

1447-2554 (On-line)

<https://museumsvictoria.com.au/collections-research/journals/memoirs-of-museum-victoria/>

DOI <https://doi.org/10.24199/j.mmv.2023.82.06>

New occurrence of Poraniidae (Valvatacea, Asteroidea) in Australia with a new genus and species from deep-sea settings

(urn:lsid:zoobank.org:pub:B48A3062-C822-4DD1-ADCC-A577C9D2CD32)

CHRISTOPHER L. MAH

¹ Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, MRC-163, PO Box 37012, Washington, D.C. 200560, United States of America [brisinga@gmail.com]

Abstract

Mah C.L. 2023. New occurrence of Poraniidae (Valvatacea, Asteroidea) in Australia with a new genus and species from deep-sea settings. *Memoirs of Museum Victoria* 82: 119–131.

The Poraniidae (Asteroidea, Valvatacea) is recorded for the first time from Australian waters at deep-sea (>200 m) depths, including, at present, Australia's deepest known asteroid occurrence from 3850 m. Three genera are reviewed, each represented by a single species, *Poraniomorpha tartarus* n. sp., *Marginaster paucispinus* Fisher 1913, and *Marginaster patriciae* McKnight 2006, which is reassigned to the new genus, *Bathymarginaster*. Comparisons with other asteroid groups similar to the Poraniidae in Australian waters is made and a key to genera of the Poraniidae is provided.

Keywords

deep-sea, Australia, abyss, *Poraniomorpha*, *Marginaster*

Introduction

Undiscovered biodiversity in marine Australian habitats, especially in deep-sea settings, is substantial, estimated at 250,000 species (Butler et al., 2010). Since Rowe and Gates (1995), no more than 14 new species have been described from Australian waters (Mah, 2006; Benavides-Serrato and O'Loughlin, 2007; Marsh, 2009; Naughton and O'Hara, 2009); most resulted from revisions of the shallow-water Asterinidae (O'Loughlin, 2002; O'Loughlin et al., 2003; Dartnall et al. 2003; O'Loughlin, 2009; O'Loughlin and Bribiesca-Contreras, 2015). Australian asteroid faunas from shallow nearshore settings have been more extensively documented (e.g. Clark, 1921, 1946; Marsh and Fromont, 2020) than those from deeper waters; for example, only 12 of 211 species recorded by Rowe and Gates (1995) were from below 1000 m. Since 1995, only three new species have been described from Australian deep-sea settings (<200 m) (Mah, 2006).

To improve understanding of this fauna, deep-water and offshore environments around Australia have been surveyed (e.g. O'Hara et al., 2020), resulting in new discoveries (e.g. Ekins et al., 2020; Zhang et al. 2020) and better characterisation of Australian biodiversity, especially for deep-sea settings.

Certain shallow-water asteroids are “keystone species” that affect community structure. Examples include *Pisaster ochraceus*, which preys on mollusks in temperate-cold-water systems (e.g. Paine 1966, 1969), and the crown-of-thorns sea star (*Acanthaster* spp.), which preys on coral reefs (e.g. Branham, 1973; Birkeland and Lucas 1990). Deep-water ecosystems are not well documented, but accounts from

remotely operated vehicles report corals and sponges as “ecosystem engineers” serving as hosts for a diversity of associates that form the basis of communities, often seen as “oases” amidst low-diversity settings (Buhl-Mortensen et al., 2010). Predation on corals and sponges by deep-sea asteroid taxa is an important consideration in understanding their ecology (Mah, 2020).

National Oceanic and Atmospheric Administration (NOAA) ship *Okeanos Explorer* has observed multiple predatory members of the Poraniidae at 300–3740 m, including *Poraniomorpha abyssicola*, *Marginaster pectinatus* and *Chondraster* sp. feeding on sponges, and corals in the North Atlantic (Mah 2020). *Bathyporania ascendens* was observed feeding on black coral (*Antipatharia*) at 2669 m in the North Pacific (Mah and Foltz, 2014). Although not observed at the same frequency or abundance as members of the Hippasterinae (Goniasteridae) (Mah, 2020, 2022) *Okeanos Explorer* regularly encountered poraniids in deep-sea settings in the North Atlantic (Mah, personal observation), suggesting unrecognised broader significance in similar habitats elsewhere.

The Poraniidae are a small family of Valvatacea that includes 11 living and one fossil genus. The family is known primarily from deep waters in cold to temperate water settings, especially at high latitudes (Mah and Foltz, 2014). Phylogenetic analysis (Mah and Foltz, 2011) unexpectedly showed the Poraniidae to be part of a basal dichotomy, and thus a sister group to the highly diverse Valvatida. Phylogenetic positioning was consistent with *Noriaster*, the fossil poraniid described from the Triassic (Blake et al., 2000).

Relatively few Poraniidae are known from the Southern Hemisphere. The high-latitude/Antarctic *Glabraster antarctica* (Smith, 1876) and two South African species, *Chondraster elattosis* H.L. Clark, 1923 and *Spoladaster veneris* (Perrier, 1879) with *Spoladaster brachyactis* (Clark, 1923) and *Tylaster meridionalis* Mortensen, 1933 having been synonymised with *S. veneris* according to Mah and Foltz (2014).

The species described herein are the first three accounts of the Poraniidae known from Australian waters. In Australia, the Poraniidae was historically represented by a single species, *Marginaster littoralis* Dartnall 1970 (Rowe and Gates, 1995). This was found to have been a misidentified species in the Asterinidae (Mah and Foltz, 2014; O'Hara et al., 2018). The three Poraniidae species presented herein are the first known from Australian waters.

A museum survey of asteroid specimens at the Museum Victoria in Melbourne, Australia revealed multiple new Poraniidae records from deep-water collections (>150 m). Poraniidae were not reported from earlier studies of Australian waters, such as Rowe and Gates (1995), Mah and Foltz (2014) and O'Hara et al. (2018), so these new taxa add to our understanding of the local marine fauna.

Methods and materials

Specimens described herein are deposited in the collections of the Museum Victoria (NMV) in Melbourne, Australia, the Muséum national d'Histoire naturelle (MNHN) in Paris and the Department of Invertebrate Zoology in the National Museum of Natural History (USNM) in Washington, D.C.

Taxonomic conventions follow the phylogenetic conclusions of Mah and Foltz (2011) and Linchangco et al. (2017). Measurements of specimens listed below are in centimetres. As a matter of convention, "R" is the distance from the disk centre to the arm tip (measured from the underside) and "r" is the distance from the disk centre to the disk edge. R/r is a ratio with no units.

Systematics

ASTEROIDEA de Blainville 1830

VALVATACEA Blake 1987

PORANIIDE Perrier 1893

Asterinidae (pt) Gray 1840: 288 (*Porania*).—Viguier 1878: 683.—1879: 220.—Perrier 1891: K107, 163

Goniasteridae (pt) Perrier 1875: 185[1876:11]

Gymnasteridae (pt) Perrier 1884: 165, 168, 229.—Sladen 1889: 355.—Verrill 1895: 137.

Poraniidae Perrier 1893: 849.—1894: 163–164.—Verrill 1914: 17.—1915: 68.—Fisher 1919: 407.—Clark 1923: 274.—Mortensen 1927: 89–90.—Fisher 1940: 154.—Djakonov 1950: 57(1968: 48).—Clark 1962: 34.—Bernasconi 1964: 263.—Tortonese 1965: 166.—Spencer and Wright 1966 (pt): U69.—Downey 1973: 81.—Hotchkiss and A.M. Clark 1976: 263–266.—Clark and Courtman-Stock 1976: 73.—Blake 1981: 380–381.—Tablado 1982: 88.—Clark 1984: 20–49.—Clark and McKnight 2001: 165.—Mah and Foltz 2014: 330.

Gymnasteridae Bell 1893: 21, 78.—Ludwig 1900: 459.—Farran 1913: 16.

Asteropidae (pt) Fisher 1911: 247–248.

Asteropidae Koehler 1921: 40–41.—1924: 151.—Mortensen 1933: 249.—Fisher 1940: 136.

Diagnostic comments. Prior detailed accounts summarise diagnoses for the Poraniidae (e.g. Clark, 1984; Clark and Downey, 1992). The account herein diagnoses the group within a more recent context, following the molecular phylogenetic treatment by Mah and Foltz (2014), which also emphasised skeletal morphology, especially those features observed on dried specimens. The diagnosis herein considers newly described genera, *Bathyporania* and *Claviporania*, as well as the reinstatement of *Glabraster* for "*Porania*" *antarctica*.

Examination of the Poraniidae in this context has compelled re-evaluation of assumed character states from the taxonomic literature. Clark and Downey (1992) and Clark (1984) used the term "resorption" in conjunction with conclusions regarding decalcification (Clark and Downey 1992) in *Culcitopsis*, which possesses a thick fleshy body wall. Composition and developmental understanding of these characters is poorly understood and further study is desirable. As best as possible, terminology herein is limited to descriptive terms, avoiding interpretations pending further understanding of these characters.

Diagnosis. Body form pentagonal to stellate, with weakly curved to straight interradial arcs. Disk and arms thick, strongly arched in many taxa, nearly all genera covered by a thick, fleshy, often stout dermis or tissue overlying the endoskeleton, which in most taxa completely obscures any plate patterns or outlines. Abactinal plate morphology variable, ranging from bar-like to more irregularly thickened and mound-like. Prominent spines present in *Poraniopsis* and variably in *Glabraster*, but otherwise the thick dermis or tissue is variably smooth or covered by granules, spinelets or other accessories. In taxa such as *Poraniomorpha* or *Glabraster*, dried specimens reveal a closely imbricate, reticulate or fenestrate skeleton overlain by the aforementioned tissue or dermis. Spines (e.g. *Poraniopsis*) or prominent knobbed projections (e.g. *Clavaporania*) variably present on abactinal and marginal plates. Marginal plates, when not obscured by dermis or tissue, appear to be imbricate but quadrate to blocky in shape.

