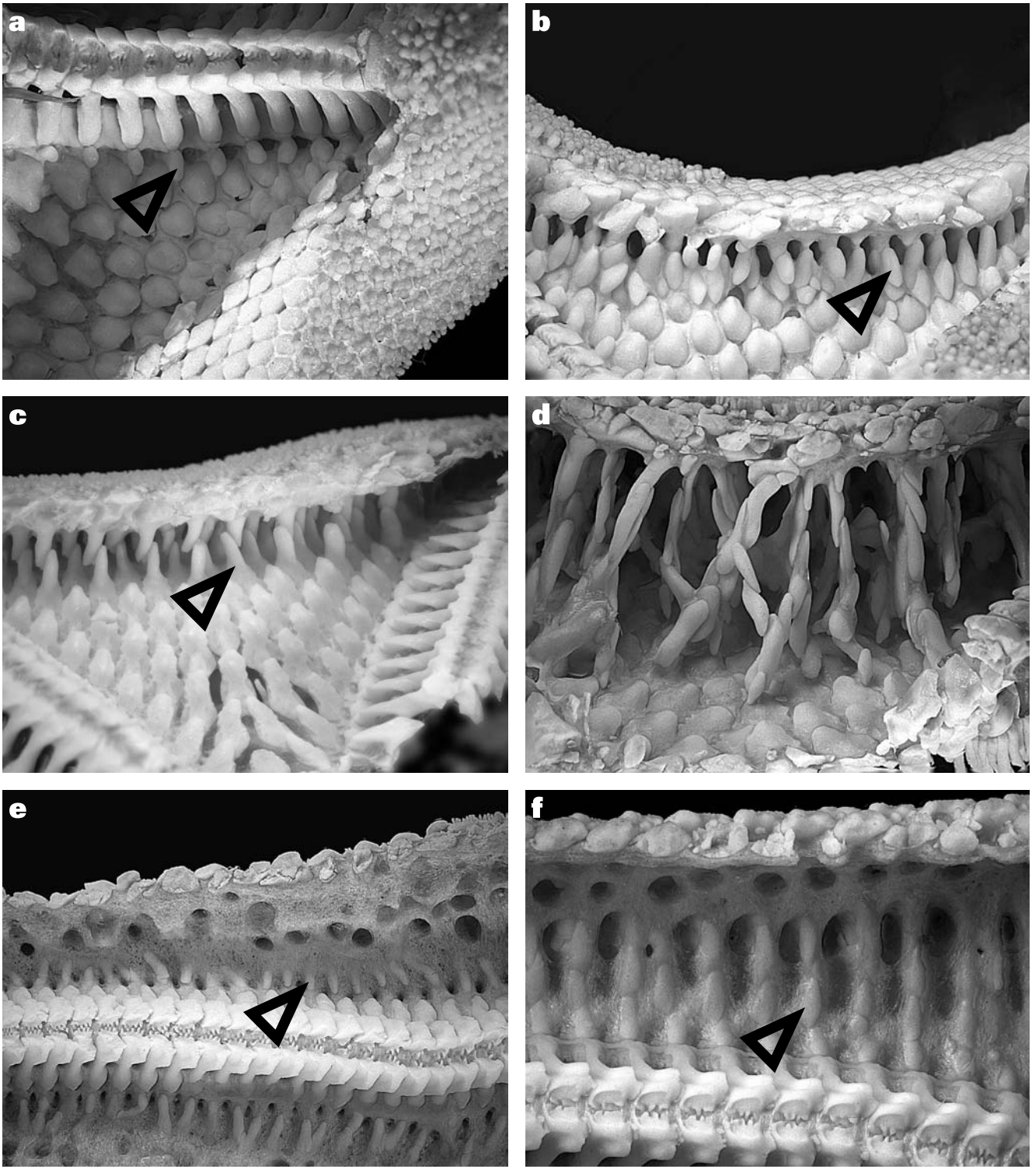


Figure 4. Abactinal views, with plates removed and cleared with bleach to show internal morphology. a–b, *Parvulastra dyscrita* (R = 24 mm, TM H854): a, series of superambulacral plates linking ambulacral and actinal plates; b, superactinal plates linking abactinal and actinal plates to support the interradial margin. c, *Meridiastra oriens* (R = 28 mm, NMV F73468): margin supported by internal contiguous projections of abactinal and actinal plates (arrow), absence of superambulacral and superactinal plates. d, *Patiria miniata* (R = 65 mm, NMV F97444): multiple superactinal plate struts supporting interradial margin. e, *Pseudonepanthia troughtoni* (R = 85 mm, NMV F73013): series of superambulacral plates, and thick internal tisue lining. f, *Nepanthia belcheri* (R = 40 mm, NMV F95806): transactinal plates extending transversely across actinal inner ray, and thick internal tissue lining.

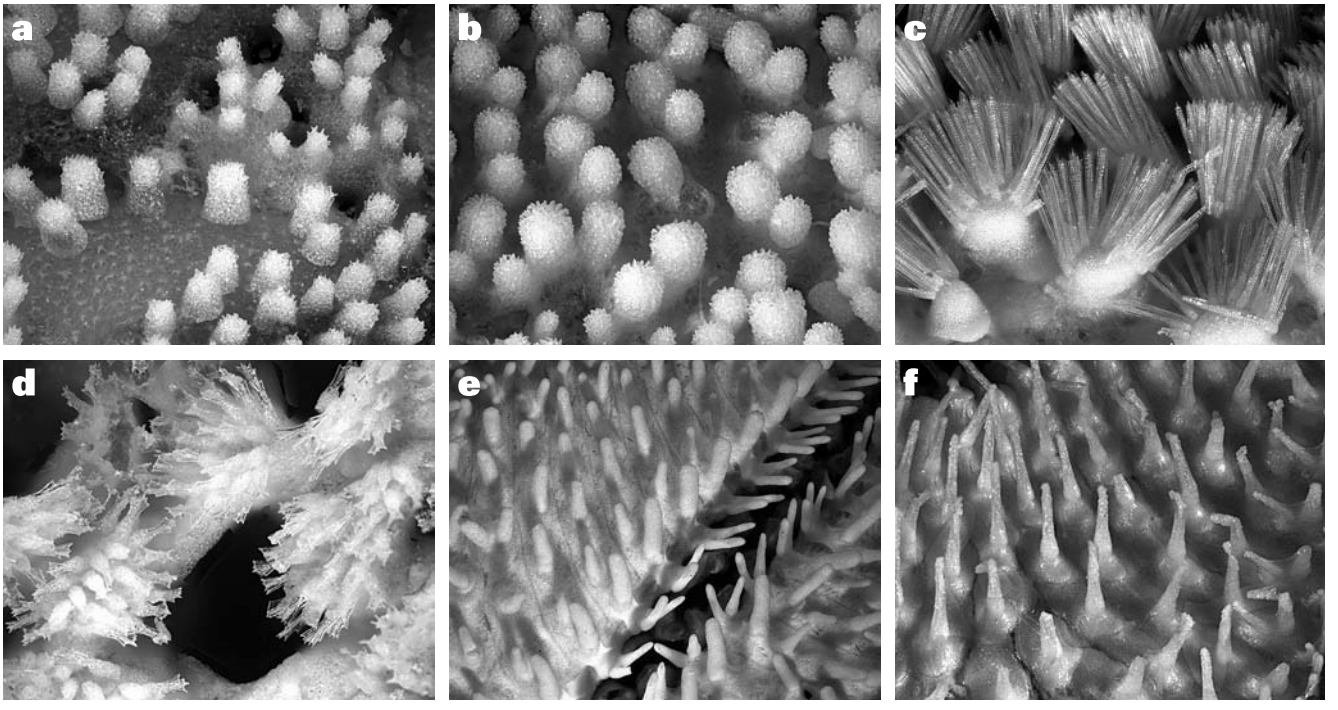


Figure 5. Forms of spinelets and spines. a, *Meridiastra gunnii* (NMV F73248): granuliform abactinal spinelets. b, *Parvulastra dyscrita* (TM H854): globose abactinal spinelets. c, *Paranepanthia grandis* (NMV F73976): acicular abactinal spinelets. d, *Pseudonepanthia gotoi* (USNM 36899): splay-pointed abactinal spinelets. e, *Parvulastra dyscrita* (TM H854): digitiform actinal spines. f, *Disasterina longispina* (WAM Z6760): sacciform actinal spines.

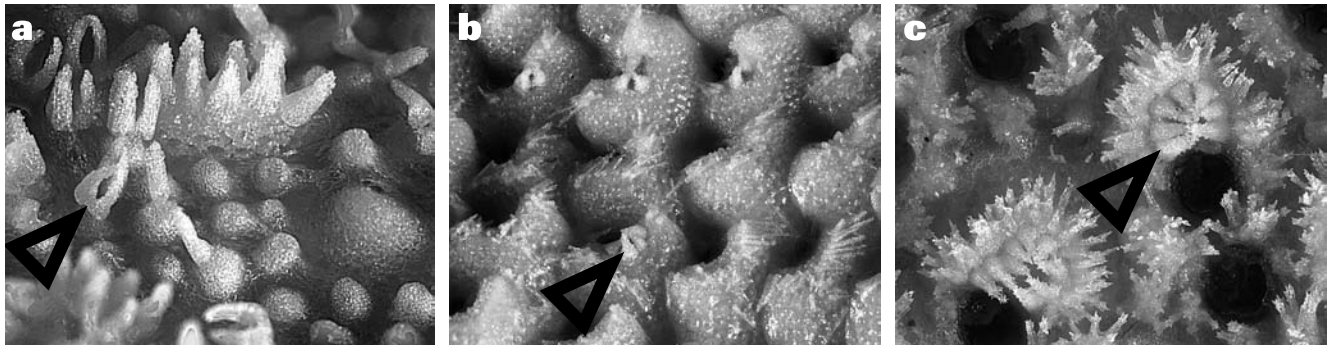


Figure 6. Forms of abactinal fasciculate pedicellariae. a, *Asterina ocellifera* (BMNH 1969.12.16.13). b, *Indianastra sarasini* (WAM Z6836). c, *Nepanthia belcheri* (NMV F95805).

rounded (*grandis, insignis, placenta*) or pointed (*rosacea*); rays slightly elevated as low ridges; size large (*grandis* up to R = 130 mm); pedicellariae present (*grandis, placenta, rosacea*); none fissiparous.

Abactinal plates thin, imbricate, narrow raised radial papulate area, extensive interradial non-papulate area; radial plates in regular (*grandis*) or irregular (*placenta*) distribution on narrow upper ray; single papulae scattered on upper ray (*rosacea, placenta*) or in 1–3 longitudinal series along each side of radial midline (*grandis*); papulae may be each surrounded by ring of up to 5 secondary plates (*placenta, rosacea*); interradial plates imbricate, rhombic to fan-shaped, in both longitudinal and oblique series, may be distally perpendicular to margin (*placenta*); disc not bordered; abactinal plates sometimes with proximal low (*placenta*) to high (*rosacea*) spinelet-bearing elevation or dome; subpaxilliform tufts of spinelets (up to about 25 in *placenta*, up to 3 in *grandis*), sometimes multiple tufts per plate (*insignis*); spinelets glassy, sacciform, pointed (*placenta, rosacea*), sometimes more stout over papulae (*grandis, placenta, rosacea*; presumed to be pedicellariae); cleared abactinal plates sometimes with reticulate glassy appearance (*rosacea*), lacking glassy convexities; superomarginal and inferomarginal plates with abactinal-type spinelets, plates slightly larger than adjacent abactinals; margin defined by projecting inferomarginal plates. Actinal plates in longitudinal and oblique series; may be distally perpendicular to margin (*placenta*).

Actinal spines per plate: oral 5–8; suboral 3–10; furrow 4–9 proximally, webbed; subambulacral 2–7; actinal 3–12, webbed,

Table 1. Selection of morphological characters present (•) in the genera of the Asterinidae

Morphological characters	Genera of Asterinidae																				
	Anseropoda	*Aquilonastra*	*Asterina*	*Asterinides*	*Callopatiria*	*Cryptasterina*	*Disasterina*	*Indianastra*	*Kampylaster*	*Meridiastra*	*Nepanthia*	*Paranepanthia*	*Parvulastra*	*Patiria*	*Patiriella*	*Pseudasterina*	*Pseudonepanthia*	*Pseudopatiria*	*Stegnaster*	*Tegulaster*	*Tremaster*
noticeable integument cover (fig. 10e)			•			•	•	•	•	•	•		•	•	•		•		•	•	•
interradii thin, inner surfaces connected (figs 2a, 7b)	•															•			•		•
habit arched, not flat (figs 3e, 17e)									•										•		•
rays usually 5 only			•		•	•	•	•	•			•	•	•	•	•		•	•	•	•
rays 5 and more	•	•		•						•	•						•				
margins straight to slightly curved (figs 2a, i, 3e)	•			•		•		•		•			•		•				•		•
rays discrete, flat actinally, wide basally (figs 2b, c)	•	•	•	•		•	•	•	•	•		•		•	•	•				•	
rays discrete, flat actinally, narrow basally (fig. 2e)					•																
rays discrete, subcylindrical (figs 2j, 3c, d, 14e)											•						•	•			
superambulacral plates present (figs 4a, 14e)		•			•	•	•	•			•		•	•	•		•			•	
transactinal plates present (fig. 4f)											•										
superactinal plates present (figs 4b, d, 15c)	•	•			•	•	•	•			•	•	•	•	•				•	•	
interradial internal articulating supports (figs 7a, b)	•																				
internal resinous body lining (figs 4e, f)					•						•						•	•			
abactinal plates imbricate (figs 8e, 10i, 15a)	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•
abactinal plates loosely contiguous (figs 12a, b)							•														
ray plates mostly in series (figs 2b, c, i, 9a, 13b)	•	•	•	•		•		•		•			•	•		•			•	•	
ray plates mostly not in series (figs 3b, 12a, b)					•		•		•		•	•			•		•	•			•
few to many papulae per space (figs 10a, 15f)			•	•	•					•		•	•	•	•			•	•		
mostly single papula per space (figs 9f, 13b)	•	•				•	•	•	•	•	•					•	•		•	•	•
spinelets opaque, stout, granuliform (figs 5a, b, 11b)						•			•	•			•	•	•	•			•		•
spinelets opaque, stout, elongate (figs 6a, 16h)			•										•		•			•			
spinelets glassy, fine, acicular (figs 5c, 13d)				•								•								•	
spinelets glassy, fine, not acicular (figs 9c-f)	•	•		•	•		•				•			•		•	•			•	
spinelets absent, or glassy, very fine, often lost (fig. 13c)							•	•		•										•	
body with integument/granule cover (figs 17a, c, d)									•										•		•
pedicellariae always present (fig. 6c)	•										•							•			
pedicellariae sometimes present (figs 6a, b)		•	•					•												•	
pedicellariae never present				•	•	•			•	•		•	•	•	•	•	•		•		•
glassy convexities always present (fig. 9c)		•			•		•		?	•	•								•	•	
glassy convexities never present	•					•			?							•	•	•			•
superomarginal plates in regular series (figs 10c, 13d)	•	•	•	•	•	•		•		•		•	•	•	•	•	•		•	•	
superomarginal plates irregular (fig. 10e)							•		•		•						•	•			
superomarginal plates absent																					•
inferomarginals project narrowly, or not at all (fig. 16g)					•	•					•					•	•	•			
inferomarginal plates loosely contiguous (fig. 10e)							•														
inferomarginal spinelets large, sacciform (fig. 10e)							•														
inferomarginal spinelets acicular, dense tufts (fig. 13d)				•				•				•									
furrow spines in longitudinal series (figs 5e, 10h, 16d)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
furrow spines in vertical series (fig. 17f)																					•
tube feet rows biserial (fig. 15b)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
tube feet rows quadriserial																					•
actinal plates in distinct oblique series (fig. 16c)					•	•	•		•			•	•	•	•	•			•	•	•

Table 2. List of genera and species of Asterinidae, including new synonymies and combinations, and species nomen dubium, nomen nudum, and incertae sedis. Type species with asterisk.

Combination, this paper, or senior synonym	Original combination
Anseropoda antarctica Fisher, 1940	*antarctica, Anseropoda,* Fisher, 1940
Anseropoda aotearoa McKnight, 1973	*aotearoa, Anseropoda*, McKnight, 1973
Anseropoda diaphana (Sladen, 1889)	*diaphana, Palmipes,* Sladen, 1889
Anseropoda fisheri Aziz and Jangoux, 1985	*fisheri, Anseropoda,* Aziz and Jangoux, 1985
Anseropoda grandis Mortensen, 1933	*grandis, Anseropoda* (*Palmipes*), Mortensen,1933
Anseropoda habracantha H.L. Clark, 1923	*habracantha, Anseropoda*, H.L. Clark, 1923
Anseropoda insignis Fisher, 1906	*insignis, Anseropoda*, Fisher, 1906
Anseropoda lobiancoi (Ludwig, 1897)	*lobiancoi, Palmipes*, Ludwig, 1897
Anseropoda ludovici (Koehler, 1909)	*ludovici, Palmipes*, Koehler, 1909
Anseropoda macropora Fisher, 1913	*macropora, Anseropoda,* Fisher, 1913
Anseropoda novemradiata (Bell, 1905)	*novemradiata, Palmipes*, Bell, 1905
Anseropoda pellucida (Alcock, 1893)	*pellucida, Palmipes*, Alcock, 1893
Anseropoda petaloides (Goto, 1914)	*petaloides, Palmipes*, Goto, 1914
**Anseropoda placenta* (Pennant, 1777)	*placenta, Asterias*, Pennant, 1777
Anseropoda rosacea (Lamarck, 1816)	*rosaceus, Asterias*, Lamarck, 1816
Anseropoda tenuis (Goto, 1914)	*tenuis, Palmipes*, Goto, 1914
Aquilonastra anomala (H.L. Clark, 1921)	*anomala, Asterina*, H.L. Clark, 1921
Aquilonastra batheri (Goto, 1914)	*batheri, Asterina*, Goto, 1914
Aquilonastra burtoni (Gray, 1840)	*burtoni, Asterina*, Gray, 1840
**Aquilonastra cepheus* (Müller and Troschel, 1842)	*cepheus, Asteriscus*, Müller and Troschel, 1842
Aquilonastra corallicola (Marsh, 1977)	*corallicola, Asterina*, Marsh, 1977
Aquilonastra coronata (Martens, 1866)	*coronata, Asterina*, Martens, 1866
Aquilonastra coronata (Martens, 1886)	*coronata fascicularis*, *Asterina*, Fisher, 1918
Aquilonastra coronata (Martens, 1886)	*spinigera, Asterina*, Koehler, 1911
Aquilonastra heteractis (H.L. Clark, 1938)	*heteractis, Asterina*, H.L. Clark, 1938
Aquilonastra iranica (Mortensen, 1940)	*cephea var. iranica*, *Asterina*, Mortensen, 1940
Aquilonastra limboonkengi (Smith, 1927)	*limboonkengi, Asterina*, Smith, 1927
Aquilonastra minor (Hayashi, 1974)	*minor, Asterina*, Hayashi, 1974
Aquilonastra rosea (H.L. Clark, 1938)	*rosea, Paranepanthia,* H.L. Clark, 1938
Aquilonastra scobinata (Livingstone, 1933)	*scobinata, Asterina*, Livingstone, 1933
Asterina fimbriata Perrier, 1875	*fimbriata, Asterina*, Perrier, 1875
Asterina gibbosa (Pennant, 1777)	*crassispina, Asterina*, H.L. Clark, 1928
**Asterina gibbosa* (Pennant, 1777)	*gibbosa, Asterias*, Pennant, 1777
Asterina gracilispina H.L. Clark, 1923	*gracilispina, Asterina*, H.L. Clark, 1923
Asterina ocellifera (Gray, 1847)	*ocellifera, Patiria*, Gray, 1847
Asterina pancerii (Gasco, 1870)	*pancerii, Asteriscus*, Gasco, 1870
Asterina phylactica Emson and Crump, 1979	*phylactica, Asterina*, Emson and Crump, 1979
Asterina stellifera (Möbius, 1859)	*siderea, Enoplopatiria*, Verrill, 1913
Asterina stellifera (Möbius, 1859)	*stellifer, Asteriscus*, Möbius, 1859
incertae sedis	*lorioli, Asterina*, Koehler, 1910
incertae sedis	*novaezelandiae*, *Asterina*, Perrier, 1875
**Asterinides folium* (Lütken, 1860)	*folium, Asteriscus*, Lütken, 1860
Asterinides hartmeyeri (Döderlein, 1910)	*hartmeyeri, Asterina*, Döderlein, 1910
Asterinides pilosa (Perrier, 1881)	*lymani, Asterina*, Perrier, 1881
Asterinides pilosa (Perrier, 1881)	*pilosa, Asterina*, Perrier, 1881
Asterinides pompom (A.M. Clark, 1983)	*pompom, Paxillasterina*, A.M. Clark, 1983
Callopatiria formosa (Mortensen, 1933)	*formosa, Parasterina*, Mortensen, 1933
**Callopatiria granifera* (Gray, 1847)	*bellula, Patiria*, Sladen, 1889
Callopatiria granifera (Gray, 1847)	*granifera*, *Patiria*, Gray, 1847
Cryptasterina hystera Dartnall and Byrne, 2003	*hystera, Cryptasterina*, Dartnall and Byrne, 2003
Cryptasterina pacifica (Hayashi, 1977)	*pseudoexigua pacifica*, *Asterina*, Hayashi, 1977
Cryptasterina pentagona (Müller and Troschel, 1842)	*obscura, Patiriella*, Dartnall, 1971
**Cryptasterina pentagona* (Müller and Troschel, 1842)	*pentagonus, Asteriscus*, Müller and Troschel, 1842
Cryptasterina pentagona (Müller and Troschel, 1842)	*pseudoexigua, Patiriella*, Dartnall, 1971
nomen nudum (this work)	*flexilis, Desmopatiria*, Verrill, 1913