Actinal plates variable, transversely rod-like to forming irregularly imbricate pavement. Adambulacral and other prominent marginal or actinal spination are similarly covered by a fleshy dermis or tissue. Furrow spines generally few (1–3). Pedicellariae absent.

Comments. Poraniids superficially appear similar to another family of Australian asteroids, the Asteropseidae, including *Petricia* and *Asteropsis*, which also have a layer of dermis or tissue covering their endoskeleton but occur primarily in shallow-water temperate to tropical settings. Hotchkiss and Clark (1976) addressed this issue, separating the two families that Spencer and Wright (1966) had merged, outlining morphological differences. Molecular data (e.g. Mah and Foltz, 2011) further supported separation between these groups.

Actinal plates are a useful diagnostic character for distinguishing the Poraniidae from the Asteropseidae (Hotchkiss and Clark, 1976; Clark, 1984). Asteropseid actinal plates are quadrate to polygonal in shape and arranged in a chevron-like arrangement. Poraniid actinal plates are arranged

in a transverse pattern from the lateral edge to the ambulacral groove. Marginal plate arrangements can be similarly diagnostic, with asteropseids showing abutted plates whereas poraniids show more fenestrate to imbricate arrangements.

Further members of the Valvatida that could be confused with the Poraniidae include the mesophotic oreasterid, *Astrosarkus* Mah, 2003 and asterinids such as *Disasterina* Perrier, 1875, which also show a thick fleshy body wall and/or a thickened dermal layer covering the body surface. *Astrosarkus* is most immediately distinguished from any poraniid by the presence of pedicellariae, with a continuous granular covering and adambulacral spines that are primarily blunt tipped, thick and present in multiple rows. Pedicellariae have not been observed on poraniids, which show pointed adambulacral spines with a well-developed dermal sheath. *Astrosarkus* also shows a broad lateral surface, whereas most poraniids display a more rounded lateral edge.

The asterinid *Disasterina*, including *D. abnormalis* Perrier 1875, possess a well-developed dermal covering over the abactinal, marginal and actinal plates on wet preserved and living specimens, which in some instances can cause them to resemble poraniids. Plate patterns in dried *Disasterina* are well developed, and plate shape and abundance is very different from those in any of the Poraniidae. *Disasterina* also occur primarily in shallow-water settings (intertidal to 3 m) (Marsh and Fromont, 2020).

Key to the Poraniidae

- (0) Prominent spines present on abactinal, marginal surface. Skeleton reticulate. (1)
- (0') Spines (if present) small and conical; otherwise, abactinal and marginal surface covered by thickened dermis, granules with round to pointed tips and/or round granules. (2)
- (1) Spines pointed. Dermis with ossicles or spinelets present or absent. Reticulation frames large papular regions, each with papulae 10–30. Sub-temperate bands in northern (Russia, Japan, west coast of North America to Galapagos) and southern hemisphere (Patagonian South America, including Brazil, Argentina, etc. southern Indian Ocean). *Poraniopsis*
- (1') Spines thickened with bifurcated tips. Dermis on abactinal, lateral and actinal surface invested with a dense covering of tiny spinelets. Papular pores single. Known only from the holotype, Macquarie Island, 1574–1693 m *Clavaporania*
- (2) Thickened, fleshy body wall at moderate to large sizes ($R > 3.0$ cm). Skeletal ossicles not clearly visible externally. ... (3)
- (2') Dermal overlay but skeleton visible, fenestrate to reticulate. (5)
- (3) Spinelets in body wall. Abactinal, actinal surface covered by numerous superficial spinelets. Inferomarginal plates with spinelets or spines. Papulae present but inconspicuous. South Africa and southern Indian Ocean. *Spoladaster* (*Tylaster* is a possible synonym)
- (3'') Body wall surface smooth and naked. Marginal plates with spines present or absent. Papulae large, conspicuous. (4)
- (4) Papulae present in continuous parallel series on adradial sides along arm. Spines variably present on marginal plates. North Atlantic and South Africa. *Chondraster*
- (4'') Papulae in discrete clusters, variably extending completely along arm, or in transverse series on abactinal surface. Spines absent. North Atlantic, North American and European coast. *Culcitopsis*
- (5) Skeleton reticulate, thick tissue or dermis variably well developed or present as an overlay obscuring plate boundaries. (6)
- (5') Skeleton fenestrate, surface variably covered by granules, which are round or spine-tipped. (9)
- (6) Marginal plates per interradius, relatively few, 8–10 per interradius (arm tip to arm tip). Overall, most individuals pentagonal to weakly stellate; size tends to be small, with most individuals with $R=0.5-1.0$ (diameter approximately 1–2.0 cm). Widely occurring, Atlantic and Pacific. *Marginaster*
- (6') Marginal plates numerous, 20–50 per interradius (at approximately $R=1.2$) (7)
- (7) Subambulacral spine large, wide and flat. Abactinal surface variably smooth or covered with prominent spines, well-developed dermis covering reticulate plates. Inferomarginal plates with bearing large, flat spines. Known only from Southern Ocean and adjacent waters (Patagonia, etc) *Glabraster*
- (7') Subambulacral spines pointed. Abactinal skeleton variably open to more close set, approaching a more fenestrate arrangement in some specimens. (8)
- (8) Abactinal, marginal, actinal surface with a rugose appearance, covered by short spines and spinose granules. Abactinal, marginal plates, multi-lobate in shape, superomarginal plates with 2–4 distinct pointed spines. Body stellate ($R/r=3.1$), arms elongate. North Pacific. *Bathyporania*
- (8'') No abactinal spines, surface mostly smooth. Abactinal skeleton imbricate, variably reticulate to more close-set, nearly fenestrate. Marginal plates more blocky in shape, imbricate, inferomarginal plates each with 4–6 pointed spinelets. Northern Hemisphere, temperate North Atlantic. *Porania*
- (9) Papular pores numerous (3–15). Marginal plates form wide periphery around body, 35–40 per interradius. Body pentagonal to weakly stellate (1.5–2.0). North Atlantic. *Poraniomorpha hispida*
- (9') Papular pores single. Marginal plates number 16–60 per interradius, indistinct with lateral facing. Body form weakly stellate to stellate, $R/r=1.6-2.5$ arms confluent with disk. (10)

- (10) Marginal plates numerous, 48–60 per interradius. Body stellate to strongly stellate, $R/r=1.9\text{--}2.5$ arms distinct with tips tapering to elongate. North Atlantic and *P. tartarus* from Australia. *Poraniomorpha abyssicola*, *P. tumida*, *P. bidens* and *P. tartarus*
- (10') Marginal plates number approximately 16 per interradius. Weakly stellate to stellate, $R/r=1.6\text{--}2.1$, arms distinct, consistently short with rounded tips. South Pacific (New Zealand & Tasmania). *Bathymarginaster n. gen.*

Taxonomic account

Bathymarginaster nov. gen.

Diagnosis and comments. As for species.

Etymology. The name alludes to the Greek *bathos* for deep and the type name *Marginaster*, referring to this taxon's presence at great depth (191–1130 m) relative to the other *Marginaster* species.

Bathymarginaster patriciae (McKnight, 2006) nov. gen, nov. comb.

Figure 1a–f

Diagnosis. Body weakly stellate to stellate ($R/r=1.6\text{--}2.1$) (Fig. 1a). Body surface, including abactinal, marginal, actinal surface all covered by dermis. Abactinal surface reticulate to imbricate, with coarse granulation/spination on each plate (Fig. 1a, b), single papulae present. Marginal plates lateral facing, approximately 16 per interradius (Fig. 1c), each plate bearing an upper and lower series, each with 2–3 spinelets present, the lower series approximately 2–3 times as large as the upper and present around the actinolateral fringe. Distinct actinolateral edge (Fig. 1e) formed by the inferomarginal plates and the actinal surface. Actinal intermediate region with approximately 16 segments, each with a spine forming a transverse series across each interradius (Fig. 1f). Furrow spines, two covered in dermis (Fig. 1d, f); no other adambulacral spination evident.

Comments. Examination of *M. patriciae* specimens relative to other *Marginaster* species, including the holotype of *Marginaster paucispinus*, led to the conclusion that *M. patriciae* is significantly different from other species assigned to *Marginaster*. '*Marginaster patriciae*' shows a much more stellate body shape, has a much denser and heavier abactinal skeleton that is weakly fenestrate. This contrasts with the skeleton in more typological *Marginaster* species, which show a more openly arranged mesh with a variably developed dermal covering (Fig. 2). *Marginaster patriciae* has laterally oriented marginal plates that form a distinct ventrolateral edge with the actinal surface, whereas the marginals, especially the inferomarginal plates, of other *Marginaster* species are extended from the superomarginals to form a distinct flattened lateral "ledge" or platform with spines.

Marginaster patriciae was originally described from New Zealand waters from near Chatham Rise at 900–1130 m.

Among poraniids, *Bathymarginaster* nov. gen. is perhaps closest to *Poraniomorpha*, which shows a fenestrate skeleton. The abactinal skeleton of the former shows a skeleton with a granular/spinose covering, rather than the more open reticulate skeleton observed in true *Marginaster* species (e.g. Fig. 2a–d). *Bathymarginaster* displays a much heavier dermal overlay (Fig. 1b) than *Poraniomorpha* that obscures the marginal and actinal plate boundaries in the former. *Bathyporania* similarly displays a granular overlay but possesses a more open, reticulate skeleton.