**Disasterina abnormalis* Perrier, 1875	*abnormalis, Disasterina,* Perrier, 1875
Disasterina abnormalis Perrier, 1875	*pulchella, Habroporina*, H.L. Clark, 1921
Disasterina ceylanica Döderlein, 1888	*ceylanica, Disasterina*, Döderlein, 1888
Disasterina longispina (H.L. Clark, 1938)	*longispina, Manasterina*, H.L. Clark, 1938
Disasterina odontacantha Liao, 1980	*odontacantha, Disasterina*, Liao, 1980
Disasterina spinosa Koehler, 1910	*spinosa, Disasterina*, Koehler, 1910
Indianastra inopinata (Livingstone, 1933)	*inopinata, Asterina*, Livingstone, 1933
Indianastra inopinata (Livingstone, 1933)	*perplexa, Asterina*, H.L. Clark, 1938
Indianastra sarasini (de Loriol, 1897)	*lutea, Asterina*, H.L. Clark, 1938
Indianastra sarasini (de Loriol, 1897)	*nuda, Asterina*, H.L. Clark, 1921
Indianastra sarasini (de Loriol, 1897)	*orthodon, Asterina,* Fisher, 1922
**Indianastra sarasini* (de Loriol, 1897)	*sarasini, Palmipes*, de Loriol, 1897
**Kampylaster incurvatus* Koehler, 1920	*incurvatus, Kampylaster*, Koehler, 1920
**Meridiastra atyphoida* (H.L. Clark, 1916)	*atyphoida, Asterina*, H.L. Cark, 1916
Meridiastra calcar (Lamarck, 1816)	*calcar, Asterias*, Lamarck, 1816
Meridiastra fissura O'Loughlin, 2002	*fissura, Meridiastra*, O'Loughlin, 2002
Meridiastra gunnii (Gray, 1840)	*brevispina, Patiriella*, H.L. Clark, 1938
Meridiastra gunnii (Gray, 1840)	*gunnii, Asterina*, Gray, 1840
Meridiastra medius (O'Loughlin et al., 2003)	*medius, Patiriella*, O'Loughlin et al., 2003
Meridiastra modesta (Verrill, 1870)	*agustincasoi, Asterina*, Caso, 1977
Meridiastra modesta (Verrill, 1870)	*modesta, Asterina* (*Asteriscus*), Verrill, 1870
Meridiastra mortenseni (O'Loughlin et al., 2002)	*mortenseni, Patiriella*, O'Loughlin et al., 2002
Meridiastra nigranota O'Loughlin, 2002	*nigranota, Meridiastra*, O'Loughlin, 2002
Meridiastra occidens (O'Loughlin et al., 2003)	*occidens, Patiriella,* O'Loughlin et al., 2003
Meridiastra oriens (O'Loughlin et al., 2003)	*oriens, Patiriella*, O'Loughlin et al., 2003
Meridiastra rapa O'Loughlin, 2002	*rapa, Meridiastra*, O'Loughlin, 2002
Nepanthia belcheri (Perrier, 1875)	*belcheri, Asterina* (Nepanthia), Perrier, 1875
Nepanthia crassa (Gray, 1847)	*crassa, Patiria*, Gray, 1847
Nepanthia fisheri Rowe and Marsh, 1982	*fisheri, Nepanthia*, Rowe and Marsh, 1982
**Nepanthia maculata* Gray, 1840	*maculata, Nepanthia*, Gray, 1840
Nepanthia pedicellaris Fisher, 1913	*pedicellaris, Nepanthia*, Fisher, 1913
incertae sedis	*brachiata, Nepanthia*, Koehler, 1910
Paranepanthia aucklandensis (Koehler, 1920)	*aucklandensis, Asterina*, Koehler, 1920
Paranepanthia grandis (H.L. Clark, 1928)	*grandis, Nepanthia,* H.L. Clark, 1928
Paranepanthia grandis (H.L. Clark, 1928)	*praetermissa, Asterinopsis*, Livingstone 1933
**Paranepanthia platydisca* (Fisher, 1913)	*platydisca, Nepanthia*, Fisher, 1913
Parvulastra calcarata (Perrier, 1869)	*calcarata, Asteriscus*, Perrier, 1869
Parvulastra dyscrita (H.L. Clark, 1923)	*dyscrita, Asterina*, H.L. Clark, 1923
**Parvulastra exigua* (Lamarck, 1816)	*1*, Lamarck, 1816
Parvulastra parvivipara (Keough and Dartnall, 1978)	*parvivipara, Patiriella*, Keough and Dartnall, 1978
Parvulastra vivipara (Dartnall, 1969)	*vivipara, Patiriella*, Dartnall, 1969
Patiria chilensis (Lütken, 1859)	*chilensis, Asterina*, Lütken, 1859
**Patiria miniata* (Brandt, 1835)	*coccinea, Patiria*, Gray, 1840
Patiria miniata (Brandt, 1835)	*miniata, Asterias*, Brandt, 1835
Patiria pectinifera (Müller and Troschel, 1842)	*pectinifera, Asteriscus*, Müller and Troschel, 1842
Patiriella inornata Livingstone, 1933	*inornata, Patiriella*, Livingstone, 1933
Patiriella oliveri (Benham, 1911)	*nigra, Patiriella*, H.L. Clark, 1938
Patiriella oliveri (Benham, 1911)	*oliveri, Asterina,* Benham, 1911
Patiriella paradoxa Campbell and Rowe, 1997	*paradoxa, Patiriella*, Campbell and Rowe, 1997
**Patiriella regularis* (Verrill, 1867)	*regularis, Asterina* (Asteriscus), Verrill, 1867
nomen dubium (this work)	*tangribensis, Patiriella*, Domantay and Acosta, 1970
**Pseudasterina delicata* Aziz and Jangoux, 1985	*delicata, Pseudasterina*, Aziz and Jangoux, 1985
Pseudasterina granulosa Aziz and Jangoux, 1985	*granulosa, Pseudasterina*, Aziz and Jangoux, 1985
Pseudonepanthia briareus (Bell, 1894)	*briareus, Patiria*, Bell, 1894
**Pseudonepanthia goto*i A.H. Clark, 1916	*gotoi, Pseudonepanthia*, A.H. Clark, 1916
Pseudonepanthia gracilis (Rowe and Marsh, 1982)	*gracilis, Nepanthia*, Rowe and Marsh, 1982
Pseudonepanthia grangei (McKnight, 2001)	*grangei, Nepanthia*, McKnight, 2001

Pseudonepanthia nigrobrunnea (Rowe and Marsh, 1982)	*nigrobrunnea, Nepanthia*, Rowe and Marsh, 1982
Pseudonepanthia reinga (McKnight, 2001)	*reinga, Nepanthia*, McKnight, 2001
Pseudonepanthia troughtoni (Livingstone, 1934)	*troughtoni, Parasterina*, Livingstone, 1934
**Pseudopatiria obtusa* (Gray, 1847)	*obtusa, Patiria*, Gray, 1847
**Stegnaster inflatus* (Hutton, 1872)	*inflatus, Pteraster*, Hutton, 1872
Stegnaster wesseli (Perrier, 1875)	*wesseli, Asterina*, Perrier, 1875
Tegulaster alba (H.L. Clark, 1938)	*alba, Asterina,* H.L. Clark, 1938
**Tegulaster emburyi* Livingstone, 1933	*emburyi, Tegulaster,* Livingstone, 1933
Tegulaster leptalacantha (H.L. Clark, 1916)	*leptalacantha, Asterina,* H.L. Clark, 1916
Tegulaster leptalacantha (H.L. Clark, 1916)	*leptalacantha var. africana, Disasterina*, Mortensen, 1933
Tegulaster praesignis (Livingstone, 1933)	*praesignis, Disasterina*, Livingstone, 1933
Tegulaster praesignis (Livingstone, 1933)	*spinulifera, Disasterina*, H.L. Clark, 1938
**Tremaster mirabilis* Verrill, 1879	*mirabilis, Tremaster*, Verrill, 1879
Tremaster mirabilis Verrill, 1879	*novaecaledoniae, Tremaster*, Jangoux, 1982

sometimes in fans (*grandis, insignis, placenta*); adradial row of actinal plates with complete series of spines; interradial actinal spines glassy, sacciform.

Superambulacral plates absent; superactinal plates absent (*rosacea*) or present proximally in multiple plate struts (*placenta*); abactinal and actinal interradial plates meet extensively internally by long thin articulating projections.

Distribution. Indo-West Pacific, South Africa, Australia, New Zealand, Antarctic Peninsula, North-East Atlantic, Mediterranean; 10–600 m.

Remarks. Molecular data are not available for any *Anseropoda* species. This restricted generic review is based on examination of specimens of *A. placenta* (type species) and *A. rosacea*, and original descriptions of *A. grandis* by Mortensen (1933) and *A. insignis* by Fisher (1906). Most of the species assigned to *Anseropoda* have not been examined and their generic placement has not been reviewed. The very thin body, and presence of extensive interradial internal thin projecting articulating supports distinguish *Anseropoda* from all other asterinid genera. The contrasting internal plate structures and presence or absence of superactinal plates in *A. placenta* and *A. rosacea* (Fig. 7) suggest that *Anseropoda* may not be monophyletic. Clark and Downey (1992) regarded the very small *Anseropoda lobiancoi* (Ludwig, 1897) from the Mediterranean (R about 8 mm) as being incompatible with *Anseropoda*.

Aquilonastra O'Loughlin gen. nov.

Figures 1 (clade IV, part), 2b, 9a–f

Diagnosis. Rays 5 (6–8 in fissiparous species); interradial margin deeply incurved, form stellate; rays discrete, broad at base, tapering, rounded distally; flat actinally, high convex abactinally; abactinal plates in longitudinal series, not perpendicular to margin; papulate areas extensive; papulae predominantly single, large, in longitudinal series along sides of rays; abactinal plates with glassy convexities; abactinal spinelets and actinal spines predominantly fine, glassy, conical or sacciform or splay-pointed sacciform, in bands or tufts, numerous (10–40 per plate); actinal plates in longitudinal, not oblique, series; superambulacral plates present for all of ray, sometimes for part of ray or absent in pedomorphic species; superactinal plates present.

Type species. Asteriscus cepheus Müller and Troschel, 1842.

Other species. A. anomala (H.L. Clark, 1921); *A. batheri* (Goto, 1914); *A. burtoni* (Gray, 1840); *A. corallicola* (Marsh, 1977); *A. coronata* (Martens, 1866) (junior synonyms: *Asterina coronata fascicularis* Fisher, 1918, possible synonymy raised by H.L. Clark, 1928, formalised by Rowe, 1995; and *Asterina spinigera* Koehler, 1911, by VandenSpiegel et al., 1998); *A. heteractis* (H.L. Clark, 1938); *A. iranica* (Mortensen, 1940) (raised to species status, this work); *A. limboonkengi* (Smith, 1927); *A. minor* (Hayashi, 1974); *A. rosea* (H.L. Clark, 1938); *A. scobinata* (Livingstone, 1933).

Material examined. A. anomala. Caroline Is, WAM Z6845 (2); Christmas I., Z6851 (1); Lord Howe I., AM J6169 (21); NMV F95593 (6); F97690 (6); F96699 (1); Maldive Is, Z6854 (1); Samoa, F96698 (2); Torres Strait, Darnley I., Z6849 (2); Western Australia, Kimberley, Z6843 (1).

A. batheri. Japan, Toyama Bay, NMV F97441 (1); AM J11564 (2); Oman, UF 70 (7).

A. burtoni. Gulf of Suez, AM J17892 (2); TM H1815 (2); Red Sea, Egyptian coast, H1814 (1).

A. cephea iranica. Syntype. Persian Gulf, S of Bushire, coral reef, AM J17891 (1).

A. cepheus. Queensland, NMV F95594 (2), AM J23331 (1); Western Australia, Abrolhos Is, WAM Z6778 (7); J8321 (5); New Guinea, Trobriand Group, J22934 (1); Hong Kong, BMNH 1981.2.6.25 (1; previously identified as *Asterina limboonkengi*).

A. corallicola. Paratypes. Caroline Is, WAM Z1704 (3).

A. coronata. Northern Territory, Darwin, NMV F95796 (4); AM J6613 (1); J8206 (2); Caroline Is, J13660 (1); Bombay, BMNH 1960.10.4.11-16 (2; previously identified as *Asterina lorioli*); Taiwan, J19956 (1); Japan, J11563 (2).

A. heteractis. Queensland, Townsville, AM J9541 (2); Heron I., J19449 (1).

A. limboonkengi. Oman, UF 1645 (2); UF 246 (1); UF 68 (6).

A. minor. Japan, NMV F96697 (2).

Paranepanthia rosea. Paratypes. Western Australia, Rottnest I., AM J6171 (3). Other material. Western Australia, Jurien Bay, AM J7437 (4).

A. scobinata. Holotype. Tasmania, AM J1241. Other material. Tasmania, Eaglehawk Neck, J9060 (3); Victoria, Phillip I., NMV F72998 (1); Port Fairy, F72985 (2); Killarney, F72997 (10).

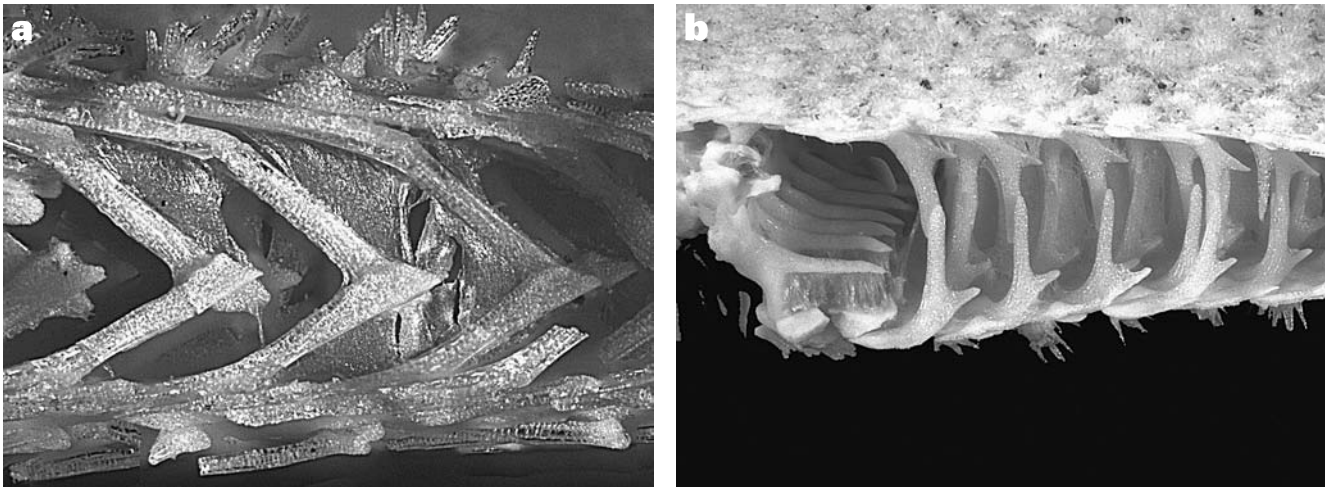


Figure 7. Longitudinal sections through interradii of *Anseropoda* species, showing internal contiguous projections from abactinal and actinal plates, and absence (b) of superambulacral plates. a, *Anseropoda placenta* (R = 56 mm, NMV F98043). b, *Anseropoda rosacea* (R = 82 mm, NMV F95811).

Description with species variations. Rays predominantly 5, or 6 (fissiparous *corallicola, heteractis*), or 6–7 (fissiparous *burtoni*), or 7–8 (fissiparous *anomala*); interradial margin deeply incurved, form stellate; rays discrete, broad at base, tapering, rounded distally; flat actinally, high convex abactinally; size medium (*iranica* up to R = 35 mm) to small (pedomorphic species *anomala, burtoni, corallicola, heteractis, minor* with R up to 10 mm); pedicellariae sometimes present, scattered (*iranica*) or few on proximal lateral rays above papulae (*batheri, coronata*); gonopores abactinal or actinal (*corallicola, scobinata*); fissiparity in 4 species.

Abactinal surface even, or very uneven with some paxilliform plates (*coronata, rosea*); plates in longitudinal series, not series perpendicular to margin; papulate areas extensive, to near distal end of rays, to near interradial margin; papular spaces small with few secondary plates and predominantly 1 large papula (rarely up to 3); 2–6 distinct longitudinal series of large papulae along each side of rays, series variably evident carinally; disc variably bordered by continuous series of 5 radial and 5 interradial plates (not in fissiparous species); abactinal plates predominantly singly notched for papulae, crescentiform on rays and interradially to near margin, round distally, with transverse or round spinelet-bearing proximal elevations; carinal series of plates absent, or proximal series of singly or doubly notched plates not widely separated by secondary plates, or doubly papulate to end of ray (*heteractis*); cleared abactinal plates with glassy convexities; abactinal spinelets glassy, conical or sacciform or splay-pointed sacciform; abactinal spinelets in transverse bands or tufts of 8–40 spinelets per plate, tufts sometimes multiple per plate (*batheri, cepheus*), spinelets sometimes 2 distinct forms (*coronata*), spinelets sometimes paxilliform (*coronata, rosea*); marginal plates with abactinal spinelets; superomarginal plates not larger than inferomarginals; acute margin formed by projecting inferomarginal plates (rounded margin in pedomorphic *corallicola*).

Actinal plates in longitudinal series, sometimes also oblique (*coronata*), or oblique (pedomorphic *heteractis*).

Actinal spines per plate: oral 5–9; suboral 3–12; furrow 3–9 proximally; subambulacral 2 up to tuft; adradial actinal plates fully spinous; actinal interradial spines similarly variable forms as abactinally, predominantly in tufts, up to 20 per plate.

Superambulacral plates present for all of ray, or distal half (pedomorphic *minor*), or absent (pedomorphic *corallicola*); superactinal plates present.

Distribution. Eastern Mediterranean, northern Indian and western Pacific Oceans, Gulf of Suez, Red Sea, Persian Gulf, Arabian Sea, southern Australia, Japan; 0–15 m.

Etymology. From the Latin *aquilonalis* (northern) and *astrum* (star), referring to the predominantly northern Indo-Pacific occurrence of the species of this genus (feminine).

Remarks. The new genus *Aquilonastra* is represented on the molecular clade of Waters et al. (2004, clade IV, part) by six species: *A. anomala, A. batheri, A. burtoni, A. coronata, A. minor, A. scobinata*. These share a consistent morphology: discrete high rays; series of single large papulae along rays; fine glassy spinelets; presence of superambulacral and superactinal plates. Other species share this morphology and are included in the genus: *cepheus, corallicola, heteractis, limboonkengi* and *rosea*. The new genus shares some characters with *Cryptasterina* Dartnall et al., 2003: extensive papulate areas; small papular spaces with few secondary plates and single papulae per space; up to four longitudinal series of papulae along each side of the rays; doubly papulate carinal plates variably present, as short or long series or absent; margin formed by projecting inferomarginal plates; superactinal plates support the interradial margin. This similarity is supported by a sister taxon relationship on the molecular tree (clade IV, part). However, there are significant morphological differences

exhibited by *Cryptasterina*: form pentagonal or subpentagonal; abactinal spinelets granuliform; at most very low raised rounded spinelet-bearing elevations along the proximal projecting edge of abactinal plates; superomarginal plates larger than inferomarginals; actinal spines fewer (oral 4–5, suboral 1–2, furrow 2–3, subambulacral 1–2 proximally, actinal interradial 0–1 proximally 1–2 distally), conical to digitiform; adradial actinal series of plates with none to few spines; superambulacral plates not in complete series, few present.

In an electrophoretic study of five *Asterina* species from Japan, Matsuoka (1981) found them to be a heterogeneous phylogenetic group with *A. batheri* and *A. coronata japonica* closely related, A. *pseudoexigua pacifica* fairly closely related, and *A. pectinifera* and *A. minor* each probably belonging to separate lineages. This result is generally congruent with the molecular phylogeny of Waters et al. (2004), except that in their clades *A. minor* was not separate but in the same lineage as *A. batheri* and *A. coronata.*

H.L. Clark (1938) described juvenile specimens of *Paranepanthia rosea* (up to R = 8 mm). Material examined in this work from Jurien Bay was significantly larger (up to R = 17 mm) and characterised by: absence of two distinct 'fields' of abactinal plates; splay-pointed sacciform spinelets and spines; predominantly large single papulae in papular spaces; numerous longitudinal series of papulae along the sides of rays; actinal plates not in oblique series; presence of series of superambulacral plates; and single superactinal plate supports. *P. rosea* is removed from *Paranepanthia*. The inferomarginal plates define the margin in *P. rosea*, not superomarginal plates as stated by H.L. Clark (1938).

Mortensen (1940) distinguished a variety *iranica* for the species *A. cepheus* on the basis of having 5–6 suboral spines per plate and *A. cepheus* two (up to four seen in this work). Further to this observation, the variety is distinguished from *A. cepheus* (characters in brackets) by having: up to eight stout sacciform spinelets in single series across proximal abactinal plates (up to 20 fine spinelets in bands across plates); up to ten stout inferomarginal spinelets per plate (more than, 20); typically two actinal spines per plate (4–8). *Asterina cepheus iranica is* raised to species status.

Marsh (1977) compared the three similar small fissiparous Indo-Pacific asterinids *A. anomala, A corallicola* and *A. heteractis*, and her confirmation of valid species status for all three is supported here. *A. heteractis* has some characters which are exceptional to those shared by other *Aquilonastra* species: regular doubly papulate carinal series for length of ray; actinal plates in oblique series; fewer actinal spines per plate, with up to four oral, sometimes no suboral, up to four furrow, up to three actinal. These differences are not sufficient to justify assignment to another genus.

Smith (1927), Liao (1980) and Liao and Clark (1995) observed that *A. limboonkengi* was close to *A. cepheus* (Smith as close to *A. burtoni* from the Philippines, *A. burtoni* presumably *A. cepheus*). Liao and Clark (1995) described the differences between *A. cepheus* and *A. limboonkengi*. Our observations confirm that the abactinal spinelets in *A. cepheus* are long and fine, and those in *A. limboonkengi* short and stout. Rowe (1995) rejected the subspecies *A. coronata fascicularis* Fisher, 1918. The possible species status of the other subspecies of *A. coronata* (*cristata* Fisher, 1916 and *euerces* Fisher, 1917) has not been examined.

Pairs of abactinal spinelets on *A. anomala, A. cepheus, A. corallicola* and *A. minor* are sometimes angled and contiguous, suggesting that they may act as pedicellariae. But the spinelets are not differentiated in form.

Asterina Nardo

Figures 1 (clade VI), 2c, 6a, 8c–e

Asterina Nardo, 1834: 716.—Clark and Downey, 1992: 177–181.—A.M. Clark, 1993: 206–214.—Liao and Clark, 1995: 129.—Rowe, 1995: 33–35.—O'Loughlin, 2002: 278.—Waters et al., 2004: 874, 875, 877 (part). (For complete synonymy and discussion see Clark and Downey, 1992).

Allopatiria Verrill, 1913: 480.—Verrill, 1914: 273.—Tortonese, 1965: 174.—Spencer and Wright, 1966: U69.—A.M. Clark, 1983: 372–373.—Clark and Downey, 1992: 172.—A.M. Clark, 1993: 204. New synonym.

Diagnosis. Rays 5; body integument noticeable; interradial margin incurved to varying extents; rays discrete, short, distally broadly or narrowly rounded or pointed; flat actinally, convex abactinally; papular spaces with numerous small papulae and secondary plates; abactinal spinelets opaque, digitiform to conical, rounded distally; actinal plates in oblique and sometimes longitudinal series; actinal interradial spines digitiform to conical, up to 5 per plate; internal contiguous projections from abactinal and actinal plates support margin; lacking superambulacral and superactinal plates.

Type species. Asterias gibbosa Pennant, 1777 (subsequent designation by Fisher, 1906; full treatment by A.M. Clark, 1983) (junior synonym: *Asterina crassispina* H.L. Clark, 1928, by Rowe, 1995).

Other species. A. fimbriata Perrier, 1875; *A. gracilispina* H.L. Clark, 1923; *A. ocellifera* (Gray, 1847); *A. pancerii* (Gasco, 1870); *A. phylactica* Emson and Crump, 1979; *A. stellifera* (Möbius, 1859) (junior synonym: *Enoplopatiria siderea* Verrill, 1913, this work).

Material examined. A. fimbriata. Argentina, Comodoro Rivadavia, AM J6411 (3).

A. gibbosa. Mediterranean, Tunisia, USNM E42476 (1); see O'Loughlin (2002).

A. gracilispina. South Africa, Cape Agulhas, BMNH 1975.10.29.47 (1).

A. ocellifera. Mauritania, Cape Lever, BMNH 1969.12.16.13 (1).

A. stellifer. Argentina, AM J6410 (1).

Enoplopatiria siderea. Holotype. Panama (assumed here to be mistaken locality), YPM No. 9830. New synonym.

Description with species variations. Rays 5; interradial margin incurved to varying extents, rays discrete, distally narrowly (*gibbosa*) or broadly (*fimbriata, gracilispina*) rounded, or pointed (*ocellifera, stellifera*); size large (*ocellifera* up to R = 81 mm) to small (*phylactica* up to R = 7.5 mm); pedicellariae numerous abactinally, predominantly 2 valves, fasciculate (*gibbosa, ocellifera, stellifer*a), or absent (*fimbriata, gracilispina*); gonopores abactinal (*fimbriata, gracilispina, ocellifera, stellifera*) or actinal (*gibbosa, phylactica*); not fissiparous.

Extensive abactinal papulate area of weakly notched or shallow crescentiform or rhombic (*ocellifera*) plates, narrow interradial non-papulate margin of proximally rounded plates; upper rays with variably developed carinal series of doubly notched plates (*fimbriata, gibbosa, gracilispina*), or irregular plates (*stellifera*), or rhombic plates (*ocellifera*); up to 4 longitudinal series of plates along each side of rays; papular spaces large, secondary plates and papulae numerous, small secondary plates may partly obscure (*ocellifera*) or encroach on (*stellifera*) primary plates; disc bordered by series of 5 radial and 5 interradial plates *(gibbosa, gracilispina*) or not (*fimbriata, ocellifera, stellifera*); abactinal plates with spinelet-bearing ridges and domes; denuded plates with glassy convexities (*gibbosa, gracilispina, ocellifera, stellifera*) or reticulations (*fimbriata*); abactinal spinelets digitiform or conical, rounded distally; spinelets spaced on plates closely (*stellifera*) or widely *(fimbriata, gibbosa, gracilispina, ocellifera*), not in tufts; interradial plates in short series perpendicular to margin (*ocellifera, stellifera*) or not (*fimbriata, gibbosa, gracilispina*); superomarginal and inferomarginal plates in distinct series, covered with abactinal-type spinelets; projecting inferomarginal plates form marginal edge.

Actinal plates in oblique series (small specimens of *A. gibbosa*; longitudinal series in large specimens of *A. gibbosa*).

Actinal spines per plate: oral 4–9; suboral 1-4; furrow 2–5 proximally, webbed; subambulacral 1–3; adradial row of actinal plates with complete series of spines; actinal interradial predominantly 2–3 in mid-interradius; interradial actinal spines digitiform to conical.

Lacking superambulacral and superactinal plates; interradial margin supported by contiguous internal tongue-like extensions of abactinal and actinal plates.

Distribution. Atlantic Ocean, Europe, SW and S Africa, SE and S South America; Mediterranean Sea; 0–250 m.

Remarks. The principal characters in this new diagnosis of *Asterina* are: papular spaces with numerous small papulae and secondary plates, not predominantly single large papulae; abactinal spinelets opaque, digitiform to conical, not glassy and fine; actinal plates in oblique and longitudinal series; internal contiguous projections from abactinal and actinal plates support the margin; lacking superambulacral and superactinal plates.

Molecular evidence (Waters et al., 2004, clade VI) places *A. phylactica* as sister species of *A. gibbosa*. On the basis of the diagnosis the following species are removed from *Asterina* to other genera: *A. alba, A. anomala, A. aucklandensis, A. batheri, A. burtoni, A. cepheus, A. chilensis, A. corallicola, A. coronata, A. hartmeyeri, A. heteractis, A. inopinata, A. miniata, A. minor, A. pectinifera, A. sarasini, A. scobinata*.

A.M. Clark (1983) considered that the rhombic and non-crescentic form of the large primary plates in the radial field, and the proliferation of small secondary plates to the extent that abactinal plates become obscured peripherally, distinguish *Allopatiria* from *Asterina*. Clark and Downey (1992) noted superficial similarity of similarly sized specimens of *Allopatiria* and *Asterina*. We have found that the form of abactinal plates and number of secondary plates are not generically significant. In diagnosing *Allopatiria*, Clark and Downey (1992) referred to "additional internal plates" supporting the margin. If such superactinal plates were present they might justify the retention of *Allopatiria*. But we did not confirm their presence. What could appear to be superactinal plates are long internal projections of distal abactinal and actinal plates. This is a character shared with *Asterina*, and *Allopatiria* is judged to be a junior synonym. A.M. Clark (1993) listed *Patiria* Gray, 1840 and *Asterinides* Verrill, 1913 as junior synonyms of *Asterina*. Rowe (1995) and Campbell and Rowe (1997) supported the validity of *Asterinides*. *Patiria* is raised out of synonymy in this work.

O'Hara (1998) synonymised *Asterina hamiltoni* Koehler, 1920 and *Cycethra macquariensis* Koehler, 1920 with *Asterina frigida* Koehler, 1917 and assigned *A. frigida* to *Cycethra* Bell, 1881 in the Ganeriidae. Rowe (1995) synonymised *Asterina crassispina* H.L. Clark, 1928 with *Asterina gibbosa*, and judged the northern Australia locality data to be incorrect. Based on an examination of the type of *Asterina spinigera,* VandenSpiegel et al. (1998) synonymised it with *Asterina coronata*.

Clark and Downey (1992) summarised the characters thought to distinguish *A. pancerii* from *A. gibbosa* as: flatter and near pentagonal shape; fewer and larger skeletal plates; plates with coarse crystal bodies; and more numerous, usually three, suboral spines. O'Loughlin (2002) noted in *A. gibbosa* material: some conspicuous glassy convexities around the margin of abactinal plates; and some plates with up to three suboral spines. The near pentagonal body form and relative size of plates have been found to show variation within species in this study. *A. pancerii* is probably conspecific with *A. gibbosa*. In the absence of molecular evidence, *pancerii* is retained here as a species of *Asterina*.

The holotype of *Enoplopatiria siderea* was examined and found to conform in all morphological features with *Asterina stellifera*. The Panama type locality must be an error, since *A. stellifera* occurs on the east and west coasts of the South Atlantic.

Specimens of *Asterina lorioli* Koehler, 1910 and *Asterina novaezelandiae* Perrier, 1875 were not examined. Based on the descriptions, assignment to *Asterina* could not be confirmed. These species are placed incertae sedis, and discussed below.

All species placed here in *Asterina* are from the Atlantic and Mediterranean.

Asterinides Verrill

Figures 2d, 8f–i

Asterinides Verrill, 1913: 479.—Verrill, 1914: 263.—Verrill, 1915: 58.—Tommasi, 1970: 14–15.—A.M. Clark, 1983: 364.—Rowe, 1995: 33.—Campbell and Rowe, 1997: 131.—Clark and Mah, 2001: 335.—O'Loughlin, 2002: 291, 293.

Paxillasterina A.M. Clark, 1983: 373.—Clark and Downey, 1992: 193.—A.M. Clark, 1993: 227. New synonym.

Diagnosis. Rays 5 or 6; form subpentagonal or subhexagonal or discrete rays; abactinal plates in longitudinal series; extensive papulate areas, predominantly single papulae; abactinal plates singly notched; abactinal spinelets glassy, acicular to

subsacciform, in tufts or subpaxilliform or on paxilliform columns; lacking pedicellariae; superomarginal plates with tuft of spinelets; inferomarginal plates with distal dense subpaxilliform tuft of larger spinelets; actinal spines subsacciform, thin; lacking superambulacral and superactinal plates, distal interradial margin supported by inward projecting tongues from abactinal and sometimes actinal plates.

Type species. *Asteriscus folium* Lütken, 1860 (original designation).

Other species. A. hartmeyeri (Döderlein, 1910); *A. pilosa* (Perrier, 1881) (junior synonym: *A. lymani* Perrier, 1881, by Clark and Downey, 1992); *A. pompom* (A.M. Clark, 1983).

Material examined. A. folium. Holotype. Atlantic Ocean, Virgin Is (ZMUC). Other material. Atlantic Ocean, Caribbean Sea, USNM E28573 (1); Gulf of Mexico, USNM 38811 (3); Bermuda, USNM 38236 (4).

A. hartmeyeri. Atlantic Ocean, Caribbean Sea, USNM E49050 (2).

A. pilosa. Atlantic Ocean, Caribbean Sea, USNM E17973 (2); Gulf of Mexico, USNM E13707 (1); Venezuela, USNM E28411 (1).

A. pompom. Atlantic Ocean, Caribbean Sea, USNM E47755 (4); E47866 (1).

Description with species variations. Rays predominantly 5 (*folium, hartmeyeri, pompom*) or 6 (*pilosa*), interradial margin straight to slightly to deeply (*pilosa*) incurved, subpentagonal or discrete rays (*pilosa*); body thick, sides of rays steep (*folium, hartmeyeri, pilosa*), or thin (*pompom*); size small (*folium* up to R = 20 mm) to very small (*hartmeyeri* up to R = 7 mm); lacking pedicellariae; gonopores abactinal; one fissiparous (*pilosa*, R up to 10 mm).

Abactinal surface uneven due to raised proximal edge of thick imbricating plates (*folium*) or paxilliform columns (*pompom*); abactinal plates in longitudinal series; denuded appearance dominated by singly notched plates, heart-shaped to crescentiform; papulate areas extensive; papulae predominantly single, large, up to 4 longitudinal series along each side of rays; doubly notched and papulate carinal series variably present for most of ray, or upper ray plates irregular (*pilosa*); papular spaces fairly large, sometimes up to 3 papulae and 3 secondary plates per space; disc bordered by series of 5 radial 5 interradial plates (*folium*), or not (*hartmeyeri, pilosa*); denuded plates with glassy convexities (*folium, hartmeyeri*) or irregular texturing (*pompom*); plates with apical ridge or dome; spination variable, up to 3 subpaxilliform tufts across each plate proximally, each tuft with up to 20 spinelets, single subpaxilliform tufts distally (*folium*), or tufts of spinelets (*hartmeyeri, pilosa*), or soft paxillar columns and rounded domes, each with up to 50 spinelets (*pompom*); spinelets glassy, acicular to subsacciform; superomarginal plates with central tuft or pompom of spinelets; inferomarginal series projects to form margin, plates bare proximally, prominent marginal tuft of larger spinelets, sometimes on elevations (*folium, pompom*).

Actinal interradial plates in longitudinal series (*folium, pompom*), sometimes oblique (*folium*), or oblique (*hartmeyeri*).

Actinal spines per plate: oral 4–7; suboral 1–10; furrow 3–5, webbed; subambulacral 2–4 or clusters (*pilosa*); adradial actinal plates with complete series of spines; actinal 1–4 or clusters (*pilosa*), webbed if more than 1; actinal interradial spines subsacciform, thin.

Lacking superambulacral and superactinal plates; distal interradial margin supported by internal contiguous tongue-like projections from abactinal and actinal plates (*folium, pompom*) or from abactinal plates only (*hartmeyeri*).

Distribution. W Atlantic, Florida, Bahamas, West Indies, Caribbean, Brazil; 0–256 m.

Remarks. Molecular data are not available for any species of *Asterinides*, and this review is based on morphology. Rowe (1995) and Rowe and Campbell (1997) considered *Asterinides* to be a valid genus. Verrill (1913) referred *Asteriscus folium* Lütken, *Asteriscus cepheus* Müller and Troschel, 1842 and *Asterina* (*Asteriscus*) *modesta* Verrill, 1870 to his new genus *Asterinides*. O'Loughlin (2002) removed *A. modesta* to his new genus *Meridiastra*. *A. cepheus* is removed here from *Asterinides* to *Aquilonastra*. The genera *Aquilonastra* and *Asterinides* share many morphological similarities, such as the multiple spinelet tufts per plate in *A. batheri* (*A. folium* also) and paxillar columns in *A. coronata* (*A. pompom* also). But the generic morphological difference evident in this study is the presence of superambulacral and superactinal internal skeletal plates in *Aquilonastra* and absence in *Asterinides*.

A.M. Clark (1983) considered the paxillar columns on many abactinal plates of *P. pompom* to be of generic significance, but Clark and Downey (1992) noted some similarity between *A. folium* and *P. pompom*. Both papers considered the paxillar columns to be otherwise unknown among Asterinidae but *Aquilonastra coronata* has similar columns. Their presence in two otherwise well-defined genera, *Asterinides* and *Aquilonastra* argues against use of paxillar columns as a generic character. *Paxillasterina* is placed in synonymy with *Asterinides*.

The description of *A. folium* by O'Loughlin (2002) was of specimens up to R = 15 mm, and is superceded by the descriptive details here based on a specimen with R = 19 mm (USNM E28573). The earlier description referred to ad-disc interradial papular spaces, each with two lateral papulae separated by one or two secondary plates. In the larger specimen these spaces have up to three papulae and three secondary plates. Multiple spinelet tufts are evident on the abactinal plates of the larger specimen, but were not evident on smaller specimens. Clark and Downey (1992) discussed differences between *A. folium* and *A. hartmeyeri* recognising separate but similar species. *Asterina hartmeyeri* also belongs to *Asterinides*. *Asterinopsis pilosa* (Perrier, 1881) is assigned here to *Asterinides* since it shares the generic diagnostic morphological characters.

Callopatiria Verrill

Figures 2e, 10a–d

Callopatiria Verrill, 1913: 480.—A.M. Clark, 1983: 367–372.—Clark and Downey, 1992: 190–191.—A.M. Clark, 1993: 217.

Diagnosis. Rays 5, discrete, narrow basally, long rayed stellate; flat actinally, high convex abactinally, sides of rays close t o perpendicular above angular margin; abactinal plate

arrangement irregular on upper rays, plates crescentiform; plates closely covered by numerous glassy spinelets, digitiform to sacciform on primary plates, thin conical pointed on secondary plates; lacking pedicellariae; papular spaces large, numerous papulae and secondary plates; inferomarginal series of plates project only slightly; actinal plates in oblique series; actinal spines digitiform, numerous per plate; interior resinous body lining; series of irregular superambulacral plates; superactinal plates fill interradial angular margin.

Type species. *Patiria bellula* Sladen, 1889 (original designation) (junior synonym of *Patiria granifera* Gray, 1847, by A.M. Clark, 1956).

Other species. *C. formosa* (Mortensen, 1933).

Material examined. *C. granifera.* South Africa, Western Cape Province, NMV F98049 (1).

Description with species variations. Rays 5, interradial margin deeply incurved, rounded proximally, rays discrete, narrow base tapering to rounded end, form long-rayed stellate; body flat actinally, wider actinally than breadth of upper ray, high convex abactinally, sides of rays close to perpendicular above angular margin; size medium, up to R = 60 mm (*granifera*); lacking pedicellariae; not fissiparous.

Abactinal surface coarse, irregularly arranged crescentiform plates only (*granifera*); sometimes also enlarged rounded plates distally, mostly bare of spinelets (*formosa*); lacking carinal series of plates; papulate areas extensive; papular spaces large, not clearly bordered, up to about 10 large to small secondary plates and up to about 10 papulae per space; abactinal plates irregularly notched for papulae, each plate with low rounded elevation, some subpaxilliform, closely covered with up to about 60 spinelets, glassy, digitiform to sacciform on primary plates, thin conical pointed on secondary plates; bare plate surface with large glassy convexities; sometimes longitudinal series of plates and papulae evident on sides of rays; series of large subequal superomarginal and inferomarginal plates, covered closely with digitiform spinelets, not in marginal tufts; inferomarginals projecting only slightly at almost right-angular margin.

Actinal plates in oblique series.

Actinal spines per plate: oral 6; suboral 5–6; furrow 4 proximally; subambulacral 3–4; actinal interradial up to 10 (fans proximally, clusters distally); adradial actinal plates with complete series of spines; actinal plates with spine-bearing low domes; interradial spines digitiform.

Superambulacral plates present as irregular series, variable size, sometimes paired or absent, contiguous with superactinals for most of ray; marginal angle filled with numerous superactinal plates; abactinal and actinal plates near margin lacking interior projections, meet at angle; superambulacral and superactinal plates embedded in resinous interior lining.

Distribution. Southern Africa; 0–82 m.

Remarks. Molecular data are not available for either species of *Callopatiria*, and this review is based on a morphological examination of a specimen of *C. granifer*a and the description of *C. formosa* by Clark and Downey (1992). *Patiria bellula* Sladen, 1889 was designated by Verrill (1913) as type species of his new genus but it was subsequently assigned to *Parasterina* by H.L. Clark (1923) and Mortensen (1933). However, *Parasterina* is a junior synonym of *Nepanthia*. *Patiria granifera* Gray, 1847 was reassigned to *Asterina* by Perrier (1875), H.L. Clark (1923) and Mortensen (1933). Mortensen (1933) thought it highly probable that *P. bellula* and *P. granifera* were synonyms and A.M. Clark (1956) was more confident. Fisher (1940, 1941) rejected *Callopatiria* as a junior synonym of *Patiria* but it was restored to generic status by A.M. Clark (1983), who noted similarities between *Callopatiria* and *Nepanthia*.

Callopatiria, Nepanthia, Pseudonepanthia and *Pseudopatiria* are unusual asterinid genera in having discrete narrow rays which are rounded abactinally. They also have irregularly arranged abactinal plates on the upper rays and narrowly or not projecting inferomarginal plates, characters shared with some other genera. *Callopatiria* is separated diagnostically by having rays that are not subcylindrical, with a flat actinal surface significantly wider at mid-ray than upper ray breadth, and by a marginal angle supported internally by many superactinal plates.

Cryptasterina Dartnall, Byrne, Collins and Hart

Figures 1 (clade IV, part), 2f, 11a

Cryptasterina Dartnall et al., 2003: 3–4.

Diagnosis. Rays 5, form pentagonal to short rays rounded distally; body with noticeable integument; low convex abactinally; abactinal plates in longitudinal series, deeply notched for papulae, many U-shaped more than crescentiform; longitudinal series of predominantly single papulae along sides of rays; nonpapulate interradial areas extensive; few (1–3) papulae per papular space; abactinal spinelets granuliform, spaced over plates; lacking pedicellariae; lacking glassy convexities; superomarginal series prominent, longitudinally subrectangular, inferomarginals predominantly project narrowly; non-plated actinal area distal to oral plates frequently present, not extensive; actinal interradial plates in oblique series; actinal spines short conical, predominantly 1 per plate, rarely 2–3 distally; very small superambulacral plates few, never as series; superactinal plates present, sometimes in multiple plate struts.

Type species. *Asteriscus pentagonus* Müller and Troschel, 1842 (original designation) (junior synonyms: *Patiriella pseudoexigua* Dartnall, 1971 and *Patiriella obscura* Dartnall, 1971, by Dartnall et al., 2003).

Other species. *C. hystera* Dartnall and Byrne, 2003; *C. pacifica* (Hayashi, 1977).

Material examined. *C. hystera*. Paratypes. Queensland, Yeppoon (Statue Bay), NMV F96255 (3). Other material. Statue Bay, F98457 (2); F97057 (6).

C. pentagona. Queensland, Cairns, NMV F96702 (2); Townsville, F97056 (2); F98452 (8); F98453 (1); Bowen (Airlie Beach), F97055 (4), F98454 (2); Mackay, F95959 (7); Hervey Bay, F98456 (2); Kurrimine, F95961 (2); Bingil Bay, F98455 (2).

Description with species variations. Rays 5 (rarely 4 or 6); interradial margin straight to slightly incurved, form pentagonal to short tapered rays rounded distally; body with

noticeable integument; flat actinally, low convex abactinally, sides of rays not steep; size small (*pentagona* up to R = 17 mm; *hystera* up to R = 12 mm); lacking pedicellariae; lacking actinal gonopores; not fissiparous.

Abactinal surface even; plates low, imbricate, deeply notched for papulae, many U-shaped more than crescentiform; plates in longitudinal series; papular spaces fairly large; papulae predominantly single, large (*pentagona*) or small (*hystera*), up to 3 per space; secondary plates 0–3 per papular space; carinal series of doubly or singly notched plates variably present; longitudinal series of papular spaces along sides of rays; disc variably bordered by 5 radial and 5 smaller interradial plates; abactinal spinelets granuliform, short columnar, spaced over plates; denuded abactinal plates with reticulate glassy ridges, not convexities; marginal plates with abactinal-type spinelets, slightly thinner and longer on inferomarginals; superomarginal series distinctive, longitudinally subrectangular; inferomarginal plates less conspicuous, predominantly project narrowly to form margin.

Actinal interradial plates in oblique series; non-plated actinal area distal to oral plates variably present, not extensive.

Actinal spines per plate: oral 5–6 (proximal separated from distal frequently in *hystera*); suboral 1–2; furrow 2–3 proximally; subambulacral 1; adradial actinal 0–1; actinal interradial predominantly 1 (rarely 2–3 distally); actinal spines short conical.

Small superambulacral plates few, especially distally, lacking series; superactinal plates present, sometimes in multiple plate struts.

Distribution. Tropical Indo-Pacific; NE Australia, Indonesia, Philippines, Solomon Is, Taiwan, Japan; littoral and shallow sublittoral.

Remarks. In the molecular clade IV of Waters et al. (2004), the label *P. pseudoexigua* (Japan) refers to *C. pacifica* and *P. pseudoexigua* (Australia) to *C. pentagona* (following Dartnall et al., 2003). These sister taxa are on a clade separate from *Aquilonastra*. Hart et al. (2003) added two additional lineages to this clade (*C. hystera* and an undescribed species from Taiwan). Dartnall et al. (2003) erected *Cryptasterina* and provided a morphological diagnosis for the three species. The principal diagnostic characters of *Cryptasterina* seen here are: integument cover; pentagonal to short-rayed form; longitudinal series of plates on rays; granuliform spinelets; predominantly single papulae per space; absence of glassy convexities; prominent longitudinally elongate superomarginal plates; narrowly projecting inferomarginal plates; actinal interradial spines predominantly single in mid-ray; some superambulacral plates present; superactinal plates present. The similarities and differences for *Cryptasterina* and *Aquilonastra* were discussed under the latter.

Disasterina Perrier

Figures 2g, 5f, 10e–f, 12a–b

Disasterina Perrier, 1875: 289.—Livingstone, 1933: 5–7.—H.L. Clark, 1946: 138.—Spencer and Wright, 1966: U69.—A.M. Clark, 1993: 218.—Liao and Clark, 1995: 131–132.—Rowe, 1995: 35.

Manasterina H.L. Clark, 1938: 157–158.—H.L. Clark, 1946: 139.—A.M. Clark, 1993: 220.—Rowe, 1995: 36. New synonym.

Diagnosis. Rays 5; body thin, covered by thick integument; form medium to long-rayed stellate, rays with wide base, tapering strongly, flat actinally, height low convex; abactinal plates thin, on broad upper rays predominantly irregular in shape, size and arrangement, loosely imbricate or contiguous or not contiguous leaving non-plated spaces; plates on lower rays in few irregular longitudinal series, sometimes weakly notched and crescentiform; interradii thin distally, small non-papulate plates in perpendicular or zig-zag series to margin; papulae few, irregular on rays; abactinal spinelets lacking or rare or few, glassy, sacciform, short or long; superomarginal plates small, not in distinct series; inferomarginal plates project widely, loosely contiguous, with distal fringe of few large sacciform spinelets; actinal interradial plates in oblique series; proximal actinal interradial areas frequently not plated; interradial actinal plates with 1–2 long sacciform spines; superambulacral plates irregularly present mid-ray and distally, lacking complete series; superactinal plates present as single plate struts.