Occurrence. Chatham Rise, central New Zealand, 900–1130 m. Note that McKnight (2006: 107) confused the depth range of *M. patriciae* with that of *M. paucispinus* (518–554 m).

Australian waters. J1 Seamount near Tasmania, Great Australian Bight. 850–1650 m.

Description. Body thick, strongly arched weakly stellate to stellate ($R/r=1.6\text{--}2.1$), arms triangular in shape, cylindrical to triangular in cross-section, actinal surface flat with distinct actinolateral edge. Plates, spines, accessories all covered by dermis (Fig. 1a, b). Arm tips upturned.

Abactinal surface fenestrate to imbricate, skeletal plates individually wide, fully enclosed over disk but forming wider, open spaces distally on arms. Individual plates ranging from larger, more irregular in shape proximally, becoming more crescentic along arms. Each plate with short, blunt spines or granules (4–15, but mostly 7–10), widely spaced, number decreasing distally along arm (Fig. 1b). Single papular pores present irregularly scattered on arms and disk on abactinal and lateral surfaces. Madreporite round, flat, adjacent to abactinal plates and slightly overlaid with tissue around edges.

Marginal plate boundaries largely obscured by dermis, but approximately 16 per interradius, eight per arm side at $R=1.0$ cm (Fig. 1c, e). At arm tip dermis sufficiently translucent as to reveal elongate plates, edges rounded, decreasing in width adjacent to arm terminus.

Superomarginal and inferomarginal plates each with spines (tips conical and pointed) in upper and lower series, approximately 2–3 in each row. Inferomarginal spines approximately twice as large as those on the superomarginal series, especially those spines on the lower series adjacent to the contact with the actinal plates. Terminal plate quadrate with a circular edge, bearing two small spines.

Actinal plates covered by dermis that shows distinct channels (Fig. 1d, f), forming segments that track from the abactinal-lateral surface via the marginal plates to the underside of the actinal surface around the marginals to each adambulacral plate (Fig. 3e). Actinal surface smooth, dermal tissue continuous from marginal plates. Each actinal intermediate segment has approximately 16 dermis-covered cone-like spines. These are single proximally, becoming double adjacent to the spines on the inferomarginal plates. These spines are in three lateral series across the actinal intermediate region.

Two furrow spines (Fig. 1d, f), covered by dermis in transverse series. No subambulacrals or other accessory adambulacral structures. Oral plate with two furrow spines, a single prominent spine projecting into mouth (Fig. 1f).

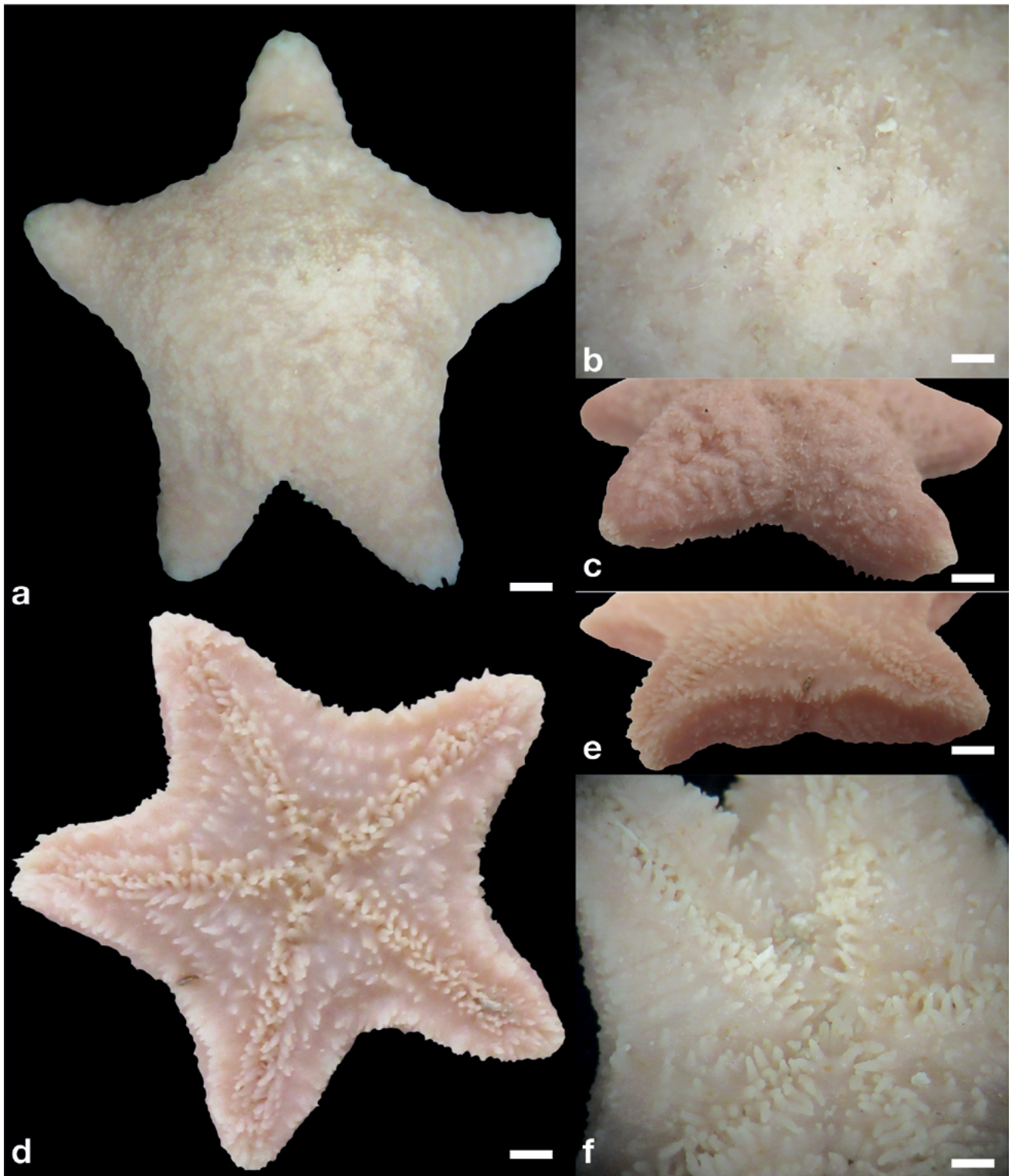


Figure 1. *Bathymarginaster patriciae* nov. gen. nov. comb. NMV F240376: a, abactinal; b, abactinal surface showing granules; c, abactinal-lateral view showing lateral surface, marginal series; d, actinolateral view showing edge and actinal surface; e, actinal view; f, closeup of actinal view showing adambulacral spination, oral view. Scale bars a=3.5 mm, b=1.5 mm, c, f=2 mm, d=2.5 mm, e=3.5 mm.

Material examined. NMV F84961 84 km SSE of South East Cape, J1 Seamont, Tasmania. -44.27° S, 147.33° E, 1300–1450 m, Coll. T. Stranks et al. CSIRO, 27 Jan 1997. 1 wet spec. R=1.3, r=0.6.

NMV F159299 Hill U. top west, Tasmania, Australia. -44.3257° S, 147.175° E, 1100–1160 m, Coll. CMBAR SS02, April 2 2007. 3 wet specs. R=1.3, r=0.7; R=1.0, r=0.5; R=1.4, r=0.6.

NMV F159300 Pedra West, south of Tasmania, -44.2585° S, 147.092° E, 850–1000 m, Coll. O'Hara et al, CMAR, 2 April 2007, 1 wet specs. R=1.3, r=0.8.

NMV F159301 Mini Matt SSW, Australia. -44.2447° S, 146.164° E, 1120–1136 m. Coll. O'Hara et al, 4 April 2007, CMAR SS02. 3 wet specs. R=1.1, r=0.6; R=1.2, r=0.7; R=1.2, r=0.6.

NMV F159302 Mini Matt site, S. of Tasmania, -44.2439° S, 146.165° E, 1120–1310 m, Coll. O'Hara et al, CMAR 4 April, 2007, 2 wet specs. R=1.1, r=0.6; R=1.3, r=0.7.

NMV F159303 Pedra West, -44.1322° S, 146.144° E, 1140–1180 m, Coll. O'Hara et al. CMAR 5 April 2007, 1 wet spec. R=0.9, r=0.5.

NMV F240386, Great Australian Bight -33.3366° S, 130.257° E, 188–191 m, Coll. IN2015_C02 GAB BP Expedition – Ichthyology Team, IN2015_C02 GAB BP Expedition – Marine Invertebrates Team, 15 Dec 2015. 1 wet spec. R=0.6, r=0.4.

NMV F240376, 82.6 km SSE of South East Cape, J1 Seamont, Tasmania, -44.24° S, 147.36° E, 1200–1450 m, Coll. T. Stranks et al. CSIRO, 27 Jan 1997. 4 wet specs. R=1.1, r=0.6; R=1.2, r=0.7; R=1.1, r=0.6; R=1.1, r=0.6.

NMV F 241095, 85.8 km SSE of South East Cape, “B1” seamont, -44.31° S, 147.27° E, 1150–1550 m, Coll. T. Stranks et al. CSIRO, 28 Jan 1997. 3 wet specs. R=1.2 r=0.5 R=1.1 r=0.5 R=0.9 r=0.6.

NMV F241096, 87.8 km SSE of South East Cape, “A1” seamont, -44.33° S, 147.27° E, 1200–1300 m, Coll. T. Stranks et al. CSIRO, 30 Jan 1997, 1 wet spec. R=1.1 r=0.5.

NMV F241097, 94.5 km SSE of South East Cape, “V” Seamont, -44.4° S, 147.15° E, 1400–1650 m, Coll. T. Stranks et al. CSIRO, 31 Jan 1997. 1 wet spec. R=1.0 r=0.6

NMV F241098, K1 seamont, 89.5 km SSE of South East Cape, Tasmania, Australia, -44.29° S, 147.41° E, 1225 m, Coll. Tim N. Stranks, CSIRO aboard RV *Southern Surveyor*, 25 Jan 1997. 4 wet specs. R=1.0, r=0.7; R=1.0, r=0.5; R=0.9, r=0.4; R=0.7, r=0.3.

NMV F241099, 81.6 km SSE of South East Cape, “38” seamont, Tasmania. -44.23° S, 147.38° E, 1200–1400 m, Coll. T. Stranks et al. CSIRO 30 Jan 1997, 1 wet spec. R=1.2, r=0.6.

NMV F241100 “Sister I” seamont, 82.9 km SSE of South East Cape, -44.27° S, 147.29° E, 1100–1122 m, Coll. T. Stranks et al. CSIRO, 23 Jan 1997, 2 wet specs. R=1.1, r=0.5; R=1.0, r=0.6.

NMV F241101 “Sister I” seamont, 82.9 km SSE of South East Cape, -44.27° S, 147.29° E, 1100–1122 m, Coll. T. Stranks et al. CSIRO, 1 wet spec. R=1.0, r=0.4

NMV F241102 Mongrel seamont, Tasmania. -44.2554° S, 147.114° E, 898 m. Coll. R. Thrasher and D. Staples, 23 Dec 2008. 1 wet spec. R=1.0, r=0.5.

NMV F241103 Mongrel seamont, Tasmania. -44.2554° S, 147.114° E, 899 m. Coll. R. Thrasher and D. Staples, 13 Oct 2008. 1 wet spec. R=0.4 r=0.2.

NMV F241573 Patience seamont, Huon Commonwealth Marine Reserve, Tasmania, Australia, -44.1206° S, 147.377° E, 1087 m, Coll. D. Bray, RV *Investigator* 12 April 2015. 2 wet specs. R=1.0, r=0.3; R=1.2, r=0.4.

NMV F270826 Punch's Hill, Tasmanian seamonts, Tasmania, -44.18556° S, 147.188333° E, 919–1085 m. Coll. A. Williams, A.A. Weber and R-L. Erickson, 13 Dec 2018. 2 wet specs. R=0.9, r=0.6; R=0.9, r=0.4.

***Marginaster* Perrier 1881**

Marginaster Perrier 1881: 16.—1884: 229.—Sladen 1889: 364.—Perrier 1894: 164–165.—Ludwig 1897: 189.—Verrill 1914: 18–19.—1915: 75–76.—Downey 1973: 82.—Clark 1984: 25–27.—McKnight 2006: 106.

Cheilaster Bell 1893: 81 (superfluous replacement name for *Marginaster* Perrier)

Poranisca Verrill 1914: 19.—Clark 1984: 25 [type: *P. lepidus* Verrill 1914]

Marginaster sp. McKnight 1968: 513.—Clark 1970: 5.—Clark and McKnight 2001: 166.

Type Species. *Marginaster paucispinus* Fisher 1913 (by subsequent designation)

Diagnostic comments. *Marginaster* has historically been considered a “provisional genus” (Clark and Downey, 1992: 205), and as such most recent diagnoses (Clark and Downey, 1992; McKnight, 2006) have been brief and incomplete. This account disagrees with prior accounts that assume *Marginaster* is a juvenile of other poraniid taxa, and as such, attempts to incorporate characters from known species, exclusive of *Marginaster* (now *Bathymarginaster*) *patriciae* and the asterinid *Marginaster* (now *Patiriella*) *littoralis* Dartnall 1970.

Diagnosis. Body small, R<2.5 cm, overall shape pentagonal to weakly stellate (R/r=1.4–2.0). Body covered by variably thickened dermis, ranging from relatively thin (Fig. 2a) to very thick and fleshy (Fig. 2e, f). Abactinal plates reticulate, forming widely open papular regions between rod-like ossicles (Fig. 2a, c, d). Plates variably with pointed, conical spinelets. Marginal plates wide, dorsal-facing, forming broad periphery (Fig. 2a, c, d), each plate series bearing 2–6 short spinelets. Inferomarginal spinelets flattened, larger than those on superomarginal plates. Actinal plates imbricate, tissue covered, relatively few overall (Fig. 2b, d, f). One to three short, pointed furrow spines. One to three subambulacral spines.

Comments. *Marginaster* Perrier 1881 has been met with skepticism throughout its taxonomic history, beginning with Verrill (1914) and later with Downey (1973) and Clark and Downey (1992), who argued *Marginaster* is the juvenile or small form of a larger, possibly unknown, poraniid. Mah and Foltz (2014) argued that *Marginaster* is a separate but small-sized taxon, and that none of the North Atlantic genera or any of the known Southern Hemisphere poraniidae, such as *Glabraster* at comparable sizes, were morphologically consistent with *Marginaster*. No other known poraniids are distributed with a comparably occurring geographic and/or bathymetric distribution (Mah, unpublished data), making it seem unlikely that *Marginaster* is the juvenile form of some other Poraniidae.

Including *B. patriciae*, addressed herein, there are four known species: *Marginaster capreensis* (Gasco, 1876), *M. paucispinus* Fisher 1913, and *M. pectinatus* Perrier, 1881. *Marginaster capreensis* and *M. pectinatus* occur in the Mediterranean and the Atlantic, whereas *M. paucispinus* occurs in the Pacific and the Indian Ocean (Reunion Island). Although a comprehensive generic review is beyond the scope of the present study, cursory examination suggests relatively few character

differences among species, particularly of inferomarginal spine number and marginal plate number, expression of the reticulate abactinal skeleton and abactinal spination.

Marginaster paucispinus Fisher, 1913

Figure 2a-f

Marginaster paucispinus Fisher 1913: 407.—Jangoux and Aziz 1988: 633, 646.—McKnight 2006: 107.—Lee et al. 2017: 274.

Marginaster sp. McKnight 1968: 513.—H.E.S. Clark 1970: 5.—McKnight in H.E.S. Clark and McKnight 2001: 166.

Diagnosis. Body pentagonal to weakly stellate ($R/r=1.1-1.7$), body thick, arms triangular, interradial arcs weakly curved. Abactinal skeleton reticulate with relatively wide openings (Fig. 2c). Transverse ribs on arms projecting from radial series (Fig. 2a, c). Marginal plates, 10–11 per interradius (Fig. 2a, c, d), each plate with 1–4 short, blunt, conical spinelets (Fig. 2a, b). Superomarginals and inferomarginals (6–7), inferomarginals forming flange-like ambitus, each with 4–5 webbed, flattened spatulate spines. Upper inferomarginal plate surface with 3–4 small spinelets. Actinal plates forming reticulate arrays that track from adambulacral plates to the inferomarginals to the abactinal surface. Open meshes between these plates. Furrow spines (1–2) (Fig. 2b, c), two subambulacral spinelets, narrowly spatulate.

Comments. *Marginaster paucispinus* has been widely recorded geographically and in depth (155–700 m) across the Indo-Pacific. Some characteristics – such as marginal plate number and marginal plate spine number, as well as abactinal plate arm patterns – appear to be consistent among individuals surveyed, whereas the two MNHN specimens from the Austral Islands and the South Pacific appear to show a more developed dermal layer. The reticulate skeleton pattern shows a similar pattern to other Indo-Pacific individuals, including the holotype. McKnight (2006) remarked on the similarity between individual *M. paucispinus* and also with other *Marginaster* spp.

This species is distinguished from the Atlantic *Marginaster* species based primarily on the lower marginal plate number per interradius (approximately 10–11) than in *Marginaster pectinatus* (15–20) and *M. capreensis* (approximately 12 or more). Number and position of marginal spines also differed but did show some overlap. A full overview was beyond the scope of this work, but based on taxonomic summaries of these species (e.g. Clark and Downey, 1992), their characteristics are very similar, suggesting further sampling could blur boundaries between established species concepts.

Occurrence. Australia. The Great Australian Bight, South Australia, 155–191 m.

Outside Australia. South China Sea, near Hong Kong (183 m), Korea, Reunion Island and Kermadec Islands (179–227 m), northern New Zealand (518–554 m). 179–554 m.

New Records: Austral Islands and the South Pacific, 480–700 m.

Material examined. NMV F 240386, Great Australian Bight, South Australia, -33.3366° S, 130.257° E, 188–191 m. Coll. IN2015_C02 GAB BP Expedition – Ichthyology Team, IN2015_C02 GAB BP

Expedition – Marine Invertebrates Team. 15 Dec 2015. 1 wet spec. $R=0.5$, $r=0.3$.

IE-2013-1518 Austral Islands, northeast of Rapa Its, South Pacific -27.566667° S, 144.27° W, 480–700 m. Coll. BENTHAUS DW 1897. 2 wet spec. $R=1.6$, $r=1.4$; $R=0.4$, $r=0.35$.

IE-2013-4675 South Pacific, south of Niue, -25.283333° S, -168.933333° W, 609–691 m. Coll. NORFOLK 2 DW 2064. 1 wet spec. $R=0.7$, $r=0.4$.

Holotype, *M. paucispinus*. USNM 32641 Approximately 250 km southeast of Hong Kong, South China Sea. 21.55° S, 116.217° E, 183 m. Coll. USFC Steamer Albatross, 4 Nov 1908. 1 wet spec. $R=1.1$, $r=0.8$.