Type species. Disasterina abnormalis Perrier, 1875 (monotypy) (junior synonym: *Habroporina pulchella* H.L. Clark, 1921, by Livingstone, 1933).

Other species. D. ceylanica Döderlein, 1888; *D. longispina* (H.L. Clark, 1938); *D. odontacantha* Liao, 1980; *D. spinosa* Koehler, 1910.

Material examined. D. abnormalis. New Caledonia, AM J5042; Queensland, Cairns, J4947 (2); Hayman I., J5699 (1); J5904 (4); J5957 (1); J7315 (1); Torres Strait, Murray I., Z6748 (1); N Western Australia, Rowley Shoals, WAM Z6749 (2); Scott Reef, Z6753-5 (3).

D. longispina. Western Australia, Houtman Abrolhos, WAM Z6758 (1); Z6760 (2).

D. odontacantha. Fiji, UF 2391 (1); UF 1116 (1); UF, 1874 (1); Guam, UF 1253 (1).

Description with species variations. Body thin, rays 5 (*abnormalis* 5–6); interradial margin deeply incurved, concave or acute proximally, form medium to long-rayed stellate; rays with wide base, tapering to narrowly or widely rounded end; body flat actinally, low convex abactinally; distal interradii wide and thin (*abnormalis*), or narrow and thin, rays rise distinctly from thin margin; body covered with thick integument; size medium (*abnormalis* up to R = 38 mm) to small (*spinosa* up to R = 14 mm); pedicellariae possibly present (*longispina*); none fissiparous.

Abactinal appearance irregular; abactinal plates on broad upper rays thin, irregular in form, size, arrangement; plates not distinguishable as primary and secondary, intergrade from large to small; plates weakly imbricating or contiguous or not contiguous leaving non-plated spaces on rays; lacking carinal series; plates on lower rays in few irregular longitudinal series; distal thin interradii with small rounded non-papulate plates in irregular series perpendicular or zig-zag to margin; plates on rays sometimes weakly notched for papulae and crescentiform (*spinosa*); papulae on rays only, single, few and sparse, large or small, irregular; disc not regularly bordered (*abnormalis*) or almost regular border (*longispina, odontacantha*); low domes sometimes present on abactinal plates (*longispina*); abactinal

plates frequently bare, or with few sacciform spinelets around disc (*abnormalis*), or sometimes with 1–2 spinelets, short proximally, long distally (*odontacantha*), or with 1–4 spinelets variable in form from digitiform to long, pointed or rounded, principally on ends of rays (*longispina*), or with 1–3 long sacciform spinelets proximally and on rays (*spinosa*); clusters of 2–4 undifferentiated spinelets possibly act as pedicellariae interradially (*longispina*); glassy convexities present on abactinal plates (*abnormalis, longispina, odontacantha*); superomarginal plates small, not in distinct series, bare (*abnormalis, longispina*) or with 1 (*odontacantha*) or few long spinelets (*spinosa*); inferomarginal plates project prominently, some elongate and almost entirely projecting (*abnormalis*, *longispina*, *odontacantha*), each plate with transverse distal fringe of 1–6 integument-covered long sacciform spinelets.

Actinal interradial plates in oblique series; proximal actinal interradial areas frequently not plated.

Actinal spines per plate: oral 4–8; suboral 1–3 (*odontacantha* 0); furrow 3–6 proximally, webbed; subambulacral 1–3; adradial bare (*abnormalis, odontacantha*) or with spines; actinal 1 or 2 (*spinosa*); interradial actinal spines long sacciform.

Superambulacral plates irregularly present mid-ray and distally (*abnormalis, longispina*), lacking complete series; superactinal plates present as single plate struts *(abnormalis, longispina*).

Distribution. Indo-West Pacific, South China Sea (Xisha Is), Ceylon, Bay of Bengal (Andaman Is), Indonesia, New Caledonia, Guam, Fiji, northern Australia, western Australia.

Remarks. Molecular data have not been obtained for species of *Disasterina* and the genus is reviewed on morphological grounds. Specimens of *D. ceylanica* and *D. spinos*a were not seen and morphological data were obtained from the original descriptions and figures by Döderlein (1888) and Koehler (1910).

Species previously assigned to *Disasterina* fall into two morphological groups, those close to the type *D. abnormalis* and retained here in *Disasterina*, and *D. leptalacantha* and *D. praesignis* (with junior synonym *D. spinulifera*) which are close to *Tegulaster emburyi* and are removed to *Tegulaster. Disasterina* differs from *Tegulaster* in having: body thin and low, not thick and high; abactinal plates thin and loosely contiguous, not thick and imbricating; non-plated abactinal spaces present, not absent; median band of irregular abactinal plates on rays wide, not narrow; distal interradial plates at margin in irregular perpendicular series, not longitudinal and thus crossed angled series; superomarginal plates small and irregular, not large and in distinct series; covering integument thick, not thin. The form and patterns of spinelets and spines are similar in the two genera. *Disasterina* also shares some morphological characters with *Indianastra* gen. nov. below, in particular spination, limited presence of superambulacral plates and presence of series of superactinal plates. The morphological differences between *Disasterina* and *Indianastra* are detailed under the latter.

Manasterina longispina H.L. Clark, 1938 was described from a single specimen and the genus distinguished from *Disasterina* by size, single minute spinelets on some abactinal plates, long spinelets on rays distally, openly spaced abactinal plates, and absence of non-plated proximal actinal areas. None of these characters is of generic value. The long spinelets on distal ray plates is unique to the species. *M. longispina* is intermediate in size amongst species of *Disasterina*; species of *Disasterina* sometimes have spinelets on abactinal plates; and the extent of non-plated abactinal and actinal body wall varies amongst specimens of *M. longispina* and amongst species of *Disasterina*. *Manasterina* is synonymised here with *Disasterina*. Clusters of 2–4 undifferentiated interradial spinelets with their distal ends angled together and contiguous were observed on preserved *D. longispina* material, and possibly act as pedicellariae.

Livingstone (1933) considered *D. spinosa* to be inappropriately assigned to *Disasterina* but gave no reason. The single long sacciform spinelets on abactinal plates distinguish the species but are not grounds for rejecting its generic placement. *Disasterina ceylanica* Döderlein (1888) was reassigned to *Tegulaster* by Livingstone (1933). *Disasterina* and *Tegulaster* have some common characters but the reassignment is inappropriate.

Material from the University of Florida extends the distribution of *D. odontacantha* from China to Guam and Fiji.

Indianastra O'Loughlin gen. nov.

Figures 2h, 6b, 13a–f

Diagnosis. Rays 5, petaloid to subpentagonal; size small; body thin, integument-covered; abactinal and actinal interradial plates in longitudinal series; abactinal plates deeply notched for papulae, short crescentiform; numerous regular longitudinal series of plates with papulae along sides of rays; abactinal spinelets fine, glassy, inconspicuous, acicular to subsacciform, few to numerous per plate, in tufts or cover over plate, not on high raised ridges or domes, fragile, readily lost; pedicellariae sometimes present over papulae; superomarginal plates with rare spinelets or bare; inferomarginal plates with distal subpaxilliform dense tufts of acicular spinelets, covered by integument; actinal interradial plates in longitudinal series; plates with small clusters of webbed short sacciform spines; lacking superambulacral series of plates, rare single plates distally; superactinal plates as single plate struts.

Type species. Palmipes sarasini de Loriol, 1897 (junior synonyms: *Asterina lutea* H.L. Clark, 1938, *Asterina nuda* H.L. Clark, 1921, and *Asterina orthodon* Fisher, 1922 by Rowe, 1995).

Other species. I. inopinata (Livingstone, 1933) (junior synonym: *Asterina perplexa* H.L. Clark, 1938, by Rowe, 1995).

Material examined. I. inopinata. Holotype, 12 paratypes. Australia, New South Wales, AM J3077. Other material. New South Wales, NMV F93460 (3); Byron Bay, AM J15254 (6);

I. lutea. Paratypes. NW Australia, Broome, AM J6167 (4).

I. orthodon. Hong Kong, BMNH 1983.2.15.116 (1).

I. sarasini. NW Australia, WAM Z6833 (1); Broome, AM J6640 (5); NMV F95802 (2); Queensland, J4123 (1).

Description with species variations. Rays 5, petaloid (rays wide basally, rounded distally, subacute to narrowly rounded junctions) to narrowing rounded to subpentagonal (interradial margin straight to shallow incurved); body integument-

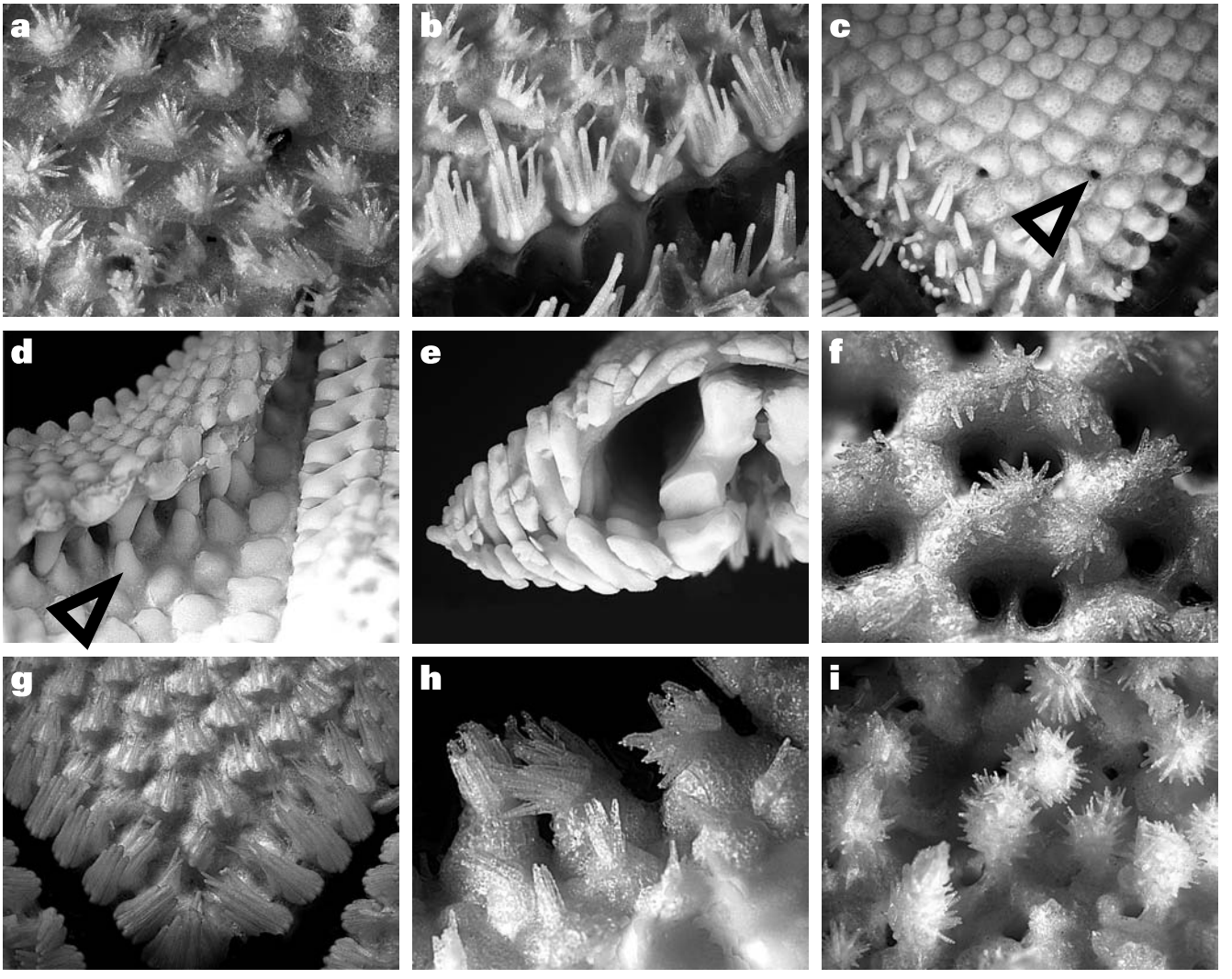


Figure 8. a, *Anseropoda placenta* (R = 56 mm, NMV F98043): abactinal plates, spinelets, papulae. b, *Anseropoda rosacea* (R = 82 mm, NMV F95811): adambulacral and actinal plates and sacciform spines. c–d, *Asterina gibbosa* (R = 19 mm, NMV F45108): c, actinal interradius with gonopores; d, margin supported by internal contiguous projections from abactinal and actinal plates, absence of superambulacral plates. e, *Asterina ocellifera* (R = 37 mm, BMNH 1969.12.16.13): margin supported by internal contiguous plate projections, absence of superambulacral and superactinal plates. f–h, *Asterinides folium* (R = 20 mm, USNM 28573): f, abactinal spinelet clusters and papulae; g, actinal interradius with sacciform spines; h, marginal plates with spinelets. i, *Asterinides pompom* (R = 14 mm, USNM 47866): abactinal plates with paxilliform elevations.

covered, flat actinally, low convex abactinally; size small (both species up to R = 20 mm); simple pedicellariae present over papulae, valves short, conical to sacciform, up to 6 valves (*sarasini* only); not fissiparous.

Abactinal appearance dominated by numerous regular longitudinal series of papulae along sides of rays; plates imbricate, deeply notched for papulae, interradially in longitudinal series to margin; papulate areas extensive, papular spaces fairly large, predominantly single large papula per space, up to 4 small papulae and 5 secondary plates per space; up to 6 longitudinal series of papulae along each side of rays; plates on narrow median upper rays irregular, carinal series of plates variably present, doubly notched; abactinal plates with low spinelet-bearing elevations, on lower rays and proximal interradii predominantly singly notched for papulae, crescentiform only (*inopinata*), additional deep to almost closed pedicellarial notch proximally (*sarasini*); fine, glassy, fragile, inconspicuous, acicular to subsacciform spinelets, sparsely present in apical tufts or numerous in crescentiform cover on projecting proximal edge of plates, spinelets readily lost; glassy convexities (*sarsini*) or reticulations (*inopinata*) on plates; disc variably bordered by continuous series of 5 large radial 5 small interradial plates; superomarginal plates in series, rare spinelets (*inopinata*) or bare (*sarasini*); inferomarginal plates in series, project to form margin, bare proximally, distal subpaxilliform dense tuft of acicular spinelets projects laterally, integument-covered.

Actinal plates in longitudinal series.

Actinal spines per plate (lower numbers in *inopinata*): oral 8–11; suboral 4–9, webbed fan; furrow 5–9 proximally, webbed; subambulacral 3–9; adradial actinal plates with complete series; actinal 2–8 in mid interradius, webbed transverse clusters; actinal interradial spines short sacciform.

Lacking series of superambulacral plates, rare single plates distally (seen in *sarasini* only); margin supported by series of single superactinal plates, and internal tongue-like projections of abactinal plates contiguous with actinal plates.

Distribution. Indian West Pacific, Sri Lanka to southern China, N and E Australia, 0–25 m.

Etymology. From the first word of "Indian West Pacific" and the Latin *astrum* (star), referring to the region of occurrence of this genus (feminine).

Remarks. Molecular data are not available for either species and this review is based on morphological evidence. *Indianastra* shares some morphological characters with both *Disasterina* and *Tegulaster*, in particular the spination, limited presence of superambulacral plates and presence of series of superactinal plates. Morphological differences between *Indianastra* and *Disasterina* are: form petaloid to subpentagonal, or rays discrete; abactinal plates small, of uniform size and imbricate, or irregular in size, form and arrangement and loosely contiguous; abactinal plates deeply, or slightly notched; longitudinal series of papulate plates numerous and regular on rays, or few and irregular on lower sides of rays; abactinal interradial plates in longitudinal series, or series perpendicular to margin; superomarginal series of plates distinct and regular, or reduced and irregular; inferomarginal spinelets acicular, in dense tufts, or few, sacciform and discrete; actinal series of plates longitudinal, or oblique; actinal interradial spines short, in clusters, or long, 1–2. Morphological differences with *Tegulaster* are given under *Tegulaster* below. These morphological differences are the basis for the erection of the new genus.

Jangoux (1985) established a lectotype and paralectotype for *Palmipes sarasini*. Rowe (1995) formalised the synonymies of *I. lutea, I. nuda* and *I. orthodon* with *I. sarasini*, which had been suggested by Clark and Rowe (1971). Dartnall (1970, 1980) recorded *A. inopinata* from northern Tasmania, but records were based on material subsequently determined by O'Loughlin as *Meridiastra nigranota* O'Loughlin, 2002 (TM H1330), *M. atyphoida* (H.L. Clark, 1916) (TM H841) and *Asterina scobinata* Livingstone, 1933 (TM H1746). The pedicellariae on *I. sarasini* are frequently difficult to detect because the valves are lost or close over the notch and are integument-covered.

Kampylaster Koehler

Kampylaster Koehler, 1920: 136–137.—Fisher, 1940: 250–252.—Bernasconi, 1973: 344.—A.M. Clark, 1993: 220.

Diagnosis. Rays 5; body small, frequently arched, abactinally covered by integument and subgranular spinelets; rays 5, short petaloid; abactinal plates thin, not notched, irregular arrangement; actinal plates in oblique series; actinal spines per plate few, subglobose; lacking superambulacral and superactinal plates; abactinal and actinal distal interradial plates lacking contiguous internal projections.

Type species. Kampylaster incurvatus Koehler, 1920 (original designation).

Material examined. K. incurvatus. Syntypes. Antarctica, Adelie Land, AM J3581 (2, A and B).

Description. Rays 5, petaloid to tapered from wide base; margin incurved and subacute interradially; body variably arched; size small, up to R = 15 mm; lacking pedicellariae; brood-protects under body.

Abactinal plates obscured by integument and close uniform cover of coarse subgranular spinelets; abactinal plates on rays large, thin, imbricating, not notched, irregular arrangement; papulae small, inconspicuous, single, irregular over rays (seen from coelomic side by Fisher, 1940; not seen here); abactinal spinelets subgranular, wide base, narrowed waist, convex and spinous distally; superomaginal plates similar to adjacent abactinal plates, covered with granular spinelets, not aligned with inferomarginals; series of thick rounded projecting inferomarginal plates define margin, covered with granular spinelets.

Actinal interradial areas small, series of plates oblique.

Actinal spines per plate: oral 3; suboral 0; furrow 2–3 proximally, webbed; subambulacral 1–2; actinal 1–3; adradial actinal plates with series of shorter spines; actinal spines short, thick, rounded, subglobose distally.

Lacking superambulacral and superactinal plates; abactinal and actinal distal interradial plates meet at an angle, lacking contiguous internal projections.

Distribution. Antarctica, Enderby Land to Scotia Sea; 93–750 m.

Remarks. Molecular data are not available for *incurvatus*, and this review is based on a morphological examination of syntypes and the observations of Fisher (1940). Distinctive diagnostic characters of *Kampylaster* are the integument and granuliform spinelet cover, irregular arrangement of thin abactinal plates, inconspicuous papulae, absence of a series of superomarginal plates, and absence of superambulacral and superactinal plates.

Koehler (1920) considered *Kampylaster* to be similar to *Tremaster* Verrill, 1880 and referrable to the subfamily Tremasterinae. Fisher (1940) rejected the similarity because of the distinctive interradial perforations of *Tremaster*, and considered *Kampylaster* to be closer to *Stegnaster* Sladen, 1889. Additional reasons for rejecting a similarity with *Tremaster* are the quadriserial arrangement of tube feet and vertical furrow spines on adambulacral plates in *Tremaster*.

Meridiastra O'Loughlin

Figures 1 (clade III), 2i, 4c, 5a, 10g–i

Meridiastra O'Loughlin, 2002: 280.—Waters et al., 2004: 874, 875, 877.

Diagnosis. Rays predominantly 5 or 6 or 7 or 8; interradial margin straight or incurved, rays not discrete; flat actinally, low

to high convex abactinally; abactinal plates in longitudinal series along rays, carinal series present for at least part ray length; papulae small, lacking longitudinal series of large papulae along sides of rays; abactinal spinelets granuliform; lacking pedicellariae; abactinal plates with glassy convexities; actinal plates in longitudinal series; actinal spines in mid-interradius digitiform or tapering or conical, 1–3; lacking superambulacral and superactinal plates, distal interradial margin supported by contiguous interior projections from abactinal and actinal plates.

Type species. Asterina atyphoida H.L. Cark, 1916 (original designation).

Other species. M. calcar (Lamarck, 1816); *M. fissura* O'Loughlin, 2002; *M. gunnii* (Gray, 1840) (junior synonym: *Patiriella brevispina* H.L. Clark, 1938, by O'Loughlin et al., 2003); *M. medius* (O'Loughlin et al., 2003); *M. modesta* (Verrill, 1870) (junior synonym: *Asterina agustincasoi* Caso, 1977 by O'Loughlin, 2002); *M. mortenseni* (O'Loughlin et al., 2002); *M. nigranota* O'Loughlin, 2002; *M. occidens* (O'Loughlin et al., 2003); *M. oriens* (O'Loughlin et al., 2003); *M. rapa* O'Loughlin, 2002.

Material examined. See O'Loughlin (2002), O'Loughlin et al. (2002, 2003).

M. calcar. Australia, Victoria, Cape Paterson, NMV F73126 (4).

Description with species variations. Rays predominantly 5 (*atyphoida, modesta, mortenseni, nigranota, rapa*), or 6 (*gunnii, medius, occidens, oriens*), or 7 (*fissura*), or 8 (*calcar*); interradial margin straight to incurved, rays sometimes distinct, narrowly rounded to pointed distally; integument noticeable; size medium (*gunnii* up to R = 56 mm) to very small (*rapa* up to R = 6.0 mm); pedicellariae absent; gonopores actinal (*nigranota*) or abactinal; fissiparity in one species (*fissura*).

Abactinal plates in longitudinal series; carinal series present to variable extent; abactinal appearance of two types, with papulate areas extensive, papular spaces large with numerous small papulae and secondary plates, plates distinctly doubly or singly notched with projecting proximal edge crescentiform except in distal plates (*calcar, gunnii, medius, mortenseni, occidens, oriens*), or with papulate areas small, papular spaces small with few small papulae and secondary plates, plates not distinctly notched and projecting proximal edge not crescentiform (*atyphoida, fissura, modesta, nigranota, rapa*); lacking distinct longitudinal series of large papulae along sides of rays; disc variably distinct with border of continuous radial and interradial plates; abactinal plates sometimes with low spinelet-bearing elevation; cleared abactinal plates with glassy convexities; abactinal spinelets over projecting anterior edge of plates, not in tufts, granuliform, and stout, opaque and firmly attached (*calcar* group above) or fine, glassy and weakly attached (*atyphoida* group above); series of subequal, spinelet-covered, superomarginal and inferomarginal plates; margin formed by projecting inferomarginal plates.

Actinal plates in longitudinal series, sometimes oblique (*atyphoida*).