Poraniomorpha Danielssen and Koren 1881

Poraniomorpha Danielssen and Koren 1881: 189.—1884: 67–70.—Verrill 1895: 139.—Grieg 1907: 41–42.—Fisher 1911: 248 (in key).—1919: 407.—Koehler 1924: 157.—Mortensen 1927: 92.—Gallo 1937: 1664–1667.—Djakonov 1950: 58–59 (1968: 48–49).—Spencer and Wright 1966: U70.—Clark 1984: 33–41.—Clark and Downey 1992: 212.—Mah and Foltz 2014: 350.

Rhegaster Sladen 1883: 155.—1889: 367.—Bell 1893: 80.—Verrill 1914: 17.

Lasiaster Sladen, 1889: 371–372.—Bell 1893: 81.—Verrill 1899: 198.

Diagnostic comments. The diagnosis herein follows Mah and Foltz (2014), who recognised *Poraniomorpha* as a separate genus from *Culcitopsis*, disagreeing with Clark and Downey (1992), who argued that *Culcitopsis* was a subgenus of *Poraniomorpha*. This includes taxa with polygonal, imbricate, fenestrate plates and a solid abactinal skeleton as separate from species within *Culcitopsis*, which demonstrate strongly expressed fleshy tissue as part of their body wall.

Diagnosis. Body shape ranges from pentagonal to strongly stellate ($R/r=1.2-2.75$, $3.7-3.9$ in this case), arms triangular, variably short to elongate. Characterised by compact, imbricate, fenestrate abactinal plates irregular in shape, but weakly convex, mound-like in overall appearance. Body surface overlaid by thick dermal tissue invested with granules bearing pointed tips, variable in abundance, density and homogeneity, covering abactinal marginal and actinal surface, obscuring plate boundaries. In other species, actinolateral fringe discrete with larger, thicker spines variably present. Actinal regions relatively large, plates imbricate in transverse series. Adambulacral armature prominent, forming a spiny fringe along tube foot groove. Two to five furrow spines.

Comments. Four species of *Poraniomorpha* are currently recognised: *P. abyssicola* (Verrill, 1895), *P. bidens* Mortensen 1932, *P. hispida* (Sars, 1872), and *P. tumida* (Stuxberg, 1878), all of which occur in the North Atlantic and adjacent waters. This is the first occurrence of *Poraniomorpha* in the Southern Hemisphere.

Poraniomorpha tartarus n. sp.

Figure 3a–e.

Etymology. The species epithet is named for Tartarus, the mythical Greek underworld, alluding to this species' occurrence at great depth. Noun held in apposition.

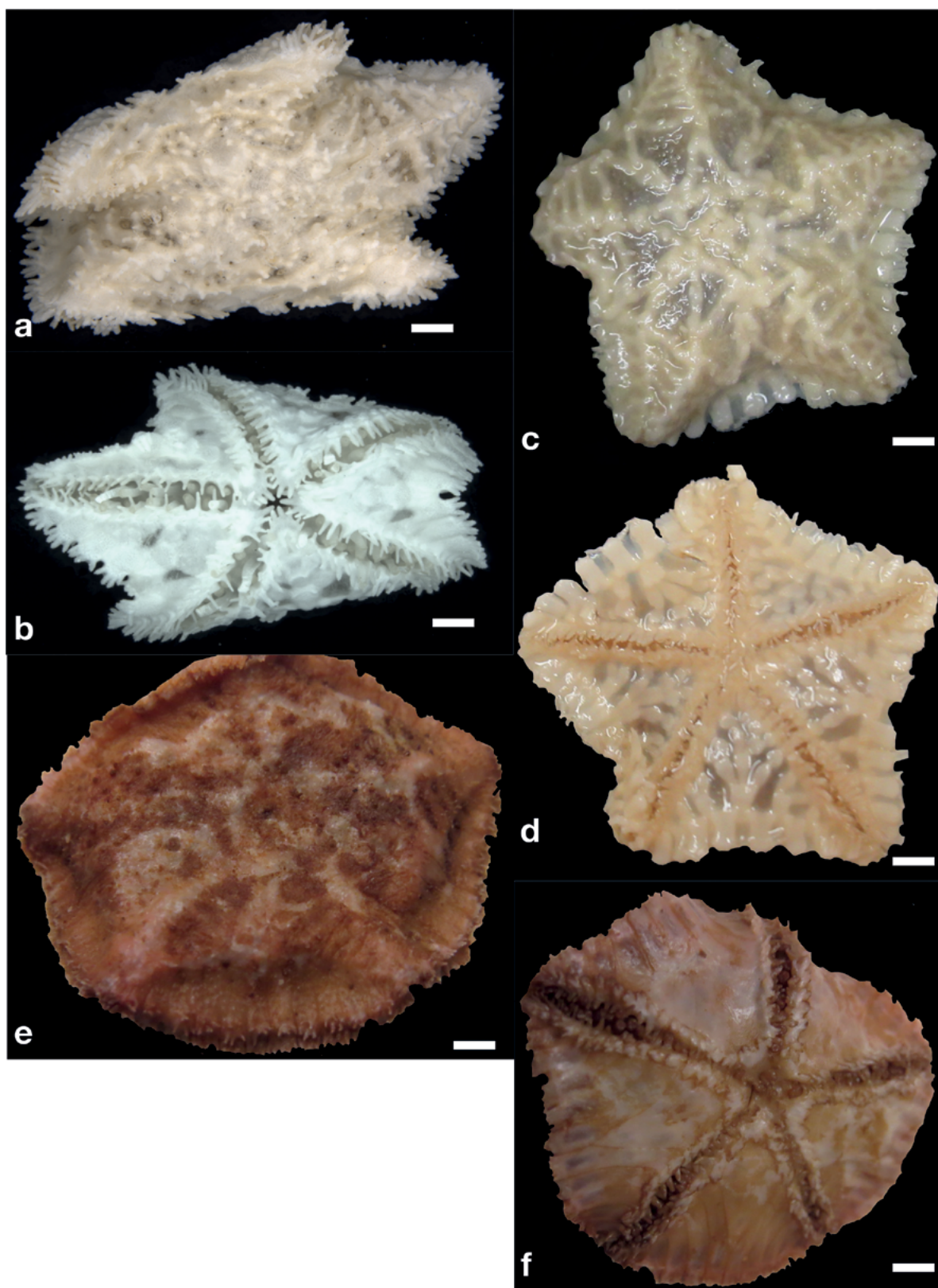


Figure 2. *Marginaster paucispinus* NMV F240386: a, abactinal view; b, actinal view; USNM holotype 032641: c, abactinal view; d, actinal view. MNHN-2013-1518: e, abactinal view; f, actinal view. Scale bars a, b=1.0 mm, c, d, e, f=1.5 mm. Photos by Melanie Mackenzie NMV.

Diagnosis. Body strongly stellate (Fig. 3a). Actinolateral fringe rounded with rounded edge (Fig. 3c, d). Abactinal surface hard, very resistant to the touch. Surface covered by minute, pointed granules embedded in dermal integument (Fig. 3b, d). Drying of specimen suggests flattened marginals are polygonal plates, approximately 48 per interradius. Actinal region narrow, surface is flat, with approximately 50 shallow segments corresponding with adambulacral and marginal plates but also bisecting the actinal intermediate region extending to the oral plate. Actinal surface also covered by small granules, covered by dermis, 5–30 per actinal segment, each with a hyaline tip invested in the dermal integument. Dark brown colour adjacent to the adambulacral spination on the disk and along the arms (Fig. 3c, d, e). One or two furrow spines, with 1–2 enlarged subambulacral spines, each approximately twice the thickness of and more elongate than the furrow spines (Fig. 3d, e).

Comments. Although *P. tartarus* n. sp. possesses a rounded actinolateral edge, unlike other *Poraniomorpha* species, several other characters – including irregular imbricate plates, the pointed granules invested in the dermal tissue, and the distinctively enlarged subambulacral and furrow spination on the adambulacral plates (Fig. 3d, e) – support placement within *Poraniomorpha*.

Poraniomorpha tartarus n. sp. invites comparison with Atlantic species such as *P. abyssicola* (Verrill, 1895) and *P. tumida* (Stuxberg, 1878), which it resembles very closely. They share similar abactinal plate morphology, displaying closely articulated irregular-shaped, imbricate, mound-like plates bearing a cover of spinose granules covering the surface such that plate boundaries are obscured. The disk in these species is strongly arched and arms are similarly elongate and tapering. Furrow spines are relatively few in both species (1–2 in *P. tartarus* n. sp. versus 2–3 in *P. abyssicola* but 3–5 in *P. tumida*). *Poraniomorpha tartarus* n. sp. is distinguished by the enlarged subambulacral spine, the absence of most papulae from the abactinal surface, and the difference in actinal plate texture, which possesses distinct transverse segments and lacks the numerous pointed spinelets seen in *P. abyssicola*. Neither *P. abyssicola* nor *P. tumida* are known to display the distinct colouration of *P. tartarus* n. sp.

Poraniomorpha tartarus n. sp. is the first known occurrence of this genus in the Southern Hemisphere and is also the deepest known species of the genus (3850–3853 m). *Poraniomorpha abyssicola* occurs at comparable depth in the Atlantic (2976–3740 m).

Although very little is known about the biology of *Poraniomorpha* spp., the NOAA vessel *Okeanos Explorer* observed *P. abyssicola* feeding on a sponge at 3403 m (Mah, 2020). *Poraniomorpha tartarus* n. sp. may feed on similar prey.

Occurrence. Known only off East Gippsland, Victoria, Tasman Sea, 3850–3853 m.

Description. Body strongly stellate ($R/r=3.7-3.9$) (Fig. 3a, c) with elongate arms, round in cross-section. Disk and arms confluent, disk strongly convex, rms thick, tips strongly upturned. Interradial arcs acute. Actinolateral fringe rounded with no distinct edge.

Disk plates not evident, thick integument covers all of body surface (Fig. 3a, b). Body texture hard to touch. General surface topology rough, presenting a wrinkled appearance, covered by minute, pointed granules invested in dermal integument (Fig. 3b). Individual plates irregular in shape, surface texture mound-like. Granular cover is complete, evenly distributed, approximately 5–6 along a 1.0 mm line. Papulae mostly absent from abactinal surface with some occurring interradially (5–8 observed between arms in each interradius), with few present proximally on the lateral sides of each arm. Anus at center of disk, flanked by 8–10 angular granules around edge. Dermal granules around anus slightly larger than those elsewhere. Madreporite convex, outline circular, large, approximately 1.5 (smaller specimen) to 3.0 (larger specimen) cm in diameter (Fig. 3a, b). On the holotype, madreporite adjacent to contact with superomarginal plates. Basal portion of madreporite covered by small dermal granules. No pedicellariae observed. Interradii each with a discrete fold each bearing 10–15 slender grooves that synchronise with those on marginal to actinal plates. Shallow transverse fasciolar channels extend from abactinal surface along lateral surface aligned with those on actinal surface and adambulacral plates.

Marginal plates completely obscured by dermal integument. Drying shows marginal plates, flattened, polygonal, approximately 48 per interradius (armtip to armtip), boundaries are obscured, exact count uncertain. Single row of approximately 5–8 papulae, in mostly single pores, along lateral surface of arm.

Actinal surface flat with approximately 50 shallow transverse grooves tracking from marginal to adambulacral plates forming segments. These grooves bisecting the actinal intermediate region tracking from the oral plate (Fig. 3d, e). Actinal surface covered by small granules, 5–30 per actinal segment, covered by dermis, each with a hyaline tip invested in the dermal integument. A dark colour pattern, especially evident on NMV F241811 (Fig. 3c), present adjacent to the adambulacral spine series and around the mouth extending interradially on to the disk.

Furrow spines (1–2) large and prominent, covered by dermal integument, conical tip, blunt spines widely spaced interlacing with furrow spines on opposing side (Fig. 3b, d, e). Subambulacral spine mostly single, but two are present on approximately 40% of adambulacrals, especially on NMV F241811, approximately twice the thickness of each furrow spine arranged transversely relative to the furrow spine. Remaining adambulacral plates with single, short subambulacral spine, variably blunt and smooth, a minority of spines with notched or roughened tip. At least one of the larger subambulacral spines comparable in size with one of the furrow spines. Those secondary subambulacrals spines smaller, less than half the height and thickness of the furrow spine. Dermal integument covers the adambulacral plate; no other accessories are present.

Oral plates with four furrow spines and one spine from each oral plate projecting into the mouth (two total). Oral plate surface, with a total of 4–6 suboral spines (two or three per half).

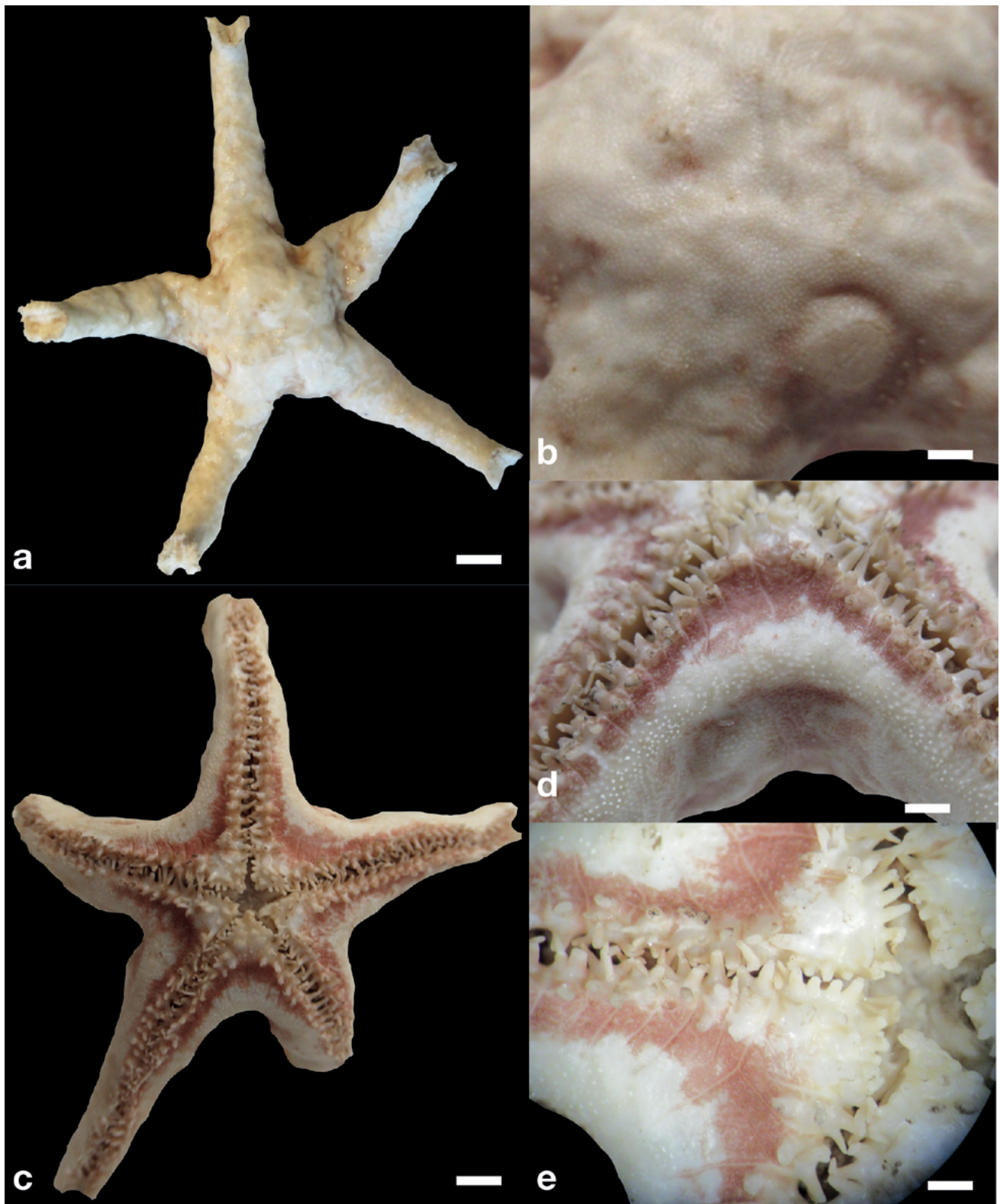


Figure 3. *Poraniomorpha tartarus* n. sp., holotype. NMV F 241811: a, abactinal; b, abactinal surface showing madreporite, surface texture; c, actinal view; d, actinal intermediate region and inferomarginals; e, actinal view furrow spines, oral region. Scale bars a=9.0 mm, b=5.0 mm, c=9.0 mm, d, e=2.0 mm.

Colour in life white to dark brown on disk, arms mottled, dark brown to white, interradii dark brown. Underside is white with dark brown in each interradius around mouth (Fig. 3c, d, e). Dark colouration present in patches along adambulacral series.

Material examined. Holotype. NMV F 241811 East Gippsland, Victoria, Tasman Sea, Australia, -38.479° S, 150.185° E, 3850–3853 m, Coll. O'Hara et al. aboard RV *Investigator* 24 May 2017, 1 wet spec. R=5.4, r=1.3.

Paratype. NMV F 241807 East Gippsland, Victoria, Tasman Sea, Australia, -38.479° S, 150.185° E, 3850–3853 m, Coll. O'Hara et al. aboard RV *Investigator* 24 May 2017, 1 wet spec. R=5.7, r=1.3.

Discussion. Deep-Sea Australian Asteroidea

To date, based on Rowe and Gates (1995), the observations of *P. tartarus* n. sp. at 3850–3853 m are the deepest known for an Australian asteroid, and comparable to the similar northern hemisphere *P. abyssicola* found at 2976–3740 m (Mah and Foltz, 2014).

The most recent taxonomic catalog of Australian asteroid species (Rowe and Gates, 1995) summarised several deep-sea groups, which are known for having widely and deeply occurring species, including the Porcellanasteridae, Benthoplectinidae, Caymanostellidae and the Zoroasteridae. However, many of these groups were represented by relatively shallow members (e.g. *Pholidaster* in the Zoroasteridae, 28–243 m), and many of these families have yet to be recorded from lower bathyal to abyssal Australian settings (1000–6000 m). For example, their account lists the porcellanasterid *Porcellanaster ceruleus*, with a depth range of 1160–6040 m; this is the global range, as indicated in Clark and Downey (1992), rather than Australian occurrence. Survey reports, such as those by O'Hara et al. (2020) and MacIntosh et al. (2018), present preliminary occurrence data from these depths (e.g. 200–5000 m) but detailed accounts of species from these expeditions await preparation.

Acknowledgements

Support for my visits to Museum Victoria would not have been possible without the efforts and generosity of Dr Tim O'Hara. I am deeply grateful for the curatorial and logistical support provided by Marine Invertebrates Collection Manager Melanie Mackenzie, who greatly facilitated progress on this project. I wish to thank the CSIRO Marine National Facility (MNF) for its support in the form of sea time on RV *Investigator*, support personnel, scientific equipment and data management. All data and samples acquired on the voyage are publicly available in accordance with MNF policy. I also thank all the scientific staff and crew who participated in voyage IN2017_V03. Project funding was provided by the Marine Biodiversity Hub, supported through the Australian Government's National Environmental Science Program. Constructive reviews by Dan Blake, professor emeritus, University of Illinois at Urbana-Champaign and Marine Fau, Department of Paleobiology, USNM greatly improved this manuscript.