Actinal spines per plate: oral 4–7; suboral 0–2; furrow 2–5 proximally, webbed; subambulacral 1–3; actinal 1–3 in mid-interradius, up to 4 distally; adradial row of actinal plates with variably complete series of spines; interradial actinal spines thick, bulbous to short tapered to conical to digitiform.

Lacking superactinal and superambulacral plates; interradial margin supported by contiguous internal projections of the abactinal and actinal plates.

Distribution. Southern Australia, New Zealand, central and eastern South Pacific, Mexico, Panama; 0–59 m.

Remarks. *Meridiastra*, erected by O'Loughlin (2002) on morphological evidence only, is supported by the molecular phylogenetic relationships of the nine species included in clade III of Waters et al. (2004). The key morphological features of these nine species are: straight to shallow incurved interradial margins, rays not discrete; longitudinal series of abactinal plates; granuliform abactinal spinelets; lack pedicellariae; presence of conspicuous glassy convexities on plates; actinal plates in longitudinal series; low numbers of thick, tapering actinal spines; lack superambulacral and superactinal plates; have internal contiguous projections of distal interradial abactinal and actinal plates supporting the margin. Most of the species of *Meridiastra* were previously assigned to *Patiriella* which has irregularly arranged abactinal plates, actinal plates in predominantly oblique series, and superambulacral and superactinal plates present. The molecular phylogeny supports the separation of *Meridiastra* and *Patiriella*. *Meridiastra* is closest morphologically to *Asterina* which also lacks internal skeletal plates but which has more discrete rays, opaque spinelets which are elongate, and actinal plates in predominantly oblique series. The molecular phylogeny also supports the separation of *Meridiastra* (Indo-Pacific) from *Asterina* (NE Atlantic). The morphological similarities of these two genera could reflect convergent evolution, or the retention of ancestral character states, or a true sister relationship; the phylogeny of Waters et al., 2004 was uninformative in this regard.

Molecular clade III provides evidence of two groups of closely related species within the clade: *M. gunnii, M. oriens, M. medius* and *M. occidens*; and *M. fissura, M. nigranota* and *M. atyphoida*. These closer molecular relationships are reflected in the morphological description above, where these two sets fall within the *M. calcar* and *M. atyphoida* groups. Our decision to combine the two groups into a single genus is subjective but supported by the significant internal skeletal similarities.

Nepanthia Gray

Figures 2j, 4f, 6c, 14a–c

Nepanthia Gray, 1840: 287.—Sladen, 1889: 386–387.—Verrill, 1913: 480.—Fisher, 1940: 270–271.—Fisher, 1941: 451–155, figs, 20–22, pl. 70 fig. 2.—Spencer and Wright, 1966: U69.—Rowe and Marsh, 1982: 93.—A.M. Clark, 1983: 370.—A.M. Clark, 1993: 220.—Liao and Clark, 1995: 132–133.—Rowe, 1995: 36–37.—McKnight (in Clark and McKnight), 2001: 158.

Asterina (*Nepanthia*) Perrier, 1875: 320.

Diagnosis. Rays 4–7, subcylindrical, to varying degrees flat actinally with distinct to slight marginal edge; plates on upper rays irregular in arrangement; secondary plates present; abactinal and actinal interradial plates with dense clusters of thick or thin glassy spinelets, frequently on spinelet-bearing elevations; pedicellariae present; glassy convexities on plates; infero-

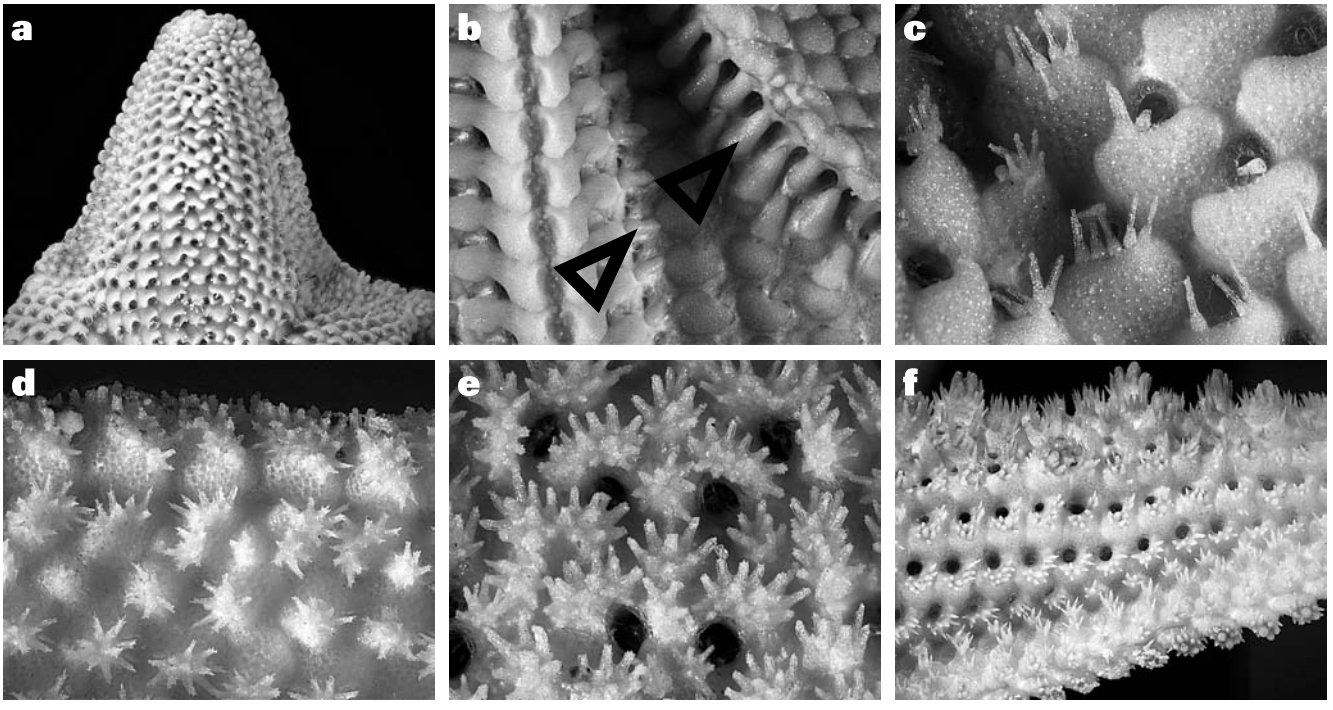


Figure 9. a–d, *Aquilonastra cepheus*: a, cleared ray (R = 17 mm, NMV F95793); b, internal superambulacral (left arrow) and superactinal (right arrow) plates (R = 22 mm, WAM Z6778); c, cleared abactinal plates with some sacciform spinelets (R = 17 mm, NMV F95793); d, abactinal margin (R = 22 mm, WAM Z6778). e, *Aquilonastra batheri* (R = 19 mm, NMV F97441): abactinal carinal plates with tufts of spinelets. f, *Aquilonastra coronata* (R = 22 mm, NMV F95796): side of ray with paxilliform elevations on upper ray.

marginal plates projecting slightly; oblique series of actinal plates variably evident; furrow spines 6 and more per plate; actinal spines predominantly thin, glassy, sometimes sacciform; superambulacral, transactinal and superactinal plates present, embedded in interior resinous lining in most species.

Type species. Nepanthia maculata Gray, 1840 (restriction by Perrier, 1875; subsequent designation by Verrill, 1913).

Other species. N. belcheri (Perrier, 1875) (junior synonym: *N. variabilis* H.L. Clark, 1938 by Rowe and Marsh, 1982); *N. crassa* (Gray, 1847); *N. fisheri* Rowe and Marsh, 1982; *N. pedicellaris* Fisher, 1913.

Material examined. N. belcheri. Queensland, Magnetic I., NMV F97721 (1); Western Australia, Dampier, F95806 (1); Exmouth Gulf, F95805 (1).

N. crassa. Western Australia, Fremantle, AM J6165 (1); Ludlow Reef, J7418 (1).

N. fisheri. Timor Sea, AM J12649 (1).

N. maculata. Australia, Timor Sea, AM J13918 (2); Gulf of Carpentaria, J7404 (2); J10536 (1); J13063 (1).

N. pedicellaris. Holotype. Philippines, USNM 32643.

N. variabilis. Paratypes. Western Australia, Broome, AM J6187 (4).

Description with species variations. Rays 4–7, elongate, subcylindrical, equal or unequal lengths, tapering strongly (*fisheri*, *pedicellaris*) or slightly; large (*maculata* up to R = 94 mm) to small (*pedicellaris* up to R = 23 mm); integument variably evident; flat actinally, distinct to slight edge at margin; pedicellariae present, 2-valve (*fisheri, maculata, pedicellaris*) or multi-valve (*belcheri, crassa*); fissiparous (*belcheri*) or not.

Abactinal plates strongly imbricating, projecting proximal edge creating uneven surface, irregularly arranged on upper rays, in regular longitudinal sloping series on sides of rays; plates predominantly irregular in shape (*crassa*) or notched (*belcheri, fisheri, maculata, pedicellaris*), with spinelet-bearing curved elevations above notch (*belcheri, pedicellaris*) or raised ridges (*fisheri, maculata*) or domes (*crassa*), lower surface with glassy convexities; disc variably bordered; papulate areas extend to near margin; papular spaces with 1–2 large papulae and 1–8 secondary plates per space; spinelets thin, glassy, variably sacciform (*fisheri, maculata, pedicellaris*), some splay-pointed distally (*belcheri, crassa*), up to more than 40 per plate; variably regular superomarginal plates, inferomarginal series of plates project slightly at margin, covered with spinelets.

Actinal plates with spine-bearing elevations, variably in oblique series.

Actinal spines per plate: oral 9–10; suboral about 10–26, tall and short; furrow 6–10; subambulacral 6–20; complete series of adradial actinal spines; interradial actinal 4–6 or dense subpaxilliform clusters, glassy, thin (*belcheri*), thick and thin (*crassa*), sometimes sacciform (*fisheri, maculata, pedicellaris*).

Superambulacral, transactinal and superactinal plates present, embedded in internal resinous lining or not (*pedicellaris*).

Distribution. N, S, E and W Australia, Lord Howe I., Indonesia, Timor Sea, New Guinea, W Indonesia, Philippines, Vietnam, Burma, Mergui Archipelago, 0–123 m.

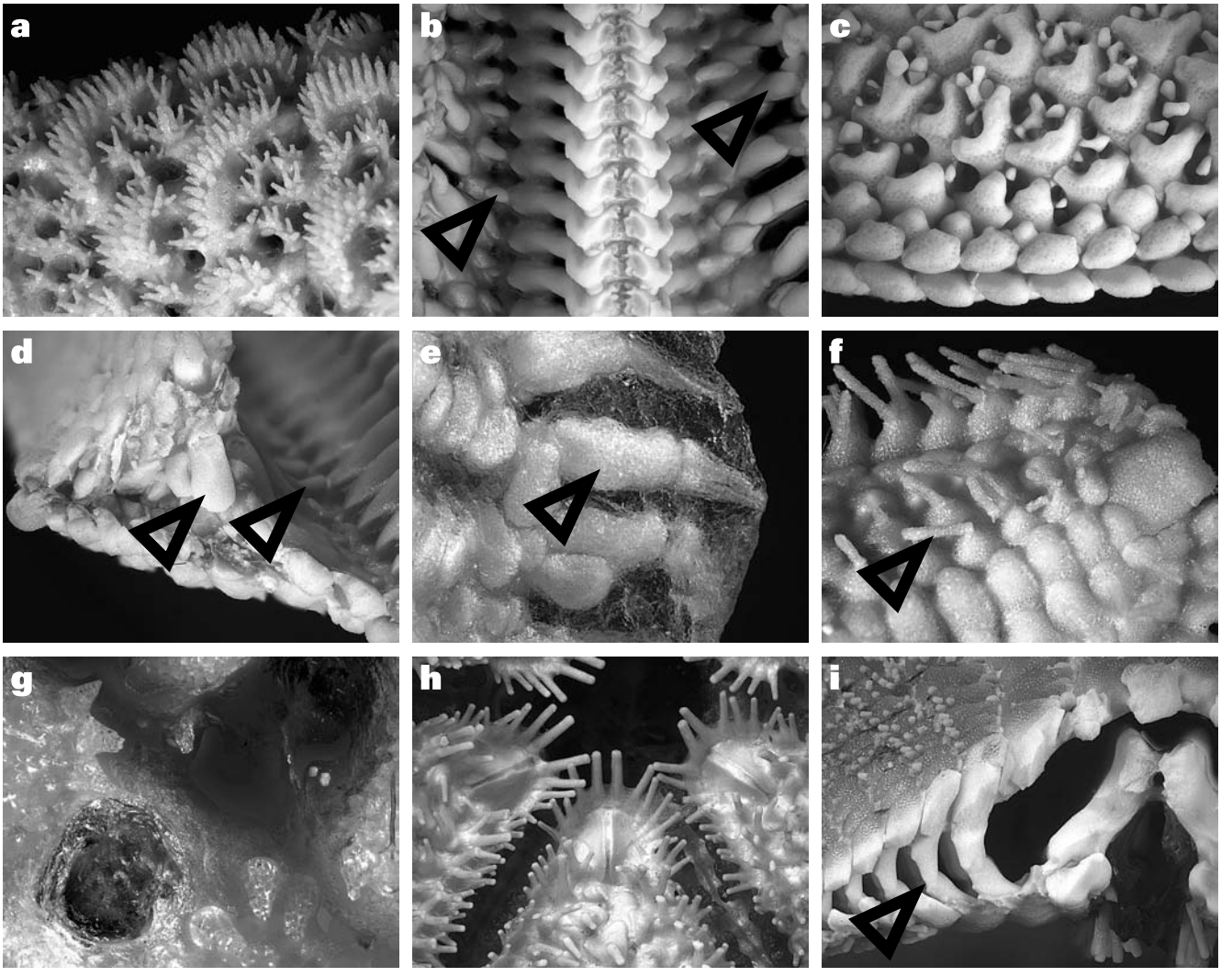


Figure 10. a–d, *Callopatiria granifera* (R = 50 mm, NMV F98049); a, mid-ray abactinal primary and secondary plates, spinelets and papulae; b, internal superambulacral (left arrow) and superactinal (right arrow) plates; c, cleared lower lateral ray, with marginal plates, glassy convexities, papulae and secondary plates; d, section through ray showing superactinal (left arrow) and superambulacral (right arrow) plates. e, *Disasterina abnormalis* (R = 38 mm, WAM Z6749): integument-covered inferomarginal plate (arrow) with two distal sacciform spinelets. f, *Disasterina longispina* (R = 20 mm, WAM Z6760): abactinal tip of ray, with margin and long upper ray spinelet (arrow). g, *Meridiastra atyphoida* (R = 12 mm, NMV F87166): minute abactinal conical spinelets. h, *Meridiastra occidens* (R = 22 mm, NMV F73186): proximal actinal interradius, with oral spines. i, *Meridiastra gunnii* (R = 40 mm, NMV F73248): interradial margin supported by contiguous projections from abactinal and actinal plates, absence of superambulacral and superactinal plates.

Remarks. Molecular data are not available for any species of *Nepanthia* and this review is based on a morphological examination. Six species previously assigned to *Nepanthia* are removed to *Pseudonepanthia*. The morphological characters which distinguish *Nepanthia* from *Pseudonepanthia* are: rays flat actinally, with a marginal edge; presence of secondary plates, pedicellariae and glassy convexities; furrow spines six and more per plate; presence of transactinal and superactinal plates.

Nepanthia pedicellaris Fisher, 1913 was referred by Fisher (1919) to *Asterinopsis* Verrill, 1913 (a nomen dubium). We return it to *Nepanthia*.

Paranepanthia Fisher

Figures 1 (clade I), 2k, 5c, 15a–c

Paranepanthia Fisher, 1917: 172.—Fisher, 1919: 419.—H.L. Clark, 1946: 136.—Spencer and Wright, 1966: U69.—A.M. Clark, 1993: 222.—Rowe, 1995: 39.—McKnight (in Clark and McKnight), 2001: 160.—Waters et al., 2004: 874, 875, 877.

Diagnosis. Rays 5, medium length, wide basally, pointed or rounded distally; flat actinally, rays elevated to low; abactinal and actinal interradial plates with subpaxilliform dense clusters of acicular subsacciform spinelets; abactinal plates mostly irregular on upper rays, mostly series perpendicular to

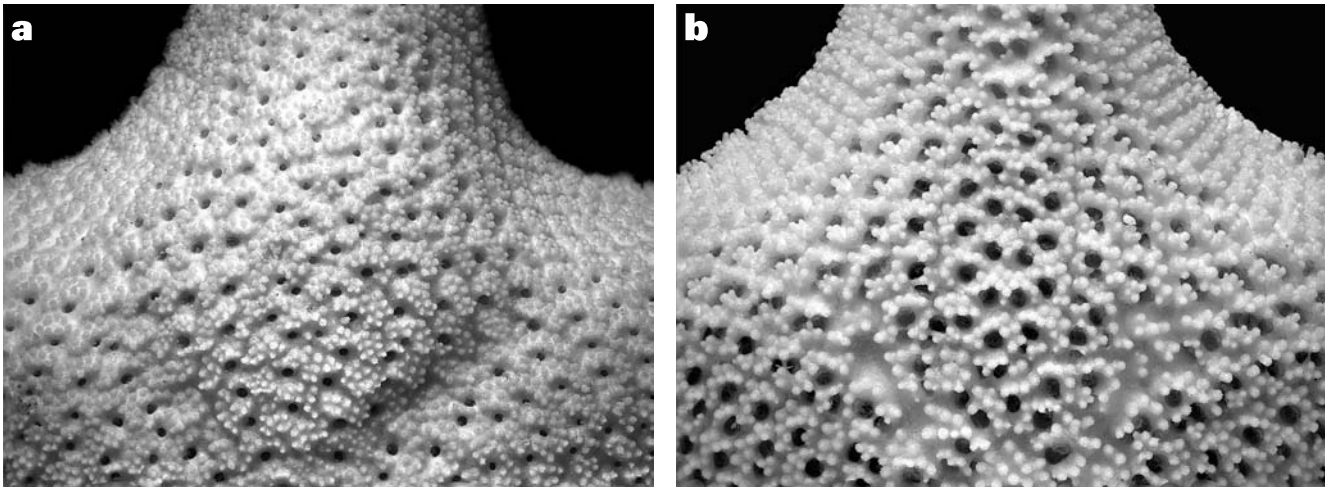


Figure 11. a, *Cryptasterina hystera* (R = 11 mm, NMV F98457): abactinal surface with small papulae and granuliform spinelets. b, *Parvulastra exigua* (R = 10 mm, NMV F98062): abactinal surface with larger papulae and granuliform spinelets.

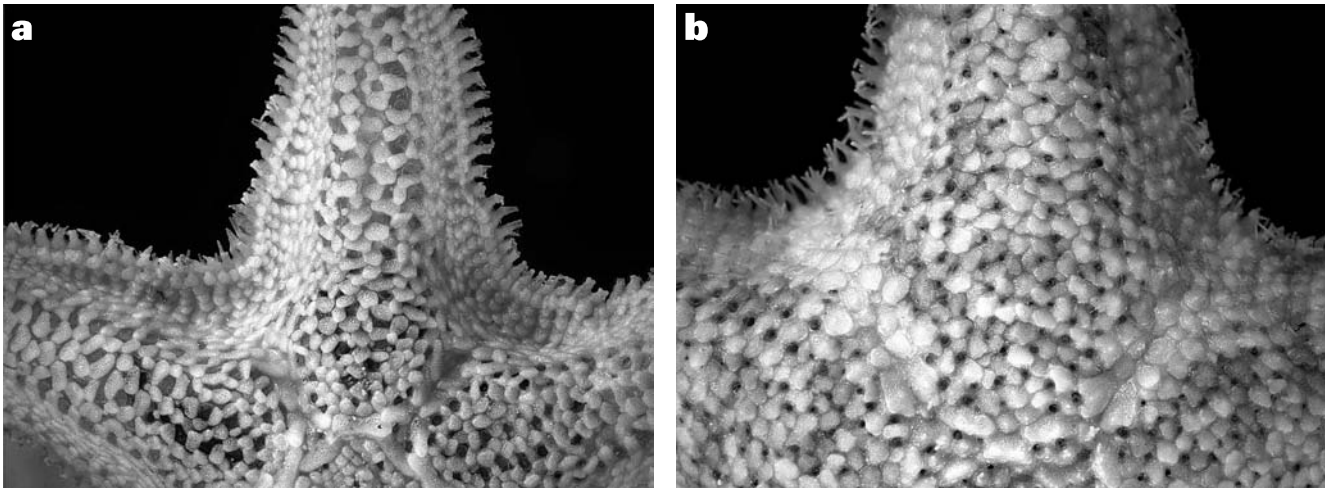


Figure 12. Abactinal views of *Disasterina* species. a, *Disasterina abnormalis* (R = 11 mm, WAM Z6753). b, *Disasterina longispina* (R = 25 mm, WAM Z6760).

margin in interradii; marginal plates subequal, in regular series, with dense tufts of spinelets, inferomarginals project prominently; actinal interradial plates in oblique series; superambulacral plates absent; superactinal plates present as multiple struts.

Type species. Nepanthia platydisca Fisher, 1913 (original designation).

Other species. P. aucklandensis (Koehler, 1920); *P. grandis* (H.L. Clark, 1928) (junior synonym *Asterinopsis praetermissa* Livingstone, 1933, by Rowe, 1995).

Material examined. P. aucklandensis. New Zealand, Auckland I., AM J5160 (2); J6023 (1).

Asterinopsis praetermissa. Holotype. Australia, New South Wales, Port Jackson, AM J4793.

Nepanthia platydisca. Holotype. Indonesia, 377 m, USNM 32644.

P. grandis. Australia, Victoria, NMV F72887 (1); Bass Strait, F98044 (1); South Australia, F73976 (4).

Description with species variations. Rays 5, interradial margin deeply incurved, rays distinct, ends of rays rounded (*aucklandensis, grandis*) or pointed (*platydisca*); body flat actinally, rays elevated or low (*platydisca*); distal interradial body thin (actinal to abactinal) or not (*aucklandensis*), area of non-papulate plates wide or not (*aucklandensis*); size medium (*grandis* up to R = 65 mm) to small (*aucklandensis* up to R = 22 mm); lacking pedicellariae; none fissiparous; gonopores abactinal.

Abactinal plates imbricate, distinct radial and interradial 'fields', plates on upper rays irregular in size, shape, arrangement (except *aucklandensis* with regular proximal carinal and upper ray series, and crescentiform plates), up to 3 fairly irregular longitudinal series along each side of rays; papular spaces large, with numbers of small papulae, variable numbers of secondary plates; interradial series of small plates perpendicular to margin (except longitudinal series in *aucklandensis*); disc not bordered or variably bordered (*aucklandensis*); abactinal plates with high (*grandis*) or low (*aucklandensis*, *platydisca*) spinelet-

bearing domes or ridges; glassy convexities on plates present (*aucklandensis*) or not (*grandis, platydisca*); subpaxilliform tufts of many acicular subsacciform spinelets; superomarginal and inferomarginal plates in distinct series, subequal; both series with spinelet-bearing domes and subpaxilliform dense tufts of acicular spinelets; inferomarginals define acute margin, projecting plates with narrowed waist (*aucklandensis, grandi*s) or not (*platydisca*).