References

- Bell, F.J. 1893. *Catalogue of the British echinoderms in the British Museum (Natural History)*. London: British Museum. 202 pp. <http://dx.doi.org/10.5962/bhl.title.11515>
- Benavides-Serrato, M., O'Loughlin, P.M., and C. Rowley. 2007. A new fissiparous micro-asteriid from southern Australia (Echinodermata: Asteroidea: Asteroidea). *Memoirs of Museum Victoria* 64: 71–78.
- Bernasconi, I. 1964. Asteroideos argentinos. Claves para los órdenes, familias, subfamilias y géneros. *Physis Buenos Aires* 24: 241–277.
- Birkeland, C., and Lucas, J.S. 1990. *Acanthaster planci: Major management problem of coral reefs*. Boca Raton, FL: CRC Press. 257 pp.
- Blake, D.B. 1981. A reassessment of the sea-star orders Valvatida and Spinulosida. *Journal of Natural History* 15: 375–394. <http://dx.doi.org/10.1080/00222938100770291>
- Blake, D. B. 1987. A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata). *Journal of Natural History* 21(2): 481–528.
- Blake, D.B., Tintori, A., and Hagdorn, H. 2000. A new, early crown-group asteroid (Echinodermata) from the Norian (Triassic) of Northern Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 106: 141–156.
- Branham, J.M. 1973. The crown of thorns on coral reefs. *Bioscience*, 23(4): 219–226. <https://doi.org/10.2307/1296587>
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., and Raes, M. 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology*, 31: 21–50.
- Butler, A.J., Rees, T., Beesley, P., and Bax, N.J. 2020. Marine biodiversity in the Australian Region. *PLoS One* 5(8): e11831. doi:10.1371/journal.pone.0011831
- Clark, A.M. 1962. Asteroidea. B.A.N.Z. Antarctic Research Expedition 1929–1931. *BANZARE Reports*, Ser. B(9): 1–104.
- Clark, A.M. 1984. Notes on Atlantic and other Asteroidea. 4. Families Poraniidae and Asteropseidae. *Bulletin of the British Museum of Natural History (Zoology)* 47(1): 19–51.
- Clark, A.M., and Courtman-Stock, J. 1976. *The Echinoderms of Southern Africa*. Publ. 766 BMNH, London, 277 pp.
- Clark, A.M. and Downey, M.E. 1992. *Starfishes of the Atlantic*. London: Chapman and Hall. 820 pp.
- Clark, H.E.S. 1970. Sea-stars (Echinodermata: Asteroidea) from *Eltanin* cruise 26, with a review of the New Zealand asteroid fauna. *Zoological Publications of Victoria University* 52: 1–34.
- Clark, H.E.S., and McKnight, D.G. 2001. The marine fauna of New Zealand, Echinodermata, Asteroidea (sea-stars), Order Valvatida. *NIWA Biodiversity Memoir* 117: 1–270.
- Clark, H.L. 1921. *The Echinoderm fauna of Torres Strait: Its composition and its origin*. Washington, D.C.: Carnegie Institution of Washington. <https://doi.org/10.5962/bhl.title.14613>
- Clark, H.L. 1923. The Echinoderm fauna of South Africa. *Annals of the South African Museum*, 13(7): 221–435.
- Clark, H.L. 1946. The Echinoderm fauna of Australia. Its composition and its origin. *Publications of the Carnegie Institution of Washington* 566: 1–567.
- Danielssen, D.C., and Koren, J. 1881. Fra den norske Nordhavsexpedition, Echinodermer. *Nyt Magazin for Naturvidenskaberne*, 26: 177–194.
- Dartnall, A. 1970. A new species of *Marginaster* (Asteroidea, Poraniidae) from Tasmania. *Proceedings of the Linnean Society of New South Wales* 94(3): 207–211.

- Dartnall, A.J., Byrne, M., Collins, J., and Hart, M.W. 2003. A new viviparous species of asterinid (Echinodermata, Asteroidea, Asterinidae) and a new genus to accommodate the species of pantropical exiguoid sea stars. *Zootaxa* 359: 1–14.
- De Blainville, H.M. 1830. Zoophytes. In *Dictionnaire des Sciences Naturelles*, 60: 1–546. Paris.
- Djakonov, A.M. 1950. Morskije Zvezdy Morei SSSR [Sea stars (Asteroids) of the USSR seas]. *Opredeliteli po faune SSSR* [Keys to the fauna of the USSR] 34: 1–203. 183 pp.
- Downey, M.E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. *Smithsonian Contributions to Zoology* 126: 1–158. <http://dx.doi.org/10.5479/si.00810282.126>
- Ekins, M., Erpenbeck, D., and Hooper, J.N.A. 2020. Carnivorous sponges from the Australian bathyal and abyssal zones collected during the RV Investigator 2017 Expedition. *Zootaxa* 4771(1): 1–159. DOI: 10.11646/zootaxa.4774.1.1
- Farran, G.P. 1913. The deep water Asteroidea, Ophiuroidea, and Echinoidea of the west coast of Ireland. *Scientific Investigations of the Fish Board of Ireland*, 1912(6): 1–66.
- Fisher, W.K. 1911. Asteroidea of the North Pacific and adjacent waters. 1. Phanerozoia and Spinulosida. *Bulletin of the United States National Museum*, 76(xiii): 1–420. <http://dx.doi.org/10.5479/si.03629236.76.i>
- Fisher, W.K. 1913. New starfishes from the Philippine Islands, Celebes, and the Moluccas. *Proceedings of the United States National Museum* 46: 201–224.
- Fisher W.K. 1919. Starfishes of the Philippine seas and adjacent waters. *Bulletin of the United States National Museum* 3(100): 1–547.
- Fisher, W.K. 1940. Asteroidea. *Discovery Reports*, 20: 69–306.
- Gallo, V.R. 1937. Sur le genre ‘Culcitopsis’ Verrill (Asteroidea). *Compte Rendu XIIIe Congres Internationale Zoologique, Lisbon*, 1935, pp. 1664–1667.
- Gasco, F. 1876. Descrizione di alcuni Echinodermi nuovi o per la prima trovati nel Mediterraneo. *Rendiconto dell'Accademia delle Scienze Fische e Matematiche*. 15: 32–41.
- Gray, J.E. 1840. XXXII. A synopsis of the genera and species of the class Hypostoma (Asterias, Linnaeus). *Annals of the Magazine of Natural History*. 6: 275–290.
- Grieg, J.A. 1907. Echinodermen von dem norwegischen Fischereidampfer Michael Sars in den Jahren 1900–1903 gesammelt. 3. Asteroidea. 1. *Bergens Museums Aarbog*, 1906 (13): 1–87.
- Hotchkiss, F.H.C., and Clark, A.M. 1976. Restriction of the family Poraniidae, sensu Spencer and Wright 1966 (Echinodermata: Asteroidea). *Bulletin of the British Museum of Natural History (Zoology)* 30(6): 263–268.
- Jangoux, M., and Aziz, A. 1988. Les astérides (Echinodermata) récoltes autour de l'île de la Réunion par le N.O. Marion Dufresne en 1982. *Bulletin du Museum National D'Histoire Naturelle (Zoologie)* 4(10): 631–650.
- Koehler, R. 1921. Echinodermes. *Faune de France* 1: 1–210.
- Koehler, R. 1924. *Les Echinodermes des Mers d'Europe*. 1. Généralités, Astérides, Ophiuridés. Paris: Librairie Octave Doin. 360 pp.
- Lee, T., Bae, S., Kim, D.-J., and Shin, S. 2017. A newly recorded sea star of the genus *Marginaster* (Asteroidea: Valvatida: Poraniidae) from the Korea Strait, Korea. *Animal Systematics, Evolution and Diversity* 33(4): 274–277.
- Linchangco, G.V., Foltz, D.W., Reid, R., Williams, J., Nodzak, C., Kerr, A.M., Miller, A.K., Hunter, R., Wilson, N.G., Nielsen, W.J., Mah, C.L., Rouse, G.W., Wray, G.A., and Janies, D.A. 2017. The phylogeny of extant starfish (Asteroidea: Echinodermata) including *Xyloplax* based on comparative transcriptomics. *Molecular Phylogenetics and Evolution* 115: 161–170. <https://doi.org/10.1016/j.ympev.2017.07.022>
- Ludwig, H. 1897. Die seesterne des mittellmeeres. *Fauna e flora del Golfo di Napoli* 24. 491 pp.
- Ludwig, H. 1900. Arktische seesterne. *Fauna Arctica* 1(3): 447–502.
- MacIntosh, H., Althaus, F., Williams, A., Tanner, J.E., Alderslade, P., Ah Yong, S.T., Bax, N., Criscione, F., Crowther, A.L., Farrelly, C.A., Finn, J.K., Goudie, L., Gowlett-Holmes, K., Hosie, A.M., Kupriyanova, E., Mah, C., McCallum, A.W., Merrin, K.L., Miskelly, A., Mitchell, M.L., Molodtsova, T., Murray, A., O'Hara, T.D., O'Loughlin, P.M., Paxton, H., Reid, A.L., Sorokin, S.J., Staples, D., Walker-Smith, G., Whitfield, E., and Wilson, R.S. 2018. Invertebrate diversity in the deep Great Australian Bight (200–5000 m). *Marine Biodiversity Records* 11: 23. <https://doi.org/10.1186/s41200-018-0158-x>
- Mah, C. L. 2003. *Astrosarkus idipi*, a new Indo-Pacific genus and species of Oreasteridae (Valvatida; Asteroidea) displaying extreme skeletal reduction. *Bulletin of Marine Science* 73(3): 685–698
- Mah, C.L. 2006. Phylogeny and biogeography of the deep-sea goniasterid, *Circeaster* (Echinodermata: Asteroidea) including descriptions of six new species. *Zoosystema* 28(4): 917–954.
- Mah, C.L. 2020. New species, occurrence records and observations of predation by deep-sea Asteroidea (Echinodermata) from the North Atlantic by NOAA Ship *Okeanos Explorer*. *Zootaxa* 4766(2): 201–260. <https://doi.org/10.11646/zootaxa.4766.2.1>
- Mah, C.L. 2022. New genera, species and occurrence of deep-sea Asteroidea (Valvatacea, Forcipulatacea, Echinodermata) collected from the tropical Pacific Ocean by the CAPSTONE Expedition. *Zootaxa* 5164(1): 1–75. <https://doi.org/10.11646/zootaxa.5164.1.1>
- Mah, C.L., and D.W. Foltz 2011. Molecular Phylogeny of the Valvatacea (Asteroidea, Echinodermata). *Zoological Journal of the Linnean Society* 161: 769–788.
- Mah, C.L., and Foltz, D.W. 2014. New taxa and taxonomic revisions to the Poraniidae (Valvatacea; Asteroidea) with comments on feeding biology. *Zootaxa* 3795(3): 327–372.
- Marsh, L.M. 2009. A new species of *Thromidia* (Echinodermata: Asteroidea) from Western Australia. *Records of the Western Australian Museum* 25: 145–151.
- Marsh, L.M., and Fromont, J. 2020. *Field guide to shallow-water seastars of Australia*. Perth: Western Australian Museum. 543 pp.
- McKnight, D.C. 1968. Some echinoderms from the Kermadec Islands. *New Zealand Journal of Marine and Freshwater Research* 2: 505–526.
- McKnight, D.C. 2006. The marine fauna of New Zealand, Echinodermata, Asteroidea (sea-stars). 3. Orders Velatdia, Spinulosida, Forcipulatida, Brisingida with addenda to Paxillosida, Valvatida. *NIWA Biodiversity Memoir* 120: 1–187.
- Mortensen, T. 1927. *Handbook of the Echinoderms of the British Isles*. London: Oxford University Press. 471 pp.
- Mortensen, T. 1932. Echinoderms of the Godthaab Expedition of 1928. *Meddelelser om Grønland* 79: 1–62.
- Mortensen, T. 1933. Echinoderms of South Africa (Asteroidea and Ophiuroidea). *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i. København* 93: 215–400.
- Naughton, K.M., and O'Hara, T.D. 2009. A new brooding species of the biscuit star *Tosia* (Echinodermata: Asteroidea: Goniasteridae), distinguished by molecular, morphological and larval characters. *Invertebrate Systematics* 23(4): 349–366.
- O'Hara, T., Mah, C. L., Hipsley, C.A., Bribiesca-Contreras, G., and Barrett, N.S. 2018. The Derwent River seastar: Re-evaluation of a critically endangered marine invertebrate. *Zoological Journal of the Linnean Society* XX: 1–8. <https://doi.org/10.1093/zoolinnea/zly057>