Actinal plates in oblique series; plates with high (*grandis*, *platydisca*) or low (*aucklandensis*) spine-bearing domes.

Actinal spines per plate: oral 8–12; suboral tufts or transverse series; furrow 7–10, webbed; subambulacral dense tufts; adradial and actinal interradial dense subpaxilliform tufts (up to about 40 spines); actinal interradial spines acicular subsacciform.

Lacking superambulacral plates; numerous superactinal plates in multiple plate struts; distal interradial margin supported by angled contiguous abactinal and actinal plates (*grandis*, *platydisca*), lacking internal projections (except *aucklandensis* with internal tongue-like projections from abactinal plates).

Distribution. E and S Australia, Indonesia, subantarctic New Zealand; 0–377 m.

Remarks. Three species cluster together in clade I of Waters et al. (2004). One of these is a species that has been assigned to *Paranepanthia* in the past and one is undescribed. The molecular evidence that *Asterina aucklandensis* is also a member of this clade is supported by morphological criteria. All three species of *Paranepanthia* were examined and the morphological integrity of the genus confirmed. *Paranepanthia* is characterised by the unique combination of subpaxilliform dense clusters of acicular spines and spinelets on the plates, absence of superambulacral plates, and presence of superactinal plates. *Paranepanthia rosea* has been removed to *Aquilonastra*.

Parvulastra O'Loughlin gen. nov.

Figures 1 (clade V), 2l, 4a–b, 5b, e, 11b, 16a–d

Diagnosis. Rays 5, pentagonal to subpentagonal; noticeable integument; carinal series variably present; abactinal plates broadly notched for papulae, crescentiform more than U-shaped; papulate areas extensive, papulae large or small, a few per space; secondary plates a few per space; abactinal spinelets clustered or spread, not paxilliform; spinelets granuliform or digitiform or thin pointed; lack pedicellariae; superomarginal and inferomarginal plate series predominantly subequal; frequently extensive non-plated actinal area distal to oral plates; actinal interradial plates in oblique series; actinal interradial plates with frequently 2 spines mid-ray to distally, spines digitiform to conical; superambulacral plates present to varying extents, superactinal plates always present.

Type species. Asterias exigua Lamarck, 1816.

Other species. P. calcarata (Perrier, 1869); *P. dyscrita* (H.L. Clark, 1923); *P. parvivipara* (Keough and Dartnall, 1978); *P. vivipara* (Dartnall, 1969).

Material examined. P. calcarata. Juan Fernandez I., NMV F96703 (1); F96704 (1); F97445 (1); F97449 (1).

P. dyscrita. South Africa, False Bay, TM H800 (1); H854 (1); Jeffrey's Bay, NMV F98059 (3).

Patiriella exigua (Lamarck, 1816). Neotype (by Dartnall, 1971). South Africa, False Bay, TM H508. Other material. Cape Town, NMV F98062 (4); Durban, F98061 (4); Jeffrey's Bay, F97450 (5); Saint Helena, F98060 (4); Amsterdam I., F98063 (2); Australia, Victoria, Apollo Bay, F97054 (6); Gabo I., F73079 (9); Port Arthur, F97451 (12).

P. vivipara. Australia, SE Tasmania, NMV F77984 (3).

P. parvivipara. South Australia, Eyre Peninsula, NMV F97720 (3).

Description with species variations. Rays predominantly 5; interradial margin straight to slightly incurved, form pentagonal to subpentagonal; noticeable integument; flat actinally, low convex abactinally, size small (*dyscrita* up to R = 24 mm) to very small (*parvivipara* up to R = 3 mm); lacking pedicellariae; 2 smallest viviparous (*parvivipara, vivipar*a); none fissiparous; gonopores abactinal (*calcarata, dyscrit*a) or actinal (*exigua*).

Abactinal surface appearance granular, upper ray plates with regular carinal series except proximally *(calcarata, dyscrita, exigua*), or irregular (*parvivipara, vivipara*); plates in longitudinal series; plates broadly notched for papulae, crescentiform more than U-shaped; papulate areas extensive, non-papulate interradial areas not extensive, papular spaces large, a few papulae and secondary plates per space; papulae large (*exigua*, *parvivipara*, *vivipara*) or small (*calcarata, dyscrita*); disc variably bordered by series of 5 large radial and 5 small interradial plates; abactinal plates with raised spinelet-bearing elevations (*calcarata*) or not; abactinal spinelets in splayed clusters (*calcarata*) or fairly close cover over plates; spinelets both digitiform on primary plates and pointed on secondary and distal interradial plates (*calcarata*), or granuliform globose (*dyscrita*), or short columnar (*exigua, parvivipara, vivipara*); glassy convexities and reticulations variably evident on denuded plates; superomarginal and inferomarginal series of predominantly subequal plates; typically widely projecting inferomarginal plates define margin, with proximal abactinal-type spinelets, distal fringe of thinner and longer spinelets.

Actinal interradial plates in oblique series; actinal proximal areas of non-plated body wall frequently extensive.

Actinal spines per plate: oral 2 tall, 3–5 short sometimes grouped separately with distalmost frequently longest; suboral 1–2, thick; furrow 2 short, thin; subambulacral 1 tall, thick; adradial actinal spines present (*dyscrita*) or few (*vivipara*) or absent *(calcarata, exigua*); actinal interradial frequently 2 midray to distally; actinal interradial spines digitiform (*dyscrita*) or pointed or short conical.

Superambulacral plates present as series (in large *dyscrita*), or rare single, or distal only plates; superactinal plates present as single or multiple-plate series (neither seen in the pedomorphic *parvivipara*).

Distribution. Southern Pacific Ocean, southern Australia, southern Indian Ocean, southern Africa, SE Atlantic Ocean; 0–10 m.

Etymology. From the Latin *parvulus* (very small) and *astrum* (star), referring to the small to very small species of the genus (feminine).

Remarks. Four species previously included in *Patiriella* belong to a monophyletic clade V in Waters et al.'s (2004) analysis. They share a consistent morphology characterised by: subpentagonal form; longitudinal series of abactinal plates on rays; oblique series of actinal plates; granuliform and digitiform spinelets; a few papulae per space; and superambulacral and superactinal plates. The clade warrants generic rank. *Asterina dyscrita* shares these morphological characters and is assigned to the genus on this basis.

Morphologically, *Parvulastra* is similar to *Cryptasterina* and *Patiriella*. Waters et al.'s cladogram suggests that these three genera are not closely related on molecular grounds. Either the similar morphological characters have remained stable while divergence has occurred in characters not considered, or there is strong morphological convergence among the three unrelated genera, or the molecular data are unreliable at levels more basal than inter-species. Nevertheless, the genera can be differentiated by morphological characters. *Cryptasterina* is differentiated by predominantly single papulae per space, elongate superomarginal plates, narrowly projecting inferomarginal plates, and single mid-actinal spines. The characters which differentiate *Patiriella* are listed under that genus.

Patiria Gray

Figures 1 (clade II), 3a, 4d, 15d–f

Patiria Gray, 1840: 290.—Gray, 1847: 82–83.—Gray, 1866: 16.—Sladen, 1889: 384.—Verrill, 1913: 480, 482.—Verrill, 1914: 263–264.—Fisher, 1919: 410.—Fisher, 1940: 269.—Fisher, 1941: 451–455, pl. 70 fig. 1.—Spencer and Wright, 1966: U69.—Bernasconi, 1973: 336.—Clark and Courtman-Stock, 1976: 78.—Campbell and Rowe, 1997: 131, 135.—Dartnall et al., 2003: 12.

Diagnosis. Rays 5, medium to short-rayed stellate, not pentagonal, rays pointed distally; noticeable integument; flat actinally, convex abactinally; primary abactinal plates strongly or weakly crescentiform, close subpaxilliform cover of short, thick or thin, columnar or subglobose spinelets, not acicular or sacciform, secondary plates with smaller spinelets; lacking pedicellariae; papulate areas extensive, papular spaces large, numerous secondary plates and papulae per papular space; series of spinelet-covered superomarginal and inferomarginal plates, spinelets on thick rounded inferomarginals extend onto actinal surface; actinal plates in oblique series; actinal spines in mid-interradius thick, combs of 4–6; lacking complete superambulacral series of plates, present distally; superactinal plates present, multiple plate struts in larger specimens.

Type species. Patiria coccinea Gray, 1840 (original designation) (junior synonym of *Asterias miniata* Brandt, 1835 mistakenly recorded from South Africa, synonymy by Mortensen, 1933).

Other species. P. chilensis (Lütken, 1859); *P. pectinifera* (Müller and Troschel, 1842).

Material examined. P. chilensis. Chile, Arica, NMV F95674 (3); Peru, NMV F97442 (1); F97443 (1).

P. miniata. California, NMV F97444 (1); F97448 (1); F98040 (1); F98041 (1); F98042 (1).

P. pectinifera. Japan, Toyama Bay, NMV F95672 (7); F95673 (2).

Description with species variations. Rays 5 (sometimes 6); noticeable integument; interradial margin incurved, medium to short-rayed stellate, not pentagonal, rays distally pointed to narrowly rounded; flat actinally, convex abactinally, body thick, sides of rays steep; size large (*miniata* up to R = 85 mm) to small (*chilensis* up to R = 21 mm); lacking pedicellariae; gonopores abactinal.

Abactinal surface uneven; appearance dominated by subpaxilliform spinous primary plates, variably crescentiform, and large papular spaces with smaller spinous secondary plates; plates in irregular longitudinal series; papulate areas extensive, to near distal end of rays and near margin; papular spaces with numerous secondary plates and small papulae (up to about 25 of each); lacking longitudinal series of large single papulae along sides of rays; disc weakly bordered by discontinuous series of larger radial and smaller interradial plates; abactinal primary plates variably crescentiform or oval or round or linear, with spinelet-bearing elevations, variably with 1 or more notches for papulae; carinal series variably present, plates separated by large papular spaces; cleared plates with glassy convexities prominent (*chilensis*) or not; abactinal spinelets opaque, short columnar, thick (*miniata*), or subglobose (*pectinifera*), or thin (*chilensis*), in section round (*chilensis, pectinifera*) or square (*miniata*); spinelets on primary plates in subpaxilliform transverse or round clusters, very close and palisade-like (*miniata*) or slightly more spaced (*chilensis, pectinifera*), on secondary plates shorter, splayed; series of subequal superomarginal and inferomarginal plates, covered with spinelets; spinelets on thick rounded inferomarginals extend onto actinal surface; projecting inferomarginals form acute margin.

Actinal plates in oblique series.

Actinal spines per plate: oral 5–7; suboral 2–7; furrow 3–4 proximally; subambulacral 2–4; adradial actinal plates fully spinous; actinal interradial in combs of 3–8 proximally, 4–6 distally; actinal interradial spines conical to digitiform to spatulate.

Superambulacral plates not present as series, sometimes present in mid-ray (*chilensis*) or absent *(miniata, pectinifera*), present distally linking with actinal or superactinal or abactinal plates; superactinal plates present, multiple plate struts in larger specimens.

Distribution. N and E Pacific Ocean, Japan, Alaska, California, Peru, Chile; 0–300 m.

Remarks. Fisher (1908, 1911), Mortensen (1933), Hayashi (1940) and A.M. Clark (1983) considered *Patiria* to be a junior synonym of *Asterina*, while Verrill (1913), Fisher (1919, 1940, 1941) and Clark and Courtman-Stock (1976) maintained *Patiria* as a valid genus. Verrill (1914) considered it to be significant that *Patiria* lacked pedicellariae. Spencer and Wright (1966) listed *Callopatiria* and *Enoplopatiria* as junior synonyms of *Patiria.* Hayashi (1973) considered *Patiria* and *Patiriella* to be junior synonyms of *Asterina*. A.M. Clark

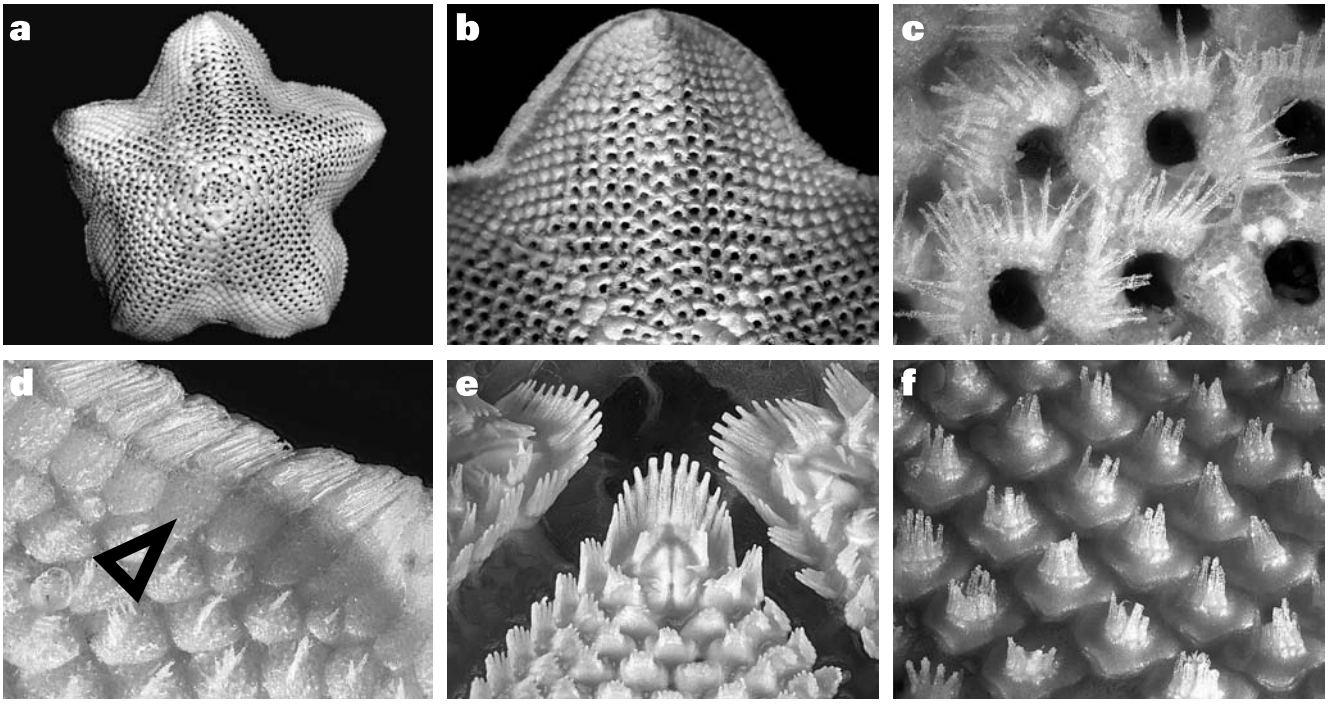


Figure 13. a, *Indianastra inopinata* (R = 19 mm, AM J15254): cleared abactinal surface. b–f, *Indianastra sarasini* (R = 14 mm, WAM Z6835): b, abactinal ray; c, abactinal elongate subsacciform spinelets, and papulae; d, bare superomarginal plates, and tufts of inferomarginal spinelets; e, oral and proximal actinal spines; f, actinal plates and spines.

(1983), Clark and Downey (1992) and A.M. Clark (1993) considered *Enoplopatiria* and *Patiria* to be junior synonyms of *Asterina*. Campbell and Rowe (1997) "accepted the separate generic status [of *Patiria*] until the matter is more clearly resolved".

Waters et al. (2004) found that the three species of *Patiria*, including the type species, constituted a single clade (II). They confirmed an earlier result, based also on molecular data (Hart et al., 1997), that confirmed the type and one of the species to be sister taxa. Together there is strong molecular evidence for the generic status of *Patiria*, remote from *Asterina* and *Patiriella*. Morphologically, *Patiria* is distinguished from *Asterina* by the presence of superambulacral and superactinal plates, and from *Patiriella* by the discrete rays, dense subpaxilliform clusters of granuliform spinelets, and more numerous actinal interradial spines.

Patiriella Verrill

Figures 1, 3b, 16e–f

Patiriella Verrill, 1913: 480, 483–484.—Verrill, 1914: 263.—Fisher, 1919: 410.—H.L. Clark, 1946: 134.—Spencer and Wright, 1966: U69.—Shepherd, 1968: 745.—Dartnall, 1970: 73–74.—Dartnall, 1971: 39–40.—Bernasconi, 1973: 341.—Clark, A.M. and Courtman-Stock, 1976: 80.—Clark, A.M., 1983: 364–367, 378, fig. 3c, 4.—Clark, A.M. and Downey, 1992: 178, 192.—Clark, A.M., 1993: 224.—Rowe, 1995: 39.—Campbell and Rowe, 1997: 129–131.—McKnight (in Clark and McKnight), 2001: 155.—O'Loughlin et al., 2002: 701.—Dartnall et al., 2003: 11–12.—Waters et al., 2004: 874, 875, 877. (Part).

Diagnosis. Rays 5, interradial margin straight to incurved, subpentagonal to short discrete rays, ends pointed or broadly or narrowly rounded; noticeable integument; plates on rays irregularly arranged; abactinal spinelets granuliform to digitiform, not webbed, in close to spaced distribution over projecting surface of plates; regular series of granuliform or digitiform spinelet-covered superomarginal and inferomarginal plates; actinal plates in oblique series; actinal adradial spines in incomplete series; actinal spines digitiform to short conical, no more than 3 per plate; superambulacral plates present from midray or distally only; superactinal plates present as single and multiple-plate supports.

Type species. Asterina (*Asteriscus*) *regularis* Verrill, 1867 (original designation).

Other species. P. inornata Livingstone, 1933; *P. oliveri* (Benham, 1911) (junior synonym: *Patiriella nigra* H.L. Clark, 1938, by Rowe, 1995); *Patiriella paradoxa* Campbell and Rowe, 1997.

Material examined. P. inornata Livingstone, 1933. Holotype. Western Australia, AM J3198.

P. nigra. Paratype. Lord Howe I., AM J4439 (1).

P. oliveri. Kermadec Is, MNZ EC4805 (2 of 7); Lord Howe I., AM G11519 (2); G2247 (1).

P. paradoxa. Holotype. Oman, BMNH 1997.1016. Paratypes. BMNH 1997.1017 (1); BMNH 1997.1018 (2).

A. regularis. Syntypes. New Zealand, Auckland, H. Edwards, 1866, YPM 988A (1), B (1, partially cleared), C (2). Other material. See O'Loughlin et al. (2002).

Description with species variations. Rays 5, rarely 6; interradial margin straight to incurved, form subpentagonal to

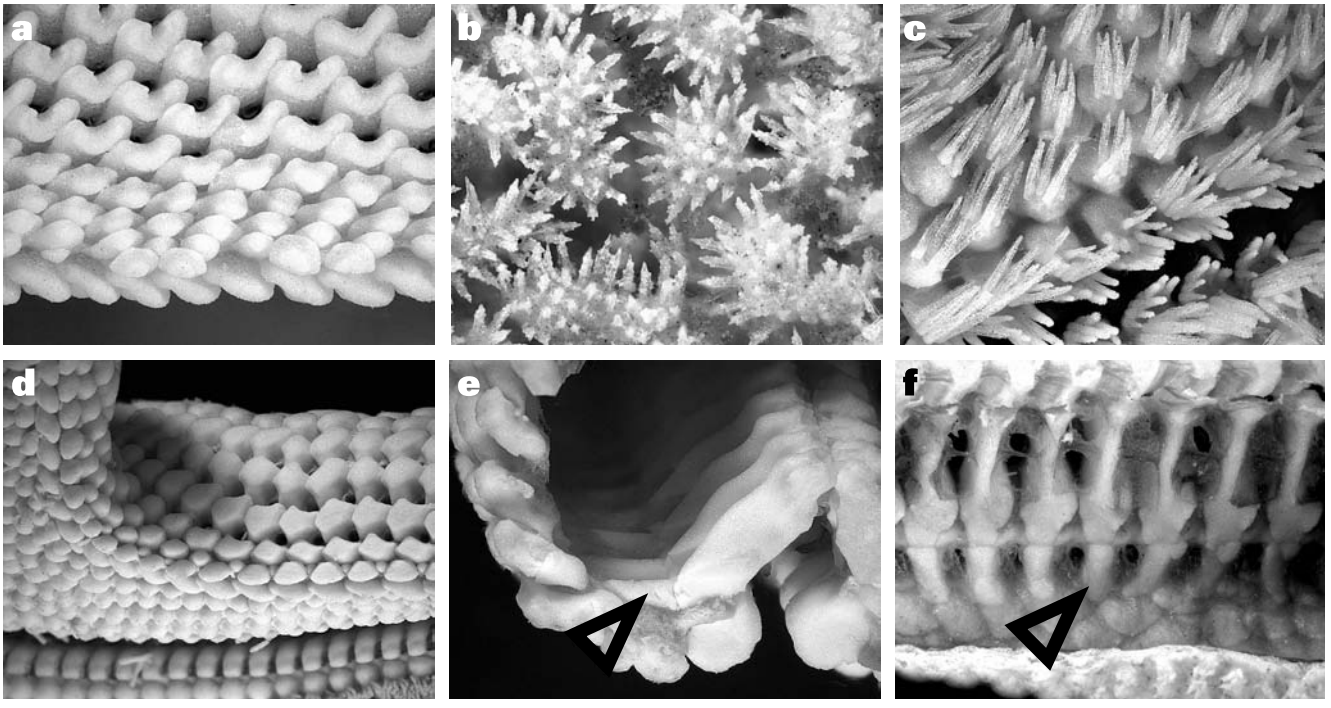


Figure 14. a–c, *Nepanthia pedicellaris* (R = 23 mm, holotype, USNM 32643): a, cleared lower lateral ray, and distinct margin; b, abactinal spinelets; c, adambulacral and actinal plates and spines. d, *Pseudonepanthia troughtoni* (R = 55 mm, NMV F73977): cleared proximal lateral lower ray, margin, and ambulacrum. e, *Pseudonepanthia nigrobrunnea* (R = 85 mm, NMV F95810): cleared section of ray with single series of superambulacral plates (arrow), and absence of transactinal and superactinal plates. f, *Pseudonepanthia gotoi* (R = 70 mm, holotype, USNM 36899): internal cleared view of ambulacral plates, with series of superambulacral plates (arrow).

discrete rays with ends broadly rounded to pointed; integument cover sometimes evident (*regularis*); body flat actinally, low convex abactinally; rays elevated, sides steep; size medium (*regularis* up to R = 39 mm); lacking pedicellariae; rare evidence of fissiparity (*regularis*); abactinal gonopores.

Abactinal plates on upper rays in longitudinally series (*oliveri*) or irregular (*inornata, paradoxa, regularis*); carinal plate series ray length (*oliveri*) or short proximal (*regularis*) or not evident *(inornata, paradoxa*), plates doubly notched; variably regular longitudinal series of crescentiform plates on lower sides of rays; papulate areas extensive, non-papulate interradial area extensive *(inornata, oliveri*) or narrow (*paradoxa, regularis*); papular spaces large, 1–4 large (*inornata, paradoxa*) or numerous small papulae and irregular secondary plates per space *(oliveri, regularis*); proximal primary abactinal plates irregular (*inornata, paradoxa*) or crescentiform (*oliveri, regularis*), with spinelet-bearing ridges (*oliveri, regularis*) or not; glassy convexities below elevations on denuded plates (*oliveri, paradoxa, regularis*), or reticulations (*inornata*); abactinal spinelets granuliform, subglobose to subconical (*inornata*, *paradoxa*), or proximally short columnar, distally short subsacciform (*regularis*), or digitiform, many slightly widened terminally (*oliveri*); spinelets not webbed, in close arrangement on plates *(oliveri, paradoxa, regularis*) or spread (*inornata*); disc variably bordered by 5 radial and 5 interradial plates; superomarginal and inferomarginal plates in regular series, with typical abactinal spinelets; margin formed by projecting inferomarginals.

Actinal plates in oblique series (irregular proximally in *inornata, paradoxa*); proximal actinal interradial areas sometimes not plated.

Actinal spines per plate: oral 4–6; suboral 0–4; furrow 2–4 proximally, short, webbed; subambulacral 1–3, tall; adradial actinal 0–1, short, incomplete series; actinal interradial 1–3 proximally, 1–2 short distally; actinal interradial spines digitiform, slightly tapered (*regularis*), slightly swollen (*oliveri*), or short conical (*inornata*), or short thick columnar (*paradoxa*).

Superambulacral plates present distally (*inornata* not examined distally); superactinal plates present as single and multiple-plate struts.

Distribution. New Zealand, North and South Is, Stewart and Chatham Is; Australia, Lord Howe I., New South Wales, Tasmania; Western Australia; Oman; 0–92 m.

Remarks. O'Loughlin et al. (2002) did not report on the four syntypes of *Asterina regularis* Verrill, 1867 in their systematic review of *Patiriella*. They have now been examined and are consistent with O'Loughlin et al.'s (2002) redescription. Waters et al. (2004) presented a molecular phylogeny in which *P. regularis* fell on a clade remote from those on which all other species of *Patiriella* were included (clades III part, IV part, and V, in Fig. 1). The species in clade III (part) were removed to *Meridiastra*, those in clade IV (part) to *Cryptasterina* by Dartnall et al. (2003), and those in clade V to *Parvulastra*.

The diagnostic characters of *P. regularis* are: subpentagonal to very short-rayed form; abactinal plates on rays not in longitudinal series; spinlets ganuliform, short columnar; large papular spaces with numerous papulae and secondary plates; actinal plates in oblique series; few superambulacral plates; superactinal plates present. *Patiriella* is distinguished from *Meridiastra* by lacking longitudinal series of plates on the rays, by oblique series of actinal plates, and by having superactinal plates. *Patiriella* is distinguished from *Cryptasterina* and *Parvulastra* by lacking longitudinal series of plates on the rays, and by having large papular spaces with numerous papulae and secondary plates.

On morphological grounds *P. inornata* and *P. paradoxa* are retained in *Patiriella*. Rowe (1995) transferred *Asterina oliveri* to *Patiriella*. *P. oliveri* has many of the characters of *Patiriella*, but is retained in *Patiriella* with reservation because of the regular carinal and longitudinal series of plates on the rays. On morphological grounds, *Asterina dyscrita* H.L. Clark, 1923 is removed from *Patiriella* to *Parvulastra*.

Patiriella tangribensis Domantay and Acosta, 1970 is judged to be nomen dubium. Domantay and Acosta (1970) established the species without type material being designated, and the description and figures are not adequate to diagnose the material (reference was made to an absence of marginal plates). It was distinguished only from *Patiriella exigua*, which does not occur in the type locality (Philippines).

Pseudasterina Aziz and Jangoux

Pseudasterina Aziz and Jangoux, 1985: 283-284.—A.M. Clark, 1993: 227.

Diagnosis. Small thin body; rays 5, discrete, broad base, rounded or pointed distally, medium-rayed stellate; abactinal upper ray plates variably regular in form and arrangement; interradial plates small, long imbricating oblique series; papulae along upper rays only, sparse, single; short columnar granuliform abactinal spinelets; superomarginal series of large plates with granuliform spinelets; inferomarginal plates project narrowly, with glassy subsacciform spinelets; actinal plates in oblique series; actinal interradial plates with numerous glassy subsacciform spines principally on proximal edge, few distally; lacking superambulacral and superactinal plates; very thin interradii, with abactinal and actinal imbricate plates angled and meeting internally throughout the interradii.

Type species. Pseudasterina delicata Aziz and Jangoux, 1985 (original designation).

Other species. P. granulosa Aziz and Jangoux, 1985.

Material examined. P. delicata. Tonga, 149–157 m, MNHN EcAs11704 (2); Wallis and Futuna Is, 250 m, MNHN EcAs11706 (1).

Description with species variations. Rays 5, discrete, broad base, distally rounded (*delicata*) or pointed (*granulosa*), medium-rayed stellate; body flat, thin; size small (*granulosa* up to R = 18 mm); lacking pedicellariae; neither fissiparous.

Abactinal appearance dominated by imbricating small interradial plates in oblique series from upper rays to margin; papulate areas confined to narrow upper rays; papular spaces small, papulae single, rare secondary plates; abactinal plates on narrow upper rays variably regular in form and arrangement, some notched, some indented for papulae, proximal doubly or singly papulate carinal series sometimes present; disc distinctly bordered; abactinal plates with short columnar stout granuliform spinelets, weakly attached, spaced not clustered, up to 10 on proximal edge or covering plate, closer and slightly larger over some papulae; glassy reticulations on plates, not convexities; superomarginal plates larger than adjacent abactinals, regular series, longitudinally subrectangular, covered with granuliform spinelets; margin formed by narrowly projecting inferomarginal plates, each with numerous conical to subsacciform to splay-pointed sacciform spinelets.

Actinal interradial plates in distinct imbricating oblique series.

Actinal spines per plate: oral up to about 10, webbed; suboral up to about 15, short, glassy conical; furrow up to about 10 on furrow edge, webbed, up to about 10 on surface of plate; subambulacral, adradial actinal, and actinal interradial about 10, predominantly on proximal edge of plates; actinal spines glassy, short, pointed, sacciform.

Lacking superambulacral and superactinal plates; thin interradii with abactinal and actinal plates imbricating and angled interiorly to meet throughout the interradii; no tongue-like inner projections from abactinal or actinal plates.

Distribution. Philippines, Wallis, Futuna and Tonga Is, 130–250 m.

Remarks. No molecular data are available and this review is based on morphology. Until recently the two species were known only from the type material from the Philippine Is (*Pseudasterina delicata* holotype, MNHN EcAs10065; paratype, MNHN EcAs10066. *P. granulosa* holotype, MNHN EcAs10067). None of the type material could be located. Recently A.J. Dartnall determined material in the MNHN collections as *P. delicata*. These specimens have been examined in this study. The distinctive characters of *Pseudasterina* are: abactinal long imbricating oblique series of small plates from narrow upper radii to margin, and similar series from furrow to margin actinally; very thin interradii, with abactinal and actinal imbricate plates angled and meeting internally throughout the interradii; short columnar, granuliform, readily-detached spinelets on abactinal and superomarginal plates, but glassy, subsacciform, sometimes splay-pointed, spinelets on the inferomarginal plates. The spination characters given by Aziz and Jangoux (1985) for distinguishing *P. delicata* and *P. granulosa* appeared to be all variably present on the *P. delicata* specimens observed here, suggesting that *P. granulosa* may be a junior synonym. Aziz and Jangoux (1985) distinguished *Pseudasterina* from all other asterinid genera by the distinctive series of large superomarginal plates. This diagnostic character is a feature of *Cryptasterina* also, from which *Pseudasterina* differs in abactinal and actinal plate arrangement and spination, and in the absence of superambulacral and superactinal plates.

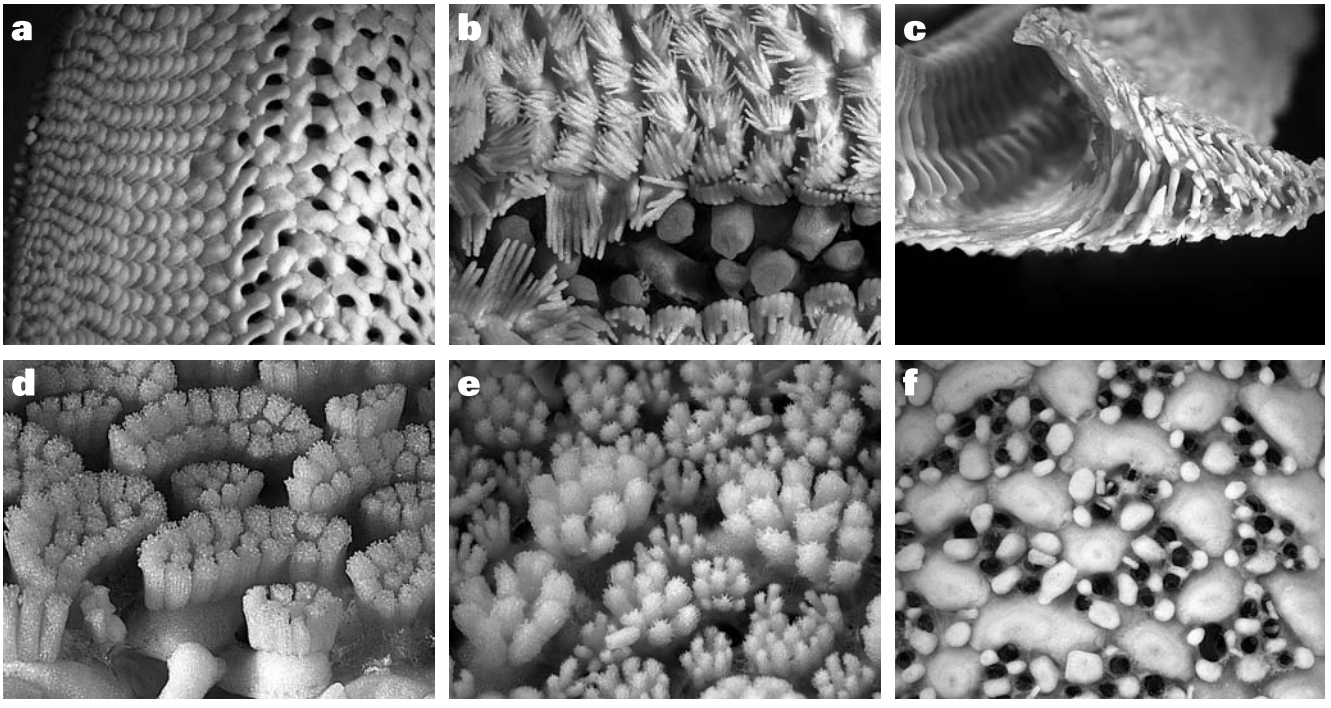


Figure 15. a–b, *Paranepanthia platydisca* (R = 55 mm, holotype, USNM 32644): a, cleared abactinal ray from upper ray to margin; b, ambulacrum with adambulacral and actinal plates and spines. c, *Paranepanthia grandis* (R = 50 mm, NMV F73976): section of ray showing superactinal plates supporting margin, and absence of superambulacral plates. d, *Patiria miniata* (R = 65 mm, NMV F97444): cleared abactinal surface with subpaxilliform clusters of granuliform spinelets. e–f, *Patiria pectinifera* (R = 40 mm, NMV F95672): e, cleared abactinal surface, with subpaxilliform globose spinelets; f, cleared abactinal surface, with papular spaces, secondary plates and papulae.

Pseudonepanthia A.H. Clark

Figures 1, 3c, 4e, 5d, 14d–f

Pseudonepanthia A.H. Clark, 1916: 118.—A.M. Clark, 1993: 227.

Diagnosis. Rays 4–10, subcylindrical, not flat actinally, lacking marginal edge; integument variably noticeable; lacking secondary plates; abactinal spinelets thick or thin or subsacciform, covering plates or in tufts; lacking pedicellariae; plates lacking glassy convexities; inferomarginal plates not projecting; furrow spines up to 5 per plate; actinal interradial spines digitiform, up to 7–30 per plate; series of superambulacral plates present, rare transactinal plates; lacking superactinal plates.

Type species. *Pseudonepanthia gotoi* A.H. Clark, 1916 (original designation).

Other species. P. briareus (Bell, 1894); *P. gracilis* (Rowe and Marsh, 1982); *P. grangei* (McKnight, 2001) (in Clark and McKnight); *P. nigrobrunnea* (Rowe and Marsh, 1982); *P. reinga* (McKnight, 2001) (in Clark and McKnight); *P. troughtoni* (Livingstone, 1934).

Material examined. P. briareus. Mariana Is, Guam, 118–152 m, UF 226 (1).

Pseudonepanthia gotoi. Holotype. Japan, Sagami Bay, 90 m, USNM 36899.

P. gracilis. Australia, New South Wales, AM J12874 (2); J11880 (2).

P. nigrobrunnea. New South Wales, Coffs Harbour, NMV F95810 (2); Byron Bay, F95804 (1).

Parasterina troughtoni. Holotype. Western Australia, Albany, AM J3978. Other material. Victoria, Cape Woolamai, NMV F73013 (1); Wilsons Promontory, F73017 (1); South Australia, Cape Jervis, F73977 (4).

Description with species variations. Rays 4–10, distinct, elongate, subcylindrical, tapered slightly (*nigrobrunnea, troughtoni*) or strongly (*briareus, gotoi, gracilis, grangei, reinga*), some irregular (*briareus, gotoi, nigrobrunnea*); integument variably noticeable; margin rounded, rays not flat actinally, lacking marginal edge; size large (*troughtoni* up to R = 87 mm) to medium (*grangei* up to R = 33 mm); lacking pedicellariae; gonopores sometimes actinal (*troughtoni*); one fissiparous (*briareus*).

Abactinal plates imbricating, projecting proximal edge creating uneven surface, irregular in form and arrangement on upper rays, oblique longitudinal series along sides of rays; lacking secondary plates; papulate areas extending to near margin; papular spaces with single large papula or a few (*nigrobrunnea*); abactinal plates with spinelet-bearing elevations or not (*troughtoni*); spinelets glassy, subsacciform with splayed points distally (*briareus, gotoi*), or subsacciform (*gracilis*), or fine columnar (*nigrobrunnea, troughtoni*); spinelets covering plates closely (*gotoi, gracilis, nigrobrunnea, troughtoni*) or in splayed groups (*briareus*); disc not bordered; cleared plates lacking glassy convexities; superomarginal plates in regular or irregular series; marginal plates covered with abactinal type spinelets; inferomarginal plates in predominantly regular series, frequently longitudinally elongate, not projecting.

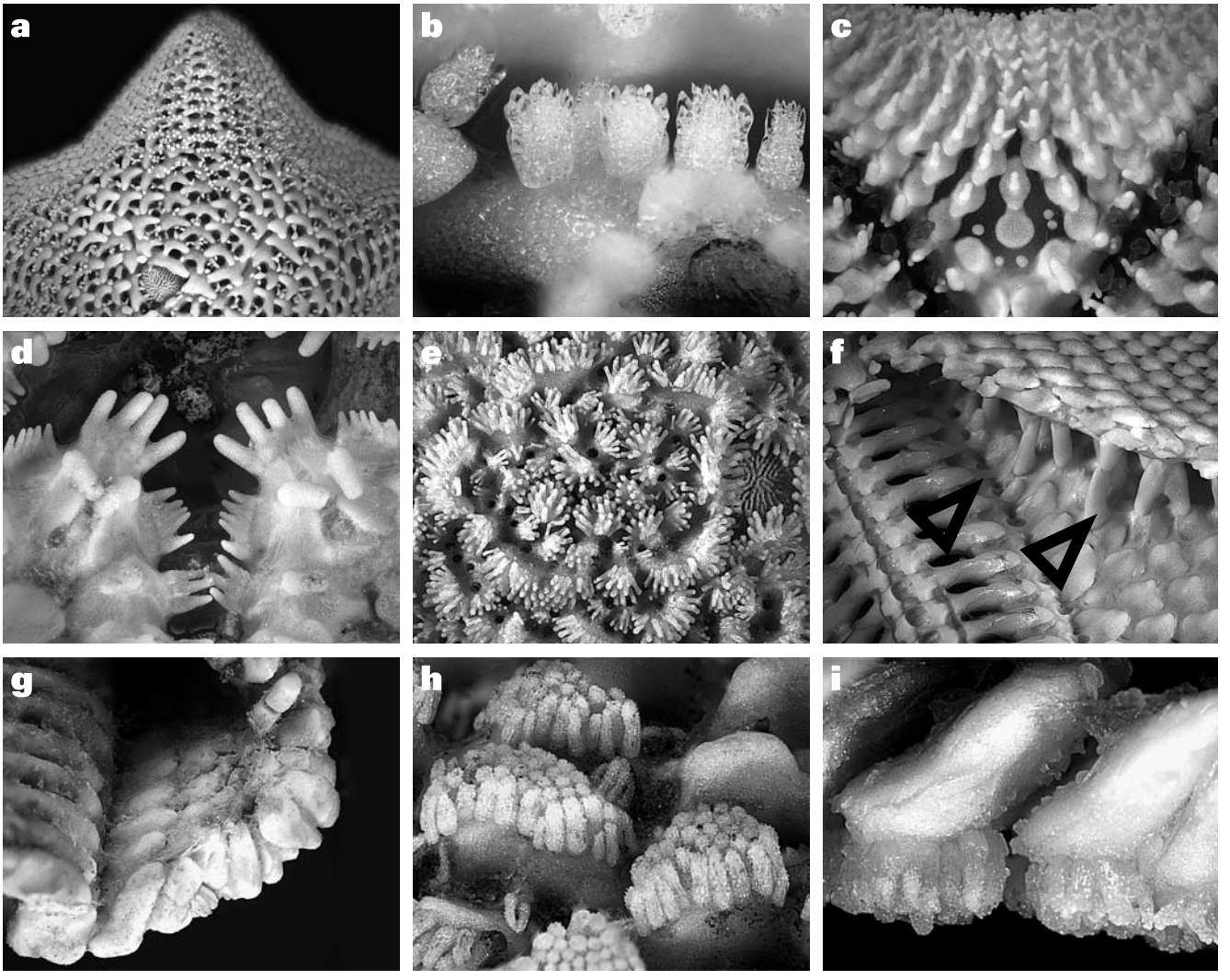


Figure 16. a–d, *Parvulastra exigua*: a, cleared ray (R = 10 mm, NMV F98062); b, denuded abactinal granuliform spinelets (NMV F98062); c, actinal interradius (R = 9 mm, NMV F98062); d, oral spines (R = 10 mm, NMV F97450). e–f, *Patiriella oliveri* (R = 28 mm, MNZ EC4805): e, abactinal disc and spinelets; f, absence of superambulacral plates (left arrow), presence of superactinal plates (right arrow). g–i, *Pseudopatiria obtusa* (R = 54 mm, holotype, BMNH 1938.6.23.24): g, section of ray with absence of both superambulacral and superactinal plates; h, abactinal subpaxilliform spinelets, and pedicellaria (lower left); i, actinal spines.

Actinal plates with spine-bearing elevations or not (*troughtoni*); not in oblique series.

Actinal spines per plate: oral 3–10; suboral 4–12; furrow 3–5; subambulacral 6–10; actinal 7–30; adradial row of actinal plates with complete series of spines; interradial actinal spines digitiform.

Superambulacral plates present as predominantly single series along ambulacrum, sometimes contiguous with inferomarginal plates across floor of ray (*briareus, troughtoni*) or with abactinal plates (*nigrobrunnea*); rare transactinal plates (sometimes irregularly present in *gracilis*); lacking superactinal plates; interior of rays with resinous lining.

Distribution. Mariana Is, SE Japan, South China Sea, Philippines, E Indonesia, E and S Australia, New Zealand; 0–540 m.

Remarks. Molecular data are available for *P. troughtoni* only. This review is based on morphology. Six species are removed from *Nepanthia* to *Pseudonepanthia* which is distinguished by: rays not flat actinally, lacking a marginal edge; absence of secondary plates, pedicellariae and glassy convexities; furrow spines fewer than 6 per plate; absence of transactinal and superactinal plates.

McKnight (in Clark and McKnight, 2001) referred *Nepanthia grangei* and *N. reinga* "provisionally" to *Nepanthia*. Material has not been examined, and internal skeletal plates not observed. Based on the descriptions, the absence of secondary plates and pedicellariae, and presence of up to five furrow spines per plate, fit the diagnosis of *Pseudonepanthia* to which both species are reassigned.

Pseudopatiria O'Loughlin gen. nov.

Figures 3d, 16g–i

Diagnosis. Rays 5; interradial margin deeply incurved, rays distinct, unequal in size, subcylindrical, narrowly flat actinally; margin weakly defined by irregular series of transversely elongate inferomarginal plates; abactinal plates irregular; abactinal spinelets opaque, digitiform to short columnar, dense subpaxilliform clusters; pedicellariae present in papular spaces; papulate areas extensive; papular spaces large, numerous secondary plates and small papulae; actinal interradial plates irregular in size and arrangement; actinal spines short columnar, dense subpaxilliform clusters; lacking superambulacral and superactinal plates; lacking interior contiguous projections of abactinal and actinal plates.

Type species. Patiria obtusa Gray, 1847.

Material examined. P. obtusa. Holotype. Panama, 11–18 m, BMNH 1938.6.23.24 (dry; poor condition).

Description. Rays 5, subcylindrical, unequal in length, up to R = 54 mm; rays narrowly flat actinally, poorly defined margin; fasciculate pedicellariae between abactinal plates, 2–3 curved digitiform valves; not fissiparous.

Abactinal surface uneven, with abactinal plates domed and irregular in size and arrangement on upper rays, in angled series on sides of rays; papulate areas extensive, to near margin; papular spaces large, numerous large secondary plates intergrading with primary plates, numerous papulae; single large madreporite; disc not bordered by regular series of radial and interradial plates; abactinal plates crescentiform or elongate or rounded, with high dome, lacking glassy convexities; spinelets thick, digitiform to short columnar, distally minutely spinous, typically 0.4 mm long, in close subpaxilliform clusters of about 40 spinelets per plate; superomarginal and inferomarginal plates in irregular series, inferomarginals frequently transversely elongate, projecting slightly to define margin.

Actinal interradial plates irregular in size and arrangement.

Actinal spines per plate: oral 6, some thick subspatulate; suboral, cluster, some thick subspatulate; furrow 3, subspatulate; subambulacral and actinal dense clusters of up to 20 per plate; spines short columnar, typically 0.5 mm long.

Superambulacral, transactinal and superactinal plates absent; margin not supported by contiguous internal projections of abactinal and actinal plates; internal resinous body lining.

Distribution. Panama; 11–18 m.

Etymology. From the Latin *pseudo* (false), with *Patiria*, referring to the significant internal skeletal differences with the genus *Patiria*.

Remarks. Gray (1866) and Verrill (1870) retained *obtusa* in *Patiria*, but Perrier (1875) referred the species to *Asterina*. Verrill (1913) referred it to *Callopatiria*. A.M. Clark (1983 figs 5a, 7) also discussed the generic placement and noted the absence of what are referred to in this work as superambulacral and superactinal plates. A.M. Clark (1993) noted the need for a reassessment of generic status and opined that the single specimen was "probably from the Pacific side of Panama". No molecular data are available, and a morphological reassessment is undertaken here. The unique characters of this asterinid genus are: subcylindrical rays; irregular abactinal and actinal plate arrangements; plates with subpaxilliform dense clusters of opaque, thick, short columnar spinelets and spines; presence of pedicellariae; and absence of superambulacral, transactinal and superactinal plates.