- O'Hara, T.D., Williams, A., Ah Yong, S.T., Alderslade, P., Alvestad, T., Bray, D., Burghardt, I., Budaeva, N., Criscione, F., Crowther, A.L., Ekins, M., Eleaume, M., Farrelly, C.A., Finn, J.K., Georgieva, M.N., Graham, A., Gomon, M., Gowlett-Holmes, K., Gunton, L.M., Hallan, A., Hosie, A.M., Hutchings, P., Kise H., Kohler, F., Kongsrud, J.A., Kupriyanova, E., Lu, C.C., Mackenzie, M., Mah, C., MacIntosh, H., Merrin, K.L., Miskelly, A., Mitchell, M.L., Moore, K., Murray, A., O'Loughlin, P.M., Paxton, H., Pogonoski, J.J., Staples, D., Watson, J.E., Wilson, R.S., Zhang, J., and Bax, N.J. 2020. The lower bathyal and abyssal seafloor fauna of eastern Australia. *Marine Biodiversity Records* 13(11). <https://doi.org/10.1186/s41200-020-00194-1>
- O'Loughlin, P.M. 2002. New genus and species of Southern Australian and Pacific Asterinidae (Echinodermata, Asteroidea). *Memoirs of Museum Victoria* 59(2): 277–296.
- O'Loughlin, P.M. 2009. New asterinid species from Africa and Australia (Echinodermata: Asteroidea: Asterinidae). *Memoirs of Museum Victoria* 66: 203–13.
- O'Loughlin, P.M., and Bribiesca-Contreras, G. 2015. New asterinid seastars from northwest Australia, with a revised key to *Aquilonastra* species (Echinodermata: Asteroidea). *Memoirs of Museum Victoria* 73: 27–40.
- O'Loughlin, P.M., Waters, J.M., Roy, M.S. 2003. A molecular and morphological review of the asterinid, *Patiriella gunnii* (Gray) (Echinodermata: Asteroidea). *Memoirs of Museum Victoria* 60(2): 181–195.
- Paine R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65–75.
- Paine R.T. 1969. The *Pisaster-Tegula* interaction: Prey patches, predator food preference and intertidal community structure. *Ecology* 50: 950–961.
- Perrier, E. 1875. Revision de la Stellerides du Museum d'Historie Naturelle de Paris. *Archives du Zoologie Experimentale et Generale* 4: 265–450.
- Perrier, E. 1879. Les Stellérides de Île Saint-Paul. *Archives du Zoologie Experimentale et Generale* 31: 47–49.
- Perrier, E. 1881. Description sommaire des espèces nouvelles de Astéries. *Bulletin of the Museum of Comparative Zoology Harvard* 9: 1–31.
- Perrier, E. 1884. Mémoire sur les d'étoiles de mer recueillies dans la Mer des Antilles et la Golfe de Mexique. *Nouvelles Archives des Musées de Histoire Naturelle*. Paris 6(2): 127–276.
- Perrier, E. 1891. Echinoderma I. Stellérides. *Mission Scientifique du Cap Horn*, 1882–83. 6. *Zoologie* (3): 1–198.
- Perrier, E. 1893. Echinodermes. *Traité de Zoologie*. 781–864.
- Perrier, E. 1894. Stellérides. *Expédition Scientifique du Travailleur-Talisman* 3: 1–431.
- Rowe F. W. E., and Gates, J. 1995. Echinodermata. Vol. 33 in: Wells, A. (ed), *Zoological Catalogue of Australia*. Melbourne: CSIRO.
- Sars, M. 1872. Nye Echinoderm fra den Norske Kyst. *Kongelige Videnskabernes Selskabsforhandling* 1871: 27–31.
- Sladen, W.P. 1883. IX. Asteroidea dredged in the Faerøe Channel during the cruise of H.M.S. Triton in August 1882. *Transactions of the Royal Society of Edinburgh* 32: 153–164. <http://dx.doi.org/10.1017/s0080456800026703>
- Sladen, W.P. 1889. Asteroidea. *Report of the Scientific Results of H.M.S. Challenger* 30: 1–893.
- Spencer, W.K., and Wright, C.W. 1966. Asterozoans, Part U, Echinodermata. Pp. U4-U107 in: R.C. Moore (ed), *Treatise on Invertebrate Paleontology*. Lawrence, KS: University Press of Kansas.
- Smith, E. A. 1876. Descriptions of species of Asteridae and Ophiuridae from Kerguelen Islands. *Annals and Magazine of Natural History*. 4th series, vol.17: 105–113.
- Stuxberg, A. 1878. Echinoderm från Novaja Semljas haf samlade under Nordenskiöldska expeditionerna 1875 och 1876. *Öfversigt af Kon gl. Vetenskaps-Akademiens Förhandlingar* 3: 27–40.
- Tablado, A. 1982. Asteroideos argentinos. Familia Poraniidae. *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, *Hidrobiologia* 2(8): 86–106.
- Tortonese, E. 1965. Echinodermata. *Fauna d'Italia* 6: 1–422. <http://dx.doi.org/10.1002/iroh.19680530111>
- Verrill, A.E. 1895. Distribution of the echinoderms of north-eastern America. *American Journal of Science* 3(49): 127–141.
- Verrill, A.E. 1899. Revision of certain genera and species of starfishes, with descriptions of new forms. *Transactions of the Connecticut Academy of Arts and Sciences* 10(1): 145–234.
- Verrill, A.E. 1914. Revision of some genera and species of starfishes, with descriptions of a few new genera. *Annals and Magazine of Natural History* 8(14): 103: 13–22. <http://dx.doi.org/10.1080/00222931408693536>
- Verrill, A.E. 1915. Report on the starfishes of the West Indies, Florida and Brazil. *Bulletin of the Laboratory of Natural History, State University of Iowa* 7(1): 1–232. <http://dx.doi.org/10.5962/bhl.title.12035>
- Viguier, C. 1878. Classification des Stellérides. *Comptes Rendus Academie des Sciences de Paris*, 84, 681–583.
- Viguier, C. 1879. Anatomie comparée du squelette des Stellérides. *Archives de Zoologie Experimentale et Generale* 7: 33–250.
- Zhang, J., Hutchings, P., Burghardt, I., and Kupriyanova, E. 2020. Two new species of Sabellariidae (Annelida, Polychaeta) from the abyss of eastern Australia. *Zootaxa* 4821(3): 487–510. DOI: 10.11646/zootaxa.4821.3.4.