Stegnaster Sladen

Figures 1, 3e, 17a–d

Stegnaster Sladen, 1889: xxxiv, 375, 376 (key).—Fisher, 1911: 254 (key).—Verrill, 1913: 481 (key).—Verrill, 1915: 65.—Spencer and Wright, 1966: U69.—Clark and Downey, 1992: 194.—A.M. Clark, 1993: 227.—McKnight (in Clark and McKnight), 2001: 161–162.

Diagnosis. Rays 5, subpentagonal, frequently arched, integument cover, rays with median ridge, body very thin interradially; abactinal cover of fine granules only; glassy convexities present; projecting inferomarginal plates lack fringe of spinelets; projecting furrow spines covered by continuous granule-covered integument; actinal interradial plates with thorn-tipped short spines; lacking superambulacral plates, proximal interradius supported by multiple superactinal plate struts, wide thin interradius supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Type species. Pteraster inflatus Hutton, 1872 (original designation).

Other species. S. wesseli (Perrier, 1875).

Material examined. S. inflatus. New Zealand, North Island, AM J1856 (1); South Island, NMV F95675 (1); no locality data, AM G2030 (1).

Description with species variations. Rays 5, narrowly elevated median ridge, interradii very thin, form subpentagonal to rounded, body frequently in high domed (arched) shape, body covered by integument; size medium (*inflatus* up to R = 53 mm) to small (*wesseli* up to R = 20 mm); lacking pedicellariae; not fissiparous; gonopores abactinal (*inflatus*), actinal (*wesseli*).

Abactinal surface even, continuous cover of granuliform spinelets partly obscured by integument, larger globose spinelets on crown of plates (*inflatus*), spinelets slightly enlarged around pores (*wesseli*); cleared plates with prominent glassy convexities; plates of radii in longitudinal series, not to end of ray; carinal series in midray raised, longitudinally oblong, not notched; plates on upper sides of rays slightly notched for papulae; secondary plates rare to absent; papulate areas not extensive, confined to narrow raised radii; papular spaces large (*inflatus*) with up to 6 small papulae per space, to small (*wesseli*) with single papulae in longitudinal series; distinct pentagonal disc bordered by 5 raised radial and 5 small interradial plates; interradial areas extensive, not papulate, small plates in regular series perpendicular to margin; superomarginal and inferomarginal plates subequal, regular series, granule and integument cover; margin formed by inferomarginals, without a fringe of spinelets, continuous with actinal series of plates.

Actinal interradial plates in oblique series.

Actinal spines per plate: oral 3; suboral 0; furrow 2–3, project actinally, continuous integument and granule cover; sub-ambulacral none to rare; adradial series present; actinal 1 proximally, up to 6 distally, partly obscured by granule-covered integument; actinal spines short, thick basally, tapering distally to needle-like glassy point (thorn).

Lacking superambulacral plates; superactinal plates numerous proximally, multiple plate struts between actinal plates and inward projecting extensions of abactinal plates; superactinals absent distally, wide thin interradius supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Distribution. West Indies, Venezuela, New Zealand, Chatham Is; 0–183 m.

Remarks. This morphological review is based on material examined and description of *S. wesseli* by Clark and Downey (1992). The phylogenetic trees of Waters et al. (2004) placed *S. inflatus* on a clade separate from three species placed in *Paranepanthia* but this distinction received only weak support. Both genera lack superambulacral plates but significant morphological differences reflect the clade separation, such as the dense subpaxilliform tufts of acicular spines and spinelets in *Paranepanthia*. Distinctive characters of *Stegnaster* are: noticeable integument and granuliform spinelet cover; furrow spines projecting actinally and covered by continuous granule-covered integument; thorn-tipped spines actinally; lacking superambulacral plates; superactinal plates proximally; wide thin interradii supported internally by downward projecting abactinal plate extensions meeting actinal plates.

Tegulaster Livingstone

Figures 3f, 18a–b

Tegulaster Livingstone, 1933: 11–12.—H.L. Clark, 1946: 143.—Spencer and Wright, 1966: U69.— A.M. Clark, 1993: 228.—Rowe, 1995: 41.

Diagnosis. Rays 5, size small, body thick, covered by thin integument; rays discrete, form medium to long-rayed stellate, flat actinally, rays elevated, narrow or broad basally; abactinal plates thick, imbricating, shallow notch and crescentiform, irregular in form and arrangement on narrow median band of upper rays; plates and papulae in few series along sides of rays; papulae predominantly single per space; secondary plates rare; abactinal spinelets few to none on plates, glassy, sacciform or conical or acicular; glassy convexities present; superomarginal plates in regular series; inferomarginal plates each with up to 7 discrete short spinelets or tuft of acicular spinelets; actinal interradial plates in oblique series; actinal interradial plates each with 1–2, long or short, sacciform spines; superambulacral plates rare, or in distal series, not in complete series; superactinal plates present as single plate struts.

Type species. Tegulaster emburyi Livingstone, 1933 (original designation).

Other species. T. alba (H.L. Clark, 1938); *T. leptalacantha* (H.L. Clark, 1916) (unrecognised subspecies: *Disasterina leptalacantha africana* Mortensen, 1933, this work); *T. praesignis* (Livingstone, 1933) (junior synonym: *Disasterina spinulifera* H.L. Clark, 1938, this work).

Material examined. Asterina alba. Paratypes. Lord Howe I., AM J6170 (5); NMV F45118 (2). Other material. J16575 (1).

T. emburyi. Holotype. Capricorn Group, Queensland, shallow sublittoral, AM J5605.

Asterina leptalacantha. Holotype. Queensland, Capricorn Group, AM J3082. Other material. J6097 (1); Mauritius, 24 m, UF 2499 (1).

Disasterina praesignis. Holotype. Queensland, Port Curtis, AM J5059. Other material. J19314 (3); NMV F94009 (1); F94010 (1).

D. spinulifera. N Western Australia, Lacepede I., WAM Z6773 (1).

Description with species variations. Body thick, covered by thin integument; rays 5, discrete, flat actinally, high convex abactinally, narrow at base (*emburyi*) or broad basally tapering distally to widely (*alba*) or narrowly (*leptalacantha, praesignis*) rounded; size small (*leptalacantha* up to R = 25 mm; *alba* up to R = 7 mm); pedicellariae present over papulae (*emburyi*, 2 conical valves), or not; none fissiparous; gonopores abactinal or actinal (*alba*).

Abactinal surface uneven, dominated by projecting proximal edges of imbricating thick plates; narrow median band of upper rays plates irregular in form and arrangement; part carinal series variably evident on upper rays (*alba, emburyi, praesignis*); secondary plates rare (*emburyi*) or absent (*alba*), or primary plates grading from large to small (*leptalacantha, praesignis*); up to 3 series of papulate plates with shallow notch and crescentiform along each side of rays; papular spaces small, predominantly single large papulae per space, irregular on upper rays, series on sides of rays; disc bordered by 5 radial and 5 interradial plates, variably regular; abactinal plates with spinelet-bearing raised rounded proximal edge (*alba*) or domes (*leptalacantha*); abactinal spinelets frequently lacking, or sometimes up to 12, glassy, sacciform to conical, spinelets across proximal edge of plates (*alba*), or present distally as tufts of small sacciform spinelets (*emburyi*), or with tufts of acicular sacciform spinelets on distal interradial plates (*leptalacantha*), or rarely a few short sacciform spinelets on apex of plates (*praesignis*); glassy convexities on bare plates; superomarginal and inferomarginal plates predominantly subequal, in regular series; superomarginal plates with a few abactinal-type spinelets (*alba*), or with spinelets only in mid-interradius (*emburyi*), or bare (*leptalacantha*), or with rare spinelets (*praesignis*); projecting inferomarginal plates with cover of up to 7 short acicular spinelets per plate (*alba*), or series of up to 6 short spinelets *(emburyi, praesignis*), or tuft of long acicular sacciform spinelets (*leptalacantha*).

Actinal interradial plates in oblique series; proximal interradial non-plated areas sometimes present (*leptalacantha, praesignis*).

Actinal spines per plate: oral 6–9; suboral 1 (*alba, leptalacantha, praesignis*) or 2 large, 4 small (*emburyi*); furrow 4–7, webbed; subambulacral 1–5; adradial actinal spines present; actinal predominantly 2 (*emburyi*) or 1; actinal interradial spines sacciform, long or short (*alba*).

Superambulacral plates rare (*alba, emburyi*) or series distally *(leptalacantha, praesignis*), not in complete series; superactinal plates present as single plate struts.

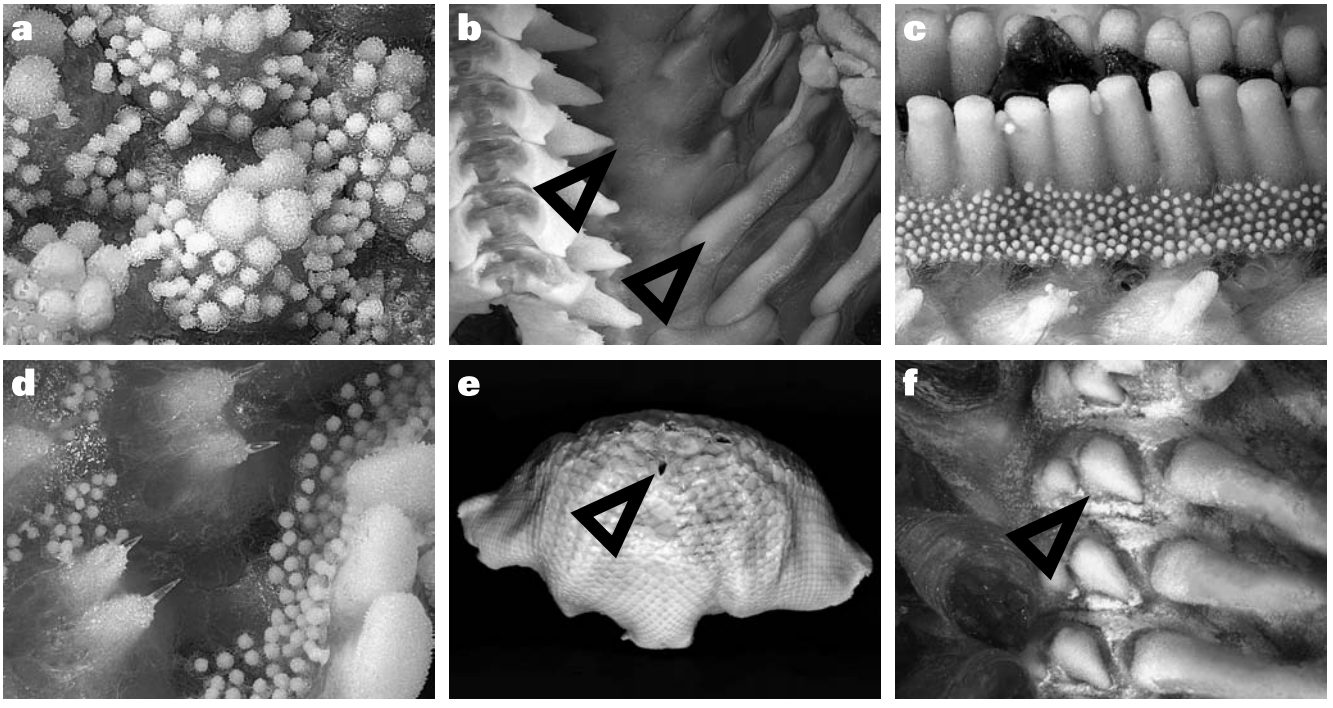


Figure 17. a–d, *Stegnaster inflatus* (cleared, R = 45 mm, NMV F95675): a, abactinal globose spinelets and granules; b, internal adradial interradius, showing absence of superambulacral plates (left) and presence of superactinal plates (right); c, actinal furrow spines, and granule-covered integument; d, actinal glassy thorn-tipped spines. e–f, *Tremaster mirabilis* (R = 60 mm, NMV F67741): e, arched body, with abactinal brood chamber pore (arrow); f, ambulacrum showing vertical series of furrow spines.

Distribution. Northern Australia, Lord Howe I., Norfolk I., Mauritius, South Africa; 0–366 m.

Remarks. Molecular data are not available and this review is based on morphological evidence. Two species have been removed from *Disasterina* to *Tegulaster* and the reasons are discussed under the former. *Tegulaster* also shares some morphological characters with *Indianastra* gen. nov. above, in particular the spination, limited presence of superambulacral plates and presence of series of superactinal plates. The features distinguishing *Tegulaster* from *Indianastra* are: body thick with discrete rays, not thin with petaloid to subpentagonal form; abactinal plates large thick in few irregular series along sides of rays, not small thin in numerous regular series along rays; abactinal plates at most slightly notched and crescentiform, not deeply notched; inferomarginal spinelets discrete, not acicular in dense integument-covered tufts; actinal interradial spines per plate up to 2, not small webbed fans; actinal interradial plates in oblique series, not longitudinal series.

Livingstone (1933) established *D. praesignis* for a single specimen (R = 14 mm) from Port Curtis (NE Australia). H.L. Clark (1938) established *D. spinulifera* for a single specimen (R = 8 mm) from Broome (NW Australia), and did not distinguish it from *D. praesignis*. Specimens of both species were compared and found to be identical; *D. spinulifera* is a junior synonym of *D. praesignis*. *Asterina alba* has all the diagnostic characters of *Tegulaster*. Livingstone (1933) assigned *Disasterina ceylanica* to his new genus *Tegulaster* but it has the characters of *Disasterina. D. leptalacantha* var. *africana* was established by Mortensen (1933) on the basis of its geographical separation (South Africa) from the *D. leptalacantha* type locality (NE Australia). Material from Mauritius has been determined as *T. leptalacantha* and no evidence found to justify the retention of variety *africana*.

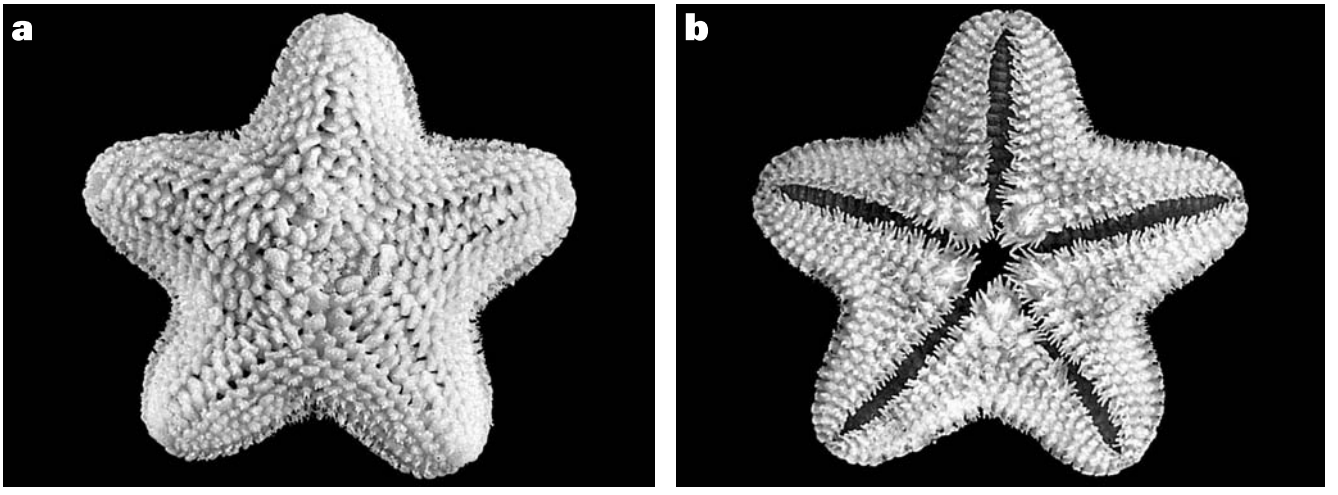
Tremaster Verrill

Figures 17e–f

Tremaster Verrill, 1879: 201.—Sladen, 1889: xxxiv, 375, 394.—Spencer and Wright, 1966: U69.—Jangoux, 1982: 155–158, 161–162.—Leeling, 1984: 263–274.—Clark and Downey, 1992: 195–196.—A.M. Clark, 1993: 228.—McKnight (in Clark and McKnight), 2001: 163.

Diagnosis. Rays 5, subpentagonal, frequently strongly arched; 5 plated ducts between proximal abactinal and proximal actinal conspicuous interradial openings; abactinal plates with integument cover and large conical (proximal) and small granuliform (overall) spinelets; lacking series of superomarginal plates; 4 rows of tube feet in each ambulacrum; furrow spines in vertical series on adambulacral plates; actinal spines single, tall, slender, spatulate, in oblique series; lacking superambulacral and superactinal plates, wide thin interradial body supported by interior distal keels on actinal plates meeting abactinal plates.

Type species. Tremaster mirabilis Verrill, 1879 (original designation) (junior synonym: *Tremaster novaecaledoniae* Jangoux, 1982 proposed by Leeling, 1984 and confirmed in this work).



Figure, 18. *Tegulaster alba* (R = 5 mm, paratype, NMV F45118): a, abactinal view; b, actinal view.

Material examined. T. mirabilis. Southern Ocean, Heard I., 226–252 m., NMV F67741 (6), F87362 (1), F67363 (1).

Description. Rays 5; interradial margin straight or slightly convex or concave; body frequently strongly arched; conspicuous proximal abactinal interradial openings to plate-lined ducts and chambers, opening actinally distal to oral plates; wide very thin body distally; size large (up to R = 85 mm); 4 rows of tube feet in each ambulacrum; lacking pedicellariae; ducts act as brood chambers.

Appearance dominated by domed form of body, 5 proximal duct openings, regular fish-scale plates, large conical spinelets on free edge of proximal plates, small granuliform spinelets on plates; abactinal proximal plates large, rhombic, thin, irregular on upper rays, singly notched for papula on upper sides of rays, distal plates small, covered by integument and weakly attached small granuliform spinelets; papular spaces small, predominantly single papula, secondary plates absent; 3–4 longitudinal series of small papulae along each upper side of rays; proximal abactinal plates with series of conical spinelets on proximal edge over papular space; cleared plates lacking conspicuous glassy convexities; abactinal interradial plates in longitudinal series, irregular distally, not in series perpendicular to margin; lacking series of superomarginal plates; acute margin formed by projecting series of inferomarginal plates; margin fragile, frequently broken off.

Actinal plates in oblique series, each plate with prominent proximal spine-bearing dome, series separated by decalcified body wall.

Actinal spines per plate: oral 1 tall proximally, adjacent pair, few upper small conical; suboral 0; furrow vertical series of 4–5, short to tall actinally; subambulacral 1 tall; adradial actinal series present; actinal 1 (rarely 2); actinal spines tall, slender, spatulate, subsacciform.

Lacking superambulacral plates; wide thin interradial margin supported by interior distal keels on actinal plates meeting abactinal plates; lacking superactinal plates.

Distribution. Atlantic, Pacific and Southern Oceans; 150–1060 m.

Remarks. No molecular data have been obtained for *T. mirabilis*, and this review is based on morphology. Leeling (1984) questioned the specific status of *T. novaecaledoniae* as its characters fell within the variation seen in *T. mirabilis*. We agree with her proposed synonymy. The significantly different characters of *Tremaster* from other asterinid genera are: abactinal and actinal duct openings, and internal plated brood chambers; absence of superomarginal series of plates; four rows of tube feet in each ambulacrum; furrow spines in vertical series on adambulacral plates; and extensive thin interradial margin supported by internal keels on actinal plates.

Incertae sedis

Asterina lorioli Koehler

Asterina lorioli Koehler, 1910: 129–131, pl., 19 figs 5–8.—A.M. Clark, 1993: 211.

Remarks. The description and illustrations by Koehler (1910) of abactinal granuliform spinelets and actinal spination suggest that A. *lorioli* is not a species of *Asterina*. Without material we have not been able to examine the internal skeleton.

Asterina novaezelandiae Perrier

Asterina novaezelandiae Perrier, 1875: 308.—Koehler, 1920: 135–136, pl. 35 figs 8–9.

Patiria novaezelandiae.—Verrill, 1913: 482.

Remarks. The single type specimen of *A. novaezelandiae* was reported by Perrier (1875) from New Zealand but A.M. Clark (1993) noted "holotype originally with specimens of *Patiriella gunnii* supposedly from New Zealand but almost certainly from southern Australia". If this is the case, it may be a five-rayed form of a species of *Meridiastra*. The description of three furrow spines and three subambulacral spines suggests *Meridiastra medius* (O'Loughlin et al., 2003). The specimen could not be found.

Nepanthia brachiata Koehler

Nepanthia brachiata Koehler, 1910: 133–135, pl., 19 figs 14–15.—Fisher, 1917: 173.—Fisher, 1919: 420.—Clark and Rowe, 1971: 70.—A.M. Clark, 1993: 222.

Remarks. Fisher (1917, 1919) and Clark and Rowe (1971) referred *N. brachiata* to *Paranepanthia*. The type specimen could not be found. Based on the description and figures by Koehler (1910), *N. brachiata* is characterised by: discrete narrow rays, flat actinally with narrow thin margins, not subcylindrical; absence of two distinct 'fields' of abactinal plates; predominantly large single papulae in papular spaces; few suboral, subambulacral and actinal interradial spines; webbed combs of digitiform actinal spines. This combination of characters is not found in *Nepanthia* or *Paranepanthia* or *Pseudonepanthia*. Without material we have not been able to examine the internal skeleton.

Biogeography

Waters et al. (2004) noted a link between the phylogeny suggested by molecular evidence and biogeographic patterns. The shallow marine genera *Paranepanthia* (clade I) in southern Australia and New Zealand, *Patiria* (clade II) in the northern and eastern Pacific, *Meridiastra* (clade III) in southern Australia and New Zealand, *Aquilonastra* and *Cryptasterina* (clade IV) in the northern Indo-West Pacific, *Parvulastra* (clade V) in the southern temperate waters from South Africa to South America, and *Asterina* (clade VI) in the north-eastern and southern coastal Atlantic and Mediterranean, all have localised distributions. Additional species added to these genera on morphological grounds do not alter this pattern. Other genera, not included in the molecular phylogeny, *Asterinides* in the West Indies, *Calloptiria* in southern Africa, *Disasterina* and *Indianastra* and *Pseudasterina* and *Tegulaster* in the northern Indo-West Pacific, *Nepanthia* and *Pseudonepanthia* around Australia and the Indo-West Pacific, and *Patiriella* in southern Australasia and the north-west Indian Ocean, are likewise regionally localised.

The remaining genera with more widespread distributions, *Anseropoda* in the Atlantic and Indo-Pacific, *Stegnaster* in the West Indies and New Zealand, and *Tremaster* in the Atlantic and Pacific and Southern Oceans, show significant morphological differences from the other asterinid genera and all occur in deeper water. *Anseropoda* also shows morphological evidence of possibly being paraphyletic.

It can be concluded that Asterinidae is a cosmopolitan family, mainly of shallow-water narrow-range genera but including some more widespread in deeper waters of all oceans.

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